Universidade de São Paulo
Instituto de Biociências
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Revisão taxonômica e morfológica da família Squalidae Blainville, 1816 (Elasmobranchii: Chondrichthyes: Squaliformes)

Taxonomic and morphological revision of the Family Squalidae Blainville, 1816 (Elasmobranchii: Chondrichthyes: Squaliformes)

Aluna: Sarah Tházia Viana de Figueirêdo
Orientador: Prof. Dr. Marcelo Rodrigues de Carvalho

São Paulo

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Ao mar.

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Introdução geral

Os tubarões da ordem Squaliformes são caracterizados por corpo cilíndrico e fusiforme, presença de espinhos dorsais situados anteriormente à pelo menos uma das nadadeiras dorsais, com ou sem sulcos laterais, e nadadeira anal ausente (Bigelow & Schroeder, 1948). Geralmente, apresentam distribuição circumglobal (e.g. *Etmopterus bigelowi* Shirai & Tachikawa, 1993), sendo encontrados desde regiões tropicais e temperadas bem como em regiões polares, localidade esta exclusiva de algumas espécies da ordem [e.g. *Somniosus microcephalus* (Bloch & Schneider, 1801)] (Compagno *et al*., 2005; Ebert *et al*., 2013). Exploram também ambientes marinhos rasos ou de grande profundidade, além de ambientes estuarinos (Ebert *et al*., 2013).

Esta ordem é constituída por seis famílias e 130 espécies atuais (Ebert *et al*., 2013) cujo monofiletismo é sustentado por quatro caracteres homoplásticos (Shirai, 1992; Carvalho, 1996): presença de fenestra subnasal; esqueleto das nadadeiras dorsais composto por cartilagem basal e espinho; dentes semelhantes em ambas as maxilas, sobrepostos uns aos outros e lineares; músculo *hyoideus dorsalis* parcialmente inserido na cartilagem hiomandibular e parte no palatoquadrado. Estudos recentes relatam sobre a grande diversidade de Squaliformes, constituindo o segundo grupo mais diverso entre os Chondrichthyes atuais (Compagno *et al*., 2005; Ebert *et al*., 2013) e cujo 1/3 das espécies foram descritas nos últimos 20 anos (e.g. Last *et al*., 2007; Last & Stevens, 2009).

A família Squalidae Blainville, 1816 abrange dois gêneros, *Squalus* Linnaeus, 1758 (gênero-tipo) e *Cirrhigaleus* Tanaka, 1912, que compartilham caracteres como presença de duas nadadeiras dorsais precedidas por espinho sem sulco lateral, ausência de entalhe subterminal na nadadeira caudal, e dentes monocuspidados e oblíquos, semelhantes em ambas as maxilas (Bigelow & Schroeder, 1957)[1]. O gênero *Squalus* pode ser distinto de *Cirrhigaleus* segundo a margem anterior da narina curta e não alongada como barbilhões, e sulco pré-caudal superior evidente (Bass *et al*., 1976). Desde Garman (1913), a diversidade de Squalidae aumentou consideravelmente de apenas duas para quase trinta espécies válidas, sendo *Squalus* o grupo com mais da metade das espécies descritas nos últimos oito anos (e.g. Last *et al*., 2007) e o segundo gênero mais diverso entre os Squaliformes, atrás apenas de *Etmopterus*.

Atualmente, são reconhecidas 26 espécies válidas de *Squalus*[2] (Last *et al*., 2007; Ebert *et al*., 2013), popularmente conhecidas como cações-bagre: *Squalus acanthias* Linnaeus, 1758 (espécie-tipo); *S. blainvillei* (Risso, 1826); *S. suckleyi* (Girard, 1854); *S. megalops* (Macleay, 1881); *S. mitsukurii* Jordan & Snyder (1903); *S. japonicus* Ishikawa, 1908; *S. brevirostris* Tanaka, 1912; *S. griffini* Phillipps, 1931; *S. montalbani* Whitley, 1931; *S. cubensis* Howell-Rivero, 1936; *S. melanurus* Fourmanoir & Rivaton, 1979; *S. rancureli* Fourmanoir & Rivaton, 1979; e mais 14 espécies recentemente descritas dos Oceanos Índico e Pacífico Sul (Baranes, 2003; Last *et al*., 2007; White & Iglésias, 2011). De maneira geral, as espécies de *Squalus* estão distribuídas entre taludes continentais, planícies insulares e montes submarinos dos oceanos Atlântico, Pacífico e Índico, abrangendo águas boreais e temperadas frias onde se encontram próximos a costa bem como águas tropicais, estando mais afastados (Compagno, 1984; Compagno *et al*., 2005).

O gênero *Cirrhigaleus* é um grupo menos diverso com apenas três espécies válidas de distribuição geográfica mais restrita nos oceanos Pacífico Ocidental, Atlântico Sul e Índico, habitando plataformas médio-continentais (Ebert *et al*., 2013): *Cirrhigaleus barbifer* Tanaka,

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[1] Informações de Squalidae retiradas da literatura. Consultar Capítulo 2 para classificação e caracterização morfológica pós-estudo.

[2] Espécies válidas anteriores a análise do presente estudo.

1912 (espécie-tipo); *C. asper* (Merrett, 1973); *C. australis* White, Last & Stevens, 2007. Apesar da família ser tratada como um grupo monofilético (Shirai, 1992; Naylor *et al*., 2012b), a correta aplicação das espécies nominais e caracterização morfológica precisa das espécies válidas de cada gênero necessitam detalhada investigação.

História taxonômica e sistemática da família Squalidae

O início da história sobre a taxonomia de Squalidae data de épocas bem anteriores ao da classificação dos animais e plantas proposto por Linnaeus. Em *História dos Animais*, escrito pelo filósofo grego Aristóteles (350B.C.), o conhecimento acerca da diversidade e morfologia dos animais foi abordado com tenacidade, representando também a primeira tentativa de classificação do Reino Animal (Aristotle *et al*., 1878). Alguns grupos de peixes cartilaginosos ("*selache*") haviam sido classificados e muitos já haviam recebido um nome na Época Antiga, mesmo que ainda não-binomial (e.g. *Squalus acanthias*; *Squalus galeus*; *Squalus zygaena*; *Squalus squatina*; *Squalus stellaris*; *Raja batus*, *Raja torpedo*). A família Squalidae, assim, foi representada nesta obra como um grupo específico de tubarões ("*acantheas*").

Peter Artedi, o pai da Ictiologia, iniciou a categorização taxonômica dos grupos de peixes que apenas foi publicada em sua obra póstuma, *Genera Piscium* (Artedi, 1738). Nesta obra, o gênero *Squalus* incluía todos as espécies de tubarões viventes enquanto *Raja* compreendia o gênero das espécies de raias. Carollus von Linnaeus, então aprendiz de Artedi, aperfeiçoou este sistema de classificação em categorias taxonômicas e elaborou a padronização da formação de nomes científicos através da nomenclatura binomial em latim, publicado oficialmente em *Systema Naturae* (1758). Linnaeus (1735, 1758) seguiu a mesma classificação em gêneros abordada por Artedi para raias e tubarões, incluindo desta vez as quimeras em um terceiro gênero, o *Chimaera*. *Squalus acanthias* Linnaeus, 1758, então, foi a primeira espécie de tubarão descrita segundo este novo sistema de classificação zoológica.

O aumento do conhecimento da diversidade de peixes elasmobrânquios nos séculos XIX e XX com a descrição de novos representantes do grupo permitiu aperfeiçoar ainda mais a organização das espécies em categorias taxonômicas superiores (e.g. Rafinesque, 1810; Blainville, 1816; Müller & Henle, 1841; Garman, 1913). O nome *Squalus*, assim, foi elevado a categoria de família (Blainville, 1816), incorporando outros gêneros de tubarões squalóides ou não (e.g. *Squatina*, *Scyliorhinus*, *Echinorhinus*) (Blainville, 1816). Até antes da institucionalização do Código Internacional de Nomenclatura Zoológica (ICZN) em 1931, porém, muitas espécies foram descritas sem a preocupação de obedecer prioridades de nomenclatura, regras de classificação e apresentação de sinonímias, sendo muitas vezes uma mesma espécie descrita sobre diferentes nomes por diferentes autores (e.g. *Squalus acanthias* e seus sinônimos). Existe um total de mais de 60 espécies nominais disponíveis dentro de Squalidae cujas descrições originais em sua maioria são bastante curta e pouco informativas. Identificações equivocadas na literatura e a perda do holótipo ou outros tipos primários de espécies nominais constituem empecilhos secundários para Squalidae, contribuindo para a aplicação desenfreada de sinônimos até hoje.

A complexidade taxonômica da família foi potencializada devido a alta sobreposição de caracteres morfológicos entre as espécies de *Squalus* já que a identificação das mesmas se dá muitas vezes através de caracteres limitados e insuficientemente consistentes como contagem de vértebras e certas medidas corporais (Last *et al*., 2007). As espécies de *Squalus* estão divididas em três complexos ou “grupos de espécies” de acordo com a similaridade morfológica, podendo ou não representar grupos monofiléticos: grupo *S. acanthias*, grupo *S. megalops* e grupo *S. mitsukurii* (Bigelow & Schroeder, 1948, 1957). Estudos taxonômicos regionais e/ou globais sobre o gênero ainda seguem esta divisão em complexos ou “grupos de espécies", refletindo claramente a dificuldade em se atribuir caracteres morfológicos eficientes para a identificação correta das espécies do grupo (e.g. Compagno *et al*., 2005; Ebert *et al*., 2010; Gomes *et al*., 2010).

Os grupos de espécies de *Squalus* são assim caracterizados (Bigelow & Schroeder, 1948, 1957; Garrick, 1960; Bass *et al*., 1976; Muñoz-Chápuli & Ramos, 1986; Compagno *et al*., 2005; Figueirêdo, 2011):

- Grupo *Squalus acanthias*: margem anterior da narina unilobada (simples); espinho da primeira nadadeira dorsal posterior a linha horizontal traçada a partir da ponta livre da nadadeira peitoral; nadadeira peitoral com ápice arredondado e margem posterior suavemente côncava; dentículos dérmicos tricuspidados; origem das nadadeiras pélvicas atinge metade da distância entre as nadadeiras dorsais; manchas brancas evidente dorsalmente no tronco mais nítidas nos indivíduos jovens que adultos. Apenas duas espécies válidas, *S. acanthias* e *S. suckleyi* são atribuídas a este grupo.

- Grupo *Squalus megalops*: espinho da primeira nadadeira dorsal anterior à linha horizontal traçada na ponta livre da nadadeira peitoral; margem anterior da narina bilobada; focinho curto; nadadeira peitoral com ponta livre pontiaguda e margem posterior evidentemente côncava; origem das nadadeiras pélvicas mais próximo da primeira nadadeira dorsal do que da segunda nadadeira dorsal; dentículos dérmicos unicuspidados e lanceolados; margem posterior da nadadeira caudal com borda uniformemente branca. O grupo inclui seis espécies válidas, entre elas, *S. brevirostris*, *S. cubensis*, *S. bucephalus* Last, Séret & Pogonoski, 2007, *S. raoulensis* Duffy & Last, 2007, *S. crassispinus* Last, Edmunds & Yearsley, 2007 e *S. megalops*, sendo esta última considerada um complexo de espécies. Mais recentemente, o grupo foi subdividido para agrupar espécies que compartilham as seguintes características (Last *et al*., 2007): espinhos dorsais bastante espessos; nadadeiras dorsais verticais e extremamente altas; dentículos dérmicos tricuspidados. Este subgrupo é chamado "highfin *megalops* group" (ou grupo *megalops* de nadadeiras altas) e abrange quatro espécies: *S. albifrons* Last, White & Stevens, 2007, *S. altipinnis* Last, White & Stevens, 2007, *S. notocaudatus* Last, White & Stevens, 2007, *S. formosus* White & Iglésias, 2011.

- Grupo *Squalus mitsukurii*: nadadeira peitoral com ponta livre arredondada e margem posterior quase reta; origem das nadadeiras pélvicas mais próxima da primeira nadadeira dorsal do que da segunda nadadeira dorsal; dentículos dérmicos tricuspidados; maior número de vértebras totais; barra caudal escura evidente na margem posterior da nadadeira caudal. As espécies deste grupo compartilham com as espécies do grupo *S. megalops* a posição do primeiro espinho dorsal em relação a nadadeira peitoral e o formato da margem anterior da narina. Estão incluídas oito espécies válidas no grupo: *S. mitsukurii*, *S. blainvillei*, *S. griffini*, *S. montalbani*, *S. grahami* White, Last & Stevens, 2007, *S. chloroculus* Last, White & Motomura, 2007, *S. lalannei* Baranes, 2003, *S. edmundsi* White, Last & Stevens, 2007. Last *et al*. (2007) também subdividiu este grupo para agrupar apenas quatro espécies que compartilham focinho conspicuamente alongado, denominando-o grupo *S. japonicus*: *S. japonicus*, *S. melanurus*, *S. rancureli*, *S. nasutus* Last, Marshall & White, 2007.

Squalus hemipinnis White, Last & Yearsley, 2007 é a única[3] espécie do gênero que evidentemente não se encaixa em um grupo de espécies particular, pois apresenta características tanto do grupo *S. megalops* quanto do grupo *S. mitsukurii* (White *et al*., 2007a).

Similaridades morfológicas também são encontradas entre espécies de *Cirrhigaleus* e *Squalus*, contribuindo para a complexidade taxonômica da família. Bigelow & Schroeder (1948, 1957), seguidos por Garrick & Paul (1971), reconheceram *Cirrhigaleus* como um gênero válido e distinto, distinguindo-o pela presença de barbilhões nasais evidentes e da ausência de sulco pré-caudal. A espécies nominal "*asper*" foi inserida no gênero *Squalus* por

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[3] Consultar Capítulo 2 para novas interpretações pós-análise quanto a separação em "grupos de espécies".

compartilharem características como dentição, número de vértebras e formato de dentículos dérmicos sem fazer, contudo, análises comparativas com *Cirrhigaleus* (Merrett, 1973). Bass *et al.* (1976) também reconheceram semelhanças entre *C. barbifer* do Japão e a espécie do oceano Índico, incorporando *C. barbifer* dentro do gênero *Squalus*, estabelecendo, assim, um quarto novo grupo de espécies, o grupo *S. asper*-*S. barbifer*. Este grupo de espécies é caracterizado por (Bass *et al*., 1976): ausência de sulco pré-caudal superior (ou fracamente evidente em alguns espécimes); margem anterior da narina com conspícuo lobo, sendo este largo na base ou bastante alongado desde a margem interna da narina a ponta interna do lobo; segunda nadadeira dorsal de comprimento similar a primeira nadadeira dorsal; dentículos dérmicos alongados; cabeça e focinho relativamente curtos e pontiagudos. Shirai (1992) e White *et al*. (2007b) depois afirmaram que os representantes do grupo *S. asper*-*S. barbifer* devem ser atribuídos ao gênero *Cirrhigaleus*.

Estudos mais recentes retomaram a discussão sobre a validade e caracterização morfológica das espécies de *Cirrhigaleus*. White *et al*. (2007b) apresentaram diferenças morfológicas e moleculares entre *C. australis* e espécies congêneres. Os autores ainda constataram que espécimes co-específicos de *C. barbifer* da Indonésia e do Japão apresentam grandes variações morfológicas, indicando a necessidade de uma investigação mais detalhada sobre as espécies do gênero ocorrentes na região. Figueirêdo (2011) constatou similaridades na morfologia externa e esquelética entre *C. asper* e espécies de *Squalus* do Oceano Atlântico Sul Ocidental, reforçando a necessidade em investigar com detalhe a correta alocação genérica desta espécie. Kempster *et al*. (2013) confirmou a ocorrência de espécimes de *C. barbifer* ainda na Austrália Ocidental e a separou de *C. australis* segundo diferenças do gene CO1 e poucos caracteres morfológicos.

Vários estudos sobre a filogenia de elasmobrânquios de altas categorias taxonômicas comprovaram o monofiletismo da família Squalidae através de caracteres morfológicos (e.g.

Shirai, 1992, 1996; Carvalho, 1996) e/ou moleculares (Naylor *et al*., 2012a,b). Shirai (1992, 1996) suporta esta hipótese apenas através de dois caracteres: dentes superiores imbricados que formam uma superfície cortante contínua (carácter 69); homodontia dignática (carácter 70).

As relações filogenéticas internas de Squalidae, contudo, ainda são intensamente discutidas na literatura. Shirai (1992) suportou o monofiletismo de *Cirrhigaleus* com base na presença de barbilhão nasal mais ou menos desenvolvido e inervado pelo nervo facial bucofaringeano. O autor constatou ainda que a presença de processos supraethmoidais no neurocrânio e do sulco pré-caudal superior evidente são caracteres exclusivos de *Squalus*. Todavia, segundo Gomes (*pers. comm.*) espécimes de *C. asper* do oceano Atlântico Sul Ocidental não apresentam a inervação no barbilhão nasal e Ramos (2009) constatou ainda a presença dos processos supraethmoidais nestes exemplares. Figueirêdo (2011) também verificou a ausência dos processos supraethmoidais em *Squalus* sp. da mesma região, sugerindo, assim, a necessidade de rever os caracteres utilizados para sustentar o monofiletismo dos gêneros da família.

Naylor *et al*. (2012b) através de análises do gene mitocondrial NADH2 afirmou que *Squalus* somente é monofilético se as espécies *C. asper* e *C. australis* forem realocadas genericamente. Outras análises moleculares baseadas no gene COI para fins de identificação (e.g. Ward *et al*., 2005, 2007; Ebert *et al*., 2010; Naylor *et al*., 2012a) também refletiram a complexidade sistemática dentro de Squalidae. Espécies válidas antes consideradas de ampla distribuição geográfica (e.g. *S. mitsukurii*, *S. megalops* e *S. acanthias*) apresentaram inúmeros clados individuais nestas análises, suportando a separação e o reconhecimento de pelo menos mais de uma espécie, nova ou não para a Ciência. Last *et al*. (2007), Ebert *et al*. (2010), e White & Iglésias (2011) são exemplos de trabalhos que reviram o *status* taxonômico destas espécies nominais em diferentes regiões após as análises moleculares. A maioria das espécies atuais de *Squalus* e *Cirrhigaleus* são consideradas monofiléticas baseados apenas em caracteres moleculares, porém estudos sobre filogenia com base em caracteres morfológicos e/ou combinados ainda não foram elaborados.

Objetivos

O presente estudo teve como objetivos:

1. Realizar uma revisão taxonômica da família Squalidae através de um estudo morfológico comparativo minucioso das espécies dos gêneros *Squalus* e *Cirrhigaleus*, delimitando as espécies válidas mundialmente e acertando a nomenclatura das espécies reconhecidas. Sinonímias completas para cada espécie são propostas aqui, além da descrição morfológica de novos representantes da família descobertos durante o estudo;
2. Investigar detalhadamente a morfologia externa e interna (esquelética) das espécies válidas, incluindo aspectos morfométricos e merísticos;
3. Fornecer subsídios morfológicos relevantes para a aplicação futura em estudos filogenéticos internos da família Squalidae.

Material e Métodos

1. Material analisado

O material biológico foi adquirido através de empréstimos, e de visitas às coleções ictiológicas nacionais e internacionais. Informações morfológicas dos espécimes-tipo de espécies nominais de *Squalus* e de *Cirrhigaleus* foram obtidos através de visitas pessoais aos museus bem como através de fotografias e radiografias enviadas pelos curadores responsáveis e outros pesquisadores. A análise morfológica de mais 1.800 espécimes da família Squalidae de várias regiões geográficas foi realizada, englobando desde indivíduos adultos, juvenis e neonatos, de ambos os sexos, conforme realizado anteriormente por Figueirêdo (2011).

A lista do material analisado está disponibilizada por Capítulo, sendo indicada para cada espécie descrita. O material comparativo utilizado para discussão do status taxonômico de cada espécie é disponibilizado ao final da seção *Remarks*. As abreviaturas das instituições seguem Sabaj Pérez (2013).

O presente projeto de Doutorado teve financiamento concedido pela Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) através dos projetos de pesquisa (Processos 2011/18861-7; 2013/11621-6; 2014/26503-1) e pelo Conselho Nacional de Pesquisa (CNPq) através do projeto (XXXX).

2. Metodologia

Dados da morfologia externa foram obtidos a partir de observações a olho nu ou com o auxílio de microscópio estereoscópico de espécimes preservados em álcool à 70%. Análises dos dentículos dérmicos foram realizados a partir de amostras de pele medindo 1x1 centímetros, retiradas abaixo da primeira nadadeira dorsal (lado direito), através de microscopia eletrônica de varredura (MEV) feitas no Instituto de Biociências, Universidade de São Paulo (IBUSP) e no Departamento de Zoologia da Rhodes University (Grahamstown, África do Sul). Amostras de dentes da mandibular e maxila inferior foram retiradas (três dentes laterais da primeira série dentária) e investigadas através de microscópio estereoscópico.

Medidas externas do corpo e cranianas foram tomadas com ajuda de paquímetro digital Mitutoyo de precisão igual a 0,1 mm (para medidas menores) ou de fita métrica milimétrica (para medidas maiores que 150 mm). Um total de 62 medidas externas foram obtidas de acordo com os protocolos estabelecidos por Last *et al.* (2007) e são expressas como porcentagem do comprimento total (% TL). Medidas cranianas (Appendix A) foram obtidas segundo Muñoz-Chápuli & Ramos (1989) e Compagno (1988) com modificações e são expressas porcentagem do comprimento total do neurocrânio (% CL). Estas medidas são definidas como: **1. Comprimento total do neurocrânio (TL):** distância do centro occipital a ponta anterior do rostro medida ao longo do eixo longitudinal do neurocrânio**; 2. Comprimento pós-cerebral:** distância entre o centro occipital e a extremidade posterior da fossa pré-cerebral medida entre os processos supraetmoidais; **3. Comprimento da fossa pré-cerebral:** distância da extremidade posterior da fossa pré-cerebral (entre os processos supraetmoidais) a ponta anterior do rostro; **4. Largura da fossa pré-cerebral:** largura máxima da fossa pré-cerebral medida a partir das extremidades internas; **5. Largura entre as cápsulas nasais:** maior distância transversal entre as laterais das cápsulas nasais; **6. Largura interorbital:** distância entre as cristas supraorbitais através do teto craniano; **7. Largura**

através dos processos pré-orbitais: distância transversal entre as extremidades distais dos processos pré-orbitais; **8. Comprimento do processo pós-orbital:** distância entre a extremidade distal do processo pós-orbital e o início da crista esfenopterótica; **9. Largura através dos processos pós-orbitais:** distância transversal entre as extremidades distais dos processos pós-orbitais; **10. Distância entre os processos orbitais:** distância entre a extremidade distal do processo pré-orbital e a extremidade distal do processo pós-orbital; **11. Distância através dos processos opistóticos:** distância transversal através dos processos opistóticos medida dorsalmente; **12. Largura através das facetas hiomandibulares:** distância transversal entre as facetas hiomandibulares medida dorsalmente a partir do processo pós-ótico; **13. Comprimento nasobasal:** distância entre o centro occipital e a extremidade posterior da quilha rostral; **14. Comprimento da quilha rostral:** distância entre as extremidades anterior e posterior da quilha rostral; **15. Largura subetmoideana:** distância transversal anterior através da região subetmoideal; **16. Largura do ângulo basal:** distância transversal através do ângulo basal; **17. Comprimento da placa basal:** distância entre o centro occipital e o sulco do ângulo basal; **18. Largura da placa basal:** distância transversal mínima através da sinuosidade anterior da placa basal (posterior ao ângulo basal); **19. Largura através do primeiro processo cartilaginoso:** distância transversal através do primeiro processo cartilaginoso da placa basal; **20. Largura através do segundo processo cartilaginoso (se presente):** distância transversal através do segundo processo cartilaginoso da placa basal; **21. Altura máxima sagital:** distância vertical entre a extremidade dorsal da crista occipital e a placa basal; **22. Largura do forâmen magnum:** distância transversal através do forâmen magnum.

Dissecções foram realizadas para análises de estruturas do esqueleto como neurocrânio, nadadeiras peitoral e pélvicas, e do clásper, sendo posteriormente, preservados em álcool a 70%. Instrumentos específicos como pinças, bisturis e tesouras de tamanhos e formatos variados foram utilizados para empregar a técnica de dissecção. Diafanizações foram realizadas em alguns espécimes, seguindo Dingerkus & Uhler (1977) para complementar as análises de estruturas do esqueleto. Radiografias (filme ou digital) também foram retiradas nos museus e coleções visitadas. Dados merísticos foram obtidos para fileira e séries de dentes, corpos vertebrais, e raios das nadadeiras peitorais e pélvicas a partir destas técnicas de preparação. Micro-CT scan da cabeça do holótipo de *Cirrhigaleus asper* foi realizado no Natural History Museum em Londres para análise do neurocrânio.

Todos os espécimes analisados foram fotografados inteiros em vistas lateral e ventral bem como estruturas particulares do corpo (e.g. nadadeiras, cláspers) com câmera digital. Espécimes preparados anatomicamente também foram fotografados antes e após a preparação de material. Estruturas específicas desarticuladas e individualizadas do esqueleto foram ilustradas através de fotografias com câmera digital e/ou desenhos científicos (técnica nanquim em papel). Dentes e outras estruturas anatômicas também foram fotografadas com câmera digital acoplada ao microscópio estereoscópico Leica. Os programas QGIS 2.4 Chugiak (QGIS Development Team, QGIS Geographic Information System, Open Source Geospatial Foundation Project; http://qgis.osgeo.org) e Google Earth foram utilizados para produzir mapas de distribuição geográfica para cada espécie descrita.

3. Terminologia

A nomenclatura, incluindo padrão de coloração segue Last *et al*. (2007). Descrição dos dentículos dérmicos é de acordo com Deynat and Séret (1996). A terminologia de estruturas do esqueleto segue Marinelle & Strenger (1959), Compagno (1988), Shirai (1992), Silva & Carvalho (2015). Terminologia do clásper foi adotada de Jungersen (1899). Radiografias (digital e filme) for a retiradas para obtenção de dados merísticos como, por exemplo, contagem de vertebras e fileiras de dentes. A contagem de vértebras segue Springer &

Garrick (1964). A contagem de dentes e nomenclatura da dentição estão de acordo com Cappetta (1987) e Herman *et al*. (1989).

4. Descrição taxonômica de espécies

As espécies aqui reconhecidas como válidas foram descritas morfologicamente em inglês obedecendo a seguinte organização: nome da espécie e autoria; nome-comum; lista de sinonímias; série-tipo (se cabível); localidade-tipo; material não-tipo analisado; diagnose; descrição morfológica; distribuição geográfica; etimologia (se cabível); *Remarks*; material comparativo.

Os sinônimos são abreviados de acordo com autoria, data, páginas e figuras quando possível. O sinal de dois-pontos (:) é empregado entre o nome da espécie e a referência quando a autoria do nome não é indicada. Para a diagnose e descrição, medidas externas com valores únicos correspondem ao holótipo enquanto a amplitude representa os valores para os parátipos seguidos por material não-tipo cujas medidas foram retiradas (exceto quando citado anteriormente à descrição).

5. Abreviaturas anatômicas

abc: condyle for anterior pelvic basal; abv: anterior pelvic basal; afs: anterior fossa of scapulae; aoc: antorbital cartilage; ap: apopyle; ax: axial cartilage; ba: basal angle; bg: glossopharyngeal base; bp: basal plate; bpt: basipterygium; btp: basitrabecular process; b1: first intermediate segment; b2: second intermediate segment; cbp: condyle for basipterygium; cg: clasper groove; co: coracoid bar; cp1: first cartilaginous process; cr: cranial roof; csa: anterior semicircular canal; csl: lateral semicircular canal; csp: posterior semicircular canal; ctq: ceratotrichia; df: diazonal foramen; drl: distal radials; ec: ethmoidal canal of the ophthalmicus superficialis nerve; eec: ectethmoid chamber; elf: endolymphatic foramen; ep:

epiphysial pit; es: eye stalk; fca: foramen for carotid artery; fd: foramen diazonale; feld: endolymphatic fossa; foa: foramen for orbital artery; fopp: profundus canal for the ophthalmicus profundus nerve; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; fbp: facet for basipterygium; fpr: facet for proterygium; hmf: hyomandibular facet; fvn: foramen for ventral fin nerves; g: end-style; hmVII: foramen for hyomandibularis facialis; hp: hypopyle; lag: lateral auditory groove; lpp: lateral prepelvic process; lra: lateral rostral appendage; mes: mesopterygium; mra: median rostral appendage; mrl: medial radials; mrp: median rostral prominence; msc: mesocondyle; mtp: metapterygium; mtx: metapterygial axis; NAO: North Atlantic Ocean; NEAO: Northeastern Atlantic Ocean; NEPO: Northeastern Pacific Ocean; ns: nasal capsule; NWAO: Northwestern Atlantic Ocean; oc: otic capsule; occ: occipital condyle; ohc: occipital hemicentrum; opp: opistotic process; otc: otic crest; pc: condyle for propterygium; pcf: precerebral fossa; pff: prefrontal fontanelle; plf: perilymphatic foramen; poc: preorbital canal of the ophthalmic superficial nerve; pop: postorbital process; potp: prootic process; pow: preorbital wall; ppe: preorbital process; prl: proximal radials; pro: propterygium; psb: efferent of pseudobranchial artery foramen; pub: puboischiadic bar; p1: pectoral fin; p1n: pectoral fin nerve; p2: pelvic fin; r: rostrum; rc: rostral carina; rd: dorsal marginal cartilage; rh: rhipidion; rk: rostral keel; rl: radials; rv: ventral marginal cartilage; scl: scapulae; sec: subethmoid chamber; sep: supraethmoidal process; SEAO: Southeastern Atlantic Ocean; SEPO: Southeastern Pacific Ocean; ser: subethmoidean ridge; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; SWAO: Southwestern Atlantic Ocean; td or claw: dorsal terminal cartilage; td2: dorsal terminal 2 cartilage; tr: transbasal canal for the pituitary vein; tv: ventral terminal cartilage; tv2: ventral terminal 2 cartilage; t3 or spur: accessory terminal 3 cartilage; II: foramen opticum; III: foramen oculomotor; IV: foramen trochlear; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve; β: beta cartilage; *: segmented ridge of scapulae.

6. Organização da Tese

A tese está organizada em três Capítulos redigidos em inglês em formato de artigos científicos com a intenção de submetê-los para publicação. A Introdução geral, Materiais e Métodos bem como Referências Bibliográficas Geral e Conclusão Geral sobre os resultados da Tese são apresentadas em Português.

O primeiro capítulo intitulado *"Comparative analysis of the skeletal anatomy of species of Squalidae Blainville, 1816 (Chondrichthyes: Squaliformes) with comments on the systematics of the family*" apresenta descrições comparativas de cada complexo esquelético analisado no presente estudo para espécies dos gêneros *Squalus* e *Cirrhigaleus*.

O segundo capítulo intitulado "*Taxonomic and morphological revision of the genus Squalus Linnaeus, 1758 (Chondrichthyes: Squaliformes: Squalidae)*" apresenta caracterização morfológica e composição da família Squalidae seguido da diagnose dos gêneros reconhecidos. Cada espécie válida reconhecida, incluindo possíveis novas espécies, para os gêneros é também descrita neste capítulo.

O terceiro capítulo é intitulado "*Taxonomic and morphological revision of the genus Cirrhigaleus Tanaka, 1912 highlights new intepretations regarding its taxonomic position within Squaliformes* Cada espécie de *Cirrhigaleus* reconhecida é descrita e o posicionamento genérico de *C. asper* e as interrelações do gênero dentro da ordem é aqui discutida.

Referências bibliográficas

Aristotle, Cresswell, R. Schneider, J.G. (1878) *Aristotle's History of animals in ten books*. William Clowes and Sons, London, 348 pp.

Artedi, P. (1738) *Genera Piscium. In quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis. Speciebus 242 ad Genera 52*. Ichthyologiæ pars III. Lugduni Batavorum, Apud Conradum Wishoff, 723 pp.

Baranes, A. (2003) Sharks from the Amirantes Islands, Seychelles, with a description of two new species of squaloids from the deep sea. *Israel Journal of Zoology*, 49, 33–65.

Bass, A.J., D'Aubrey, J.D. & Kistnasamy, N. (1976) Sharks of the east coast of southearn Africa. VI The families Oxynotidae, Squalidae, Dalatiidae and Echinorhinidae. *Investigational Report*, 45, Oceanographic Research Institute, Durban, 1–103.

Bigelow, H.B. & Schroeder, W.C. (1948) Sharks. *In*: J.Tee-Van *et al*. (Eds.), *Fishes of the Western North Atlantic. Part 1*. Memoir Sears Foundation for Marine Research, Yale University, New Haven, pp. 1–576.

Bigelow, H.B. & Schroeder, W.C. (1957) A study of the sharks of the suborder Squaloidea. *Bulletin of the Museum of Comparative Zoology at Harvard College in Cambridge*, 117 (1), 1–150.

Blainville, H. (1816) Prodrome d'une nouvelle distribution systématique du règne animal. *Bulletin de la Société Philomathique de Paris*, 8, 105–112.

Cappetta, H. (1987) Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. *In*: Schultze, H.P. (Ed.), *Handbook of Paleoichthyology. Vol. 3B*. Verlag Dr. Friedrich Pfeil, München, pp. 1–193.

Carvalho, M.R. de (1996) High-level Elasmobranch Phylogeny, Basal Squaleans, and Paraphyly. *In*: Stiassny, M.L. J.; Parenti, L.R. & Johnson, G.D. (Eds.), *Interrelationships of fishes*. Academic Press Inc., San Diego, pp. 35–62.

Compagno, L.J.V. (1984) *FAO Species Catalogue. Vo. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes*. FAO Fisheries Synopsis, Rome, 4 (125), 249 pp.

Compagno, L.J.V. (1988) *Sharks of the Order Carcharhiniformes*. Princeton University Press, Princeton, 486 pp.

Compagno, L.J.V., Dando, M. & Fowler, S. (2005) *Sharks of the World – Princeton Field Guides*. Harper Collins Publishers Ltd., London, 368 pp.

Deynat, P.P. & Séret, B. (1996) Le revêtement cutané des raies (Chondrichthyes, Elasmobranchii, Batoidea). I: Morphologie et arrangement des denticules cutanés. *Annales des Sciences Naturalles, Zoologie*, 17, 65–83.

Dingerkus, G. & Uhler, L.D. (1977) Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Technology*, 52 (4), 229–232.

Ebert, D.A., Fowler, S. & Compagno, L.J.V. (2013) *Sharks of the World: A Fully Illustrated Guide*. Wild Nature Press, London, 528 pp.

Ebert, D.A., White, W.T., Goldmann, K.J., Compagno, L.J.V., Daly-Engel, T.S. & Ward, R.D. (2010) Resurrection and redescriptions of *Squalus suckleyi* (Girard, 1854) from the North Pacific, with comments on the *Squalus acanthias* subgroup (Squaliformes: Squalidae). *Zootaxa*, 2612, 22–40.

Figueirêdo, S.T.V. (2011) Revisão taxonômica e morfológica do gênero *Squalus* Linnaeus, 1758 do oceano Atlântico Sul Ocidental (Chondrichthyes: Squaliformes: Squalidae). Unpublished MSc Thesis. Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, 348 pp.

Garman, S. (1913) *The Plagiostoma (sharks, skates and rays)*. Memoirs of the Museum of Comparative Zoology at Harvard College, 36, Cambridge, 515 pp.

Garrick, J.A.F. (1960) Studies on New Zealand Elasmobranchii. Part XII. The species of *Squalus* from New Zealand and Australia; and a general account and key to the New Zealand Squaloidea. *Transactions of the Royal Society of the New Zealand*, 88 (3), 519–557.

Garrick, J.A.F. & Paul, L.J. (1971) *Cirrhigaleus barbifer* (Fam. Squalidae), a little known Japanese shark from New Zealand waters. *Zoology Publications, Victoria University, Wellington*, 154, 1–13.Gomes, U.L., Signori, C.N., Gadig, O.B.F. & Santos, H.R.S. (2010) *Guia para Identificação de Tubarões e Raias do Rio de Janeiro*. Technical Books, Rio de Janeiro, 234 pp.

Herman, J., Hovestadt-Euler, M. & Hovestadt, D.C. (1989) Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyes fishes. Part A: Selachii. N° 3: Order Squaliformes – Families Echinorhinidae, Oxynotidae and Squalidae. *Bulletin de l'Institute Royal des Sciences Naturalle de Belgique*, Biologie, 59, 101–157.

Jungersen, H. F. E. (1899) *On the appendices genitales in the greenland shark Somniosus microcephalus (Bl. Schn.) and other selachians*. The Danish Ingolf-Expedition, 2, Bianco Luno, Copenhagen: Bianco Luno, 88 pp.

Kempster, R.M., Hunt, D.M. Human, B.A., Egeberg, C.A. & Collin, S.P. (2013) First record of the mandarin dogfish *Cirrhigaleus barbifer* (Chondrichthyes: Squalidae) from Western Australia. Marine Biodiversity Records, *Marine Biodiversity Records*, 6 (25), 1–4. doi:10.1017/S175526721300002X.

Last, P.R. & Stevens, J.D. (2009) *Sharks and Rays of Australia*, 2nd edition. Harvard University Press, Cambridge, 644 pp.

Last, P.R., White, W.T. & Pogonoski, J.J. (2007) *Descriptions of new dogfishes of the genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, 130 pp.

Linnæus, C. (1735) *Systema naturæ, sive regna tria naturæ systematice proposita per classes, ordines, genera, & species*. Lugduni Batavorum. (Haak). 13 pp.

Linnaeus, C. (1758) *Systema Naturae. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decimal, reformata.*. Tomus I, Sweden, Holmiae, 824 pp.

Marinelli, W. & Strenger, A. (1959) *Vergleichende Anatomie und Morphologie der Wirbeltiere III Lieferung (Squalus acanthias)*. Franz Deuticke, Vienna, 308 pp.

Merrett, N.F. (1973) A new shark of the genus *Squalus* (Squalidae, Squaloidea) from the equatorial western Indian Ocean, with notes on the *Squalus blainvillei*. *Journal of Zoological Society of London*, 171, 93–110.

Müller, J. & Henle, J. (1841) *Systematische Beschreibung der Plagiostomen*. Berlim, 300 pp.

Muñoz-Chápuli, R. & Ramos, F. (1989) Morphological comparisons of *Squalus blainvillei* and *S. megalops* in the Eastern Atlantic, with notes on the genus. *Japanese Journal of Ichthyology*, 36 (1), 6–21.

Naylor, G.J.P., Caira, J.N., Jensen, K., Rosana, A.M., White, W. T. & Last, P.R. (2012a) A DNA sequence-based approach to the identification of shark and rays species and its implication of global elasmobranch diversity and parasitology. *Bulletin of the American Museum of Natural History*, 367, 262 pp.

Naylor, G. J. P., Caira, J.N., Jensen, K., Rosana, A.M., Straube, N. & Lakner, C. (2012b) Elasmobranch Phylogeny: A mitochondrial estimate based on 595 species. *In*: Carrier, J.C., Musick, J.A., & Heithaus, M.E. (Eds.). *Biology of Sharks and their relatives.* 2nd edn. CRC Press. pp. 31–56.

Rafinesque, C.S. (1810) *Indice d'ittiologia siciliana; ossia, catalogo metodico dei nomi latini, italiani, e siciliani dei pesci, che si rinvengono in Sicilia disposti secondo un metodo naturale e seguito da un appendice che contiene la descrizione de alcuni nuovi pesci sicilian*. Messina, 70 pp.

Ramos, S.G.A.C. (2009) Descrição e comparação do condrocrânio de *Cirrhigaleus* Tanaka, 1912 e *Squalus* Linnaeus, 1758 (Squaliformes, Squalidae). Unpublished Monograph. Instituto de Ciências Biológicas e Ambientais, Universidade Santa Úrsula, Rio de Janeiro. 40 pp.

Sabaj Pérez, M.H. (2013) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 4.0 (28 June 2013). Electronically accessible at http://www.asih.org/, *American Society of Ichthyologists and Herpetologists*, Washington, DC.

Shirai, S. (1992) *Squalean phylogeny: a new framework of "squaloid" sharks and related taxa*. Hokkaido University Press. Sapporo, 151 pp.

Shirai, S. (1996) Phylogenetic Interrelationships of Neoselachians (Chondrichthyes: Euselachii). *In*: Stiassny, M. L. J.; Parenti, L. R.; Johnson, G. D. (Eds). *Interrelationships of fishes*. Academic Press Inc., San Diego, pp. 9–34.

Silva, J.P.C.B. & Carvalho, M.R. (2015) Morphology and phylogenetic significance of the pectoral articular region in elasmobranchs (Chondrichthyes). *Zoological Journal of the Linnean Society,* 175 (3), 525–568.

Springer, V.G. & Garrick, J.A.F. (1964) A survey of vertebral numbers in sharks. *Proceedings of the United States National Museum*, 116 (3496), 73–96.

Ward, R.D., Zemlak, T.S., Innes, B.H., Last, P.R. and Hebert, P.D.N. (2005) DNA barcoding Australia's fish species. *Philosophical Transactions of the Royal Society of London*, Series B, 360, 1847–1857.

Ward, R.D., Holmes, B.H., Zemlak, T.S. & Smith, P.J. (2007) DNA barcoding discriminates spurdogs of the genus *Squalus*. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.). *Descriptions of new dogfishes of the genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, pp. 117–130.

White, W.T. & Iglésias, S.P. (2011) *Squalus formosus*, a new species of spurdog shark (Squaliformes: Squalidae), from the Western North Pacific Ocean. *Journal of Fish Biology*, pp. 1-15.

White, W.T., Last, P.R. & Stevens, J.D. (2007) *Cirrhigaleus australis* n. sp., a new Mandarin Dogfish (Squaliformes: Squalidae) from the south-west Pacific. *Zootaxa*, 1560, 19–30.

White, W. T., Last, P.R. & Yearsley, G.K. (2007) *Squalus hemipinnis* sp. nov, a new short-snout spurdog from eastern Indonesia. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.). *Descriptions of new dogfishes of the genus Squalus (Squaloidea: Squalidae).* CSIRO Marine and Atmospheric Research Paper No. 014 (part 10): 101-108.

Chapter 1

Comparative skeletal anatomy of species of Squalidae Blainville, 1816 (Elasmobranchii: Chondrichthyes: Squaliformes) with comments on the systematics of the family

Abstract

Skeletal components of species of *Squalus* and *Cirrhigaleus* are poorly investigated, except for *S. acanthias*, *S. megalops* and *C. barbifer* that have been described with more accuracy. Characters based on studies of the neurocranium and cartilages of the clasper seem to be more effective for separating species. Other comparative analyses provided characteristics that support the monophyly of genera. However, recent investigations noticed that the synapomorphies attributed to *Squalus* and *Cirrhigaleus* are not consistent because they vary between species. The present study aimed to investigate these variations in Squalidae with more accuracy and to provide better morphological support that could be integrated with future Systematic analysis of the family. Neurocranium, pectoral fin and girdle, pelvic fin and girdle, and cartilages of the clasper of a variety of species are described comparatively. Characteristics of the skeleton in Squalidae appear to be more complex than previously thought. A total of 20 morphological characters are provided in the current study and compared with other members within Squaliformes. New insights regarding the position of *Cirrhigaleus* in Squalidae and the interrelationships between species of *Squalus* are discussed.

Resumo

Componentes do esqueleto em espécies de *Squalus* e *Cirrhigaleus* são pouco analisados, exceto para *S. acanthias, S. megalops* and *Cirrhigaleus barbifer* que tem sido descritos com detalhe. Estudos do neurocrânio e cartilagens do clásper revelaram eficientes caracteres diagnósticos para separar as espécies. Outros estudos comparativos forneceram características que suportam o monofiletismo dos gêneros. Contudo, investigações mais recentes do esqueleto notam que tais sinapomorfias não são consistentes devido a variações observadas entre as espécies. O presente estudo objetivou investigar estas variações em Squalidae e fornecer subsídios morfológicos eficientes para serem incorporados a futuras análises filogenéticas da família. Neurocrânio, nadadeiras e cinturas peitoral e pélvica, e cartilagens do clásper são descritos comparativamente aqui. Características do esqueleto em Squalidae apresentam complexidade e variação maior do que antes descrito na literatura. Ao todo, 20 caracteres esqueléticos são apresentados no presente trabalho e comparados com outros membros de Squaliformes. Novas interpretações sobre o posicionamento de *Cirrhigaleus* dentro da família e as interrelações entre as espécies de *Squalus* são discutidas.

Introduction

Squalidae Blainville, 1816 is a family of dogfish sharks whose monophyly is supported by two external characters of dentition: teeth imbricated with continuous cutting edge (character 69); homodonty dignatic (character 70) (Shirai, 1992). It comprises two genera, *Squalus* Linnaeus, 17158 and *Cirrhigaleus* Tanaka, 1912 with complex taxonomic history and whose systematics is intensively discussed in the literature (e.g. Shirai, 1992; White *et al*., 2007b; Figueirêdo, 2011;Naylor *et al*., 2012b).

Characters of the skeleton such as neurocranium and claspers have not been used yet to support the monophyly of the family but genera. It is also often used for separating species of *Squalus*. Skeletal anatomy in *Squalus* and *Cirrhigaleus* is still poorly investigated and most of the published studies describe structures for only a few species (e.g. Jungersen, 1899; Marinelle & Strenger, 1959; Gilbert, 1973; Yano, 1986; Maia & Wilga, 2013), including *Squalus acanthias*, *S. megalops*, *S. blainvillei* and *Cirrhigaleus barbifer*. Muñoz-Chápuli & Ramos (1989) noticed differences in the basal plate of the neurocranium between *Squalus megalops* from the Eastern Atlantic Ocean and *Squalus blainvillei.* These authors also provided 19 cranial measurements that were helpful on differentiating them. Terminal cartilages of the claspers also varied among these species, according to length and thickness (Muñoz-Chápuli & Ramos, 1989). Marouani *et al*. (2012) supported the separation between these two species in Tunisian waters based on characters of the neurocranium and clasper as well. Other studies on the taxonomy of the genus followed the methodology of Muñoz-Chápuli & Ramos (1989) and corroborated its effectiveness in separating nominal species or groups of species of *Squalus* (e.g. Marques, 1999; Figueirêdo, 2011). The diversity of the family requires a broader analysis of the skeletal anatomy for better understanding of inter- and intraspecific character variations and to evaluate their usefulness for taxonomic and phylogenetic purposes.

Shirai (1992) was the first author who analyzed inner phylogenetic relationships within the Squalidae. He supported *Squalus* as monophyletic, using the presence of supraethmoidal process (his character 19) and conspicuous upper precaudal pit (his character 181) as synapomorphies. The nominal species *Squalus asper* and *Cirrhigaleus barbifer* lack these two characteristics, which supported the allocation of the former species into the genus *Cirrhigaleus* (Shirai, 1992). According to Shirai (1992), *Cirrhigaleus* is monophyletic based on the innervation of the nasal barbels by a branch of the buccopharyngeal facialis nerve (his character 175). These three synapomorphies, however, were debated in recent studies due to variations observed in species of *Squalus* and *Cirrhigaleus*. Ramos (2009) pointed out that a specimen of *C. asper* from the Southwestern Atlantic Ocean has two prominent supraethmoidal processes in the neurocranium, supporting its morphological similarities with species of *Squalus*. Figueirêdo (2011) on the other hand noticed its absence in a specimen of *Squalus* sp. from this region. Gomes (*pers. comm.*) did not find innervation on the nasal barbel of *C. asper*, indicating that the characters that support the monophyly of each genus require further investigation.

The present study aimed to investigate skeletal components in species of *Squalus* and *Cirrhigaleus*, and to describe and discuss comparatively their morphological variations. New characters are provided for integrating future analysis on interrelationships of the family.

Material and methods

The present study follows the methodology outlined in the section “Materiais e Métodos” of the current PhD thesis.

Analyzed material (91 specimens). *Squalus acanthias* (34 specimens): AMNH 38181, unknown sex and TL, off Woods Hole, Massachusetts, The United States of America (all skeleton); AMNH 40802, neonate female, 190 mm TL, off Woods Hole, Massachusetts, The United States of America (all skeleton); AMNH 97545, unknown sex and TL, The United States of America (all skeleton); AMNH 97554, unknown sex and TL, The United States of America (all skeleton); AMNH 97561, unknown sex and TL, The United States of America (all skeleton); AMNH 53052, The United States of America (all skeleton); AMNH 225783, unknown sex and TL, off North Carolina, The United States of America (all skeleton); BMNH 1888.2.6.72, adult male, 690 mm TL, United Kingdom, Northeast Atlantic Ocean (radiograph); BMNH 1929.10.20.1, adult female, 875 mm TL, United Kingdom, Northeast Atlantic Ocean (radiograph); BMNH 1931.8.10.1, adult male, 785 mm TL, New Zealand (syntype of *Squalus kirki*) (radiograph); BMNH 1976.7.30.20, adult female, 523 mm TL, France, Mediterranean Sea (radiograph); BMNH 1999.5.4.4, juvenile male, 550 mm TL, Falkland Islands, Southwest Atlantic Ocean (neurocranium, pelvic fin and girdle, claspers); CAS 13381, adult male, 670 mm TL, Gregory Bay, Strait of Magellan, Chile (radiograph); CAS 21968, neonate female, 285 mm TL, off Alameda, California, The United States of America (all skeleton); HUMZ 30173, adult male, unknown TL, off Patagonia, Argentina, 47°S, 65°16’W (neurocranium, pelvic fin and girdle, claspers); HUMZ 30291, adult male, 595 mm TL, off Patagonia, Argentina, 47°S, 65°16’W (pectoral fin and girdle, pelvic fin and girdle); HUMZ 107285, juvenile female, 340 mm TL, off Argentina, 46°59.5’S, 65°16’W (neurocranium, pectoral fin); NMW 50118, adult male, 805 mm TL, Bergen, Norway (all skeleton); NRM 85, neonate female, 177 mm TL, unknown locality, from the King Adolf

Fredrik's collection at Ulriksdal (syntype of *S. acanthias*) (radiograph); NRM 21763, adult male, 645 mm TL, Öresund, near Råå, Sweden (radiograph); RMNH.PISC. 4315, juvenile female, 465 mm TL, The Netherlands (radiograph); RMNH.PISC. 27099, juvenile female, 466 mm TL, Schulpengat, The Netherlands (radiograph); SAIAB 21873, adult male, 675 mm TL, Cape Columbine, South Africa, 32.59°S, 17.36°E (neurocranium, pelvic fin and girdle, claspers); SAIAB 25918, adult male, 700 mm TL, West coast of South Africa, 31.48°S, 17.27°E (radiograph); SAIAB 26301, adult female, 670 mm TL, West coast of South Africa, 32.70°S, 17.20°E (radiograph); SAM 38271, juvenile male, 240 mm TL, unknown locality, Northwestern Atlantic Ocean; SAM 38276, adult male, 670 mm TL, unknown locality, Northwestern Atlantic Ocean (neurocranium, pectoral fin and girdle, pelvic fin and girdle, claspers); SAM 41629, adult female, 900 mm TL, unknown locality, Northwestern Atlantic Ocean (neurocranium); UUZM 159, juvenile male, 346 mm TL, unknown locality, from the King Adolf Fredrik's collection at Ulriksdal, Donation by J. Alströmer (syntype of *S. acanthias*) (radiograph); UUZM 160, neonate female, 380 mm TL, dried material, unknown locality, Donation by J. Alströmer (syntype of *S. acanthias*) (radiograph); UUZM 287, adult male, 700 mm TL, stuffed specimen, unknown locality, Donation by Gustav IV Adolf (syntype of *S. acanthias*) (radiograph); ZMH 101004, two juvenile males, 555, 635 mm TL, Canada, 47°40N, 59°24W (radiograph); ZMH 104416, adult male, 725 mm TL, near Peninsula del Valdes, Argentina, 59°48'W,43°8'S (neurocranium, pelvic fin and girdle, claspers); ZMB 4504 adult male, 650 mm TL, The North Sea (pelvic fin and girdle).

Squalus suckleyi (10 specimens): CAS 21424, neonate female, 285 mm TL, off Alameda, California, The United States of America (all skeleton); CAS 21971, neonate female, 290 mm TL, off Alameda, California, The United States of America (all skeleton); CAS 34815, neonate male, 228 mm TL, San Francisco Bay, California, The United States of America, 37°45N, 122°22’E (all skeleton); CAS 40592, neonate male, 185 mm TL, San

Francisco Bay, California, The United States of America (all skeleton); CAS 40868, neonate female, 160 mm TL, between Pt. Bonita and Pt. Reyes, Marin, California, The United States of America, (all skeleton); CAS 40873, neonate male, 330 mm TL, Point Roberts, Washington State, The United States of America (neurocranium, pelvic fin and girdle, claspers); CAS 56093, neonate male, 256 mm TL, San Francisco Bay, California, The United States of America (all skeleton); CAS 227267 (neotype of *S. suckleyi*), adult male, 674 mm TL, Hood Canal, Puget Sound, Washington, USA, 47°22N, 123°05W (pectoral girdle and fin, claspers) (radiograph); SAM 38346, adult female, 850 mm TL, Oakland, San Francisco Bay, California (neurocranium, pectoral fin and girdle); SAM 38355, unknown sex, 783 mm TL, San Francisco, California (neurocranium)

Squalus cf. *suckleyi* (4 specimens): HUMZ 87643, adult male, 665 mm TL, Usujiri, Mimamikayakabie, Hokkaido, Japan (neurocranium, pelvic fin and girdle, claspers); HUMZ 87733, juvenile male, 495 mm TL, off Shiretoko, Hokkaido, Japan (neurocranium); NSMT-P 79501, adult male, 740 mm TL, Northern Japan, Japan (radiograph); NSMT-P 92640, adult female, 740 mm TL, Northern Japan, Japan (radiograph).

Squalus megalops (1 specimen): AMS I 46093-001, adult male, 650 mm TL, Derwent Hunter Seamount, New South Wales, Australia (neurocranium, pelvic fin and girdle, claspers)

Squalus brevirostris (2 specimens): HUMZ 37664, adult female, unknown total length, off northwest Borneo, 3°07.8’N,110°45.4’E (neurocranium, pelvic fin and girdle); HUMZ 189762, adult male, 433 mm TL, East China Sea (neurocranium, pelvic fin and girdle, claspers).

Squalus albifrons (2 specimens): CSIRO H 2619-12, unknown sex and TL, Western Australia, 33°22'S,114°31'E (neurocranium); MZUSP uncatalogued (formely CSIRO uncatalogued), adult male, 760 mm TL, East of Ballina, New South Wales, Australia (all skeleton).

Squalus blainvillei (1 specimen): BMNH 1963.5.14.13-18, juvenile male, 382 mm TL, France, Mediterranean Sea (neurocranium, pelvic fin and girdle, claspers).

Squalus cf. *blainvillei* (1 specimen): SAIAB 6021, adult male, 670 mm TL, Durban, South Africa, 29.85°S,31°E (neurocranium, pelvic and girdle, claspers).

Squalus mitsukurii (2 specimens): HUMZ 68767, adult male, 620 mm TL, Emperor Sea Mount, Kinmei, 35°07.3'N, 171°41.4'E (neurocranium, pectoral fin and girdle); NSMT-P 44381, juvenile male, 770 mm TL, unknown locality, Southern Japan (neurocranium, pelvic fin and girdle, claspers).

Squalus montalbani (1 specimen): MZUSP uncatalogued (formerly CSIRO uncatalogued), adult male, 713 mm TL, East of Ballina, New South Wales, Australia (all skeleton).

Squalus chloroculus (2 specimens): CSIRO H 2867-07, adult male, 746 mm TL, Great Australian Bight, Southern Australia, 33°25'S, 129°55'E (neurocranium); CSIRO H 2867-08, adult female, 750 mm TL, same locality as CSIRO H 2867-07 (neurocranium).

Squalus grahami (4 specimens): CSIRO 1362-3, adult male, unknown TL, Northeast of Hinchibrook Island, Queensland, Australia, 17°55'S, 147°06'E (neurocranium); CSIRO 1372-1, adult female, 710 mm TL, North of Townville, Queensland, Australia, 17°57'S, 147°00'E (neurocranium); MZUSP uncatalogued (formely CSIRO uncatalogued), adult male, 565 mm TL, East of Ballina, New South Wales, Australia (all skeleton); MZUSP uncatalogued (formely CSIRO uncatalogued), adult male, 560 mm TL, East of Wooli, New South Wales, Australia (all skeleton).

Squalus griffini (1 specimen): NMNZ TMP 30388, adult female, 1000 mm TL, New Zealand (all skeleton).

Squalus japonicus (3 specimens): HUMZ 80223, adult male, unknown TL, near Okinawa, Japan, 25°33.8’N, 126°25.2’E (pectoral fin, pelvic fin and girdle, claspers); HUMZ 95213, unknown sex and TL, East China Sea, 27°46’N, 126°15.3’E (neurocranium); HUMZ 189737, adult male, 560 mm TL, East China Sea (neurocranium, pelvic fin and girdle, claspers).

Squalus nasutus (1 specimen): CSIRO H 2591-18, juvenile female, 520 mm TL, West of Leander Point, Western Australia, 29°18’S, 113°56’E (neurocranium).

Squalus sp. 1 (2 specimens): BMNH 1912.12.10.45-46, juvenile female, 441 mm TL, South Africa (neurocranium); SAIAB 21858, adult male, 455 mm TL, Jakkalsbaai, South Africa, 29.85°S, 15.18°E (claspers).

Squalus sp. 3 (1 specimen): SAIAB 25370, adult male, 500 mm TL, Algoa Bay, South Africa, 34.03°S, 25.70°E (neurocranium, pelvic fin and girdle, claspers).

Squalus sp. 4 (3 specimens): UERJ 1112, adult male, 635 mm TL, Rio Grande do Sul, Brazil (neurocranium, pelvic fin and girdle, claspers); UERJ 1661 (paratype), adult male, 640 mm TL, unknown locality Brazil (neurocranium, pelvic fin and girdle, claspers); UERJ 1173, adult female, unknown TL and locality, off Brazilian coast (neurocranium).

Squalus sp. 7 (1 specimen): MNRJ 30184, adult male, 480 mm TL, Salvador, Bahia, Brazil, 13°8'54"S, 38°28'41"W (paratype).

Cirrhigaleus barbifer (3 specimens): HUMZ 95177, juvenile female, 584 mm TL, East China Sea, 28°54.2’N, 128°29.3’E (neurocranium, pectoral fin, pelvic fin and girdle); TPM 38074, adult male, 1020 mm TL, Southern Norfolk ridge, New Zealand, 32°40’S, 167°37’E (pelvic fin and girdle, claspers); SU 13901, adult female, 730 mm TL, Honshu Island, Misaki Bay, Chiba, Japan (holotype of *Phaenopogon barbulifer*) (radiograph).

Cirrhigaleus asper (4 specimens): BMNH 1972.10.10.1 (holotype of *Cirrhigaleus asper*), adult male, 880 mm TL, off Aldabra Island, Seychelles, 09°27’S, 46°23.5’E (radiograph and CT scan of head); SAIAB 6092, neonate male, 270 mm TL, unknown locality, South Africa (neurocranium); SAM 38269, adult female, 1045 mm TL, off Coffee Bay, Transkei, South Africa (all skeleton); UERJ 1641, adult male, 990 mm TL, off Rio de Janeiro, Brazil (pelvic fin and girdle, claspers).

Cirrhigaleus australis (4 specimens): AMS I 45670-001, juvenile male, 630 mm TL, Britannia Seamount, New South Wales, Australia (radiograph); CSIRO H 5789-01, adult female, 970 mm TL, East of Bicheno, Tasmania, 41°55'S, 148°37'E (holotype of *Cirrhigaleus australis*) (radiograph); CSIRO H 7042-04, juvenile female, 605 mm TL (neurocranium, pectoral fin and girdle, pelvic fin and girdle); CSIRO H 7048-01, adult male, 993 mm TL, East of Tweed Heads, New South Wales, Australia, 28°17'S, 153°53'E (radiograph).

1. Neurocranium

Anatomical description (Tabs. 1–8; Figs. 1–27). The neurocranium in Squalidae is described in detail for five nominal species: *Squalus acanthias*, *S. mitsukurii*, *S. japonicus* and *Cirrhigaleus barbifer*. Each description represents a major morphological condition within the family. The remaining species that share similar morphological condition are briefly described and the variations observed among them are indicated in detail.

In *Squalus acanthias* (Table 1; Figs. 1), neurocranium with greatest width across postorbital processes (its width 49.2%–54.9% of CL), narrower in the interorbital region (its width 24.5%–60.8% of CL) and between the opistotic processes in the otic region (its width 32.0%–42.2% of CL). Rostrum spoon-like, constituted by an elongate (its length 35.8%–42.3% of CL) and profound precerebral fossa, slender proximal and distally, and wide medially, its width 11.5%–20.7% of CL; lateral rostral cartilages cylindrical, somewhat depressed anteriorly; ventrally, two lateral rostral appendages thick and hook-like, connecting to the nasal capsule on each side by ligament; median rostral prominence modest, placed between lateral rostral appendages and connecting to the rostral keel by a thick ligament; rostral keel conspicuous and well elongate (its length 17.3%–38.5% of CL); rostral carina subtle, placed anteriorly from anterior base of the rostral keel until median rostral prominence. Prefrontal fontanelle rounded and tapered, located at the base of the rostrum and afore the cerebrum. Nasal capsules oval and strongly oblique, very narrow, located on each side of the rostrum, width across them 41.4%–50.4% of CL; nasal cracks evident ventrally, and anterior nasal margin with an unique cartilaginous lobe; subnasal fossa oval, large and vertical, located ventrally on each side of the rostral keel. Two supraethmoidal processes prominent and triangular, although not elongate, placed in the dorsal base of the prefrontal fontanelle; epiphyseal pit rounded, broad and vertical, posteriorly to the supraethmoidal processes; ethmoidal canal rounded and narrow, placed in the base of each nasal capsule; ectethmoidal chamber flattened, somewhat constricted ventrally with antorbital cartilage triangular and prominent, attached anteriorly to a nasal capsule on each side; subethmoidal ridge small and prominent, posterior to the rostral keel and extending to the subethmoidean region; the latter elongate and very narrow, its width 10.5%–13.6% of CL.

Cranial roof strongly concave medially in the interorbital region; supraorbital crest prominent laterally; longitudinal sulcus at the medial base of this crest, markedly profound anteriorly, carrying the profundus canal for the ophthalmicus profundus nerve, the preorbital canal and a series of foramina (7–9 foramina) of the branch superficial ophthalmic of the trigeminal and facial nerves (V-VII); preorbital canal rounded and markedly large, placed anteriorly to the series of foramina; profundus canal rounded and small, located previous to the preorbital canal and aside the ethmoidal canal; ventral-lateral aperture of the profundus canal small, placed in the interorbital wall just prior the preorbital canal. Preorbital processes inconspicuous, although wide across them (it width 44.3%–55.7% of CL). Postorbital process prominent and triangular, although not well elongate (its length 6.7%–10.3% of CL). Distance between the orbital processes, corresponding to 26.0%–33.9% of CL.

Orbital region with preorbital wall concave, carrying a single orbitonasal canal on its base; interorbital wall very narrow with foramen optic (II) very elongate and rounded, placed middle-ventrally; foramen trochlear (IV) small, located more dorsal-anteriorly to the foramen optic (II); eye stalk with distal disc, located more posteriorly in the interorbital wall between the foramen oculomotor (III) and the foramen abducens (VI); these foramina are placed, respectively, dorsal and ventrally to the eye stalk; foramen prooticum, for the trigeminal (V) and facial (VII) nerves single and large in the posterior base of the interorbital wall, just before postorbital process; two foramina for hyomandibular branch of the facial nerve (VII) opens on the anterior base of the hyomandibular facet. Species of *Squalus* share same arrangement of cranial nerves and blood vessels in the interorbital wall. *Squalus acanthias* also has basal angle conspicuous (its width 16.5%–21.5% of CL), placed ventral-medially in the interorbital wall for supporting the orbital articulation; basal angle also carries dorsally foramen for an efferent of the pseudobranchial artery which is small and rounded.

Basal plate flattened and large (its length 36.9%–49.5% of CL), narrower anteriorly in the basitrabecular process, turning broader posteriorly (its anterior width between 16.9%–26.4% of CL); basitrabecular processes conspicuous and bean-shaped, perpendicular to the basal plate axis; one or two sinuous lateral prominences on each side, among the basitrabecular processes and the first cartilaginous process; single cartilaginous process on each side of the basal plate, somewhat cylindrical (width across them 29.7%–34.2% of CL); one foramen for the carotid artery, located medial-anteriorly in the basal plate with two inner apertures; foramina for the orbital artery with its ventral opening in the anterior base of the cartilaginous process and the lateral opening in the subotic shelf.

Otic region strongly deep anterior-dorsally between otic capsules; one otic capsule on each side, narrow and heptagonal; dorsally, two anterior and two posterior semicircular canals, both conspicuous, the former placed almost in parallel to the longitudinal axis of the neurocranium; endolymphatic fossa oval and small, placed posteriorly between otic capsules; this fossa carries two anterior endolymphatic foramina, slightly oblique, and two posterior and vertical perilymphatic foramina; otic crest strong and posterior, running from endolymphatic fossa to foramen magnum; sphenopterotic ridge weak with anterior process, placed on each side of the otic region; opisthotic process rather subtle, placed posteriorly to the sphenopterotic ridge; laterally, otic wall delimited dorsally by one prominent lateral semicircular canal, ventral-posterorly by hyomandibular facet, and anteriorly by deep lateral auditory groove; hyomandibular facet shallow, ending on markedly pointed postotic process (width across the hyomandibular facets 36.8%–48.6% of CL).

Occipital region with two occipital condyles distally, triangular and broad; foramen magnum rounded and large between occipital condyles (its width 7.2%–18.3%% of CL); foramen for the vagus nerve (X) rounded aside each occipital condyle; glossopharyngeal base thick and subtriangular, although not very prominent, located more laterally in the occipital region and carrying foramen for the glossopharyngeal nerve (IX); the latter oval and large.

Squalus suckleyi and *Squalus* cf. *suckleyi* (Table 2; Figs. 2–3) share with *Squalus acanthias* many characteristics of the neurocranium, such as: greatest width at postorbital processes (width across than 47.2%–54.9% of CL for *S. suckleyi*; 52.9%–58.9% of CL for *Squalus* cf. *suckleyi*) than at nasal capsules (width across them 41.4%–54.1% of CL for *S. suckleyi*; 49.6%–51.2% of CL for *Squalus* cf. *suckleyi*); rostral keel markedly elongate with moderate rostral carina; one cartilaginous process on each side of the basal plate; two lateral rostral appendages; profundus canal with its dorsal aperture aside ethmoidal canal; otic crest robust; a single foramen for carotid artery; foramen for orbital artery at the base of each cartilaginous process. However, *Squalus suckleyi* can be distinguish from them by: median rostral prominence conspicuous (vs. median rostral prominence modest for *Squalus acanthias* and *Squalus* cf. *suckleyi*); epiphyseal pit horizontal (vs. vertical for *S. acanthias* and *Squalus* cf. *suckleyi*); sphenopterotic ridge lacking anterior process (vs. sphenopterotic ridge with prominent anterior process for *S. acanthias* and *Squalus* cf. *suckleyi*); antorbital cartilage less pointed distally (vs. very pointed for *S. acanthias* and *Squalus* cf. *suckleyi*); first cartilaginous process somewhat rounded (vs. strongly pointed for *S. acanthias* and *Squalus* cf. *suckleyi*). It is also distinguished by shorter nasobasal length than *S. acanthias* and *Squalus* cf. *suckleyi* (58.5%–60.6% of CL vs. 61.0%–68.5% of CL for *S. acanthias* vs. 63.1%–65.0% of CL for *Squalus* cf. *suckleyi*). In contrast to *S. suckleyi* and *S. acanthias*, the species *Squalus* cf. *suckleyi* bears two epiphyseal pits medial-dorsally in the cranial roof, interorbital concavity much more tapered, two lateral sinuosity in the basal plate between basitrabecular process and first cartilaginous process. *Squalus* cf. *suckleyi* has 8–10 foramina of the branch superficial ophthalmic of the trigeminal and facial nerves (V-VII). This species can also be distinguished from *S. suckleyi* by having larger distance across opisthotic processes (37.7%–38.3% of CL vs. 31.3%–34.3% of CL) and wider distance across hyomandibular facets (45.7%–45.8% of CL vs. 37.4%-44.9% of CL).

Squalus megalops (Tab. 3; Fig. 5) shows cranial morphology similar to those observed for *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*. However, the former species has neurocranium much more wide than these species as it is shown through some cranial measurements: width across nasal capsules 52.3% of CL; width across postorbital processes 59.1% of CL; distance across opisthotic processes 43.2% of CL. *Squalus megalops* also differs from them by having smaller precerebral fossa (its length 29.9% of CL), shorter rostral keel (its length 19.1% of CL), larger distance between orbital processes (distance 38.4% of CL), and very elongate nasobasal length 74.1% of CL. *Squalus megalops* carries 7–

8 series of foramina of the branch superficial ophthalmic of the trigeminal and facial nerves (V-VII). This species has postorbital process more elongate (its length 11.0% of CL), conical and directed laterally than it is noticed for *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*. In contrast to these three nominal species, *S. megalops* has subethmoidal region markedly small, anterior and lateral semicircular canals inconspicuous, hyomandibular facet profound, and opisthotic processes robust. It also lacks median rostral prominence, otic crest, and ventral aperture of the foramen for orbital artery. *Squalus megalops* also bears transbasal canal for the pituitary vein, placed ventral to the foramen prooticum, which it is not observed in the latter three species.

Squalus brevirostris, *S. albifrons*, *Squalus* sp. 1, *Squalus* sp. 3, and *Squalus* sp. 7 (Tables 3, 7; Figs. 6–12) have neurocranium very similar to those of *S. megalops* regarding width and length of neurocranium, although all these species also share general cranial morphology observed for *S. acanthias*. With exception to *S. albifrons*, these species share median rostral prominence very small and subtle as it is noticed for *S. acanthias* and *Squalus* cf. *suckleyi*. In contrast to *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*, these five nominal species have otic crest very short and inconspicuous. *Squalus brevirostris*, *S. albifrons*, *Squalus* sp. 1 and *Squalus* sp. 7 share neurocranium with its greatest width at level of the postorbital processes (60.5%–63.2% for *S. brevirostris* vs. 52.5%–64.3% for *S. albifrons* vs. 61.7%–62.8% for *Squalus* sp. 1 vs. 57.1% for *Squalus* sp. 7) than at nasal capsules (56.7%–59.1% for *S. brevirostris* vs. 49.3%–62.6% for *S. albifrons* vs. 54.4%–59.5% for *Squalus* sp. 1 vs. 52.8% for *Squalus* sp. 7), two lateral rostral cartilages and a single cartilaginous process on each side of the basal plate like it is noticed for *Squalus acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*. The number of series of foramina of the branch superficial ophthalmic of the trigeminal nerve (V-VII) varies among *S. albifrons*, *Squalus* sp. 1, *Squalus* sp. 7, and *S. brevirostris* (11–13 for *S. albifrons* vs. 9–9 for *Squalus* sp. 1 vs. 11–11 for *Squalus* sp. 7 vs. 8–9 for *S. brevirostris*).

Squalus albifrons, Squalus sp. 1 and *Squalus* sp. 7 differ from *S. brevirostris* and *S. megalops* by having anterior semicircular canal conspicuous (vs. inconspicuous). *Squalus brevirostris* can also be distinguished from these species by having sphenopterotic ridge more elongate with lateral concavity strongly broad. *Squalus albifrons* has median rostral prominence well developed and otic crest thick, although very short. Two external apertures of the foramen for carotid artery are also noticed in *Squalus albifrons*. Foramen for orbital artery small and rounded placed near the base of each cartilaginous process in the basal plate for *S. albifrons*, *Squalus* sp. 1, and *S. brevirostris* in contrast to *S. megalops*. *Squalus* sp. 7 is clearly distinguished from *S. albifrons*, *Squalus* sp. 1, *S. brevirostris* and *S. megalops* by having first foramen of the series of foramina of the branch superficial ophthalmic of the trigeminal nerve (V-VII) as large as preorbital canal while this foramen is much smaller than preorbital canal in other species.

Squalus blainvillei (Table 4; Fig.13) also has neurocranium similar to *S. acanthias*, sharing characteristics such as: profundus canal for the branch deep opththalmic of the trigeminal nerve (V) small and rounded, located medially aside the ethmoidal canal; a single foramen for carotid artery, and one foramen for orbital artery on each side at the base of first cartilaginous process; otic crest markedly small and subtle. However, the neurocranium of *S. blainvillei* resembles generally those for *S. megalops*, regarding cranial measurements: rostral keel markedly short (its length 20.1% of CL). *Squalus blainvillei* has preorbital canal elliptical and strongly large, all semicircular canals well prominent, and seven series of tiny foramina of the branch superficial ophthalmic of the trigeminal and facial nerves (V-VII). A second pair of cartilaginous processes, rounded and small, is conspicuously observed in *Squalus blainvillei* in the basal plate. These second cartilaginous processes are placed more posteriorly and laterally settled in the anterior base of hyomandibular facet, which suggests additional support for the cranium-hyomandibular articulation. This nominal species also present the neurocranium with greatest width across both nasal capsules and postorbital processes (60.8% vs. 59.4% of CL, respectively), in contrast to what it is observed for *Squalus acanthias*, *S. suckleyi*, *Squalus* cf. *suckleyi*, *S. megalops*, *S. brevirostris*, *S. albifrons*, *Squalus* sp. 1, and *Squalus* sp. 7.

In *Squalus mitsukurii* (Table 5; Fig. 14), neurocranium with circular prefrontal fontanelle, somewhat narrow, located between the nasal capsules and anteriorly to the cranial cavity; precerebral fossa markedly profound, placed just before prefrontal fontanelle and forming the rostrum trough; rostrum spoon-like, very wide (precerebral fossa width 14.8% of CL), although slenderer at its proximal end, and elongated (precerebral fossa length 39.9% of CL); lateral rostral cartilages thick distally near the nasal capsules, turning depressed, expanded and soft anteriorly to it until it reaches the rostral tip; rostral appendages prominent ventrally, hook-like and thick, one medial and two laterals, contrasting to species of *Squalus* described previously; rostral keel large (its length 25.4% of CL) and prominent; rostral carina small, not reaching the medial rostral appendage; subethmoidal ridge small and inconspicuous; subnasal fenestra large and rounded, placed on each side of the rostral keel and at the ventral base of prefrontal fontanelle. Nasal capsules oval, narrow and oblique, irregular in shape ventrally with unchondrified cracks and a small internal lobe.

Neurocranium with its greatest width across postorbital processes rather than at nasal capsules (57.1% vs. 54.0% of CL, respectively). Cranial roof concave medially, its proximal region with two conspicuous supraethmoidal processes, although not elongated, thick and triangular in shape; epiphyseal pit rounded, small, placed posteriorly to the supraethmoidal processes; small protrusion evident between these two structures; supraorbital crest arched and C-shaped; longitudinal sulcus profound, carrying preorbital canal and 8–10 foramina of the branch superficial ophthalmic of the trigeminal nerve (V-VII); ethmoidal canal small, rounded, located at the base of each nasal capsule; profundus canal for the branch deep opththalmic of the trigeminal nerve (V), small and rounded, placed dorsally between the preorbital canal and ethmoidal canal, and ventral-laterally just prior the preorbital canal in the interorbital wall; preorbital canal markedly large and rounded, much wider than the profundus canal, located in front of the series of foramina for the ophthalmic nerve (V-VII); preorbital processes inconspicuous; interorbital region widely concave laterally, its width among 31.6% of CL; postorbital processes prominent, subtriangular and somewhat short, its length 10.9% of CL. Ethmoidal region very broad, moderately arched with antorbital cartilage wide, triangular and pointed ventral-posteriorly; subethmoidal region elongate and broad anteriorly (its width 14.7% of CL).

Preorbital wall very tall and concave; interorbital wall elongate and profound; foramen optic (II) large and rounded, located anterior-ventrally in the interorbital wall; foramen oculomotor (III) just above the eye stalk and foramen abducens (VI) near its base; foramen trochlear (IV) placed middle-dorsally, close to the series of foramina of the branch superficial ophthalmic of the trigeminal nerve (V-VII); trigeminal (V) and facial (VII) nerves share same foramen, the foramen prooticum, located ventral-posteriorly in the interorbital wall, near the lateral commissure; transbasal canal for the pituitary vein present, placed just anterior to foramen prooticum in the interorbital wall (this canal is absent in *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*); a branch hyomandibular of facial nerve (VII) have two apertures that open laterally in the subotic shelf at the anterior base of the hyomandibular facet. *Squalus mitsukurii* has basal angle prominent (its width 16.9% of CL), ventral-medially in the interorbital wall for supporting the orbital articulation, and carrying dorsally small and rounded foramen for an efferent of the pseudobranchial artery.

Otic region with two hexagonal otic capsules on each side; two broad anterior semicircular canals and two narrow posterior semicircular canals, both prominent and oblique; endolymphatic fossa between the otic capsules, pentagonal and profound, supporting two endolymphatic foramina and two perilymphatic foramina; the latter oval, oblique and much larger than the former; otic crest stout and longitudinal, running medially from endolymphatic fossa to foramen magnum with protuberance small and pointed at its proximal edge; sphenopterotic ridge well marked, laterally to the otic capsules; opisthotic processes conspicuous, strongly pointed and expanded laterally; lateral otic wall surrounded anteriorly by lateral auditory groove, ventrally by hyomandibular facet, and dorsally by lateral semicircular canal; hyomandibular facet shallow, ending posteriorly on prominent postotic process; width across hyomandibular facets 48.1% of CL.

Occipital region with two occipital condyles triangular and narrow, placed ventrally; foramen magnum broad (its width 7.9% of CL); foramina for vagus nerve (X) oval, placed laterally on each side of the occipital region; glossopharyngeal base markedly heavy and subtriangular, located lateral-posteriorly on each side of the occipital region, carrying foramen for the glossopharyngeal nerve (IX); the latter with its posterior aperture oval and conspicuously wide, and its ventral aperture elliptical and small.

Basal plate narrower anteriorly than posteriorly (its width 19.7% of CL) and well elongate (its length 33.2% of CL); basitrabecular processes been-shaped and subtle; an unique cartilaginous process on each side of the basal plate, small and rounded (distance between them 31.5% of CL); basal plate sinuous laterally between basitrabecular process and first cartilaginous processes; foramen for carotid artery large placed in the midline of the basal plate near basitrabecular processes; foramen for orbital artery at the base of each cartilaginous process. *Squalus* sp. 4 (Table 7; Fig. 20) from Brazilian coast and *Squalus* cf.

blainvillei (Table 4) from South Africa have neurocranium with morphology similar to those of *S. mitsukurii*.

In contrast to other species, *Squalus montalbani*, *S. chloroculus*, *S. grahami* and *S. griffini* (Table 5; Figs. 15–19) have neurocranium with its greatest width at nasal capsules (its width 54.8% of CL vs. 50.9%–51.9% of CL vs. 41.5%–56.8% of CL vs. 58.3% of CL) rather than across postorbital processes (its width 53.3% of CL vs. 42.8%–49.0% of CL vs. 53.1% of CL). These three nominal species show cranial condition similar to *S. mitsukurii*, such as: three rostral cartilages ventrally; otic crest thick and large; elongate rostral keel (its length 24.0% of CL for *S. montalbani* vs. 22.9%-29.6% of CL for *S. grahami* vs. 24.2% of CL for *S. griffini*); transbasal canal for the pituitary vein present. *Squalus montalbani* and *S. chloroculus* can be distinct from them by having: profundus canal with two dorsal apertures, placed between ethmoidal canal and preorbital canal; anterior semicircular canal inconspicuous; foramen optic (II) subtriangular and large. Few differences on cranial measurements are noticed between *Squalus montalbani* and *S. chloroculus*, including postcerebral length, length if precerebral fossa, width at nasal capsules and distance between orbital processes. *Squalus montalbani*, *S. chloroculus*, *S. grahami* and *S. griffini* have, respectively, 12–12, 12–12, 11–9 and 11–11 series of foramina of the branch superficial ophthalmic of the trigeminal nerve (V-VII) in contrasting to *S. mitsukurii* and *Squalus* sp. 4. The former four species also share rostral carina well developed, reaching the median rostral appendage, which differs from the latter two species.

Squalus grahami and *S. griffini* differ from *S. montalbani*, *S. chloroculus*, and *S. mitsukurii* by having rostral projection, very small and somewhat rounded, located dorsally on each side of the rostrum, although in *S. griffini* it is located more posteriorly while in *S. grahami* it is anteriorly. The latter species also differs from these three species by: narrower interorbital width (its width 25.7%–28.3% of CL for *S. grahami* vs. 29.7% of CL for *S.*

montalbani vs. 31.6% of CL for *S. mitsukurii* vs. 30.0% of CL for *S. griffini*); much shorter postorbital process (its length 4.6%–5.7% of CL vs. 8.1% of CL vs. 10.9% of CL vs. 6.8% of CL for *S. griffini*); narrower width across preorbital processes (its width 44.2%–47.4% of CL vs. 50.5% of CL vs. 48.6% of CL vs. 51.3% of CL); narrower width across hyomandibular facets (its width 36.7%–40.7% of CL vs. 41.6% of CL vs. 48.1% of CL vs. 45.7% of CL). *Squalus grahami* also differs from *S. montalbani* by having shorter distance between orbital processes (its length 28.5%–32.3% of CL vs. 35.2% of CL). *Squalus griffini* can be distinguished from these three species by having first cartilaginous process strongly prominent, cylindrical and very elongate (its length 30.8% of CL), directed laterally, and nasal capsule with ventral projection, very large and directed medial-posteriorly.

Squalus japonicus (Table 6; Fig. 21–22) shows cranial condition similar to *S. mitsukurii*, although its neurocranium has its greatest width equally across nasal capsules and across postorbital processes (its width 44.8%–45.0% of CL vs. 43.1%–44.5% of CL). Contrary to other species of *Squalus*, this species can be easily recognized by: precerebral fenestra shallow and conspicuously slender (its width 8.4%–10.9% of CL); prefrontal fontanelle evidently constricted and rounded; rostrum markedly elongate (its length 53.4%–59.2% of CL) and narrow, especially on its proximal and distal ends. It also differs from its congeners by having: rostral keel prominent and well elongate (its length 25.9% of CL); rostral carina strongly robust anteriorly, reaching the median rostral appendage; subethmoidal ridge markedly developed, posteriorly; sinuosity conspicuous and thick between basitrabecular process and first cartilaginous processes. As it is observed in *S. mitsukurii*, *S. montalbani*, *S. chloroculus*, *S. grahami*, *S. griffini* and *Squalus* sp. 4, *Squalus japonicus* has three rostral appendages ventrally, although it differs from them by having small lateral crests, slim and large on each rostral appendage, placed proximally. It also exhibits nasal capsules very constricted (width across nasal capsules 44.8%–45.0% of CL), oval and irregular in shape ventrally; subnasal fenestra oval and large at the ventral base of the prefrontal fontanelle; antorbital cartilage bifurcate distally; subethmoidal region rather large, markedly slender distally near the basitrabecular processes (its anterior width to 12.1% of CL); longitudinal sulcus, carrying 10 foramina of branch superficial ophthalmic of trigeminal nerve (V-VII).

In *S. japonicus*, otic region very deep anteriorly between otic capsules on each side; anterior and posterior semicircular canals small and inconspicuous; lateral semicircular canal somewhat prominent; hyomandibular facet shallow and markedly small (width across hyomandibular facets 36.5%–37.7% of CL); endolymphatic fossa pentagonal and tapered, placed among otic capsules with two tiny anterior endolymphatic foramina, and two large and oval posterior perilymphatic foramina; opisthotic processes conspicuously pointed posteriorly, showing condition similar to *S. grahami* (width across them 31.0%–33.5% of CL). *Squalus nasutus* (Table 6) exhibits cranial morphology like those of *S. japonicus*, including precerebral fenestra shallow, rostrum conspicuously large, small lateral crests on rostral appendages, and sinuosity conspicuous between basitrabecular process and first cartilaginous process. It also has 10 foramina of the branch superficial ophthalmic of the trigeminal nerve (V-VII), as in *S. japonicus*. Some differences in cranial measurements are noticed between these two species, in which *S. nasutus* show smaller values such as smaller precerebral fossa length (45.5% of CL vs. 46.4%–45.65% of CL for *S. japonicus*), width across postorbital processes (41.4% of CL vs. 43.1%–44.5% of CL for *S. japonicus*), and width at basal angle (12.5% of CL vs. 13.5%–13.9% of CL for *S. japonicus*).

In *Cirrhigaleus barbifer* (Table 8; Figs. 23, 26), neurocranium very thick, broader anteriorly across nasal capsules than posteriorly across postorbital processes (width across nasal capsules 68.2% of CL vs. width across postorbital processes 62.2% of CL); neurocranium narrower in the interorbital region (its width 37.5% of CL) and posteriorly in the occipital region (width across opistotic processes 41.6% of CL). Precerebral fossa very deep distally, and shallow proximally. Prefrontal fontanelle markedly narrow. Rostrum spoon-like and very short (its length 39.9% of CL), uniform on its extension with somewhat cylindrical lateral cartilages, rounded at the tip; in contrast to species of *Squalus*, this species lacks rostral appendages; rostral keel prominent, although markedly short (its length 22.6% of CL), not reaching the anterior margin of the nasal capsules. Nasal capsules conspicuously large, oval dorsally and rounded ventrally, slightly oblique; many large nasal foramina evident lateral and ventrally in each nasal capsule, rarely in dorsal view; nasal capsule cracks present ventrally. Subnasal fenestra oval, slender and small on each side of the rostral keel at the base of prefontal fontanelle.

Ethmoidal region strongly narrow; epiphysial pit large and rounded, located anterior-dorsally just posteriorly to the prefrontal fontanelle with thick anterior crest. In contrast to species of *Squalus*, *Cirrhigaleus barbifer* has ectethmoidal chamber markedly narrow ventrally, and antorbital cartilage tapered, continuous and convex at its distal margin. Subethmoidal region conspicuously short and slender, its width 15.2% of CL; subethmoidal ridge prominent. This species lacks supraethmoidal processes.

Cranial roof rather flattened with superficial longitudinal sulcus, carrying 10 tiny foramina of the branch superficial ophthalmic of the trigeminal and facial nerves (V-VII) plus preorbital canal; the latter conspicuously large and rounded, placed in front of the series of foramina for the ophthalmic nerve (VII); ethmoidal canal large, located well anteriorly in the base of the nasal capsule; profundus canal for the deep ophthalmic of the trigeminal nerve (V) with two apertures, one dorsal, very small and rounded, and another lateral, small and rounded, located in the interorbital wall just before the preorbital canal; the dorsal aperture of the profundus canal is placed between the ethmoidal canal and preorbital canal as it is noticed for *Squalus mitsukurii*. Interorbital region concave with supraorbital crest slender and C-shaped; distance between orbital processes very small, its length 34.0% of CL; preorbital process inconspicuous; postorbital process triangular and small, its length 13.4% of CL; width across postorbital processes slightly greater than the width across preorbital processes (the former 62.2% of CL vs. the latter 60.8% of CL).

Preorbital wall convex and short. Interorbital wall profound with eye stalk small and wide, carrying distal disc, and located more posteriorly; foramen optic (II) very large and rounded, placed more ventral-anteriorly near the preorbital wall; foramen trochlear (IV) dorsally near the series of foramina of the branch superficial ophthalmic of the trigeminal nerve (V-VII); foramen oculomotor (III) just above the eye stalk while foramen abducens (VI) is near its base; trigeminal (V) and facial (VII) nerves with a common aperture, the foramen prooticum, posteriorly in the orbital wall; foramen prooticum also opens lateral-posteriorly to a branch hyomandibular of facial nerve (VII) in the hyomandibular facet through two small apertures. *Cirrhigaleus barbifer* shows basal angle prominent (its width 25.5% of CL), ventral-posteriorly in the interorbital wall for supporting the orbital articulation; foramen for an efferent of the pseudobranchial artery small and rounded, placed dorsally in the basal angle. Transbasal canal was not observed for this species as in *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*.

Otic region with endolymphatic fossa hexagonal and profound, carrying two anterior endolymphatic foramina and two posterior perilymphatic foramina, with similar sizes; otic capsule pentagonal and wide on each side; anterior semicircular canal inconspicuous; posterior and lateral semicircular canals well prominent on each otic capsule; the latter placed laterally in the otic capsule above the hyomandibular facet; otic crest very small and prominent, placed posteriorly between endolymphatic fossa and foramen magnum; sphenopterotic ridge subtle; opisthotic process somewhat pointed; hyomandibular facet shallow; lateral auditory groove markedly deep in the anterior edge of the lateral otic wall; inconspicuous lateral commissure.

Occipital region with occipital condyles small and triangular, ventrally; foramen magnum broad (its width 7.9% of CL); foramen for vagus nerve (X) also large aside the foramen magnum; glossopharyngeal base broad, thick, and subtriangular, carrying glossopharyngeal foramen (IX) with two apertures; one aperture rounded and large placed posterior-dorsally, and a second aperture small and oval, located lateral-ventrally.

Basal plate flattened and elongate (its length 51.5% of CL), narrower anteriorly (its width 25.0% of CL) than posteriorly in the glossopharyngeal base; basitrabecular processes been-shaped, prominent and very narrow, directed lateral-posteriorly; a single cartilaginous process, short and rounded, width across them 36.0% of CL, placed laterally in each side of the subotic shelf; an unique foramen for carotid artery, rounded, placed mesial-anteriorly between basitrabecular processes and first cartilaginous processes; foramen for orbital artery, oval and small, located laterally near the base of each cartilaginous process.

Cirrhigaleus asper and *C. australis* (Table 8; Figs. 24, 25, 27) have neurocranium of morphological condition similar to *C. barbifer*. *Cirrhigaleus asper*, however, differs from them by: median rostral prominence conspicuous vs. absent for *C. barbifer* and *C. australis*; foramen for carotid artery with two apertures vs. a single aperture for *C. barbifer* and *C. australis*; anterior semicircular canal prominent vs. inconspicuous for *C. barbifer* and *C. australis*; hyomandibular facet profound vs. very shallow for *C. barbifer* and *C. australis*. Foramina of the branch superficial ophthalmic of the trigeminal nerve (V-VII) varies from 8–11 in *C. asper* while in *C. australis* varies from 7–9 foramina.

Cirrhigaleus asper is further distinguished from *C. barbifer* and *C. australis* by: shorter precerebral fossa length (39.9% of CL in *C. barbifer* vs. 38.7% of CL in *C. australis* vs. 32.3%–32.4% of CL in *C. asper*); more elongate distance between orbital processes (34.0%

of CL in *C. barbifer* vs. 32.2% of CL in *C. australis* vs. 36.0%–40.4% of CL in *C. asper*); larger rostral keel (22.6% of CL in *C. barbifer* vs. 22.8% of CL in *C. australis* vs. 27.4%–30.4% of CL in *C. asper*). *Cirrhigaleus asper* can also be separated from *C. barbifer* by: subethmoidal chamber broader in *C. asper* than in *C. barbifer* (subethmoideal width 17.3%–17.6% of CL vs. 15.2% of CL); narrower interorbital width (37.5% of CL in *C. barbifer* vs. 30.6%–34.3% of CL in *C. asper*).

Remarks.

Morphological variations of the neurocranium. Despite of the neurocranium is very conservative in general morphology within Squalidae, three major morphological conditions are observed among its species. Each cranial condition is represented herein by descriptions of the neurocranium of *Squalus acanthias, S. mitsukurii* and *Cirrhigaleus barbifer*. The first condition (or *S. acanthias* condition) is observed for *Squalus acanthias*, *S. suckleyi*, *Squalus* cf. *suckleyi*, *S. megalops*, *S. brevirostris*, *S. albifrons*, *S. blainvillei*, *Squalus* sp. 1, *Squalus* sp. 3 and *Squalus* sp. 7, and it is characterized by: neurocranium with its greatest width across postorbital processes rather than across nasal capsules; two lateral rostral appendages; median rostral prominence; profundus canal with its dorsal aperture aside ethmoidal canal near the base of the nasal capsule; a pair of supraethmoidal processes; single cartilaginous process on each side of the basal plate. *S. megalops*, *S. brevirostris*, *S. albifrons*, *S. blainvillei*, *Squalus* sp. 1 and *Squalus* sp. 7 can also represent a subgroup within this condition for sharing proportional cranial measurements much smaller than for *Squalus acanthias*, *S. suckleyi*, *Squalus* cf. *suckleyi*, and having transbasal canal in the interorbital wall (vs. absent in these three latter species).

The second cranial condition (or *S. mitsukurii* condition) share with the first condition a pair of supraethmoidal processes and neurocranium with its greatest width across postorbital processes. This condition has three rostral appendages (two laterally and one medially), and profundus canal with its dorsal aperture placed between ethmoidal canal and preorbital canal. *Squalus mitsukurii, S. montalbani, S. chloroculus, S. grahami, S. griffini, S. japonicus, S. nasutus, Squalus* cf. *blainvillei*, and *Squalus* sp. 4 share this condition. Within the second condition, the species *S. grahami* and *S. griffini* have neurocranium wider across nasal capsules than across postorbital process while *S. montalbani, S. chloroculus, S. japonicus* and *S. nasutus* have neurocranium almost equally wide at both nasal capsules and postorbital processes.

The third cranial condition is observed for *Cirrhigaleus barbifer, C. australis* and *C. asper*. It is characterized by lacking rostral appendages and supraethmoidal processes, and having antorbital cartilage markedly narrow and convex posteriorly. Neurocranium has its greatest width across nasal capsules rather than across postorbital processes with proportional measurement across nasal capsules with 6%–8% of CL more than width across postorbital processes. In contrast, *Squalus grahami* and *S. griffini* exhibit width across nasal capsules with 2%–4% of CL greater than those across postorbital processes. The third cranial condition is further characterized by having neurocranium equally broad across preorbital and postorbital processes (its proportional measurements ranging less than 2% of CL from each other). It shares with the second condition the placement of the profundus canal between preorbital canal and ethmoidal canal.

The characteristics of each cranial condition are not useful for identification purposes at species-specific level but it helps to support recognition of more than two morphological groups in Squalidae. Our assumptions, however, need to be confirmed after integrating all morphological characters proposed for the family into phylogenetic analysis.

Morphological particularities of the neurocranium are also noticed for some species. *Squalus albifrons* and *Cirrhigaleus asper*, for instance, is distinguished from its congeners of similar condition by having foramen for carotid artery with two apertures (vs. a single aperture). The same condition is observed for *Chlamydoselachus*, *Trygonognathus, Zameus*, *Oxynotus*, *Squaliolus* and *Deania*, although Yano (1986) and Shirai (1992) stated that the foramen varies from paired to unpaired in Squaliformes. *Squalus* sp. 1 and *Squalus* sp. 7 can be differentiated within this condition by having first foramen of the series of foramina of the branch superficial ophthalmic of the trigeminal nerve (V-VII) as large as preorbital canal (vs. much smaller than preorbital canal). *Squalus japonicus* and *S. nasutus* show small lateral crests on each lateral rostral appendage. *Squalus grahami* has dorsal projection on the midline of each lateral rostral cartilage while in *Squalus griffini* the projection is more distally placed at the base of the lateral cartilage. *Cirrhigaleus asper* has rostral keel much more elongate than in *C. barbifer* (its length 27.4%–30.4% of CL vs. 22.6% of CL), transcending greatly the anterior margin of the nasal capsule. Epiphyseal pit is present in all species of Squalidae, contrasting to the statement of Shirai (1992) about the intraspecific variation in *Squalus* and *Etmopterus*. *Cirrhigaleus barbifer* and *C. australis* also have epiphyseal pit large and rounded with single and independent aperture, and it is not fused to the dorsal base of the prefrontal fontanelle as it was illustrated in Shirai (1992).

Squalus blainvillei is the only species of Squalidae that can be distinguished taxonomically through characteristics of the neurocranium. A second pair of cartilaginous processes in the basal plate is found exclusively in the Mediterranean species, which strongly supports its autapomorphy. Previous studies (e.g. Muñoz-Chápuli & Ramos, 1989; Marouani *et al*., 2012) addressed this structure to the nominal species *S. megalops* from Northeast Atlantic Ocean instead. However, species of *Squalus* that occurs in this region exhibit a single pair of cartilaginous processes. These results indicate that *S. blainvillei* has been possibly misidentified by Muñoz-Chápuli & Ramos (1989) and Marouani *et al*. (2012) and that a redescription of this species is imperative in order to better understand its morphological limits and geographical distribution between Mediterranean Sea and waters of Northern Africa.

Cranial measurements support separation among species of similar morphological condition, representing characters of great taxonomic value. For instance, *Squalus albifrons*, *Squalus* sp. 1 and *Squalus* sp. 7, *S. brevirostris* and *S. megalops* can be also distinguished by postcerebral length, precerebral fossa width, length of postorbital process, width across hyomandibular facets, length of rostral keel, width of basal plate, width across first cartilaginous processes, and maximum sagittal length. *Squalus grahami*, *S. japonicus* and *S. nasutus* differs greatly from *S. mitsukurii*, *S. montalbani*, *S. chloroculus* and *S. griffini* by much smaller proportional cranial measurements (e.g. width across hyomandibular facets; interorbital width). *Cirrhigaleus barbifer* also can be distinct from *C. asper* and *C. australis* by these measurements.

Variations of cranial measurements are observed for specimens of *S. acanthias* from different localities, especially between specimens from SEAO and SWAO: neurocranium wider at nasal capsules and interorbital region in specimens from SWAO than SEAO (width across nasal capsules 44.0%–50.4% of CL vs. 41.7%–43.2% of CL; interorbital width 29.6%–60.8% of CL vs. 24.5%–27.3% of CL). Specimens from SEAO still have slightly larger nasobasal length (67.5% of CL vs. 62.8%–67.4% of CL) and narrower basal angle (its width 16.6% of CL vs. 16.8%–20.0% of CL) than specimens from SWAO. It is also distinct from those of NAO and SWAO by having smaller width across preorbital processes (44.3% of CL vs. 45.3%–50.7% of CL vs. 47.9%–55.7% of CL, respectively), shorter postorbital process (its length 6.7% of CL vs. 9.0%–10.1% of CL vs. 7.8%–10.3% of CL), and more elongate basal plate (its length 49.5% of CL vs. 41.2%–42.6% of CL vs. 36.9%–42.2% of CL). Specimens from NAO still can be distinguished from those of SEAO by neurocranium narrower at opistotic process (width across them 32.0%–33.2% of CL vs. 38.7%–42.2% of

CL) and deeper (its sagittal length 18.6%–19.3% of CL vs. 10.0%–18.5% of CL). *Squalus acanthias* is the only nominal species of Squalidae whose cranial anatomy varies greatly among its population, indicating that cryptic species might potentially exhist. Intraspecific variations are not observed for other species of *Squalus* and *Cirrhigaleus* regarding cranial measurements or general morphology. The limited number of specimens for each nominal species in which the neurocranium was analysed may have contributed for unrevealing these variations.

2. Pectoral apparatus

Anatomical description (Tab. 9; Figs. 28–38). All species of *Squalus* and *Cirrhigaleus* present pectoral girdle constituted by a ventral transverse element, the coracoid bar, and a pair of scapulae that is continuous to the coracoid bar, ending into a pointed tip, the scapular processes. Coracoid bar together with the scapulae forms the scapulocoracoid cartilage. Suprascapula articulates dorsally to each scapular process, running freely aside the horizontal axis of the body without connection to the vertebral column.

In *Squalus acanthias* (Fig. 28–31), scapulocoracoid is U-shaped, somewhat sinuous and cylindrical in general morphology, and placed transversely in relation to the body axis with scapular processes directed dorsal-posteriorly. Coracoid bar straight and horizontal with its anterior margin convex and posterior margin strongly concave, compressed and narrow on its midline, forming a prominent dorsal fossa for the insertion of the hypobranchial longitudinal muscles; ventral posterior margin of coracoid bar conspicuously pointed and convex on its midline; subrectangular prominence observed lateral-ventrally on each side of the coracoid bar. Posteriorly, a pair of lateral fossa supports the origin of the *parietalis pars epaxonica* muscle on the coracoid bar; a robust and slightly rounded process, also called caudal process or posterior process of coracoid bar, is evident on the hindmost part of each fossa that together with the base of the articular process supports the origin of *pterygii ventralis* muscle.

Scapulae placed more dorsal-posteriorly, very broad ventrally and tapering cylindrically to its dorsal extremities where it turns into a pointed scapular process; its anterior margin markedly convex and posterior margin concave; there is a conspicuous and expanded lateral-anterior fossa on each side of scapulae for origin of the *pterygii cranialis* muscle; this anterior fossa also carries a small and rounded foramen for the pectoral fin nerve, the foramen diazonale; foramen for pectoral artery located laterally just above the mesocondyle. Specimens of *S. acanthias* carry a pair of segmented processes on the scapulae, located lateral-dorsally to the anterior fossa and attached ventrally to the scapulae (Figs. 28, 29). These segmented processes are named herein as segmented ridge of scapulae that is constituted by three to seven units of barrel-shaped cartilages, organized into longitudinal series and separated from each other by connective tissue. Neonate specimens of *S. acanthias*, however, vary from 16 to 18 units for each segmented process of scapulae. Suprascapula somewhat cylindrical, tapering to its dorsal tip and directed medially to the body horizontal axis; suprascapula attached proximally to the scapular process. Posteriorly, the *pterygii dorsalis* fossa, placed more distally above the articular region of the pectoral girdle, supports the origin of the *pterygii dorsalis* muscle in the scapulae.

Articular region between pectoral girdle and fin comprises by two distinct regions. Propterygium of the pectoral fin articulates through a facet that is elliptical and somewhat vertical, placed lateral-posteriorly in the scapulae base (Fig. 31). Mesopterygium articulates through a separate and conspicuous mesocondyle, located ventrally in the posterior rear base of the scapulae. Metapterygium does not have a direct articulation with the pectoral girdle and it is attached laterally to the mesopterygium on their proximal edges. The same pattern of pectoral articulation is noticed for *Squalus suckleyi*.

Propterygium small and subrectangular, broader proximally than distally, carrying one series of segmented radials. Mesopterygium markedly wide and subtriangular, very narrow proximally and broad distally, carrying 9 series of segmented radials. Metapterygium markedly narrow and elongate, wider distally than proximally, carrying 9 series of segmented radials; metapterygium do not reach the scapulae base; metapterygium axis evident lateral-distally to the metapterygium, carrying few irregular radials. Pectoral radials flattened and usually segmented series into three elements (proximal, medial and distal radials); distal radials longer than the proximal and mesial radials in propterygium and mesopterygium, while it is smaller than the proximal and mesial radials in metapterygium; first series of radials in the mesopterygium and the last series of radials in the metapterygium are often segmented into two elements only.

Squalus suckleyi (Fig. 31, 32) differs from *Squalus acanthias* on having: prominence pointed and triangular observed lateral-ventrally on each anterior side of coracoid bar; ventral posterior margin of coracoid bar pointed and convex on its midline in adult specimens only; posterior process of coracoid bar markedly pointed and triangular. Anterior fossa of scapulae cylindrical and does not have segmented ridge dorsally as in *S. acanthias*.

Squalus albifrons, *S. grahami*, *S. griffini* and *S. montalbani* (Figs. 33–35) differs from *Squalus acanthias* by having: coracoid bar with anterior margin strongly convex and pointed, and ventral margin completely straight; posterior process of coracoid bar pointed and triangular; both diazonal foramen and foramen for pectoral artery much larger than in *S. acanthias* and *S. suckleyi*; scapulae with anterior fossa conspicuously wide and profound with cylindrical dorsal ridge, although not segmented like noticed for *S. acanthias*. In contrast to *Squalus acanthias*, the species *Squalus albifrons*, *S. grahami*, *S. montalbani* and *S. griffini* have pectoral articulation constituted by two regions: facet for the propterygium located lateral-posteriorly near meso-metacondyle; one condyle for mesopterygium and metapterygium placed ventral-posteriorly in the scapulae. Facet for propterygium is much more elongated in *Squalus albifrons*, *S. montalbani* and *S. grahami* than in *S. acanthias* and *S. griffini*. Meso-metacondyle is larger in *Squalus albifrons* and *S. montalbani* than in *S. grahami* and *S. griffini*.

Pectoral fin of *Squalus mitsukurii*, *S. japonicus*, *S. albifrons*, *S. montalbani*, *S. grahami* and *S. griffini* exhibit its basal elements similar in shape to those of *Squalus acanthias*, differing on number of radials. However, *Squalus albifrons* has propterygium strongly broader than its congeners, and mesopterygium subrectangular while subtriangular in other species of *Squalus*.

Cirrhigaleus barbifer has pectoral fin equivalent to *Squalus acanthias*, differentiating from it regarding the propterygium that is divided into two pieces, one proximal, well elongate and conical, slenderer distally, and one distal, rectangular and cylindrical, shorter than the proximal one; propterygium carries one series of segmented radials in *Cirrhigaleus barbifer*. This species has mesopterygium triangular, much broader distally than proximally, carrying 8 series of segmented radials. Metapterygium triangular, thin, and elongated, narrower than the mesopterygium, carrying 8 series of segmented radials; metapterygium axis with an element rectangular, carrying one series of radials and another lateral and subtriangular element with three small radials attached to it. Pectoral radials segmented into three elements as well; distal radials longer than the proximal and mesial radials in propterygium and mesopterygium, while in metapterygium is shorter than the proximal and mesial radials; first series of radials in the mesopterygium is segmented into two elements only.

Cirrhigaleus asper and *C. australis* (Figs. 36–37) share similar morphology of pectoral fin with *C. barbifer*. It also shares with *S. acanthias* the general morphology of pectoral girdle, although it is much more robust and larger in the former two species. It differentiates from *S. acanthias* by: anterior margin of coracoid bar conspicuously pointed and triangular; lateral prominence very narrow on each side of coracoid bar; posterior process of coracoid bar triangular; posterior ridge in the scapulae prominent, placed more dorsally near scapular process; much larger foramen diazonale with smaller posterior aperture that is placed more laterally between the two articular regions. *Cirrhigaleus australis* bears same number of pectoral radials for each element as it is noticed for *C. barbifer*. *Cirrhigaleus asper* and *C. australis* are distinguished from species of *Squalus* by pattern of pectoral articulation, which comprises two distinct regions by two condyles: procondyle elliptical, oblique and well prominent, located lateral-dorsally in the scapulae base; meso-metacondyle rounded and very large, placed posterior-ventrally in the scapulae base.

Remarks.

Autapomorphy of *Squalus acanthias*. The recognition of species of *Squalus* is usually based on characters of the external morphology or vertebral counts (e.g. Müller & Henle, 1841; Fowler, 1941; Bigelow & Schroeder, 1957; Last *et al*., 2007) and have never involved the comparative analysis of the skeletal anatomy. *Squalus acanthias* is the only species of the family that have segmented ridge of scapulae process in the dorsal anterior margin of the scapulae, which comprises a great taxonomic character for distinguishing this species from its congeners. The autapomorphy of *Squalus acanthias* supported herein is the first tentative on providing skeletal characters for separating species within Squalidae and in particular from *Squalus suckleyi* that occurs in the North Pacific Ocean. These two nominal species are subject to intensive discussions on the literature about their taxonomic status due to its intrinsic morphological similarities (e.g. Bigelow & Schroeder, 1957; Jones & Geen, 1976; White *et al*., 2007c; Ebert *et al*., 2010). Recent studies that combined molecular and morphological data have supported the latter species as valid, despite of overlapping of morphological characters proposed for differentiating them (e.g. Ward *et al*., 2005; Ebert *et al*., 2010). The lacking of the segmented process of the scapulae in specimens of the North Pacific Ocean represent an additional support for the validity of *S. suckleyi*.

Phylogenetic analyses have also revealed that *S. acanthias* represents a complex group of cryptic species that includes two large and distinct subpopulations (Ward *et al*, 2007; Veríssimo *et al*., 2010), one restricted to the North Pacific Ocean and a second subpopulation that comprises specimens from all remaining areas. Consistency of segmented ridge of scapulae in specimens from the South Pacific, North Atlantic and South Atlantic Oceans supports *S. acanthias* as a single taxonomical unit rather than a complex of cryptic species in these areas. Despite of it, some morphological variations such as vertebra counts, morphometric and dentition often observed among these specimens are still relevant to consider in further taxonomic investigations on this species.

Analysis of the pectoral girdle and fin rarely contribute for taxonomic purpose because its skeletal variations within species of sharks and rays are not often observed interspecifically but intraspecifically (e.g. Loboda & Carvalho, 2013; Vaz & Carvalho, 2013). Segmented ridge of scapulae also varies among specimens of *Squalus acanthias* from different geographical regions concerning the number of barrel-shaped units (Tab. 3). Specimens from the North and South Atlantic Oceans varies from three to six units while those from the South Pacific Ocean have constantly five barrel-shaped cartilages in segmented ridge of scapulae. Specimens from Baltic Sea have greater number of units of segmented ridge of scapulae, ranging from five to seven. A single neonate specimen from the North Pacific Ocean presents much greater number of these units that varies from 16 to 18 in each side of the scapulae.

Home (1823) first illustrated the barrel-shaped process for the pectoral girdle of *Squalus acanthias* when comparing the morphological apparatus for swimming within all animals in general. Later, Molin (1859) compared the skeleton of species of sharks and rays, describing the pectoral fin and girdle of *Squalus acanthias* in detail. The author also illustrated the segmented process of the scapulae and mentioned it for the first time as “a crest comprised by bony structures and divided into three joints” (page 413). Subsequent studies on the anatomy of *Squalus acanthias* have omitted segmented ridge of scapulae in the descriptions and/or illustrations of the pectoral girdle (e.g. Compagno, 1999), indicating that comparative investigations on the pectoral apparatus of species of Squalidae were always very superficial. Its functionality is not yet understood because no other musculature or nerves are apparently related to segmented ridge of scapulae. Future analysis on the ontogeny and embryology regarding morphological formation of the pectoral girdle in *Squalus acanthias* probably will answer this question and will give light for understanding its origin during the development.

3. Pelvic apparatus

Anatomical description (Figs. 39–47). *Squalus acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi* (Figs. 39A-B, 46) share same morphological pattern of pelvic apparatus. It is characterized by having puboichiadic bar horizontal, rectangular, short and slightly slender; anterior margin somewhat straight; posterior margin conspicuously convex medially and concave laterally; pelvic condyle conspicuous and rounded, small, placed posterior-laterally on each side of puboischiadic bar for articulating to anterior pelvic basal element of pelvic fin; posterior facet slender and rectangular on each side, placed more medially for articulating puboischiadic bar to basipterygium of pelvic fin; foramen for pelvic nerve single, small and rounded on each side of puboischiadic bar. Anterior pelvic basal element of pelvic fin subrectangular and wide with three series of radials irregular and tiny (first one not segmented), articulating proximally to pelvic condyle and lateral-proximally to the basipterygium (these vary from 2–3 radials in *S. suckleyi* and two radials for *Squalus* cf. *suckleyi*); basipterygium vertical, elongate and markedly slender, cylindrical and sinuous on its extension, articulating proximally to posterior pelvic facet; pelvic radials large, thin and cylindrical, segmented into proximal and distal elements, the former much larger than the latter. Females with unique intermediate segment, rectangular and strongly slender medial-distally with one small radial laterally, connected proximally to distal end of basipterygium. 14 total pelvic radials for *Squalus acanthias* and *Squalus* cf. *suckleyi*. 14 neotype (14–16 non-type specimens) total pelvic radials for *Squalus suckleyi*.

In *Squalus brevirostris* (Fig. 39D), pelvic girdle with puboischiadic bar transverse, small and thin with anterior and posterior margins slightly convex medially and concave laterally; two foramina for pelvic nerves located laterally on each side of puboischiadic bar. Pelvic fin with basipterygium vertical, small and broad, slenderer distally with medial margin straight and lateral margin convex; anterior pelvic basal element subtriangular, small and much broader than in *S. acanthias*; pelvic radials cylindrical, flattened distally, subdivided into proximal and distal elements; 3–4 tiny radials allied to anterior pelvic basal element (first one not segmented). Females of *S. brevirostris* with one intermediate segment, rectangular and broad, attached to distal end of basipterygium, followed by a modified and bifurcated radial. 13–14 total pelvic radials for *S. brevirostris*. The pelvic apparatus of *Squalus megalops* (Fig. 39C) and *S. blainvillei* is similar to those of *S. brevirostris* but it can be distinct from it by having single foramen for pelvic nerve and 13–15 total pelvic radials for *S. megalops* and 11–13 total pelvic radials for *S. blainvillei*. The latter species also has both anterior and posterior margins of puboischiadic bar completely straight.

Squalus albifrons (Fig. 39E) has pelvic apparatus similar to *S. brevirostris* and *S. megalops* but it differs from them by having: puboischiadic bar with anterior margin almost straight on all its extension; posterior margin with a small posterior process laterally on each side; anterior foramen for pelvic nerve larger than posterior foramen; three tiny radials allied to anterior pelvic basal element (first two radials not segmented); 14 total pelvic radials for *S. albifrons*. *Squalus brevirostris*, *S. megalops* and *S. albifrons* (Fig. 40) have two regions of articulation between pelvic girdle and fin that is comprised by lateral pelvic condyle and posterior facet like it is observed for *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*. The morphological condition of the pelvic apparatus in *Squalus* sp. 7 (Fig. 39L) resembles those observed for *S. megalops* and *S. blainvillei.* Total pelvic radials vary 12–13 radials for *Squalus* sp. 7.

Squalus mitsukurii, *S. japonicus* and *S. grahami* (Fig. 39F-I) have pelvic apparatus similar to those of *S. acanthias* but differ from it by having basipterygium with lateral and medial margins straight, although slightly concave distally, and tapered on its edges. *Squalus mitsukurii* has a single foramen for pelvic nerve while *S. japonicus* (Fig. 39I) and *S. grahami* have two foramina, small and rounded as it is shown for *S. brevirostris*. *Squalus japonicus* and *S. grahami* have anterior and posterior margins somewhat convex medially and concave laterally as it is noticed for *S. brevirostris* and *S. megalops*. In contrast to *S. acanthias*, *Squalus mitsukurii* has the last two pelvic radials not segmented. 15 and 17 total pelvic radials for holotype and paratype of *S. mitsukurii*, respectively; 14 total pelvic radials for *S. japonicus;* and 13 total pelvic radials for *S. grahami*. *Squalus grahami* differ from these species by having pelvic girdle with puboischiadic bar very narrow and short, lateral prepelvic process strongly prominent, and anterior pelvic basal element more elongate and slender. It also has pelvic condyle and posterior process of puboischiadic bar markedly thin and elongate. Its anterior foramen for pelvic nerve larger than posterior one as it is noticed for *S. albifrons*. *Squalus* sp. 4 has pectoral apparatus that resembles those of *S. mitsukurii*. Total pelvic radials vary from 14–15 radials for *Squalus* sp. 4.

Squalus montalbani (Fig.39G) has a very distinct puboischiadic bar, markedly narrow and short with anterior margin conspicuously convex medially and posterior margin straight on all its extension. Its lateral prepelvic process is conspicuously prominent and elongate, and anterior foramen for pelvic nerve larger than posterior one, a condition similar to those of *S. grahami*. A posterior-lateral process, rounded and large is observed on each side of the puboischiadic bar in *S. montalbani*, which distinguish clearly this species from its congeners. Anterior pelvic basal element in *S. montalbani* is markedly broad, carrying five series of small radials (first two radials not segmented) in contrast to those of *Squalus mitsukurii*, *S. japonicus* and *Squalus grahami*. As it is observed for other species of *Squalus*, *S. montalbani* and *S. grahami* (Figs. 41–42) have two regions of pelvic articulation that is comprised by pelvic condyle and inner posterior facet. Pelvic condyle in the puboischiadic bar of *S. montalbani* is much broader than those of these three latter species.

In *Squalus griffini*, pelvic girdle is also very unique in morphology. Its puboischiadic bar is conspicuously narrow and elongate with both anterior and posterior margins slightly convex but markedly concave medially. Lateral prepelvic processes resemble those of *S. grahami* and *S. montalbani* but it differs from them by directing more posteriorly (vs. anteriorly). Pelvic fin in *S. griffini* is very similar to those of *S. montalbani,* comprising by basipterygium very large and slender, and anterior pelvic basal element wide with three series of small radials associated to it. *Squalus griffini* also share same pattern of pelvic articulation noticed for *S. acanthias*. Females of *S. griffini* present one intermediate segment rectangular and large, cylindrical and bifurcated distally, connecting to distal end of basipterygium. In contrast to *Squalus acanthias, S. suckleyi, Squalus* cf. *suckleyi* and *S. brevirostris*, this species lacks radials associated to the intermediate segment. 15 total pelvic radials for *S. griffini*.

Cirrhigaleus barbifer, *C. asper* and *C. australis* (Fig. 43) share skeletal pattern of the pelvic apparatus that it is distinct from those observed for species of *Squalus*. In *C. barbifer*, pelvic girdle with pubosichiadic bar transverse, large and narrow with anterior and posterior margins straight, although slightly convex medially; two small foramina for pelvic nerves evident laterally in the pubosichiadic bar, although anterior-most foramen is located right in the edge of lateral prepelvic process in contrast to what it is noticed for *S. brevirostris*, *S. albifrons*, *S. japonicus*, *S. grahami*, *S. griffini* and *S. montalbani* that is placed more medially in the puboischiadic bar. Pelvic fin of *C. barbifer* with anterior pelvic basal element subtriangular, small and conspicuously broad with two series of radials associated to it (first radial is markedly broad and segmented, differing from species of *Squalus*); basipterygium elongate, cylindrical and thin, slightly broader on its proximal end than on its distal end; pelvic radials large, cylindrical and segmented into proximal and distal elements, the former much larger than the distal elements as it is shown for species of *Squalus*; 16–18 total pelvic radials for *C. barbifer* and 18 total pelvic radials for *C. australis*. Females of *C. barbifer*, *C. asper* and *C. australis* have one intermediate segment, small, barrel-shaped, attached proximally to the distal end of basipterygium, and a modified pelvic radial attached to the intermediate segment. In *C. barbifer* and *C. asper* this latter cartilage is rectangular, wide, bifurcated and cylindrical distally while in *C. australis* is ray-like, thin and cylindrical.

These three species of *Cirrhigaleus* (Fig. 44) have two regions of pelvic articulation as observed for species of *Squalus*, although it differentiates by having pelvic condyle much more prominent, rounded and elongate for articulating to anterior pelvic basal element, and second articulating region in the inner posterior margin of puboischiadic bar comprised by both second condyle and pelvic facet for articulating to basipterygium. Second condyle is smaller than first condyle and located more dorsally in this region for articulating to dorsal portion of the basipterygium that is comprised by a hollow small and rounded. Pelvic facet is flattened and rectangular, placed ventrally in this region for articulating to ventral portion of the basipterygium.

Cirrhigaleus asper and *C. australis* differs from *C. barbifer* by having anterior foramen for pelvic nerve not completely enclosed in the lateral prepelvic process. This foramen is placed more posteriorly in *C. australis* while is more anteriorly in *C. asper*. Anterior pelvic basal element of pelvic fin is rectangular and much larger in *C. asper* and *C. australis* than in *C. barbifer*. Four series of radials thin, cylindrical and segmented (except first one) are shown in *C. asper* while *C. australis* and *C. barbifer* exhibit two series of radials broad in which first series is wider than second one. *Cirrhigaleus asper* is further distinguished from *C. barbifer* and *C. australis* by: puboischiadic bar with anterior margin conspicuously convex medially; posterior margin of puboischiadic bar concave with paired convexity medially.

Remarks. Morphological pattern of the pelvic apparatus in species of *Squalus* is very conservative in its general morphology and regarding the pelvic articulation. The majority of its variations among congeners, however, are noticed in the puboischiadic bar of pelvic girdle rather than in skeletal structures of pelvic fin. Anterior and posterior margins of puboischiadic bar vary medially from straight to conspicuously convex. Number of foramen for pelvic nerve varies from one to two foramina in species of *Squalus*. Total pelvic radials range greatly from 11–16 in *Squalus* and 3–4 series of small radials associated to the anterior pelvic basal element. These variations, however, are not useful for identification purposes with few exceptions. *Squalus albifrons* has posterior process on each side of puboischiadic bar that help to differentiate from its congeners. *Squalus griffini* has both anterior and posterior margins of puboischiadic bar with conspicuous concavity medially.

Species of *Cirrhigaleus* also present its greatest variations in the puboischiadic bar. *Cirrhigaleus asper* is distinguished from all species of the family Squalidae by having two conspicuous convexities in the posterior margin of puboischiadic bar, and its anterior foramen for pelvic nerve not totally enclosed. Intraspecific variations into these three species of the family still need to be investigated in order to verify the efficiency of these characters for separating species.

4. Cartilages of the clasper

Anatomical description (Figs. 47–58). *Squalus acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi* (Figs. 46–49) have clasper with similar morphology. The pelvic fin of mature males has an intermediate segment barrel-shaped, attaching basipterygium to axial cartilage of the clasper. It is also observed a single beta cartilage, rod-like, slender and cylindrical, located lateral-dorsally over intermediate segment and axial cartilage for articulating basipterygium to axial cartilage. These species have claspers with axial cartilage markedly slender and large, somewhat straight with conspicuous medial process on its proximal edge; end-style elongate and thin, placed in the distal end of axial cartilage and medially between dorsal terminal and ventral terminal cartilages. Dorsal marginal cartilage slim and short, located dorsal-laterally over axial cartilage and reaching its midline. Dorsal terminal cartilage hook-like and markedly concave lateral-distally, conspicuously elongate (its length almost equal to length of axial cartilage), although not reaching tip of ventral terminal cartilage, connected proximally to dorsal marginal cartilage and axial cartilage, and medially to end-style. Dorsal terminal 2 cartilage leaf-like and flattened with lateral margin convex, attached medially to dorsal terminal cartilage, and proximally to dorsal marginal cartilage, supporting externally the rhipidion; dorsal terminal 2 cartilage is markedly elongate, its length is greater than one-half length of dorsal terminal cartilage. Ventral marginal cartilage slightly thick, convex and narrow, although wider distally, its inner side with lateral groove profound and large that forms a folded plate where accessory terminal cartilage is inserted. Ventral terminal cartilage conspicuously elongate (its length almost equal to length of axial cartilage), slender and spatula-like with distal tip convex and somewhat sinuous laterally, located at distal end of the clasper, attached proximally to ventral marginal cartilage and medially to end-style. Accessory terminal 3 cartilage (or spur) markedly slender, conspicuously cylindrical or pin-like, pointed and tapered distally with dorsal and medial furrows prominent; accessory terminal 3 cartilage elongate (its length corresponds to more than two-thirds length of ventral terminal cartilage, reaching distal tip of dorsal terminal 2 cartilage) with its proximal edge rounded, inserted laterally into folded plate of ventral margin cartilage. *Squalus* cf. *suckleyi* (Fig. 48C,D) differs slightly from *S. acanthias* (Figs. 48A,B, 49) and *S. suckleyi* by having accessory terminal 3 cartilage much thicker and carrying three furrows (medial, ventral and dorsal).

Squalus montalbani (Figs. 48O,P, 52) has its clasper morphology very similar to those of *S. acanthias*, *Squalus suckleyi* and *Squalus* cf. *suckleyi*. It differs from these species by having: accessory terminal 3 cartilage with a single furrow dorsally and its tip not reaching distal tip of dorsal terminal 2 cartilage; dorsal terminal 2 cartilage is connected partially to dorsal marginal cartilage at its proximal edge and its length is almost equal to length of dorsal terminal cartilage; dorsal terminal cartilage almost reaching the tip of ventral marginal cartilage; length of ventral marginal cartilage greater than one-half length of axial cartilage; dorsal marginal cartilage much greater in length, transcending one-half length of axial cartilage. Mature male of *S. montalbani* is very distinct regarding cartilages that connect the basipterygium of pelvic fin to axial cartilage of clasper. Two intermediate segments, barrel-shaped and large (although the second element is smaller than the first element) are observed in this species. Its beta cartilage is conspicuously elongate, transcending the medial process of axial cartilage. In contrast to *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*, beta cartilage of *S. montalbani* is placed over distal end of basipterygium, intermediate segment and proximal end of axial cartilage.

Squalus mitsukurii (Fig. 48M,N) has a single intermediate segment and one beta cartilage very similar to those observed for *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*. The latter cartilage, however, is located more medially in *S. mitsukurii*. The clasper of this species has axial cartilage elongate, thick and sinuous, tapered distally with small medial process on its proximal edge, although this process is much less prominent than in *S. acanthias*; end-style cylindrical, short and thick, placed medially aside ventral marginal and ventral terminal cartilages. Dorsal marginal cartilage short (not reaching half of axial cartilage), subtle and markedly slim placed medial-dorsally over the axial cartilage. Ventral marginal cartilage thick and convex, markedly narrow, rather broader distally, located ventral-laterally aside axial cartilage; ventral marginal cartilage with lateral groove profound that forms a folded plate in which accessory terminal cartilage is inserted. Ventral terminal cartilage thick and spoon-like, convex at its posterior tip, and conspicuously elongate (its length three times greater than length of ventral marginal cartilage), placed at distal end of clasper. Dorsal terminal cartilage (or claw) conspicuously elongated (in contrast to *S. acanthias* its length almost equal to length of ventral terminal cartilage) with its distal tip reaching tip of ventral terminal cartilage; dorsal terminal cartilage hook-like, concave and pointed distally, attached proximally to dorsal marginal cartilage and end-style. Dorsal terminal 2 cartilage flattened and leaf-like with lateral edge free and convex, supporting the rhipidion; dorsal terminal 2 cartilage also very large (its length equal to length of dorsal terminal cartilage), attached medially to dorsal terminal cartilage and also connecting partially to dorsal marginal cartilage on its proximal edge. Accessory terminal 3 cartilage thick and pointed distally with mesial furrow; it is also elongate, although in contrast to *S. acanthias* its tip not reaches distal edge of dorsal terminal 2 cartilage.

Squalus grahami (Figs. 48Q,R, 53*), Squalus* cf. *blainvillei* (Fig. 56) and *Squalus* sp. 4 (Fig. 57) have clasper morphology very similar to those of *S. mitsukurii*. *Squalus grahami* differs from the latter by having beta cartilage placed over basipterygium, intermediate segment and axial cartilage as it is observed for S. *montalbani,* although it does not transcend medial process. This process is well prominent in *S. grahami* and the tip of dorsal terminal cartilage (or claw) is directed laterally (vs. anteriorly), contrasting to those of *S. mitsukurii*. In contrast to *S. acanthias*, *S. suckleyi*, *Squalus* cf. *suckleyi*, *S. montalbani* and *S. mitsukurii*, end-style of *S. grahami* is much more elongate and thin, and its dorsal marginal cartilage almost reaches the proximal edge of axial cartilage.

Squalus japonicus (Fig. 48S,T) also has one intermediate segment and a single beta cartilage that are similar in morphology to those observed for *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi*, although its beta cartilage is placed over distal end of basipterygium, intermediate segment and proximal end of axial cartilage as it is noticed for *S. montalbani*. The general morphology of the clasper in the Japanese species is though similar to those of *S. mitsukurii* but differs from it by having axial cartilage with prominent medial process and dorsal marginal cartilage markedly thick and elongate, reaching midline of axial cartilage. *Squalus japonicus* also has cartilages of the clasper much smaller than *S. acanthias*, *S. suckleyi*, *Squalus* cf. *suckleyi* and *S. mitsukurii*. Ventral marginal cartilage of *S. japonicus* heavy, broad, and convex with lateral groove markedly profound, forming folded plate where the accessory terminal 3 cartilage is attached. Ventral terminal cartilage spatula-like, convex distally and concave laterally, very short (its length slightly greater than length of ventral marginal cartilage), attached proximally to ventral marginal cartilage. In contrast to these four species, ventral terminal cartilage of *S. japonicus* is also inserted proximal-medially to folded plate of ventral marginal cartilage. Dorsal terminal cartilage (or claw) thick and weakly hook-like, markedly small (its length one-third the length of axial cartilage) with its distal end reaching the tip of ventral terminal cartilage, connected proximally to axial cartilage and dorsal marginal cartilage; in contrast to *S. acanthias*, *S. suckleyi*, *Squalus* cf.

suckleyi and *S. mitsukurii*, tip of dorsal terminal cartilage of *S. japonicus* is straight or slightly concave distally with its tip directed laterally (vs. sinuous and conspicuously concave with its tip directed anteriorly). Dorsal terminal 2 cartilage of *S. japonicus* markedly narrow and thin, connected medially to dorsal terminal cartilage and anteriorly to the dorsal marginal cartilage, supporting the rhipidion externally; its length is equal to length of dorsal terminal cartilage. Accessory terminal 3 cartilage (or spur) thick and blade-like with prominent medial furrow, inserted into the folded plate of ventral marginal cartilage; accessory terminal 3 cartilage is markedly short (its length equal to length of dorsal terminal cartilage), not reaching midline of dorsal terminal 2 cartilage.

Squalus megalops (Fig. 48E,F) share with some congeners one intermediate segment and a single beta cartilage. The former cartilage, however, is more rectangular and larger than in other species. Beta cartilage is much wider in this species, covering the intermediate segment totally. This species also has cartilages of the clasper very short and its morphology similar to those observed for *S. japonicus*, although it differs from it by having: medial process of axial cartilage absent; dorsal marginal cartilage conspicuously thick and large, transcending midline of axial cartilage; dorsal terminal cartilage sinuous and thinner with its tip directed posteriorly. *Squalus* sp. 7 (Fig. 48I,J) shares with *S. megalops* and *S. japonicus* dorsal terminal cartilage weakly hook-like and thick, and accessory terminal 3 cartilage conspicuously heavy and blade-like. *Squalus* sp. 7 (Fig. 55) differs from *S. megalops* by having beta cartilage placed laterally as it is observed for all species of *Squalus* (except *S. mitsukurii*). It differs from *S. megalops* and *S. japonicus* for having accessory terminal 3 cartilage with both mesial and ventral furrows.

Squalus albifrons (Fig. 51) and *S. brevirostris* (Figs. 48G,H, 50) have clasper morphology similar to *S. megalops*, *S. japonicus*, and *Squalus* sp. 7. *Squalus albifrons* differs from all these species for showing beta cartilage over distal edge of basipterygium, intermediate segment and proximal edge of axial cartilage, a condition similar to *S. montalbani* and *S. japonicus*. Beta cartilage is also placed laterally as it is shown for *Squalus* sp. 7. *Squalus albifrons* also can be distinguished from them by having accessory terminal 3 cartilage cylindrical and markedly slender, directed laterally, and dorsal terminal 2 cartilage smaller than dorsal terminal cartilage. *Squalus brevirostris* can be distinguished from all congeners by having dorsal marginal cartilage and ventral marginal cartilage markedly elongate, reaching, respectively, beta cartilage and intermediate segment. Three furrows (mesial, dorsal and ventral) are observed in accessory terminal cartilage of *Squalus brevirostris*, which it is a condition similar to *Squalus* cf. *suckleyi*.

In *Cirrhigaleus barbifer* (Fig. 58), two intermediate segments, barrel-shaped and thick are connecting basipterygium to axial cartilage as it is also noticed for *S. montalbani*. In contrast to this species, first intermediate segment of *C. barbifer* is smaller than second one. *Cirrhigaleus australis* and *C. asper* apparently also have two intermediate segments that articulate basipterygium of pelvic fin to axial cartilage of claspers as it is shown for *C. barbifer*. Beta cartilage in *C. barbifer* is conspicuously stout and placed laterally over distal edge of basipterygium, first and second intermediate segments and proximal edge of axial cartilage in which transcends its mesial process.

Cartilages of the clasper of *C. barbifer* are strongly heavy. Its axial cartilage is almost straight and very elongate (its length equal to length of basipterygium of pelvic fin) with mesial process. Dorsal marginal cartilage strongly thick, although short (its length less than one-half length of axial cartilage), placed laterally over axial cartilage. Dorsal terminal cartilage thick, somewhat blade-like and elongate (its length one-half length of axial cartilage), located distally and connect proximally to dorsal marginal cartilage and axial cartilage. Dorsal terminal 2 cartilage leaf-like and conspicuously slender, although wider proximally, and large (its length one-third greater than length of dorsal terminal cartilage, although not reaching tip of dorsal terminal cartilage), connected proximal-medially to dorsal marginal cartilage and medial-distally to dorsal terminal 2 cartilage. Ventral marginal cartilage subtriangular and conspicuously broad distally, very elongate (it transcends midline of axial cartilage), attached to distal edge of axial cartilage; ventral marginal cartilage has folded plate markedly profound in which accessory terminal 3 cartilage is inserted. Accessory terminal 3 cartilage blade-like and heavy, although somewhat slender and cylindrical distally. Ventral terminal cartilage spatula-like, convex at its tip and laterally, markedly large (its length twice length of ventral marginal cartilage), attached proximally to ventral marginal cartilage. In contrast to all species of *Squalus*, accessory ventral marginal 2 cartilage is present in *C. barbifer*, located over proximal edge of ventral terminal cartilage. It is rectangular and elongate (its length one-half length of ventral terminal cartilage).

Remarks.

Morphological variations. Jungersen (1899) provided measurements of some cartilages (axial and terminal parts) and stated its importance for distinguishing genera as well as separating species of sharks. The current study noticed that axial, marginal and terminal cartilages often vary in length and thickness rather than in shape itself within Squalidae. Based on that, two morphological patterns of the clasper are observed among its species. The first pattern is characterized by having axial, marginal and terminal cartilages conspicuously elongate and slender with medial process strongly prominent proximally in the axial cartilage. Beta cartilage is placed more lateral-dorsally in the first pattern (except for *S. mitsukurii*). It also has dorsal terminal cartilage markedly hook-like, and accessory terminal 3 cartilage cylindrical and thin. The species *Squalus acanthias*, *S. suckleyi*, *Squalus* cf. *suckleyi*, *S. mitsukurii*, *S. grahami*, *S. montalbani*, and *Cirrhigaleus barbifer* share this morphological condition of the clasper.

Within this pattern, *S. acanthias*, *S. suckleyi* and *Squalus* cf. *suckleyi* comprise a subgroup of species that share ventral terminal cartilage conspicuously elongate, its length almost equal to length of axial cartilage. These three species also share accessory terminal 3 cartilage strongly cylindrical and pin-like. Despite of adult males of *S. suckleyi* were not analyzed through dissection in the present study, its clasper morphology was analyzed from juveniles that have already developed the main cartilages or through radiographs of the neoptype of *S. suckleyi*. Further investigations are required for this species in order to better understand its morphology.

Another morphological pattern of the clasper is characterized by having axial, marginal and terminal cartilages very short with medial process of axial cartilage inconspicuous or absent. It also shows dorsal terminal cartilage weakly hook-like and heavy, and accessory terminal 3 cartilage strongly stout and blade-like. Beta cartilage is placed right over intermediate segment and axial cartilage dorsally or more medially in some species. *Squalus japonicus*, *S. megalops*, *S. brevirostris*, *S. albifrons*, *Squalus* sp. 7 share this condition. Most of these species also have certain proximity of its external morphology, indicating that the morphological patterns of the clasper described here might facilitate recognition of species with similar characteristics of the skeletal and external morphology. Few exceptions, however, are noticed (e.g. *S. japonicus* and *C. barbifer*), requiring attention on the use of characters of the clasper for identification keys rather than diagnosis.

Many variations are observed among species within each pattern of clasper. However, its intraspecific or interspecific significance are not yet understood due to the limited number of specimens analyzed for each species. Beta cartilage over distal edge of basipterygium or not, and presence of ventral and dorsal furrows in the accessory terminal 3 cartilage are examples of these variations. Skeletal variations of the clasper in species of *Squalus* are often reported in the literature (e.g. Muñoz-Chápuli & Ramos, 1989; Marques, 1999; Marouani *et* *al*., 2012; Figueirêdo, 2011). Muñoz-Chápuli & Ramos (1989) further stated that intraspecific variations are slighter than interspecific variations in *Squalus*, suggesting its taxonomic value for separating species. Dorsal terminal cartilage and accessory terminal 3 cartilage were significantly distinct among *S. acanthias*, *S. blainvillei*, *S. megalops*, *S. acutirostris* and *S. cubensis*, according to these authors.

The current results indicate that cartilages of the clasper are not useful for identification purposes on species-specific level in Squalidae because these cartilages are subject to change with growth and maturity on males even though some species exhibit morphological particularities when adults. *Squalus brevirostris*, for example, has both dorsal and ventral marginal cartilages reaching proximal edge of axial cartilage (vs. these cartilages often extends to midline of axial cartilage in other species). *Squalus grahami* has end-style extremely thin and large (vs. thick and markedly small). The two morphological patterns of clasper described herein on the other hand exhibit characteristics that might be useful for integrating future systematics analysis among species of the family. Observations of the cartilages of clasper in some species (e.g. *C. australis*, *C. asper*, *S. suckleyi*, *S. blainvillei*, *S. acutipinnis*) were based on radiography, which provides very few information about its precise morphology. Further investigations on these species as well as a large number of specimens of different species (e.g. *S. raoulensis*, *S. griffini*, *S. notocaudatus*) are still required in order to better understand the variations of the cartilages of clasper in Squalidae.

Discussion.

General characterization of the neurocranium. The present study analyzed and described comparatively the neurocranium for 22 species of *Squalus* and *Cirrhigaleus*. In Squalidae, it is characterized by a rostrum comprised of a single rostral cartilage, spoon-like with precerebral fenestra dorsally and rostral keel ventrally, placed between nasal capsules;

prefrontal fontanelle small, rounded and located at anterior base of ethmoidal region; nasal capsule oval and oblique on each side and attached posteriorly to the preorbital wall, a pair of subnasal fenestra vertical, oval and large at the ventral base of prefrontal fontanelle, unchondrified antorbital cartilage. These species also bear conspicuous C-shaped supraorbital crest, longitudinal sulcus carrying series of small foramina for the superficial ophthalmic branch of the trigeminal nerve (V), profundus canal with two apertures (one dorsal and another ventral), preorbital canal markedly enlarged in front of the series of foramina of the trigeminal nerve (V), otic capsule hexagonal and large on each side of the cranium, endolymphatic fossa small and oval between otic capsules, carrying two pairs of foramina, subethmoidal region well developed and elongate, basitrabecular processes very prominent and bean-shaped, trigeminal and facial nerves sharing the same foramen, the foramen prooticum, and placed posteriorly in the interorbital wall, conspicuous basal angle for supporting the orbital articulation, basal plate with a single cartilaginous process on each side; hyomandibular facet broad, placed ventral-posteriorly in the lateral otic wall and carrying two foramina for a branch hyomandibular of facial nerve (VII), glossopharyngeal base prominent and subrectangular, carrying large glossopharyngeal foramen (IX) on each side of occipital region.

These cranial features represent a morphological pattern that is typically observed within Squaliformes and some basal groups of squaloid sharks (e.g. Chlamydoselachiidae, Hexanchiidae) (Yano, 1986; Shirai, 1992), and could potentially be synapomorphic characters for defining and supporting phylogenetic relationships at higher taxonomic levels in Chondrichthyes (e.g. Maisey, 1984; Shirai, 1992; Carvalho, 1996). The superorder Squalea, for instance, is supported as monophyletic through two synapomorphies that are consistent in Squalidae: presence of basal angle and basitrabecular processes (Maisey, 1980; Shirai, 1992). The ethmoidal canal partially enclosed in the nasal capsule is synapomorphic for Hexanchiformes, Echinorhiniformes, Squaliformes and some species of Hypnosqualea (Yano, 1986; Shirai, 1992). Subnasal fenestra is sinapomorphic for Hexanchiformes, Squaliformes and Hypnosqualea (Shirai, 1992). Other cranial characters are plesiomorphies for all living forms of euselachian fishes that are also in Squalidae are (Yano, 1986; Shirai, 1992): nasal capsules with unchondrified cracks ventrally; presence of prefrontal fontanelle; preorbital canal perforating supraorbital crest; presence of profundus canal; eye stalk with distal disc; foramina of endolymphatic fossa.

Characters of the neurocranium have not been used to support the monophyly of Squalidae, while in other groups within Squalea in which they were included in at least one synapomorphy for each family (e.g. Echinorhinidae, Etmopteridae, Somniosidae, Oxynotidae) (Yano, 1986; Shirai, 1992). In *Squalus* and *Cirrhigaleus,* the hyomandibular branch of the facial nerve (VII) runs through a canal with two apertures placed antero-lateralluin the hyomandibular facet. This is in contrast to other squaloid sharks that have a single aperture. This condition seems to be a derived condition for the Squalidae, although Yano (1986) and Shirai (1992) illustrated similar condition for *Dalatias*. Hook-like rostral appendages (laterals and medial) are exclusive for all species of *Squalus*, but are vestigial or absent in species of *Cirrhigaleus*. *Deania* apparently has lateral rostral appendages (Yano, 1986; Shirai, 1992) but their precise morphology and variation are uncertain.

The presence of supraethmoidal processes in *Squalus* is the only cranial feature that has been used for supporting the monophyly of the genus (Shirai, 1992). Similar processes at the dorsal base of the prefrontal fontanelle were illustrated for *Cirrhigaleus barbifer* even though Shirai (1992) stated its absence in this species. Ramos (2009) discussed the synapomorphy of *Squalus* based on investigations of the neurocranium in *C. asper* from the Southwestern Atlantic Ocean but her assumptions were based on misidentifications[1].

[1] See Chapter 2 for discussions on *Squalus* from this region.

Analysis of the specimen of *C. barbifer* examined by Shirai (1992) corroborates the absence of supraethmoidal processes for this species and reveals considerable mistakes in rendering the illustration of the neurocranium of *C. barbifer* that also compromised the understanding of other cranial characteristics of this species. The illustrations of *Dalatias* and *Centrophorus* in Shirai (1992) also show similar processes, although they are rather inconspicuous when compared to species of *Squalus*. The current analysis further reveals that *Cirrhigaleus asper* and *C. australis* also lack supraethmoidal processes and supports its exclusivity in species of *Squalus*, as well as the synapomorphies provided in Shirai (1992).

Some cranial characteristics in the family were not yet analyzed or discussed comparatively and with accuracy in members of the Squaliformes. The profundus canal, for example, perforates first the preorbital wall through a dorsal aperture located just in front of preorbital canal, and then it perforates the supraorbital crest through a dorsal aperture. Shirai (1992) apparently illustrated this condition for *Zameus* and *Squaliolus* but he restricted the perforation of the profundus canal to the supraorbital crest in all squalean-like sharks. The first cartilaginous process is a small lateral extension of the basal plate that supports the suborbital shelf in species of Squalidae and always carries a foramen for the orbital artery. This condition is apparently observed for *Centroscylium* and *Squaliolus* while *Zameus*, *Dalatias*, *Isistius*, *Deania* and *Squatina* have similar process, although lacking the orbital artery foramen (Shirai, 1992).

Variability of the pectoral apparatus. The pectoral girdle in species of *Squalus* and *Cirrhigaleus* is generally U-shaped and comprised by the scapulocoracoid cartilage, a typical pattern in species of elasmobranch fishes (Daniel, 1928; Compagno, 1973, 1977, 1988). Both pectoral girdle and fin are very conservative in members of the Squalidae, although some anatomical variations are observed. Pectoral girdle varies, for instance, in the convexity of the anterior margin of the coracoid bar, which is more or less pointed in some species of *Squalus* and *Cirrhigaleus*. The *depressor pectoralis* facet of the scapulae also has variations in its length and depth among them.

The greatest differences, however, reside in the articulation region with the pectoral fin. Three different pectoral articulations are observed in Squalidae. *Squalus acanthias* and *S. suckleyi* share the same pattern through two articulating regions, a facet for propterygium and a mesocondyle. Metapterygium in these species do not articulate with the girdle but proximally with the mesopterygium. Other species of *Squalus* analyzed in the present study share a second pattern that differes in having the mesopterygium and metapterygium articulating through a single condyle, the meso-metacondyle. These two variations on the pectoral articulation in species of *Squalus* were reported recently by Silva & Carvalho (2015) when analyzing *S. acanthias* and *S. megalops* that highlited the necessity of undertaking morphological investigations even at low taxonomic levels.

Species of *Cirrhigaleus*, on the other hand, share a procondyle and a meso-metacondyle in the scapulae that articulates with the pectoral fin. This pattern matches the one recently described for *Etmopterus pusillus* in Silva & Carvalho (2015). However, it differs in having a procondyle that is much more conspicuous and elliptical (vs. small and rounded), and a meso-metacondyle located postero-ventrally (vs. laterally) in the scapulae. It is also distinct from the former species by lacking a small ridge in the condyle for mesopterygium and metapterygium that isolates the specific articular regions for each pectoral basal.

Pelvic morphology. *Cirrhigaleus barbifer*, *C. australis* and *C. asper* exhibit a second pattern of the pelvic apparatus that is very disparate within the family regarding the skeleton of the pelvic fin and its articulation to the pelvic girdle. It differes from those observed for *Squalus* in the following characteristics: anterior foramen for pelvic nerve placed right in the edge of lateral prepelvic process (vs. more medially in puboischiadic bar); females with one intermediate segment, short and barrel-shaped connected to the distal end of basipterygium (vs. rectangular and elongate). The articulation region between puboischiadic bar and basipterygium of pelvic fin is formed by both the second condyle and the inner posterior facet in species of *Cirrhigaleus* while it consists of the single posterior facet in *Squalus*. Silva (2015) showed a similar pattern of pelvic articulation in species of *Etmopterus* and *Pristiophorus*. The differences in pelvic articulation in Squalidae are described herein for the first time and comprise an efficient character for cladistics analysis.

Cartilages of the claspers. Clasper skeletal morphology in Squalidae is very conservative regarding the number of axial, marginal and terminal cartilages, as well as concerning its shape. There are two marginal cartilages (dorsal and ventral) and four terminal cartilages (dorsal terminal, dorsal terminal 2, ventral terminal, and accessory terminal 3). These findings are in accordance to the description of Jungersen (1899) for *S. acanthias*. However, this author described a fifth terminal cartilage for this species as an uncalcified membrane attached to the proximal lateral edge of ventral terminal cartilage and connecting it to accessory terminal 3 cartilage and ventral marginal cartilage. Jungersen (1899) identified such cartilage as ventral terminal 2 cartilage that was also present in *Etmopterus* and *Somniosus*. In the current investigation, none of the species of the family showed this cartilage according to his description, suggesting that Jungersen (1899) probably misidentified it with proximal extension of accessory terminal 3 cartilage that is covered by connective tissue and inserted into the folded plate of the ventral terminal cartilage.

Two marginal cartilages and at least two terminal cartilages (dorsal and ventral) are present in all extant species of sharks and rays (Jungersen, 1899). According to this author, the number of terminal cartilages is useful for differentiating genera and some species within the Squaliformes. *Somniosus* and *Etmopterus* have five terminal cartilages while *Dalatias* shows only three terminal cartilages (Jungersen, 1899). *Squalus* and *Cirrhigaleus* can be differentiated by having, respectively, four and five terminal cartilages. *Cirrhigaleus barbifer* is the only species of the family that has an additional terminal cartilage, herein identified as ventral terminal 2 cartilage. This cartilage corresponds to the ventral cartilage (*v*) in *Squatina argentina* in Jungersen (1899) and ventral terminal 2 cartilage (*vt2*) in *Squatina guggenheim* in Vaz & Carvalho (2013). The condition of the ventral terminal 2 cartilage in *Cirrhigaleus asper* and *C. australis* still needs to be confirmed by dissection for better understanding of this character in this genus. Comparative investigations of ventral terminal 2 cartilage of *Cirrhigaleus* are also required with other species of sharks in order to correctly trace its morphological condition as derived or primitive character.

In Chondrichthyes the primary skeleton of the ventral appendix is composed by the basipterygium, the intermediate segments, the beta cartilage, and the appendix-stem (Jungersen 1899). In males, appendix-stem corresponds to axial cartilage of clasper from where marginal and terminal cartilages (so called secondary skeleton) will be developed with growth through different degrees of calcification (Jungersen, 1899). Analysis of clearing and staining material in neonates and young juveniles of *S. acanthias*, *S. suckleyi* and *S. blainvillei* (Figs. 46–47) showed that these cartilages are still under development or not yet calcified, supporting this hypothesis. The beta cartilage seems to be already developed in embryos of *S. acanthias*, according to Jungersen (1899), which is in disagreement to the current findings. Beta cartilage is only found in males of *Squalus* and *Cirrhigaleus*, articulating with the distal edge of the basipterygium, intermediate segment and axial cartilage, but does not reach the basipterygium in some species (e.g. *S. acanthias*, *Squalus* cf. *suckleyi*, *S. mitsukurii*, *S. megalops*, *S. brevirostris*). These findings are in agreement with Jungersen (1899) for other species of sharks.

The intermediate segments vary in number and shape in Squalidae as observed for other Squaliformes (e.g. Jungersen, 1899). These cartilages, however, do not bear radials in species of *Squalus* and *Cirrhigaleus,* in contrast to the observations of Jungersen (1899). *Etmopterus spinax* and *Somniosus microcephalus* exhibit more than one intermediate segment and the latter species has a third intermediate segment (Jungersen, 1899). Species of *Cirrhigaleus* and *S. montalbani* show two intermediate segments, although *Cirrhigaleus* can be distinguished from *E. spinax* and *S. montalbani* by having the first intermediate segment much smaller than the second one (vs. first segment larger than second one). *Squalus acanthias* and *Dalatias licha* have a single intermediate segment, still according to Jungersen (1899), as has been observed in all remaining species of Squalidae analyzed herein.

Sexual dimorphism is observed for the intermediate segments that vary in shape, but not in number in Squalidae. Females have modified distal cartilages of the pelvic fin that often are more expanded and enlarged, lacking radials. In females of *Cirrhigaleus*, the first intermediate segment is always barrel-shaped and short, like in males, followed by a wide and bifurcate cartilage that may correspond to the fusion of the second intermediate segment to the appendix-stem. This assumption is in contrast to the observations of Jungersen (1899) for females of *Somniosus microcephalus* in which the first and second intermediate segments are fused together, forming a broad cartilage between the basipterygium and the appendix-stem. In this species the latter cartilage is ray-like that is believed to correspond to the axial cartilage of males (Jungersen, 1899). Females of *Squalus* have a single cartilage, very broad and elongate with its distal edge bifurcated and cylindrical, almost ray-like, placed just posteriorly to the basipterygium. Intermediate segment and appendix-stem are fused to form this unique cartilage because no barrel-shaped cartilage is observed in this case. Based on this finding, it is further possible to state that females of *Cirrhigaleus* retain two intermediate segments with the first one separated and barrel-shaped while those of *Squalus* retain one intermediate segment that it is fused to the appendix-stem.

Taxonomic and phylogenetic considerations. The skeleton of species of the Squalidae reveals greater complexity than previously described in the literature. Characteristics of the neurocranium, pectoral and pelvic apparatus, and claspers are more useful for phylogenetic analysis rather than for identification purposes. The morphological patterns described are helpful in recognizing species that also exhibit certain similarity in external morphology. Interestingly, characters of the neurocranium, pectoral and pelvic apparatus, and clasper conduct to formation of possible distinct lineages that are associated to these groups of species in the family with distinct external morphology. Three groups are recognized: a group with species of spotted dogfish sharks, a second group with all remaining species of *Squalus*, and a third group with three species of *Cirrhigaleus*. These groups may represent three distinct supraspecific taxa in the Squalidae. Bigelow & Schroeder (1948, 1957) and Bass *et al*. (1976), using external morphology, and more recently Ward *et al*. (2007) and Naylor *et al*. (2012b) recognized four similar assemblages of species: groups *S. acanthias, S. megalops, S. mitsukurii* and *S. asper*. In contrast, the groups *S. megalops* and *S. mitsukurii* are merged into one according to the current analysis.

The morphological characteristics of the pelvic girdle and the clasper are also shared among certain species, leading to the formation of at least two major groups. One comprises all the species of *Squalus*; the second group includess the three species of *Cirrhigaleus*. Furthermore, the latter genus shares many characteristics of the neurocranium (e.g. absence of rostral appendages and supraethmoidal processes), pelvic and pectoral fins (e.g. articulation between fin and girdle), and cartilages of clasper (e.g. number of terminal cartilages) with other members of the Squaliformes rather than with *Squalus*. These findings suggest that *Cirrhigaleu*s may have evolved as a more distinctive lineage within the order Squaliformes than previously thought. Innervation of the nasal barbel in *Cirrhigaleu*s still needs investigation to corroborate its monophyly. Characteristics of the skeleton usually vary among groups of high taxonomic categories rather than at the genus and species levels (e.g. Compagno, 1973, 1977; Maisey, 1980; Carvalho, 1996; Shirai, 1996), indicating that the differences noticed here within Squalidae may support new interpretations regarding the phylogenetic relationships of its species. The taxonomic classification of species of *Squalus* may have to be re-evaluated in this context.

A total of 20 morphological characters of the skeleton are raised in the present study that will be integrated in a future phylogenetic analysis. The family Dalatiidae is the outgroup, according to recent findings on the relationships of the Squaliformes by Naylor *et al*. (2012b). These potential characters are defined and discussed below:

1. Character 1: Number of regions for pectoral articulation

Refers to the number of surfaces in the scapulae for articulation between the pectoral fin and pectoral girdle. Silva & Carvalho (2015) defined it according to the number of condyle and/or facets. *Dalatias* and *Isistius* have articulation by a single articular region (character state 0). *Squalus* and *Cirrhigaleus* have two articular regions (character state 1).

2. Character 2: The pectoral articular surface

The shape of the pectoral articular surfaces varies between facet and condyle in species of sharks, according to Silva & Carvalho (2015). *Dalatias* and *Isistius* have single condyle for articulation (character state 0). *Squalus* has both facet and condyle for articulation (character state 1) while *Cirrhigaleus* has two separate condyles (procondyle and meso+metacondyle) for articulation (character state 2).

3. Character 3: Dorsal ridge of scapulae

Depressor pectoralis fossa exhibits a cylindrical dorsal ridge in the scapulae in *Dalatias* and *Isistius* as well as in *Cirrhigaleus* (character state 0). Species of *Squalus* also show cylindrical ridge in this region. *Squalus acanthias* has segmented ridge with small barrel-shaped units lateral-dorsally to the *depressor pectoralis* fossa (character state 1).

4. Character 4: Rostral keel

Rostral keel is evident in *Squalus* and *Cirrhigaleus*, although its length varies greatly between these two genera. *Dalatias* and *Isistius* lack rostral keel (character state 0). *Squalus* has rostral keel very elongate, transcending anteriorly the nasal capsules (character state 1). *Cirrhigaleus* has short rostral keel, never transcending anteriorly the nasal capsules.

5. Character 5: Number of rostral appendages in the neurocranium

Rostral appendages may be present laterally and medially for connecting lateral sensory canals to the ventral base of the rostrum. *Dalatias* and *Isistius* have no rostral appendages (character state 0). These are also absent in species of *Cirrhigaleus*. In *Squalus*, some species have two rostral appendages (character state 1) while others have three (character state 2).

6. Character 6: Supraethmoidal processes in the neurocranium

Dalatias and *Isistius* lack supraethmoidal processes in the neurocranium (character state 0). These processes are also absent in species of *Cirrhigaleus* while *Squalus* has two supraethmoidal processes at anterior dorsal base of the ethmoidal region (character state 1).

7. Character 7: Dorsal aperture of profundus canal

Profundus canal has one ventral aperture placed in the interorbital wall and a second aperture that goes up to the ethmoidal region, called herein dorsal aperture. Shirai (1992) and Shirai & Nakaya (1992) stated that the profundus nerve runs together with superficial nerves in the preorbital canal in *Dalatias* and *Isistius*, thus, profundus canal is absent (character state 0). In some species of *Squalus*, profundus canal has its dorsal aperture placed aside the ethmoidal canal, at the base of the nasal capsule (character state 1). In other species of *Squalus* and in *Cirrhigaleus*, the dorsal aperture is between the ethmoidal canal and the preorbital canal at the longitudinal sulcus (character state 2).

8. Character 8: Greatest width of the neurocranium

Neurocranium has its greatest width at nasal capsules and/or across postorbital processes. In *Dalatias* and *Isistius*, neurocranium is wider across postorbital processes (character state 0) as it is observed for many species of *Squalus*. *Squalus japonicus* has neurocranium equally wide at nasal capsules and postorbital processes (character state 1). *S. montalbani*, *S. grahami* and *S. griffini* show the neurocranium broader at nasal capsules with its width 2%–4% of CL greater than across postorbital processes (character state 2). *Cirrhigaleus* has its greatest width at nasal capsules, its width 6%–8% of CL greater than postorbital processes (character state 3).

9. Character 9: Antorbital cartilage in the neurocranium

The antorbital cartilage is an extension of the subethmoidal region that is triangular and directed posteriorly, forming the ventral base of the preorbital wall. It is vestigial in *Dalatias* and *Isistius* (character state 0) as well as in *Cirrhigaleus*. In *Squalus*, the antorbital cartilage is well developed and expanded posteriorly (character state 1).

10. Character 10: Number of cartilaginous processes in the basal plate

Cartilaginous process is evident ventrally on each side of the basal plate as a lateral extension of the suborbital shelf, usually carrying the foramen for orbital artery. In *Dalatias* and *Isistius*, as well as in *Squalus* and *Cirrhigaleus*, there is a single pair of cartilaginous processes (character state 0). *Squalus blainvillei* has two cartilaginous processes on each side (character state 1).

11. Character 11: Shape of surfaces for pelvic articulation

Two regions in the pelvic girdle articulate with the pelvic fin. According to Silva (2015), one pelvic condyle articulates to the anterior pelvic element of the pelvic fin, and a posterior inner facet articulates to the basipterygium. *Dalatias* and *Isistius* exhibit this pattern of pelvic articulation (character state 0). *Squalus* also has a single pelvic condyle and an inner posterior facet for articulation. *Cirrhigaleus* is similar in having a lateral pelvic condyle that articulates to the anterior pelvic element, but differs in a combined inner facet and condyle articulating together to the basipterygium (character state 1).

12. Character 12: Number of pelvic foramen

The pubosichiadic bar has one or two foramina for pelvic nerve, laterally near the lateral prepelvic process on each side. Silva (2015) stated that it varies from one to two foramina within Squaliformes. *Dalatias* and *Isistius* have a single pelvic foramen on each side (character state 0). *Squalus acanthias*, *S. suckleyi*, *Squalus* cf. *suckleyi, S. megalops*, *S. brevirostris* and *Squalus* sp. 1 show single foramen as well. The remaining species of *Squalus* have two pelvic foramina on each side that are completely enclosed in the pubosichiadic bar (character state 1). *Cirrhigaleus* shows two pelvic foramina, although the anteriormost foramen is not completely enclosed in the pubosichiadic bar (character state 2).

13. Character 13: Lateral prepelvic process

Found on the anterior margin of the pubosichiadic bar, the lateral prepelvic process varies from inconspicuous to prominent within the Squalidae. *Dalatias* and *Isistius*, as well as *Cirrhigaleus* and most species of *Squalus*, have an inconspicuous lateral prepelvic process on each side (character state 0). *Squalus montalbani*, *S. grahami* and *S. griffini* exhbit very prominent lateral prepelvic process (character state 1). This latter condition, however, is still within the definition of the short lateral prepelvic process of Silva (2015).

14. Character 14: Number of intermediate segments between the basipterygium and the axial cartilage of the clasper in males (Jungersen, 1899)

Intermediate segments vary from one to three units in Squaliformes, according to Jungersen (1899). *Dalatias* has a single intermediate segment in adult males (character state 0). *Squalus* also shows single intermediate segment, except *S. montalbani* that has two intermediate segments with the first element much larger than the second (character state 1). *Cirrhigaleus* has two intermediate segments, with first one much smaller than second segment (character state 2).

15. Character 15: Position of beta cartilage in claspers

Jungersen (1899) stated that the beta cartilage varies greatly in position among species of sharks and rays. *Dalatias* has its beta cartilage over the intermediate segment and partially at proximal edge of the axial cartilage (character state 0). *Squalus acanthias*, *Squalus* cf. *suckleyi*, *S. megalops, S. brevirostris* and *S. mitsukurii* exhibit the same pattern. All remaining species of *Squalus* and *Cirrhigaleus* show beta cartilage over the distal edge of basipterygium, the first intermediate segment and the axial cartilage (character state 1).

16. Character 16: Number of terminal cartilages of the clasper

According to Jungersen (1899), sharks and rays have at least two terminal cartilages of the clasper. *Dalatias* has three terminal cartilages (character state 0). *Squalus* shows four terminal cartilages (character state 1). *Cirrhigaleus* has five terminal cartilages (character state 2).

17. Character 17: Mesial process in the axial cartilage of the claspers

The axial cartilage of the clasper is usually straight, although some sinuosity may occur. A mesial process on the proximal edge of the axial cartilage is described here for the first time. In *Isistius,* this process is absent (character state 0). *Squalus megalops* and *S. albifrons* share this condition with *Isistius*. *Squalus brevirostris* and *Squalus* sp. 7 show an inconspicuous mesial process (character state 1). *Squalus acanthias*, *S. suckleyi*, *Squalus* cf. *suckleyi*, *S. mitsukurii*, *S. grahami*, *S. montalbani*, *S. japonicus* and *C. barbifer* exhibit a conspicuous mesial process on the axial cartilage (character state 1).

18. Character 18: Thickness and length of cartilages of the clasper

Jungersen (1899) and Muñoz-Chápuli & Ramos (1986) reported variation in the length and thickness of the cartilages of the clasper in the Squaliformes. *Isistius* has very short and thick terminal and marginal cartilages with the ventral terminal cartilage much smaller than the axial cartilage (character state 0), according to Pettean (2015). *Squalus megalops*, *S. brevirostris*, *S. albifrons*, *Squalus sp. 5* and *S. japonicus* show the same condition. *Squalus mitsukurii*, *S. grahami*, *S. montalbani* and *C. barbifer* have the terminal and marginal cartilages markedly elongate and thin, with the ventral marginal cartilage one-third the length of the axial cartilage (character state 1). *Squalus acanthias*, *S. suckleyi*, *S. wakiyae* also have terminal and marginal cartilages elongate and thin, but their ventral marginal cartilage is equal in length to the axial cartilage (character state 2).

19. Character 19: Shape of dorsal terminal cartilage (td or claw)

Muñoz-Chápuli & Ramos (1986) described differences in the shape of the dorsal terminal cartilage in species of *Squalus*. This cartilage is absent in *Isistius*, according to Pettean (2015) (character state 0). *Squalus megalops, S. brevirostris, S. albifrons, Squalus sp. 5* and *S. japonicus* have a weakly hook-like dorsal terminal cartilage (character state 1), while *Squalus acanthias, S. suckleyi, Squalus* cf. *suckleyi, S. mitsukurii, S. grahami, S. montalbani* and *C. barbifer* show a dorsal terminal cartilage that is strongly hook-like (character state 2).

20. Character 20: Shape of the accessory terminal 3 cartilage (t3 or spur)

The acessory terminal 3 cartilage is stout and blade-like in *Isistius* (character state 0). The same condition is observed for *Squalus megalops*, *S. brevirostris*, *S. albifrons*, *Squalus* sp. 7 and *S. japonicus*. In *S. mitsukurii*, *S. grahami*, *S. montalbani* and *C. barbifer*, this cartilage is thin and blade-like (character state 1), while for *S. acanthias*, *S. suckleyi*, *Squalus* cf. *suckleyi* it is thin and pin-like (character state 2).

Few skeletal elements are useful for identification purposes in Squalidae. Autapomorphy of *Squalus acanthias* and *S. blainvillei* are strongly supported based on characteristics of the pectoral girdle and neurocranium, respectively. However, skeletal characters are not overall useful for differentiating species in contrast to findings of Jungersen (1899), Muñoz-Chápuli & Ramos (1989), and Marouani *et al*. (2012) but revealed to be more efficient for integrating analysis of the phylogenetic relationships in the family as previously noticed by Yano (1986) and Shirai (1992). Few studies provided descriptions of cartilages of the clasper in sharks (e.g. Daniel, 1928; White, 1937; Compagno, 1988; Carvalho & Gomes, 1991; Cunha & Gomes, 1996) and even less for species of Squaliformes (e.g. Jungersen, 1899; Yano, 1986), which makes it harder to identify correctly the cartilages and trace homologies. The same problem is observed for characteristics of the neurocranium (e.g. profundus canal and rostral appendages) and pelvic fin (e.g. number of intermediate segments).

Shirai (1992) previously provided characters of the neurocranium and nasal nerves for supporting squalid relationships at the generic level. The generic allocation of species of *Cirrhigaleus* has been debated in the literature (e.g. Merret, 1973; Garrick & Paul, 1971; Bass *et al*., 1976; Shirai, 1992; White *et al*., 2007b) and its elucidation depends strictly on morphological analysis. Recent molecular studies examined interrelationships at species level in Squalidae (e.g. Ward *et al*, 2005, 2007; Naylor *et al.*, 2012b). Naylor *et al*. (2012b) and concluded that *S. acanthias* and *S. suckleyi* are a sister group of species of *Cirrhigaleus* and that these two groups together are separated from all remaining *Squalus* species, thus making *Squalus* paraphyletic. In contrast, the current results support *Cirrhigaleus* as a genus separated from *Squalus* by structures of the skeleton and that *C. asper* is correctly allocated in the family, as previously supported by Shirai (1992). Studies of the comparative anatomy of skeletal components in other groups of the Squaliformes are imperative in order to correctly elucidate their evolutionary condition in Squalidae as well as to understand the intraspecific and interspecific significance of their variations.

Literature cited

Bass, A.J., D'Aubrey, J.D. & Kistnasamy, N. (1976) Sharks of the east coast of southearn Africa. VI The families Oxynotidae, Squalidae, Dalatiidae and Echinorhinidae. *Investigational Report,* 45, Oceanographic Research Institute, Durban, 1–103.

Bigelow, H.B. & Schroeder, W.C. (1957) A study of the sharks of the suborder Squaloidea. *Bulletin of the Museum of Comparative Zoology at Harvard College in Cambridge*, 117 (1), 1–150.

Carvalho, M.R. de (1996) High-level Elasmobranch Phylogeny, Basal Squaleans, and Paraphyly. *In*: Stiassny, M.L. J.; Parenti, L.R. & Johnson, G.D. (Eds.), *Interrelationships of fishes*. Academic Press Inc., San Diego, pp. 35–62.

Carvalho, M.R. de & Gomes, U.L. (1991) Reinterpretation of the clasper morphology of *Prionace glauca* (Chondrichthyes, Carcharhiniformes) with notes on clasper terminology. *Anais da Academia Brasileira de Ciências*, 64 (1), 199–206.

Compagno, L.J.V. (1973) Interrelationships of living elasmobranchs. *In*: Greenwood, P. H. *et al*. (Eds). *Interrelationships of Fishes*. Academic Press. Zoological Journal of the Linnean Society, London, v. 53, p. 15–61

Compagno, L.J.V. (1977) Phyletic relationships of living sharks and rays. *American Zoology*, 17, 303–322.

Compagno, L.J.V. (1988) *Sharks of the Order Carcharhiniformes*. Princeton University Press, Princeton, 486 pp.

Compagno, L.J.V. (1999) Systematic and body form. *In*: Hamlett, W.C. (Ed.). Sharks, skates, and rays: The biology of elasmobranch fishes. The John Hopkins University Press, Baltimore, p.1–47.

Cunha, M.R. & Gomes, U.L. (1994) Estudo comparativo da morfologia dos órgãos copuladores de *Rhizoprionodon lalandii* (Valenciennes, 1839) e *Rhizoprionodon porosus* (Poey, 1861) (Elasmobranchii, Carcharhinidae). *Revista Brasileira de Biologia*, 54 (4), 575–586.

Daniel, J.F. (1928) *The elasmobranch fishes*. 2nd ed. University of California Press, Berkeley, 332 pp.

Ebert, D.A., White, W.T., Goldmann, K.J., Compagno, L.J.V., Daly-Engel, T.S. & Ward, R.D. (2010) Resurrection and redescriptions of *Squalus suckleyi* (Girard, 1854) from the North Pacific, with comments on the *Squalus acanthias* subgroup (Squaliformes: Squalidae). *Zootaxa*, 2612, 22–40.

Figueirêdo, S.T.V. (2011) Revisão taxonômica e morfológica do gênero *Squalus* Linnaeus, 1758 do oceano Atlântico Sul Ocidental (Chondrichthyes: Squaliformes: Squalidae). Unpublished MSc Thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo, 348 pp.

Fowler, H.W. (1941) Contributions to the biology of the Philippine archipelago and adjacent regions. The fishes of the groups Elasmocephalii, Holocephali, Isospondyli, and Ostariophysi obtained by the United States Fisheries Steamer "Albatross" in 1907 to 1910, chiefly in the Philippine islands and adjacent seas. *Bulletin of the United States National Museum*, 100, 1–879.

Garrick, J.A.F. & Paul, L.J. (1971) *Cirrhigaleus barbifer* (Fam. Squalidae), a little known Japanese shark from New Zealand waters. *Zoology Publications, Victoria University, Wellington*, 154, 1–13.Gomes, U.L., Signori, C.N., Gadig, O.B.F. & Santos, H.R.S. (2010) *Guia para Identificação de Tubarões e Raias do Rio de Janeiro*. Technical Books, Rio de Janeiro, 234 pp.

Gilbert, S.G. (1973) Pictorial anatomy of the dogfish. University of Washington Press, Seatle, 59 pp.

Home, E. 1823. *Lectures on comparative anatomy: in which are explained the preparations in the Hunterian collection*. Illustrated by Engravings. vol. 3, Longman, Hurst, Rees, Orme, and Brown Press, London, 586 pp.

Jones, B.C. & Geen, G.H. (1976) Taxonomic Reevaluation of the Spiny Dogfish (*Squalus acanthias* L.) in the Northeastern Pacific Ocean. *Journal of the Fisheries Research Board of Canada*, 33 (11), 2500–2506

Jungersen, H. F. E. (1899) *On the appendices genitales in the greenland shark Somniosus microcephalus (Bl. Schn.) and other selachians*. The Danish Ingolf-Expedition, 2, Bianco Luno, Copenhagen: Bianco Luno, 88 pp.

Last, P.R., White, W.T. & Pogonoski, J.J. (2007) *Descriptions of new dogfishes of the genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, 130 pp.

Loboda, T.S. & DE Carvalho, M.R. (2013) Systematic revision of the *Potamotrygon motoro* (Müller & Henle, 1841) species complex in the Paraná-Paraguay basin, with description of two new ocellated species (Chondrichthyes: Myliobatiformes: Potamotrygonidae). *Neotropical Ichthyology*, 11 (4), 693-737.

Maia, A. & Wilga, C.D. (2013) Anatomy and muscle activity of the dorsal fins in Bamboo sharks and Spiny Dogfish during turning Maneuvers. *Journal of Morphology*, 274, 1288–1298.

Maisey, J.G. (1980) An evaluation of jaw suspension in sharks. *American Museum Novidates*, 2706, 1–17.

Maisey, J.G. (1984) Higher elasmobranch phylogeny and biostratigraphy. *Zoological Journal of the Linnean Society*, 82 (1-2), 33–54

Marinelli, W. & Strenger, A. (1959) *Vergleichende Anatomie und Morphologie der Wirbeltiere III Lieferung (Squalus acanthias)*. Franz Deuticke, Vienna, 308 pp.

Marouani, S., Chaâba, R., Kadri, H., Saidi, B., Bouain, A., Maltagliati, F., Last., P.R., Séret, B. & Bradai, M.N. (2012) Taxonomic research on *Squalus megalops* (Macleay, 1881) and *Squalus blainvillei* (Risso, 1826) (Chondrichthyes: Squalidae) in Tunisian waters (Central Mediterranean Sea). *Scientia Marina*, 76 (1).

Marques, A.R. (1999) O gênero *Squalus* no Brasil: caracterização do grupo megalops e determinação do status taxonômico das formas brasileiras. Unpublished Msc. Thesis. Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 117 pp.

Merrett, N.F. (1973) A new shark of the genus *Squalus* (Squalidae, Squaloidea) from the equatorial western Indian Ocean, with notes on the *Squalus blainvillei*. *Journal of Zoological Society of London*, 171, 93–110.

Molin, R. (1860) Sullo scheletro degli Squali. Instituto Veneto di Scienze, lettre ed Arti 8, 1–93.

Müller, J. & Henle, J. (1841) *Systematische Beschreibung der Plagiostomen*. Berlim, 300 pp.

Muñoz-Chápuli, R. & Ramos, F. (1989) Morphological comparisons of *Squalus blainvillei* and *S. megalops* in the Eastern Atlantic, with notes on the genus. *Japanese Journal of Ichthyology*, 36 (1), 6–21.

Naylor, G. J. P., Caira, J.N., Jensen, K., Rosana, A.M., Straube, N. & Lakner, C. (2012b) Elasmobranch Phylogeny: A mitochondrial estimate based on 595 species. *In*: Carrier, J.C., Musick, J.A., & Heithaus, M.E. (Eds.). *Biology of Sharks and their relatives.* 2nd edn. CRC Press. pp. 31–56.

Pettean, F.F. (2015) Revisão taxonômica e morfologia comparada das espécies do gênero *Isistius* Gill, 1864 (Chondrichthyes: Squaliformes: Dalatiidae). Unpublished MSc. Thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo, 350 pp.

Ramos, S.G.A.C. (2009) Descrição e comparação do condrocrânio de *Cirrhigaleus* Tanaka, 1912 e *Squalus* Linnaeus, 1758 (Squaliformes, Squalidae). Unpublished Monograph. Instituto de Ciências Biológicas e Ambientais, Universidade Santa Úrsula, Rio de Janeiro. 40 pp.

Shirai, S. (1992) *Squalean phylogeny: a new framework of "squaloid" sharks and related taxa*. Hokkaido University Press. Sapporo, 151 pp.

Shirai, S. (1996) Phylogenetic Interrelationships of Neoselachians (Chondrichthyes: Euselachii). *In*: Stiassny, M. L. J.; Parenti, L. R.; Johnson, G. D. (Eds). *Interrelationships of fishes.* Academic Press Inc, San Diego, p. 9–34.

Shirai, S. & Nakaya, K. (1992) Functional morphology of feeding apparatus of the cookie-cutter shark, *Isistius brasiliensis* (Elasmobranchii, Dalatiinae). *Zoological Science,* 9 (4), 811-821.

Silva, J.P.C.B. (2014) Filogenia dos principais grupos de Chondrichthyes baseada na anatomia comparada do esqueleto das nadadeiras pares e suas cinturas. Unpublished PhD Thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo, 703 pp.

Silva, J.P.C.B. & Carvalho, M.R. (2015) Morphology and phylogenetic significance of the pectoral articular region in elasmobranchs (Chondrichthyes). *Zoological Journal of the Linnean Society*, 175 (3), 525–568.

Vaz, D.F.B. & Carvalho, M.R. (2013) Morphological and taxonomic revision of species of Squatina from the Southwestern Atlantic Ocean (Chondrichthyes: Squatiniformes: Squatinidae). *Zootaxa*, 3695 (1), 1–81.

Veríssimo, A. & MacDowell, J.R. & Graves, J.E. (2010) Global population structure of the spiny dogfish Squalus acanthias, a temperate shark with an antitropical distribution. *Molecular Ecology*, 19 (8), 1651–1662.

Ward, R.D., Zemlak, T.S., Innes, B.H., Last, P.R. and Hebert, P.D.N. (2005) DNA barcoding Australia’s fish species. *Philosophical Transactions of the Royal Society of London*, Series B, 360, 1847–1857.

Ward, R.D., Holmes, B.H., Zemlak, T.S. & Smith, P.J. (2007) DNA barcoding discriminates spurdogs of the genus *Squalus*. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.). *Descriptions of new dogfishes of the genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, pp. 117–130.

White, E.G. (1937) Interrelationships of the elasmobranchs with a key to the Order Galea. *Bulletin of the American Museum of Natural History,* 74, 25–138.

White, W.T., Last, P.R. & Stevens, J.D. (2007b) *Cirrhigaleus australis* n. sp., a new Mandarin Dogfish (Squaliformes: Squalidae) from the south-west Pacific. *Zootaxa*, 1560, 19–30.

White, W.T., Yearsley, G.K. & Last, P.R. (2007c) Clarification of the status of *Squalus tasmaniensis* and a diagnosis of *Squalus acanthias* from Australia, including a key to the Indo-Australasian species of *Squalus*. *In*: Descriptions of new dogfishes of the genus *Squalus* (Squaloidea: Squalidae). CSIRO Marine and Atmospheric Research Paper, 14 (part 11), 109–115.

Yano, K. (1986) Studies on morphology, phylogeny, taxonomy and biology of Japanese Squaloid sharks, Order Squaliformes. Unpublished PhD Thesis. Tokai University, Shimizu, 335pp.

Table 1. Cranial measurements of *Squalus acanthias* expressed as percentage of total length of the neurocranium (% CL). CL: expressed in milimeters (mm). N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	North Atlantic Ocean				Southeastern Atlantic Ocean				Southwestern Atlantic Ocean			
	N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD
1	3	80.2 - 115.2	96.6	17.6	2	83.2 - 93.0	88.1	6.9	4	48.4 - 92.7	71.7	19.0
2	3	59.0 - 65.2	62.3	3.1	2	57.8 - 62.4	60.1	3.2	4	57.8 - 64.7	62.5	3.2
3	3	35.9 - 39.6	37.7	1.9	2	35.8 - 37.8	36.8	1.4	4	36.0 - 42.3	38.8	2.7
4	3	15.0 - 16.1	15.5	0.5	2	13.2 - 20.7	16.9	5.3	4	11.5 - 16.9	14.4	2.4
5	3	41.4 - 45.8	43.6	2.2	2	41.7 - 43.2	42.5	1.1	4	44.0 - 50.4	47.6	2.7
6	3	25.3 - 30.6	28.3	2.7	2	24.5 - 27.3	25.9	2.0	4	29.6 - 60.8	38.7	14.8
7	3	45.3 - 50.7	48.8	3.0	1	-	44.3	-	4	47.9 - 55.7	50.8	3.4
8	3	9.0 - 10.1	9.4	0.6	1	-	6.7	-	4	7.8 - 10.3	9.4	1.1
9	3	49.2 - 51.2	50.3	1.0	2	49.6 - 50.8	50.2	0.8	4	50.0 - 54.9	52.1	2.4
10	3	26.7 - 33.9	30.2	3.6	2	26.0 - 32.9	29.5	4.9	4	28.4 - 28.7	28.6	0.1
11	3	32.0 - 33.2	32.6	0.6	2	38.7 - 42.2	40.4	2.4	4	32.6 - 40.1	35.9	3.1
12	3	44.3 - 46.8	45.2	1.4	2	42.7 - 48.6	45.6	4.2	4	36.8 - 46.3	42.3	4.1
13	3	61.0 - 68.5	64.1	3.9	1	-	67.5	-	4	62.8 - 67.4	65.2	2.1
14	3	24.2 - 38.5	29.1	8.1	2	24.4 - 27.3	25.9	2.1	4	17.3 - 26.1	22.5	3.9
15	3	11.6 - 12.6	12.1	0.5	2	12.5 - 13.6	13.0	0.8	4	10.5 - 13.6	12.4	1.5
16	3	16.5 - 21.5	18.4	2.7	1	-	16.6	-	4	16.8 - 20.0	18.7	1.4
17	3	41.2 - 42.6	42.0	0.7	1	-	49.5	-	4	36.9 - 42.2	40.5	2.5
18	3	16.9 - 21.6	18.6	2.6	1	-	17.8	-	4	17.8 - 26.4	21.2	3.7
19	3	29.7 - 34.2	31.9	2.3	1	-	30.3	-	4	28.1 - 34.0	30.8	3.1
20	-	-	-	-	-	-	-	-	-	-	-	-
21	3	18.6 - 19.3	19.0	0.4	2	10.0 - 18.5	14.2	6.0	4	17.5 - 23.1	20.7	2.5
22	3	7.4 - 10.8	9.1	1.7	2	7.7 - 18.3	13.0	7.4	4	7.2 - 10.9	9.2	1.9

Table 2. Cranial measurements of *Squalus suckleyi* and *Squalus wakiyae* expressed as percentage of total length of the neurocranium (% CL). CL: expressed in milimeters (mm). N: number of specimens; *x*: mean; SD: standard deviation.

	Measurements	***Squalus suckleyi***				***Squalus wakiyae***			
		N	Range	*x*	SD	N	Range	*x*	SD
1	Total length of neurocranium (CL)	4	36.4 - 109.8	76.3	38.8	2	67.4 - 80.4	73.9	9.2
2	Postcerebral length	4	59.1 - 64.8	62.3	2.5	2	60.2 - 66.5	63.4	4.5
3	Precerebral fossa length	4	36.5 - 40.4	37.9	1.7	2	33.1 - 39.9	36.5	4.8
4	Precerebral fossa width	4	11.7 - 15.1	14.0	1.6	2	11.6 - 14.5	13.1	2.1
5	Width across nasal capsules	4	41.4 - 54.1	46.7	5.4	2	49.6 - 51.2	50.4	1.2
6	Interorbital width	4	29.3 - 35.8	33.0	3.0	2	32.7 - 34.6	33.6	1.3
7	Width across preorbital processes	4	48.7 - 52.7	50.6	1.8	2	52.7 - 56.3	54.5	2.6
8	Postorbital process length	4	6.6 - 12.7	8.9	2.6	2	9.8 - 10.1	10.0	0.2
9	Width across postorbital processes	4	47.2 - 54.9	50.1	3.4	2	52.9 - 58.9	55.9	4.3
10	Distance between orbital processes	4	25.0 - 33.5	28.2	3.7	2	26.4 - 27.0	26.7	0.4
11	Distance across opistotic processes	4	31.3 - 34.6	33.2	1.5	2	37.7 - 38.3	38.0	0.4
12	Width across hyomandibular facets	4	37.4 - 44.9	42.2	3.3	2	45.7 - 45.8	45.7	0.1
13	Nasaobasal length	4	58.5 - 60.6	59.6	1.1	2	63.1 - 65.0	64.1	1.4
14	Rostral keel length	4	24.5 - 36.3	29.1	5.0	2	25.7 - 26.7	26.2	0.8
15	Subethmoidean width	4	11.6 - 15.1	13.4	1.4	2	12.5 - 13.9	13.2	1.0
16	Basal angle width	4	17.5 - 19.4	18.3	0.8	2	17.4 - 18.9	18.1	1.1
17	Basal plate length	4	35.9 - 43.3	40.3	3.2	2	42.4 - 42.7	42.5	0.2
18	Basal plate width	4	18.0 - 20.9	19.3	1.2	2	20.1 - 21.7	20.9	1.1
19	Width across first cartilaginous processes	4	29.6 - 31.9	30.9	1.1	2	31.5 31.7	31.6	0.2
20	Width across second cartilaginous processes	-	-	-	-	-	-	-	-
21	Maximum sagital length	4	18.5 - 23.5	20.2	2.3	2	20.1 20.2	20.2	0.0
22	Foramen magnum width	4	7.0 - 9.5	8.2	1.1	2	7.8 - 8.6	8.2	0.5

Table 3. Cranial measurements of species of *Squalus* expressed as percentage of the total length of the neurocranium (% CL). CL: expressed in milimeters (mm). N: number of specimens; x: mean; SD: standard deviation.

Measurements	*Squalus megalops*		*Squalus albifrons*				*Squalus brevirostris*			
	N	*x*	N	Range	*x*	SD	N	Range	*x*	SD
1	1	69.2	2	98.4 - 108.4	103.4	7.1	2	55.2 - 60.3	57.8	3.6
2	1	66.8	2	59.9 - 61.5	60.7	1.2	2	64.5 - 68.3	66.4	2.7
3	1	29.9	2	38.0 - 40.2	39.1	1.6	2	31.9 - 37.3	34.6	3.8
4	1	14.7	2	11.7 - 14.0	12.9	1.6	2	15.2 - 15.3	15.2	0.0
5	1	52.3	2	49.3 - 62.6	55.9	9.4	2	56.7 - 59.1	57.9	1.7
6	1	31.2	2	28.0 - 33.3	30.6	3.8	2	30.4 - 33.5	32.0	2.2
7	1	53.0	2	48.6 - 56.5	52.6	5.6	2	52.0 - 55.1	53.5	2.2
8	1	11.0	2	7.8 - 8.3	8.1	0.3	2	9.3 - 10.1	9.7	0.6
9	1	59.1	2	52.5 - 64.3	58.4	8.4	2	60.5 - 63.2	61.9	1.9
10	1	38.4	2	32.6 - 38.9	35.7	4.5	2	35.1 - 37.0	36.1	1.3
11	1	43.2	2	35.2 - 40.0	37.6	3.4	2	39.1 - 43.4	41.3	3.1
12	1	47.1	2	40.4 - 47.6	44.0	5.1	2	47.8 - 49.1	48.5	0.9
13	1	74.1	2	60.3 - 68.5	64.4	5.8	2	60.4 - 67.4	63.9	5.0
14	1	19.1	2	15.2 - 20.8	18.0	4.0	2	22.5 - 27.4	24.9	3.5
15	1	13.6	2	14.1 - 17.5	15.8	2.4	2	15.6 - 20.9	18.2	3.8
16	1	18.6	2	16.8 - 20.0	18.4	2.3	2	19.0 - 39.1	29.1	14.2
17	1	43.6	2	38.7 - 45.9	42.3	5.1	2	21.2 - 42.0	31.6	14.7
18	1	20.8	2	18.9 - 23.0	20.9	2.9	2	23.4 - 39.8	31.6	11.6
19	1	33.8	2	27.2 - 32.7	30.0	3.9	2	34.7 - 34.8	34.7	0.1
20	-	-	-	-	-	-	-	-	-	-
21	1	20.5	2	15.1 - 18.7	16.9	2.5	2	20.7 - 20.7	20.7	0.1
22	1	9.0	2	6.6 - 8.9	7.8	1.6	2	7.0 - 9.8	8.4	2.0

Table 4. Cranial measurements of *Squalus blainvillei* and *Squalus* cf. *blainvillei* expressed as percentage of the total length of the neurocranium (% CL). CL: expressed in milimeters (mm). N: number of specimens.

	Measurements	***Squalus blainvillei***		***Squalus* cf. *blainvillei***	
		N	*x*	N	*x*
1	Total length of neurocranium (CL)	1	50.8	1	101.8
2	Postcerebral length	1	65.4	1	62.4
3	Precerebral fossa length	1	35.0	1	37.2
4	Precerebral fossa width	1	18.1	1	18.6
5	Width across nasal capsules	1	60.8	1	52.0
6	Interorbital width	1	30.3	1	31.6
7	Width across preorbital processes	1	52.8	1	48.8
8	Postorbital process length	1	11.0	1	9.0
9	Width across postorbital processes	1	59.4	1	53.2
10	Distance between orbital processes	1	31.3	1	33.1
11	Distance across opistotic processes	1	43.9	1	43.5
12	Width across hyomandibular facets	1	50.6	1	54.3
13	Nasaobasal length	1	73.2	1	63.1
14	Rostral keel length	1	20.1	1	21.8
15	Subethmoidean width	1	16.3	1	14.6
16	Basal angle width	1	17.1	1	37.6
17	Basal plate length	1	41.7	1	47.7
18	Basal plate width	1	18.1	-	-
19	Width across first cartilaginous pro	1	33.3	-	-
20	Width across second cartilaginous p	1	34.6	-	-
21	Maximum sagital length	1	24.0	1	17.5
22	Foramen magnum width	1	7.5	1	4.1

Table 5. Cranial measurements of *S. mitsukurii*, *S. montalbani*, *S. chloroculus*, *S. grahami* and *S. griffini* expressed as percentage of the total length of the neurocranium (% CL). CL: expressed in milimeters (mm). N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Squalus mitsukurii***		***Squalus montalbani***		***Squalus chloroculus***				***Squalus grahami***				***Squalus griffini***	
	N	*x*	N	*x*	N	Range	*x*	SD	N	Range	*x*	SD	N	*x*
1	1	103.2	1	106.2	2	110.6 - 120.3	115.5	6.9	4	85.5 - 110.2	93.2	11.6	1	141.9
2	1	61.4	1	58.7	2	62.1 - 63.5	62.8	1.0	4	54.0 - 61.3	57.6	3.2	1	58.6
3	1	39.9	1	41.8	2	36.7 - 37.6	37.2	0.6	4	39.4 - 45.6	42.8	2.7	1	41.3
4	1	14.8	1	12.9	2	14.3 - 16.1	15.2	1.3	4	10.8 - 13.3	12.1	1.4	1	13.2
5	1	54.0	1	54.8	2	50.9 - 51.9	51.4	0.7	4	45.1 - 56.8	50.4	6.1	1	58.3
6	1	31.6	1	29.7	2	28.2 - 29.3	28.8	0.8	4	25.7 - 28.3	27.1	1.1	1	30.0
7	1	48.6	1	50.5	2	52.0 - 53.4	52.7	1.0	4	44.2 - 47.4	45.5	1.4	1	51.3
8	1	10.9	1	8.1	2	8.3 - 8.6	8.5	0.2	4	4.6 - 5.7	5.1	0.4	1	6.8
9	1	57.1	1	53.3	2	56.2 - 56.3	56.3	0.0	4	42.8 - 49.0	46.3	2.7	1	53.1
10	1	32.2	1	35.2	2	33.4 - 33.9	33.7	0.3	4	28.5 - 32.3	30.7	1.8	1	32.6
11	1	37.0	1	36.0	2	37.7 - 38.6	38.1	0.6	4	31.6 - 36.5	33.7	2.2	1	35.9
12	1	48.1	1	41.6	2	43.7 - 43.9	43.8	0.1	4	36.7 - 40.7	38.9	2.0	1	45.7
13	1	54.7	1	57.0	2	64.3 - 66.5	65.4	1.6	4	54.5 - 57.9	56.7	1.5	1	61.9
14	1	25.4	1	24.0	2	20.4 - 22.8	21.6	1.7	4	22.9 - 29.6	25.5	3.0	1	24.2
15	1	14.7	1	15.3	2	15.5 - 16.5	16.0	0.6	4	13.2 - 15.4	14.2	1.1	1	15.4
16	1	16.9	1	19.7	2	19.4 - 20.3	19.9	0.6	4	13.8 - 18.4	15.6	2.0	1	19.0
17	1	33.2	1	35.0	2	43.1 - 43.4	43.3	0.2	4	31.9 - 36.5	34.2	2.2	1	39.0
18	1	19.7	1	19.0	2	17.6 - 20.6	19.1	2.1	4	17.1 - 18.9	18.1	0.8	1	17.2
19	1	31.5	1	29.1	2	29.3 - 30.0	29.6	0.5	4	24.8 - 29.5	27.0	2.1	1	30.8
20	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21	1	18.9	1	18.4	2	18.5 - 19.6	19.0	0.8	4	13.8 - 17.9	15.5	1.8	1	18.5
22	1	7.9	1	7.1	2	5.7 - 6.5	6.1	0.5	4	5.0 - 8.4	6.8	1.8	1	7.2

Table 6. Cranial measurements of *Squalus japonicus* and *Squalus nasutus* expressed as percentage of the total length of the neurocranium (% CL). CL: expressed in milimeters (mm). N: number of specimens; *x*: mean; SD: standard deviation.

	Measurements	*Squalus japonicus*				*Squalus nasutus*	
		N	Range	*x*	SD	N	*x*
1	Total length of neurocranium (CL)	2	85.7 - 94.2	90.0	6.0	1	97.4
2	Postcerebral length	2	53.4 - 59.2	56.3	4.1	1	53.3
3	Precerebral fossa length	2	46.4 - 46.5	46.5	0.0	1	45.4
4	Precerebral fossa width	2	8.4 - 10.9	9.6	1.7	1	12.5
5	Width across nasal capsules	2	44.8 - 45.0	44.9	0.2	1	43.3
6	Interorbital width	2	23.6 - 27.8	25.7	3.0	1	23.4
7	Width across preorbital processes	2	40.2 - 42.2	41.2	1.4	1	42.4
8	Postorbital process length	2	6.1 - 7.3	6.7	0.9	1	8.9
9	Width across postorbital processes	2	43.1 - 44.5	43.8	1.0	1	41.4
10	Distance between orbital processes	2	28.4 - 28.9	28.6	0.4	1	26.9
11	Distance across opistotic processes	2	31.0 - 33.5	32.2	1.8	1	30.5
12	Width across hyomandibular facets	2	36.5 - 37.7	37.1	0.8	1	33.4
13	Nasaobasal length	1	-	55.8	-	1	53.8
14	Rostral keel length	1	-	25.9	-	1	26.5
15	Subethmoidean width	1	-	12.1	-	1	13.6
16	Basal angle width	2	13.5 - 13.9	13.7	0.3	1	12.5
17	Basal plate length	2	31.3 - 37.0	34.2	4.0	1	34.2
18	Basal plate width	2	16.8 - 18.3	17.5	1.0	1	16.1
19	Width across first cartilaginous proces	2	23.8 - 27.1	25.4	2.3	1	22.4
20	Width across second cartilaginous pro	-	-	-	-	-	-
21	Maximum sagital length	2	16.8 - 17.4	17.1	0.4	1	15.2
22	Foramen magnum width	2	6.7 - 7.9	7.3	0.9	1	5.4

Table 7. Cranial measurements of *Squalus* sp. 1, *Squalus* sp. 3, *Squalus* sp. 4 and *Squalus* sp. 7 expressed as percentage of the total length of the neurocranium (% CL). CL: expressed in milimeters (mm). N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Squalus* sp. 1				*Squalus* sp. 3		*Squalus* sp. 4		*Squalus* sp. 7	
	N	Range	*x*	SD	N	*x*	Paratype UERJ 1661	Other material UERJ 1112	N	*x*
1 Total length of neurocranium (CL)	2	61.8 - 62.7	62.3	0.6	1	70.6	90.2	80.9	1	70.4
2 Postcerebral length	2	62.8 - 64.4	63.6	1.1	1	64.0	58.3	65.0	1	58.5
3 Precerebral fossa length	2	35.4 - 37.2	36.3	1.2	1	37.1	40.6	36.1	1	40.1
4 Precerebral fossa width	2	14.2 - 16.3	15.3	1.4	1	14.7	13.6	15.6	1	14.9
5 Width across nasal capsules	2	54.4 - 59.4	56.9	3.6	1	58.6	52.3	57.8	1	52.8
6 Interorbital width	2	32.7 - 33.3	33.0	0.5	1	29.3	30.2	28.8	1	28.8
7 Width across preorbital processes	2	53.9 - 58.4	56.1	3.2	1	49.4	52.3	54.6	1	48.9
8 Postorbital process length	2	11.7 - 14.2	12.9	1.8	1	7.9	6.9	9.4	1	10.2
9 Width across postorbital processes	2	61.7 - 62.8	62.3	0.8	1	59.9	55.8	57.2	1	57.1
10 Distance between orbital processes	2	32.2 - 38.5	35.4	4.5	1	39.9	35.0	39.1	1	34.7
11 Distance across opistotic processes	2	40.5 - 42.3	41.4	1.3	1	43.1	37.9	39.3	1	36.5
12 Width across hyomandibular facets	2	47.2 - 49.1	48.2	1.3	1	51.3	43.5	51.3	1	41.5
13 Nasobasal length	2	65.1 - 66.8	66.0	1.2	1	64.0	64.5	63.7	1	64.9
14 Rostral keel length	2	21.1 - 26.4	23.7	3.8	1	27.8	20.8	30.0	1	25.0
15 Subethmoidean width	2	15.7 - 15.8	15.7	0.1	1	27.5	15.3	16.9	1	16.5
16 Basal angle width	2	17.9 - 18.3	18.1	0.3	1	18.8	18.1	19.0	1	16.1
17 Basal plate length	2	34.6 - 40.0	37.2	3.8	1	40.5	42.4	41.5	1	38.6
18 Basal plate width	2	20.1 - 27.0	23.6	4.9	1	20.1	19.8	20.8	1	17.9
19 Width across first cartilaginous processes	2	34.0 - 38.5	36.2	3.2	1	33.7	30.6	31.1	1	30.3
20 Width across second cartilaginous processes	-	-	-	-	-	-	-	-	-	-
21 Maximum sagital length	2	22.6 - 23.0	22.8	0.2	1	22.9	18.5	20.0	1	18.9
22 Foramen magnum width	1	-	7.7	-	1	10.2	8.8	8.4	1	9.2

Table 8. Cranial measurements of *Cirrhigaleus barbifer, C. asper* and *C. australis* expressed as percentage of total length of the neurocranium (% CL). CL: expressed in milimeters (mm). N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Cirrhigaleus barbifer*		*Cirrhigaleus asper*				*Cirrhigaleus australis*	
	N	*x*	N	Range	*x*	SD	N	*x*
1	1	71.7	2	37.6 - 123.5	80.6	60.7	1	78.2
2	1	60.8	2	67.1 - 73.1	70.1	4.3	1	62.9
3	1	39.9	2	32.3 - 32.4	32.4	0.1	1	38.7
4	1	14.9	2	14.5 - 19.1	16.8	3.3	1	14.6
5	1	68.2	2	62.5 - 70.5	66.5	5.6	1	68.0
6	1	37.5	2	30.6 - 34.3	32.5	2.6	1	33.1
7	1	60.8	2	57.7 - 58.9	58.3	0.8	1	53.5
8	1	13.4	2	11.2 - 13.1	12.1	1.4	1	10.0
9	1	62.2	2	55.1 - 64.1	59.6	6.4	1	59.7
10	1	34.0	2	36.0 - 40.4	38.2	3.1	1	32.2
11	1	41.6	2	40.6 - 43.1	41.9	1.7	1	43.0
12	1	50.6	1	-	50.4	-	1	48.3
13	1	66.4	2	66.6 - 68.9	67.8	1.6	1	65.7
14	1	22.6	2	27.4 - 30.4	28.9	2.2	1	22.8
15	1	15.2	2	17.3 - 17.6	17.4	0.2	1	17.8
16	1	25.5	2	17.8 - 24.8	21.3	4.9	1	18.8
17	1	51.5	2	44.0 - 48.7	46.4	3.3	1	41.6
18	1	25.0	2	21.8 - 23.9	22.8	1.5	1	20.3
19	1	36.0	1	-	35.4	-	1	33.5
20	-	-	-	-	-	-	-	-
21	1	22.6	2	20.5 - 20.6	20.6	0.1	1	22.9
22	1	7.9	2	7.6 - 11.2	9.4	2.5	1	4.1

Table 9. Units in the segmented ridge of the scapulae of *Squalus acanthias*. *x*: mean; SD: standard deviation.

	N	Range			*x*	SD	Mode
Paralectotypes	2		-		*5*	-	5
Baltic Sea	3	5	-	7	5	1	5
North Atlantic	11	3	-	6	5	1	5
South Atlantic	6	3	-	6	4	1	4
North Pacific	1	16	-	18	16	-	-
South Pacific	2		-		5	-	5

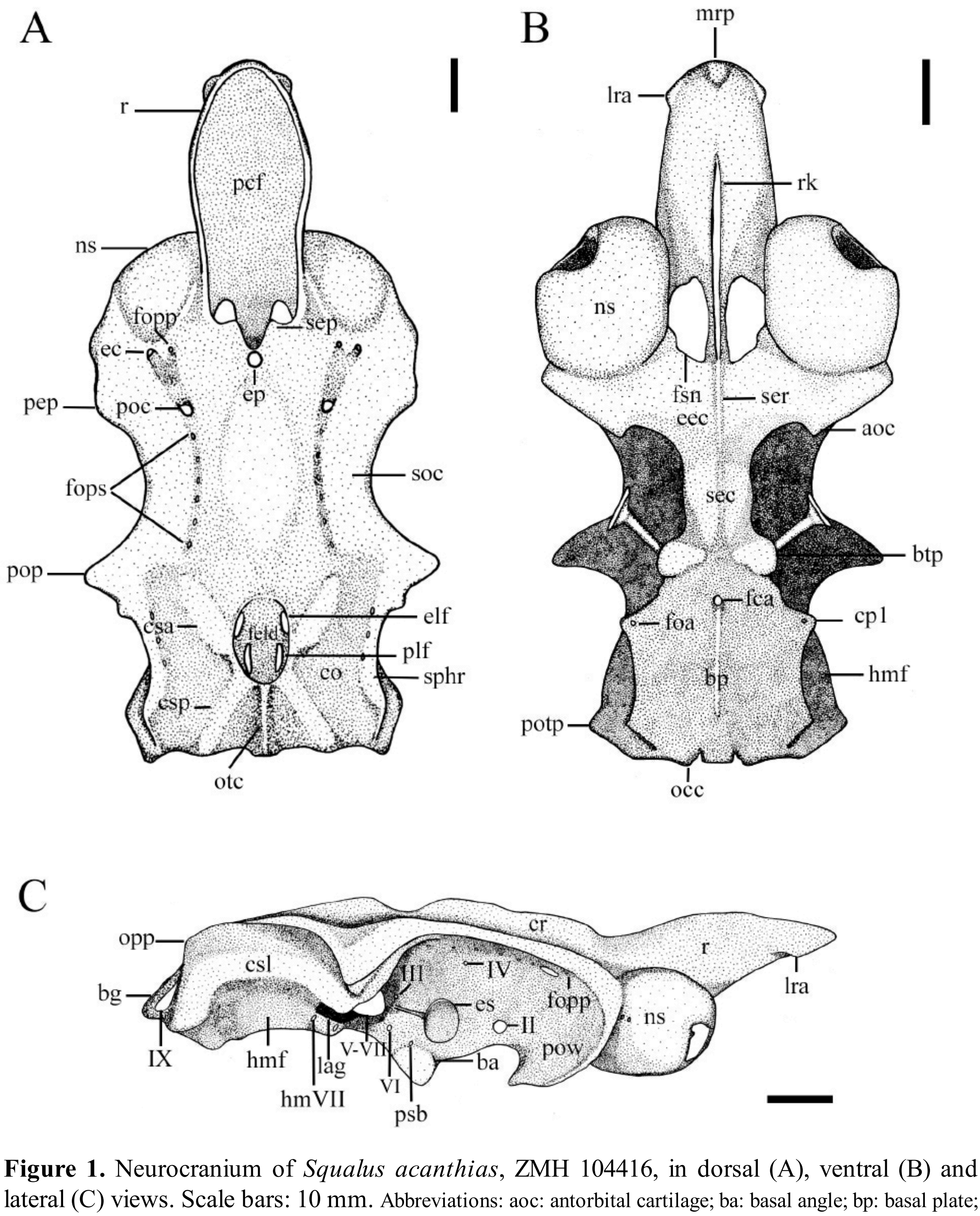

Figure 1. Neurocranium of *Squalus acanthias*, ZMH 104416, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; bp: basal plate; btp: basitrabecular process; cp1: first cartilaginous process; cr: cranial roof; csa: anterior semicircular canal; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; eec: ectethmoid chamber; elf: endolymphatic foramen; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; feld: endolymphatic fossa; foa: foramen for orbital artery; fopp: profundus canal; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; gb: glossopharyngeal base; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; lag: lateral auditory groove; oc: otic capsule; occ: occipital condyle; otc: otic crest; pcf: precerebral fossa; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; potp: prootic process; pow: preorbital wall; ppe: preorbital process; psb: foramen for efferent of pseudobranchial artery; r: rostrum; lra: lateral rostral appendage; mrp: median rostral prominence; rk: rostral keel; sec: subethmoid chamber; sep: supraetmoidal process; ser: subethmoidean ridge; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; II: foramen opticum; III: foramen oculomotor; IV: foramen trochlear; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve.

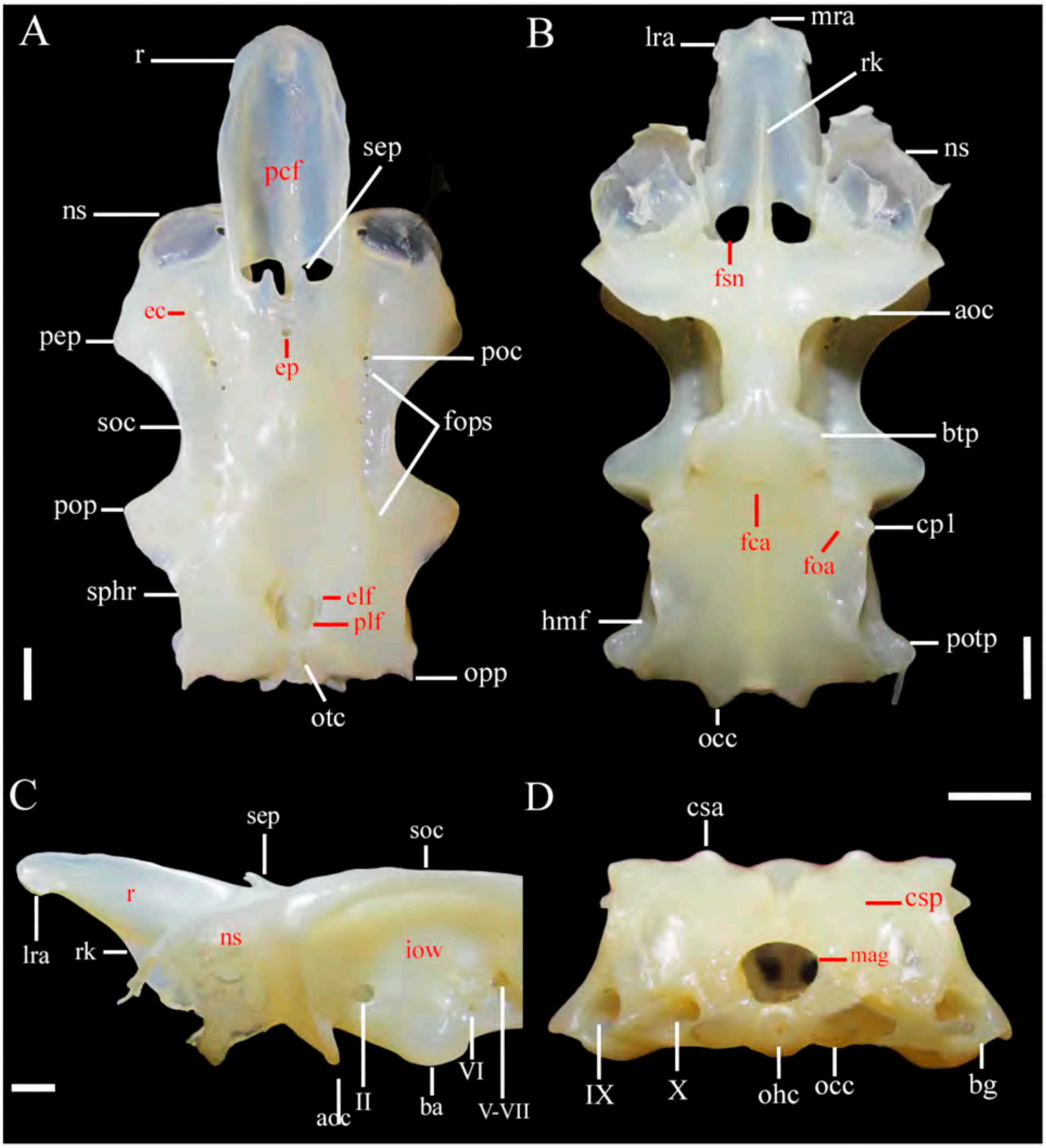

Figure 2. Neurocranium of *Squalus suckleyi* in dorsal (A), ventral (B), anterior-lateral (C), and occipital (D) views. Scale bars: 10 mm. A–C: SAM 38346; D: SAM 38346. Abbreviations: aoc: antorbital cartilage; ba: basal angle; bg: glossopharyngeal base; btp: basitrabecular process; cp1: first cartilaginous process; csa: anterior semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; fca: foramen for carotid artery; feld: endolymphatic fossa; foa: foramen for orbital artery; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; hmf: hyomandibular facet; iow: interorbital wall; mag: foramen magnum; ns: nasal capsule; occ: occipital condyle; ohc: occipital hemicentrum; otc: otic crest; pcf: precerebral fossa; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; potp: prootic process; ppe: preorbital process; r: rostrum; lra: lateral rostral appendage; mrp: median rostral prominence; rk: rostral keel; sep: supraetmoidal process; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; II: foramen opticum; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve; X: foramen vagus.

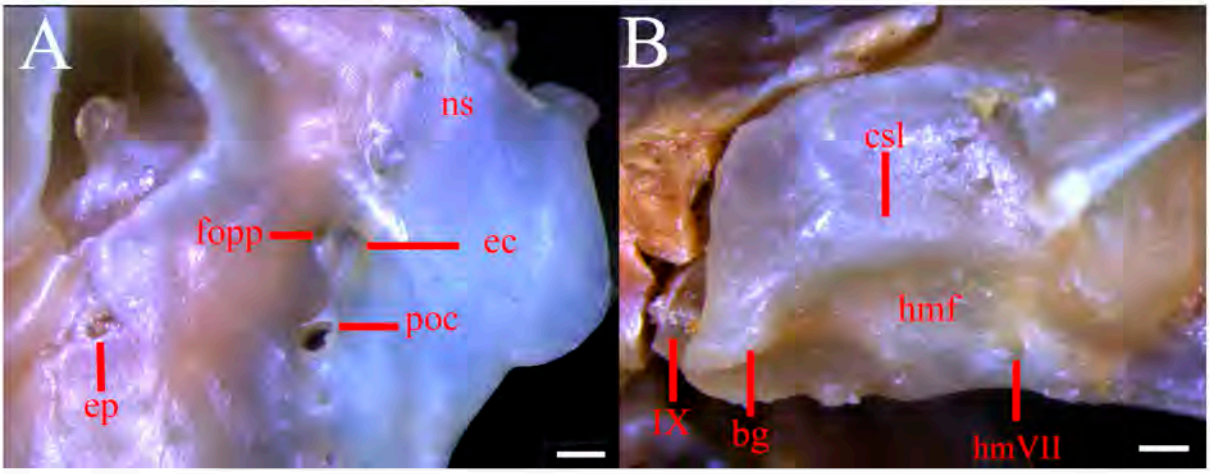

Figure 3. Detail of neurocranium of *Squalus suckleyi* (CAS 40873): A: dorsal view; B: posterior-lateral view. Scale bars: 1 mm. Abbreviations: bg: glossopharyngeal base; csl: lateral semicircular canal; ec: ethmoidal canal; ep: epiphysial pit; fopp: profundus canal for the ophthalmicus profundus nerve; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; poc: preorbital canal; IX: foramen for glossopharyngeal nerve.

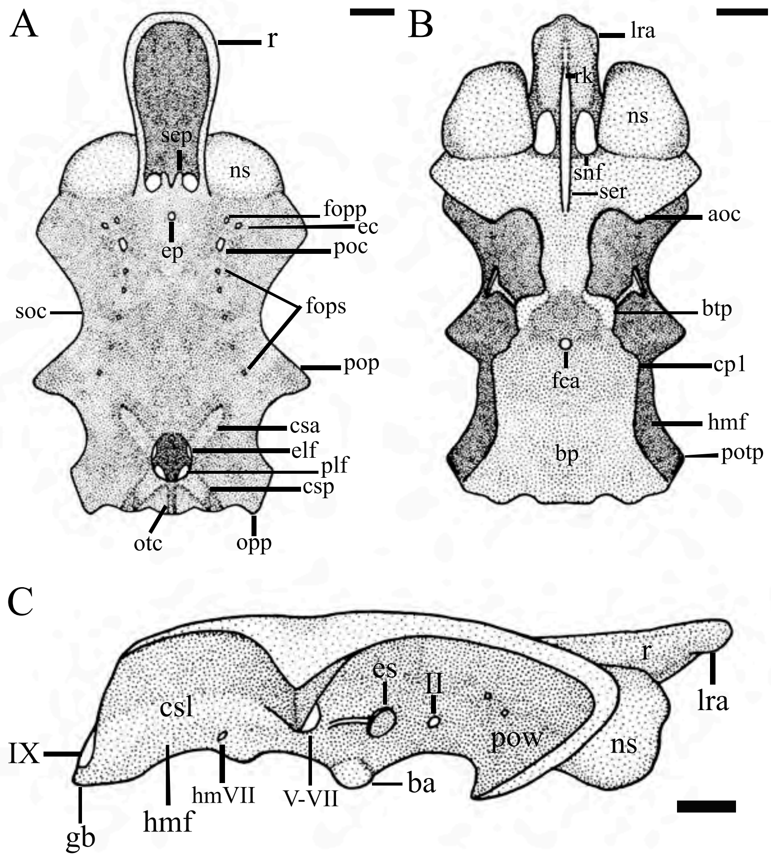

Figure. 4. Neurocranium of *Squalus wakiyae*, HUMZ 87643, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; btp: basitrabecular process; cp1: first cartilaginous process; csa: anterior semicircular canal; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; fopp: profundus canal; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; gb: glossopharyngeal base; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; opp: opistotic process; otc: otic crest; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; potp: prootic process; pow: preorbital wall; r: rostrum; lra: lateral rostral appendage; rk: rostral keel; sep: supraethmoidal process; snf: subnasal fenestra; soc: supraorbital crest; II: foramen opticum; V-VII: foramen prooticum; IX: foramen for glossopharyngeal nerve.

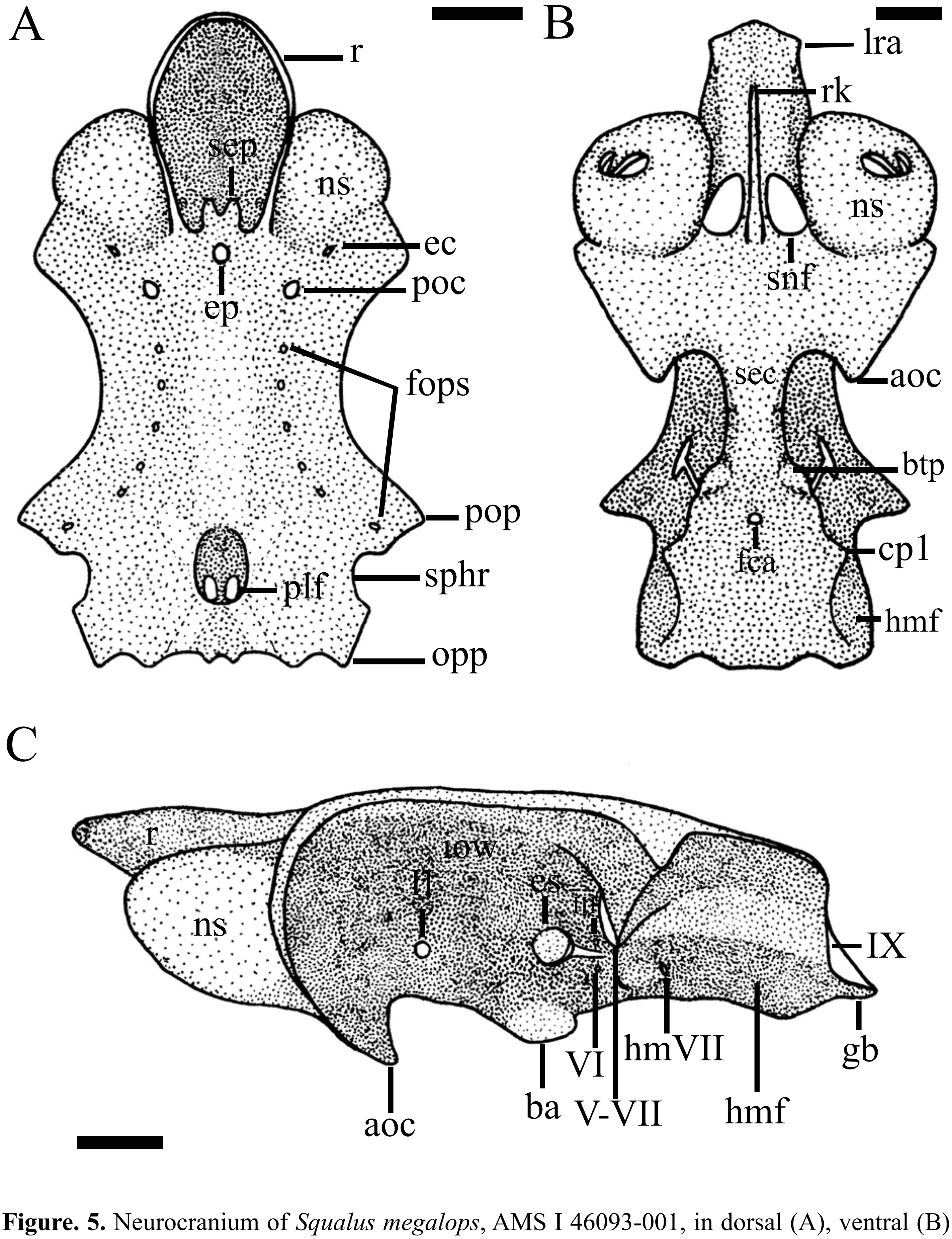

Figure. 5. Neurocranium of *Squalus megalops*, AMS I 46093-001, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; btp: basitrabecular process; cp1: first cartilaginous process; ec: ethmoidal canal; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; fopp: profundus canal; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; gb: glossopharyngeal base; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; iow: interorbital wall; ns: nasal capsule; opp: opistotic process; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; pow: preorbital wall; r: rostrum; lra: lateral rostral appendage; rk: rostral keel; sec: subethmoid chamber; sep: supraethmoidal process; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; II: foramen opticum; III: foramen oculomotor; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve.

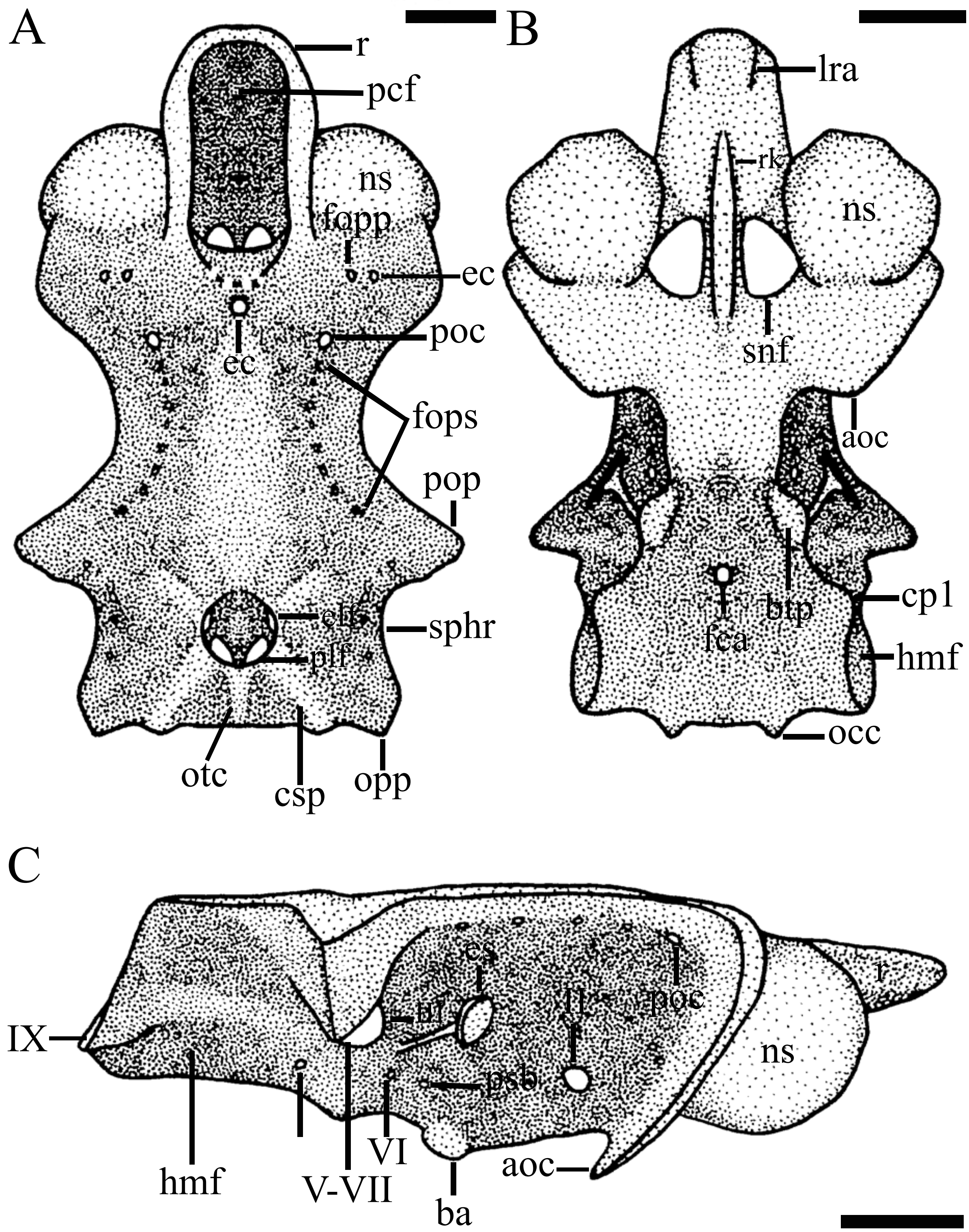

Figure. 6. Neurocranium of *Squalus brevirostris*, HUMZ 189762, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; btp: basitrabecular process; cp1: first cartilaginous process; csp: posterior semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; fopp: profundus canal; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; occ: occipital condyle; opp: opistotic process; otc: otic crest; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; psb: foramen for efferent of pseudobranchial artery; r: rostrum; lra: lateral rostral appendage; rk: rostral keel; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; II: foramen opticum; III: foramen oculomotor; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve.

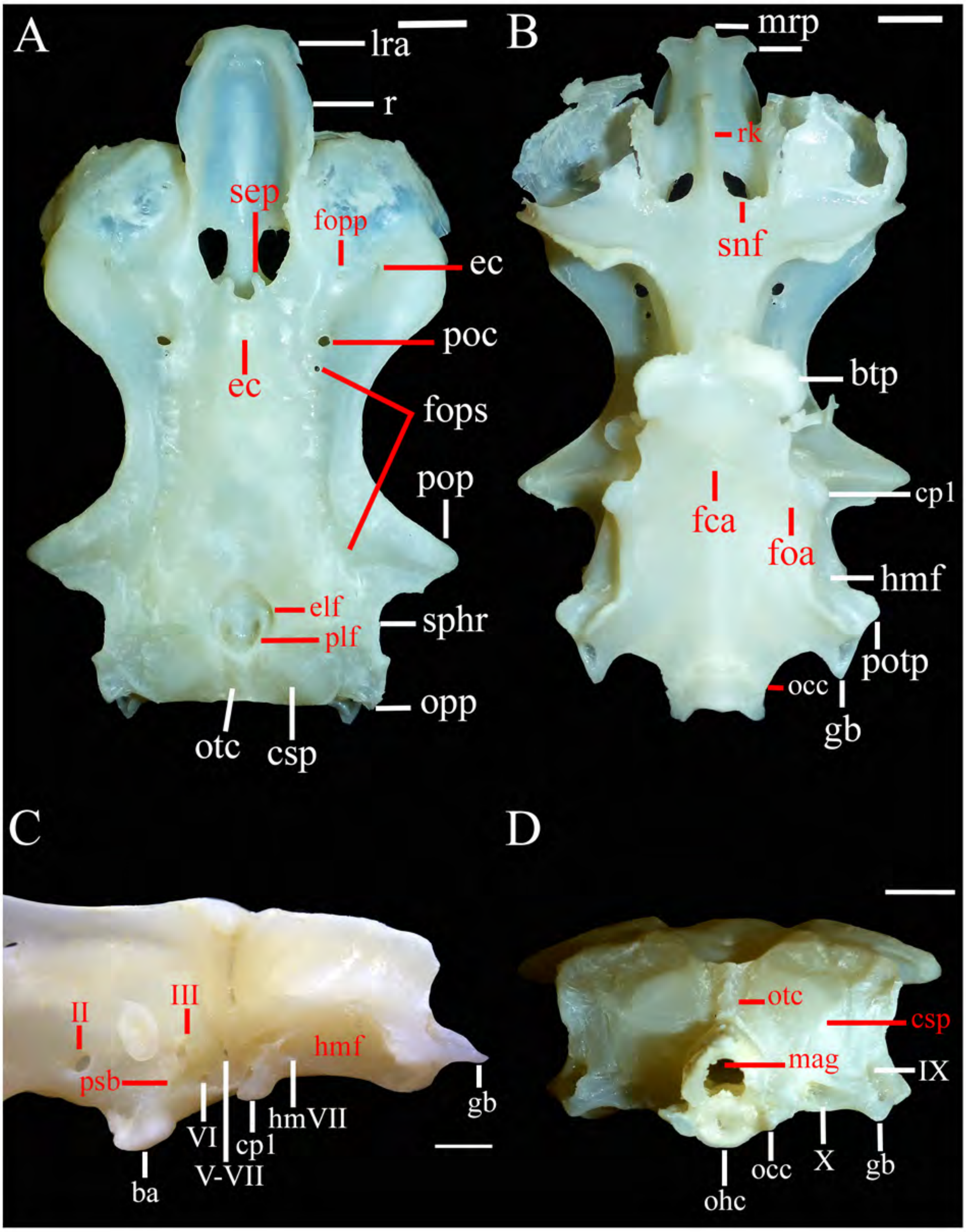

Figure 7. Neurocranium of *Squalus albifrons*, MZUSP not catalogued, 760 mm TL in dorsal (A), ventral (B), posterior-lateral (C), and occipital (D) views. Scale bars: 10 mm. Abbreviations: ba: basal angle; gb: glossopharyngeal base; btp: basitrabecular process; cp1: first cartilaginous process; csp: posterior semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; fca: foramen for carotid artery; feld: endolymphatic fossa; foa: foramen for orbital artery; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; hmf: hyomandibular facet; mag: foramen magnum; occ: occipital condyle; ohc: occipital hemicentrum; otc: otic crest; plf: perilymphatic foramen; poc: preorbital canal; potp: prootic process; r: rostrum; lra: lateral rostral appendage; mrp: median rostral prominence; sep: supraetmoidal process; snf: subnasal fenestra; sphr: sphenopterotic ridge; II: foramen opticum; III: foramen oculomotor; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve; X: foramen vagus.

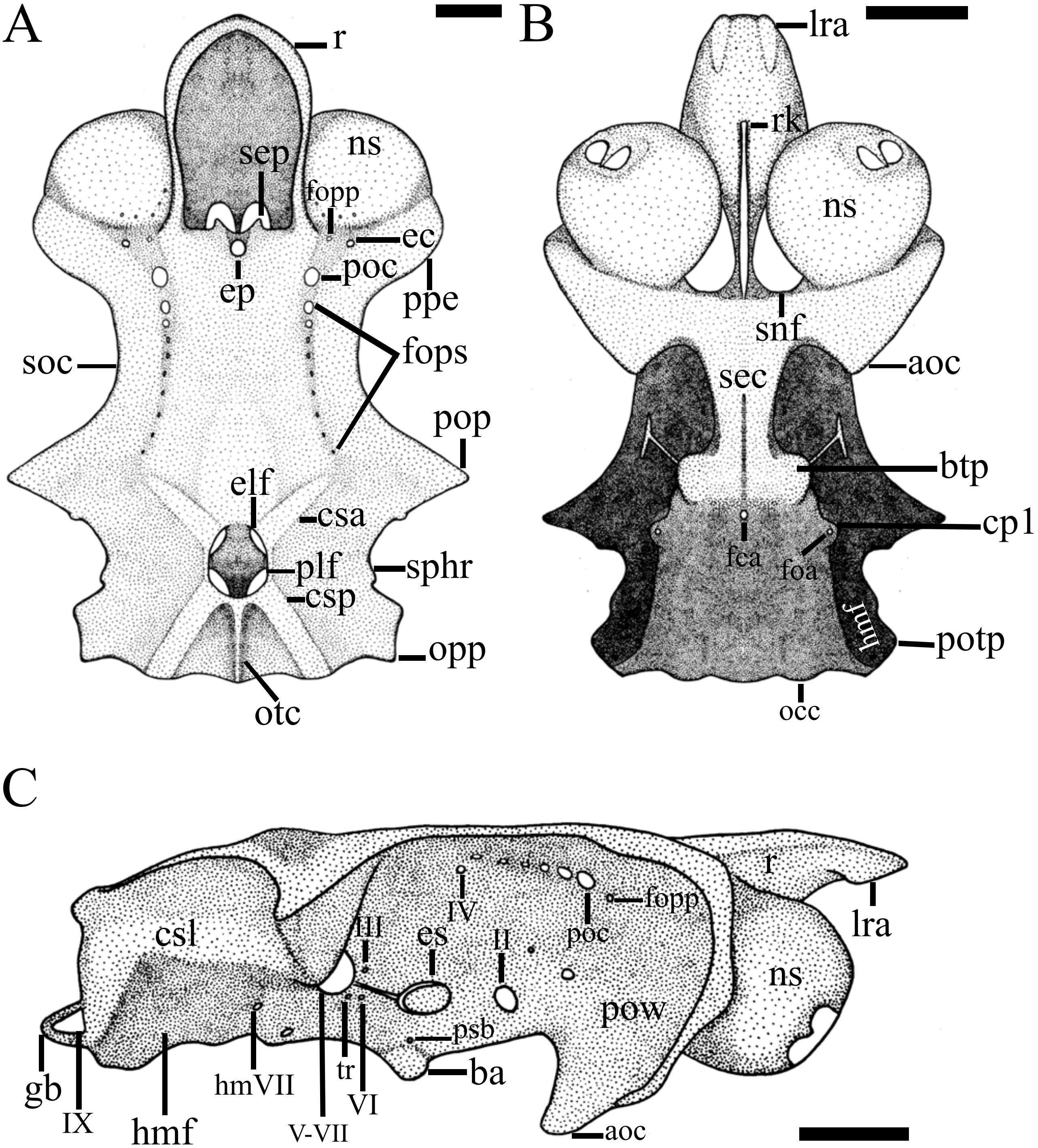

Figure. 8. Neurocranium of *Squalus* sp. 1, BMNH 1912.12.10.45-46, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; btp: basitrabecular process; cp1: first cartilaginous process; csa: anterior semicircular canal; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; foa: foramen for orbital artery; fopp: profundus canal; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; gb: glossopharyngeal base; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; occ: occipital condyle; opp: opistotic process; otc: otic crest; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; potp: prootic process; pow: preorbital wall; ppe: preorbital process; psb: foramen for efferent of pseudobranchial artery; r: rostrum; lra: lateral rostral appendage; rk: rostral keel; sec: subethmoid chamber; sep: supraethmoidal process; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; tr: transbasal canal; II: foramen opticum; III: foramen oculomotor; IV: foramen trochlear; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve.

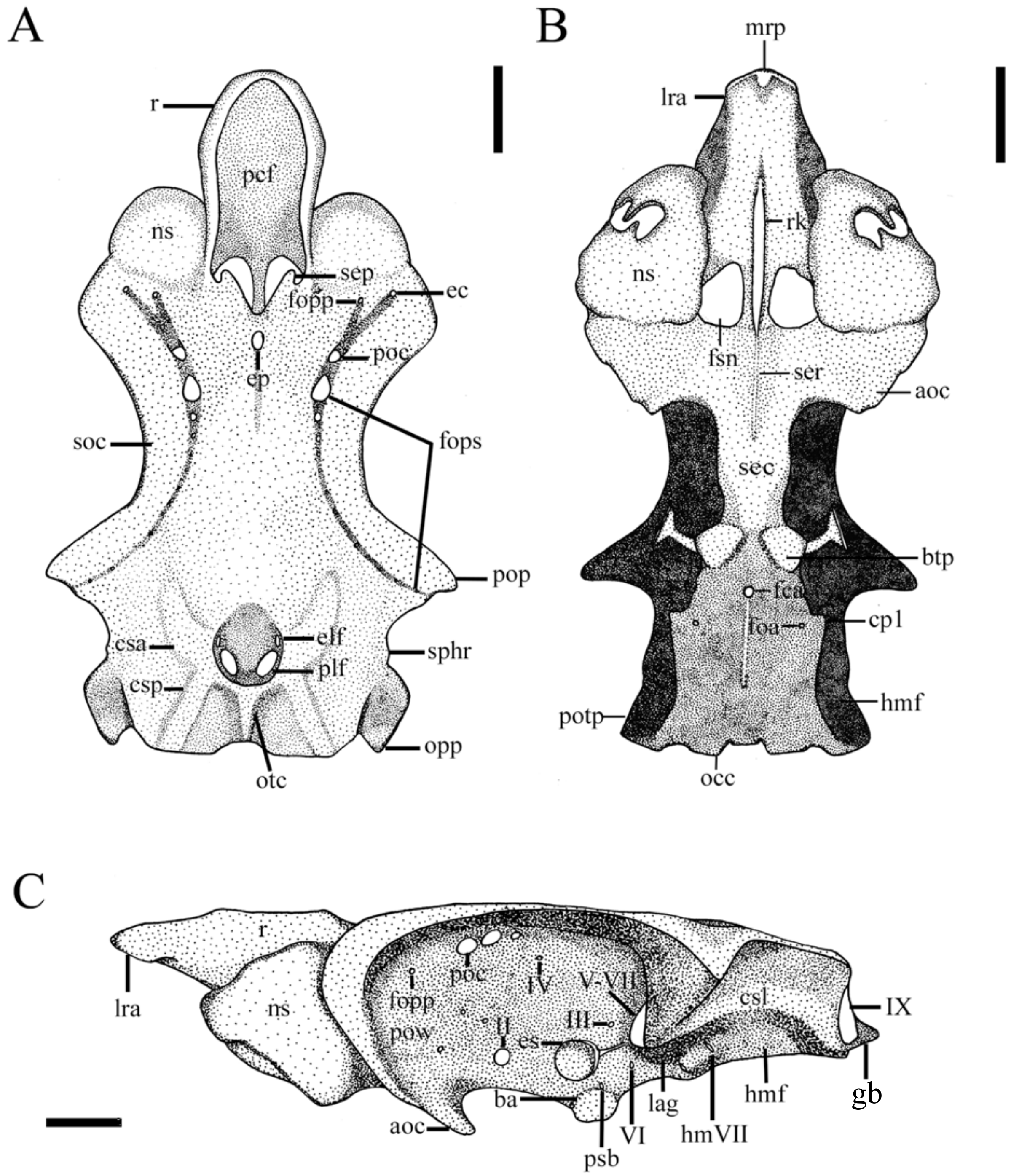

Fig. 9. Neurocranium of *Squalus* sp. 7, MNRJ 30184, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; btp: basitrabecular process; cp1: first cartilaginous process; csa: anterior semicircular canal; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; eec: ectethmoid chamber; elf: endolymphatic foramen; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; feld: endolymphatic fossa; foa: foramen for orbital artery; fopp: profundus canal; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; gb: glossopharyngeal base; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; lag: lateral auditory groove; occ: occipital condyle; opp: opistotic process; otc: otic crest; pcf: precerebral fossa; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; potp: prootic process; pow: preorbital wall; ppe: preorbital process; psb: foramen for efferent of pseudobranchial artery; r: rostrum; lra: lateral rostral appendage; mra: median rostral appendage; mrp: median rostral prominence; rk: rostral keel; sec: subethmoid chamber; sep: supraetmoidal process; ser: subethmoidean ridge; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; II: foramen opticum; III: foramen oculomotor; IV: foramen trochlear; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve.

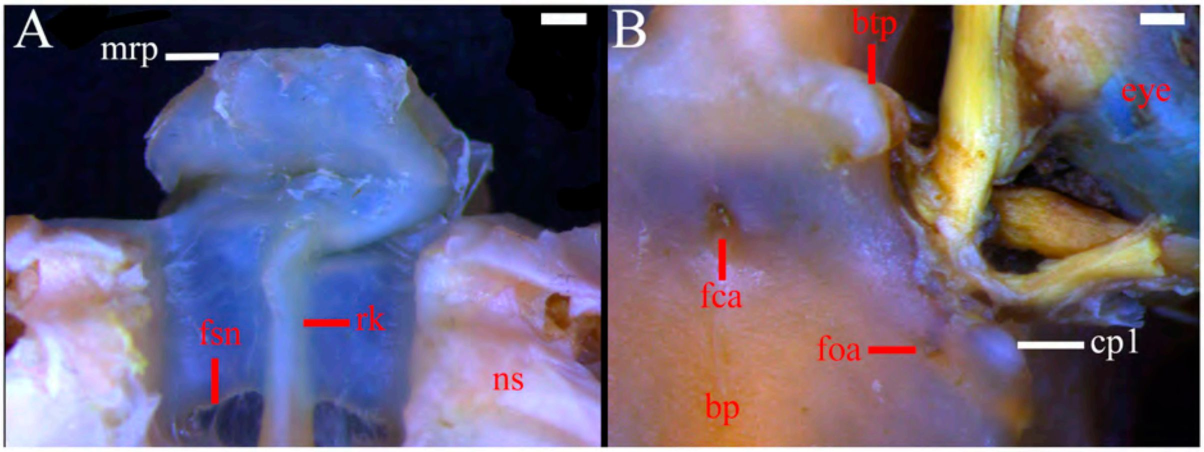

Figure 10. Detail of neurocranium of *Squalus brevirostris* (HUMZ 189762): A: rostrum ventrally; B: region of basal plate. Scale bars: 1 mm. Abbreviations: bp: basal plate; btp: basitrabecular process; cp1: first cartilaginous process; fca: foramen for carotid artery; foa: foramen for orbital artery; fsn: subnasal fossa; mrp: median rostral prominence; ns: nasal capsule; rk: rostral keel.

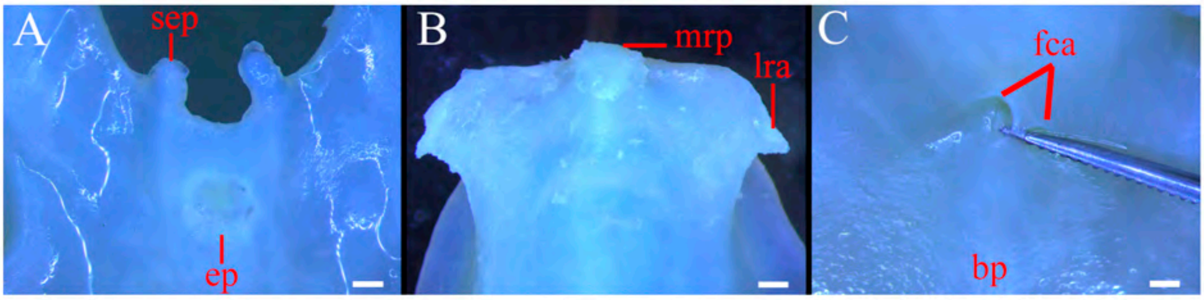

Figure 11. Detail of neurocranium of *Squalus albifrons* (MZUSP uncatalogued): A: ethmoidal region; B: rostrum ventrally; C: region of basal plate. Scale bars: 1 mm. Abbreviations: bp: basal plate; ep: epiphysial pit; fca: foramen for carotid artery; lra: lateral rostral appendage; mrp: median rostral prominence; sep: supraethmoidal process.

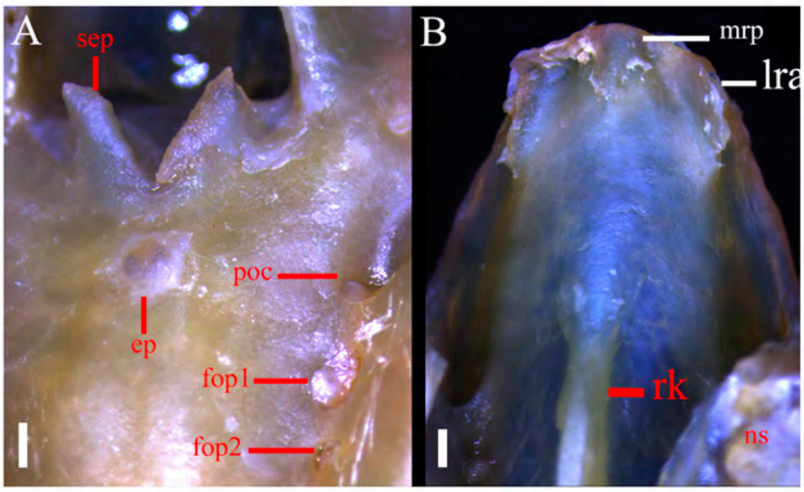

Figure 12. Detail of neurocranium of *Squalus* sp. 7, MNRJ 30184: A: ethmoidal region; B: rostrum ventrally. Scale bars: 1 mm. Abbreviations: ep: epiphysial pit; fop1: first foramen of series V-VII; fop2: second foramen of series V-VII; lra: lateral rostral appendage; mrp: median rostral prominence; ns: nasal capsule; poc: preorbital canal; rk: rostral keel; sep: supraethmoidal processes;

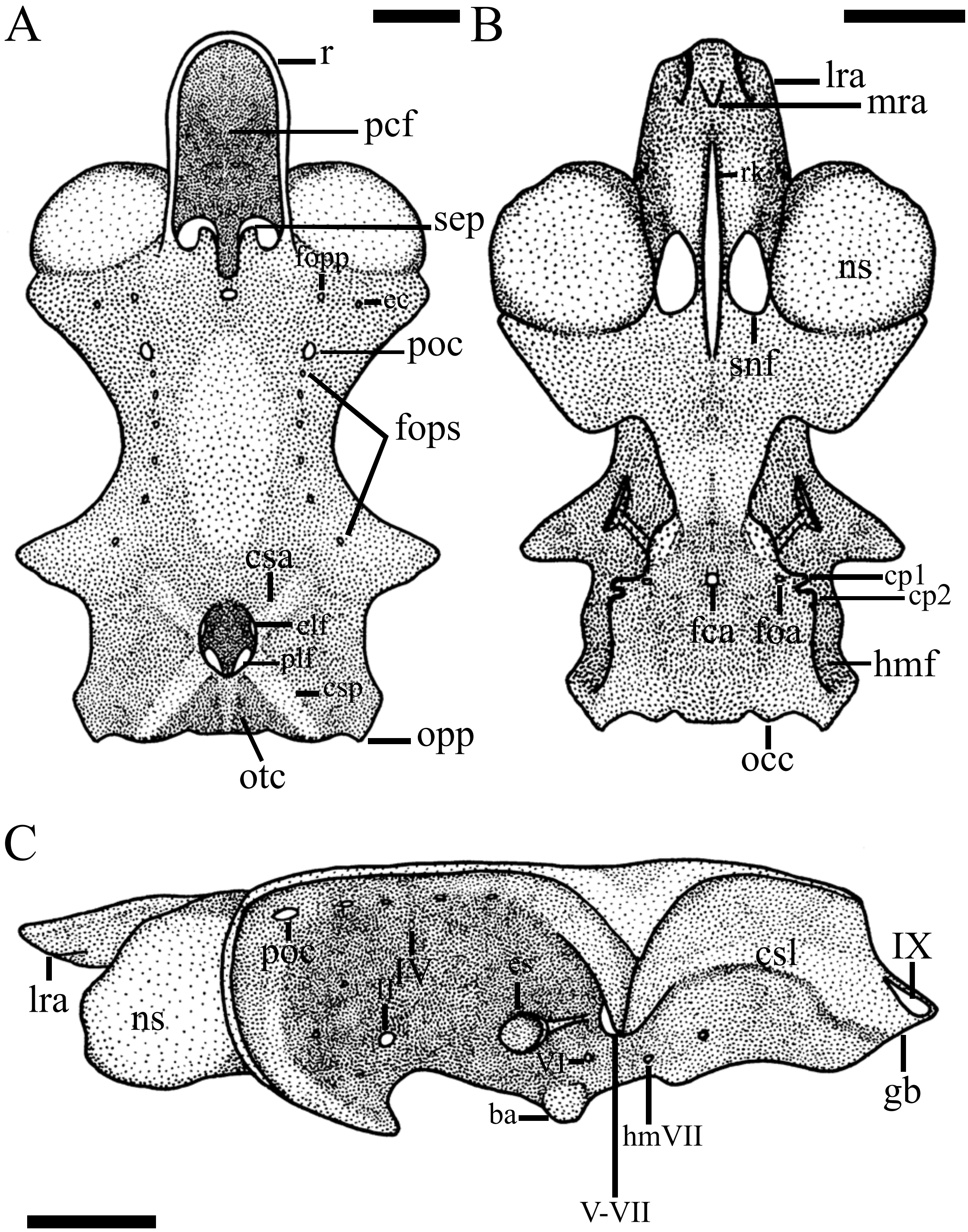

Figure. 13. Neurocranium of *Squalus blainvillei*, BMNH 1963.5.14.13-18, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: ba: basal angle; cp1: first cartilaginous process; cp2: second cartilaginous process; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; feld: endolymphatic fossa; foa: foramen for orbital artery; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; occ: occipital condyle; opp: opistotic process; plf: perilymphatic foramen; poc: preorbital canal; lra: lateral rostral appendage; mra: median rostral appendage; r: rostrum; rk: rostral keel; sep: supraetmoidal process; snf: subnasal fenestra; II: foramen opticum; IV: foramen throclear; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve.

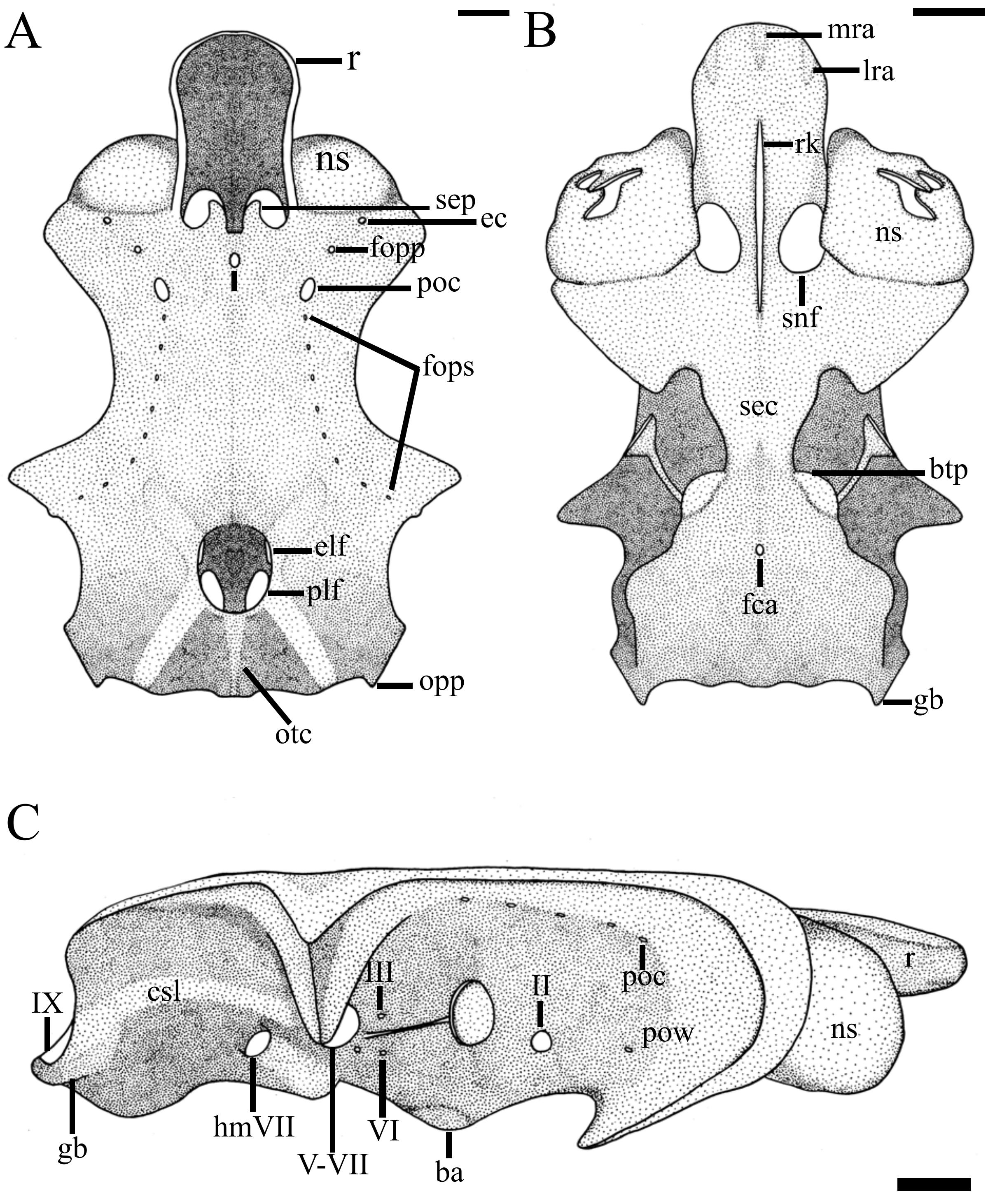

Figure. 14. Neurocranium of *Squalus mitsukurii*, NSMT 44381, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: ba: basal angle; csl: lateral semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; fca: foramen for carotid artery; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; opp: opistotic process; plf: perilymphatic foramen; poc: preorbital canal; lra: lateral rostral appendage; mra: median rostral appendage; r: rostrum; rk: rostral keel; sec: subethmoidean chamber; sep: supraetmoidal process; snf: subnasal fenestra; II: foramen opticum; III: foramen oculomotor; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve.

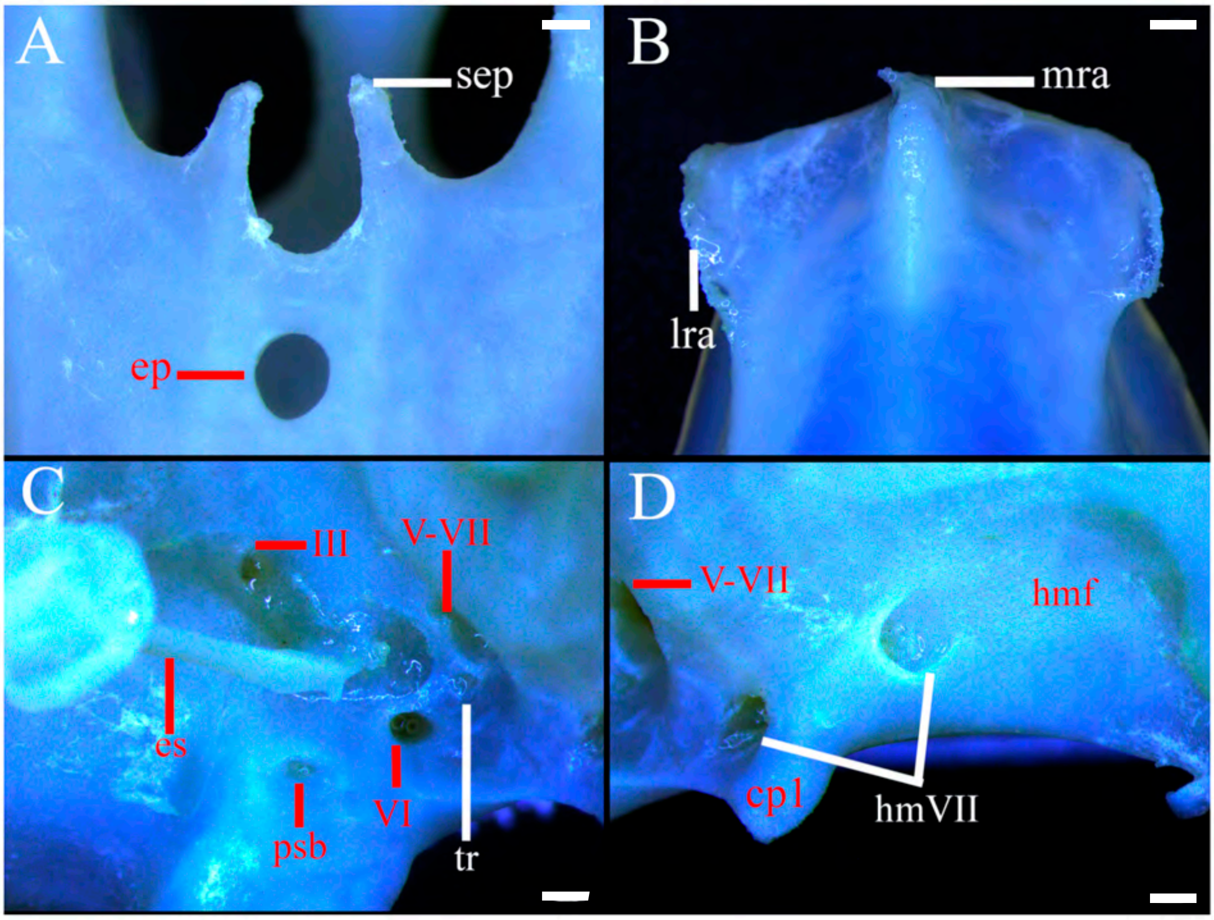

Figure. 15. Detail of neurocranium of *Squalus montalbani,* MZUSP uncatalogued, 560 mm TL. A: ethmoidal region; B: rostrum ventrally; C: interorbital wall; D: hyomandibular facet. Scale bars: 1 mm. Abbreviations: cp1: first cartilaginous process; ep: epiphysial pit; es: eyes stalk; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; lra: lateral rostral appendage; mra: median rostral appendage; psb: efferent of pseudobranchial artery foramen; sep: supraethmoidal processes; tr: transbasal canal for pituitary vein; III: foramen oculomotor; V-VII: foramen prooticum; VI: foramen abducens.

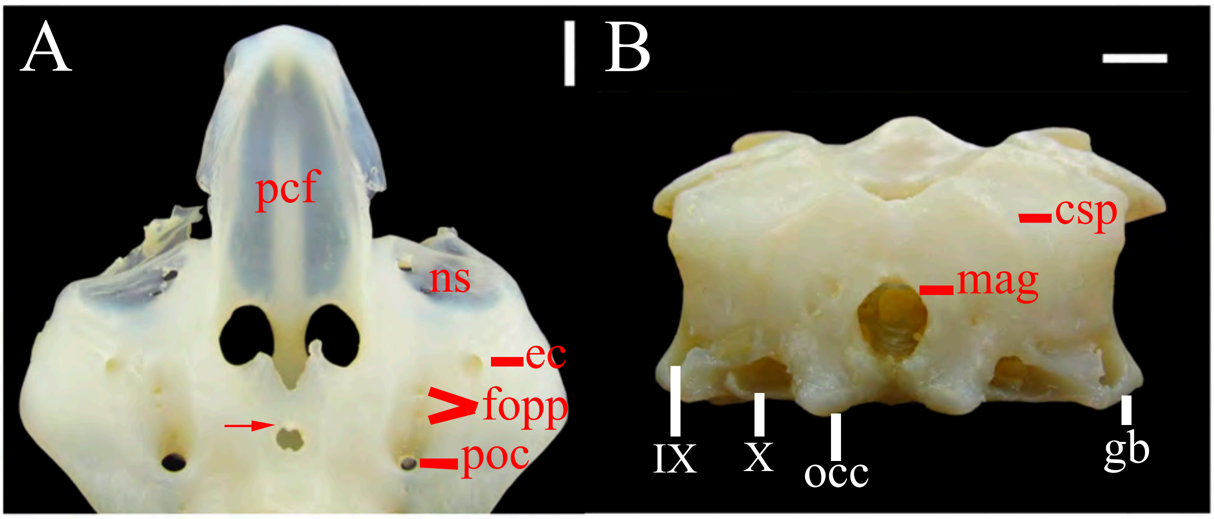

Figure. 16. Neurocranium of *Squalus chloroculus*, CSIRO H2867-08, in anterior-dorsal (A), and occipital (B) views. Scale bars: 10 mm. Abbreviations: csp: posterior semicircular canal; ec: ethmoidal canal; fopp: profundus canal; gb: glossopharyngeal base; mag: foramen magnum; ns: nasal capsule; occ: occipital condyle; poc: preorbital canal; IX: foramen for glossopharyngeal nerve; X: foramen for vagus nerve. Red arrow: epiphysial protusion.

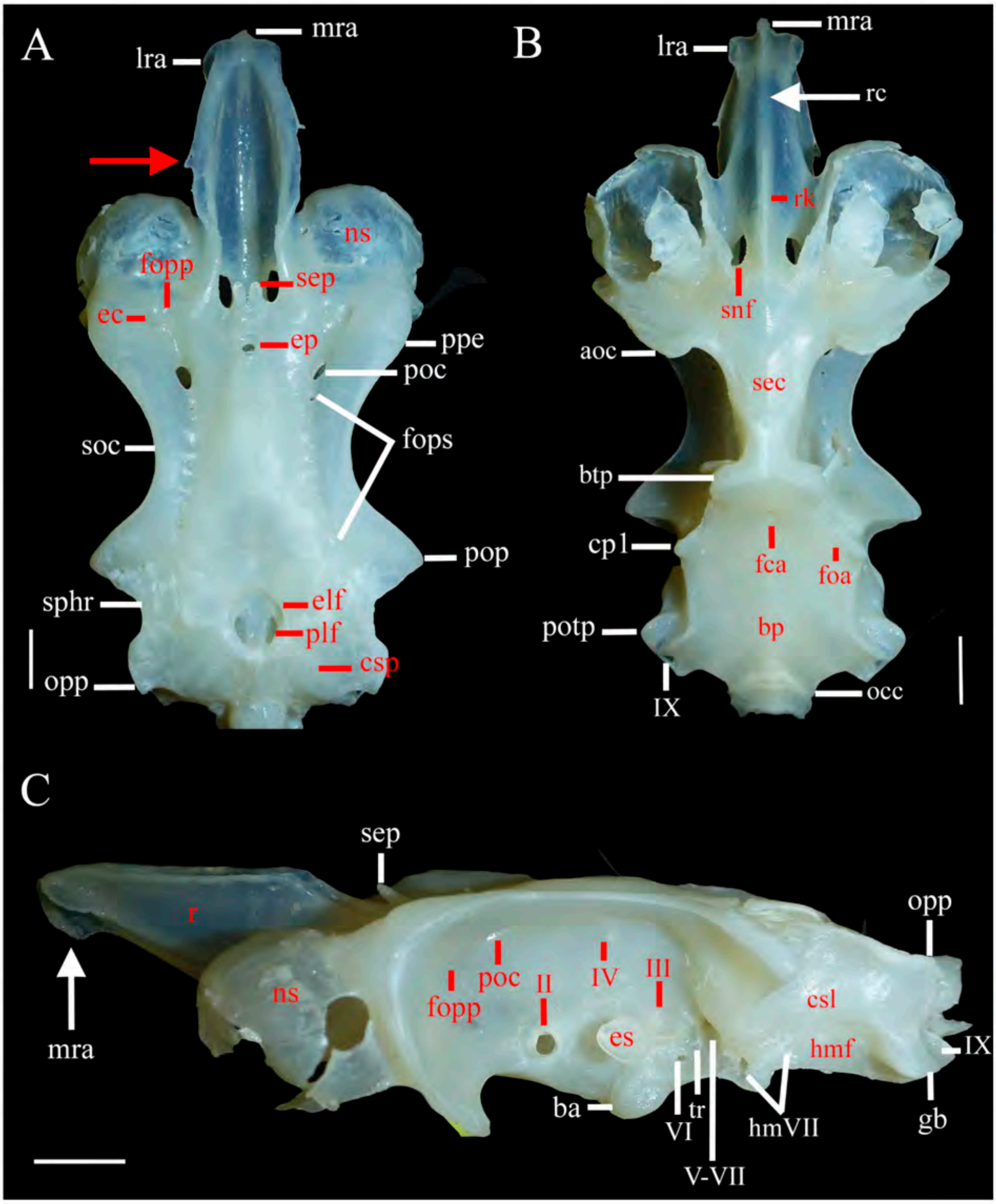

Figure. 17. Neurocranium of *Squalus grahami*, MZUSP uncatalogued, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; bp: basal plate; btp: basitrabecular process; cp1: first cartilaginous process; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; feld: endolymphatic fossa; foa: foramen for orbital artery; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; occ: occipital condyle; opp: opistotic process; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; potp: prootic process; ppe: preorbital process; lra: lateral rostral appendage; mra: median rostral appendage; r: rostrum; rc: rostral carina; rk: rostral keel; sec: subethmoidean chamber; sep: supraetmoidal process; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; tr: transbasal canal; II: foramen opticum; III: foramen oculomotor; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve. Red arrow: rostral projection.

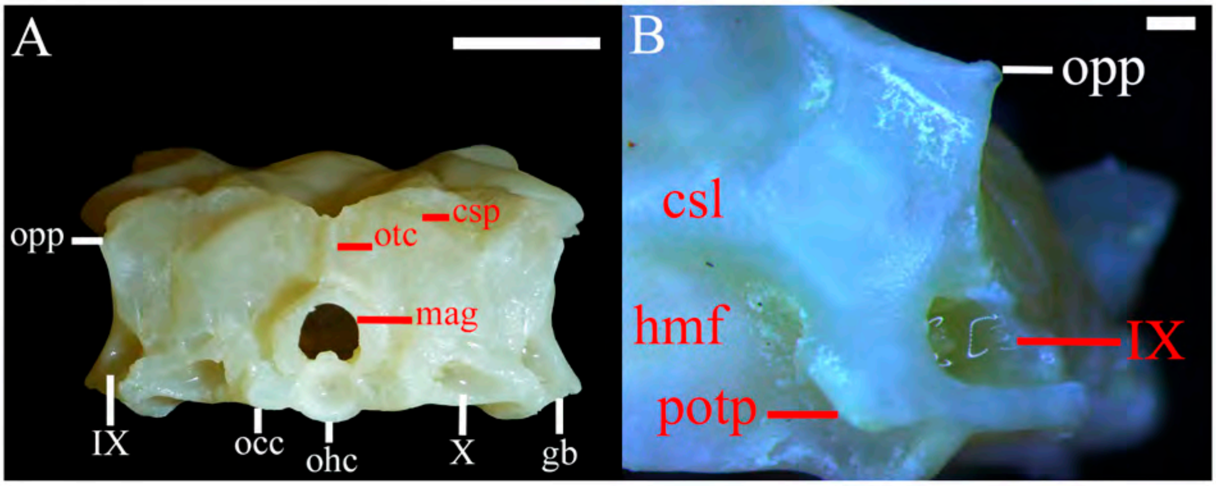

Figure. 18. Detail of neurocranium of *Squalus grahami*, MZUSP uncatalogued, adult male, 565 mm TL: A: occipital view; B: lareal-posterior view. Scale bars: 1 mm. Abbreviations: csl: lateral semicircular canal; csp: posterior semicircular canal; hmf: hyomandibular facet; gb: glossopharyngeal base; mag: foramen magnum; occ: occipital condyle; ohc: occipital hemicentrum; opp: opistotic process; otc: otic crest; potp: prootic process; IX: foramen for glossopharyngeal nerve; X: foramen for vagus nerve.

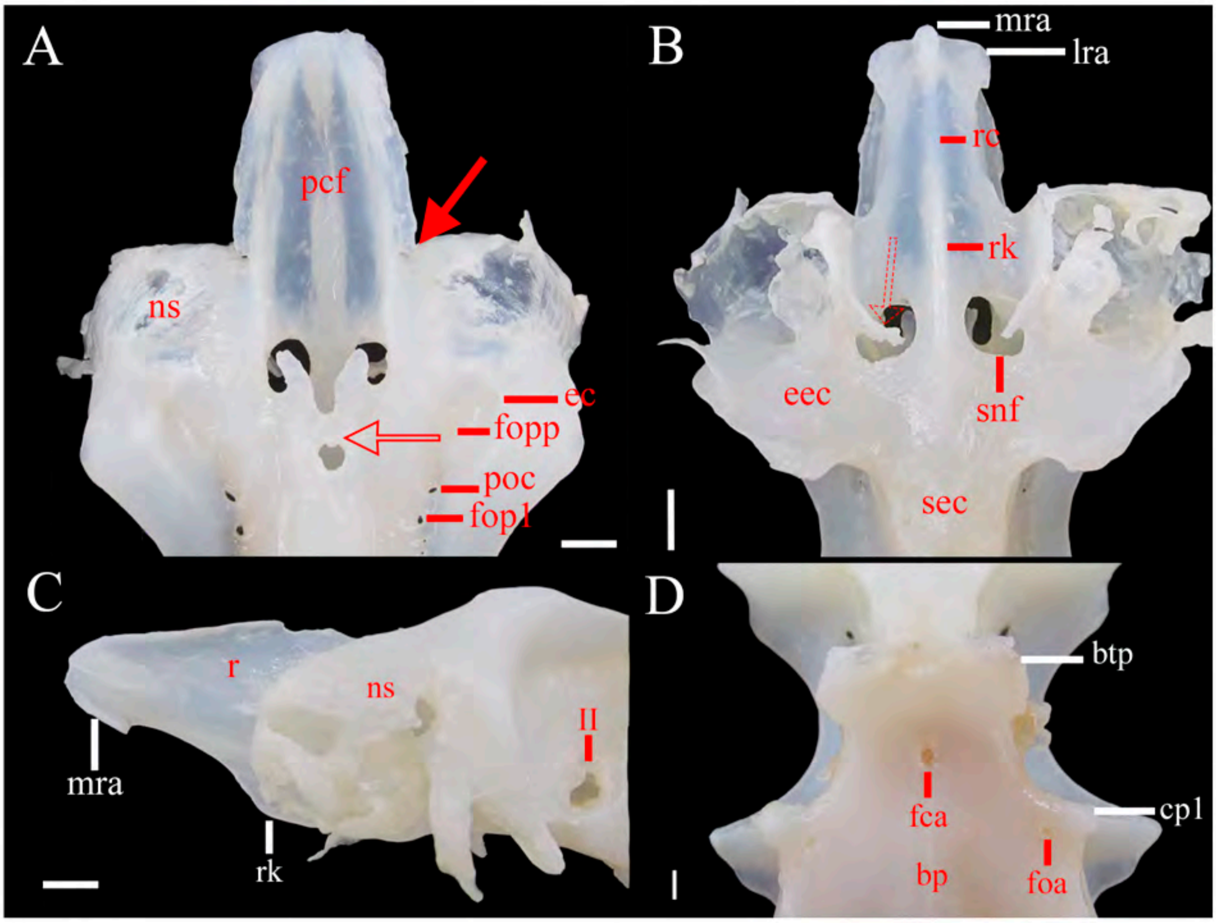

Figure 19. Neurocranium of *Squalus griffini*, TMP 10388, in dorsal (A), anterior-ventral (B), anterior-lateral (C), and posterior-ventral (D) views. Scale bars: 10 mm. Abbreviations:bp: basal plate; btp: basitrabecular process; cp1: first cartilaginous process; ec: ethmoidal canal; ep: epiphysial pit; fca: foramen for carotid artery; foa: foramen for orbital artery; fop: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; ns: nasal capsule; poc: preorbital canal; r: rostrum; lra: lateral rostral appendage; mra: median rostral appendage; rc: rostral carina; rk: rostral keel; sec: subethmoidean chamber; sep: supraetmoidal process; snf: subnasal fenestra; soc: supraorbital crest; II: foramen opticum. Full red arrow: rostral projection. Continuous red arrow: epiphysial protusion. Dotted red arrow: nasal process.

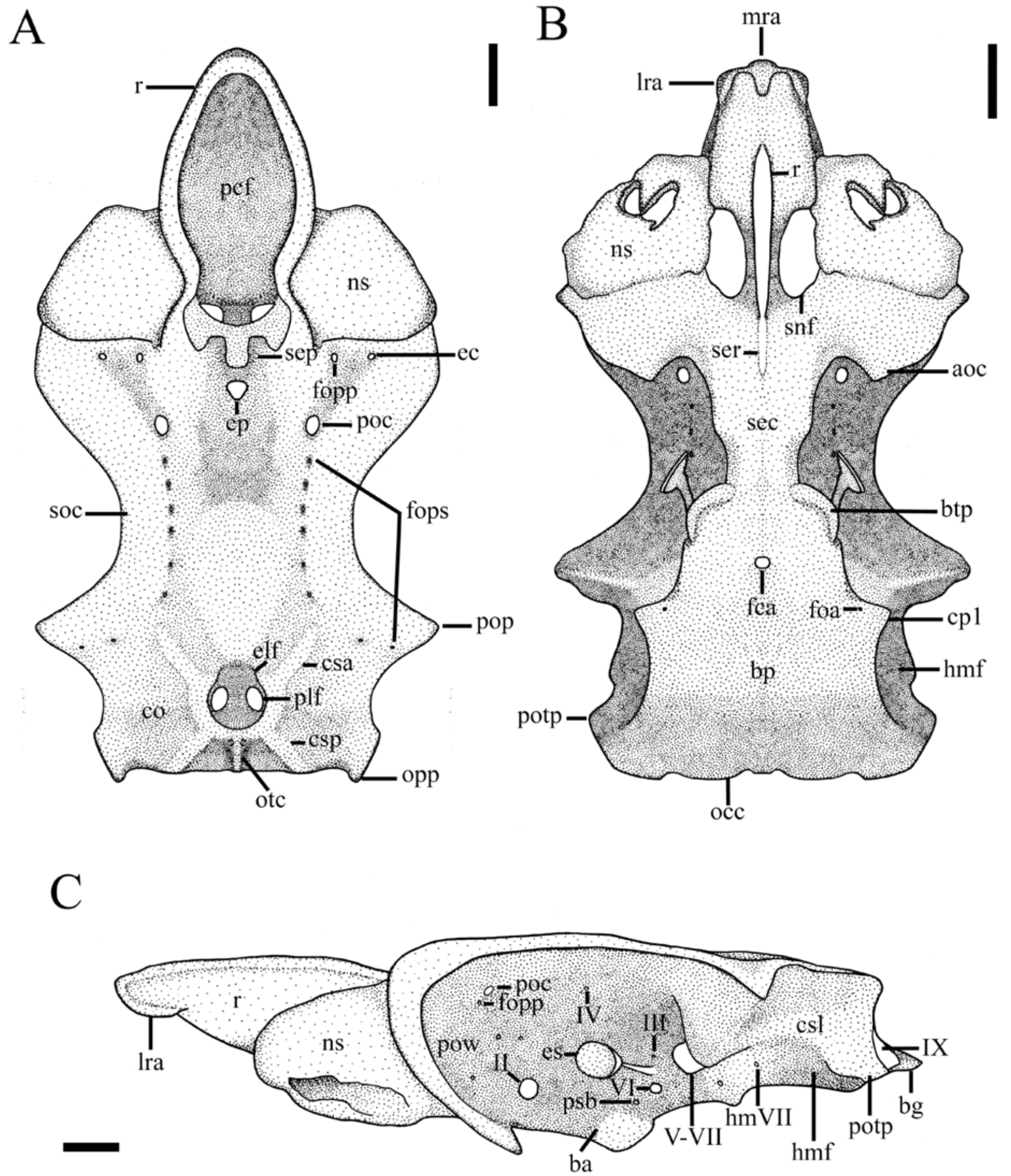

Figure. 20. Neurocranium of *Squalus* sp. 4, UERJ 1661, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; btp: basitrabecular process; cp1: first cartilaginous process; csa: anterior semicircular canal; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; eec: ectethmoid chamber; elf: endolymphatic foramen; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; feld: endolymphatic fossa; foa: foramen for orbital artery; fopp: profundus canal; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; gb: glossopharyngeal base; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; lag: lateral auditory groove; oc: otic capsule; occ: occipital condyle; opp: opistotic process; otc: otic crest; pcf: precerebral fossa; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; potp: prootic process; pow: preorbital wall; ppe: preorbital process; psb: foramen for efferent of pseudobranchial artery; r: rostrum; lra: lateral rostral appendage; mra: median rostral appendage; rk: rostral keel; sec: subethmoid chamber; sep: supraethmoidal process; ser: subethmoidean ridge; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; II: foramen opticum; III: foramen oculomotor; IV: foramen trochlear; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve.

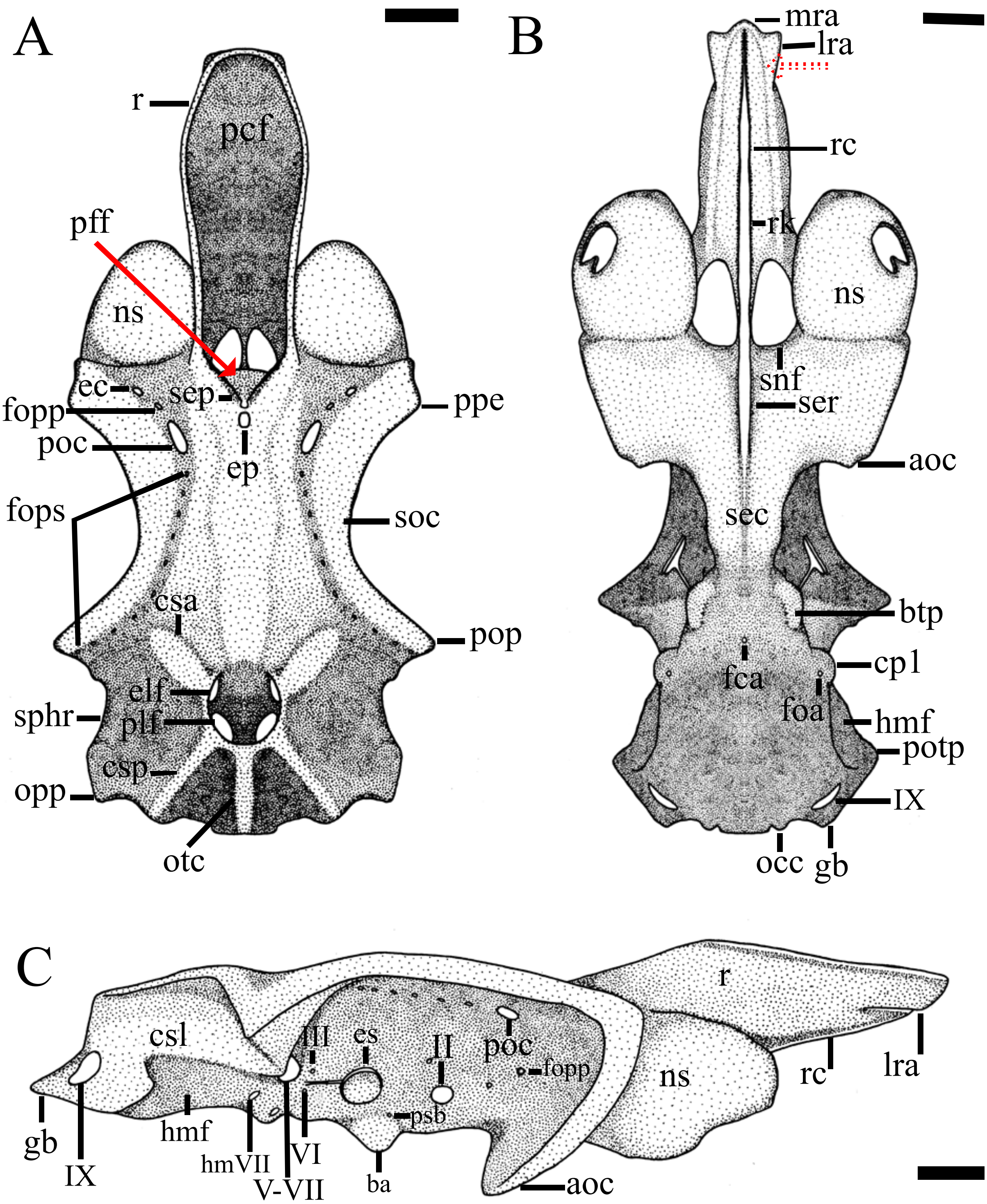

Figure 21. Neurocranium of *Squalus japonicus*, HUMZ 189737 in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; btp: basitrabecular process; cp1: first cartilaginous process; csa: anterior semicircular canal; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; es: eye stalk; fca: foramen for carotid artery; foa: foramen for orbital artery; fopp: profundus canal; fops: s eries of foramina of the branch superficial ophthalmic of trigeminal nerve; gb: glossopharyngeal base; hmf: hyomandibular facet; hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; occ: occipital condyle; opp: opistotic process; otc: otic crest; pcf: precerebral fossa; pff: prefrontal fontanelle; plf: perilymphatic foramen; poc: preorbital canal; pop: postorbital process; potp: prootic process; ppe: preorbital process; psb: foramen for efferent of pseudobranchial artery; r: rostrum; lra: lateral rostral appendage; mra: median rostral appendage; rc: rostral carina; rk: rostral keel; sec: subethmoid chamber; sep: supraethmoidal process; ser: subethmoidean ridge; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; II: foramen opticum; III: foramen oculomotor; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen for glossopharyngeal nerve. Full red arrow: constricted prefrontal fontanelle. Dotted red arrow: small ridges.

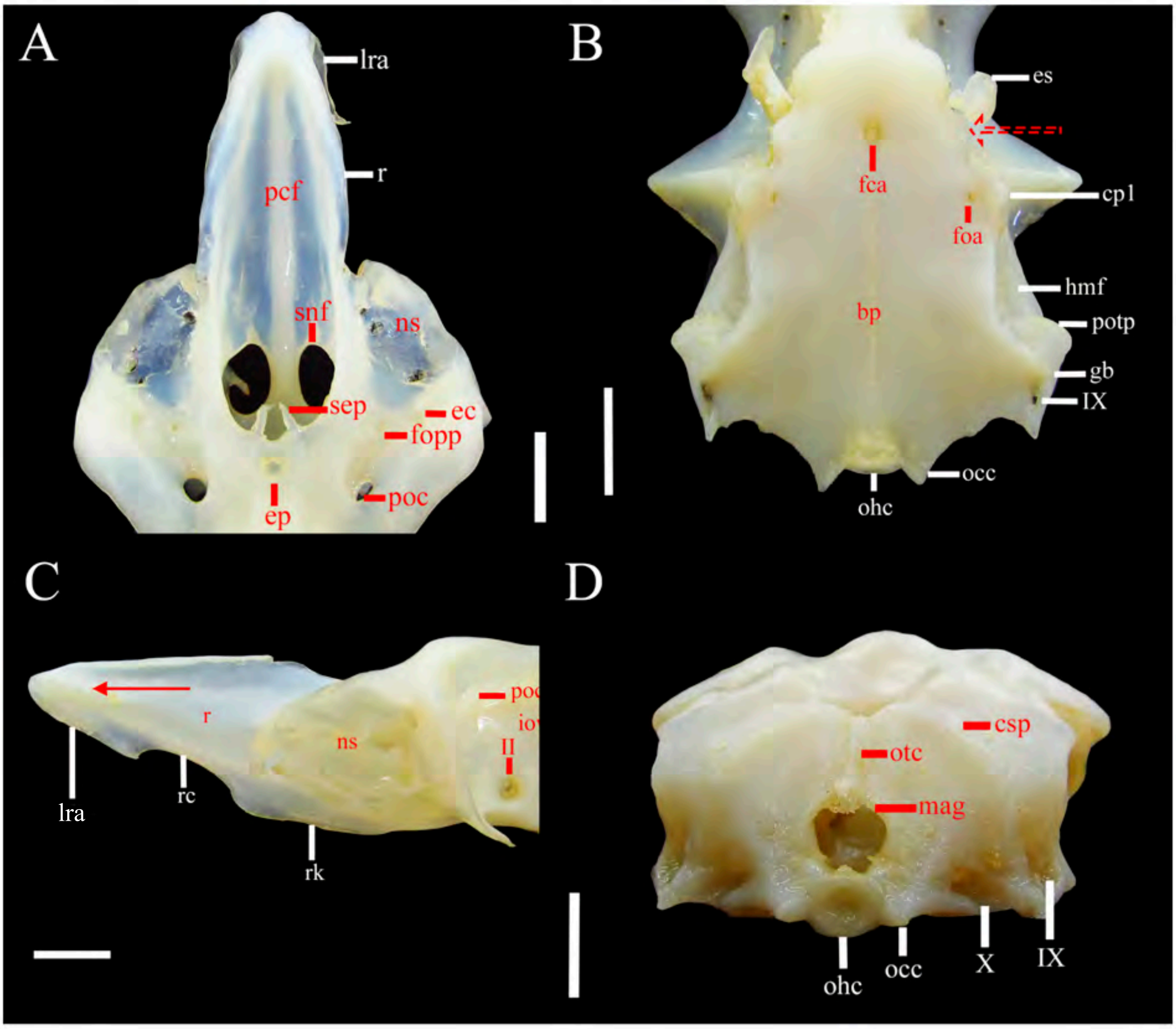

Figure. 22. Neurocranium of *Squalus nasutus*, CSIRO H2591-18, in anterior-dorsal (A), region of basal plate (B), anterior-lateral (C), and occipital (D) views. Scale bars: 10 mm. Abbreviations: bp: basal plate; cp1: first cartilaginous process; csp: posterior semicircular canal; ec: ethmoidal canal; ep: epiphysial pit; es: eye stalk; foa: foramen for orbital artery; fca: foramen for carotid artery; fopp: profundus canal; gb: glossopharyngeal base; hmf: hyomandibular facet; iow: interobital wall; lra: rostral appendage; mag: foramen magnum; ns: nasal capsule; occ: occipital condyle; ohc: occipital hemicentrum; otc: otic crest; pcf: precerebral fossa; poc: preorbital canal; potp: prootic process; r: rostrum; rc: rostral carina; rk: rostral keel; sep: supraethmoidal process; IX: foramen for glossopharyngeal nerve; X: foramen for vagus nerve. Full red arrow: lateral crests of rostral appendage. Dotted red arrow: sinuosity of basal plate.

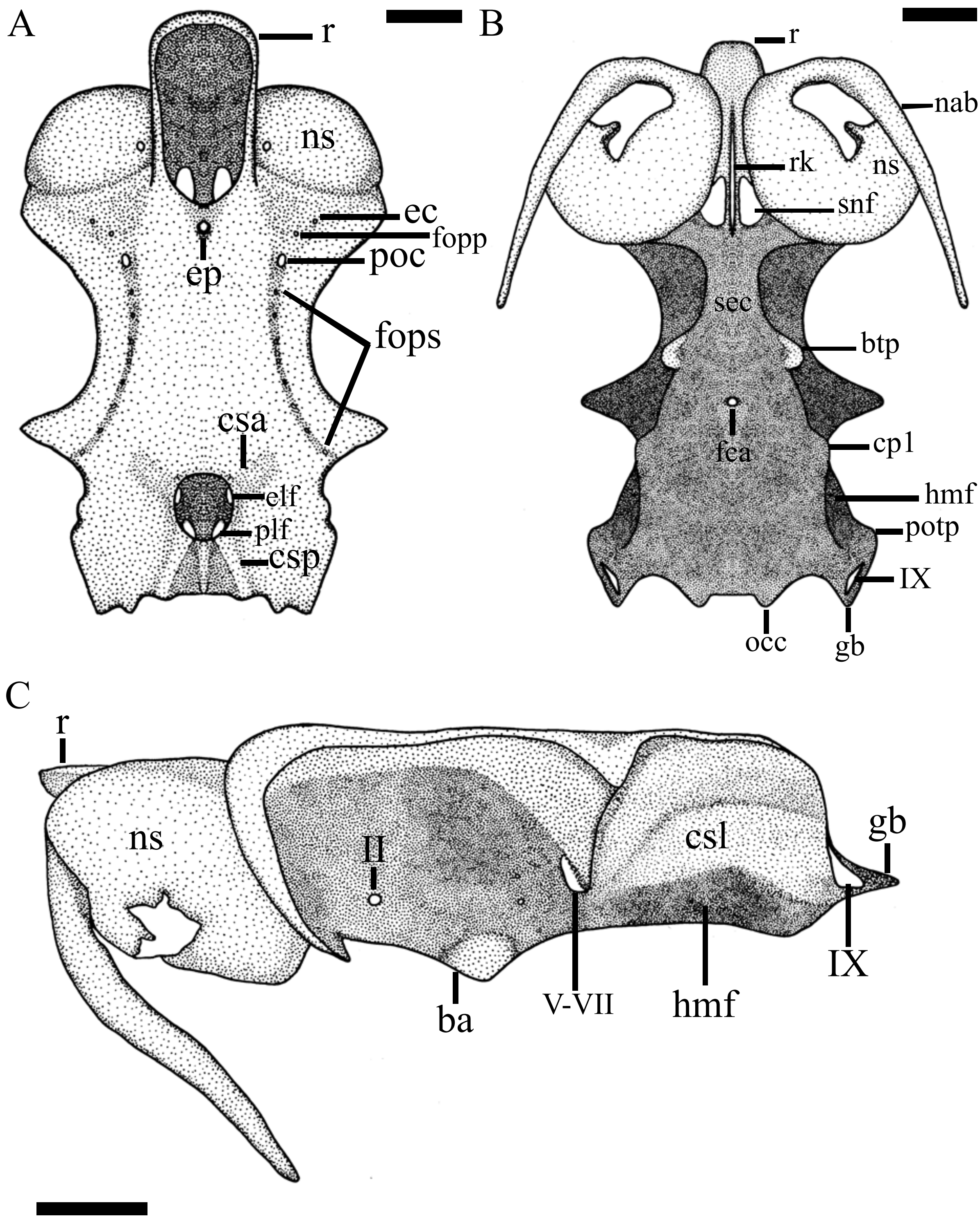

Figure. 23. Neurocranium of *Cirrhigaleus barbifer*, HUMZ 95177, in dorsal (A), ventral (B) and lateral (C) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; btp: basitrabecular process; cp1: first cartilaginous process; csa: anterior semicircular canal; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; elf: endolymphatic foramen; ep: epiphysial pit; fca: foramen for carotid artery; fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; hmf: hyomandibular facet; ns: nasal capsule; occ: occipital condyle; plf: perilymphatic foramen; poc: preorbital canal; potp: prootic process; r: rostrum; rk: rostral keel; sec: subethmoidean chamber; snf: subnasal fenestra; II: foramen opticum; V-VII: foramen prooticum; IX: foramen for glossopharyngeal nerve.

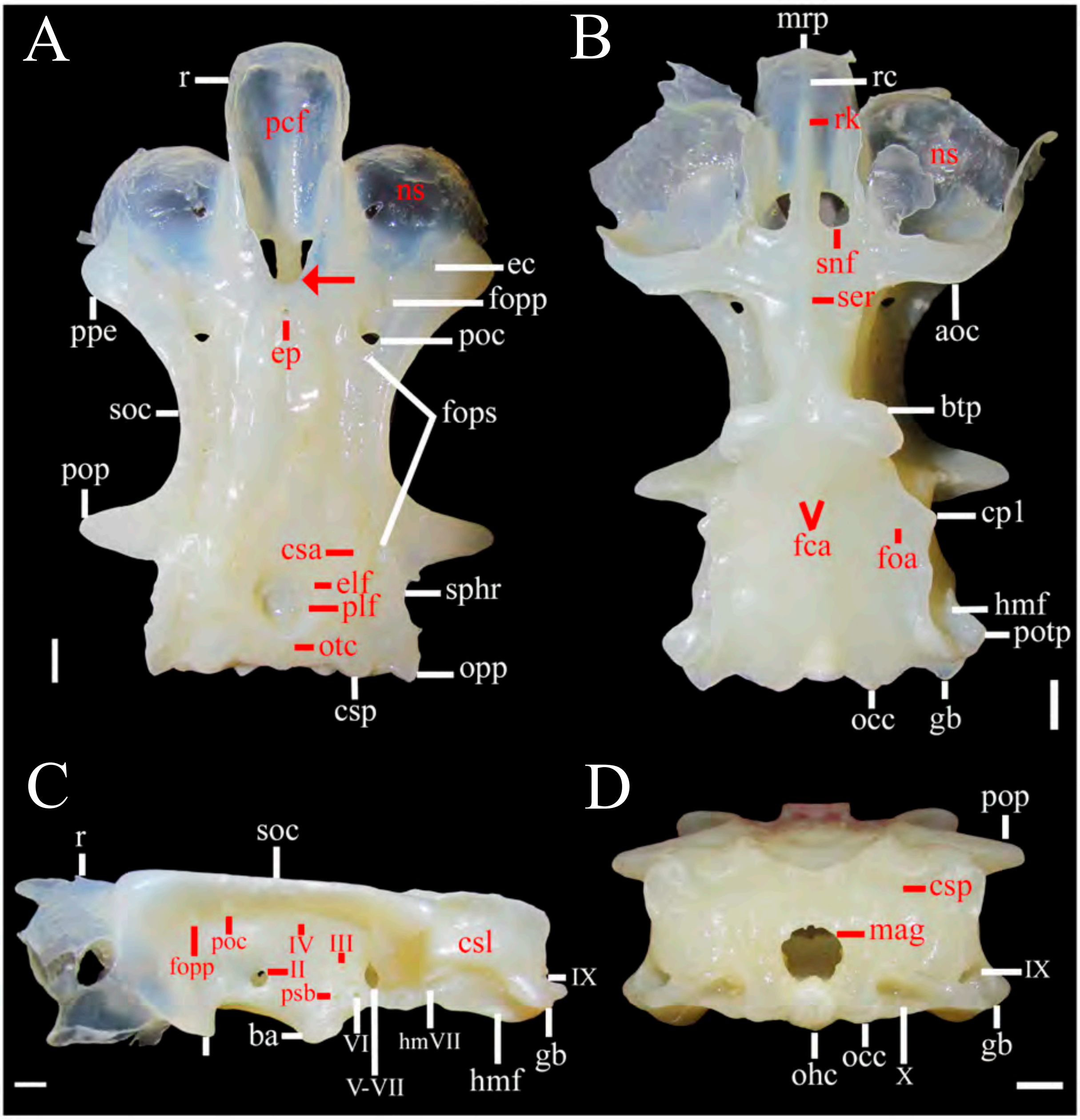

Figure. 24. Neurocranium of *Cirrhigaleus asper*, SAM 38269, in dorsal (A), ventral (B) and lateral (C), occipital (D) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; ba: basal angle; btp: basitrabecular process; cp1: first cartilaginous process; csa: anterior semicircular canal; csl: lateral semicircular canal; csp: posterior semicircular canal; ec: ethmoidal canal; ep: epiphysial pit; elf: endolymphatic foramen; fca: foramen for carotid artery; foa: foramen for orbital artery; fopp: profundus canal; fops: fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; gb: glossopharyngeal base; hmf: hyomandibular fossa; hmVII: foramen for hyomandibularis facialis; mag: foramen magnum; mrp: median rostral prominence; ns: nasal capsule; occ: occipital condyle; ohc: occipital hemicentrum; opp: opistotic process; otc: otic crest; pcf: precerebral fossa; plf: perilymphatic foramen; pop: postorbital process; potp: prootic process; ppe: preorbital process; r: rostrum; rc: rostral carina; rk: rostral keel; ser: subethmoidean ridge; snf: subnasal fenestra; soc: supraorbital crest; sphr: sphenopterotic ridge; II: foramen opticum; III: foramen oculomotor; IV: foramen trochlear; V-VII: foramen prooticum; VI: foramen abducens; IX: foramen glossopharyngeal; X: foramen vagus.

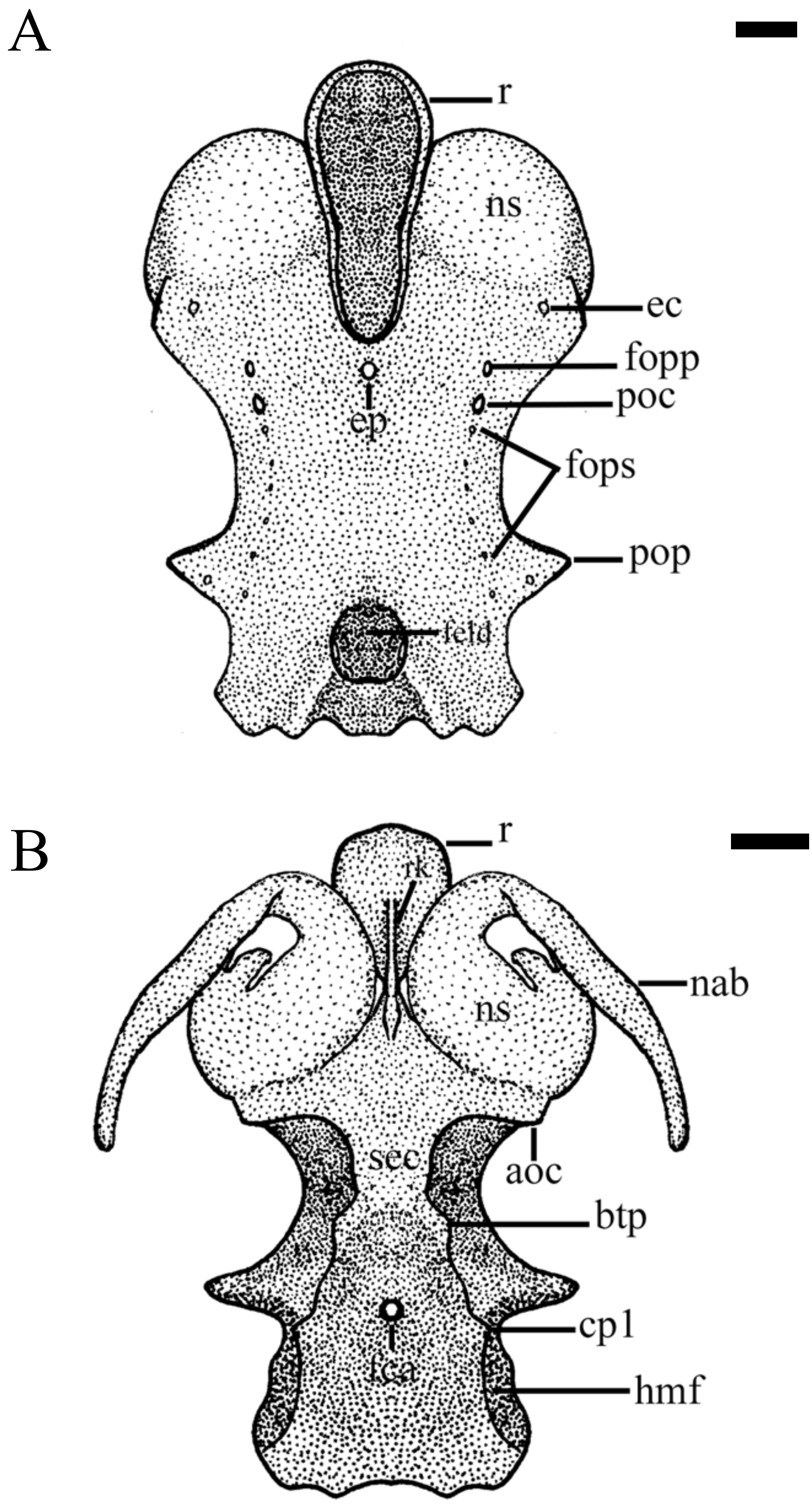

Figure. 25. Neurocranium of *Cirrhigaleus australis*, CSIRO H7042-04, in dorsal (A) and ventral (B) views. Scale bars: 10 mm. Abbreviations: aoc: antorbital cartilage; btp: basitrabecular process; cp1: first cartilaginous process; ec: ethmoidal canal; ep: epiphysial pit; fca: foramen for carotid artery; fopp: profundus canal; fops: fops: series of foramina of the branch superficial ophthalmic of the trigeminal nerve; hmf: hyomandibular fossa; ns: nasal capsule; pop: postorbital process; r: rostrum; rk: rostral keel.

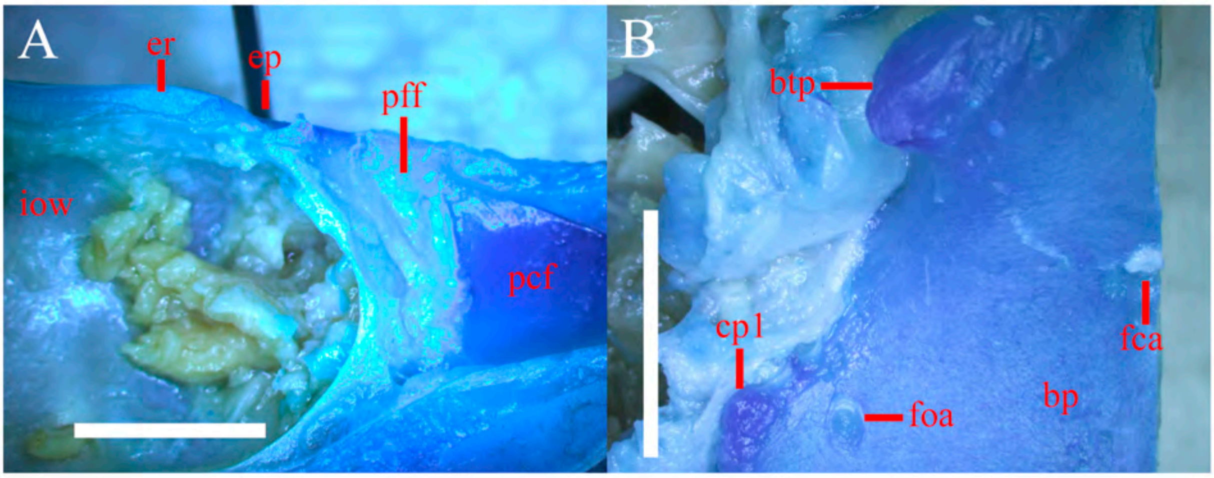

Figure 26. Detail of neurocranium of *Cirrhigaleus barbifer*, HUMZ 95177, in inner sagittal (A) and ventral views (B). Scale bars: 5 mm.Abbreviations: bp: basal plate; btp: basitrabecular process; cp1: first cartilaginous process; ep: epiphysial pit; er: ethmoidal region; fca: foramen for carotid artery; foa: foramen for orbital artery; iow: interorbital wall; pcf: pff: precerebral fossa; pff: prefrontal fontanelle.

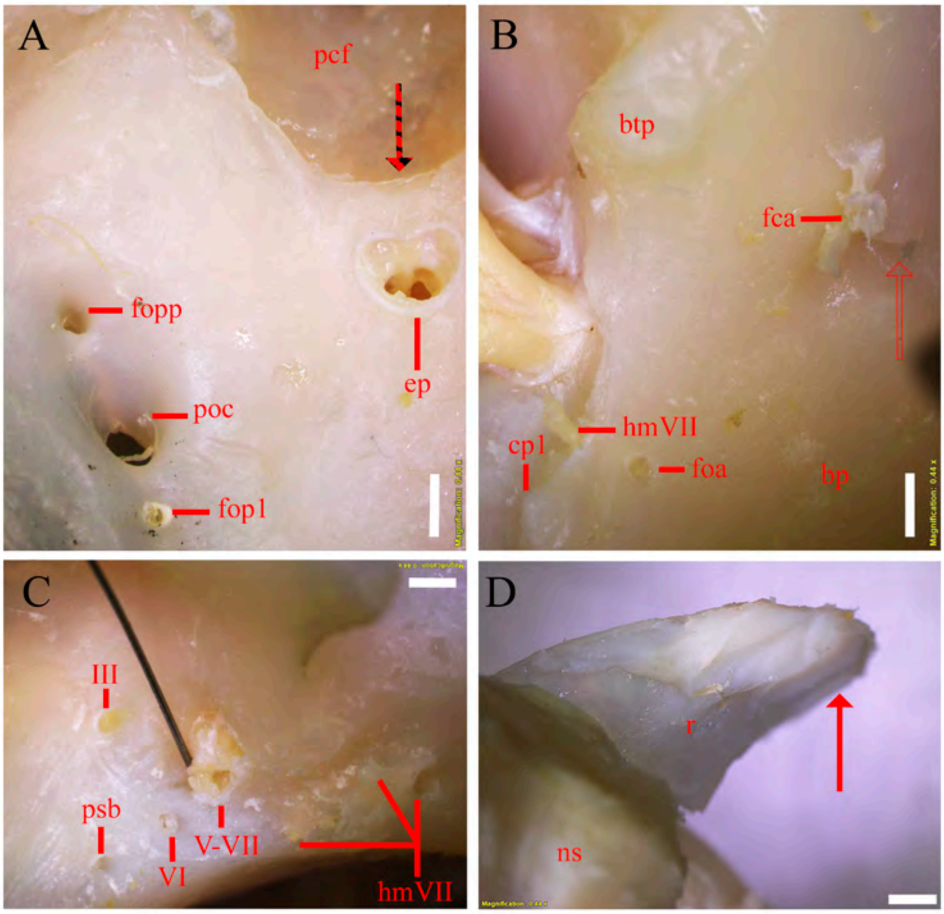

Figure 27. Detail of neurocranium of *Cirrhigaleus australis*, CSIRO H7042-04, in ethmoidal (A), basal plate (B), interorbital (C), and rostral (D) views. Scale bars: 2 mm. Abbreviations: bp: basal plate; btp: basitrabecular process; cp1: first cartilaginous process; ep: epiphysial pit; fca: foramen for carotid artery; foa: foramen for orbital artery; fopp: profundus canal; fop1: first foramen of branch superficial ophthalmic of the trigeminal nerve; hmVII: hmVII: foramen for hyomandibularis facialis; ns: nasal capsule; pcf: precerebral fossa; poc: preorbital canal; psb: psb: foramen for efferent of pseudobranchial arter; r: rostrum; III: foramen oculomotor; VI: foramen abducens; V-VII: foramen prooticum. Red arrow with black dots: absence of supraethmoidal processes. Empty red arrow: furrow. Red arrow: rostrum tip lacking appendages.

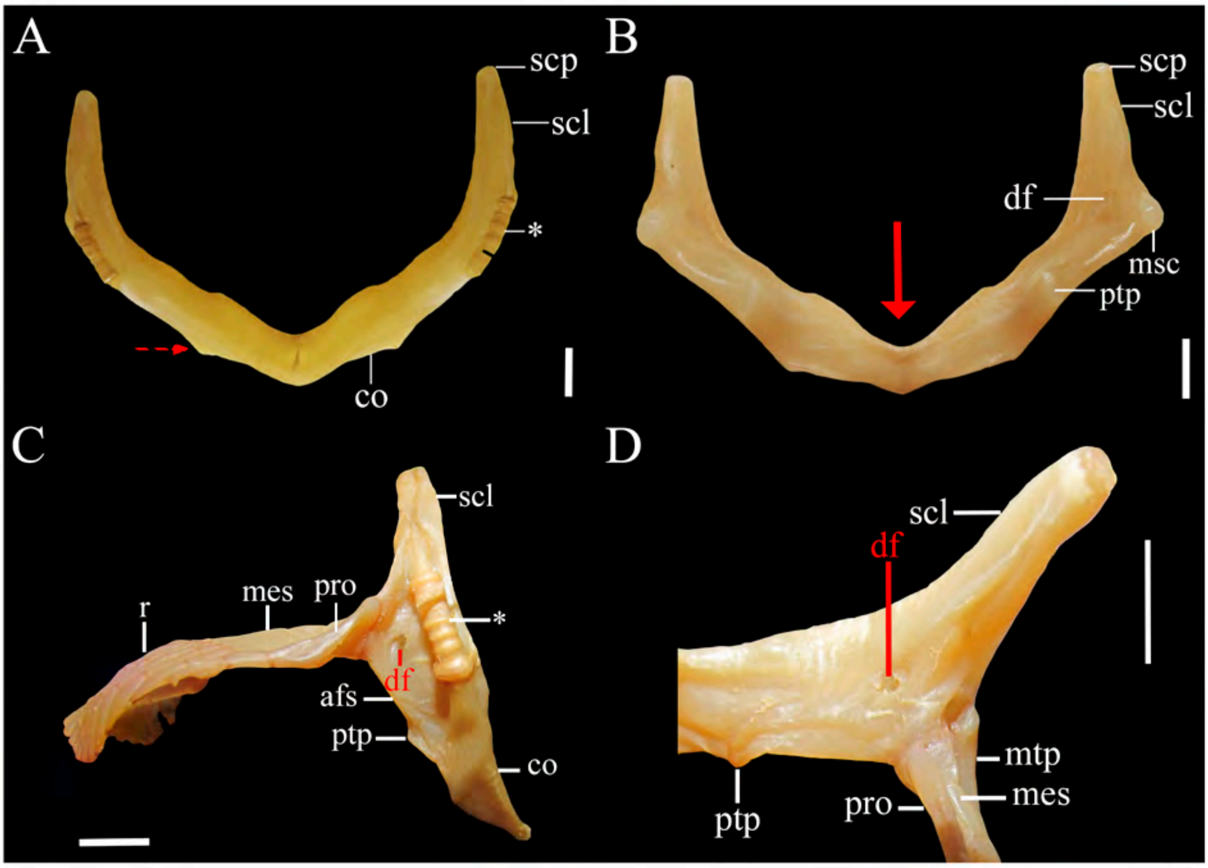

Figure 28. Pectoral girdle of *Squalus acanthias*: A: anterior view; B: posterior view; C: lateral view; D: detail of pectoral articulation. A-B: AMNH 53052; C-D: SAM 38276. Scale bar: 10 mm. Abreviations: afs: anterior fossa of scapulae; co: coracoid bar; df: diazonal foramen; mes: mesopterygium; msc: mesocondyle; mtp: metapterygium; pro: propterygium; ptp: posterior process of coracoid bar; scl: scapulae; scp: scapular process; *: segmented ridge of scapulae. Dotted red arrow: subrectangular prominence of coracoid bar. Red arrow: mesial concavity of coracoid bar.

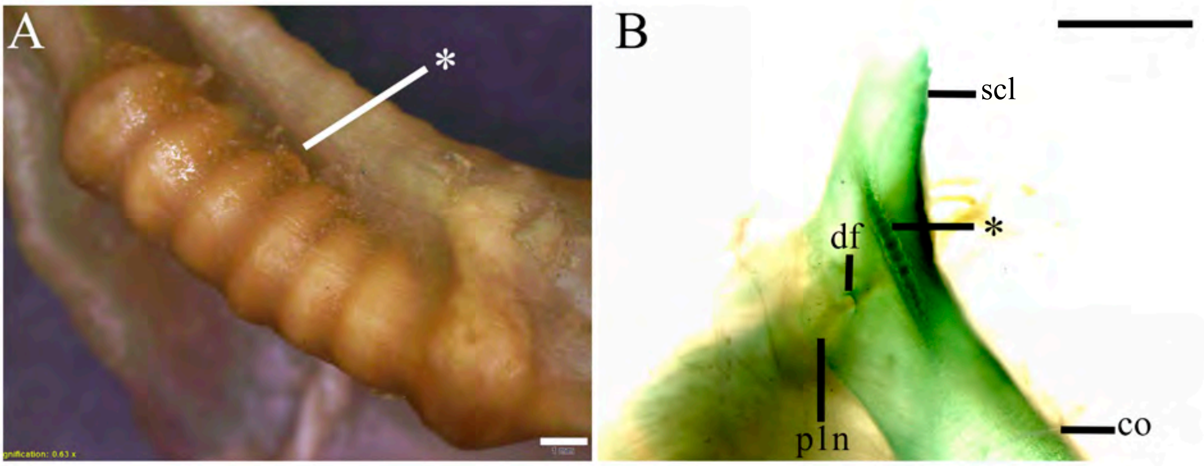

Figure 29. Pectoral girdle in anterior-lateral view, showing segmented ridge of scapulae in *Squalus acanthias*: A) SAM 38276, adult male; B) CAS 21968, neonate female, 285 mm TL. Scale bar: 1mm. Abbreviations: co: coracoid bar; df: diazonal foramen; p1n: pectoral nerve; scl: scapulae; *: segmented ridge of scapulae.

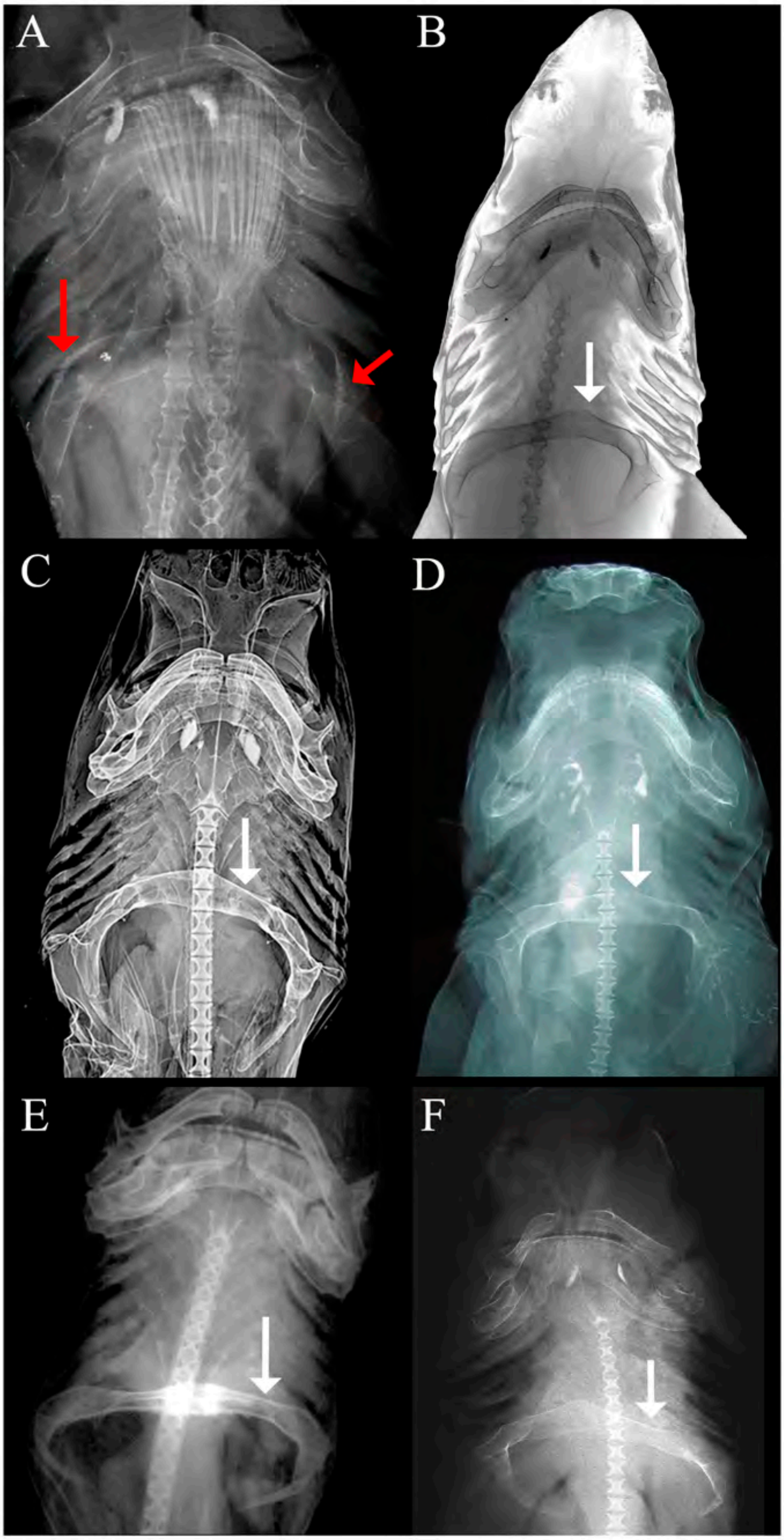

Figure 30. Radiographs of pectoral girdle of syntype of *Squalus acanthias*, UUZM 159 (A), and holotypes of *Squalus suckleyi*, CAS 227267 (B), *Squalus megalops*, AMS I.16255-001 (C), *Squalus mitsukurii*, SU 12793 (D), and paratypes of *Cirrhigaleus asper*, BMNH 1972.10.10.2 (E) and *Cirrhigaleus australis*, AMS I.19154-001 (F). Red arrow showing segmented ridge of scapulae in *S. acanthias*. White arrows show pectoral girdle in other species.

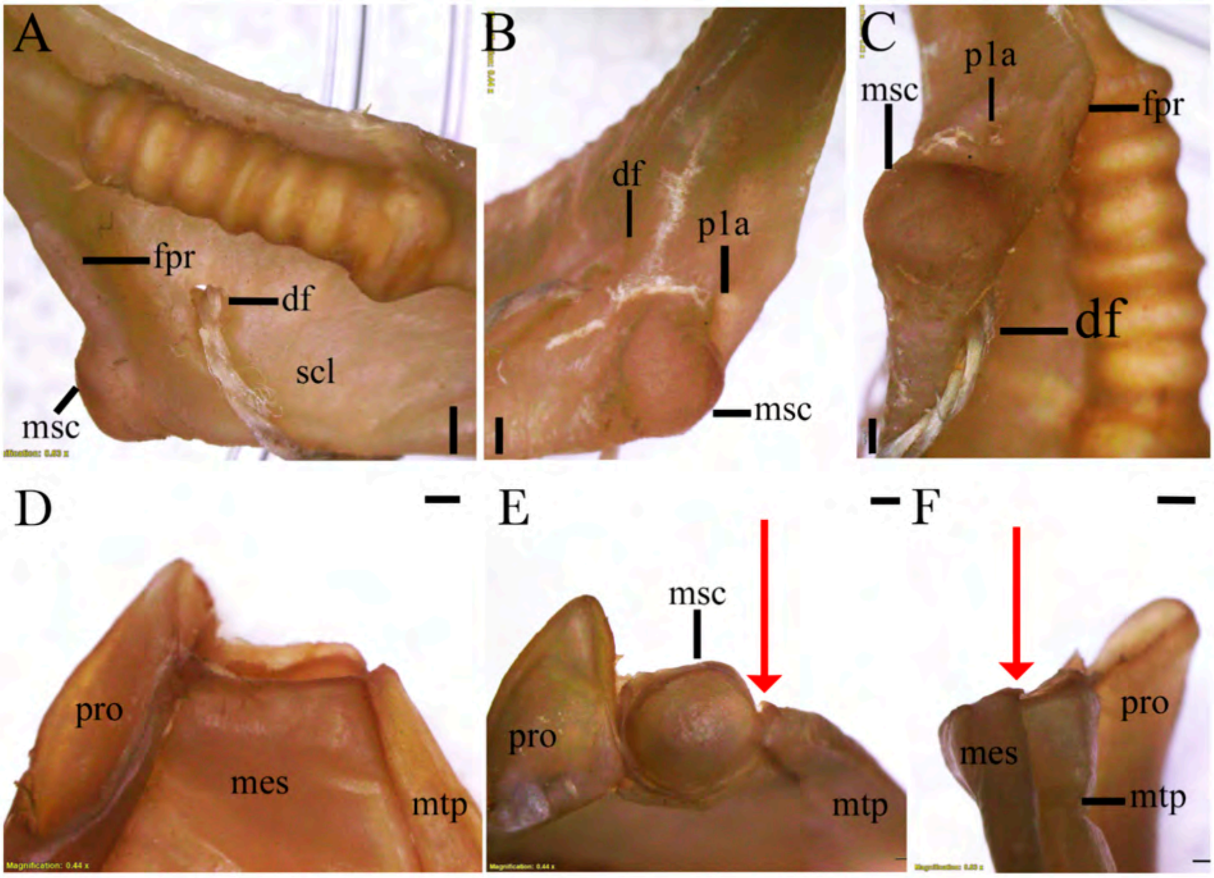

Figure 31. Surfaces for pectoral articulation in *Squalus acanthias*, SAM 38276, adult male, 670 mm TL. A: anterior view of scapulae; B: posterior view of scapulae; C: posterior view of scapulae; D: dorsal proximal view of pectoral basal; E: anterior proximal view of pectoral basal; F: lateral proximal view of pectoral basal. Scale bar: 1mm. Abbreviations: df: diazonal foramen; fpr: facet for propterygium; mes: mesopterygium; msc: mesocondyle; mtp: metapterygium; pro: propterygium; p1a: foramen for pectoral artery; scl: scapulae. Red arrows shows propterygium articulating to

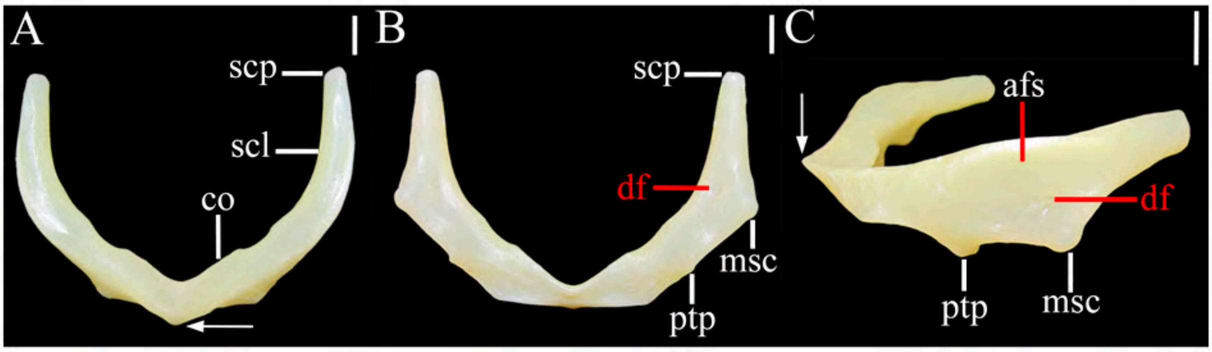

Figure 32. Pectoral girdle of *Squalus suckleyi*, SAM 38346, adult female: A: anterior view; B: posterior view: C: lateral view. Scale bar: 10 mm. Abbreviations: afs: anterior fossa of scapulae; co: coracoid bar; df: diazonal foramen; msc: mesocondyle; ptp: posterior process of coracoid bar; scl: scapulae; scp: scaular process. White arrows shows ventral margin of coracoid bar pointed anteriorly.

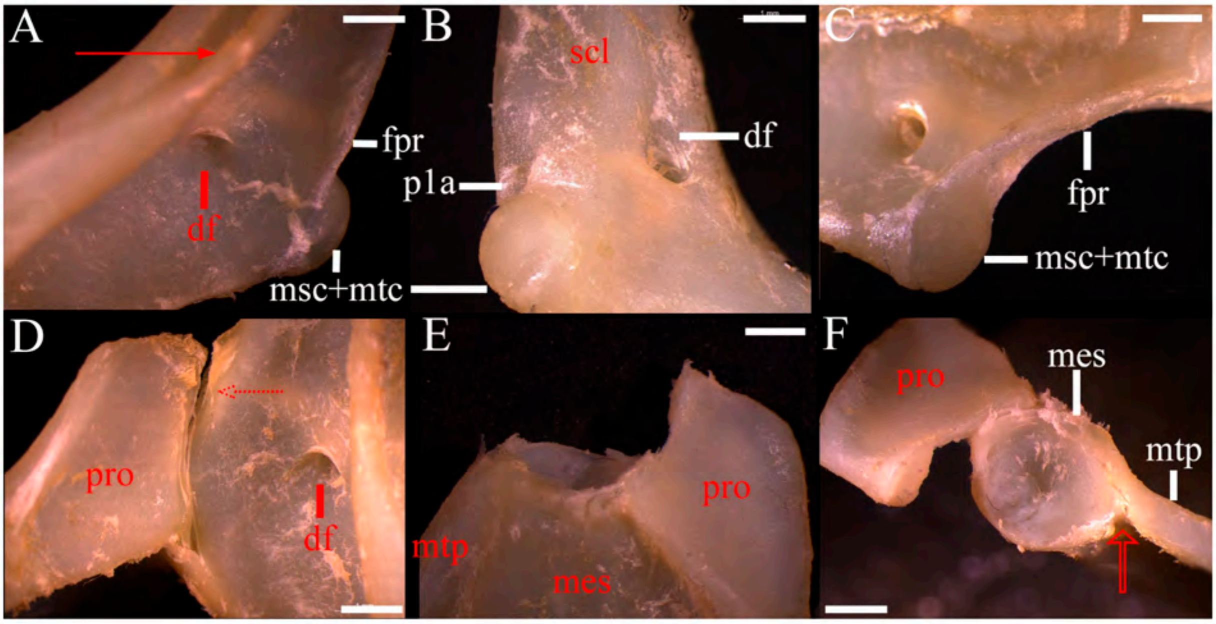

Figure 33. Pectoral articulation of *Squalus albifrons*, MZUSP uncatalogued, adult male, 760 mm TL: A: anterior view of scapulae; B: posterior view of scapulae; C: lateral view of scapulae; D: anterior view of articulation between propterygium and pectoral fin; E: dorsal proximal view of pectoral basal; F: anterior proximal view of pectoral basal. Scale bar: 1mm. Abbreviations: df: diazonal foramen; fpr: facet for propterygium; mes: mesopterygium; msc+mtc: condyle for mesopterygium and metapterygium; mtp: metapterygium; pro: propterygium; p1a: foramen for pectoral artery; scl: scapulae. Full red arrow: ridge of scapulae. Dotted red arrow: articulation region with propterygium. Empty red arrow: metapterygium attached to mesopterygium.

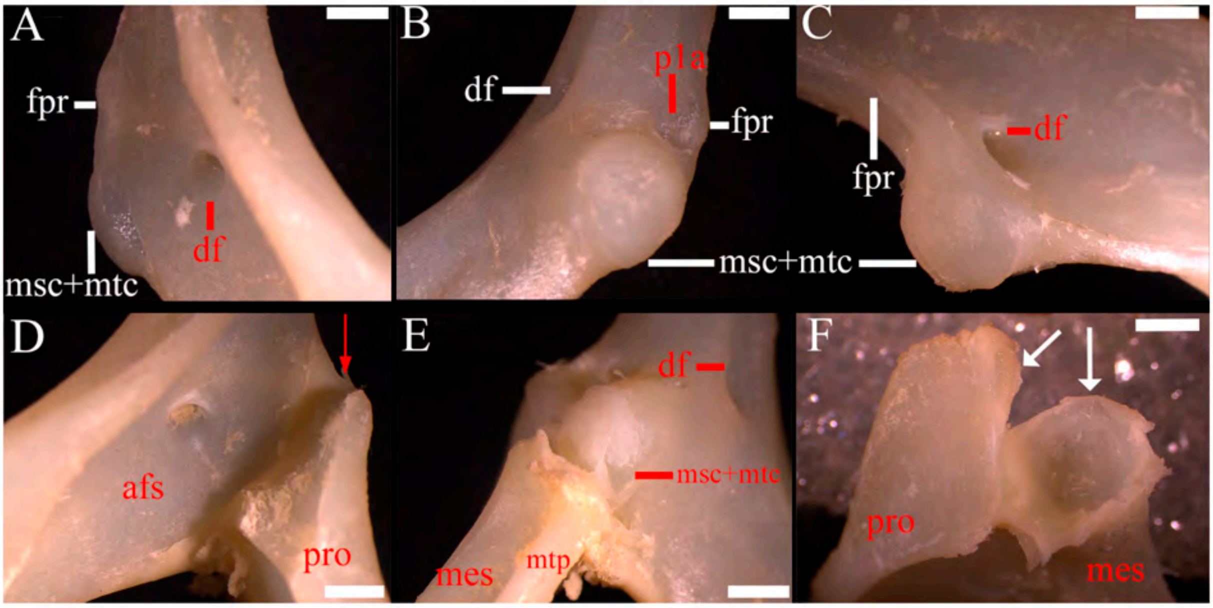

Figure 34. Pectoral articulation of *Squalus montalbani*, MZUSP uncatalogued, adult male, 713 mm TL: A: anterior view of scapulae; B: posterior view of scapulae; C: lateral view of scapulae; D: anterior view of pectoral articulation with propterygium; E: posterior view of mesopterygium and metapterygium articulating with condyle; F: anterior proximal view of pectoral basal. Scale bar: 1mm. Abbreviations: afs: anterior fossa of scapulae; df: diazonal foramen; fpr: facet for propterygium; mes: mesopterygium; msc+mtc: condyle for mesopterygium and metapterygium; mtp: metapterygium; pro: propterygium; p1a: foramen for pectoral artery. Red arrow: region of articulation between propterygium and scapulae. White arrows: articulation region in propterygium (left) and metapterygium (right).

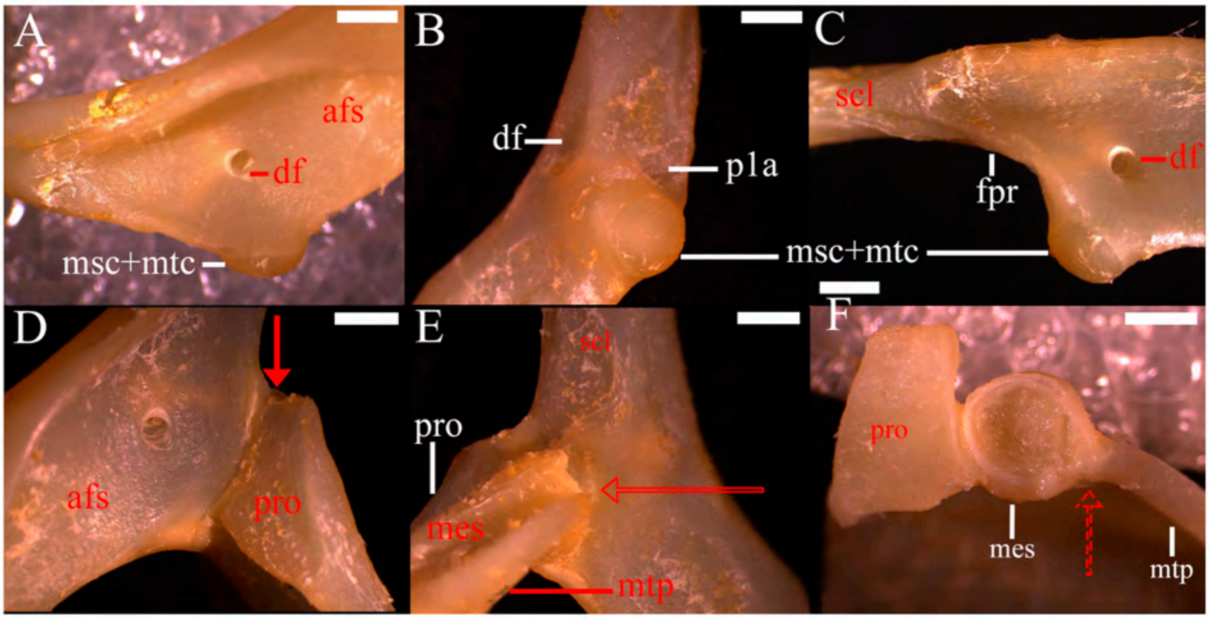

Figure 35. Pectoral articulation of *Squalus grahami*, MZUSP uncatalogued, adult male, 565 mm TL: A: anterior view of scapulae; B: posterior view of scapulae; C: lateral view of scapulae; D: anterior view of pectoral articulation with propterygium; E: posterior view of mesopterygium and metapterygium articulating with condyle; F: anterior proximal view of pectoral basal. Scale bar: 1mm. Abbreviations: afs: anterior fossa of scapulae; df: diazonal foramen; fpr: facet for propterygium; mes: mesopterygium; mtp: metapterygium; msc+mtc: condyle for mesopterygium and metapterygium; pro: propterygium; p1a: foramen for pelctoral artery; scl: scapulae. Full red arrow: artculation region between propterygium and pectoral girdle. Empty red arrow: region of articulation between pectoral girdle and mesopterygium and metapterygium. Dashed red arrow: metapterygium attached to mesopterygium.

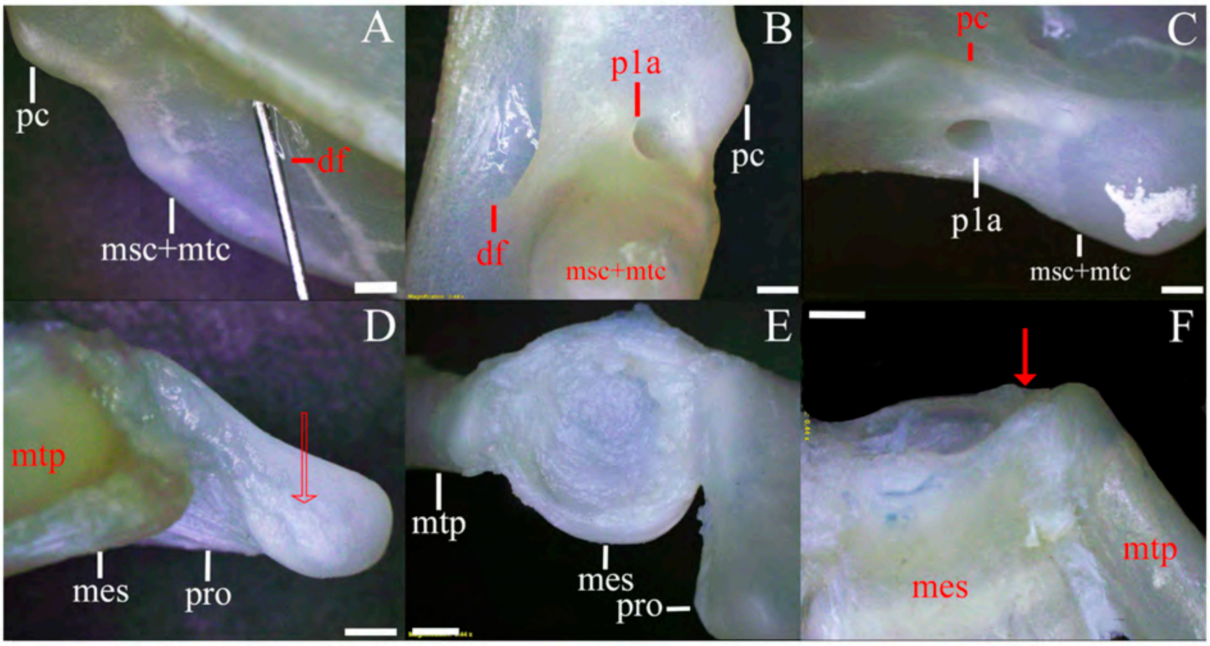

Figure 36. Pectoral articulation of *Cirrhigaleus asper*, SAM 38269, adult female: A: dorsal anterior view of scapulae; B: posterior view of scapulae; C: lateral view of scapulae; D: lateral proximal view of pectoral basal; E: anterior proximal view of pectoral basal; F: dorsal proximal view of pectoral basal. Scale bar: 2mm. Abbreviations: df: diazonal foramen; mes: mesopterygium; msc+mtc: condyle for mesopterygium and metapterygium; mtp: metapterygium; pc: condyle for propterygium; pro: propterygium; p1a: foramen for pectoral artery. Lined red arrow: region in propterygium where it articulates with procondyle. Full red arrow: connection between metapterygium and mesopterygium.

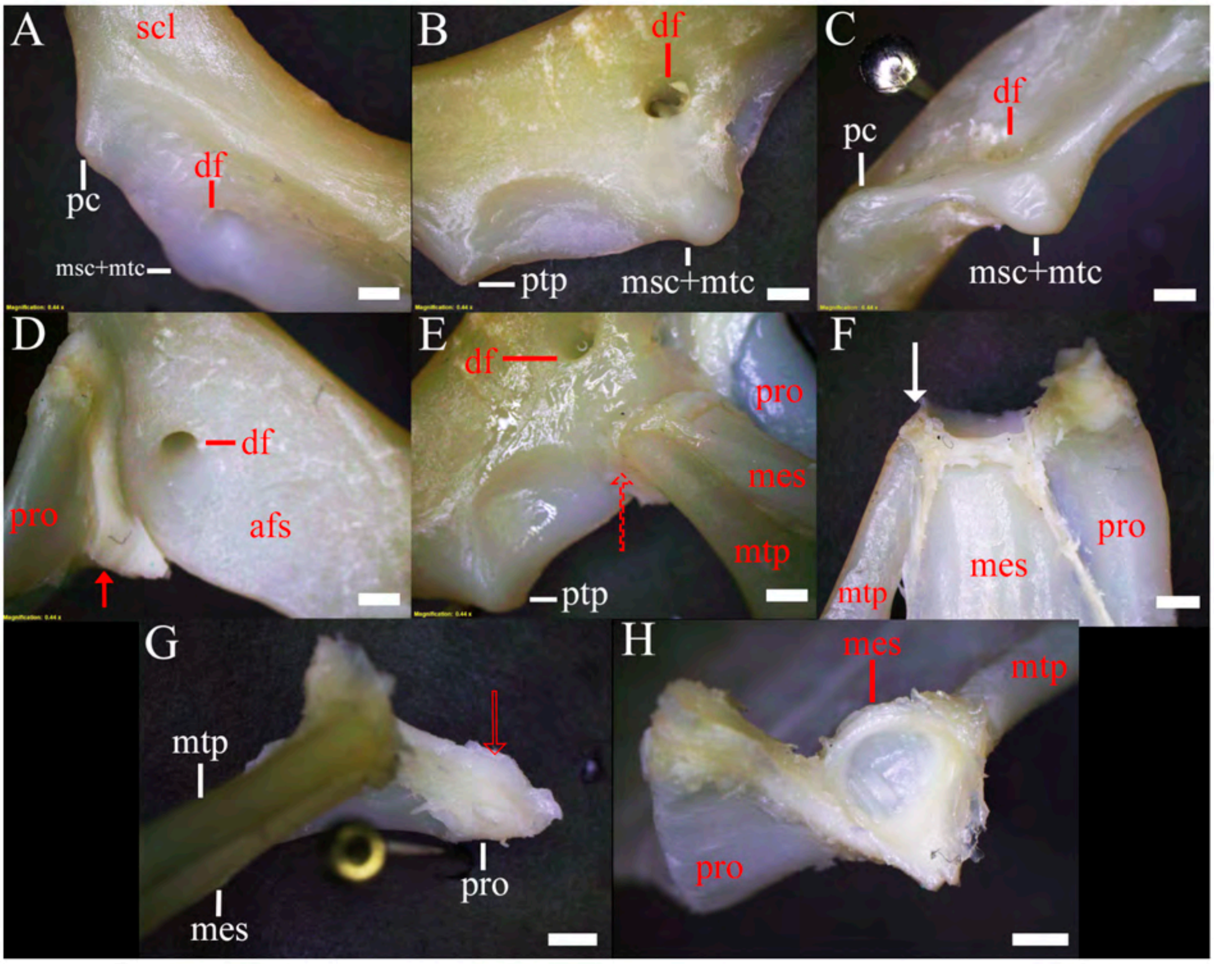

Figure 37. Pectoral girdle of *Cirrhigaleus australis*, CSIRO H 7042-04, juvenile female: A: dorsal anterior view of scapulae; B: posterior view of scapulae; C: lateral view of scapulae; D: anterior view of articulation between propterygium and girdle; E: posterior view of articulation between condyle and mesopterygium and metapterygium; F: dorsal proximal view of pectoral basal; G: lateral proximal view of pectoral basal; H: anterior proximal view of pectoral basal. Scale bar: 2mm. Abbreviations: afs: anterior fossa of scapulae; df: diazonal foramen; mes: mesopterygium; mtp: metapterygium; msc+mtc: condyle for mesopterygium and metapterygium; pc: procondyle; pro: propterygium; ptp: posterior process of scapulae. Full red arrow: articulation region of propterygium. Dashed red arrow: articulation region of metapterygium and condyle. Lined red arrow: region of propterygium where articulates with procondyle. White arrow: metapterygium attached to mesopterygium.

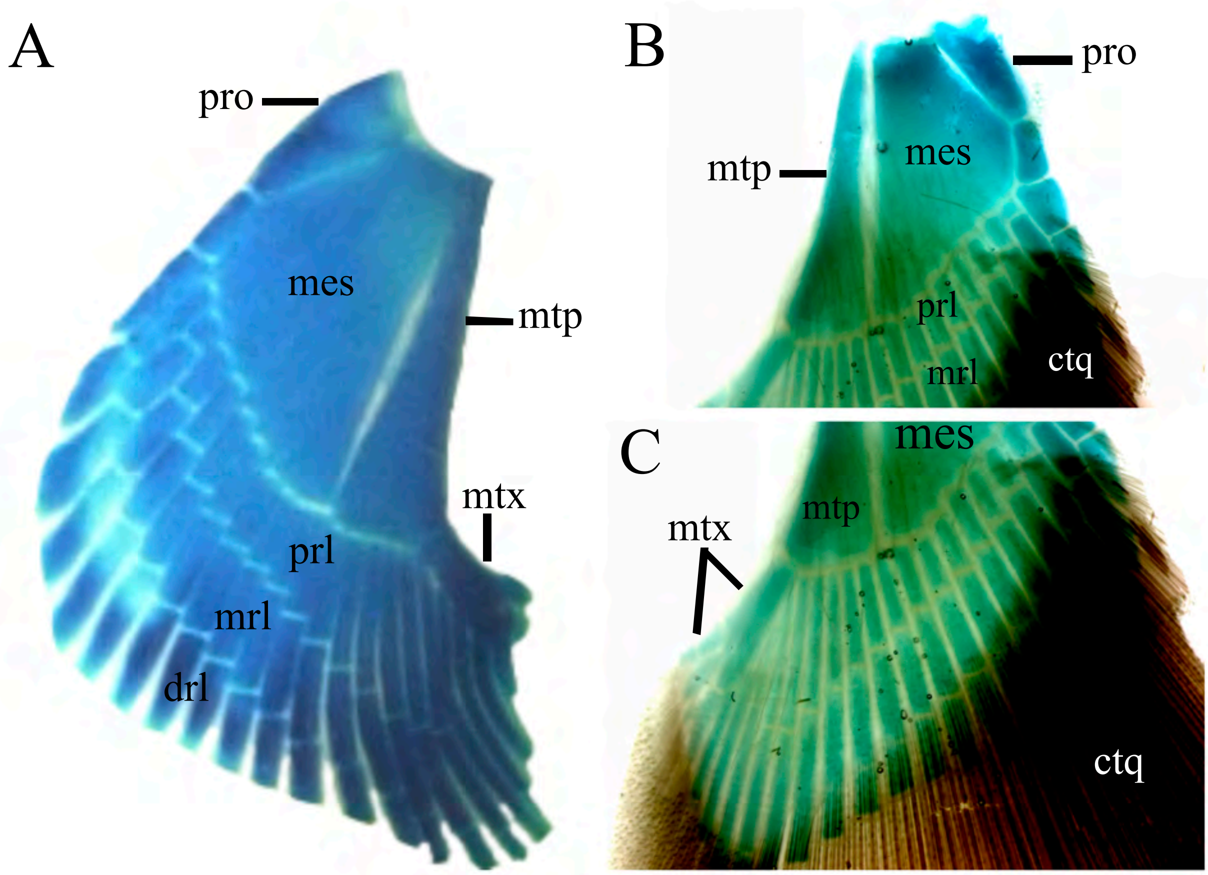

Figure 38. Cleared and stained pectoral fin of *Squalus acanthias*, AMNH 38181 (A) and *Squalus suckleyi*, CAS 21424 (B-C), showing pectoral basals and radials. Abbreviations: ctq: ceratotrichia; drl: distal radial; mes: mesopterygium; mrl: medial radial; mtp: metapterygium; mtx: metapterygial axis; prl: proximal radial.

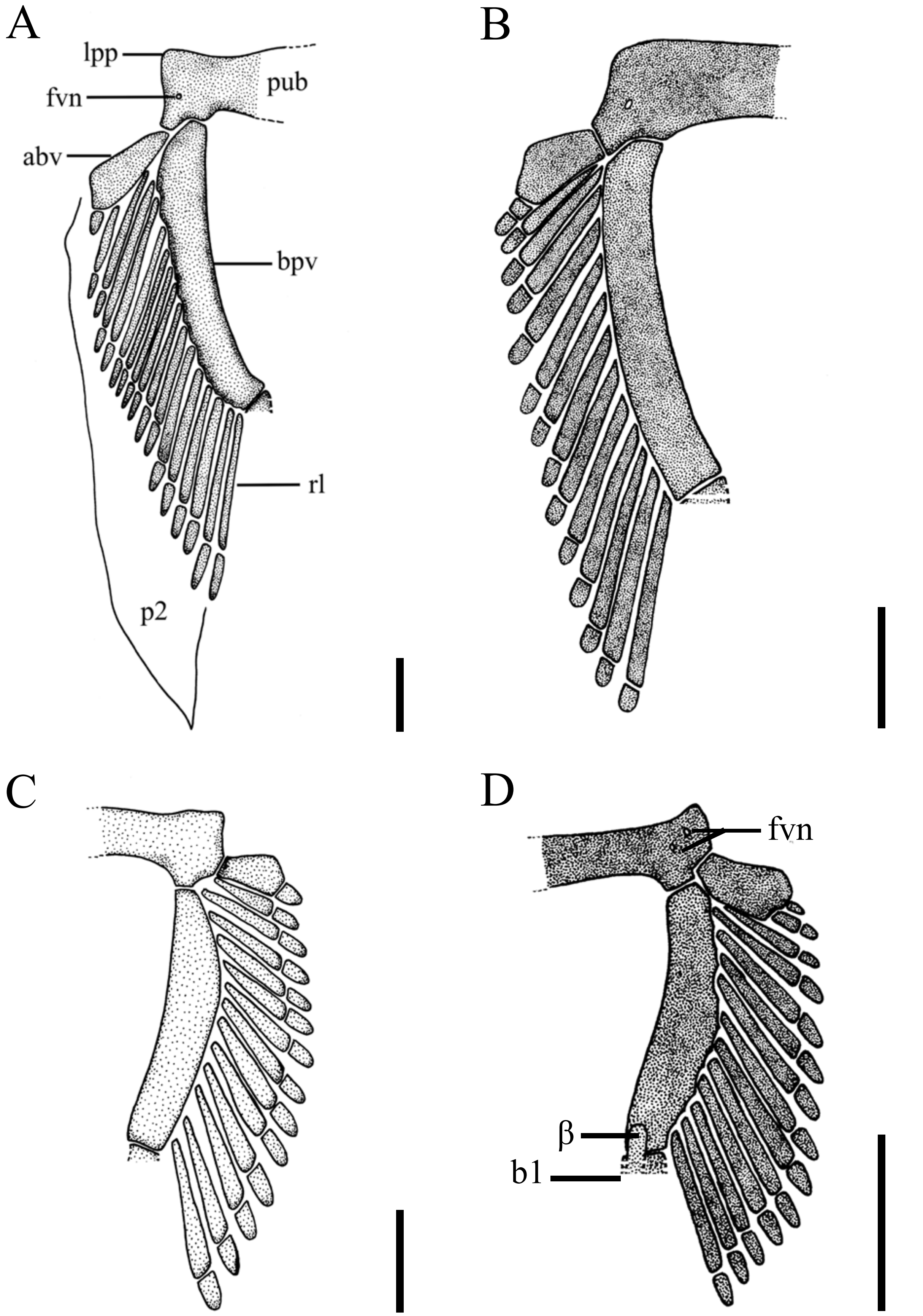

Figure 39. Pelvic girdle and fin of *Squalus*. A: *S. acanthias*, ZMH 104416; B: *Squalus* cf. *suckleyi*, HUMZ 87643; C: *S. megalops*, AMS 46093-001; D: *S. brevirostris*, HUMZ 189762. A-C: ventral view: D: dorsal view. Scale bar: 10 mm.

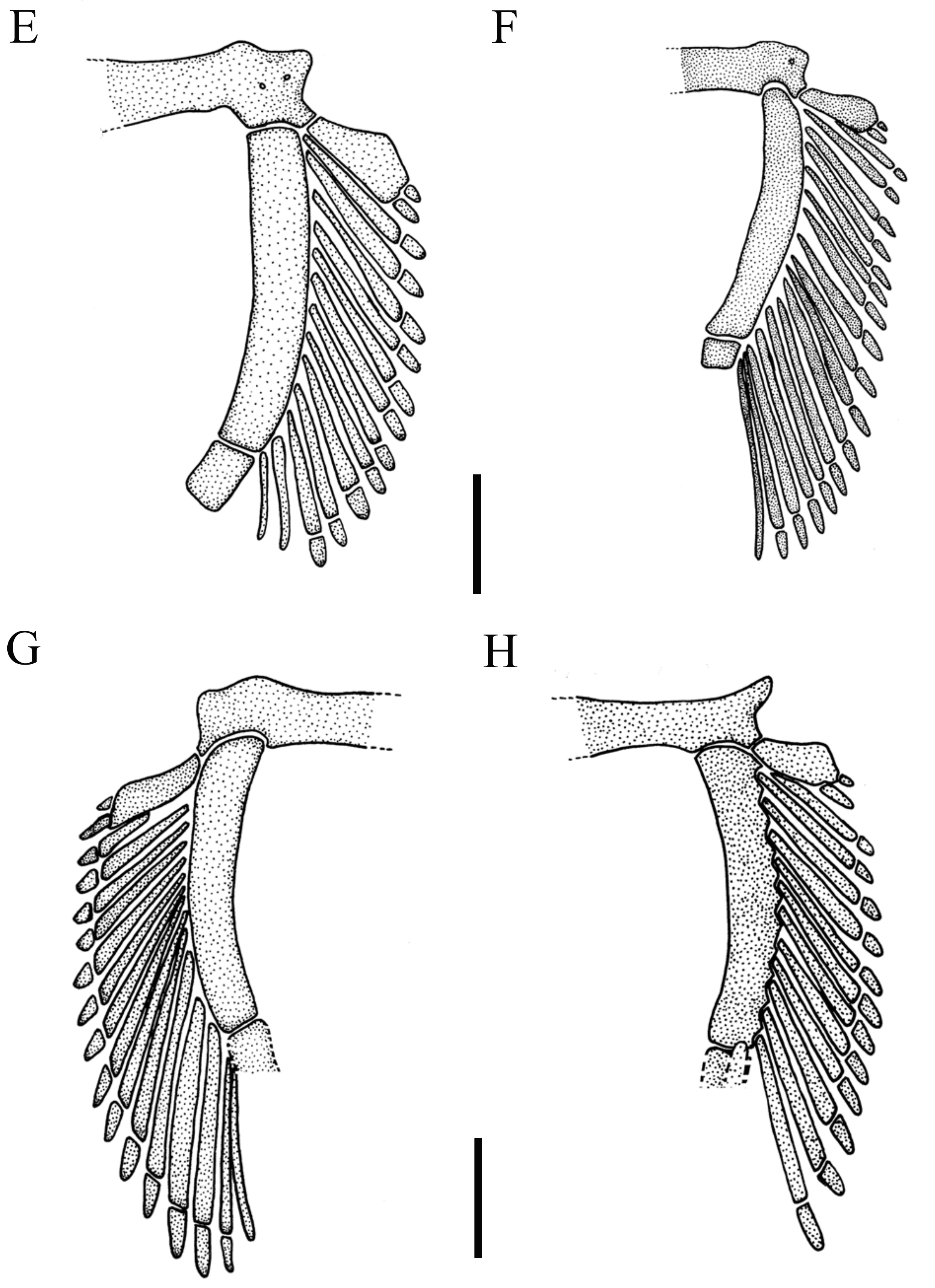

Figure 39 cont. Pelvic girdle and fin of *Squalus*. E: *S. albifrons*, MZUSP uncatalogued, adult male, 760 mm TL; F: *S. mitsukurii*, NSMT P 44381; G: *S. montalbani*, MZUSP uncatalogued, adult male, 713 mm TL; H: *S. grahami*, MZUSP uncatalogued, adult male, 565 mm TL. E-G: ventral view; H: dorsal view. Scale bar: 10 mm.

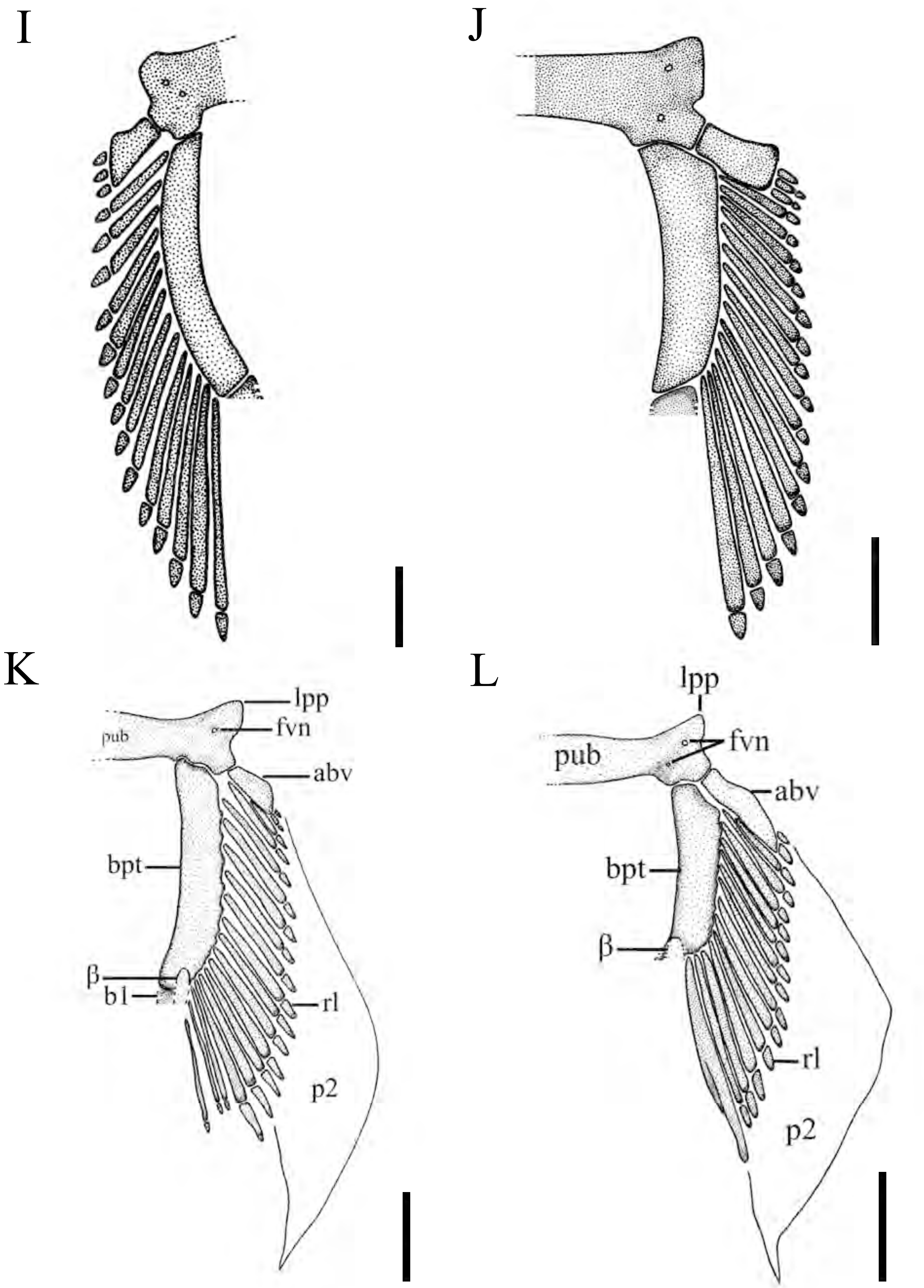

Figure 39 cont. Pelvic girdle and fin of *Squalus*. I: *S. japonicus*, HUMZ 189737; J: *Squalus* sp. 1, SAIAB 21858; K: *Squalus* sp. 4, UERJ 1661; L: *Squalus* sp. 7, MNRJ 30184. Scale bar: 10 mm. I-J: ventral view; K-L: dorsal view. Abbreviations: abv: anterior pelvic basal; bpt: basipterygium; b1: intermediate segment; fvn: foramen for ventral fin nerves; lpp: lateral prepelvic process; pub: puboischiadic bar; p2: pelvic fin; rl: radials; β: beta cartilage.

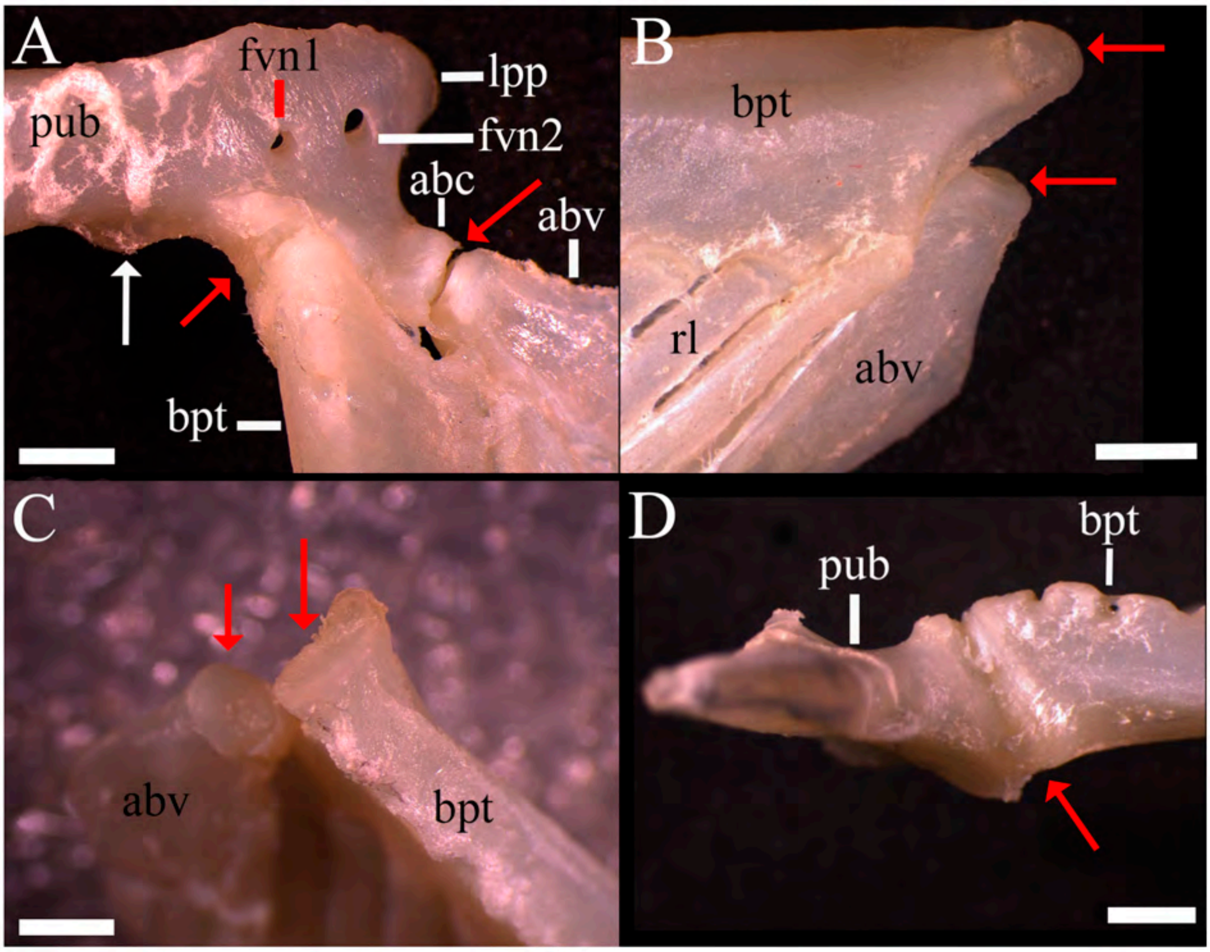

Figure 40. Pelvic articulation of *Squalus albifrons*, MZUSP uncatalogued, adult male, 760 mm TL. A: right dorsal view of pelvic girdle and fin; B: dorsal proximal view of basipterygium and anterior basal element; C: anterior proximal view of basipterygium and anterior pelvic basal; D: mesial view of basipterygium articulating to puboischiadic bar. Scale bar: 1mm. Abbreviations: abc: condyle for anterior plevic basal; abv: anterior pelvic basal; bpt: basipterygium; fvn: foramen for ventral fin nerve; lpp: lateral prepelvic process; pub: puboischiadic bar; rl: radials. Full white arrow: posterior process. Full red arrow: articulation region between basipterygium or anterior pelvic basal and puboischiadic bar.

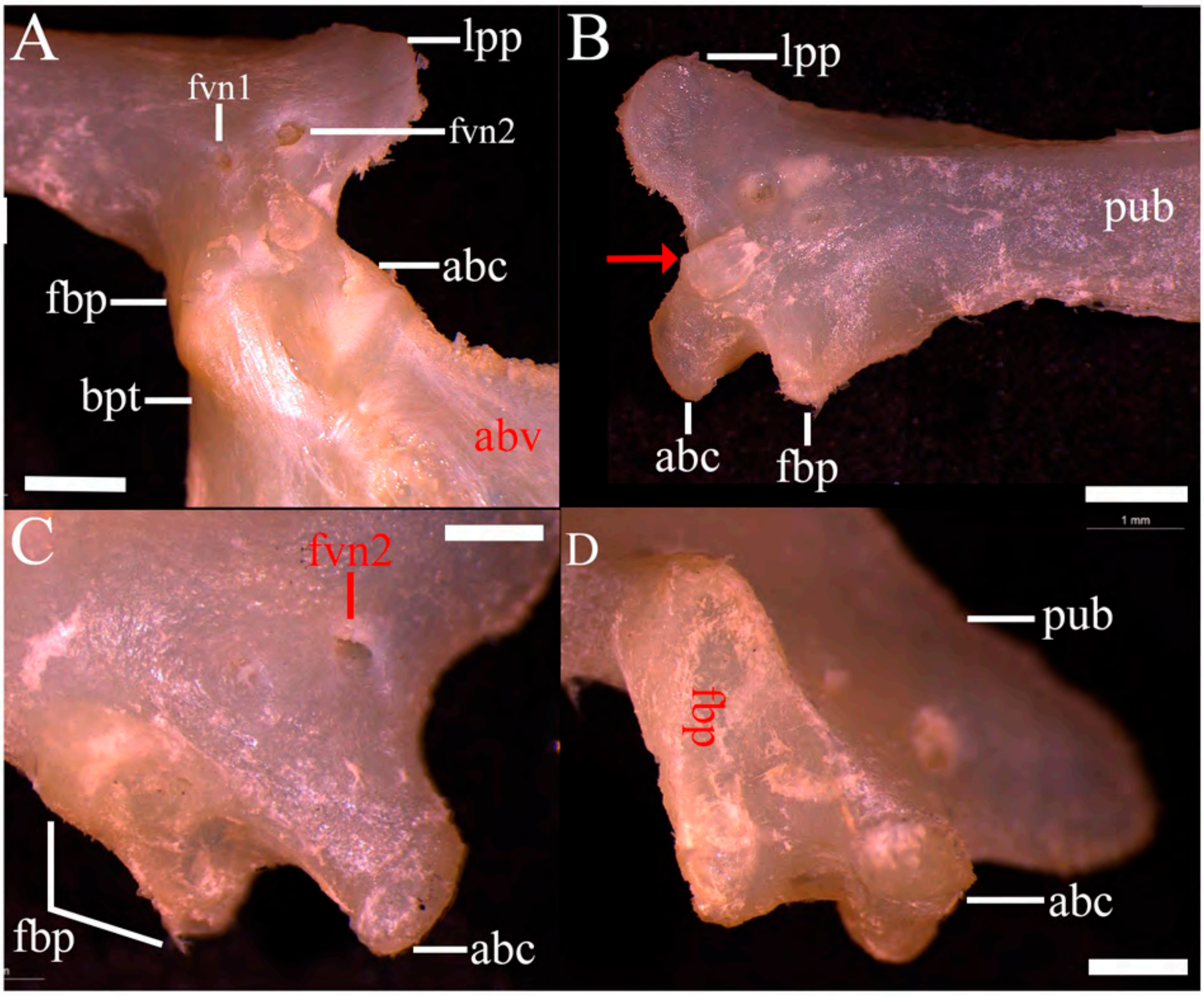

Figure 41. Puboischiadic bar of *Squalus montalbani*, MZUSP uncatalogued, adult male, 713 mm TL, showing regions of pelvic articulation. A: right dorsal view of pelvic girdle and fin; B: left dorsal view; C: left ventral view; D: left posterior view. Scale bar: 1mm. Abbreviations: abc: condyle for anterior pelvic basal; abv: anterior pelvic basal; bpt: basipterygium; fbp: facet for basipterygium; fvn: foramen for ventral fin nerve; lpp: lateral prepelvic process; pub: puboischiadic bar. Full red arrow: dorsal process of puboischiadic bar.

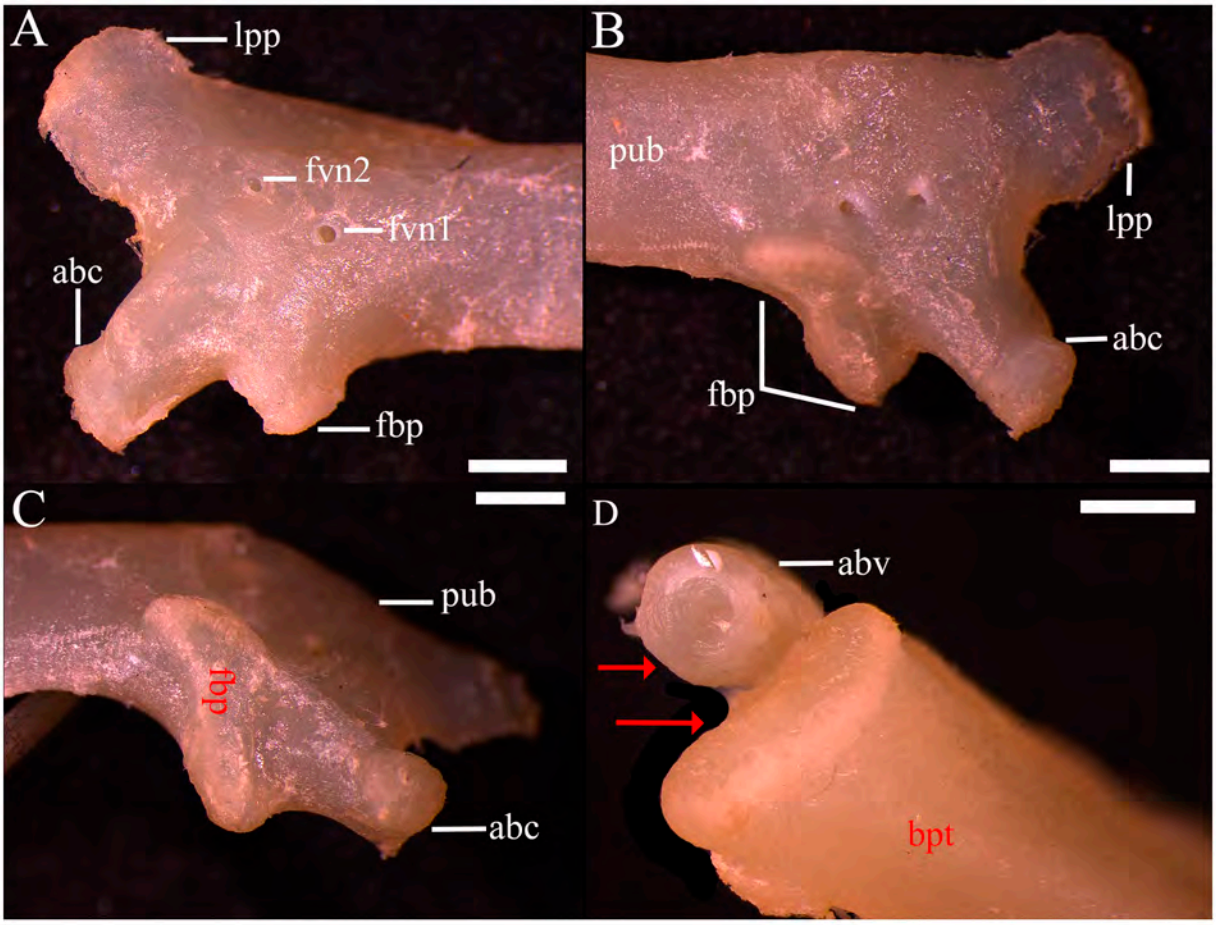

Figure 42. Pelvic articulation of *Squalus grahami*, MZUSP uncatalogued, adult male, 565 mm TL. A: left dorsal view of puboischiadic bar; B: left ventral view of puboischiadic bar; C: posterior view of puboischiadic bar; D: anterior proximal view of basipterygium and anterior pelvic basal. Scale bar: 1mm. Abbreviations: abc: condyle for anterior pelvic basal; abv: anterior pelvic basal; bpt: basipterygium; fbp: facet for basipterygium; fvn: foramen for ventral fin nerve; lpp: lateral prepelvic process; pub: puboischiadic bar. Full red arrow: articulation regions in pelvic fin.

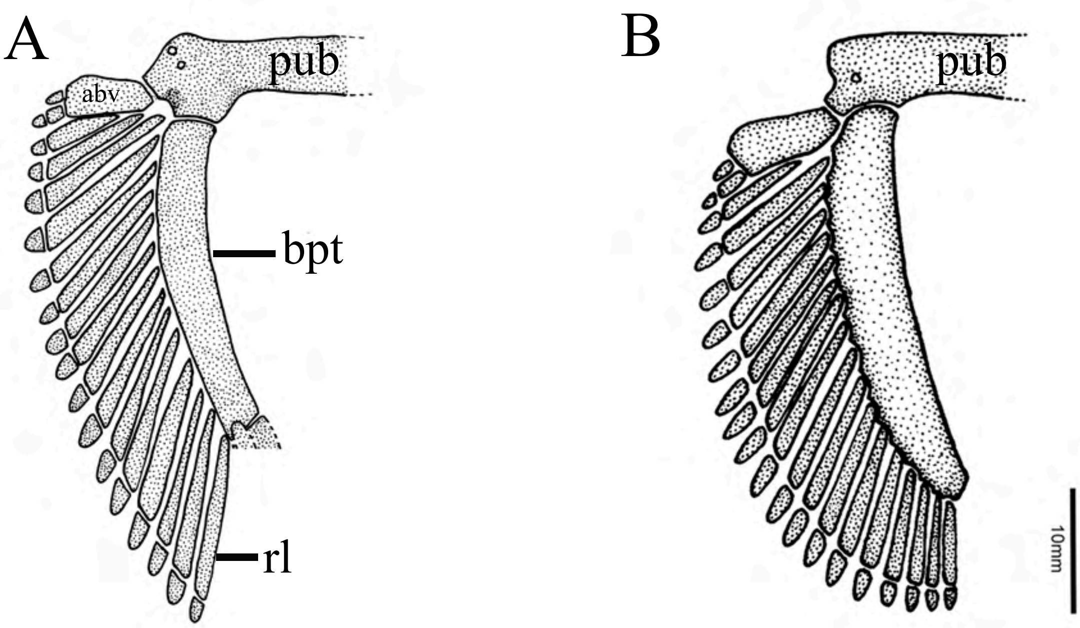

Figure 43. Pelvic girdle and fin of *Cirrhigaleus*. A: *Cirrhigaleus barbifer*, TPM 38074; B: *Cirrhigaleus australis*, CSIRO H 7042-04.

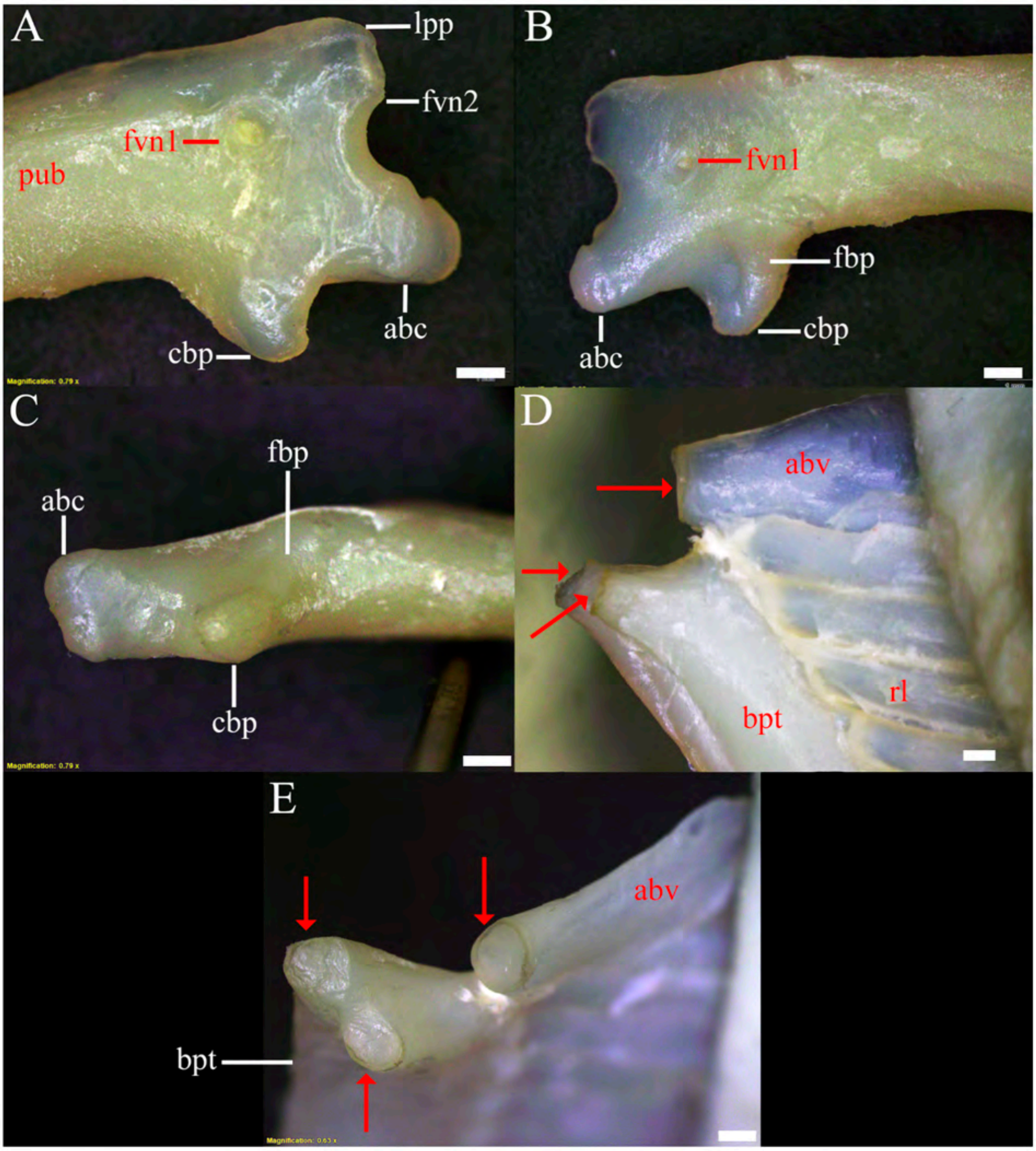

Figure 44. Pelvic articulation of *Cirrhigaleus australis*, CSIRO H 7042-04. A: right dorsal view of puboischiadic bar; B: right ventral view of puboischiadic bar; C: right posterior view of puboischiadic bar; D: dorsal proximal view of basipterygium and anterior pelvic basal; E: anterior proximal view of basipterygium and anterior pelvic basal. Scale bar: 1mm. Abbreviations: abc: condyle for anterior pelvic basal; abv: anterior pelvic basal; bpt: basipterygium; cbp: condyle for basipterygium; fbp: facet for basipterygium; fvn: foramen for ventral fin nerve; lpp: lateral prepelvic process; pub: puboischiadic bar; rl: radials. Full red arrow: articulating regions in the pelvic fin.

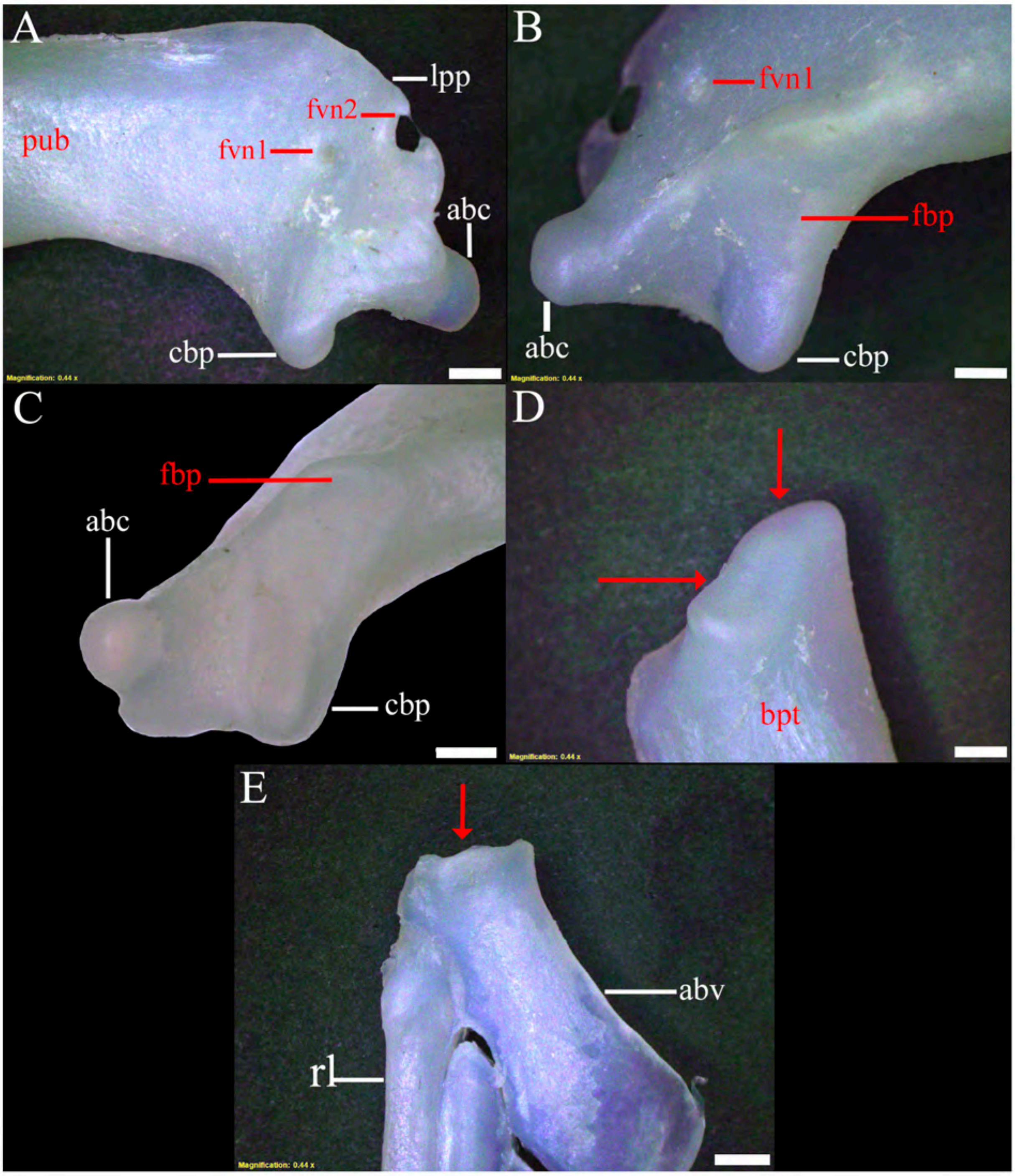

Figure 45. Pelvic articulation of *Cirrhigaleus asper*, SAM 38269. A: right dorsal view of puboischiadic bar; B: right ventral view of puboischiadic bar; C: right posterior view of puboischiadic bar; D: dorsal proximal view of basipterygium; E: dorsal proximal view of anterior pelvic basal. Scale bar: 2 mm. Abbreviations: abc: condyle for anterior pelvic basal; abv: anterior pelvic basal; bpt: basipterygium; cbp: condyle for basipterygium; fbp: facet for basipterygium; fvn: foramen for ventral fin nerve; lpp: lateral prepelvic process; pub: puboischiadic bar; rl: radials. Full red arrow: articulating regions in the pelvic fin.

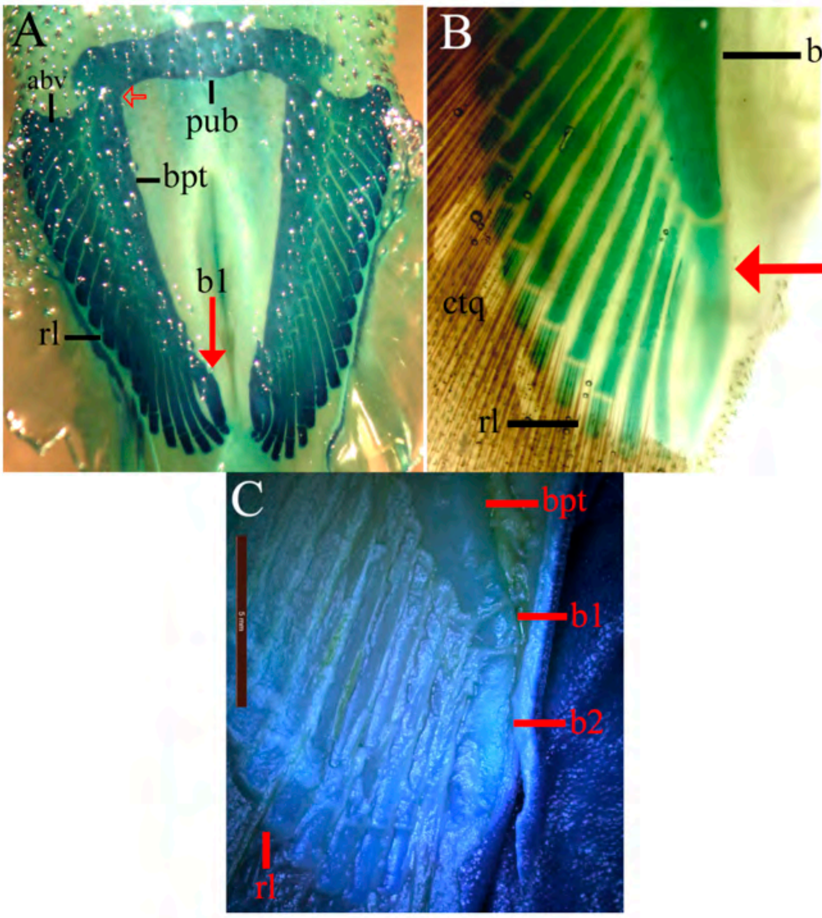

Figure 46. Clearing and staining of pelvic fin and girdle in females of *Squalus acanthias* (A) and *S. suckleyi* (B) and *Cirrhigaleus barbifer* (C), showing intermediate segments. A: AMNH 40802. B: CAS 21424; C: HUMZ 95177. Scale bar: 5mm. Abbreviations: abv: anterior pelvic basal; bpt: basipterygium; b1: first intermediate segment; b2: second intermediate segment; ctq: ceratotrichia; fvn: foramen for ventral fin nerves; lpp: lateral prepelvic process; pub: puboischiadic bar; rl: radials. Full red arrow: single intermediate segment.

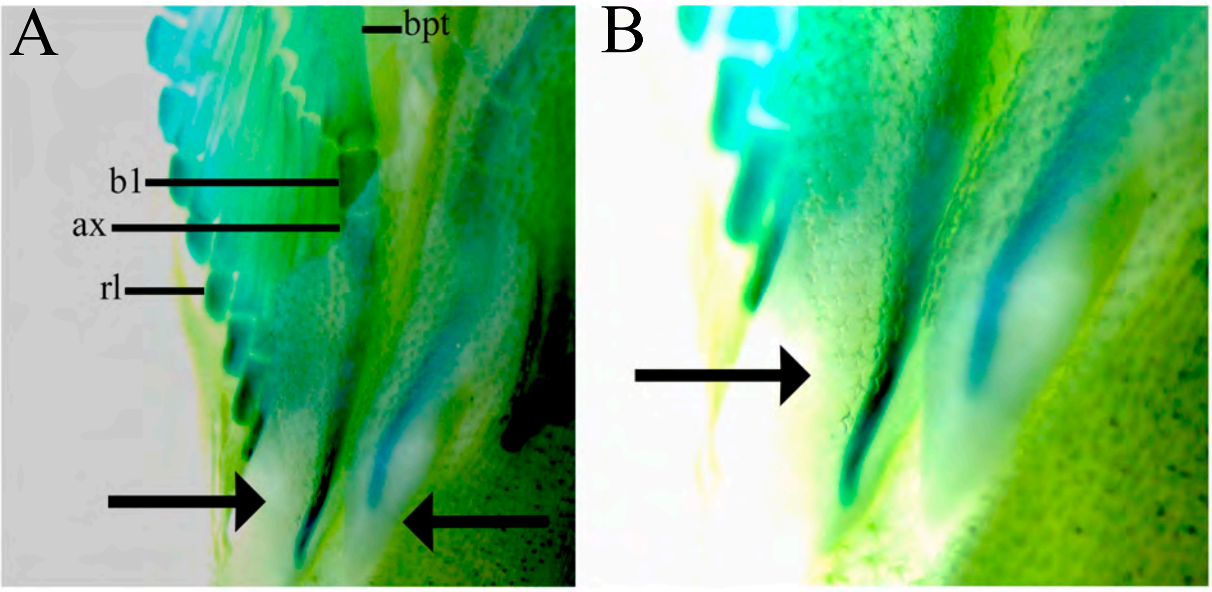

Figure 47. Ventral appendix in neonate male of *Squalus suckleyi*, CAS 56093, showing intermediate segment (A) and appendix-stem (A, B) in ventral view. Abbreviations: ax: axial cartilage; bpt: basipterygium; b1: first intermediate segment; rl: radials. Full black arrow: clasper under development, lacking terminal and marginal cartilages.

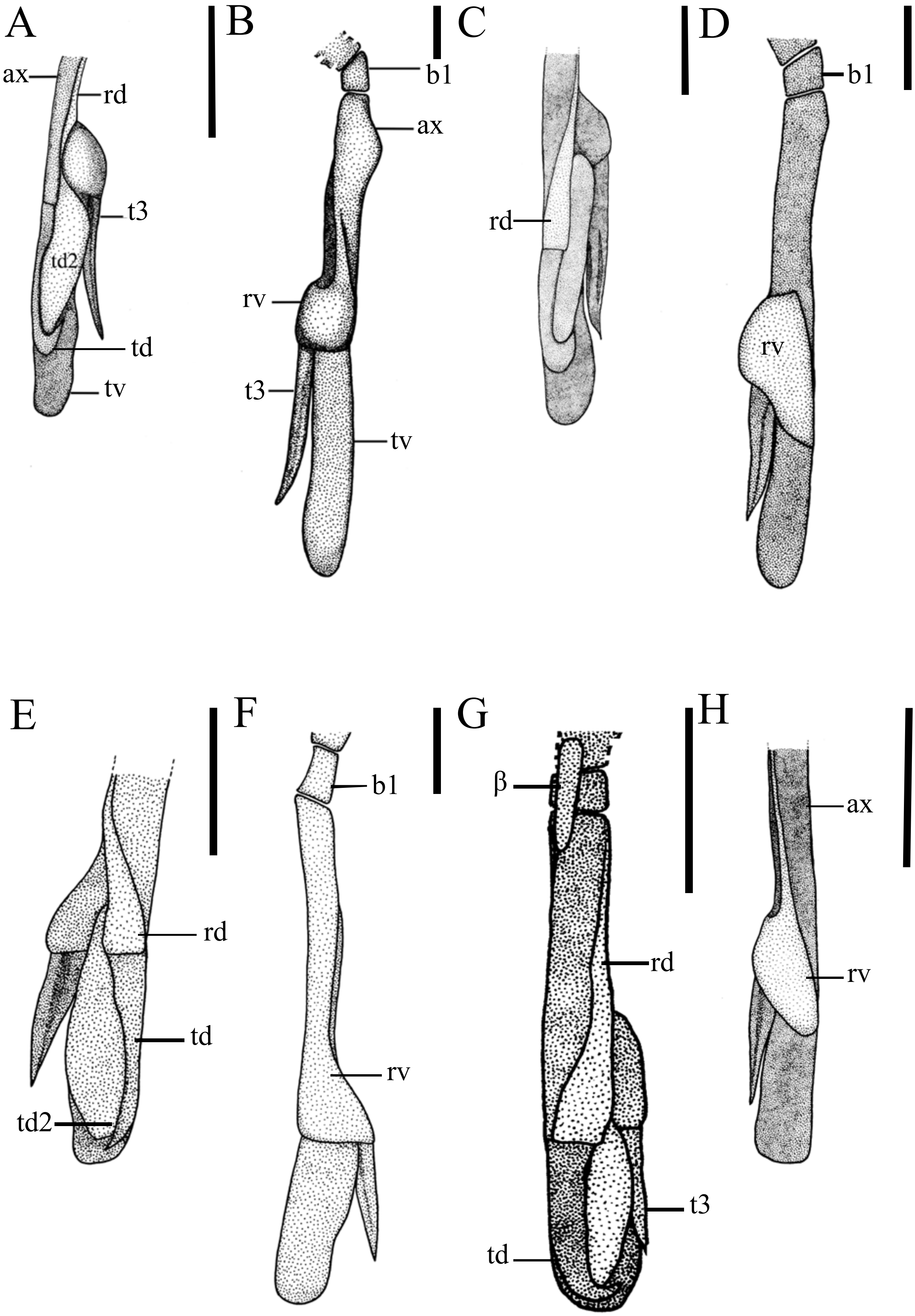

Figure 48. Cartilages of the clasper of *Squalus*. A,B: *S. acanthias*, ZMH 104416; C,D: *Squalus* cf. *suckleyi*, HUMZ 87643; E,F: *S. megalops*, AMS I 46093-001; G,H: *S. brevirostris*, HUMZ 189762. dorsal (a,c,e,g) and ventral views (b,d,f,h). Scale bars: 10 mm.

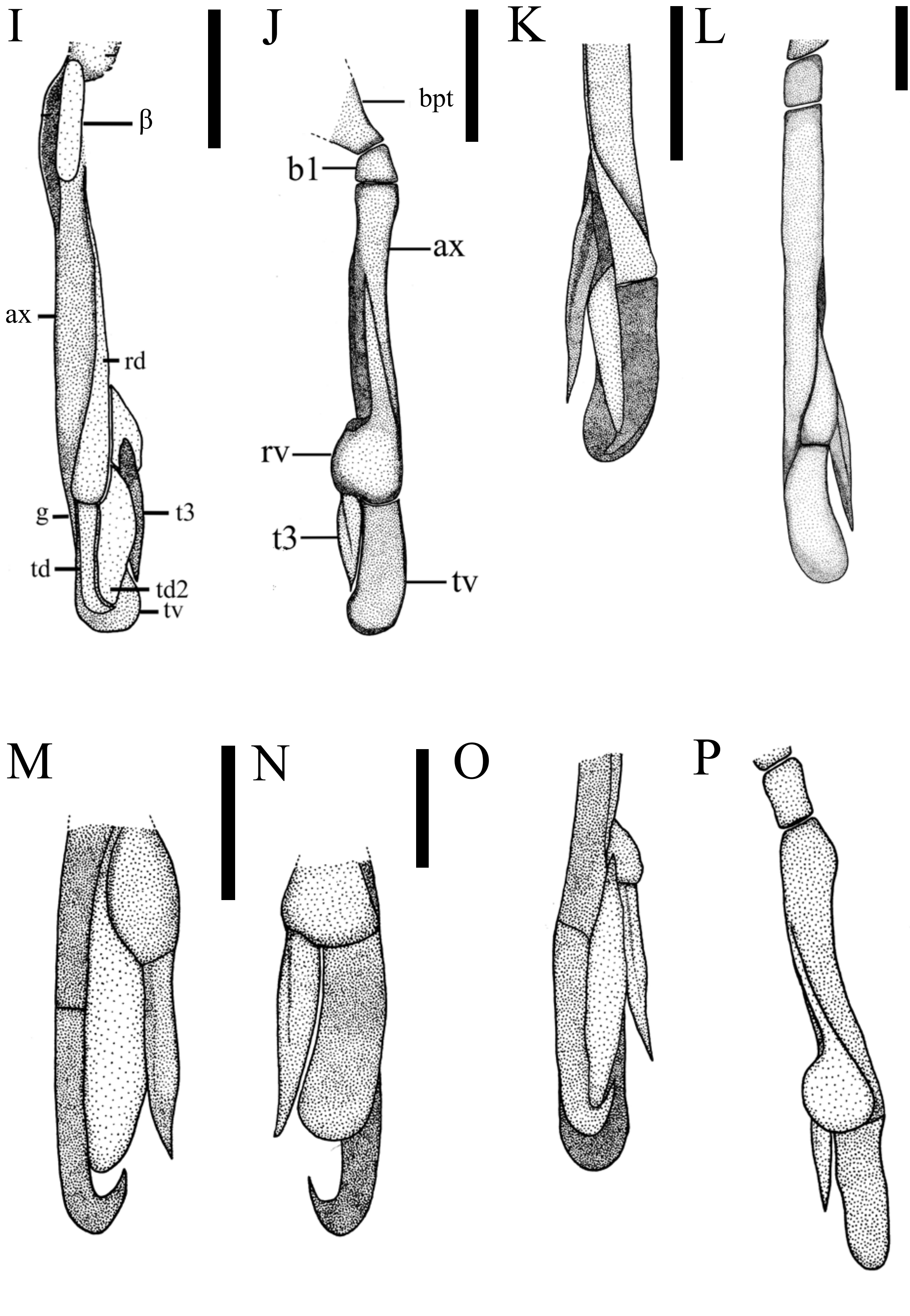

Figure 48 cont. Cartilages of the clasper of *Squalus*. I-J: *Squalus* sp. 7, MNRJ 30184; K-L: *Squalus* sp. 1, SAIAB 21858; M-N: *S. mitsukurii,* NSMT 44381; O-P: *S. montalbani*, MZUSP not catalogued. Dorsal (i,k,m,o) and ventral (j,l,n,p) views. Scale bars: 10 mm.

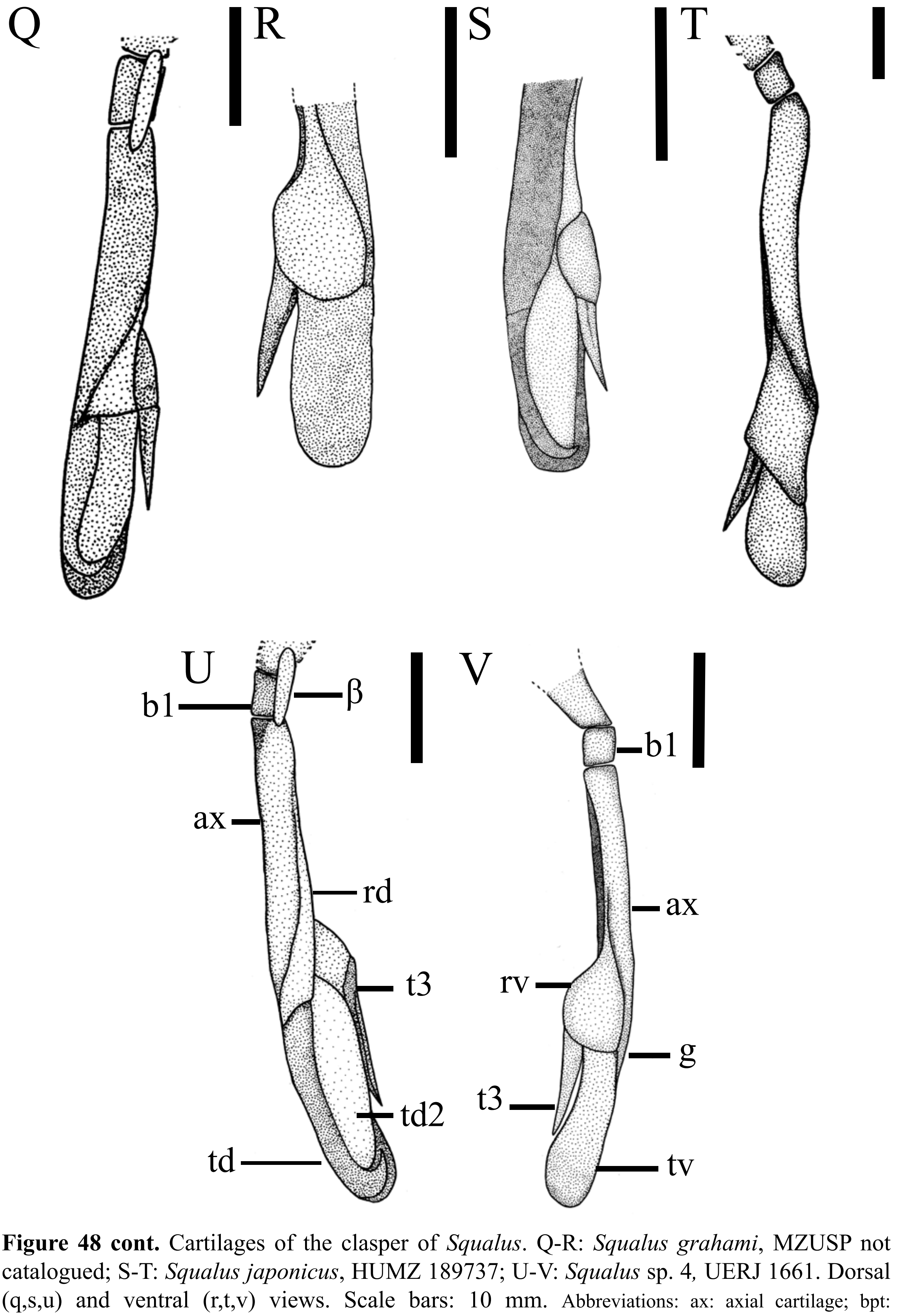

Figure 48 cont. Cartilages of the clasper of *Squalus*. Q-R: *Squalus grahami*, MZUSP not catalogued; S-T: *Squalus japonicus*, HUMZ 189737; U-V: *Squalus* sp. 4*,* UERJ 1661. Dorsal (q,s,u) and ventral (r,t,v) views. Scale bars: 10 mm. Abbreviations: ax: axial cartilage; bpt: basipterygium; b1: intermediate segment; g: end-style; rd: dorsal marginal cartilage; rv: ventral marginal cartilage; td: dorsal terminal cartilage; td2: dorsal terminal 2 cartilage; tv: ventral terminal cartilage; t3: acessory terminal 3 cartilage; β: beta cartilage.

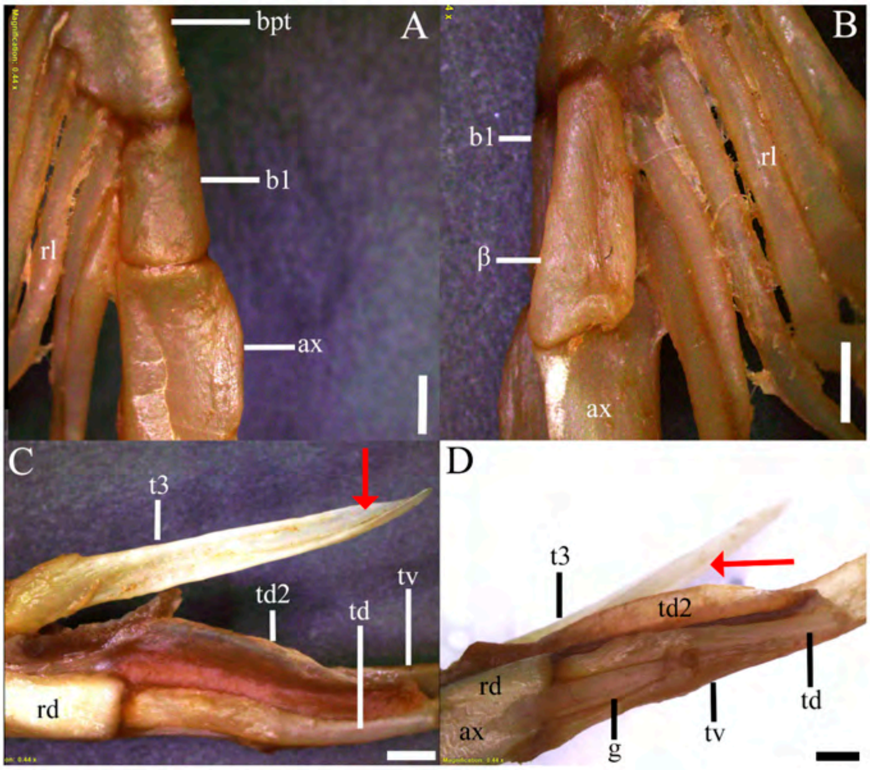

Figure 49. Detail of cartilages of the clasper in *Squalus acanthias*, SAM 38276. A: ventral view; B: dorsal view; C: dorsal distal view; D: medial distal view. Scale bar: 2 mm. Abbreviations: ax: axial cartilage; bpt: basipterygium; b1: intermediate segment; g: end-style; rl: radials; rd: dorsal marginal cartilage; td: dorsal terminal cartilage; td2: dorsal terminal 2 cartilage; tv: ventral terminal cartilage; t3: acessory terminal 3 cartilage; β: beta cartilage. Full red arrow: furrows of spur.

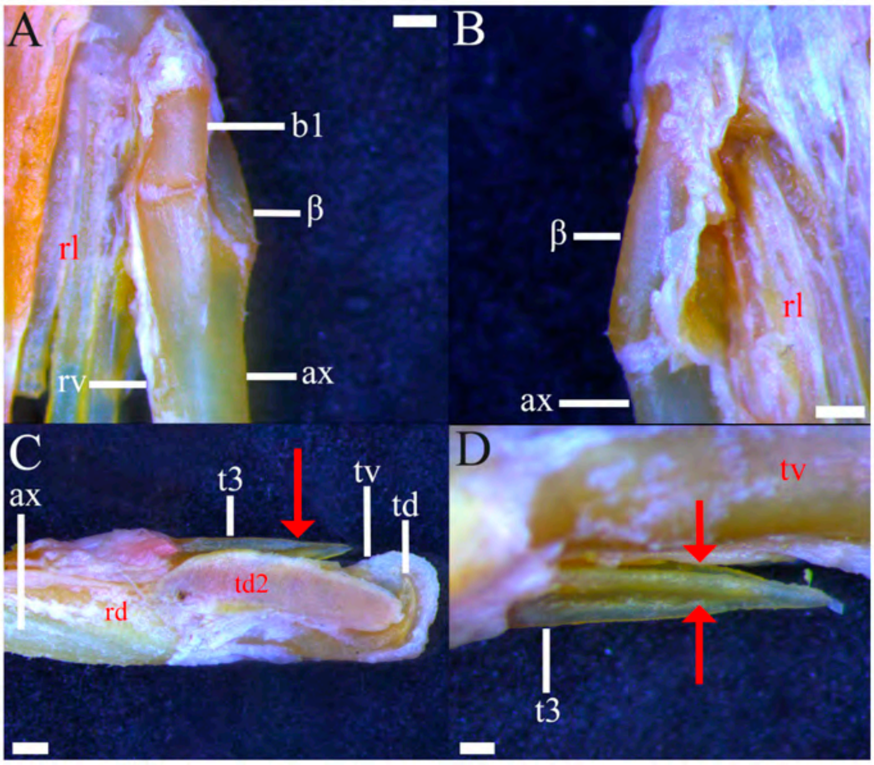

Figure 50. Detail of cartilages of the clasper in *Squalus brevirostris*, HUMZ 189762. A: ventral view; B: dorsal view; C: dorsal distal view; D: spur. Scale bar: 1 mm. Abbreviations: rv: ventral marginal cartilage. Full red arrow: furrows of spur.

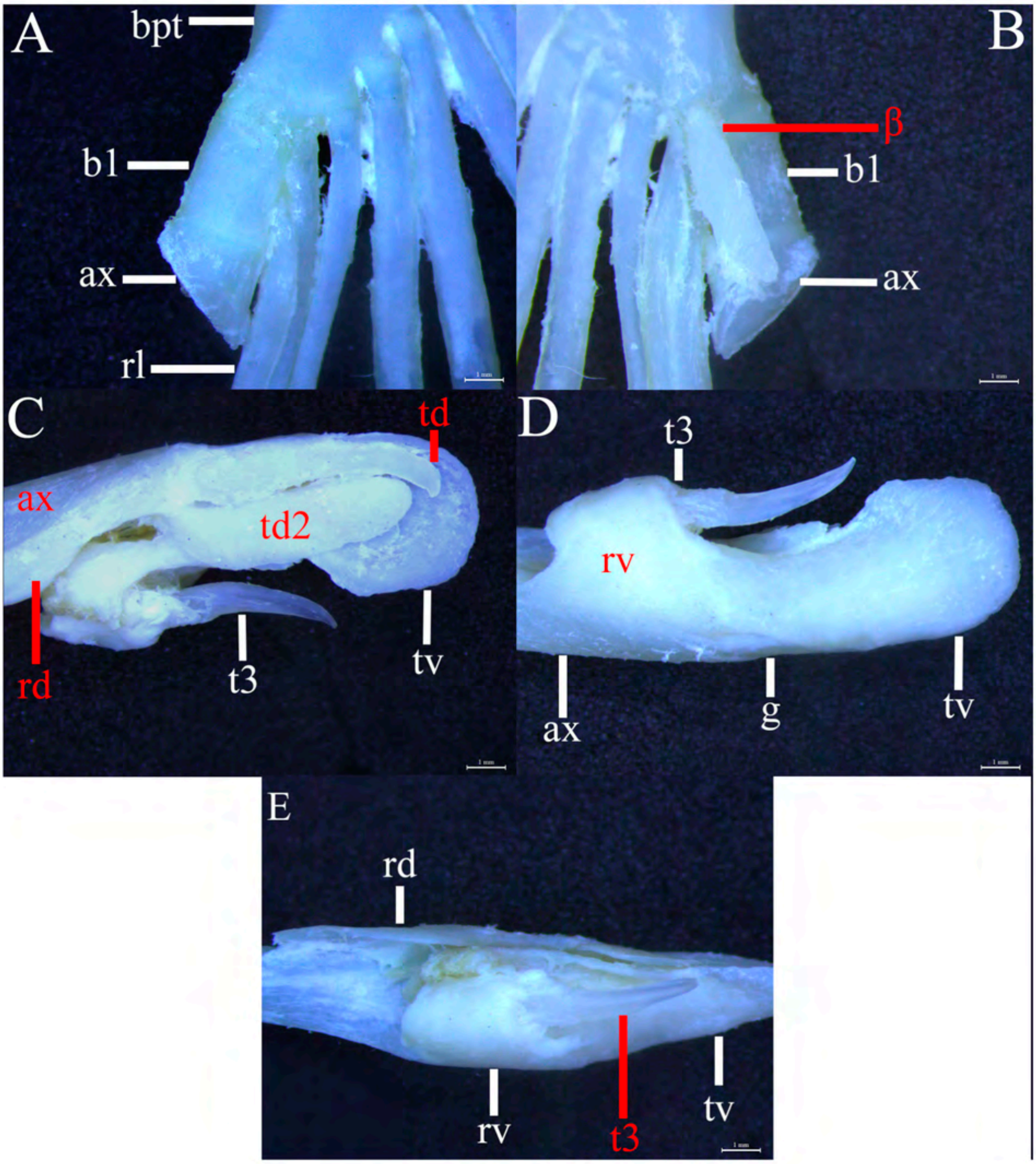

Figure 51. Detail cartilages of the clasper in *Squalus albifrons*, MZUSP uncatalogued, adult male, 760 mm TL. A: ventral view; B: dorsal view; C: distal dorsal view; D: distal ventral view; E: medial distal view. Scale bar: 1 mm. Abbreviations: ax: axial cartilage; bpt: basipterygium; b1: intermediate segment; g: end-style; rl: radials; rd: dorsal marginal cartilage; rv: ventral marginal cartilage; td: dorsal terminal cartilage; td2: dorsal terminal 2 cartilage; tv: ventral terminal cartilage; t3: acessory terminal 3 cartilage; β: beta cartilage.

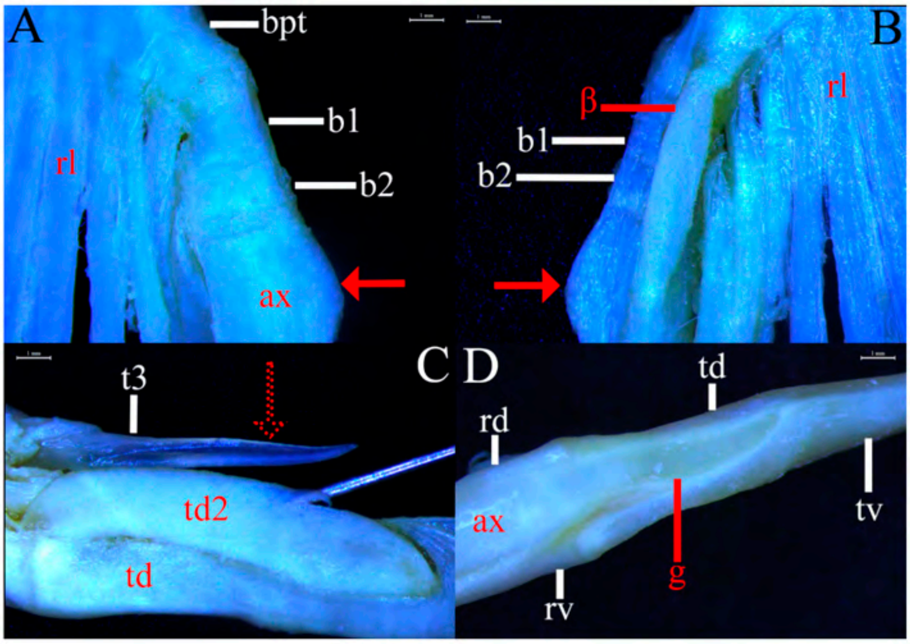

Figure 52. Detail cartilages of clasper in *Squalus montalbani*, MZUSP uncatalogued, adult male, 713 mm TL. A: ventral view; B: dorsal view; C: distal dorsal view; D: lateral view. Scale bar: 1 mm. Abbreviations: ax: axial cartilage; bpt: basipterygium; b1: first intermediate segment; b2: second intermediate segment; g: end-style; rl: radials; rd: dorsal marginal cartilage; rv: ventral marginal cartilage; td: dorsal terminal cartilage; td2: dorsal terminal 2 cartilage; tv: ventral terminal cartilage; t3: acessory terminal 3 cartilage; β: beta cartilage. Full red arrows: medial process; Dotted red arrow: furrow of spur.

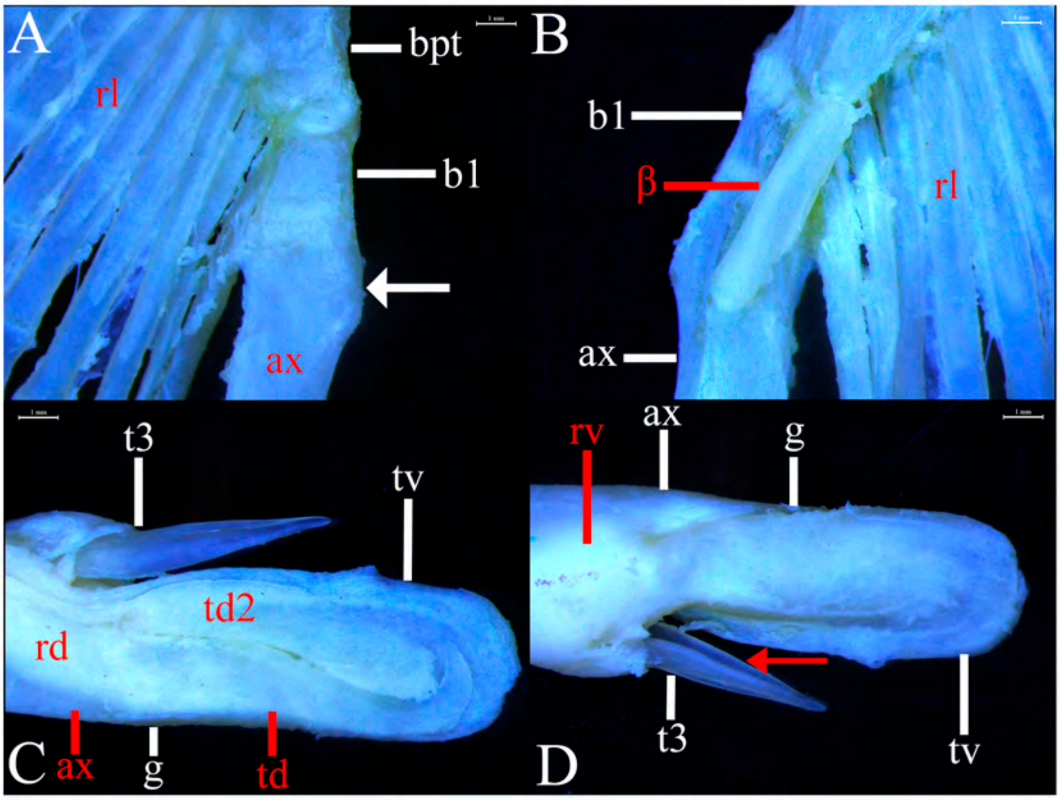

Figure 53. Detail cartilages of the clasper in *Squalus grahami*, MZUSP uncatalogued, adult male, 565 mm TL. A: ventral view; B: dorsal view; C: distal dorsal view; D: distal ventral view. Scale bar: 1 mm. Full white arrow: medial process. Full red arrow: furrow of spur.

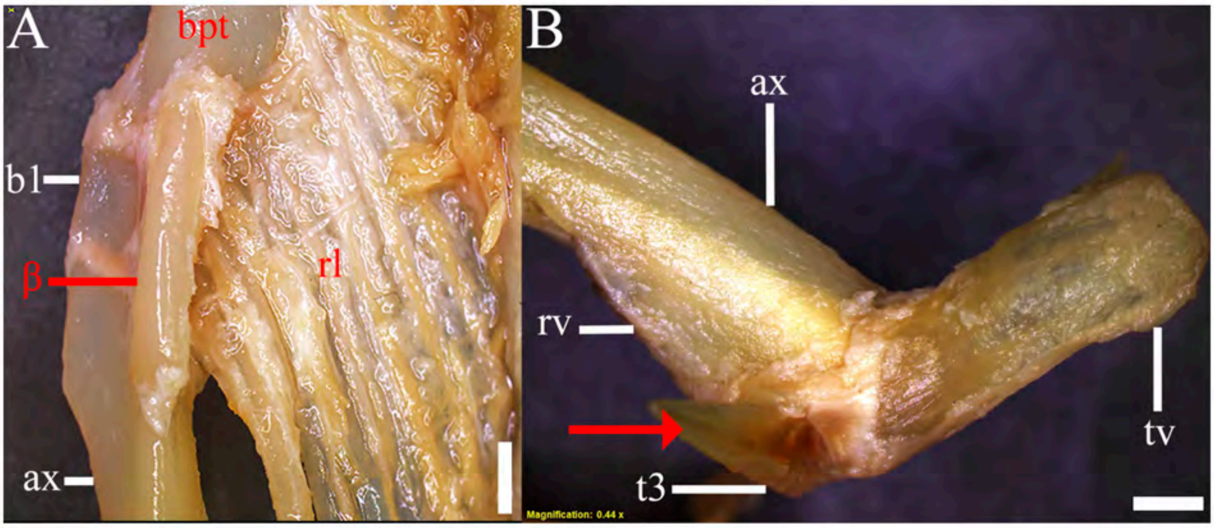

Figure 54. Detail cartilages of the clasper in *Squalus* sp. 3, SAIAB 25370. A: dorsal view; B: distal ventral view. Scale bar: 2 mm. Abbreviations: ax: axial cartilage; bpt: basipterygium; b1: first intermediate segment; rl: radials; rd: dorsal marginal cartilage; rv: ventral marginal cartilage; tv: ventral terminal cartilage; t3: acessory terminal 3 cartilage; β: beta cartilage. Full red arrow: furrow of spur.

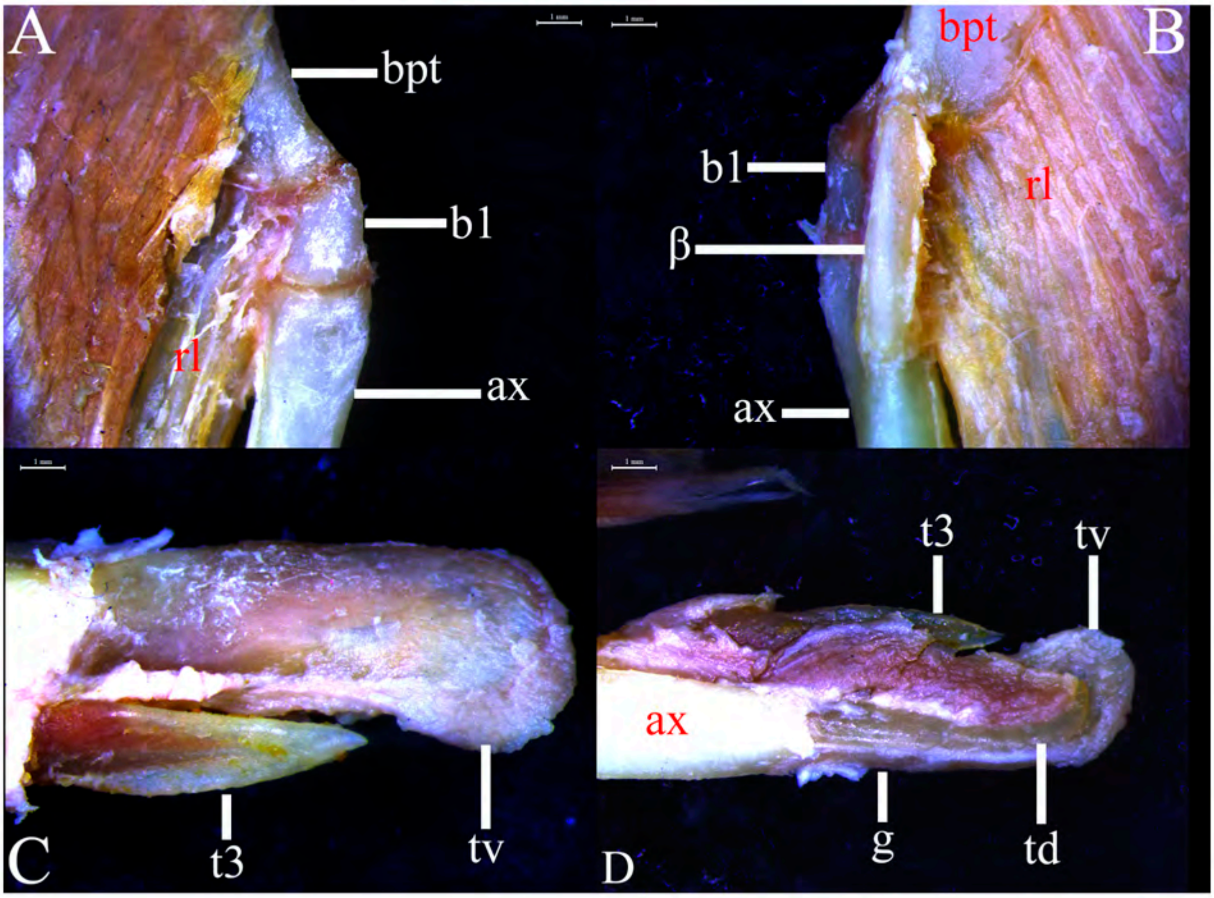

Figure 55. Detail cartilages of the clasper in *Squalus* sp. 7, MNRJ 30184. A: ventral view; B: dorsal view; C: distal ventral view; D: distal dorsal view. Scale bar: 1 mm. Abbreviations: ax: axial cartilage; bpt: basipterygium; b1: first intermediate segment; g: end-style; rl: radials; td: dorsal terminal cartilage; tv: ventral terminal cartilage; t3: acessory terminal 3 cartilage; β: beta cartilage.

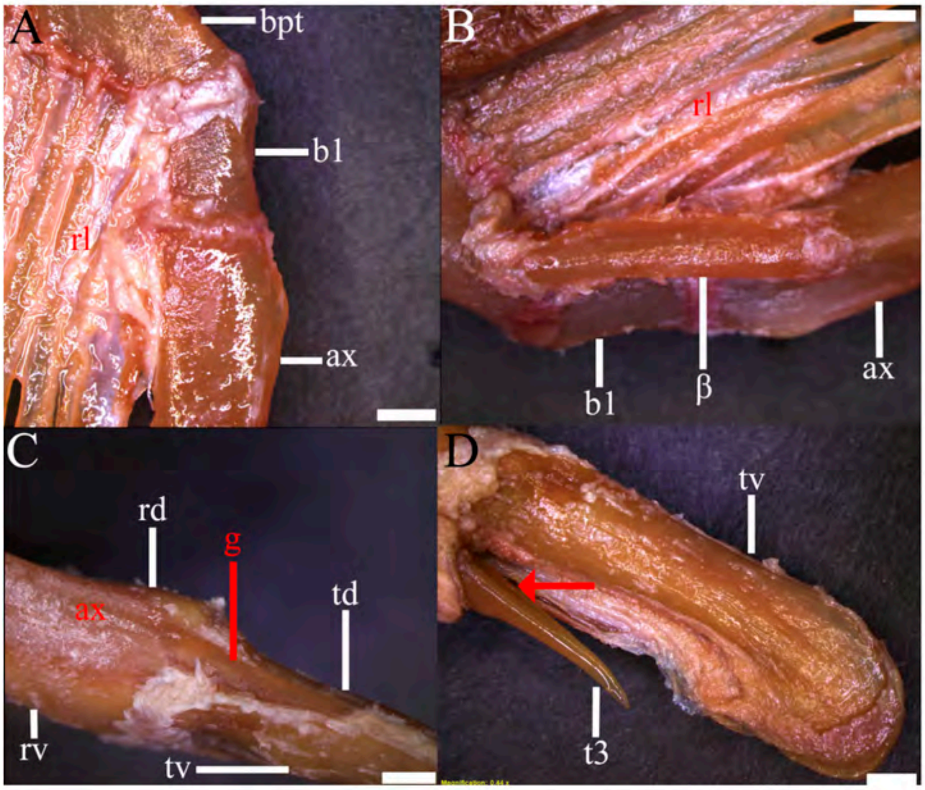

Figure 56. Detail cartilages of the clasper in *Squalus* cf. *blainvillei*, SAIAB 6021. A: ventral view; B: dorsal view; C: lateral view; D: distal ventral view. Scale bar: 2 mm. Abbreviations: ax: axial cartilage; bpt: basipterygium; b1: first intermediate segment; g: end-style; rl: radials; rd: dorsal marginal cartilage; rv: ventral marginal cartilage; td: dorsal terminal cartilage; tv: ventral terminal cartilage; t3: acessory terminal 3 cartilage; β: beta cartilage.

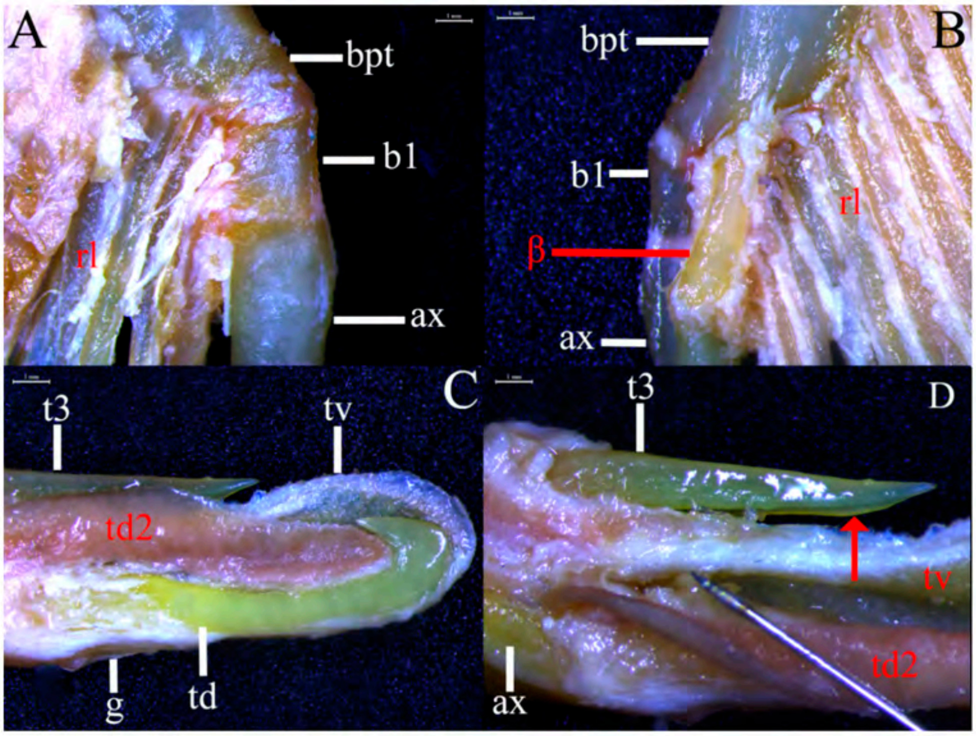

Figure 57. Detail cartilages of the clasper in *Squalus* sp. 4, UERJ 1661. A: ventral view; B: dorsal view; C, D: distal dorsal view. Scale bar: 1 mm. Abbreviations: td2: dorsal terminal 2 cartilage. Full red arrow: furrow of spur.

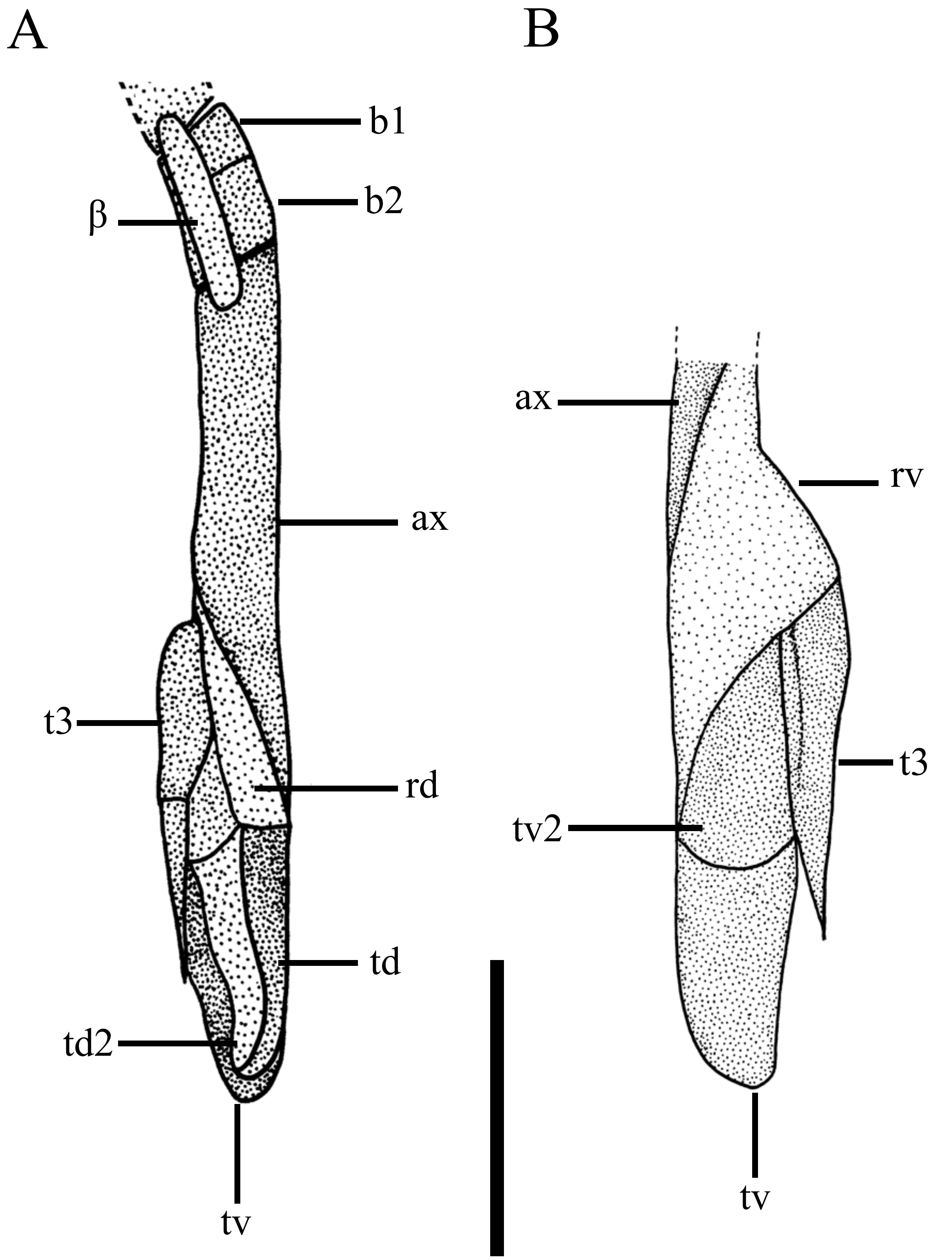

Figure 58. Cartilages of the clasper of *Cirrhigaleus barbifer*, TPM 38074, adult male, 1020 mm TL. A: dorsal view; B: ventral view. Scale bar: 10 mm. Abbreviations: ax: axial cartilage; b1: first intermediate segment; b2: second intermediate segment; rd: dorsal marginal cartilage; rv: ventral marginal cartilage; td: dorsal terminal cartilage; td2: dorsal terminal 2 cartilage; tv: ventral terminal cartilage; tv2: ventral terminal 2 cartilage; t3: acessory terminal 3 cartilage; β: beta cartilage.

Chapter 2

Taxonomic and morphological revision of the genus *Squalus* Linnaeus, 1758 (Elasmobranchii: Chondrichthyes: Squaliformes)

Abstract

Squalus comprises a group of sharks with complex taxonomic history due to the difficulty of morphological distinction between its species, associated to an uncertainty in relation to the application of the available nominal species. A taxonomic and morphological revision of the genus was conducted in order to globally delimitate the valid species and provide efficient morphological characters for distinction among them through a detailed analysis of both external and skeletal morphology. More than 1,800 specimens of *Squalus* were analyzed, including type material from its nominal species collected from the Atlantic, Pacific and Indian Oceans. The genus *Squalus* is herein recognized as a smaller group, which comprises three valid species of spotted-dogfish shark. A second genus is raised and revalidated with 27 valid species of non-spotted dogsharks. Seven possible new species are described in this separated genus. Two nominal species are resurrected as valid and five species are proposed as new synonyms from other valid species within this context. The genera are redefined based on new morphological characteristics and compared with other members of Squaliformes. Each valid species is described and compared with its congeners. Diagnosis and illustrations as well as identification keys to genera and species are also provided in this study.

Resumo

Squalus compreende um grupo de tubarões com história taxonômica complexa devido a dificuldade na diferenciação morfológica entre as espécies, associada a uma incerteza em relação a aplicação das espécies nominais disponíveis. A revisão taxonômica e morfológica do gênero foi conduzida com o intuito de delimitar globalmente as espécies válidas e fornecer caracteres morfológicos eficientes para a diferenciação entre as mesmas através de uma análise detalhada da morfologia externa e dados merísticos. Mais de 1.800 espécimes de *Squalus* foram analisados provenientes dos Oceanos Atlântico, Pacífico e Índico, incluindo material-tipo das espécies nominais. O gênero *Squalus* é aqui reconhecido como um grupo menor que abrange três espécies válidas de tubarões com manchas brancas no corpo. Um segundo gênero, separado de *Squalus*, é reconhecido e revalidado com 20 espécies de tubarões sem manchas no dorso. Sete possíveis espécies novas são apresentadas para este gênero. Duas espécies nominais são ressuscitadas como válidas e cinco espécies são propostas como novos sinônimos de outras espécies válidas dentro deste contexto. Os dois gêneros são redefinidos baseados em novas caraterísticas morfológicas e são comparados com outros membros da ordem Squaliformes. Cada espécie válida é descrita e comparada com os congêneres. Diagnoses e ilustrações bem como chaves de identificação para gênero e espécies são também fornecidas no presente estudo.

Introduction

Squalidae Blainville, 1816 comprises a family of the order Squaliformes of sharks that currently includes two genera, *Squalus* Linnaeus, 1758 (type-genus) and *Cirrhigaleus* Tanaka, 1912, which share morphological characters such as two dorsal fins with dorsal spines without lateral grooves, absence of subterminal notch in the caudal fin, and teeth monocuspid, oblique and similar in both jaws (Bigelow & Schroeder, 1957; Compagno *et al*., 2005). *Squalus* is often distinct from *Cirrhigaleus* by a prominent upper precaudal pit and lacking nasal barbels in the anterior margin of the nostrils (Bass *et al*., 1976).

Squalus has a complex taxonomic history due to overlapping of morphological characters between its species, whose identification is presently done using limited and inconsistent characters such as vertebral counts and some external body measurements (Last *et al*., 2007). Currently, *Squalus* comprises 26 valid species (of 60 available nominal species) with occurrences all over the world (Last *et al*., 2007; Ebert *et al*., 2013a). Among these are: *Squalus acanthias* Linnaeus, 1758 (type-species); *S. acutipinnis* Regan, 1908; *S. albifrons* Last, White & Stevens, 2007; *S. altipinnis* Last, White & Stevens, 2007; *S. blainvillei* (Risso, 1826); *S. brevirostris* Tanaka, 1912; *S. bucephalus* Last, Séret & Pogonoski, 2007; *S. chloroculus* Last, White & Motomura, 2007; *S. crassispinus* Last, Edmunds & Yearsley, 2007; *S. cubensis* Howell-Rivero, 1936; *S. edmundsi* White, Last & Stevens, 2007; *S. formosus* White & Iglésias, 2011; *S. grahami* White, Last & Stevens, 2007; *S. griffini* Phillipps, 1931; *S. hemipinnis* White, Last & Yearsley, 2007; *S. japonicus* Ishikawa, 1908; *S. lalannei* Baranes, 2013; *S. megalops* (Macleay, 1881); *S. melanurus* Fourmanoir & Rivaton, 1979; *S. mitsukurii* Jordan & Snyder (1903); *S. montalbani* Whitley, 1931; *S. nasutus* Last, Marshall & White, 2007; *S. notocaudatus* Last, White & Stevens, 2007; *S. rancureli* Fourmanoir & Rivaton, 1979; *S. raoulensis* Duffy & Last, 2007; *S. suckleyi* (Girard, 1854).

Species of the genus are usually divided into "groups/complex of species" according to their morphological similarity: *S. acanthias*, *S. megalops* and *S. mitsukurii* groups (Bigelow & Schroeder, 1948, 1957; Compagno *et al*., 2005; Last *et al*., 2007). Recent taxonomic investigations on the genus (Figueirêdo, 2011; Viana & Carvalho, *in press*; Viana *et al*., *in prep*.) have revealed that the recognition of "group of species" is unnecessary due to overlapping of morphological characteristics among these groups. Last *et al*. (2007) noticed that *S. hemipinnis* from Indonesian waters relay into two different groups of species, *S. megalops* and *S. mitsukurii* groups, indicating that these overlaps can potentially occur on species-level as well. Uncertainty regarding the classification of some nominal species means that a thorough taxonomic and morphological revision of *Squalus* is imperative.

Despite of the monophyly of the genus *Squalus* (Shirai, 1992; Naylor *et al*., 2012a), the correct application of its nominal species and a better morphological characterization of the valid species still need to be investigated in more detail. The present study aimed to recognize the valid species of *Squalus* around the world and their synonyms as well as provide efficient morphological characters for their correct identification through an exhaustive comparative analysis (external and skeletal) of all species.

Material and methods

Methodology follows the outline provided in the section "Materiais e Métodos" of this Thesis.

Squalidae Blainville, 1816

Squalinidae Leach, 1812: 61-62 (cited, listed; global).
Squalus Blainville, 1816: 121 (revision; global; first established as both family and genus level; *Acanthorhinus* is indicated as new subgeneric name for all species of Squaliformes); Cuvier, 1817: 123-132 (cited); Van der Laan *et al*., 2014: 22 (listed).
Squalides Risso, 1826: 115 (revision; Northeastern Atlantic Ocean; it includes all species of sharks into the same family); Van der Laan *et al*., 2014: 22 (listed).
Squali Müller & Henle, 1841: 1 (systematics; global; it comprises all groups of sharks and rays); Van der Laan *et al*., 2014: 22 (listed).
Squalidae Bonaparte, 1832: 41, 63, 64 (systematics; it included all species of sharks); Bonaparte, 1838: 4, 5, 8, 9 (systematics; Spinacini as subfamily); Gill, 1893: (cited); Jordan & Evermann, 1896: 53, 54 (systematics; North Atlantic Ocean); Jordan & Snyder, 1903: 628-630 (revision; Northwestern Pacific Ocean); Smith, 1912: 677-685 (revision; Southwest Pacific Ocean); Garman, 1913: 13, 188-233 (systematics; global); Jordan & Snyder, 1913: 18 (revision); Regan, 1914: 14 (systematics); Fowler, 1935: 66-87 (systematics; Northeastern Atlantic Ocean); Whitley, 1939: 242 (listed; Southeastern Pacific Ocean); Whitley, 1940: 137-150 (revision; Southwest Pacific Ocean); Fowler, 1941: 223 (revision; Southwest Pacific Ocean); Phillipps, 1946: 14 (cited; Southwest Pacific Ocean); Bigelow & Schroeder, 1948: 17-18, 450-499 (revision; Northwestern Atlantic Ocean); Poll, 1951: 15, 57 (systematics; Southeastern Atlantic, Western Indian Oceans); Smith & Smith, 1953: 57-60 (cited; global); Yuanding, 1960: 106-112 (description; Northwest Pacific Ocean); Compagno, 1973: 26 (listed; global); McEachran & Branstetter, 1984: 128 (cited, listed; Northeast Atlantic Ocean, Mediterranean Sea); Bass *et al*., 1986: 49 (cited; global); Last & Stevens, 1994: 31, 47 (cited; Southwest Pacific Ocean); Compagno & Niem, 1998: 1213-1232 (listed; Western Central Pacific Ocean); Compagno, 1999: 472 (listed; global); Yuanding & Qingwen, 2001: 271-320 (listed, description; Northwest Pacific Ocean); Compagno, 2002: 379-385 (cited; Western Central Atlantic Ocean); Serena, 2005: 18, 19, 26 (listed, revision; Mediterranean Sea, Black Sea); Ebert, 2013: 51 (revision; Indian Ocean); Ebert & Stehmann, 2013: 56 (revision; North Atlantic Ocean); Van der Laan *et al*., 2014: 22 (listed); Ebert *et al*., 2013: 73-95 (cited, description; global); Nakabo, 2013: 194–196 (listed; Western Pacific Ocean).
Spinaces Müller & Henle, 1841: 83 (systematics; global; it comprises species of *Acanthias*, *Spinax*, *Centrina*, *Centrophorus* and *Centroscyllium*); Duméril, 1865: 435 (systematics; global; it was also called Spinaceans by this author with same subdivision as provided by Müller & Henle, 1841).
Spinacoidae Gill, 1861: 60 (systematics; North Atlantic Ocean; the genus *Acanthias* (=*Squalus*) and *Centroscyllium* belonged to subfamily Spinacinae); Gill, 1862: 38 (systematics; global); Macleay, 1881: 366 (revision; genus *Acanthias* comprises all species of *Squalus*).
Spinacidi Poey, 1868: 211, 454 (revision; Central Atlantic Ocean);
Spinacidae: Ogilby, 1886: 4 (listed; Southwest Pacific Ocean); Günther, 1870: 417 (description; global).
Squalinae: Fowler, 1941: 223 (as subfamily; revision; Southwest Pacific Ocean); Compagno, 1973: 26 (listed as subfamily, including *Squalus*, *Cirrhigaleus* and *Centrophorus*; global)
Squalinidae: Van der Laan *et al*., 2014: 22 (listed).
Seláciens: Van der Laan *et al*., 2014: 22 (listed).
Acanthidae: Van der Laan *et al*., 2014: 22 (listed).

Type genus: *Squalus* (Artedi) Linnaeus, 1758
Content: Squalidae comprises two genera, *Squalus* and *Flakeus*.

Definition. Members of Squalidae share the following morphological characteristics: dorsal spines ungrooved in front of each dorsal fin; caudal fin without subterminal notch in the post-ventral caudal margin. It differs from other Squaliformes on having supraethmoidal processes in the neurocranium, and upper and lower precaudal pits present while these characteristics are absent in other families. Squalidae shares with Centrophoridae anterior margin of nostrils very short and lobe-like, upper and lower labial furrows present, although lower one without a fold. Squalidae shares with *Cirrhigaleus* and *Centrophorus* teeth with cuspid short, oblique or somewhat vertical. It also shares with Centrophoridae, Oxynotidae, Dalatiidae, and Somniosidae teeth unicuspid, although it is distinguished from them (except *Centrophorus* and *Cirrhigaleus*) and Etmopteridae on having teeth similar in both jaws (vs. dissimilar). Squalidae, Dalatiidae and *Cirrhigaleus* share lateral keel present in the caudal peduncle.

Comparisons within Squaliformes. Species of *Squalus* and *Flakeus* differ from species of *Oxynotus* and *Cirrhigaleus* on having body fusiform (vs. trihedral) and transition between upper and lower caudal lobes discontinuous (vs. continuous). Squalidae is separated from Oxynotidae on lacking anterior and posterior ocular membrane and lateral-ventral keel in the body. Species of Squalidae is distinguished from Dalatiidae, Etmopteridae and Somniosidae on having spiracles lateral-posteriorly to the eyes (vs. dorsally in the head). *Squalus* and *Flakeus* are easily distinguished from *Oxynotus* and *Isistius* on lacking lips surrounding the mouth (vs. conspicuous lips). Etmopteridae also differs from Squalidae on having teeth tricuspid at least in one of the jaws, and lacking upper labial furrow.

Remarks. Jordan & Evermann (1896) and Jordan & Snyder (1903) erroneously pointed out that Rafinesque (1810) first considered the name *Squalus* for a group of species that lacks anal fin and it has spiracles, contributing to the confusion of the correct authorship of Squalidae. Rafinesque (1810) did not consider family level in his classification, placing genera just after orders, following Artedi (1738). *Squalus* was restricted to a group of three nominal species, including *Squalus acanthias* in this study. Rafinesque (1810) raised many other taxa to new genera (e.g. *Oxynotus*, *Etmopterus*, *Dalatias*) that also have the same characteristics pointed out by Jordan & Evermann (1896) and Jordan & Snyder (1903) for *Squalus*.

Blainville (1816) raised *Squalus* to family and genus level at the same time for a larger group of species of sharks. *Acanthorhinus* Blainvillei, 1816 (= *Squalus*), then, was provided as subgeneric name for a group that retains *S. acanthias* and all species that lacks anal fin and have spiracles, which nowadays correspond to species of the order Squaliformes. According to Article 11.7 from ICZN, the authorship of Squalidae is attributed to Blainvillei (1816) because he clearly stated it to denote a suprageneric taxon and in reference to *Squalus* as a valid generic name. Later, Bonaparte (1832) corrected its suffix by adding *–idae* into the name for the first time, the original authorship and date still must be attributed to Blainville (ICNZ, Art. 11.7).

Comparative material: *Isistius brasiliensis* (1 specimen): SAIAB 64998, juvenile female, 403 mm TL, Angola. *Oxynotus centrina* (1 specimen): SAIAB 192249, adult female, 545 mm TL, Madagascar. *Centrophorus moluccensis* (2 specimens): SAIAB 189434, adult female, 833 mm TL, off Northern Madagascar; SAIAB 189448, juvenile male, 435 mm TL, off Northern Madagascar. *Centrophorus granulosus* (1 specimen): SAIAB 189432, adult male, 763 mm TL, off Northern Madagascar. *Deania calcea* (1 specimen): SAIAB 192867, juvenile male, 453 mm TL, off Southern Madagascar. *Deania quadrispinosa* (2 specimens): SAIAB 189437, adult female, 890 mm TL, adult male, 825 mm TL, off Northern Madagascar. *Etmopterus pusillus* (1 specimen): SAIAB 192260, adult male, 395 mm TL, Madagascar. *Etmopterus sensotus* (4 specimens): SAIAB 189442, juvenile female, 170 mm TL, juvenile male, 146 mm TL, off Northern Madagascar; SAIAB 191641, juvenile female, 200 mm TL, Madagascar; SAIAB 199441, adult male, 225 mm TL, off Northern Madagascar. *Centroscyllium fabricci* (1 specimen): SAIAB 26424, juvenile female, 520 mm TL, off West coast, South Africa. *Centroselachus crepidater* (1 specimen): SAIAB 25724, adult female, 810 mm TL, off Cape Peninsula, South Africa. *Zameus squamulosus* (1 specimen): SAIAB 6093, juvenile female, 645 mm TL, Kwazulu-Natal, South Africa.

Identification key to genera of Squalidae

1. – Body with white spots dorsally; anterior margin of nostrils unilobate in adults; origin of first dorsal fin posterior to pectoral free rear tips; first dorsal spine smaller than second dorsal spine, not reaching half of its fin height; dermal denticles unicuspid with single ridge……….…..……………...………………......***Squalus* Linnaeus, 1758 (type-genus)**

– Body uniformly colored, lacking spots; anterior margin of nostrils bilobate; origin of first dorsal fin anterior or over pectoral free rear tips; first dorsal spine as large as second dorsal spine, often reaches fin apex; dermal denticles unicuspid or tricuspid with three ridges….…………………...………………….……..…………………***Flakeus* Whitley, 1939**

Squalus (Artedi) Linnaeus, 1758

Squalus Artedi, 1735: 102-103 (description); Artedi, 1738: 504 (description); Linnaeus, 1758: 233 (original description; "Oceano Europaeo"; type posteriorly designated by Gill, 1861); Molina, 1782: 188, 189 (catalogued; Chile); Rafinesque, 1810: 45 (catalogued; Sicily); Bonaparte, 1832: 63 (listed); Girard, 1855 (catalogued; Chile); Gill, 1861: 59 (catalogued; Eastern coast of North America); Gill, 1862: 38-39 (cited, listed; subsequent designation of type species *Squalus acanthias*; global); Poey, 1868: 211, 213, 454 (listed; Cuba); Berg, 1895: 5, 6 (catalogued; Argentina and Uruguay); Jordan & Evermann, 1898: 53, fig. 24 (catalogued; North and Central America); Jordan & Fowler, 1903: 629, 630 (listed, Japan); Schreiner & Ribeiro, 1903: 79 (listed; Brazil); Jordan, 1907: 202 (cited); Miranda-Ribeiro, 1907: 167, 168 (catalogued; Brazil); Regan, 1908: 39, 45, 48 (identification key, listed); Smith, 1912 (or 1914??): 677-679 (revision; Southwest Pacific Ocean); Garman, 1913: 191 (description); Jordan *et al.*, 1913: 18 (catalogued; Japan); Miranda-Ribeiro, 1923 (catalogued; Brazil); Phillipps, 1931: 360-361 (cited; Southwest Pacific Ocean); Daniel, 1934 (general description); Fowler, 1935: 67, 69-71 (systematics; Northeastern Atlantic Ocean); Howell-Rivero, 1936: 45 (revision; Cuba); Fowler, 1936: 69-71 (description; Western Africa); Whitley, 1939: 242 (listed; Southeastern Pacific Ocean); Fowler, 1941: 223, 255-262 (cited, revision; Southwest Pacific Ocean); Fowler, 1941: 129 (listed; Brazil); Bigelow & Schroeder, 1948: 451-480, figs 87-90 (revision; Northwestern Atlantic); Poll, 1951: 15, 57 (systematics; Southeastern Atlantic, Western Indian Oceans); Bigelow, Schroeder & Springer, 1953: 220-222 (cited; Western Atlantic); Smith & Smith, 1953: 57, 59-60 (cited, description; Southeast Atlantic Ocean, West Indian Ocean); Bigelow & Schroeder, 1957: 26-37, figs 3, 4 (description); Garrick, 1960: 519-557 (revision; New Zealand); Yuanding, 1960: 106-112 (description; Northwest Pacific Ocean); Ledoux, 1970, 65-69 (revision; Mediterranean Sea); Bass *et al.*, 1976 (revision; Eastern South Africa); Figueiredo, 1977: 8 (catalogued; Southeastern Brazil); Cadenat & Blache, 1981: 46-52; figs 28-31 (revision; Mediterranean Sea); Figueiredo, 1981: 17 (listed; Brazil); Lucena & Lucena, 1981: 2-4 (catalogued; Brazil); Compagno, 1984: 109-123 (catalogued); Kondyurin & Myagkov, 1984: 118-120, (revision; Western Atlantic); McEachran & Branstetter, 1984: 146 (cited; Northeast Atlantic Ocean, Mediterranean Sea); Menni *et al.*, 1984: 62, 83, 84 (catalogued; Argentina, Uruguay); Muñoz-Chápuli, 1985: 396-400 (description); Bass *et al.*, 1986: 49, 60-62 (cited; Southeast Atlantic Ocean); Myagkov & Kondyurin, 1986: 1-20 (revision; Atlantic); Parin, 1988: 43-49 (cited; Southeast Pacific Ocean); Muñoz-Chápuli & Ramos, 1989 (revision; Eastern Atlantic); Gadig & Moreira, 1992: 112, 118 (cited;

Brazil); Calderón, 1994 (cited; Brazil); Marques, 1994 (description; Brazil); Last & Stevens, 1994: 47-49, 91-102 (cited, description; Southwest Pacific Ocean); Gomes *et al*., 1997: 93-98 (catalogued; Brazil); Cervigón & Alcalá, 1999: 122 (revision; Venezuela); Compagno & Niem, 1998: 1215-1217, 1229-1232 (cited; Western Central Pacific Ocean); Compagno, 1999: 472 (listed; global); Compagno & Niem, 1999: 1229-1232 (revision; Western-Central Pacific); Lessa *et al*., 1999 (cited, listed; Brazil); Marques, 1999 (description; Brazil); Mazzoleni & Schwingel, 1999: 114 (listed; South Brazil); Gadig *et al*., 2000: 129 (cited; Ceará, Brazil); Szpilman, 2000: 75 (listed; Brazil); Gadig, 2001: 54-59 (catalogued; Brazil); Soto, 2001: 94-96 (listed; Brazil); Yuanding & Qingwen, 2001: 310-313 (description; Northwest Pacific Ocean); Compagno, 2002: 380-385 (revision; Western Central Atlantic); Nion *et al*., 2002: 4, 65 (listed; Uruguay); Haimovici *et al*., 2003 (cited; Brazil); Meneses & Paesch, 2003: 7, 8, 25 (guide); FIP, 2005: 51, 52 (cited; Chile); Heemstra & Heemstra, 2004 (cited, Southern Africa): 49, 53-54; Soto & Mincarone, 2004: 73-82 (catalogued; Brazil); Compagno *et al*., 2005: 72 (catalogued); Serena, 2005: 19, 26 (listed, revision; Mediterranean Sea, Black Sea); Haddad & Gadig, 2005 (cited; Brazil); Lamilla & Bustamante, 2005: 9, 26 (cited; Chile); Hazin *et al*., 2006 (cited; Norteastern Brazil); Jablonski *et al*., 2006 (cited; Brazil); Nelson, 2006: 66 (listed); Last *et al*., 2007 (revision; Australia); Louro & Rossi-Wongtschowski, 2007 (cited; Brazil); Menni & Lucifora, 2007: 2, 3 (listed; Argentina, Uruguay); Pon & Gandini, 2007 (cited; Argentina); Last & Stevens, 2009 (revision; Australia); Carrier *et al*., 2010: 44, 127, 139 (cited); Gomes *et al*., 2010: 44, 45 (cited; Brazil); Menni *et al*., 2010 (cited; Southwestern Atlantic); Saéz *et al*., 2010: 623, 624 (identification key; Chile); Tomás *et al*., 2010 (cited; Brazil); Eschmeyer & Fricke, 2011 (catalogued); Bornatowski & Abilhoa, 2012: 35 (cited; Brazil); Ebert, 2013: 51-64 (revision; Indian Ocean); Ebert & Stehmann, 2013: 56-66 (revision; North Atlantic Ocean); Ebert *et al*., 2013: 73-95 (cited, description; global); Nakabo, 2013: 194 (cited; Western Pacific Ocean); Rosa & Gadig, 2014: 92, 97 (listed, cited; Brazil).

Squallus Scopoli, 1777: 464 (misspelling for *Squalus*).

Acanthias Leach, 1812: 62 (original description; global; type species by originally included nominal species); Risso, 1826: 131 (description, not illustrated; Mediterranean Sea); Bonaparte, 1838: 8 (description; North Atlantic Ocean); Müller & Henle, 1841: 83 (listed); Gill, 1861: 60 (catalogued; North and Central America); Duméril, 1865: 435, 436 (description); Günther, 1866: 384, 396 (listed; Central America); Günther, 1870: 417–419 (description; global); Vaillant, 1888: 7 (cited; Argentina); Bigelow & Schroeder, 1948: 452 (synonymy of *Squalus*).

Acanthorhinus Blainville, 1816: 121 (subgenus of *Squalus*; original description, not illustrated; type species by absolute tautonymy); Fowler, 1936: 61 (cited); Bigelow & Schroeder, 1948: 452 (listed).

Spinax: Cuvier, 1817: 130 (cited); Cuvier, 1863: 320 (listed); Bigelow & Schroeder, 1948: 452 (listed).

Koinga Whitley, 1939: 242 (subgenus of *Squalus*; original description; Australia; *Squalus whitleyi*, type species by original designation); Whitley, 1940: 140, fig. 153 (revision; Australia); Bigelow & Schroeder, 1948: 452 (synonymy of *Squalus*); Whitley, 1964: 33 (listed; Australia); Compagno, 1984: 109 (revision; global) (synonymy of *Squalus*).

Type species: *Squalus acanthias* Linnaeus, 1758

Content: *Squalus acanthias*, *S. suckleyi*, and *S. wakiyae.*

Definition. The dogfish sharks of the genus *Squalus* are morphologically characterized by having body with white spots dorsally, pectoral fin conspicuously narrow, anterior margin of nostrils unilobed at least in adults, and dermal denticles unicuspid with single median ridge. It differs from other genera of Squalidae in having: first and second dorsal fins equal in length; dorsal fins with length of its inner margin equal to its height; distance between pectoral and pelvic fins equal to distance between pelvic and caudal fins; space between dorsal fins 1.8 times greater than dorsal-caudal space. In contrast to *Flakeus*, *Squalus* has first dorsal spine markedly small, never reaching one-half of dorsal fin height, and length of second dorsal spine twice larger than length of first dorsal spine.

Identification key to species of *Squalus*

1. – Origin of first dorsal fin posterior to vertical line traced at pectoral free rear tips; pelvic fins nearest second dorsal fin than first dorsal fin……………………..........……..………….**2**

– Origin of first dorsal fin prior to vertical line traced at pectoral free rear tips; pelvic fins placed in the midline between first and second dorsal fins fin……………...……………………………………………………..……..…***Squalus suckleyi***

2. – White spots large and numerous (8–13 pairs), distributed into two rows on each side of the body; dermal denticles very narrow at crown with cusp directed posteriorly; presence of segmented ridge in the scapulae…………………............................……***Squalus acanthias***

– White spots tiny and few (1–6 pairs), distributed into single row on each side of the body; dermal denticles markedly broad at crown with cusp forming 45 degrees with body axis; absence of segmented ridge in the scapulae……………................…***Squalus wakiyae***

Squalus acanthias **(Artedi) Linnaeus, 1758**

(Spotted spiny dogfish; piked spurdog; whitespotted spurdog)

Figs. 59–69, Tables 10–13, 15

Galeus acanthias Artedi, 1735: 102-103 (cited).

Squalus acanthias Linnaeus, 1758: 233 (original description, "Oceano Europaeo"); Rafinesque, 1810: 45 (catalogued; Sicily); Cuvier, 1817: 130 (cited); Bonaparte, 1838: 8 (listed; North Atlantic Ocean); Gill, 1862: 39 (cited; global); Poey, 1868: 213, 454 (cited; Cuba); Berg, 1895: 5, 6 (catalogued; Argentina, Uruguay); Jordan & Evermann, 1896: 54 (catalogued; North and Central America); Waite, 1901: 33, 34 (cited; Southwest Pacific Ocean, Atlantic Ocean); Schreiner & Ribeiro, 1903: 79 (listed; Brazil); Jordan, 1907: 202, fig. 144 (description); Regan, 1908: 45, 46 (identification key, listed); Garman, 1913: 192, plates 14 (figs. 1-4), 43 (figs. 9, 10), 59 (figs. 1, 2) (description); Daniel, 1934 (cited); Fowler, 1935: 69-71 (systematics; North Atlantic Ocean); Fowler, 1936: 69-71, figs. 19, 20 (revision; Eastern Atlantic); Fowler, 1941: 257-258 (description; Southwest Pacific Ocean); Bigelow & Schroeder, 1948: 455-473, figs. 87 (A-D), 88 (revision; Northwestern Atlantic); Bigelow & Schroeder, 1953: 47-51, fig. 17 (description, cited); Bigelow, Schroeder & Springer, 1953: 221 (cited; Western Atlantic); Smith & Smith, 1953: 59-60 (cited, description; Southeast Atlantic Ocean); Bigelow & Schroeder, 1957: 30, fig. 3D (description); Garrick, 1960: 520, figs. 1 (A-C), 3(G-M), 5 (revision; New Zealand); Bass *et al*., 1976: 13, 14, figs. 8 (F-G) , 9 (revision; Eastern South Africa); Cadenat & Blache, 1981: 46-48; fig. 28(A-E) (revision; Mediterranean

Sea); Lucena & Lucena, 1981: 2, fig. 3 (catalogued; Brazil); Compagno, 1984: 109-113 (catalogued); Kondyurin & Myagkov, 1984: 118-120, fig. 1A (revision; Western Atlantic); McEachran & Branstetter, 1984: 128, 146 (cited, description; Northeast Atlantic Ocean, Mediterranean Sea); Menni *et al.*, 1984: 62, 83, 84 (catalogued; Argentina, Uruguay); Bass *et al.*, 1986: 60-61 (cited, description; global); Myagkov & Kondyurin, 1986: 1-20, fig. 1 (A, E, F, H) (revision; Atlantic); Parin, 1988: 43-49 (cited, listed; Southeast Pacific Ocean); Wheeler, 1991: 157 (listed); Last & Stevens, 1994: 48, 98-99 (cited, description; Southwest Pacific Ocean); López *et al.*, 1996: 7, 8 (listed; Argentina); Cousseau & Perrotta, 1998: 34-35 (description; Argentina); Compagno, 1999: 472 (listed; global); Lessa *et al.*, 1999: 26, 61, 150 (cited, listed; Brazil); Mazzoleni & Schwingel, 1999: 114 (listed; Itajaí, Brazil); Szpilman, 2000: 75 (listed; Brazil); Gadig, 2001: 29, 36, 54-57, fig. 27 (catalogued; Brazil); Soto, 2001: 94, 95 (listed; Brazil); Yuanding & Qingwen, 2001: 310-311 (cited; global); Compagno, 2002: 380, 381, 383 (description; North and Central Atlantic); Nakabo, 2002: 155 (listed; global); Nion *et al.*, 2002: 4 (listed; Uruguay); Haimovici *et al.*, 2003: 38, 39 (cited; Brazil); Meneses & Paesch, 2003: 7, 25, 45 (cited; Argentina); Smith & Heemstra, 2003: 61, 62, fig. 5.24 (identification key; description; South Africa); Heemstra & Heemstra, 2004 (cited, Southern Africa): 54; Soto & Mincarone, 2004: 73, 74 (catalogued; Brazil); FIP, 2005: 51, 52 (cited; Chile); Lamilla & Bustamante, 2005: 9, 26 (cited; Chile); Nelson, 2006: 66 (listed); Menni & Lucifora, 2007: 3 (cited; Argentina and Uruguay); Pon & Gandini, 2007 (cited; Argentina); Carrier *et al.*, 2010: 44, 127, 139 (cited); Gomes *et al.*, 2010: 44, 45 (cited; Brazil); Menni *et al.*, 2010 (cited; Southwestern Atlantic); Saéz *et al.*, 2010: 623 (identification key; Chile); Menezes, 2011: 4 (listed; Southern Brazil); Ebert & Stehmann, 2013: 56-62 (revision; North Atlantic Ocean); Ebert *et al.*, 2013: 76, 83 (cited, description; Atlantic Ocean, South Pacific Ocean); Nakabo, 2013; 194 (listed; Japan); Rosa & Gadig, 2014: 92 (listed; Brazil).

Squalus fernandinus Molina, 1782: 188, 189, 285 (original description, not illustrated; Southeast Pacific Ocean); Regan, 1908a: 45, 46 (cited); Waite, 1909: 142; Lahille, 1928: 326; Bigelow, Schroeder & Springer, 1953: 220-222 (cited; Western Atlantic); Eschmeyer & Fricke, 2011 (catalogued).

Acanthorhinus acanthias Blainville, 1816: 121 (original description; not illustrated; type by originally included nominal species); Bigelow & Schroeder, 1948: 452 (cited).

Spinax acanthias: Cuvier, 1817: 130 (cited); Bonaparte, 1832: 64 (listed; Central Atlantic Ocean); Cuvier, 1863: 320 (listed); Bigelow & Schroeder, 1948: 452 (cited).

Acanthias vulgaris Risso, 1826: 13 (original description; Mediterranean Sea); Müller & Henle, 1841: 83 (description); Duméril, 1865: 437 (description); Günther, 1866: 384, 396 (listed; Central America); Günther, 1870: 418–419 (description; global); Macleay, 1881: 366 (catalogued; Australia); Vaillant, 1888: 5 (listed; Argentina).

Acanthias americanus Storer, 1846: 506 (original description; United States of America); Gill, 1861: 60 (listed; North America).

Spinax acantheus: Cuvier, 1863: 320 (cited).

Acanthias lebruni Vaillant, 1888: 5, 13, 14, 33, 34, fig. 2 (original description; type by original designation [MNHN 1883-190, adult male, 655 mm TL, Santa Cruz, Argentina, 50°03'S,68°34'59''W]; Southeast Pacific Ocean).

Squalus lebruni Berg, 1895: 6 (catalogued; Argentina, Uruguay); Menni *et al.*, 1984: 62, 84 (catalogued; Southwest Atlantic Ocean).

Squalus blainvillei: Schreiner & Ribeiro, 1903: 79 (listed; Brazil); Miranda-Ribeiro, 1907: 168 (in part; catalogued; Brazil).

Squalus kirki Phillipps, 1931: 360-361 (original description, not illustrated; illustration provided in previous publication from Phillipps, 1929; BMNH 1931.8.10.1, adult male, 785 mm TL, New Zealand [syntype hereby designated]; Southwest Pacific Ocean); Fowler, 1941: 256 (listed; Southwest Pacific Ocean); Phillipps, 1946: 14-16, fig. 4 (description; Southwest Pacific Ocean).

Squalus whitleyi Phillipps, 1931: 361 (name only, not illustrated; original description by McCoy, 1886; Southwest Pacific Ocean).

Squalus barbouri Howell-Rivero, 1936: 47, 48 (original description, not illustrated; Cuba).

Squalus tasmaniensis Howell-Rivero, 1936 (original description, not illustrated; Southwest Pacific Ocean); Last *et al.*, 2007: 109-113, figs. 1B, 2B (revision; Southwest Pacific Ocean); Fowler, 1941: 256 (description; Southwest Pacific Ocean); Eschmeyer & Fricke, 2011 (catalogued).

Flakeus tasmaniensis Whitley, 1940: 139, fig. 150 (description; Southwest Pacific Ocean).

Koinga whitleyi Whitley, 1940: 139, figs. 151, 152 (description; Southwest Pacific Ocean).

Koinga kirki Whitley, 1940: 140, fig. 153 (listed; Southwest Pacific Ocean).

Squalus sp. of *acanthias* group: Figueiredo, 1981: 17 (listed; Brazil); Gomes *et al.*, 1997: 93 (catalogued; Brazil); Marques, 1999 (cited; Brazil).

Lectotype: NRM 85, neonate female, 177 mm TL, unknown locality, Donation by King Gustav IV Adolf from the collection at Ulriksdal in 1745 with printed label from 1764 or before. Lectotype hereby designated.

Paralectotypes (3 specimens): UUZM 159, juvenile male, 346 mm TL, unknown locality, Donation by Jonas Alströmer in 1749 with printed label from 1787 or before; UUZM 160, neonate female, 380 mm TL, dried material, Donation by Jonas Alströmer in 1749 with printed label from 1787 or before; UUZM 287, adult male, 700 mm TL, stuffed specimen, Donation by Museum Gustavo-Adolphianum in 1803 (formerly from King Gustav IV Adolf's collection).

Type locality: "Oceano Europaeo", and possibly west coast of Sweden.

Non-type material: NEAO (220 specimens): AMS I 2893, neonate female, 175 mm TL, Faroe Islands; AMS B 5143, juvenile male, 242 mm TL, England; AMS B 5144, juvenile female, 237 mm TL, England; AMS B 5145, juvenile female, 237 mm TL, England; AMS B 5408, juvenile male, 395 mm TL, England; BMNH 1845.6.22.120, neonate female, 244 mm TL, neonate male, 238 mm TL, Mediterranean Sea; BMNH 1888.2.6.72, adult male, 690 mm TL, United Kingdom; BMNH 1888.5.23-52, juvenile male, 415 mm TL, United Kingdom; BMNH 1902.6.9.15-16, two juvenile females, 198-208 mm TL, Italy, Mediterranean Sea; BMNH 1928.9.18.7-12, nine embryos, 40-80 mm TL, Republic of Ireland; BMNH 1929.8.7.2-3, two juvenile males, 278-280 mm TL, Ukraine, Black Sea; BMNH 1929.10.20.1, adult female, 875 mm TL, United Kingdom; BMNH 1930.3.21.1, juvenile female, 310 mm TL, Ukraine, Black Sea; BMNH 1931.4.27.2, adult female, 800 mm TL, United Kingdom; BMNH 1950.7.26.2, juvenile female, 570 mm TL, Republic of Ireland; BMNH 1960.9.8.2-3, two juvenile females, 246-250 mm TL, Republic of Ireland; BMNH 1968.1.15.2, juvenile female, 258 mm TL, unknown locality; BMNH 1968.8.21.2, neonate female, 173 mm TL, unknown locality; BMNH 1976.7.30.20, adult female, 523 mm TL, France, Mediterranean Sea; BMNH 1983.3.8.1, juvenile male, 266 mm TL, United Kingdom; BMNH 1989.11.14.1, neonate female, 230 mm TL, Thames, United Kingdom; BMNH 2013.9.3.1-2, two neonate females, 210-219 mm TL, Republic of Ireland; BMNH 2013.9.3.3, neonate female, 288 mm TL, United Kingdom,; BMNH 2013.9.3.5, neonate female, 282 mm TL, United Kingdom; MNHN 1959-564, neonate female, 220 mm TL, neonate male, 224 mm TL, Aber-vrach, France, 48°36'N,4°34'59''W; MNHN 1974-281, adult male, 590 mm TL, Concarneau, France, 47°49'59''N,3°55'01''W; NMW 2091, adult female, 840 mm TL, Helgoland, The North Sea; NMW 18853, two neonate males, 183-185 mm TL, neonate female, 185 mm TL, Triest, Italy; NMW 22445, two neonate females, 195-208 mm TL, Dalmatien, Croatia; NMW 50119, adult female, 910 mm TL, Dalmatien, Croatia; NMW 59659, juvenile male, 345 mm TL, The North Sea; NMW 60875, two neonate males, 208-210 mm TL, five neonate females, 198-210 mm TL, Triest, Italy; NMW 61518, neonate male, 178 mm TL, Triest, Italy; NMW 78036, neonate male, 207 mm TL, Dalmatien, Croatia; NMW 83676, juvenile male, 340 mm TL, The North Sea; NMW 83709, neonate male, 204 mm TL, Dalmatien, Croatia; NMW 83711, neonate female, 275 mm TL, Dalmatien, Croatia; NMW 83710, juvenile female, 337 mm TL, Spalato, Croatia; NMW 83978, adult female, 620 mm TL, Spalato, Croatia; NMW 84778, three neonate females, 133-145 mm TL, Triest, Italy; NMW 84781, adult female, 525 mm TL, Triest, Italy; NMW 86034, two juvenile males, 495-660 mm TL, adult male, 750 mm TL, Bergen, Norway; NMW 86149, juvenile male, 565 mm TL, two adult females, 590-615 mm TL, Bergen, Norway; NMW 87204, juvenile female, 510 mm TL, adult female, 705 mm TL, adult male, 803 mm TL, Bergen, Norway; NMW 90131, adult female, 983 mm TL, Triest, Italy; NRM 9012, juvenile female, 277 mm TL, juvenile male, 355 mm TL, Napoli, Italy, 14°25'N,408°333'W; NRM 9015, neonate male, 185 mm TL, neonate female, 185 mm TL, The North Sea; NRM 9016, two neonate males, 130 mm TL, neonate female, 130 mm TL, Northern Norway; NRM 21755, neonate male, 158 mm TL, Northwest of Bergen, Norway, 532°472’N,603°911’W; NRM 21756, three neonate females, 164-170 mm TL, eight neonate males, 162-226 mm TL, Northwest of Bergen, Norway, 532°472’N,603°911’W; NRM 21757, adult male, 690 mm TL, Bohuslän, Sweden, 11°8’N,582°333’W; NRM 21758, adult female, 715 mm TL, Bohuslän, Sweden; NRM 21759, adult female, 775 mm TL, Bohuslän, Sweden; NRM 21760, neonate male, 177 mm TL, four neonate females, 140-177 mm TL, Koster, Sweden; NRM 21762, juvenile female, 420 mm TL, Sweden; NRM 21763, adult male, 645 mm TL, Öresund, near Råå, Sweden; NRM 21764, juvenile female, 260 mm TL, Strömstad, Sweden, 111°667’N,588°667’W; NRM 21765, two neonate males, 87 mm TL, Swede; NRM 21768, three juvenile males, 250-260 mm TL, two juvenile females, 252-256 mm TL, Gullmarn Fjord, Sweden, 114°333’N,58°25’W; NRM 21769 neonate male, 158 mm TL, juvenile female, 243 mm TL, Sweden; NRM 36020, adult female, 745 mm TL, Bohuslän, Sweden, 11°08’N,582°333’W; NRM 37566, juvenile female, 255 mm TL, Venice, Italy; NRM 44740, adult female, 830 mm TL, Bohuslän, Sweden, 11°08’N,585°667’W; NRM 46678, juvenile male, 260 mm TL, juvenile female, 218 mm TL, Skagerrak, 100°167’N,58°7’W; NRM 46690, juvenile male, 255 mm TL, Skagerrak, 104°333’N,584°167’W; NRM 46694, juvenile female, 300 mm TL, Skagerrak, 100°833’N,587°167’W; NRM 46764, juvenile female, 355 mm TL, Sweden; NRM 48733, adult male, 682 mm TL, Sweden; RMNH.PISC. 4315, juvenile female, 465 mm TL, The Netherlands; RMNH.PISC. 27099, juvenile female, 466 mm TL, Schulpengat, The Netherlands; ZMA 112.249, three neonate females, 242-255 mm TL, four neonate males, 240-250 mm TL, The North Sea; ZMA 112.251, neonate female, 255 mm TL, neonate male, 246 mm TL, near England, 55°19’N,05°25’E; ZMA 112.252, three neonate females, 200-213 mm TL, three neonate males, 198-203 mm TL, The North Sea, 57°10’N,03°5’E; ZMA

112.253, two neonate females, 190-200 mm TL, seven neonate males, 115-195 mm TL, The North Sea; ZMA 112.254, three neonate females, 190-195 mm TL, three neonate males, 180-200 mm TL, lichtschip Haaks, The North Sea; ZMA 112.255, four neonate females, 206-215 mm TL, three neonate males, 205-210 mm TL, The North Sea, 56°15’N,05°18’E; ZMA 112.256, neonate female, 204 mm TL, neonate male, 200 mm TL, The North Sea, 54°44’N,06°55’E; ZMA 112.258, juvenile male, 425 mm TL, Clyde, United Kingdom, 55°10’N,05°15’E; ZMA 113.457, three neonate females, 195-200 mm TL, three neonate males, 202-207 mm TL, off Morecambe Bay, England, 54°N,03°50’E; ZMB 4504, adult male, 650 mm TL, The North Sea; ZMB 4505, juvenile male, 435 mm TL, The North Sea; ZMB 4507, juvenile male, 225 mm TL, The North Sea; ZMB 6459, juvenile female, 220 mm TL, Lissabon; ZMB 8397, juvenile female, 550 mm TL, The Netherlands; ZMB 17404, adult male, 670 mm TL, The North Sea; ZMB 17405, adult male, 660 mm TL, juvenile male, 470 mm TL, The North Sea; ZMB 19994, juvenile female, 321 mm TL, Rovigno; ZMB 23134, juvenile female, 292 mm TL, The North Sea; ZMB 23688, juvenile male, 250 mm TL, The North Sea; ZMH 14, juvenile female, 265 mm TL, two juvenile males, 275-294 mm TL, The North Sea, 58°14'N,0°28'W; ZMH 24, juvenile male, 318 mm TL, The North Sea, 55°40'N,04°45'W; ZMH 36, adult female, 730 mm TL, Doggerbank, Germany, 54°40'N,03°10'W; ZMH 10217, three juvenile males, 282-290 mm TL, The North Sea; ZMH 10219, neonate female, 265 mm TL, Neustädter Bucht, Ostsee, Germany; ZMH 10220, neonate female, 245 mm TL, neonate male, 247 mm TL, The North Sea; ZMH 10221, neonate female, 140 mm TL, two neonate males, 145-147 mm TL, North of Norway; ZMH 10222, neonate female, 200 mm TL, 10 neonate males, 195-212 mm TL, Sylt, The North Sea; ZMH 10225, adult female, 600 mm TL, Helgoland, The North Sea; ZMH 11165, neonate female, 179 mm TL, neonate male, 172 mm TL, Mediterranean Sea; ZMH 11167, neonate male, 172 mm TL, Smith Channel; ZMH 100813, adult female, 595 mm TL, juvenile male, 570 mm TL, Artic Sea, 61°14’N,01°47’W; ZMH 100853, two neonate males, 159-163 mm TL, The North Sea, 60°47'N,03°0'W; ZMH 101117, adult male, 700 mm TL, Artic Sea, 64°03’N,53°03’W; ZMH 101766, three neonate females, 251-258 mm TL, neonate male, 250 mm TL, North Atlantic Ocean, 57°59'N,08°49'W; ZMH 101886, adult female, 565 mm TL, adult male, 625 mm TL, Artic Sea, 62°28’N,04°25’E.

NWAO (18 specimens): BMNH 1879.10.9.64, adult female, 620 mm TL, off east coast, The United States of America; BMNH 1881.3.14.249, neonate female, 137 mm TL, off east coast, The United States of America; NRM 36067, adult female, 935 mm TL, Gulf of Maine, Massachusetts, The United States of America; NSMT-P 41928, adult female, 715 mm TL, Atlantic Ocean; SAM 26386, three neonate females, 185-200 mm TL, neonate male, 200 mm TL, Caso Bay, off Maine, The United States of America, 43.65ºS,68.96 ºE; SAM 38271, juvenile male, 240 mm TL, unknown locality, Northwestern Atlantic Ocean; SAM 38276, adult male, 670 mm TL, unknown locality, Northwestern Atlantic Ocean; USNM 116902, neonate male, 220 mm TL, neonate female, 228 mm TL, Florida, The United States of America; USNM 22660, neonate female, 175 mm TL, neonate male, 178 mm TL, Massachusetts, The United States of America; ZMH 11170, juvenile male, 536 mm TL, British Columbia, Canada; ZMH 101004, two juvenile males, 555-635 mm TL, Canada, 47°40’N,59°24’W; ZMH 119920, juvenile female, 314 mm TL, The United States, 40°05’N,72°08’W.

SEAO (88 specimens): HUMZ 151302, juvenile male, 520 mm TL, off Namibia, 22°46’S,12°57’E; SAIAB 4195, neonate female, 145 mm TL, two neonate male, 145-170 mm TL, Cape St. Francis, South Africa, 34.21°S,24.83°E; SAIAB 6034 juvenile male, 460 mm TL, Saldanha Bay, South Africa, 32.83°S,17.66°E; SAIAB 6035 neonate female, 215 mm TL, two neonate males, 210-215 mm TL, Saldanha Bay, South Africa, 32.83°S,17.66°E; SAIAB 10446, neonate female, 240 mm TL, unknown locality; SAIAB 21873, adult male, 675 mm TL, Cape Columbine, South Africa, 32.59°S,17.36°E; SAIAB 21874, adult male, 670 mm TL, Strandfontein, South Africa, 31.89°S,16.53°E; SAIAB 21876, juvenile male, 610 mm TL, Cape Columbine, South Africa, 32.71°S,17.33°E; SAIAB 21877, juvenile male, 590 mm TL, Cape Columbine, South Africa, 32.46°S,17.31°E; SAIAB 21878, juvenile male, 340 mm TL, Port Nolloth, South Africa, 29.06°S,16.66°E; SAIAB 25312, juvenile male, 635 mm TL, west coast of South Africa, 33.23°S,17.68°E; SAIAB 25313, juvenile female, 480 mm TL, west coast of South Africa, 32.25°S,16.88°E; SAIAB 25314, juvenile male, 650 mm TL, west coast of South Africa, 31.63°S,16.34°E; SAIAB 25315, juvenile female, 560 mm TL, west coast of South Africa, 30°S,16.25°E; SAIAB 25316, juvenile male, 620 mm TL, west coast of South Africa, 32.25° S,16.88°E; SAIAB 25317, adult male, 640 mm TL, west coast of South Africa, 31.70°S,17.02°E; SAIAB 25318, juvenile male, 625 mm TL, west coast of South Africa, 31.91°S,17.83°E; SAIAB 25319, juvenile male, 610 mm TL, west coast of South Africa, 32.16°S,16.86°E; SAIAB 25320, juvenile male, 580 mm TL, west coast of South Africa, 30.08°S,15.96°E; SAIAB 25325, juvenile male, 560 mm TL, west coast of South Africa, 32.04°S,16.60°E; SAIAB 25326, juvenile male, 440 mm TL, unknown locality; SAIAB 25327, juvenile male, 535 mm TL, west coast of South Africa, 29.06°S,16.57°E; SAIAB 25719, juvenile male, 600 mm TL, west coast of South Africa, 33.51°S,17.61°E; SAIAB 25918, adult male, 700 mm TL, west coast of South Africa, 31.48°S,17.27°E; SAIAB 26300, adult male, 650 mm TL, west coast of South Africa, 32.70°S,17.20°E; SAIAB 26301, adult female, 670 mm TL, same locality as SAIAB 26300; SAIAB 26302, adult male, 650 mm TL, same locality as SAIAB 27168; SAIAB 26300, adult female, 850 mm TL west coast of South Africa, 29.16°S,14.80°E; SAIAB 40864, neonate female, 200 mm TL, neonate male, 200 mm TL, Algoa Bay, South Africa, 34.03°S,25.70°E; SAIAB 48524, neonate female, 146 mm TL, East London, South Africa, 33.03°S,27.89°E; SAIAB 63974, two neonate males, 243-245 mm TL, near Bay of Cape Doring, South Africa,

31.38°S,17.79°E; SAM 12994, two juvenile females, 460-480 mm TL, Atlantic Ocean; SAM 12995, neonate male, 190 mm TL, Atlantic Ocean; SAM 32450, adult male, 643 mm TL, 30.59ºS,17.08ºE; SAM 32444, juvenile female, 505 mm TL; two juvenile males, 490-620 mm TL, 30.35ºS,15.93ºE; SAM 32505, neonate female, 190 mm TL, 32.83ºS, 17.32ºE; SAM 32584, adult male, 705 mm TL, 31.08ºS, 16.51ºE; SAM 33158, four adult males, 615-670 mm TL, 30.93ºS,16.61ºE; SAM 33159, five juvenile females, 275-515 mm TL; six juvenile males, 285-585 mm TL, 29.83ºS,15.54ºE; SAM 33184, juvenile female, 527 mm TL, 29.91ºS,16.17ºE; SAM 33258, juvenile male, 605 mm TL, 32.75ºS,16.94ºE; SAM 33281, juvenile female, 465 mm TL, 32.66ºS,16.67ºE; SAM 33365, neonate female, 158 mm TL, two neonate males, 160 mm TL, 32.99ºS,17.62ºE; SAM 34464, two juvenile males, 260-500 mm TL, Namibia, 28.91ºS,16.49ºE; SAM 36711, neonate female, 145 mm TL, neonate male, 145 mm TL, 34.62ºS,21.25ºE; SAM 36993, neonate female, 155 mm TL, two neonate males, 160 mm TL, 32.99ºS,17.62ºE; SAM 36995, two neonate females, 195-203 mm TL, neonate male, 205 mm TL, 30.68ºS,16.06ºE; SAM 37950, three adult males, 590-705 mm TL, 32.05ºS,16.37ºE; SAM 38280, neonate male, 125 mm TL, South Africa, 30.83ºS,16.08ºE; ZMB 21982, adult male, 555 mm TL, juvenile female, 460 mm TL, Southeast Atlantic Ocean; ZMB 22989, adult male, 562 mm TL, Southeast Atlantic Ocean; ZMH 11166, neonate male, 100 mm TL, three neonate females, 90-137 mm TL, Walvis Bay, Namibia.

SWAO (65 specimens): BMNH 1868.9.16.11, neonate male, 222 mm TL, Falkland Islands; BMNH 1936.8.26.17, adult male, 635 mm TL, near Strait of Magellan, Argentina, 52.18°S,68°W; BMNH 1999.5.4.4, juvenile male, 550 mm TL, Falkland Islands; BMNH 1999.5.4.11, juvenile female, 465 mm TL, Falkland Islands; BMNH 1999.5.4.13, juvenile female, 448 mm TL, Falkland Islands; BMNH 1999.5.4.15, adult female, 535 mm TL, Falkland Islands; BMNH 1999.5.4.16, juvenile male, 496 mm TL, Falkland Islands; BMNH 1999.5.4.28, juvenile male, 470 mm TL, Falkland Islands; NMW 83924, neonate male, 215 mm TL, unknown locality, Brazil; ZMH 104416, adult male, 725 mm TL; adult female, 755 mm TL, near Peninsula del Valdes, Argentina, 59°48'W,43°8'S; ZMH 104461, two juvenile females, 510-557 mm TL, adult female, 742 mm TL, near Peninsula del Valdes, Argentina, 60°8'W,43°3'S; ZMH 104519, two adult females, 670-745 mm TL, near Cabo Blanco, Argentina, 61°12'W,47°8'S; ZMH 104930, juvenile female, 462 mm TL, near Santa Cruz, Argentina, 57°11'W,39°56'S; ZMH 104946, adult male, 595 mm TL, near Santa Cruz, Argentina, 66°07'W,46°10'S; ZMH 104951, adult male, 715 mm TL, near Santa Cruz, Argentina, 63°40'W,49°0'S; ZMH 104955, seven neonates males, 187-192 mm TL, five neonate females, 185-200 mm TL, near Santa Cruz, Argentina, 65°46'W,47°50'S; ZMH 104968, six juvenile males, 226-233 mm TL, four juvenile females, 225-235 mm TL, near Cabo Blanco, Argentina, 65°18'W,47°0'S; ZMH 107911, four juvenile males, 213-225 mm TL, six juvenile females, 215-223 mm TL, near Santa Cruz, Argentina, 64°0'W,46°0'S; ZMH 108038, adult male, 670 mm TL, near Cabo Blanco, Argentina, 65°0'W,47°0'S; ZMH 113349, adult male, 880 mm TL, near Santa Cruz, Argentina, 123°26'W,37°55'S; ZMH 115469, juvenile male, 322 mm TL, near Santa Cruz, Argentina, 63°24'W,45°51'S; HUMZ 30178, adult male, 693 mm TL, off Patagonia, Argentina, 47°S,65°16’W; HUMZ 30200, adult male, 655 mm TL, off Patagonia, Argentina, 47°S,65°16’W; HUMZ 30221, adult male, 670 mm TL, off Patagonia, Argentina, 47°S,65°16’W; HUMZ 30282, adult male, 718 mm TL, off Patagonia, Argentina, 47°S,65°16’W; HUMZ 30285, adult male, 720 mm TL, off Patagonia, 47°S,65°16’W; HUMZ 30291, adult male, 595 mm TL, off Patagonia, Argentina, 47°S,65°16’W; HUMZ 30295, adult male, 660 mm TL, off Patagonia, Argentina, 47°S,65°16’W; HUMZ 30303, juvenile female, 487 mm TL, off Patagonia, 47°S,65°16’W; HUMZ 30310, juvenile female, 520 mm TL, off Patagonia, Argentina, 47°S,65°16’W; HUMZ 30324, adult male, 760 mm TL, off Patagonia, 47°S,65°16’W; HUMZ 107285, juvenile female, 340 mm TL, off Argentina, 46°59.5’S,65°16’W.

SWPO (47 specimens): CSIRO H 2921-01, adult female, 605 mm TL, upper Pitt Water, near Shark Point, Tasmania, Australia, 42°48.32'S,147°29.64'E; CSIRO H 2921-02, adult male, 522 mm TL, same location of CSIRO H 2921-01; CSIRO H 4226-01, juvenile female, 430 mm TL, off Seven Mile Beach, Frederick Henry Bay, Tasmania, Australia, 42°50.45'S,147°33.23'E; CSIRO H 4876-01, adult male, 612 mm TL, off Woodbridge Marine Discovery Centre, Tasmania, Australia, 43°10'S,147°15'E; CSIRO H 6205-01, neonate male, 276 mm TL, Battery Point, Tasmania, Australia, 42°53'S,147°20'E; CSIRO H 6485-01, juvenile female, 485 mm TL, off Port Davey, Tasmania, Australia; CSIRO H 6851-01, neonate female, 217 mm TL, 1 nautical miles South Betsey Island, Tasmania, Australia, 43°04'S,147°20'E; CSIRO H 6851-02, neonate female, 202 mm TL, same location of CSIRO H 6851-01; CSIRO T 480, neonate male, 118 mm TL, Little Roaring Beach, Tasmania, Australia; CSIRO T 712, adult male, 570 mm TL, off Port Davey, Tasmania, Australia; CSIRO T 783, adult male, 660 mm TL, same location as CSIRO T 712; CSIRO T 1099, neonate male, 218 mm TL, three neonate females, 205-220 mm TL, Nutgrove Beach, Sandy Bay, Tasmania, Australia; HUMZ 65447, adult male, 755 mm TL, New Zealand, 38°40.6'S,167°445.5'E; NMNZ P 942, adult female, 773 mm TL, Queen Charlotte Sound, Marlborough, South Island, New Zealand, 41°13.000'S,174°2.5000'E; NMNZ P 1255, two adult females, 993-935 mm TL, Cape Campbell, Marlborough, South Island, New Zealand, 41°44.000'S,174°16.000'E; NMNZ P 2645, neonate male, 230 mm TL, off Cape Campbell, Marlborough, South Island, New Zealand, 41°44.000'S,174°16.000'E; NMNZ P 5877, three neonate females, 197-214 mm TL, Pegasus Bay, Canterbury, South Island, New Zealand, 43°11.000'S,173°25.000'E; NMNZ P 10579, neonate female, 255 mm TL, neonate male, 255 mm TL, off Oamaru, Otago, South Island, New Zealand, 45°10.000'S,171°5.000'E; NMNZ P 16844, adult female, 610 mm TL, East of Snares Islands, New Zealand, 48°1.000'S,166°39.000'E; NMNZ P 20924, neonate female, 237 mm TL, Chattam Islands, New Zealand, 43°33.6000'S,176°0.5000'E; NMNZ P 25182, neonate male, 248 mm TL, Long Beach, Otago, South Island, New Zealand, 45°43.630'S,170°39.320'E; NMNZ P 26808, juvenile female, 405 mm TL, Snares Islands, Auckland Islands, New Zealand, 48°49.1000'S,167°9.0000'E; NMNZ P 36873, juvenile female, 570 mm TL, St. Anne Bay, Southland, South Island, New Zealand, 44°34.533'S,167°46.933'E; NMNZ P 38064, two neonate males, 237-240 mm TL, Northern Solander Trough, Southland, South Island, New Zealand, 46°2.0500'S,166°12.8000'E; NMNZ P 41292, adult female, 769 mm TL, Western Palliser Bay, Wellington, South Island, New Zealand, 41°24.000'S,175°8.000'E; NMNZ P 42107, juvenile male, 635 mm TL, unknown locality; NMNZ P 47304, adult male, 769 mm TL, Oamaru, Otago, South Island, New Zealand, 45°13.058'S,171°6.542'E; NMNZ P 47623, neonate female, 295 mm TL, Lyttleton Port, Canterbury, South Island, New Zealand, 43°36.333'S,172°43.103'E; NMNZ P 48084, neonate male, 268 mm TL, Lyttleton Port, Canterbury, South Island, New Zealand, 43°36.465'S,172°42.868'E; NMNZ P 48123, neonate female, 236 mm TL, Timaru Port, Canterbury, South Island, New Zealand, 44°23.242'S,171°15.602'E; NMNZ P 48164, neonate female, 257 mm TL, Lyttleton Port, Canterbury, South Island, New Zealand, 43°36.333'S,172°43.103'E; NMNZ P 53677, adult female, 795 mm TL, off Otago Peninsula, Otago, South Island, New Zealand, 45°47.1110'S,170°56.8300'E; NMNZ P 53678, neonate female, 243 mm TL, same location as NMNZ P 53677; NRM 9031, neonate male, 135 mm TL, two neonate females, 137-142 mm TL, Jakarta, Indonesia; ZMB 22735, juvenile female, 225 mm TL, Nepal; ZMB 12835, adult female, 580 mm TL, Nepal.

SEPO (10 specimens): ZMH 10216, six neonate males, 153-190 mm TL, four neonate females, 150-183 mm TL, Coronel, Chile.

Diagnosis. *Squalus acanthias* can be distinguished from its congeners by having: dermal denticles unicuspid and narrow with cusp directed posteriorly; teeth with cusp conspicuously vertical in adult males. In contrast to *S. suckleyi* and *S. wakiyae*, *S. acanthias* has 8–13 pairs of large white spots on each side of the body (vs. 16–17 vs. 1–6 pairs, respectively). It differs from these two nominal species of spotted dogfish sharks by larger number of vertebrae: 48 monospondylous vertebrae in paralectotype and 46–48 for specimens of Baltic Sea (vs. 44, 37–43 for *S. suckleyi* vs. 40–42 for *S. wakiyae*). It is also distinguished from all species of the family Squalidae by having segmented ridge on scapulae with barrel-shaped units.

Descriptions. Description is based on specimens from the Baltic Sea. Single values are for lectotype. Range values are for paralectotypes and non-type specimens from the Baltic Sea.

External morphology (Tabs. 10–12; Figs. 59–67). Body fusiform and slender for all its extension, rather arched anteriorly since posterior margin of spiracle until vertical traced at insertion of pectoral fins; head height 1.0 (0.9-1.0; 0.8-0.9) times trunk height and 1.3 (0.7-1.2; 0.9-1.1) times abdomen height. Head flattened anteriorly, small (its length 23.4%, 19.5%-21.6%; 19.2%-23.3% of TL), and broad with its width 1.3 (0.9-2.0; 1.1-1.3) times trunk width and 2.0 (1.1-1.3; 1.1-1.8) times abdomen width. Snout elongate (its length 5.2%, 4.2%-4.5%; 3.8%-5.3% of TL) and obtuse at the tip. Nasal apertures located ventral-laterally, oblique and small; anterior margin of nostril unilobate or bilobate in young specimens; distance from nostrils to snout tip 0.9 (0.9-1.3; 0.9-1.1) times distance from nostrils to upper labial furrow; prenarial length corresponding to two-fourths the preoral length in lectotype; internarial distance 0.7 (0.6-0.9; 0.6-0.9) times eye length. Eyes oval with anterior margin convex and posterior margin angular, although not notched with spiracle; eyes closest to snout tip than first branchial arch; eye length 1.6 (2.2-6.5; 1.3-2.0) times its height.

Mouth arched and markedly broad, its width 1.5 (1.5-1.8; 1.3-1.8) times prenarial length and 2.0 (2.2-2.9; 1.8-2.3) times internarial space; upper labial furrow thin and large (its length corresponding to 2.8%, 1.6%-3.3%; 2.0%-3.3% of TL), carrying a thin fold; lower labial furrow also elongate, lacking fold. Teeth unicuspid, similar in both jaws, flattened labial-lingually and alternate; teeth broad, although short at the crown; upper teeth smaller than lower teeth; cusp thick and elongate, oblique and directed laterally; mesial cutting edge convex; both distal and mesial heels rounded; apron large and thick on both jaws; in adult males, cusp conspicuously vertical; two series of functional teeth on upper and lower jaws for paralectotypes (vs. three series for non-types); teeth rows varying from 13-14 on the upper jaw and 11-10 on the lower jaw in paralectotypes (vs. 13-1-13 and 11-1-11 for non-types).

Prespiracular length 1.6 (1.8-1.8; 1.6-1.8) times greater than preorbital length and 0.6 (0.5-0.6; 0.5-0.6) times pre-pectoral length. Spiracles half-moon shaped, located posterior-dorsally to the eyes, directed obliquely in relation to longitudinal axis of the body; spiracle diameter at least one-third the eye length. Pre-branchial length 1.5 (1.3-1.6; 1.4-1.6) times larger than pre-spiracular length. Gill slits concave, placed in front of pectoral fins, evidently tall with fifth gill slit 1.4 (1.1-1.5; 1.1-1.5) times higher than first gill slit.

Origin of first dorsal fin conspicuously posterior to free rear tips of pectoral fin (in young specimens, the origin is almost over free rear tip of pectoral fin but still posterior to it); horizontal distance between the origins of pectoral fin and first dorsal fin 1.5 (1.6-3.2; 1.5-2.7) times preorbital length. First dorsal fin vertical and markedly wide on its fin web, relatively small (its length 12.1%, 9.7%-12.5%; 11.0%-13.7% of TL) and low (its height 6.6%, 4.2%-6.6%; 5.9%-7.5% of TL); first dorsal length 1.9 (1.5-2.3; 1.6-2.1) times greater than its height; first dorsal height 0.8 (0.7-1.2; 0.8-1.2) times preorbital length; first dorsal anterior margin convex, posterior margin moderately concave near the free rear tip, its apex rounded, and free rear tips triangular and pointed; inner margin length of first dorsal fin 0.8

(0.8-1.0; 0.7-0.9) times first dorsal height. Origin of first dorsal spine markedly behind free rear tips of the pectoral fins. First dorsal spine ungrooved, conspicuously thin and markedly low (its length 1.2%, 1.7%-2.7%; 1.2%-2.3% of TL), its length not greater than one-third first dorsal fin height, never reaching the fin apex.

Interdorsal distance 0.8 (0.9-1.4; 0.8-1.2) times prepectoral length and 1.6 (1.7-2.5; 1.6-2.4) times greater than dorsal-caudal space. Pre-second dorsal length 5.3 (3.4-6.3; 4.1-5.3) times larger than anterior margin length of pectoral fin and 2.8 (2.2-4.3; 2.8-3.3) times greater than dorsal caudal margin length. Second dorsal fin rather oblique, narrow on its fin web, and relatively large (its length 2.5, 2.6-5.4; 1.9-2.6 times its height); second dorsal length almost equal to first dorsal length, corresponding to 1.0 (1.0-1.2; 0.8-1.0) times first dorsal fin length; second dorsal anterior margin convex and posterior margin falcate; apex evidently rounded and free rear tip pointed; its inner margin well elongate (its length 1.0, 0.9-2.2; 0.6-1.0 times second dorsal height). Second dorsal spine lightly inclined, conspicuously slender and low, its length 0.5 (0.9-1.9; 0.4-0.9) times second dorsal fin height, and not reaching the fin apex; second dorsal spine 2.0 (1.6-2.0; 1.8-2.2) times larger than first dorsal spine length; second spine 1.8 (1.2-1.9; 1.0-1.8) times broader at base than first dorsal spine.

Pre-pectoral length 0.7 (0.5-0.7; 0.5-0.7) times pre-first dorsal length and 0.5 (0.3-0.4; 0.4-0.4) times pre-vent length. Pectoral fins very narrow with both anterior and inner margins convex, and posterior margin straight; anterior margin length 1.6 (1.5-2.1; 1.4-1.6) times posterior margin length, although its tip reaches the same level of its apex; apex and free rear tips evidently rounded, although not lobulated; pectoral fin base length varying from 4.1% (4.5%-4.9%; 3.5%-4.9%) of TL.

Pelvic fins very narrow and short (its length 9.3%, 9.2%-10.4%; 8.5%-11.5% of TL); pelvic anterior margin slightly convex and posterior margin straight; apex and free rear tips rounded, the latter lobulated; origin of the pelvic fins 3.9 (3.3-3.8; 3.4-4.0) times distance between the origins of two dorsal fins; pelvic fin placed in the midline between two dorsal fins in lectotype, although it is nearest second dorsal fin in other specimens; pectoral-pelvic distance usually equal to pelvic-caudal distance, the former corresponding to 1.1 (1.0-1.2; 1.0-1.2) times the latter. Clasper cylindrical, compressed dorsal-ventrally throughout all its extension, transcending greatly the free rear tips of pelvic fin in adults; clasper outer length 1.3%-6.1% of TL for paralectotypes (vs. 1.6%-5.3% of TL for non-type specimens); clasper with elongate siphon, located medial-ventrally from the anteriormost end of the puboischiadic bar until the level of intermediate segment; clasper groove longitudinal, sinuous and deep, large, placed dorsal-medially; apopyle broad, located more anteriorly in the clasper groove; hypopyle narrow, placed posteriorly in the clasper groove, although prior the rhipidion; rhipidion elongate, blade-like, located laterally at the distal end of clasper.

Caudal peduncle with discreet lateral keels, its origin behind insertion of the second dorsal fin; upper and lower precaudal furrows well marked. Caudal fin with upper lobe conspicuously rectangular; dorsal-caudal margin straight and large (its length 21.0%, 16.4%-25.9%; 19.3%-21.3% of TL); upper postventral caudal margin strongly convex; posterior caudal tip rounded; caudal fork markedly concave and broad, its width corresponding to 8.2% (5.3%-6.8%; 6.1%-8.0% of TL); dorsal-caudal margin length 0.9 (0.8-1.2; 0.8-1.0) times head length and 1.8 (1.9-2.1) times larger than preventral caudal margin length; lower postventral caudal margin also convex; preventral caudal margin convex and elongate, its length 2.5 (1.7-2.8; 1.7-2.8) times greater than inner margin length of pelvic fin.

Dermal denticles (Fig. 65). Dermal denticles unicuspid, not imbricated with single ridge (lateral ridges absent); median ridge pronounced and narrow, equally thick proximal to distally, lacking furrows; median ridge convex and short, its cusp pointed posteriorly in parallel to the horizontal axis of the body; dermal denticles with crown thin or weakly expanded; crown base strongly broad and diamond-like with four thick pedicels. In neonates, dermal denticles are smaller, markedly sparse one to another and little developed throughout the body.

Coloration (description based on newest preserved specimens of *S. acanthias*). Body dark grey dorsal and laterally, although light grey more posteriorly from the lower lateral half of the body just in front of the pectoral fin origin to the caudal fin; white ventrally; white spots large and numerous with two rows on each side of the body (8–13 pairs), placed dorsal-laterally until behind second dorsal fin. Both dorsal fins dark grey with its apex slightly darker at the tip than the rest of the fin, white at the fin base and in the free rear tips; dorsal fin spines dark grey to brownish anteriorly and whitish at its tips. Pectoral fins also dark grey dorsoventrally with both inner and posterior margins broadly whitish. Pelvic fins grey dorsal and ventrally, although lighter ventrally, with anterior and posterior margins evidently white. Caudal fin grey, darker at the posterior tip, slightly white in the dorsal caudal margin, forming the white caudal bar, and at the vertebral column; black caudal stripe prominent and wide, placed dorsally to the vertebral column; postventral caudal margins discreetly white; preventral caudal margin white, including at the ventral tip.

In young specimens, body usually light grey with numerous white spots, often fusioned; dorsal fins markedly darker at the tip; caudal fin conspicuously dark grey with broad white caudal bar at dorsal caudal margin; black upper caudal blotch near tip of vertebral column to the posterior tip; preventral and postventral caudal margins largely white.

Vertebral counts (Tab. 15). Monospondylous vertebrae 48 for paralectotypes (46–50 for specimens from Baltic Sea); precaudal vertebrae 81 (79–86); caudal vertebrae 28–31 (28–31); total vertebrae 110–112 (109–117).

Geographical distribution (Fig. 68). *Squalus acanthias* has worldwide geographic distribution in the North and South Atlantic Oceans, and South Pacific Ocean. It is also occurs in the Mediterranean and Artic Seas. Its occurrence in the Indian Ocean is rare.

Etymology. The epithet *acanthias* refers to αγκάθι, which means spine in greek.

Remarks.

Considerations on the type specimens of *Squalus acanthias*. Understanding the taxonomy of Squalidae means to go back almost three hundred years in history of Ichthyology. Peter Artedi, founder of Systematic Ichthyology, first described the genus *Squalus* as a single major group that comprised all nominal species of sharks known to that time. These descriptions were based on material of several collections of natural history in Europe, including Leiden in Netherlands, London in England and Uppsala University in Sweden where Artedi started his studies in Zoology and developed a modern classification system of animals (Wheeler, 1987). Nowadays these collections belong to NHM in London, Naturhistoriska riksmuseet, Uppsala University and Naturalis where specimens of *Squalus acanthias* analyzed by Artedi could be possibly deposited. A single specimen of shark from Artedi is unknown, according to Wheeler (1987) and the present study, which discards any possibility of addressing type specimens to him.

Artedi formerly prepared manuscripts with diagnosis, descriptions and list of synonyms of several species (e.g. “Ichthyologia Scripsi Londini, 1735”; “Thesaurus, third volume”), including the book “Catalogus Piscium Maris Balthici” that focus on the diversity of species from the coast of Sweden (Wheeler, 1987). These studies include *S. acanthias,* indicating that the description of this nominal species was based on material from Swedish waters. Linnaeus compiled several descriptions of species from Artedi's works that were included in studies before 10th edition of *Systema Naturae* (1758) (e.g. Linnaeus, 1746, 1748, 1754) in which *S. acanthias* was also described. At this stage, Linnaeus was working in the scientific collection of King Adolf Fredrik in Stockholm where he has based most of his publications. Fernholm & Wheeler (1983) stated that these descriptions together with old labels in the jar of the specimen NRM 85 support it as syntype of *S. acanthias*. In the present study, this hypothesis is also supported and the specimen is designated as lectotype for this nominal species. Its type locality, even though previously whereabouts undetermined, it is assumed to regard to the oldest and first available label in the jar of this specimen that it is from Ulriksdal in Sweden.

Designation of paralectotypes of *S. acanthias* is based on material from the Linnaean collections and old descriptions provided in several studies from Linnaeus as well. Wheeler (1991) previously refuted these specimens from Uppsala University as potential types because it comes from the donation of Jonas Alströmer in 1749 that Linnaeus did not mention on publications. Many specimens that came from this donation lack labels and/or are poorly documented on its location and history. According to Wheeler (1991), the majority of specimens were collected in Sweden once Alströmer was the Councilor of Commerce. In that time, Linnaeus published (e.g. Linnaeus, 1746a [page 100], 1747 [page 174], 1748 [page 40]) descriptions of Swedish fishes, which supports the assumption he analyzed material from Alströmer donation as well. A third specimen from Uppsala comes from the *Museum Gustavo Adolphianum* that also received several specimens from the collection of the King Adolf Fredrik as donation (Dr. Mejlon, *pers. comm.*; Wheeler, 1991). Linnaeus (1754) made autoreference to specimens from the latter on page 53.

Preserved conditions of the lectotype of *S. acanthias* are very fragile because of many years of storage in ethanol. Its natural color is completely lost as well as its skin is partially eviscerated dorsally and laterally in the head. Pectoral, pelvic and caudal fins are still intact, although left pectoral fin is somewhat fringed on its posterior margin. Both dorsal fins are completely well preserved, including its spines. Region of the head, however, is damaged with snout tip squashed anteriorly, and dorsally with a large hole. Profound furrow from snout tip to mouth is noticed ventrally, indicating that this specimen was labeled previously in this region. Another specimen, the paralectotype UUZM 159, is also well preserved in ethanol and shows the same good conditions of the lectotype. This specimen exhibits a large ventral cut in the trunk between mouth and pectoral fins. It is also slightly damaged in the right nostril and right side of the trunk upon gill slits. However, other two paralectotypes are not well conserved because they are dried material. Both specimens lost its natural color and shape of the body as well as few teeth are also missing. Despite of the fins are smashed or fringed in these two type specimens, they are still complete and not fragmented into pieces.

Morphological variations on specimens of *S. acanthias*. *Squalus acanthias* is the only species that occurs worldwide within Squalidae with its populations spread into the Atlantic and Pacific Oceans. Previous studies (e.g. Bigelow & Schroeder, 1948; Springer & Garrick, 1964; Figueirêdo, 2011) on the taxonomy of this nominal species pointed out some variations of the external morphology and vertebral counts among its specimens that are still observed in the current study. For instance, a single intermediate tooth is present in specimens from the Baltic Sea, and populations of the North and South Atlantic Oceans but absent in specimens from the Pacific Ocean. Intermediate tooth is usually smaller than the following tooth with cusp vertical and apron short, and both distal and mesial heels markedly rounded. Dentition is commonly used for defining the genus *Squalus* and separating its nominal species as well (e.g. Smith, 1912; Phillipps, 1946). Phillipps (1931, 1946) separated the nominal species *S. kirki* from *S. acanthias*, according to the shape of mesial and distal heels more or less deflect, and apron more or less elongate which it is in agreement with the current study. However, apron is equally elongate in both jaws for *S. acanthias*. Differences on these aspects were also observed between *S. acanthias, S. suckleyi* and *S. wakiyae* and will be further discussed in this chapter.

Vertebrae counts also varies among populations of *S. acanthias* from different regions in which specimens from Baltic Sea and North Atlantic Ocean (both sides) show greater number of monospondylous, diplospondylous, precaudal and total vertebrae than specimens from the South Atlantic (both sides) and South Pacific (both sides). These results are in accordance to Springer & Garrick (1964), Bass *et al*. (1976), White *et al*. (2007a) and Figueirêdo (2011). Holotypes of the nominal species *S. barbouri* and *S. tasmaniensis* are very young specimens whose calcification of vertebrae is not yet complete, impeding on taking radiographs for additional comparisons.

External measurements are overlapped among specimens of *S. acanthias* from these locations. Few exceptions, however, are noticed between specimens from the Black Sea and specimens from the remaining areas. First and fifth gill slits are much lower in specimens from the Black Sea than other specimens (first gill slit height 1.0% of TL for Black Sea vs. 1.5%-2.2% for Baltic Sea vs. 1.4%-2.5% for Atlantic Ocean vs. 1.4%-2.1% for South Pacific; fifth gill slit height 1.1% vs. 2.0%-2.8% vs. 1.2%-3.0% vs. 1.5%-2.8% of TL, respectively). Inner margin of pectoral fin is smaller in specimens from the Black Sea (its length 6.3% vs. 6.9%-8.9% for Baltic Sea vs. 6.8 %-9.6% for Atlantic Ocean vs. 7.5%-8.4% of TL for Southeast Pacific Ocean).

Major variations are noticed among specimens from Black Sea and specimens from the Northwest Atlantic and South Atlantic Oceans (both sides). These specimens are distinct from those of the Northwest Atlantic Ocean by having wider distance between nostrils (its width 3.8% vs. 3.0%-3.7% of TL), more elongate eyes (its length 4.1% vs. 1.9%-3.6% of

TL), and larger distance between pectoral and pelvic fins (21.0%, 23.0%-28.6% of TL). Specimens from the Black Sea can also be separated from those of Southeast Atlantic Ocean on showing narrower mouth (its width 6.4% vs. 7.0%-8.7% of TL), and shorter anterior margin of pectoral fin (its length 11.5% vs. 11.8%-16.6% of TL). The current analysis was based on a single juvenile specimen from the Black Sea that might interfere in these differentiations because external measurements in specimens of *S. acanthias* are subject to change with maturity.

Ontogenetic variations need to be considered for this species in order to avoid misidentifications and/or unnecessarily application of new synonyms. Howell-Rivero (1936a), for instance, failed in this manner when describing *Squalus barbouri* and *S. tasmaniensis* as two new species from the Central Atlantic and South Pacific Oceans, respectively, and distinct from *S. acanthias*. Garrick (1960) previously attempted to these modifications with the growth regarding location of pelvic fins related to the dorsal fins in which it was measured as from insertion of first dorsal fin to origin of second dorsal fin. Young specimens of *S. acanthias* show pelvic fins nearest to the first dorsal fin while it is nearest the midline between both dorsal fins, according to this author. Garrick (1960), however, did not attempt that free rear tip of first dorsal fin also vary in shape and length with growth in specimens of *S. acanthias*, suggesting that his assumptions were equivocated. In order to avoid this, the position of pelvic fins related to dorsal fins must be measured as the distance between the origin of first dorsal fin to the origin of second dorsal fin. In the current analysis, young specimens have its pelvic fins nearest the midline between two dorsal fins while it is nearest second dorsal fin in adults.

Taxonomic status of the piked dogfish *Squalus acanthias*. Several nominal species of spotted piked dogfish were described from different regions of the world due to morphological variability between specimens, contributing to the taxonomic complexity of *S. acanthias*. Many of these species had its taxonomic status unclear or were not yet properly investigated till now. Original descriptions are very brief for these nominal species and its diagnostic characters were not clearly expressed or are overlapped with those of *S. acanthias* and other synonyms. Difficulties on finding its type specimens have contributed in this manner as well and many authors applied them as junior synonyms of *S. acanthias* without detailed explanations (e.g. Bigelow & Schroeder, 1948, 1957; Fowler, 1941; Compagno, 1984; White *et al*., 2007; Eschmeyer & Fricke, 2015).

Acanthias vulgaris, *Acanthias americanus* and *S. barbouri* are nominal species of spotted dogfish described from the North Atlantic Ocean. Its original descriptions together with analysis of available type material and other specimens suggest that these species are conspecific with *S. acanthias* from the Baltic Sea. No morphological variations were noticed with regards to specimens from Northwest and Northeast Atlantic Oceans, which supports this hypothesis.

Squalus kirki Phillipps, 1931 (Fig. 69) from New Zealand was described as differentiating from *S. acanthias* on number of labial folds and teeth morphology (Phillipps, 1931, 1946) but no type material was expressly denoted in the original description even though Phillipps states he analyzed 10 specimens of spotted dogfish. Whitley (1940), later, referred to its holotype as an adult male with about 813 mm TL based on illustration provided by Phillipps and reproduced later in Phillipps (1946). Such act invalidates the designation of this specimen as holotype of *Squalus kirki* by means of specimen illustrated because it was no reproduced in the original description or fixed by the original author. W.J. Phillipps sent a specimen of *S. kirki* to the NHM in London after completion of his publication as gratefulness for the help of both Regan Tate and J.R. Norman on the manuscript. Correspondent letters between these three ichthyologists from October, 1930 and August, 1931 supports this assumption. The specimen is BMNH 1931.8.10.1 herein designated as the only survival syntype of *Squalus kirki* once no other material of this nominal species exists in the fish collection of Auckland Museum (formerly Dominion Museum) and Te Papa Museum. The current analysis verifies that the syntype has a single upper labial fold, elongate and thin, and another small fold in the lower jaw. The latter, however, is not a labial fold by definition because there is no lateral furrow associated to it but an inner fold in the lower lip for sustaining the lower labial cartilage as it is defined in Wilga & Motta (1998). Few wrinkles are observed near the lower labial furrow in the syntype but its appearance is due to preservation process as it was stated by Norman in one of the letters. All other species of the family Squalidae exhibit the same pattern of labial furrow and fold, which dismiss it as consistent diagnostic character to validate *S. kirki*.

Syntype of *S. kirki* differs from specimens of *S. acanthias* from Baltic Sea regarding the shape of dermal denticles (which assemblages those of *S. wakiyae*). Teeth are also slightly distinct in *S. kirki*, which has apron markedly thin (vs. thick in specimens of *S. acanthias* from Baltic Sea). Differences on feeding preferences might contribute to teeth variation (Phillipps, 1946). Specimens from Australia (White *et al*., 2007a) and New Zealand also show fewer numbers of total, precaudal and monospondylous vertebrae than those from the Baltic Sea like it is also observed for specimens from South Atlantic Ocean (both sides). No differences on external measurements were observed between specimens of *S. acanthias* from these regions. Additionally, segmented ridge of scapulae are noticed for all of them, which supports that these two nominal species are conspecific.

Further investigations on specimens from South Pacific (both sides), including Chilean waters, are required in order to elucidate these morphological variations. If it is verified to be separate from the Atlantic *S. acanthias*, the nominal species *Squalus fernandinus* Molina, 1782 from Chile is the first available name and may be resurrected. The original description of this nominal species is a compilation from the description of Linnaeus (1758) for *S. acanthias* as Molina (1782) expressly stated in the beginning of the index of his book. Then, it clearly denotes that *S. fernandinus* is an available name by indication. Regan (1908a) was the first author to provide better description of this nominal species and it differentiated from *S. acanthias* by having shorter preoral length, which it is in disagreement with the current study. Analysis of specimens from Southeast Pacific Ocean, however, was based on limited number of representatives and often very old material that impede to properly verify the existence of any other morphological disparity besides vertebral counts with *S. acanthias* from Baltic Sea. No type material is known for *S. fernandinus* and most descriptions provided for it have not consistent diagnostic characters, indicating that it must be considered junior synonym of *S. acanthias*.

Acanthias lebruni Vaillant, 1888 (Fig. 69) was described as a result of the Scientific Mission from Cape Horn in Chile. Its description was based on an adult specimen measuring 700 mm TL that was expressly stated as “type”, together with six other small specimens “measuring 230-280 mm TL” (Vaillant, 1888). Only two paratypes were known as the remaining specimens held by MNHN while other type material was considered lost or not found in the fish collection (Eschmeyer & Fricke, 2015; Pruvost *per. comm.*, 2013). During the visit to MNHN in 2013, an adult male with 655 mm TL (MNHN 1883-190) collected in 1883 from Santa Cruz, Argentina was found, which it is the only specimen whose total length is closest to those mentioned in the original description for the holotype. Its collecting date is also coincident with paratypes of this nominal species, although the collector is differently regarded as Sir Lebrun (and not Scientific Mission from Cape Horn). Vaillant (1888) clearly mentioned that the descriptions of fishes were based on donated specimens from Tierra del Fuego in Argentina, Falkland Islands, and South Georgie Islands. Thus, the specimen MNHN 1883-190 also belongs to the series of specimens collected during the visit to Cape Horn.

Based on the original description and this information, it is assumed that this specimen represents the holotype of *Acanthias lebruni*. Other four specimens also collected during this visit are herein considered paratypes once they all have total length ranging between 230–280 mm TL.

Punta Arenas in Chile is the type locality of *Acanthias lebruni*, according to Vaillant (1888) but only five of seven specimens at MNHN collected in 1883 come from this region. So, we assume that the author made his statement based on major number of specimens that were collected in this area. It is important to clarify herein, however, that the correct type locality must be related to its holotype, which in this case it is Punta Arenas, Argentina. The analysis of the types of *Acanthias lebruni* in the current study, however, does not show any greater morphological differences with specimens of *S. acanthias* from Baltic Sea. Specimens from Southwest Atlantic Ocean also overlap in many morphological aspects (e.g. color pattern, dermal denticles, dentition, and segmented ridge on scapulae) to specimens from North Atlantic Ocean, except vertebral counts, supporting that *Acanthias lebruni* is junior synonym of *S. acanthias*.

Previous studies (e.g. Lindberg & Legeza, 1959; Myagkov & Kondyurin, 1986) recognized five subspecies for *S. acanthias* based on differences of meristic data and external measurements in order to facilitate its identification in different localities: *Squalus acanthias acanthias* for North Atlantic Ocean, *S. acanthias ponticus* for Black Sea, *S. acanthias africana* for Southeast Atlantic Ocean, *S. acanthias* subsp. for Southwest Pacific Ocean, and *Squalus acanthias suckleyi* for North Pacific Ocean. Currently, the only subspecies raised to species level is the latter (Ebert *et al*., 2010) and it will be discussed further in this chapter. Proportional distance of prepelvic length, pre-first dorsal length, and interdorsal distance were used to support this hypothesis. It is important to notice that most of the specimens analyzed by Myagkov & Kondyurin (1986) were neonates or young juveniles that are subject to changes on body proportions with growth as it is noticed in the present and past studies (e.g. Garrick, 1960; Jones & Geen, 1976; Reiss & Bonnan, 2010), implying that the recognition of subspecies of *S. acanthias* are equivocated. Differences on the teeth formula and vertebral counts between populations pointed out by these authors are in congruency with the current results but the characters alone are not useful for separating *S. acanthias* into subspecies level, which it is in accordance to findings of Jones & Geen (1976).

Populations from North Atlantic coasts (both sides) are more similar morphologically than populations from the South Atlantic (both sides) and South Pacific Oceans, according to the present analysis. Overlapping of morphological characters such as body coloration, shape of dermal denticles, teeth morphology, external measurements as well as skeletal components[1] between these populations support that *Squalus acanthias* comprises a single valid species with broader geographical distribution. These results are consistent with molecular-based analysis in which no divergence of CO1 and NADH2 genes was significant among *S. acanthias* from the Atlantic and South Pacific waters (e.g. Ward *et al*., 2007; Veríssimo *et al*., 2010; Naylor *et al*., 2012a). Variations on vertebral counts of this species must be due to environmental changes on patterns of temperature and salinity between North and Southern hemispheres as it is noticed for other sharks and bony fishes (e.g. Jordan, 1891; Applegate, 1967; McDowall, 2008).

Studies on migration, reproduction and feeding also noticed that specimens from both West and East sides of the Atlantic share similar biological patterns (e.g. Gallucci *et al*., 2009; Gračan *et al*., 2013). Despite of these aspects are still poorly investigated for populations in the South Atlantic and Pacific Oceans, most results are also congruent with those of population from the North Atlantic Ocean (e.g. Oddone *et al*., 2015). Further investigations on this species from the Southeast Pacific Ocean and Black Sea are needed

[1] Skeletal anatomy of *S. acanthias* is descibed on Chapter 1.

using morphological and/or molecular data in order to better understand the morphological variations pointed out in this study and in previous analysis of biological parameters (e.g. Avsar, 2001; Demirhan & Seyhan, 2007). DNA samples of specimens of *S. acanthias* from the South Atlantic Ocean (both sides), Black Sea, and Chilean waters are also required for integrating new molecular analysis and for comparative purposes with the current results.

Comparative material (6 specimens). BMNH 1931.8.10.1 (syntype of *Squalus kirki*), adult male, 785 mm TL, New Zealand; MCZ 146-S (holotype of *Squalus tasmaniensis*), neonate female, 245 mm TL, Hobart, Australia; MCZ 1463-S (holotype of *Squalus barbouri*), neonate female, 267 mm TL, Jaimanitas Beach, Cuba; MNHN 1883-190 (holotype of *Acanthias lebruni*), adult male, 655 mm TL, Santa Cruz, Argentina, 50°03'S,68°34'59''W; MNHN 1888-201 (paratype of *Acanthias lebruni*), juvenile female, 268 mm TL; MNHN 1888-202 (paratype of *Acanthias lebruni*), juvenile male, 295 mm TL.

Squalus suckleyi **(Girard, 1854)**

(Spotted spiny dogfish; Northeast Pacific spiny dogfish)

Figs. 70–74, Tables 14,16,18

Acanthias vulgaris: Müller & Henle, 1841 (in part): 83-84 (revision; North Pacific Ocean).
Spinax (Acanthias) suckleyi Girard, 1854: 196 (original description; no types originally designated or known; Fort Steilacoom, Puget Sound, Washington State, The United States of America).
Acanthias sucklii Jordan & Evermann, 1896: 54 (listed; North and Central Atlantic Ocean); Garman, 1913: 194 (description).
Squalus suckleyi Fowler, 1941 (in part): 258-260 (description; North Pacific Ocean); Bigelow & Schroeder, 1948: 453 (cited; Northwest Atlantic Ocean); Ebert *et al*., 2010: 22-40 (redescription, DNA barcoding, designation of neotype; North Pacific Ocean); Ward *et al*., 2007: 119 (cited; North Pacific Ocean); Naylor *et al*., 2012a: 57 (DNA barcoding; North Pacific Ocean); Orlov *et al*., 2012 (in part): 1-12 (life history; North Pacific Ocean); Ebert & Stehmann, 2013: 62 (cited; North Pacific Ocean); Ebert *et al*., 2013 (in part): 78, 95 (cited, description; Northeast Pacific Ocean).
Squalus acanthias: Bigelow & Schroeder, 1957: 30 (revision; Northwest Pacific Ocean); Jones & Geen, 1976: 2500-2506 (taxonomy; North Pacific Ocean); Ward *et al*., 2007: 118-130 (DNA barcoding; North Pacific Ocean).
Squalus acanthias suckleyi: Myagkov & Kondyurin, 1986: 1-18 (cited; North Pacific Ocean); Bass *et al*., 1976: 10 (cited; North Pacific Ocean).

Neotype: CAS 227267, adult male, 674 mm TL, Hood Canal, Puget Sound, Washington State, The United States of America, 47°22N,123°05W, 30 meter depth. Collected on August, 3rd 2007. Neotype designated by Ebert *et al*. (2010).

Type locality: Puget Sound, Washington State, The United States of America.

Non-type material (48 specimens): BMNH 1890.11.15.365, adult male, 810 mm TL, off central western coast, The United States of America; BMNH 1895.12.31.60, adult female, 955 mm TL, The United States of America, Northeast Pacific Ocean; CAS 13127, neonate male, 380 mm TL, Roberts reef, Puget Sound, Washington, The United States of America; CAS 21424, four neonate females, 235-290 mm TL; two neonate males, 235-300 mm TL; juvenile male, 375 mm TL, San Francisco Bay, California, The United States of America; CAS 21898, neonate female, 250 mm TL, neonate male, 260 mm TL, San Francisco Bay, California, The United States of America; CAS 21971, seven neonate females, 250-285 mm TL, two juvenile females, 310-315 mm TL, four neonate males, 232-305 mm TL, three juvenile males, 310-330 mm TL, San Francisco Bay, California, The United States of America; CAS 34815, neonate male, 228 mm TL, San Francisco Bay, California, The United States of America, 37°45’N, 122°22’E; CAS 40592, neonate male, 185 mm TL, San Francisco Bay, California, The United States of America; CAS 40863, juvenile male, 340 mm TL, California, The United States of America; CAS 40868, neonate female, 160 mm TL, between Pt. Bonita and Pt. Reyes, Marin, California, The United States of America; CAS 40873, two juvenile females, 340-355 mm TL, five juvenile males, 320-390 mm TL, Roberts reef, Puget Sound, Washington State, The United States of America; CAS 56093, four neonate females, 270-265 mm TL, neonate male, 260 mm TL, San Francisco Bay, California, The United States of America; SAM 38273, adult male, 825 mm TL, Moss Landing, California, The United States of America, 36°80’N, 121°78’E; SAM 38274, juvenile female, 619 mm TL, Steinhart Aquarium, San Francisco, California, The United States of America; SU 13023, adult male, 710 mm TL, San Diego Bay, California, The United States of America; SU 58376, juvenile male, 480 mm TL, Monterey Bay, California, The United States of America.

Diagnosis. A species that can be differentiated from its congeners by a combination of characters: origin of first dorsal fin prior to horizontal line traced over pectoral free rear tips; pelvic fins located in the midline between the two dorsal fins; 16–17 pairs of white spots on each side of the body. *Squalus suckleyi* is further distinguished from *S. acanthias* and *S. wakiyae* by having: teeth with cusp thin and elongate (vs. thick and short); dermal denticles markedly narrow with cusp forming right angle with horizontal axis of body. *Squalus suckleyi* has smaller number of monospondylous vertebrae than *S. acanthias* (44, 37-43 vs. 48, 46-50, respectively).

Description. Single values are for neotype (taken from Ebert *et al*., 2010). Range is for non-type specimens in which data were taken.

External morphology (Figs. 70–73; Tab. 16). Fusiform and slender body, arched dorsally since posterior margin of spiracle to insertion of pectoral fin; head height 0.7 (0.8-1.2) times trunk height and 0.9-1.4 times abdomen height. Head large (its length 23.0%, 21.3%-24.5% of TL), compressed dorsally near between snout and eyes, narrower anteriorly than posteriorly with its width 1.0-2.1 times greater than its width at the nostrils; head width 1.0 (0.7-1.5) times trunk width and 0.9-2.4 times abdomen width. Snout rounded at tip, and large (preorbital length 6.4%, 6.7%-13.4% of TL); anterior nasal flap unilobated (weakly bilobated in neonates); nostrils somewhat nearest to mouth than to snout tip; prenarial length 0.9-1.4 times distance from nostril to upper labial furrow. Eyes oval with anterior margin convex and posterior margin slightly notched; eyes elongate, its length 2.4 (1.2-2.2) times its height. Prespiracular length 1.8 (1.5-2.9) times larger than preorbital length. Spiracles crescentic and constricted, located posterior-dorsally to the eyes; spiracle length at least one-third the eye length. Prebranchial length 1.6 (0.8-1.6) times larger than prespiracular length. Gill slits vertical and tall, with fifth gill slit height 1.1 (1.0-1.5) times first gill slit height.

Mouth arched and conspicuously wide (its width 1.5, 1.6-2.7 times wider than internarial width); preoral distance 1.5 (1.1-1.6) times mouth width; upper labial furrow large (its length 2.2%, 2.1%-3.3% of TL) with slender fold; lower labial furrow also elongate, lacking fold. Teeth similar in both jaws, although upper teeth smaller than lower teeth, labial-lingually flattened and alternate; teeth unicuspid, narrow and small at the crown; cusp slender and somewhat large, oblique and directed laterally; mesial cutting edge straight on upper teeth and somewhat convex on lower teeth; mesial and distal heels rounded, although the latter is thinner than former; apron markedly thin and large on both jaws; two series of functional teeth on upper jaw and three series on lower jaw; teeth rows varying from 15-0-13 on upper jaw, and 14-1-12 on lower jaw.

First dorsal fin origin prior to free rear tips of pectoral fin, including juveniles. Pre-first dorsal length 1.5 (1.4-1.6) times larger than prepectoral length. First dorsal fin triangular with anterior and posterior margins straight, and rounded at the apex; first dorsal broad at the base (its base length 1.0, 0.5-1.1 times preorbital length); first dorsal fin low, its height 0.8 (1.1-1.4) times its inner margin length; first dorsal spine slender (its base length 0.4%-0.8% of TL) and short, never reaching half of fin height, its length 0.2-0.4 times fin height. Interdorsal space 1.1 (0.8-1.0) times prepectoral length and 2.1 (1.4-2.0) times larger than dorsal-caudal space. Second dorsal fin broad at its base, corresponding to 0.9 (0.5-1.0) times preorbital length; second dorsal very low, its height 0.6 (0.9-1.0) times its inner margin length; first dorsal anterior margin convex, and posterior margin concave, rounded at the apex; second dorsal spine convex and thick at its base (its base width 1.3-7.2 times wider than base of first spine); second dorsal spine larger than first one, its length 1.6-2.8 times greater than length of first dorsal spine, almost reaching the fin apex.

Pectoral fin very narrow with anterior and inner margins straight, posterior margin concave; both apex and free rear tips rounded and lobulated, not reaching the same length when a horizontal line is traced between them; pectoral anterior margin length 2.0 (1.3-1.8) times larger than inner margin length; pectoral posterior margin length 1.1 (0.7-1.5) times trunk height. Pectoral-pelvic space equal to pelvic-caudal space in adults, its distance corresponding 0.7-1.2 times the latter. Pelvic fins located in the midline between first and second dorsal fins. Pelvic fins narrow with anterior margin somewhat convex, posterior margin straight; pelvic free rear tips slightly rounded and lobulated. Adult males with claspers slender and elongate, transcending greatly free rear tips of pelvic fin; clasper inner length 0.4-0.8 times length of pelvic inner margin; clasper with clasper groove large, located dorsal-laterally; apopyle and hypopyle with narrow apertures; apopyle placed anterior to clasper groove; hypopyle located posterior to clasper groove and anterior to rhipidion; rhipidion flattened and blade-like, markedly elongate, located at lateral-distal end of clasper.

Upper and lower precaudal pits conspicuous. Caudal keel inconspicuous, placed laterally since second dorsal fin insertion to caudal fin origin. Caudal fin rectangular with dorsal caudal margin straight, upper postventral margin convex, and dorsal tip rounded; dorsal caudal margin markedly large, its length 0.8 (0.9-1.1) times head length, and 1.9 (1.7-2.1) times larger than length of preventral caudal margin; lower postventral margin somewhat convex; preventral margin markedly convex and large, its length 1.7-3.1 times length of pelvic inner margin; ventral tip rounded; caudal fork between lobes strongly concave; caudal fin broad at caudal fork, its width 5.6%-7.6% of TL.

Dermal denticles (Fig. 72). Dermal denticles unicuspid, very small, and not imbricated with a single ridge (lateral ridges absent); median ridge conspicuous, narrower distally than proximally without furrows; median ridge markedly tall and erect, forming right angle with horizontal axis of the body; dermal denticles conspicuously thin at the crown; crown base broad and lozenge-like with four prominent pedicels.

Coloration. Body light grey dorsally and pale ventrally; numerous white spots dorsally (16-17 pairs on each side), rounded and small, distributed symmetrically within two rows on each side of body from posterior of spiracles to origin of caudal fin (although over vertebral column in the caudal fin of neonates and juveniles). Dorsal fins grey, darker from apex tip to midline of posterior margin, whitish at distal end of posterior margin and free rear tips; dorsal fins also white at its base; dorsal spines grey and white at the tip. Pectoral fins dark grey dorsal and ventrally with posterior margin slightly white, although not uniform. Pelvic fins light grey with posterior and inner margins slightly white. Caudal fin grey, whitish near the vertebral column; dorsal caudal margin somewhat white proximally; postventral caudal margins narrowly white; preventral caudal margin white; black caudal stripe conspicuous above the vertebral column.

Vertebral counts (Tab. 18). Monospondylous vertebrae 44 for neotype (37-43 for non-type specimens); diplospondylous vertebrae 58 (60-76); precaudal vertebrae 73 (72-84); total vertebrae 102 (102-114).

Geographical distribution (Fig. 74). It occurs in the Northeast Pacific Ocean from Washington to California in the U.S.A.

Etymology. The epithet "*suckleyi*" is honor to Dr. George Suckley, collector of the specimen in which Girard (1854) based his original description.

Remarks.

The original description of *Squalus suckleyi* (Girard, 1854) is very brief and generic, whose most of the diagnostic characteristics are applied to any species within Squalidae. Previously, this nominal species was distinguished from *S. acanthias* by having smaller number of vertebrae and through divergence on sequences of the mitochondrial CO1 gene only (e.g. Springer & Garrick, 1964; Ward *et al*., 2007; Ebert *et al*., 2010). In contrast to these studies, most of vertebrae count overlap between these two species, according to the current results. Despite of *S. suckleyi* is distinguished from *S. acanthias* from North Atlantic by fewer monospondylous vertebrae, there is no such variation when compared to the southern population of *S. acanthias*. New morphological differentiation with *S. acanthias* is provided herein and it is based on teeth morphology, shape of dermal denticles, and number of white spots. These results support *S. suckleyi* as a valid nominal species, which is in agreement with findings of Lindberg & Legeza (1959), Ebert *et al*. (2010) and Naylor *et al*. (2012a).

No type material was known for *S. suckleyi*, which contributed to its application as junior synonym of *S. acanthias* for more than 150 years. Taxonomic and biological studies (e.g. Springer & Garrick, 1964; Lindberg & Legeza, 1959; Gallucci *et al*., 2009) had revealed strong variations between specimens from East and West coast of The United States of America, suggesting being no conspecific. Only recently Ebert *et al*. (2010) designated a neotype and resurrected *S. suckleyi* as a valid species. These authors proposed new diagnosis based on a combination of characters that, however, also overlay on other species within Squalidae besides *S. acanthias*. Proportional measurements (e.g. trunk height; eye length) were also included as diagnostic despite of showing to be congruent between *S. suckleyi* and *S. acanthias*, with exception to proportional ratios of mouth width and prenarial length, and preoral length. No morphometric differences were noticed between these two nominal species in the present study, indicating that these characters cannot be integrated to the diagnosis of *S. suckleyi*.

Lindberg & Legeza (1959) and Ebert *et al*. (2010) further stated that the North Pacific species is distinguished from *S. acanthias* by pelvic-fin midpoint to first dorsal-fin insertion (PDI) and pelvic-fin midpoint to second dorsal-fin insertion (PDO). Other proportional ratios were also considered to be helpful for taxonomic separation such as first dorsal-fin midpoint to pectoral-fin insertion (DPI) and first dorsal-fin midpoint to pelvic-fin origin (Ebert *et al*., 2010) that indicates the position of first dorsal fin related to the pectoral fin, and pelvic fins related to the dorsal fins. Jones & Geen (1976) and Al-Badri & Lawson (1985), however, did not find any significant difference on these parameters.

None of these parameters were integrated for comparisons in the methodology of this current analysis because the definition of fin midpoint is biased rather than external measurement whose starting point is defined by the origin of the fin. In contrast to Lindberg & Legeza (1959), Garrick (1960), Jon & Geen (1976), Al-Badri & Lawson (1985), and Ebert *et al*. (2010), the results presented herein indicate that origin of first dorsal fin is prior to pectoral fin (vs. posterior to it for *S. acanthias*), and pelvic fins are in the midline between two dorsal fins in *S. suckleyi* (vs. nearest to second dorsal fin), when considering adult specimens.

Our analysis of specimens from Japanese and Russian coasts reveals greatly differentiation on external morphology on specimens of *S. suckleyi*, indicating to be a separate and distinct species (see further in this Chapter). Recent studies on reproduction, feeding and migration on this nominal species (e.g. Orlov *et al*., 2012a,b) also noticed variations on these biological patterns between populations from the east and west coasts, which it is in agreement with the current taxonomic analysis. *Squalus suckleyi* then is restricted to East side of the North Pacific Ocean, in contrast to Ebert *et al*. (2010), Naylor *et al*. (2012a), and Ebert *et al*. (2013a) that previously stated to inhabit both sides.

Comparative material. Same material listed previously for *S. acanthias*.

Squalus wakiyae Tanaka, 1917

(Northwest Pacific spiny dogfish)

Figs. 75–80, Tables 14, 17–18

Squalus wakiyae Tanaka, 1917: 471-475, pl. 130, figs. 368-370 (original description; illustrated; type by original designation from Watanoha, Japan; Northwest Pacific Ocean).
Squalus suckleyi not Girard: Fowler, 1941 (in part): 258-260 (description; North Pacific Ocean); Ebert *et al*., 2013 (in part): 78, 95 (cited, description; Northwest Pacific Ocean).
Squalus acanthias not Linnaeus: Yuanding, 1960: 107–109 (description; Northwest Pacific Ocean); Yuanding & Qingwen, 2001: 310-313 (description; Northwest Pacific Ocean); Nakabo, 2002: 155 (listed; Japan); Nakabo, 2013: 194 (listed; Japan); Shinohara *et al*. 2014: 233 (listed; Northwest Pacific Ocean); Dyldin, 2015: 56-57 (listed; Northwest Pacific Ocean).

Holotype: ZUMT 7632 (lost), juvenile female, 525 mm TL, Watanoha, Rikuzen Province, Japan.

Type locality: Ishinomaki, Miyag Prefecture (formerly Rikuzen), Japan.

Non-type material (42 specimens): HUMZ 68927, adult female, 952 mm TL, Yamasedomari Fish Market, Hakodate, Hokkaido, Japan; HUMZ 75718, juvenile female, 500 mm TL, Usujiri, Mimamikayakabie, Hokkaido, Japan; HUMZ 81094, adult female, 565 mm TL, Usujiri, Mimamikayakabie, Hokkaido, Japan; HUMZ 87643, adult male, 665 mm TL, Usujiri, Mimamikayakabie, Hokkaido, Japan; HUMZ 87733, juvenile male, 495 mm TL, off Shiretoko, Hokkaido, Japan; HUMZ 87752, juvenile female, 455 mm TL, off Muroran, Hokkaido, Japan; HUMZ 90963, adult female, 784 mm TL, Notori Misaki oki, Japan; HUMZ 107865, juvenile female, 465 mm TL, off Sekinai, Kumaishi, Hokkaido, Japan; HUMZ 107869, adult female, 650 mm TL, off Sekinai, Kumaishi, Hokkaido, Japan; HUMZ 117845, adult male, 720 mm TL, off Irifune, Hakodate, Hokkaido, Japan; HUMZ 123859, adult male, 815 mm TL, north Japan, 44°00.1’N, 155° 00.1’E; NSMT-P 10540, adult female, 625 mm TL, Northern Japan, Japan; NSMT-P 42569, adult male, 597 mm TL, unknown locality; NSMT-P 61090, adult female, 915 mm TL, Northern Japan, Japan; NSMT-P 74887, juvenile male, 445 mm TL, Northern Japan, Japan; NSMT-P 77186, adult male, 835 mm TL, unknown locality; NSMT-P 79501, adult male, 740 mm TL, Northern Japan, Japan; NSMT-P 92640, adult female, 740 mm TL, Northern Japan, Japan; ZUMT 3231, neonate male, 272 mm TL, Nagasaki, Japan; ZUMT 4684, neonate male, 265 mm TL, Tokyo Fish Market, Tokyo, Japan; ZUMT 4685, neonate female, 270 mm TL, Tokyo Fish Market, Tokyo, Japan; ZUMT 10536, neonate female, 120 mm TL; ZUMT 10789, neonate female, 238 mm TL, Hokkaido, Japan; ZUMT 36806, neonate female, 202 mm TL, Sakhalin Island, Russia; ZUMT 36807, neonate female, 200 mm TL, Sakuharin, Japan; ZUMT 36825, neonate female, 202 mm TL, Sakhalin Island, Russia; ZUMT 36836, neonate female, 202 mm TL, Sakuharin, Japan; ZUMT 40117, neonate male, 257 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 41539, neonate male, 284 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 45801, neonate male, 270 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46116, neonate male, 284 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46123, neonate male, 254 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46124, neonate male, 288 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46151, neonate male, 272 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46670, neonate male, 258 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46671, neonate female, 250 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46672, neonate male, 230 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46673, neonate female, 260 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46674, neonate male, 270 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 46675, neonate male, 245 mm TL, Uozu, Toyama Prefecture, Japan; ZUMT 51256, neonate female, 165 mm TL, East China Sea.

Diagnosis. *Squalus wakiyae* differs from its congeners by having body markedly dark grey with white spots tiny and very few in number, spread into a single row on each side (1–6 pairs). It also has dermal denticles conspicuously expanded at crown with cups directed in acute angle with longitudinal axis of body. It differs from *S. suckleyi* by showing origin of first dorsal fin posterior to horizontal line traced over pectoral free rear tips, and pelvic fins nearest second dorsal fin than first dorsal fin. It further distinguished from *S. acanthias* by having fewer vertebrae: 58–62 monopondylous vertebrae (vs. 46–50 for specimens from Baltic Sea); 58–62 (vs. 63–68) diplospondylous vertebrae; 71–73 (vs. 79–86) precaudal vertebrae; 99–104 (vs. 109–117) total vertebrae.

Description. Range values are for non-type specimens in which data were taken.

External morphology (Figs. 75–80; Tab 17). Fusiform and robust body (slender in younger specimens), arched dorsally since the anterior margin of the eye to the first dorsal fin origin, turning slenderer to the tail; head height 0.7-1.0 times the trunk height and 0.8-1.2 times the abdomen height. Head well elongate (its length 20.0%-24.2% of TL), flattened dorsally near the snout and narrower anteriorly than posteriorly, its width 1.2-2.2 times than its width at the nostrils; its width 0.9-1.5 times the trunk width and 1.2-1.8 times the abdomen width. Snout rounded at the tip, well elongated (preorbital length 6.3%-8.2% of TL); anterior nasal flap unilobated (bilobated in neonates and very young juveniles); nostrils nearest to the mouth than to the snout tip; prenarial length 0.9-1.3 times the distance from the nostril to the upper labial furrow. Strongly rounded eyes with anterior margin concave and notched posterior margin, strongly large, its length 1.6-2.8 times its height. Prespiracular length 1.5-1.7 times the preorbital length. Spiracles crescentic, very broad, located posterior-dorsally to the eyes; its length at least one-fourth the eye length. Prebranchial length 1.5-1.7 times the prespiracular length. Gill slits vertical, markedly tall with fifth gill slit height 1.0-1.6 times the first gill slit height.

Mouth slightly arched, conspicuously wide, its width 1.7-2.3 times the internarial width; preoral distance 1.1-1.5 times the mouth width; elongated upper labial furrow (its length 1.7%-3.2% of TL) with slim fold; lower labial furrow also elongate, lacking fold. Teeth unicuspid, broad and large at the crown; teeth similar in both jaws with upper teeth slightly smaller than lower teeth; teeth labial-lingually flattened and alternate; cusp short and thick, oblique and directed laterally; mesial cutting edge conspicuously convex on both upper and lower teeth; mesial heel rounded; distal heel notched; apron markedly thin and elongate on both jaws; two series of functional teeth on upper and lower jaws; teeth rows varying from 13-1-13 on upper jaw, and 11-1-11 on lower jaw.

First dorsal fin origin posterior to the free rear tips of the pectoral fin, including neonates. Pre-first dorsal length 1.4-1.7 times prepectoral length. First dorsal fin somewhat triangular in shape with somewhat convex anterior margin, straight posterior margin, conspicuously narrower and rounded at the apex; broad at the base, its base length 0.8-1.1 times the preorbital length; first dorsal fin low with its height 1.2-1.5 times its inner margin length; first dorsal spine extremely slim (its base length 0.3%-0.6% of TL) and small, never reaching half of the fin height with its length 0.2-0.3 times the fin height. Interdorsal space 0.7-1.1 times the prepectoral length and 1.5-2.1 times the dorsal-caudal space. Second dorsal fin also broad at its base, corresponding to 0.7-1.2 times the preorbital length; second dorsal also very low with its height 0.8-1.3 times its inner margin length; convex anterior margin, rounded at the apex; concave posterior margin, slightly falcate; second dorsal spine convex and thicker at its base (its base width 1.0-2.1 times base of first spine); second dorsal spine 1.4-3.0 times larger than first one, although never reaching the fin apex.

Pectoral fin narrow with convex anterior and inner margins, posterior margin somewhat concave; both apex and free rear tips rounded and widely lobulated, reaching the same length when a horizontal line is traced between them; anterior margin length 1.5-2.0 times the inner margin length; posterior margin length 0.7-1.1 times the trunk height. Pectoral-pelvic space almost equal to the pelvic-caudal space, its distance corresponding 1.0-1.2 times the latter. Pelvic fin nearest to the second dorsal fin than to the first dorsal fin. Pelvic fins also very narrow with convex anterior margin and straight posterior margin, rounded and lobulated free rear tips (pointed in males). Adult males with very slender and large clasper, transcending greatly the free rear tips of the pelvic fin, its inner length 0.5-1.6 times the inner margin length of the pelvic fin; clasper with profound clasper groove, located dorsal-laterally; apopyle with large aperture; hypopyle with narrow aperture anterior to the rhipidion; rhipidion flattened and blade-like, somewhat elongate, supporting the dorsal terminal 2 cartilage, located at lateral-distal end of the clasper.

Upper and lower precaudal pits conspicuous. Caudal keel somewhat prominent, placed laterally since the second dorsal fin insertion to posteriorly the caudal fin origin. Caudal fin conspicuously rectangular with convex dorsal caudal margin, strongly convex upper postventral margin and rounded dorsal tip; dorsal caudal margin very large, its length 0.8-1.1 times the head length and 1.0-2.4 times the ventral lobe length; lower postventral margin also strongly convex; preventral margin convex and well elongate, its length 1.9-5.9 times the inner margin of the pelvic fin; ventral tip rounded, although somewhat slender; caudal fork continuous and strongly broad, its width 6.3%-11.2% of TL.

Dermal denticles (Fig. 79). Dermal denticles unicuspid, small, and not imbricated with an unique ridge (lateral ridges absent); median ridge very prominent, narrower distally than proximally with furrow anterior and profound; median ridge very tall and convex, forming 45 degrees angle with horizontal axis of the body; crown base strongly broad and diamond-like with four prominent pedicels; dermal denticles conspicuously expanded laterally at the crown. A single adult male shows few dermal denticles with weak lateral cusps, although lateral ridges are still absent.

Coloration. Body dark grey dorsally with very few and inconspicuous white spots (1–6 pairs), rounded, distributed symmetrical in a single row on each side, and laterally at the body; white spots commonly absent in some large specimens, although clearly evident in young juveniles; white to greyish white ventrally. Both dorsal fins grey, brownish in the apex, slightly darker from the apex tip to the midline of the posterior margin, white distally at posterior margin and free rear tips; fin base discreetly white; dorsal spines dark brown, white at the tip. Pectoral fins dark grey dorsal and ventrally with white posterior margin, although not uniform. Pelvic fins also dark grey with posterior and inner margins slightly white. Caudal fin grey, darker at the tip of the dorsal lobe and in the lower caudal lobe, white over vertebral column; proximal end of dorsal caudal margin white; postventral caudal margins narrowly white; preventral caudal margin slightly white; black caudal stripe conspicuous above vertebral column.

Vertebral counts. (Table IX) 99-104 total vertebrae; 40-42 monospondylous vertebrae; 71-73 precaudal vertebrae; 27-31 caudal vertebrae.

Geographical distribution (Fig. 80). It occurs in the Northwest Pacific Ocean from Russia to South Japan.

Etymology. The epithet "*wakiyae*" is in honour to Mr. Yojiro Wakiya.

Remarks.

Types specimens of *Squalus wakiyae.* Tanaka (1917) stated that *Squalus wakiyae* was described and illustrated based on a juvenile female with 525 mm TL, whose catalogue number is ZUMT 7632, collected in Watanoha, Rikuzen Province (currently Ishinomaki, Miyag Prefecture) in Japan by the Miyagiken Fisheries Experiment Station. According to Dr. Sakamoto, curator of the Zoological University Museum of Tokyo, the holotype of this nominal species is lost or no longer exists in the fish collection. I myself verified this information by visiting the museum personally where I analyzed all specimens of *S. wakiyae* that were deposited there. Interestingly, no one of these specimens was collected in the same location of the holotype, which excludes any possible curatorial mistake on mixing specimens. Once the original description was based in a single specimen, there is no syntypes for this nominal species, suggesting that a neotype is needed for supporting *Squalus wakiyae* as a valid nominal species, and distinct from its congeners.

Taxonomic status of *Squalus wakiyae.* A single nominal species of spotted spiny dogfish was described from the Northwestern Pacific Ocean under the name of *Squalus wakiyae* Tanaka, 1917. Its original description was related to *S. mitsukurii* because Tanaka (1917) did not realized earlier that the picture and description present in Jordan & Snyder (1903) are not correspondent to the same nominal species. Despite of later Tanaka (1917) promptly corrected his mistake and proposed a new scientific name for the spotted dogfish from

Japanese waters, it is possible to notice that Tanaka combined characteristics from both nominal species for describing *S. wakiyae*. For instance, dermal denticles tricuspid with three ridges that resembles those of *S. japonicus*, and body bluish brown are attributed to *S. mitsukurii*. Other characteristics provided by Tanaka (1917) are overlapped to those of *S. acanthias* and *S. suckleyi*, and contributed to its application as synonym of these nominal species by many authors (e.g. Fowler, 1941). Later studies (e.g. Chen *et al*., 1979; Figueirêdo, 2011) noticed that the specimen illustrated in Jordan & Snyder (1903) belongs to *S. acanthias*, then definitely placing *S. wakiyae* as its junior synonym.

Other common synonyms that are often applied for Japanese waters are the nominal species *Acanthias vulgaris*, *S. tasmaniensis*, *S. acanthias*, and *S. suckleyi* (Bigelow & Schroeder, 1957; White *et al*., 2007a). As discussed previously in this chapter, the first two nominal species are junior synonyms of *S. acanthias* that occurs from the North Atlantic to South Atlantic Oceans as well as South Pacific Ocean. *Squalus suckleyi* is the next available name for spotted dogfish in this region to which *S. wakiyae* is been misidentified till now (e.g. Ebert *et al*., 2010; Eschmeyer & Fricke, 2015). Morphological comparisons were never achieved between specimens from East and West side of the North Pacific Ocean in order to support these assumptions but through DNA barcoding only (e.g. Ward *et al*., 2007; Ebert *et al*., 2010; Naylor *et al*., 2012a). It is important to notice that these authors used very few representatives from Japan, indicating that possible molecular distinction between these specimens would be unrevealed. Despite of molecular conspecificity among these populations, White *et al*. (2007a) stated that *S. wakiyae* should be resurrected, although no additional data was provided.

The current results show great morphological variations between specimens from these areas, and with specimens of *S. acanthias* for the first time. *Squalus wakiyae* is then revalidated herein as a nominal species restricted to Northwest Pacific Ocean. It is easily distinguished from *S. acanthias* and *S. suckleyi* by having body conspicuously dark grey dorsally with few white spots distributed in a single row on each side of the body (vs. light grey body with many white spots in two rows), and rounded snout tip (vs. obtuse snout tip). In contrast to what it is observed for *S. suckleyi*, *Squalus wakiyae* is easily distinct from *S. acanthias* from different localities by smaller number of vertebrae (monospondylous, diplospondylous, precaudal and total vertebrae). It further has teeth with oblique and short cusp (vs. teeth with vertical and rather longer cusp for adult males of *S. acanthias*). *Squalus wakiyae* also exhibits teeth broad at crown with medial cutting edge markedly convex on both jaws while tooth is narrow with mesial cutting edge convex in the lower teeth only in *S. suckleyi*.

Dermal denticles are also useful for distinguishing *S. wakiyae* from *S. acanthias* and *S. suckleyi*. The former species always show median ridge forming acute angle with longitudinal axis of body (vs. in parallel for *S. acanthias* vs. in right angle for *S. suckleyi*) with a profound anterior furrow (vs. absent in both latter species). Besides, the crown is conspicuously expanded in *S. wakiyae* (vs. very thin in the latter two species). Specimens of *S. wakiyae* have pelvic fin nearer second dorsal fin than first dorsal fin, and it is agreement with Tanaka (1917). It is important to notice that no ontogenetic variation is showed for this species regarding position of pelvic fin, which it is in contrast to what it is observed for *S. suckleyi* and *S. acanthias*.

External measurements are overlapped between *S. wakiyae* and *S. suckleyi*, although the former species shows broader range: length of inner margin of first and second dorsal fin much greater in NEPO than NWPO (4.8%-5.9% vs. 4.4%-5.3% of TL; 4.5%-5.4%-3.7%-4.8% of TL); length of inner pectoral margin larger in NEPO (7.3%-10.2% vs. 7.3%-8.7% of TL). However, great morphometric differences with the neotype of *S. suckleyi* (taken from Ebert *et al.*, 2010) are shown and support *S. wakiyae* as a separate species: greater prepelvic length in *S. suckleyi* than in specimens from the NWPO (51.5% of TL for neotype vs. 47.2%-50.6% of TL, respectively); greater pre-vent length in *S. suckleyi* (54.9% of TL vs. 50.1%-53.6% of TL, respectively); narrower mouth in *S. suckleyi* (6.2% of TL vs. 6.9%-8.2% of TL, respectively); lower head height (6.5% of TL vs. 7.8%-10.6% of TL, respectively); pectoral fin broader at the base in *S. suckleyi* (6.4% of TL vs. 3.5%-4.9% of TL, respectively); lower second dorsal fin in *S. suckleyi* (3.0% of TL vs. 3.6%-5.0% of TL).

Squalus wakiyae is also distinct from types of the nominal species *Acanthias lebruni* from Chile and *Squalus tasmaniensis* from Australia by, respectively: larger pre-first dorsal length (32.6%-35.6% of TL vs. 29.6%-32.1% of TL vs. 30.6% of TL); smaller dorsal-caudal space (9.9%-11.5% of TL vs. 12.1%-12.8% of TL vs. 11.9% of TL); lower first dorsal fin (first dorsal height 5.9%-6.7% of TL vs. 6.8% of TL vs. 6.9% of TL); smaller second dorsal spine (1.9%-3.5% of TL vs. 3.8%-4.0% of TL vs. 4.4% of TL); greatest width of head (9.5%-12.6% of TL vs. 8.8%-9.1% of TL vs. 8.7% of TL); deepest head (its height 7.8%-10.6% of TL vs. 7.4%-7.6% of TL vs. 6.2% of TL).

Recent investigations on the biology of *S. suckleyi* notice variations with specimens from the West side of North Pacific Ocean that additionally support the current hypothesis of *S. wakiyae* as a separate and valid species. Differences on diet and reproduction were provided by Orlov *et al*. (2012a) for specimens from off Kuril Islands, Kamchatka and Sea of Japan. Later, Orlov *et al*. (2012b) also revealed large differences on vertical migration and size composition.

Comparative material. Same material listed previously for *S. acanthias* and *S. suckleyi*.

Flakeus Whitley, 1939

Flakeus Whitley, 1939: 242 (original description; Australia; subgenus of *Squalus*; type by original designation); Whitley, 1940: 137–139, figs. 147–152 (revision; Australia; new replacement name for *Squalus*); Bigelow & Schroeder, 1948: 452 (cited; Australia); Whitley, 1964: 33 (listed; Australia).

Type species: *Flakeus megalops* (Macleay, 1881), type by original designation.

Definition. Species of the genus *Flakeus* are morphologically characterized by having body uniformly colored lacking spots, anterior margin of nostrils bilobate, origin of first dorsal fin anterior or over the vertical traced at pectoral free rear tips, first dorsal spine as large as second dorsal spine at least, and dermal denticles unicuspid or tricuspid with three ridges. It differs from *Squalus*: first dorsal fin greater in length and height than second dorsal fin; dorsal fins with length of its inner margin much smaller than its height; distance between pectoral and pelvic fins much smaller than distance between pelvic and caudal fins; space between dorsal fins 2.5 times greater than dorsal-caudal space. In contrast to *Squalus*, *Flakeus* has first dorsal spine elongate, over one-half of first dorsal fin height, and length of second dorsal spine 1.6 times larger than length of first dorsal spine.

Content. *Flakeus megalops, F. acutipinnis, F. brevirostris, F. cubensis, F. crassispinus, F. bucephalus, F. raoulensis, F. albifrons, F. notocaudatus, F. blainvillei, F. hemipinnis, F. mitsukurii, F. japonicus, F. montalbani, F. griffini, F. melanurus, F. probatovi, F. lalannei, F. grahami, F. edmundsi, Flakeus* sp. 1, *Flakeus* sp. 2, *Flakeus* sp. 3, *Flakeus* sp. 4, *Flakeus* sp. 5, *Flakeus* sp. 6, and *Flakeus* sp. 7.

Remarks. Whitley (1939) proposed two subgenera for *Squalus*: *Flakeus* and *Koinga*. The former group comprised species characterized by having: eye length four times in head length; origin of first dorsal fin over or just posterior to vertical at pectoral free rear tips, and nearest to snout tip than second dorsal fin; body with uniform color. *Squalus megalops* was designated as its type species, and included *S. tasmaniensis* and *S. griffini* into this subgenus as well (Whitley, 1939). Later, Whitley (1940, 1964) raised *Flakeus* and *Koinga* to genus-level and suppressed *Squalus* without comments. The genus-name *Flakeus* is derived from the English word, flake, commonly used in the fish shops from Australia for sharks, according to Dr. Hoese (*pers. comm.*, 2015). Whitley (1939, 1940, 1964) did not mentioned its etymology, even though he was the only author that considered it as a valid genus for all species of dogfish from Australian and New Zealand waters. *Koinga* includes the nominal species *Squalus whitleyi* Phillipps, 1931, as type species, wich it is junior synonym of *S. acanthias*. Thus, this genus is an unnecessary replacement name for *Squalus* and also an unavailable name because it directly derived from vernacular Maori word, *koinga*, that means spine and also a common-name for the white spotted dogfish (Article 11, ICNZ).

Bigelow & Schroeder (1948) considered both genera as synonyms of *Squalus*, followed by many authors (e.g. Garrick, 1960; Compagno, 1984). The former authors proposed the subdivision of the genus into “group of species” instead due to similarities of external morphology among the species, even though the characteristics for defining each group are somewhat overlapped between species that belongs to different group of species as verified in the present study, and Figueirêdo (2011) and Viana *et al*. (*in prep*.). Since then, many authors (e.g. Bass *et al*., 1976; Compagno *et al*., 2005; Last *et al*., 2007) recognized the subdivisions within *Squalus* despite of recent studies on its Systematics has shown two to three inner clades in the family (e.g. Ward *et al*., 2007; Naylor *et al*., 2012a,b).

In the present study, *Flakeus* is ressurected as a valid genus and separated from *Squalus* based on a broader morphological analysis of members of Squalidae and new intepretations over recent studies on its inner phylogenetic relationships.

Identification key to species of *Flakeus*

1. – Body small (adults between 378–830 mm TL); snout very short, its preorbital length 6.1%–9.6% of TL in adults); prenarial length equal or smaller than distance from nostrils to upper labial furrow; dermal denticles unicuspid and lanceolate……………………………**2**

– Body elongate (adults between 465–1120 mm TL); snout conspicuously large, its preorbital length 6.6%–10.7% of TL in adults); prenarial length equal or larger than distance from nostrils to upper labial furrow; dermal denticles tricuspid and rhomboid…………………...…………………………………………………….……….........**15**

2. – First dorsal spine very short (its length 1.8%–3.7% of TL in adults), never reaching one-half of height of first dorsal fin…………………………….………..….***Flakeus megalops***

– First dorsal spine elongate (its length 3.0%–6.3% of TL in adults), transcending one-half height of first dorsal fin………………………………..………………………....**3**

3. – Dorsal spines markedly heavy with base width of first dorsal spine greater than 1.1% of TL and base width of second dorsal spine broader than 1.2% of TL; caudal fin conspicuously pale with no uniform white postventral caudal margins……………..................…………..……………………….***Flakeus crassispinus***

– Dorsal spines markedly slender with base width of first dorsal spine not greater than 1.1% of TL and base width of second dorsal spine not broader than 1.0% of TL; caudal fin grey or brownish with uniform white postventral caudal margins……………..….............…**4**

4. – Pectoral fins with free rear tips pointed or L-shaped; first dorsal fin oblique and low, its greatest height between 8.0%–9.1% of TL…..……………….………..………..**5**

– Pectoral fins with free rear tips rounded and lobe-like; first dorsal fin conspicuously upright and tall, its greatest height between 9.1%–10.4% of TL…..……..........………..**10**

5. – Pectoral fins markedly broad posteriorly, its posterior margin transcends trunk height when adpressed on body……………………………………………………...……**6**

– Pectoral fins markedly narrow posteriorly, its posterior margin never transcends trunk height when adpressed on body…………………….……………………..……..**7**

6. – First dorsal fin rounded at apex; caudal fin continuous at caudal fork; dermal denticles somewhat narrow at crown, its length equal to its width with lateral expansions asymmetrical…………………………...……………………….…***Flakeus acutipinnis***

– First dorsal fin triangular at apex; caudal fin discontinuous; dermal denticles broad at crown, its length greater than its width with lateral expansions symmetrical..…***Flakeus* sp. 1**

7. – First and second dorsal fins with conspicuous black markings at apex…………………………...…………………….………….***Flakeus cubensis***

– First and second dorsal fins lacking black markings at apex……………………….……**8**

8. – Body light grey dorsally; internarial space very narrow (3.4%–3.8% of TL); dorsal-caudal distance 10.0%–10.6% of TL; first dorsal spine thin, its base width 0.5%–0.7% of TL…………………....……………………………..………….***Flakeus brevirostris***

– Body dark grey dorsally; internarial space broad (3.6%–5.1% of TL); dorsal-caudal distance 10.7%–14.1% of TL; first dorsal spine stout, its base width 0.7%–1.1% of TL..…………….……………………………………………………………...…..**9**

9. – Upper labial furrow more elongate, its length 2.5%–2.7% of TL; first dorsal spine large, its length 4.2%–4.9% of TL……………………………….……….………***Flakeus* sp. 3**

– Upper labial furrow small, its length 2.1%–2.5% of TL; first dorsal spine short, its length 2.3%–4.1% of TL……….……………………………………….……....***Flakeus* sp. 7**

10. – Head conspicuously humped dorsally and broad, its width at mouth 12.9%–13.5% of TL; mouth straight and conspicuously broad, its width 8.1%–8.7% of TL; pelvic-caudal space, corresponding to 23.5%–24.9% of TL; 99 precaudal vertebrae……………..…………...……..…………………………..…***Flakeus bucephalus***

– Head flattened dorsally and narrow, its width at mouth 9.2%–12.4% of TL; mouth arched and narrow, its width 6.7%–8.3% of TL; pelvic-caudal space, corresponding to 25.5%–33.9% of TL; 74–97 precaudal vertebrae……………….………….…………..**11**

11. – Snout obtuse at tip; fewer monospondylous (37), precaudal (74) and total (97–98) vertebrae; caudal fin slender at lobes……………..………...…………***Flakeus hemipinnis***

– Snout rounded at tip; more number of monospondylous (40–48), precaudal (80–97) and total (107–126) vertebrae; caudal fin somewhat rectangular...……………......………..**12**

12. – First dorsal spine short, its length 2.1%–4.3% of TL in adults; dermal denticles lacking cusplets; head elongate, its length 22.6%–26.6% of TL; distance from nostrils to upper labial furrow 4.8%–6.4% of TL; snout large, its preorbital length 7.1%–9.1% of TL…………………...…………………………………..……..……***Flakeus raoulensis***

– Conspicuously elongate first dorsal spine, its length 4.2%–6.3% of TL in adults; dermal denticles with posterior cusplets; head very small, its length 19.8%–22.4% of TL; distance from nostrils to upper labial furrow 4.1%–4.7% of TL; snout short, its preorbital length 6.1%–7.1% of TL……………………………………………………….………**13**

13. – Interdorsal space smaller than 25.1% of TL in adults; dorsal-caudal space between 10.3%–11.7% of TL; internarial distance 3.2%–3.8% of TL; dermal denticles with cusplets comprised by extension of posterior margin of crown; 67–69 diplospondylous vertebrae; 80–84 precaudal vertebrae; 107–111 total vertebrae…..……………………..…***Flakeus blainvillei***

– Interdorsal space between 25.2%–26.4% of TL in adults; dorsal-caudal space between 9.3%–10.3% of TL; internarial distance 4.1%–4.6% of TL; dermal denticles with cusplets comprised by an posterior extension of the lateral ridges; 72–78 diplospondylous vertebrae; 90–97 precaudal vertebrae; 115–126 total vertebrae..………………..…………..**14**

14. – Eyebrow white; body brown dorsally; caudal fin without upper caudal fringe; pectoral fins small, its anterior margin length between 15.0%–15.9% of TL; pectoral posterior margin concave……...............................……………………………….……***Flakeus albifrons***

– Eyebrow absent; body light grey dorsally; caudal fin with black upper caudal fringe; pectoral fins markedly elongate, its anterior margin length between 16.6%–18.7% of TL; pectoral posterior margin conspicuously falcate……….…………***Flakeus notocaudatus***

15. – Snout conical at tip and conspicuously elongate, its prenarial length 5.8%–8.4% of TL; preorbital length 8.3%–10.9% of TL; mouth very narrow, its width 5.3%–7.4% of TL……………………………………………………………………………...………..**16**

– Snout obtuse at tip and small, its prenarial length 4.0%–5.6%; preorbital length 6.6%–8.7%; mouth broad, its width 7.0%–9.4% of TL……………………………………...**17**

16. – Head very narrow, its width at mouth 9.7%–10.5% of TL in adults; first dorsal fin low, its height 6.6%–7.5% of TL; pectoral fin very narrow, its posterior margin length 8.3%–9.2% of TL in adults; caudal fin uniformly grey on ventral lobe…..……***Flakeus japonicus***

– Head wide, its width at mouth 10.8%–12.7% of TL in adults; first dorsal fin tall, its height 8.2%–10.3% of TL; pectoral fin wide, its posterior margin length 9.3%–12.0% of TL; caudal fin with black ventral lobe……………..……..…………………***Flakeus melanurus***

17. – Pectoral fins with anterior and inner margins markedly straight; caudal fin with upper and lower lobes symmetrical with tips pointed; dorsal caudal margin short, its length 17.6% of TL, corresponding to 1.5 times length of preventral caudal margin; 67–69 precaudal and 93–95 total vertebrae……..…………………...……………………...….***Flakeus lalannei***

– Pectoral fins with anterior and inner margins convex; caudal fin with upper and lower lobes asymmetrical with tips rounded; dorsal caudal margin elongate, its length 18.6%–23.7% of TL, corresponding to 1.7–2.1 times length of preventral caudal margin; 80–92 precaudal and 112–121 total vertebrae…………………………………………..…......….**18**

18. – Head very large, its length 25.6%–28.8% of TL in adults; mouth width 8.2%–9.4% of TL; prepectoral length 23.5%–27.8% of TL in adults; dorsal spines conspicuously elongate with first dorsal spine length 5.5%–6.5% of TL and second dorsal spine length 6.1% of TL in adults...…...…………………………………………………………***Flakeus edmundsi***

– Head small, its length 20.6%–25.2% of TL in adults; mouth width 6.6%–8.4% of TL; prepectoral length 20.0%–24.7% of TL in adults; dorsal spines small with first dorsal spine length 2.7%–5.3% of TL and second dorsal spine length 3.0%–5.6% of TL in adults……………………………..……………...………………………..………….**19**

19. – Dorsal fins upright; first dorsal fin tall, its height 8.2%–10.4% of TL in adults; origin of first dorsal fin just behind vertical at origin of pectoral fin; pelvic-caudal space 15.3%–20.3% of TL in adults…………………..........……………………..……***Flakeus probatovi***

– Dorsal fins vertical; first dorsal fin low, its height 6.9%–8.9% of TL; origin of first dorsal fin prior to pectoral free rear tips; pelvic-caudal space 20.1%–26.3% of TL……………………………………………………………………...………………..**20**

20. – Body dark grey to black; eyes small, its length 3.4%–4.0% of TL in adults; prenarial length 4.1%–5.2% of TL in adults; preoral length 7.6%–9.9% of TL in adults; fifth gill slit tall, its height 2.4%–2.6% of TL in adults; caudal fin narrow, its width at caudal fork 6.1%–6.8% of TL…………………..……………..……………..………***Flakeus mitsukurii***

– Body light grey; eyes large, its length 3.9%–5.3% of TL in adults; prenarial length 5.0%–6.1% TL in adults; preoral length 9.5%–11.2% of TL in adults; fifth gill slit low, its height 1.8%–2.4% of TL in adults; caudal fin wide, its width at caudal fork 6.4%–7.7% of TL……………………………………………………………………………………..…**21**

21. – Body light grey dorsally and whitish laterally from pectoral fin to behind origin of caudal fin; pelvic fins nearest to second dorsal fin than first dorsal fin; conspicuous white caudal bar at fork; 46–49 monospondylous vertebrae…………….…………***Flakeus griffini***

– Body grey dorsally and laterally; pelvic fins placed in the midline between dorsal fins; conspicuous black caudal bar at fork; 38–45 monospondylous vertebrae…………...………..…………………………………………………………...…**22**

22. – Black caudal bar at caudal fork and black upper caudal fringe present……………..**23**

– Black caudal bar and black upper caudal fringe absent……………..………………**24**

23. – Body slender; snout obtuse at tip; preoral length 1.4–1.6 times greater than mouth width; mouth width 1.1–1.2 times greater than prenarial length; dorsal fins slender at fin web; pectoral fin with its posterior margin concave; pelvic-caudal space 26.1%–29.0% of TL…………………………………………..……………………….***Flakeus grahami***

– Body robust; snout rounded at tip; preoral length 1.2–1.4 times greater than mouth width; mouth width 1.3–1.7 times greater than prenarial length; dorsal fins very broad at fin web; pectoral fin with its posterior margin straight; pelvic-caudal space 22.0%–26.3% of TL………………………………………………………...………***Flakeus montalbani***

24. – Body markedly humped dorsally and robust; first dorsal fin conspicuously slender from its midline to the apex; second dorsal fin upright and markedly tall, its height 4.0%–5.3% of TL; dermal denticles markedly imbricate and broad at the crown.……………………………………………………………....…….***Flakeus* sp. 6**

– Body very slightly arched dorsally and slender; first dorsal fin uniformly thin; second dorsal fin raked and low, its height 3.7%–4.4% of TL; dermal denticles not imbricate and slender and crown……..……….……………………………………………..…………**25**

25. – First dorsal fin high, its height 7.5%–9.0% of TL in adults; prebranchial length 19.1%–22.4% of TL in adults; preorbital length 7.6%–8.4% of TL; dermal denticles with anterior margin of crown constricted and conspicuously rounded……........….***Flakeus* sp. 3**

– First dorsal fin low, its height 6.5%–7.5% of TL; prebranchial length 17.7%–18.8% of TL; preorbital length 7.0%–7.4% of TL; dermal denticles with anterior margin of crown broad and arrow-shaped…………………………………………………….……………..**26**

26. – First and second dorsal fins narrow; caudal fin light grey with dorsal caudal margin white and ventral caudal lobe mostly white; interdorsal space 24.4%–26.8% of TL; dorsal caudal space 11.0%–12.2% of TL; pectoral-caudal space 19.5%–20.3% of TL; pectoral inner margin 8.4%–8.9% of TL……...……...……………..….…………………..***Flakeus* sp. 5**

– First and second dorsal fins very broad; caudal fin mostly dark grey with dorsal caudal margin light grey and ventral caudal lobe uniformly dark grey; interdorsal space 21.9%–24.1% of TL; dorsal caudal space 10.4%–10.9% of TL; pectoral-caudal space 20.3%–24.4% of TL in adults; pectoral inner margin 9.2%–10.6% of TL…..……..… ***Flakeus* sp. 4**

***Flakeus megalops* (Macleay, 1881)**

(Piked spurdog; Skittle dogfish)

Figs. 81–87; Tables 19, 23, 24

Acanthias megalops Macleay, 1881: 367 (original description, not illustrated; Port Jackson, Australia; type by original designation); Ogilby, 1886: 4 (listed; Southwest Pacific Ocean).

Squalus megalops Waite, 1901: 33-34 (cited; Southwestern Pacific Ocean); Regan, 1908: 45, 47 (cited, listed; Southwest Pacific Ocean); Smith, 1912: 679 (cited; Southwest Pacific Ocean); Phillipps, 1931: 361 (cited; Southwest Pacific Ocean); Fowler, 1941: 256 (cited; Southwest Pacific Ocean); Phillipps, 1946: 16 (cited; Southwest Pacific Ocean); Last & Stevens, 1994: 48, 99-100 (cited, description; Southwest Pacific Ocean); Compagno & Niem, 1998: 1222, 1230 (listed, cited; Southwest Pacific Ocean); Compagno, 1999: 472 (listed); Last *et al*., 2007: 17-22 (redescription; Southwest Pacific Ocean); Last & Stevens, 2009: 45, 55, 56 (listed, description; Southwest Pacific Ocean); Ebert *et al*., 2013 (in part): 76, 91 (cited, description; Southeast Pacific Ocean).

Squalus fernandinus: Garman, 1913 (in part): 195 (description; Southwest Pacific Ocean); Fowler, 1941 (in part): 260 (described; Southwest Pacific Ocean).

Flakeus megalops Whitley, 1939: 242 (description; new combination; type species of the subgeneric name *Flakeus*); Whitley, 1940: 137-138 (description; Southwest Pacific Ocean); Whitley, 1964: 33 (listed; Southwest Pacific Ocean).

Squalus brevirostris: Compagno & Niem, 1998: 1230 (cited; Northwest Pacific Ocean).

Holotype. AMS I 16255-001, adult female, 550 mm TL, Port Jackson, New South Wales, Australia.

Paratypes: Not mentioned.

Type locality: Port Jackson, New South Wales, Australia.

Non-type material (52 specimens): AMS I 23359-002, three adult females, 557-625 mm TL; adult male, 665 mm TL, off Nowra, New South Wales, Australia; AMS I 45622-001, neonate male, 198 mm TL; two neonate females, 191, 193 mm TL, Queensland Seamount, Australia; AMS I 45658-001, two adult females, 625 mm TL, Barcoo Seamount, New South Wales, Australia; AMS I 46033-001, adult male, 475 mm TL, Barcoo Seamount, New South Wales, Australia; CSIRO C 3931, juvenile female, 490 mmm TL, off Laurieton, New South Wales, Australia, 31°40’S,152°52’E; CSIRO H 624-02, adult male, 415 mm TL, Southeast of Eddystone Point, Tasmania, Australia, 41°04’S,148°24’E; CSIRO H 822-17, juvenile female, 259 mm TL, Southeast of Shark Bay, Western Australia, 27°03’S,112°40’E; CSIRO H 822-18, juvenile female, 205 mm TL, Southeast of Shark Bay, Western Australia, 27°03’S,112°40’E; CSIRO H 1264-16, adult female, 515 mm TL, North of Maria Island, Tasmania, Australia, 42°33’S,148°15’E; CSIRO H 1264-17, adult female, 526 mm TL, North of Maria Island, Tasmania, Australia, 42°33’S,148°15’E; CSIRO H 1310-3, juvenile male, 335 mm TL, South of Saumarez Reef, Queensland, Australia, 22°35’S,153°40’E; CSIRO H 1345-1, juvenile female, 328 mm TL, between Saumarez Reef and Fraser Island, Queensland, Australia, 22°53’S,152°59’E; CSIRO H 1403-01, juvenile female, 487 mm TL, Southeast

Tasmania, Australia; CSIRO H 2225-01, adult male, 449 mm TL, Storm Bay, Tasmania, Australia; CSIRO H 2365-01, adult female, 505 mm TL, Northwest of Cape Naturaliste, Western Australia, 33°20’S,114°30’E; CSIRO H 2599-04, juvenile female, 219 mm TL, West of Gree Head, Western Australia, 29°58’S,114°26’E; CSIRO H 2605-09, juvenile male, 460 mm TL, Northwest of Rottnest Island, Western Australia, 31°43’S,114°58’E; CSIRO H 2688-03, juvenile male, 399 mmm TL, East off Coffs Harbour, New South Wales, Australia, 30°24’S,153°24’E; CSIRO H 2688-04, juvenile female, 371 mmm TL, East off Coffs Harbour, New South Wales, Australia, 30°24’S,153°24’E; CSIRO H 2688-05, juvenile male, 310 mmm TL, East off Coffs Harbour, New South Wales, Australia, 30°24’S,153°24’E; CSIRO H 2967-05, juvenile male, 362 mmm TL, East off Coffs Harbour, New South Wales, Australia, 30°20’S,153°24’E; CSIRO H 2967-08, juvenile male, 365 mmm TL, East off Coffs Harbour, New South Wales, Australia, 30°20’S,153°24’E; CSIRO H 3522-06, juvenile female, 232 mm TL, South of Cape Everard, Victoria, Australia, 38°11’S,149°34’E; CSIRO H 3762-01, adult female, 500 mm TL, Bass Strait, Victoria, Australia, 38°32’S,148°25’E; CSIRO H 3969-14, adult female, 545 mm TL, Southwest of Fremantle, Western Australia, 32°20’S,114°20’E; CSIRO H 5320-01, neonate male, 200 mm TL, Southeast Cape Everard, Victoria, Australia, 38°10’S,149°38’E; CSIRO H 5737-02, juvenile female, 477 mm TL, West of Port Davey, Tasmania, Australia, 43°20’S,145°32’E; CSIRO H 6368-01, juvenile female, 207 mm TL, Southwest of Shark Bay, Western Australia, 27°08’S,112°45’E; CSIRO H 6449-01, juvenile male, 241 mm TL, off Trial Harbour, Tasmania, Australia, 42°S,145°E; CSIRO H 6482-01, adult male, 410 mm TL, Storm Bay, Tasmania, Australia, 43°S,147°30’E; CSIRO H 6482-02, adult male, 426 mm TL, Storm Bay, Tasmania, Australia, 43°S,147°30’E; CSIRO H 7053-01, neonate female, 200 mm TL, East of Terrigal, New South Wales, Australia, 33°21’S,152°11’E; CSIRO H 7053-02, neonate male, 223 mm TL, East of Terrigal, New South Wales, Australia, 33°21’S,152°11’E; CSIRO H 7053-03, neonate female, 218 mm TL; two neonate males, 215, 223 mm TL, East of Terrigal, New South Wales, Australia, 33°21'S,152°11'E; CSIRO H 7226-03, neonate female, 197 mm TL, Britannia Seamount, Queensland, Australia, 27°5'S,155°32'E; CSIRO H 7226-04, neonate male, 195 mm TL, Britannia Seamount, Queensland, Australia, 27°5'S,155°32'E; CSIRO H 7226-05, neonate male, 184 mm TL; neonate female, 196 mm TL, Britannia Seamount, Queensland, Australia, 27°5'S,155°32'E; CSIRO T 1516, juvenile female, 438 mm TL, Maria Island, Tasmania, Australia, 42°51'S,148°19'E; QM I 18629, juvenile female, 343 mm TL, East of Bunker Group, Queensland, Australia, 23°36'S,152°43'E; QM I 18737, juvenile female, 345 mm TL, East of Bunker Group, Queensland, Australia, 23°36'S,152°43'E; QM I 21519, juvenile male, 290 mm TL, Queensland, Australia; QM I 34026, juvenile male, 295 mm TL, Swain Reefs, Queensland, Australia, 22°36'S,153°17'E; QM I 34028, juvenile male, 376 mm TL, Whitsunday Island, Queensland, Australia, 20°23'S,151°14'E.

Diagnosis. Small Australian species (adults between 415–665 mm TL) distinguished from its congeners by a combination of characters: snout obtuse at tip and markedly short (prenarial length 4.2%, 3.9%–5.4% of TL); pectoral fins with posterior margin concave and free rear tips rounded; dorsal fins triangular and very low (first dorsal fin height 5.3%, 7.8%–10.5% of TL; second dorsal fin height 5.7%, 4.8%–7.6% of TL); first dorsal spine conspicuously short, never reaching one-half height of first dorsal fin (first dorsal spine length 1.8%–3.7% of TL); second dorsal spine short, never reaching apex of second dorsal fin (its length 2.5%, 3.6%–6.1% of TL); dermal denticles unicuspid and lanceolate, bearing three ridges, very narrow at crown with its length much greater than its width. It is also distinct from its congeners by having postventral caudal margins uniformly white.

Flakeus megalops is separated from *F. brevirostris*, *F. cubensis*, *F. crassispinnus*, *Flakeus* sp. 3, and *Flakeus* sp. 7, by having pectoral free rear tips often rounded (vs.

markedly pointed). It is also separated from *F. acutipinnis* pectoral fins narrow, never reaching trunk height when adpressed (vs. transcending trunk height), caudal fork discontinuous and markedly concave (vs. caudal fork continuous), and dermal denticles narrow at crown. It is distinguished from *F. acutipinnis* and *F. blainvillei* by having larger claspers (its outer length 2.6%–5.6% of TL vs. 1.8% of TL for *F. acutipinnis* vs. 1.3%–1.8% of TL for *F. acutipinnis*). Adult specimens of *Flakeus megalops* has shorter first dorsal spine (its length 1.8%–3.7% of TL) than those of *F. crassispinus* (5.9%–6.4% of TL), *F. blainvillei* (4.2%–5.6% of TL), *F. albifrons* (4.8%–6.3% of TL), and *F. notocaudatus* (4.4% of TL).

Flakeus megalops is easily distinct by having fewer monospondylous (37–40 vs. 39–42 for *F. crassispinus* vs. 41–43 for *F. raoulensis* vs. 45 for *F. bucephalus* vs. 43–47 for *F. albifrons* vs. 48 for *F. notocaudatus*), precaudal (79–86 vs. 93 for *F. bucephalus* vs. 90–93 for *F. albifrons* vs. 97 for *F. notocaudatus*), and total vertebrae (107–112 vs. 114–115 for *F. raoulensis* vs. 124 for *F. bucephalus* vs. 115–124 for *F. albifrons* vs. 126 for *F. notocaudatus*).

Description. Single values are for holotype. Range values are for non-type specimens in which data were taken.

External morphology (Fig. 81–86; Tabs. 19, 23). Body fusiform and somewhat robust, arched dorsally since posterior margin of spiracle to pelvic fin insertion, turning slender to the tail; body broader at head with head width 1.3 (0.9-1.5) times the trunk width and 2.0 (1.2-1.7) times broader than abdomen width; head height equal to trunk and abdomen heights (1.0, 1.0 for holotype; 0.9-1.0, 0.8-1.0 for non-type material, respectively); head elongate, its length 24.7% (20.7%-24.8%) of TL. Snout obtuse at tip, very short with preorbital length 7.5% (6.6%-7.7%) of TL internarial space 4.5% (3.6-4.8%) of TL; anterior margin of nostrils strongly bilobate and broad; prenarial length 0.8 (0.7-1.1) times the distance between nostril and upper labial furrow. Eyes oval and large, its length 2.2 (1.8-3.8) times greater than its height; both anterior and posterior margins of the eyes concave. Prespiracular length 1.8 (1.7-1.9) times larger than preorbital length and 0.6 (0.5-0.6) times prepectoral length; spiracles subtriangular and tapered, placed laterally right behind the eyes and below dorsal margin of the eye, its length 1.1% (1.0%-2.0%) of TL. Prebranchial length 1.7 (1.4-1.6) times greater than prespiracular length. Gill slits oblique and vertical; fifth gill slit 1.5 (1.0-2.1) higher than first gill slit.

Preoral length 1.0 (1.0-1.3) times mouth width. Mouth almost straight and very wide, its width 2.3 (1.5-2.2) times prenarial length and 2.2 (1.8-2.2) times internarial space; upper labial furrow large, its length 2.7% (2.2%-3.0%) of TL, and upper labial fold thin; inconspicuous lower labial furrow and fold. Teeth unicuspid, similar in both jaws, labial-lingually compressed, wide at crown; upper teeth a little narrower than the lower teeth; cusp thick and short, oblique; mesial cutting edge straight; distal heel markedly rounded; mesial heel pointed in upper teeth and rounded in lower teeth; apron short and thick in both jaws; two series of functional teeth in both jaws in holotype. 13-13 (13-12) teeth in upper jaw and 12-12 (11-11) in lower jaw.

Pre-first dorsal length 34.5% (28.7%-31.4%) of TL, corresponding to 1.5 (1.3-1.5) times prepectoral length; origin of first dorsal fin located just anterior to the vertical at pectoral free rear tips. First dorsal fin triangular and elongate, its length 1.4 (1.0-1.2) times length of second dorsal fin; first dorsal fin low and wide, its height 0.8 (1.3-2.3) times its inner margin length; width of first dorsal fin base 8.5% (7.1%-8.8%) of TL; first dorsal posterior margin straight, rounded at apex; free rear tip pointed. First dorsal spine thick at its base (base width 0.8%, 0.5%-0.8% of TL), located anterior to free rear tip of pectoral fins; first dorsal spine short, its length 1.8%-3.7% of TL in non-type specimens (broken in holotype), never reaching half of fin height. Pre-second dorsal length 3.0 (2.6-3.1) greater than prepectoral length. Interdorsal space 2.5 (2.1-2.5) greater than dorsal-caudal space. Second dorsal fin rather wide and large, its length 10.9% (10.4%-13.9%) of TL, very low with its height 1.3 (1.0-1.4) times its inner margin length; markedly falcate posterior margin; narrow and lobulate at apex; free rear tips pointed. Second dorsal spine slender, also small and never reaching the fin height, although its length 1.1-2.9 greater than first dorsal spine length; its length 0.4 (0.5-0.9) times second dorsal fin height.

Pectoral fins narrow anteriorly and broad posteriorly; anterior margin slightly convex, inner margin convex, and posterior margin concave; anterior margin length 1.6 (1.2-1.8) much greater than inner margin length, and 1.4 (1.1-1.5) times length of posterior margin; posterior margin length never reaching the trunk height when adpressed laterally to the body, although its length 1.1 (0.9-1.3) times the trunk height; both apex and free rear tips of pectoral fin conspicuously rounded and lobulate; apex and free rear tip reaching equally the horizontal line traced among them.

Pectoral-pelvic space 1.0 (0.6-1.0) times pelvic-caudal space. Pelvic fins in the midline between first and second dorsal fins, although few adults show pelvic fins nearest to second dorsal fin. Pelvic fins narrow with anterior and inner margins straight; pelvic fin length 10.9% (6.1%-12.7%) of TL and its inner margin length 5.4% (4.9%-7.0%) of TL; pelvic free rear tips strongly rounded and lobulate. Claspers in adult males short, slightly beyond the free rear tip of the pelvic fins with clasper inner length 0.5-1.4 times pelvic fin inner margin length; siphon prominent, short, located medial-ventrally from the midline of the basipterygium to the intermediate cartilage; clasper groove well elongated, dorsal and longitudinal; apopyle with broad aperture, well anteriorly; hypopyle with narrow aperture, above the rhipidion; rhipidion large, blade-like, located at the posterior end of the clasper.

Caudal keel prominent, placed laterally from behind the first dorsal fin insertion to little beyond the caudal fin origin. Upper and lower pre-caudal furrows well prominent. Caudal fin slender with dorsal caudal margin straight and elongate, its length 0.8-1.0 times the head length and 1.7-3.5 times larger than length of preventral caudal margin; post-ventral caudal margins convex; preventral caudal margin markedly convex, also elongate with its length 1.6 (1.1-2.6) times pelvic inner margin length; both dorsal and ventral caudal tips rounded; caudal fork discontinuous with deeply concavity between lobes; caudal fork narrow, its width 6.0% (6.5%-8.1%) of TL.

Dermal denticles (Fig. 85). Dermal denticles unicuspid and lanceolate, not imbricated; length of the crown much greater than its width; denticles slender at the crown, although broader anteriorly at the base of each ridge; cusp posterior and rounded; three ridges, often bifurcated anteriorly; median ridge large, thick and tall; lateral ridges thin and tall, smaller than median ridge.

Coloration. Body dark grey dorsal and laterally, white ventrally. First and second dorsal fins grey, slightly darker at apex; whitish posterior margin since just anterior to its midline to the free rear tips. Dorsal spines brownish anteriorly and white at tip. Pectoral fins dark grey dorsally and light grey ventrally; inner and posterior margins of pectoral fins uniformly white. Pelvic fins grey dorsally and white ventrally, somewhat whitish margins. Caudal fin grey with postventral caudal margins uniformly white since dorsal caudal tip to ventral caudal tip; black caudal stripe discreet. In neonates and young juveniles: body light grey dorsally and laterally, although whitish from pelvic fin insertion to caudal fin origin; white ventrally; dorsal fins dark grey, markedly blackish at the apex and whitish at fin base with posterior margin and free rear tips white; pectoral fins light grey dorsally, white ventrally with large grey spot near the anterior margin, and posterior margin conspicuously broadly white. Caudal fin dark grey, uniform and broad white post-ventral margins, especially near the tips, and both dorsal caudal margin and pre-ventral margin slightly white.

Vertebral counts (Tab. 24). 86 (79-83) precaudal vertebrae; 40 (39-41) monospondylous vertebrae; 107-112 total vertebrae.

Geographical distribution (Fig. 86). It occurs in the South Indo-Pacific Ocean from New South Wales to Western Australia.

Etymology. The epithet "*megalops*" is not indicated in the original description.

Remarks.

Holotype of *Flakeus megalops*. The holotype of *Flakeus megalops* is in very poor condition of preservation. Natural coloration was lost with few regions of the body (e.g. snout, pelvic fins, dorsal fins, caudal fin, and laterals of body) missing skin and dermal denticles due to many years preserved in ethanol. Part of its caudal fin is missing, in which upper and lower caudal lobes are mostly broken. Right pectoral fin is also broken from its base to the apex. Pelvic fin are still intact, slightly fringed on its anterior and posterior margins. Dorsal fins are in better conditions, although its posterior margin is fringed. Both dorsal spines are worn down.

Morphological variations within *Flakeus megalops*. Intraspecific variations are observed for *F. megalops* regarding shape of pectoral fins, and dermal denticles. Specimens from Tasmania and some specimens from Western Australia exhibit pectoral free rear tips often pointed with posterior margin concave that assemblage those of *F. brevirostris* and *F. cubensis*, although free rear tips of pectoral fin also may differ within a same specimen from pointed to rounded.

Pectoral fins with free rear tips not reaching horizontal line traced at its apex for specimens from Southern and Western Australia as in the holotype while free rear tips transcending greatly the horizontal line for those from Victoria and Tasmania. Dermal denticles also vary in *F. megalops*, regarding the thickness of the crown. Specimens from Victoria have dermal denticles much broader at the crown than specimens from Southern and Western Australia.

In contrast to Last *et al*. (2007), the current analysis did not find differences on external measurements (e.g. pectoral-pelvic space; pelvic-caudal space; length of pectoral anterior margin) within this species. In particular, a neonate specimen from Queensland shows great differences with those from Southern Australia but it is preferable to suggest that this might be due to ontogenetic variation within the species. These authors also reported variations regarding color pattern of body, particularly to the postventral caudal margins, dorsal fins, and pectoral and pelvic fins especially between specimens from Western Australia and *F. megalops* elsewhere in the Australian territory, which it is in disagreement with the present study. In fact, another morphological group besides *F. megalops* are recognized in Western Australia, although it is more similar morphologically to *F. crassispinus* that will be described and discussed later in this Chapter.

Taxonomic status of *Flakeus megalops*. Macleay (1881) provided a brief description of *F. megalops* based on external characteristics of the body, including coloration and few morphometric. The current results are in congruence with its original description, although it is important to notice that the description of Macleay (1881) is also applicable to other species of Squalidae with similar morphology. No additional information regarding dentition, shape of dermal denticles and external measurements of *F. megalops* from Australian waters were provided in the literature for long periods of time (e.g. Regan, 1908a; Whitley, 1939, 1940, 1964), which together with its original description contributed to the recognition and application of this nominal species in many other geographical regions, such as, Northeastern Atlantic, especially in North Africa and Mediterranean Sea (e.g. Marouani *et al*., 2012), Indo-West Pacific and Southeast Atlantic (e.g. Bass *et al*., 1976; Heemstra & Heemstra, 2004; Naylor *et al*., 2012a), and Southwestern Atlantic (e.g. Gomes *et al*., 1997; Gomes *et al*., 2010; Figueirêdo, 2011).

Bigelow & Schroeder (1948, 1957) proposed the division of the genus *Squalus* into groups of species with similar external morphology based on the shape of pectoral fins and position of the dorsal and pelvic fins, which it is the first attempt to provided diagnostic characters for identifying the Australian species. *Squalus megalops* was included in the *brevirostris-cubensis* group together with *S. cubensis* from the West Central Atlantic Ocean and *S. brevirostris* from North Pacific Ocean for sharing pelvic fins placed in the midline between two dorsal fins, and first dorsal fin located prior the vertical line traced over free rear tips of pectoral fins (Bigelow & Schroeder, 1948, 1957). According to these authors, *S. megalops* also share with these two nominal species pectoral fins with posterior margin markedly concave and free rear tip pointed, based on comparisons with an illustration of a specimen from Tasmania taken from McCullogh (1927). Then, the morphological group was renamed after *S. megalops* to denote the earliest described species. Since then, the Australian species is considered a complex of species with large distribution in the Pacific and Atlantic Oceans rather than a single species (e.g. Bass *et al*., 1976; Gomes *et al*., 1997; Compagno *et al*., 2005; Ebert *et al*., 2013a).

The current results show that *Flakeus megalops* comprises a single valid species and endemic to Australian waters with occurrences in Western Australia, Queensland and New South Wales to the south in Victoria and Tasmania. No specimens from the Northern Territory were founded it here. These findings are in agreement with Last & Stevens (1994, 2009). Recently, molecular analyses have supported this hypothesis as well rather than a species of worldwide distribution (e.g. Ward *et al*., 2005, 2007; Naylor *et al*., 2012a,b). Morphological variations, however, are observed on specimens along the coast of Australia (see in detail above), which it is expected for a species well distributed within a territory subject to great differences in environmental pressures (e.g. water temperature; marine topography; bathymetric). Specimens from Southern and Western Australia, and Tasmania overlap generally in external morphology, including dentition, color pattern, shape of dorsal, pelvic and caudal fins, as well as external measurements and vertebral counts, which all support its conspecificity.

These results are in contrast to previous studies that recognized *F. megalops* in the West Indian and Eastern Atlantic Oceans (e.g. Bass *et al*., 1976, 1986; Muñoz-Chápuli & Ramos, 1989; Heemstra & Heemstra, 2004; Ebert & Stehmann, 2013) as well as Southwest Atlantic Ocean (e.g. Figueirêdo, 2011). A combination of morphological characters that includes shape and length of pectoral and dorsal fins, shape of dermal denticles, vertebral counts, and more barely body coloration help to support the hypothesis that at least four separated and different species are recognized in these regions[1]. Recently, Last *et al*. (2007) described six new species with occurrences in Australian, New Zealand and New Caledonian waters that were considered synonym of *F. megalops* for long periods of time (e.g. Regan, 1908a; Whitley, 1940; Last & Stevens, 1994) based on the same combination of different characters. In the current study, similar situation is observed for identification and separation of *F. megalops* from these new forms because no exclusive characteristics were observed for this species.

External measurements rarely help for its differentiation, however, it is more apparent when adult specimens are compared. *Flakeus megalops* shows slight differences on internarial space (3.6%–4.6% of TL) with *F. blainvillei* (3.2%–3.8% of TL) and *F.*

[1] Species recognized elsewhere as *S. megalops* are described later in this Chapter.

brevirostris (3.4%–3.8% of TL). It has larger pre-first dorsal length than *F. albifrons* (29.4%–31.4% of TL vs. 27.0%–29.8% of TL), and larger prespiracular length than *F. acutipinnis* (11.6%–13.2% of TL vs. 7.7%–11.8% of TL). It further has smaller first dorsal spine than in *F. acutipinnis* (1.8%–3.7% of TL vs. 3.5%–4.3% of TL), and thinner than in *F. albifrons* (its base lenfgth 0.5%–0.8% of TL vs. 0.8%–1.4% of TL). *Flakeus megalops* exhibits more elongate pelvic fins than *F. acutipinnis* and *F. albifrons* (its length 5.4%–6.8% of TL vs. 4.2%–5.4% of TL vs. 5.2%–5.5% of TL). It also shows larger inner length of claspers than *F. acutipinnis* and *F. blainvillei* (4.5%–7.6% of TL vs. 4.3% of TL vs. 2.6%–4.5% of TL).

Comparative material: All specimens listed for *F. acutipinnis*, *F. brevirostris*, *F. cubensis*, *F. crassispinus*, *F. bucephalus*, *F. raoulensis* in this Chapter.

Flakeus blainvillei (Risso, 1827)

(**Mediterranean dogfish; L'agullat de blainville, Mangin** in French)

Figs. 88–93; Tables 33, 37–38

Acanthias blainville Risso, 1826: 133, pl. 3, fig. 6 (original description; illustrated; Nice and Mediterranean Sea).

Acanthias blainvillii Risso, 1826: 478 (listed, misspelling); Müller & Henle, 1841: 84 (described; Mediterranean Sea); Duméril 1865: 438 (description; Spain, Italy, France); Günther, 1870 (in part): 419 (description; Portugal, France, New Holland, and Mediterranean and Adriatic Seas).

Acanthias blainvillei Macleay, 1881: 367 (listed; New Holland).

Squalus blainvillii Regan, 1908a: 247 (cited; Mediterranean Sea); Garrick, 1960: 533-537, figs. 1 (D-F), 2, 3 (A-F), 6 (revision; New Zealand).

Squalus blainvillei Regan, 1908b: 45, 47 (identification key, listed; Mediterranean Sea, Portugal); Bigelow & Schroeder, 1948: 454, 455 (cited, identification key; Portugal, Mediterrranean and Black Seas); Garrick, 1961: 843 (cited); Ledoux, 1970: 65-69, figs. 1, 2 (A, B), 3 (C-F) (revision; Mediterranean Sea); Cadenat & Blache, 1981: 49-51; figs. 29, 30 (revision; Mediterranean Sea); Compagno, 1984: 110, 115, 116 (catalogued); McEachran & Branstetter, 1984: 128, 147 (cited, description; Mediterranean Sea); Muñoz-Chápuli, 1985: 397, 398, fig. 1 (cited); Myagkov & Kondyurin, 1986 (in part): 12 (description; Mediterranean Sea); Muñoz-Chápuli & Ramos, 1989 (in part): 6–21, figs. 1, 2B and 2E, 3B (revision; Morrocco, Spain); Compagno, 1999: 472 (listed); Fricke, 1999: 27 (catalogued; Mascarene Island); Compagno *et al.*, 2005 (in part): 74, 75, pl. 3 (listed; Mediterranean Sea); Marouani *et al.*, 2012: 1–13 (description; Tunisia); Ebert *et al.*, 2013 (in part): 76, 85 (cited, description; Mediterranean Sea).

Squalus blainville Ebert & Stehmann, 2013 (in part): 62–64 (description: Mediterranean Sea, Black Sea).

Squalus fernandinus not Molina: Garman, 1913 (in part): 195–196 (description; Mediterranean Sea); Bigelow, Schroeder & Springer, 1953: 222 (cited); Bigelow & Schroeder, 1957 (in part): 32–36 (cited; Portugal, Mediterranean and Black Seas).
Squalus megalops not Macleay: Muñoz-Chápuli & Ramos, 1989 (in part): 1–21, figs. 1, 2E, 3D (description; Alboran Sea); Marouani *et al*., 2012: 1–13 (description; Tunisia).

Type specimens: Unknown.

Type locality: Nice, France.

Non-type material (63 specimens): BMNH 1866.5.28.1, adult male, 480 mm TL, France, Mediterranean Sea; BMNH 1868.2.12.22, neonate male, 160 mm TL, unknown locality; BMNH 1902.6.9.17, embryo female, 75 mm TL, Italy, Mediterranean Sea; BMNH 1928.8.14.1-2, two neonate males, 200–205 mm TL, Cyprus, Mediterranean Sea; BMNH 1963.5.14.13-18, six juvenile males, 242–382 mm TL, France, Mediterranean Sea; BMNH 1963.5.14.19-22, juvenile male, 270 mm TL, three juvenile females, 285–315 mm TL, France, Mediterranean Sea; BMNH 1971.7.21.25-27, three neonate females, 210–240 mm TL, Portugal, Northeast Atlantic Ocean; BMNH 2013.9.3.6, adult female, 540 mm TL, Lisbon, Portugal; MNHN 1162, juvenile male, 368 mm TL, Algeria, 40°N,5°E; MNHN 1163, juvenile female, 328 mm TL, Baleares Islands, Ibiza, Spain, 38°52”1’N,1°28”1’E; MNHN 1164, adult male, 490 mm TL, Sicily, Italy; MNHN 1166, juvenile male, 465 mm TL, Sicily, Italy, 38°13”1’N,15°33”0’E; MNHN 5604, neonate female, 196 mm TL, Nice, France, 43°42”0’N,7°16”1’E; MNHN 1898-1235, juvenile female, 502 mm TL, Nice, France, 43°42”0’N,7°16”1’E; MNHN 1987-2091, juvenile male, 396 mm TL, juvenile female, 403 mm TL, Mediterranean Sea; MNHN 2002-1523, adult male, 485 mm TL, Latakia, Syria, 35°30”58’N,35°46”59’E; MNHN A-7665, juvenile male, 510 mm TL, Algeria, 40°N,5°E; NMW 18901, juvenile female, 303 mm TL, Split, Croatia; NMW 50124, adult female, 700 mm TL, Nice, France; NMW 50125, adult male, 530 mm TL, Palermo, Italy; NMW 78035, neonate male, 220 mm TL, Naples, Italy; NMW 78037, juvenile female, 275 mm TL, Cádiz, Spain; NMW 78038, neonate male, 230 mm TL, Adriatic Sea; NMW

78786, juvenile female, 436 mm TL, Izmir, Turkey; NMW 83937, juvenile female, 262 mm TL, Split, Croatia; NMW 83938, juvenile male, 243 mm TL, Naples, Italy; NMW 83939, two juvenile males, 260–416 mm TL, neonate female, 243 mm TL, Dalmatia, Croatia; NMW 84003, adult male, 478 mm TL, Izmir, Turkey; NMW 84901, juvenile female, 495 mm TL, Trieste, Italy; NMW 85503, adult male, 560 mm TL, Europe; NMW 85903, juvenile female, 268 mm TL, two juveniles males, 378–455 mm TL, adult male, 480 mm TL, Morrocco; NMW 86101, adult female, 575 mm TL, unknown locality; NRM 9017, neonate female, 171 mm TL, Calabria, Italy; NRM 9038, juvenile female, 535 mm TL, Genoa, Italy; RMNH.PISC. 4187, juvenile male, 352 mm TL, Dalmatia, Croatia; RMNH.PISC. 15781, two juvenile males, 242–322 mm TL, three juvenile females, 240–268 mm TL, Cascais, Portugal; RMNH.PISC. 34092, neonate male, 245 mm TL, three neonate females, 230–252 mm TL, Banyuls, France; ZMA 113.606, juvenile male, 385 mm TL, Cádiz, Spain, 36°10” N,06°26”W; ZMB 4510, adult male, 495 mm TL, Nice, France; ZMH 25478, juvenile female, 283 mm TL, Naples, Italy.

Diagnosis. Small species of dofish shark from the Mediterranean Sea that is characterized by a combination of characters: snout conspicuously rounded at tip and very short (its prenarial length 3.6%–4.8% of TL); first dorsal spine elongate, almost reaching fin apex (its length 3.5%–5.6% of TL); second dorsal spine also large, transcending the fin apex (its length 5.0%–7.3% of TL). *Flakeus blainvillei* differs from its congeners by having two cartilaginous processes on each side of the basal plate in the neurocranium. It is also distinguished from them by having dermal denticles lanceolate, uniscuspid and markedly slender at crown and weakly tricuspid in adults.

Flakeus blainvillei is distinct from *F. crassispinus, F. raoulensis, F. bucephalus, F. albifrons* and *F. notocaudatus* by having fewer vertebrae (41–43 monospondylous vertebrae;

67–69 diplospondylous vertebrae; 80–84 precaudal vertebrae; 107–111 total vertebrae). It is also differentiated from *F. crassispinus*, *F. brevirostris*, and *F. cubensis* by having pectoral fins with posterior margin almost straight and free rear tips somewhat rounded (vs. posterior margin conspicuously concave and free rear tips pointed). *Flakeus blainvillei* is distinct from *F. acutipinnis* by: smaller head in *F. blainvillei* (its length 19.8%–22.4% of TL vs. 22.7%–24.3% of TL for *F. acutipinnis*); shorter interdorsal space (its length 21.3%–24.3% of TL vs. 24.5%–25.4% of TL for *F. acutipinnis*); larger second dorsal fin (its anterior margin length 10.2%–12.1% of TL vs. 8.9%–10.0% of TL for *F. acutipinnis*, its base length 7.1%–8.6% of TL vs. 5.7%–6.7% of TL for *F. acutipinnis*).

Description. Range values are for specimens in which data were taken.

External morphology (Figs. 88–92; Tabs. 33, 37). Body fusiform and slender throughout all its extention, its height at head 0.8–1.0 times trunk height and 0.8–1.1 times abdomen height; body slightly arched dorsally since posterior margin of spiracle to insertion of second dorsal fin; its greatest width at head, corresponding to 1.1–1.5 times trunk width and 1.2–2.0 times abdomen height; head length 19.8%–23.1% of TL. Snout conspicuously rounded at tip and very short (its preorbital length 6.1%–8.4% of TL); anterior margin of nostrils bilobed; prenarial length 0.8–1.0 times the distance between nostrils and upper labial furrow, and 0.4–0.5 times preoral length; internarial space very short, corresponding to 0.7–0.9 times eye length. Eyes oval and elongate, its length 1.6–4.5 times greater than its height; eyes with anterior margin concave and posterior margin notched. Prespiracular length small, its length 10.8%–13.8% of TL and corresponding to 1.6–1.9 times greater than preorbital length. Spiracles crescent, placed laterally and posterior to the eyes; spiracles short, its length 1.1%–1.8% of TL.

Preoral length 1.0–1.3 times greater than mouth width. Mouth arched and narrow, its width 1.6–2.1 times greater than prenarial length and 1.8–2.6 times broader than internarial space; upper labial furrow large (its length 2.3%–2.8% of TL) with slender fold; lower labial furrow very elongate, lacking fold. Teeth unicuspid, flattened labial-lingually and similar in both jaws; upper teeth smaller than lower ones; mesial cutting edge concave; cusp very short and thin, slightly oblique; mesial heel notched, and distal heel strongly rounded; apron short and thick. Two series of functional teeth on upper and lower jaws. 14–14 upper teeth rows and 11–11 lower teeth rows. Pre-branchial length 1.4–1.6 times larger than prespiracular length. Gill slits concave and vertical; fifth gill slit 1.0–2.3 times higher than first gill slit.

Pre-first dorsal fin length 1.3–1.5 times prepectoral length; origin of first dorsal fin anterior to vertical traced at pectoral free rear tips. First dorsal fin somewhat triangular and slender at the tip, its anterior margin straight, posterior margin slightly concave near distally, not falcate; first dorsal fin upright and tall, its height 1.4–1.8 times greater than its inner margin length. First dorsal spine conspicuously thin (its base length 0.6%–1.0% of TL) and elongate, although not reaching the fin apex, its length 3.5%–5.6% of TL and corresponding to 0.3–0.6 times height of first dorsal fin. First dorsal fin length 1.0–1.1 times length of second dorsal fin. Interdorsal space 0.9–1.2 times prepectoral length and 1.7–2.3 times larger than dorsal-caudal distance. Pre-second dorsal fin 2.6–3.5 times larger than prepectoral length. Second dorsal fin with anterior margin straight posterior margin conspicuously falcate, and slender at apex; second dorsal fin upright and low, its height 1.0–1.4 times greater than its inner margin length. Second dorsal spines thin (its base length 0.7%–1.2% of TL) and conspicuously elongate, transcending the apex of second dorsal fin, its length 0.8–1.2 times height of second dorsal fin (in juveniles, it reaches the fin apex or very close to it); second dorsal spine 1.2–1.8 times larger than first dorsal spine.

Prepectoral length 19.0%–22.3% of TL. Pectoral fins with anterior and inner margins convex, and posterior margin almost straight; pectoral apex rounded; free rear tips slightly rounded (markedly rounded in juveniles), reaching longitudinal line traced at apex; pectoral fins narrow, its posterior margin 9.5%–13.2% of TL and corresponding to 0.8–1.4 times trunk height, never transcending the trunk (except in small juveniles); pectoral anterior margin 1.2–1.6 times larger than posterior margin length and 1.3–1.7 times greater than inner margin length.

Distance from pectoral to pelvic fin 0.6–0.8 times pelvic-caudal distance. Prepelvic length 39.6%–44.9% of TL, placed in the midline between two dorsal fins. Pelvic fins with margins somewhat convex, apex and free rear tips conspicuously rounded, the latter evidently lobe-like; pelvic fins narrow and small, its length 10.0%–12.9% of TL. Claspers with clasper groove oblique and dorsal, small; apopyle broad and placed anteriorly in the clasper groove; hypopyle constricted, placed distally in the clasper groove; rhipidion narrow and very short, flap-like with lateral margin free, placed medial-distally in the clasper; clasper short and transcending pelvic free rear tips, its inner length 0.5–1.3 times inner length of pelvic fin.

Upper and lower precaudal pits prominent; caudal keel inconspicuous laterally in the caudal peduncle. Caudal fin with dorsal caudal margin straight, postventral caudal margins slightly convex, and preventral caudal margin straight; caudal fin slender at posterior caudal tip; ventral caudal tip slightly pointed; dorsal caudal margin short, its length 0.9–1.1 times head length and 1.8–2.0 times larger than preventral caudal margin; preventral caudal margin very short, its length 1.6–2.4 times larger than pelvic inner margin; caudal fork discontinuous between lobes, its width 6.3%–7.6% of TL.

Dermal denticles (Fig. 92). Unicuspid and lanceolate, not imbricate, conspicously narrow at crown, its length greater than its width; cusp posterior and pointed; median ridge prominent, elongate and markedly thin with anterior furrow oval, large and shallow; median ridge with anterior margin spatula-like; lateral ridges markedly thin and symmetrical, much shorter than median ridge. Adult specimens have denticles weakly tricuspid, broader at the crown, lateral cusps very short and forming weak concavity with median cusp. Adult females has tricuspid denticles much more evident than adult males.

Coloration. Body reddish brown dorsally, pale ventrally and laterally from just before the pelvic fin to the tip of the vertebral column in preserve specimens. First dorsal fin brown, slightly darker at the tip and near the spine, white at the fin base and posterior margin, although very slender, to the free rear tip. Second dorsal fin light brown, also white at the fin base and posterior margin until the free rear tip. Dorsal spines white, lighter at the tip and light brown anteriorly. Pectoral fins brown dorsla and ventrally with inner and posterior margins broadly white. Pelvic fins totally pale. Caudal fin brown, whitish over vertebral column; postventral caudal margins white except at the caudal fork and not uniform; dorsal caudal margin white; black caudal stripe discreet and short.

Vertebral counts (Tab. 38). 41–43 monospondylous vertebrae; 67–69 diplospondylous vertebrae; 80–84 precaudal vertebrae; 107–111 total vertebrae.

Geographical distribution (Fig. 93). It occurs in the Mediterranean Sea with few occurences in the Atlantic coast of Portugal and Spain.

Etymology. The name "*blainvillei*" is in honor to the French zoologist Henri-Marie Ducrotay De Blainville.

Remarks. Different speeling of this species name are present in the literature, for instance, "*blainville*" (e.g. Risso, 1826; Ebert & Stehmann, 2013; Eschmeyer & Fricke, 2015), "*blainvilii*" (e.g. Müller & Henle, 1841; Regan, 1908a), and "*blainvillei*" (e.g. Macleay, 1881; Garrick, 1961). Recently, Eschmeyer & Fricke (2015) stated that the original speeling "*blainville*" is also accepted as a name in apposition to the generic name. However, according to ICZN (Art. 31.1), it is recommended to form names in the genitive case rather than noun in apposition in order to avoid confusion between the species-name and the generic authorship. In this case, it also must add *–i* to the stem of the modern personal name. Thus, the correct speeling of this species is "*blainvillei*" as it was suggested previously by Garrick (1961).

Morphological variations in *Flakeus blainvillei*. *Flakeus blainvillei* has uniform body coloration that varies from light brown to pinkish brown in preserved specimens. No dark brown and oblique stripes are noticed, which it is in disagreement with Risso (1826). It is possible that these stripes concern to bundles of muscles that are noticed throughout the body when the specimens are preserved for long time in ethanol.

Ledoux (1970) reported variations on the pectoral fins in this species that show four different shapes among adults. In contrast, the current study reveals slight ontogentic differences in which pectoral posterior margin is concave and free rear tips rounded in neonates and young juveniles (Fig. 2A of Ledoux, 1970) while adults have its posterior margin almost straight and free rear tips weakly rounded to pointed (Fig. 2B, 2C of Ledoux, 1970). It is possible that the shape of Fig. 2D from Ledoux (1970) corresponds to an individual variation because it was not noticed in the present analysis. Pectoral fins in adults of *F. blainvillei* are similar to those of *F. acutipinnis*, although the latter species has its posterior margin transcending the trunk height when adpressed on body. In contrast to these two species, *F. cubensis*, *F. brevirostris* and *F. crassispinus* have pectoral posterior margin conspicuously concave and free rear tips markedly pointed.

Variations on dermal denticles are also observed herein and it is in congruence with Leadoux (1970) regarding the ontogenetic differences in size and shape. He also observed that the shape of the dermal denticles in *F. blainvillei* is intermediary between those observed for *F. megalops* and *F. cubensis*, and *F. montalbani*, which it is in congruence with the current results because the Mediterranean species shows denticles weakly tricuspid in late juveniles and adults, specially females. These cusps, however, are not homologous to those observed for *F. notocaudatus* and *F. albifrons* because it is formed as a posterior extention of the crown base on each side of the denticle (vs. posterior extention of the lateral ridge in these two species).

Type specimens of *Flakeus blainvillei*. Risso (1826) did not mention any particular material in the original description of *F. blainvillei*. Besides, possible syntypes are unknown because the material analysed by him was not found in the European fish collections. Designation of a neotype is still necessary for redescribing properly this species as valid. However, very old specimens were analyzed in the current study that are not in good condition of preservation for designation as type. Fresh specimens are in need for this purpose.

Taxonomic status of *Flakeus blainvillei*. According to the present study, *F. blainvillei* is a species endemic to the Mediterranean Sea and the only species of Squalidae to occur in this area besides *Squalus acanthias*. These findings are in contrast to Garman (1913), Garrick (1960), Compagno (1984), Muñoz-Chápuli & Ramos, (1989), Compagno *et al*. (2005), Marouani *et al*. (2012), and Ebert *et al*. (2013a) that recognized *F. blainvillei* as a species with broad geographical distribution in the Southeast Atlantic, Indo-Pacific, and Southwest

Pacific Oceans. Many authors reported its occurrence in the NEAO from Morrocco down to Namibia and South Africa (e.g. Bass *et al*., 1976; Muñoz-Chápuli & Ramos, 1989; Ebert & Stehmann, 2013), and Tunisian waters (e.g. Marouani *et al*., 2012; Iglésias, 2012). Others consider it to represent a species-complex (e.g. Bigelow & Schroeder, 1948, 1957; Ledoux, 1970; Compagno, 1984) due to morphological variations observed on shape of pectoral fins and dermal denticles. These variations are currently addressed to two nominal species *Squalus blainvillei* and *S. megalops* in these regions (Muñoz-Chápuli & Ramos, 1989; Marouani *et al*., 2012).

Specimens from the Mediterranean Sea are characterized by having dorsal spines conspicuously large with at least second spine exceeding apex of second dorsal fin. This is in congruence with descriptions of Risso (1826), Müller & Henle (1841), Duméril (1865), Bigelow & Schroeder (1948) and Ledoux (1970). It also has snout very short and rounded, pectoral free rear tips weakly rounded, and dermal denticles unicuspid and lanceolate to weakly tricuspid, as it was noticed by Ledoux (1970). Two lateral cartilaginous processes in the basal plate are present in these specimens and support the autapomorphy of *F. blainvillei*[2]. All these features, however, are often recognized for *F. megalops* from the Northeastern Atlantic Ocean and Mediterranean Sea (e.g. Muñoz-Chápuli & Ramos, 1989; Marouani *et al*., 2012). These authors separated it from *F. blainvillei* regarding shape of dermal denticles, cranial measurements and morphology, and clasper morphology even though overlapping of external measurements and vertebral cunts were clearly noticed. These differences were not noticed among specimens within the Mediterranean waters, suggesting conspecificity. Another form from outside these waters was used by Muñoz-Chápuli & Ramos (1989) for recognizing *F. megalops* in the Eastern Atlantic Ocean.

[2] See description of neurocranium in Chapter 1.

More recently, these features were also addressed to *F. acutipinnis* that could possibly inhabit the Mediterranean Sea (Ebert & Stehmann, 2013). *Flakeus blainvillei* and *F. acutipinnis* are undoubtfully distinct. Despite of morphometric differences are subtle between them it is more evident when adult specimens are compared. *Flakeus blainvillei* is further distinct from *F. acutipinnis* by: head narrower at nostrils in *F. blainvillei* (5.9%–7.1% of TL vs. 6.9%–7.8% of TL for *F. acutipinnis*); more elongate first (its length 4.2%–5.6% of TL vs. 3.5%–4.3% of TL of TL for *F. acutipinnis*) and second dorsal spines (its length 5.0%–7.3% of TL vs. 4.5%–5.6% of TL of TL for *F. acutipinnis*). Once *F. acutipinnis* exclusively occurs in the Indian Ocean (Viana & Carvalho, *in press*), the current results indicates that *F. blainvillei* was misidentified with another species of *Flakeus* that occurs from the west coast of Northern Africa to the Southern tip of South Africa.

A second species of *Flakeus*[3] occurs in the Eastern Atlantic Ocean that are separated and different from *F. blainvillei*, indicating the confusion regarding the taxonomy of the Mediterranean species is much more complex than previously thought. Muñoz-Chápuli & Ramos (1989) characterized *F. blainvillei* as a species with dermal denticles tricuspid, low dorsal fins, pectoral inner margin very small, and hook-like dorsal terminal cartilage of the clasper. These features, however, are applied for both *F. blainvillei* and this second species, indicating that the authors examined more than one form to describe *F. blainvillei* in the region. The latter character also varies from weak to strongly concave tip, according to their study, which give additional support to assume that they analyzed two different species. Muñoz-Chápuli & Ramos (1989) noticed a single cartilaginous process in the neurocranium of the nominal species "*S. blainvillei*" that we believe was cautch off the Atlantic coast of Morocco or Spain but not off Mediterranean Sea. The current analysis of the material at

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[3] These two species are described later in the current Chapter.

MNHN from North African waters identified by Dr. Muñoz-Chápuli also supports this hypothesis.

Problems regarding lost of type specimens, concise original description and misunderstanding of morphological information from the literature contributed to the complexity of the taxonomic status of *F. blainvillei*. Garman (1913) was the first author to consider it as well as many other nominal species (e.g. *S. megalops, S. acutipinnis, S. phillipinus*) as synonym of *Squalus fernandinus* from Juan Fernandez. Many characteristics provided by Garman (1913), for instance, pectoral free rear tips rounded and dermal denticles tricuspid it is clearly not applicable to all these nominal species, including *F. blainvillei*, according to the present study. Later authors (e.g. Garrick, 1960; Compagno, 1984; Bass *et al*., 1976) recognized this species as belonging to the "*S. mitsukurii* group" and stated that the Mediterranean species bears dermal denticles tricuspid and rhomboid, and snout blunt and markedly elongate that assemblages those of the *F. mitsukurii* from Japan. Muñoz-Chápuli & Ramos (1989) clearly stated the difficulty to correctly apply *S. blainvillei* of Risso (1826) to these forms from the Eastern Atlantic Ocean and preferred to follow the characteristics provided by the latter authors. All these information suppressed the morphological particularities of *F. blainvillei* and contributed to the difficulty on properly identifying it, which are also observed for other species within Squalidae.

Comparative material: Specimens of *F. megalops, F. cubensis, F. brevirostris, F. albifrons, F. notocaudatus, F. crassispinus, F. acutipinnis,* and *F. montabani* listed in this Chapter.

Flakeus acutipinnis[4] (Regan, 1908)

[4] Article submitted and accepted for publication in *Copeia* in 2015 (Viana & Carvalho, *in press*).

(**Bluntnose spiny dogfish; Stompneus-penhaai** in Afrikaans)

Figs. 94–99; Tables 20, 23–24

Squalus acutipinnis Regan 1908a: 241, 248, pl. XXXVII (original description, illustrated; type locality: Kwazulu-Natal, South Africa [not NE of Bird Island as stated on p. 241]; 40 ftm/ 73.152 m; lectotype: BMNH 1905.6.8.8 [see below]). Regan, 1908b: 45, 47 (cited; South Africa, Mauritius). Regan, 1921: 412 (listed; Kwazulu-Natal, South Africa). Krefft, 1968 (in part): 34, 51–54, pl. III A (cited, description, designation of lectotype; South Africa). Merrett, 1973: 94, 104, 108, 109 (cited; South Africa). Kondyurin and Myagkov, 1979 (revision, South Africa [not seen, cited in Myagkov and Kondyurin, 1986]). Cadenat and Blache, 1981: 47, 51, 52, fig. 31f–g (cited; South Africa). Myagkov and Kondyurin, 1986: 8–10, 15 (description; Southern Africa). Last *et al*., 2007: 11 (cited; Southwest Indian Ocean). Ebert et al., 2010: 22, 23 (cited; Southern Africa). Ebert and Stehmann, 2013 (in part): 66 (cited as possibly valid; Southern Africa).

Squalus fernandinus (not Molina 1782): Garman, 1913: 195–196 (synonymy, description). Bigelow and Schroeder, 1948: 480 (cited, South Africa). Bigelow and Schroeder, 1957: 32, 35 (cited, South Africa). Smith, 1961: 59, 61 (brief account, South Africa).

Squalus megalops (not Macleay 1881): Bass *et al*., 1976 (in part): 11, 9–13, 16–18, 60; fig. 11; pl. 3 (description, illustrated; Southern Africa). Compagno, 1984 (in part): 118, 119 (description, illustrated; South Africa). Bass et al., 1986 (in part): 61, 62, fig. 5.26 (description; Southern Africa). Parin, 1988: 49 (cited; Southeastern Atlantic Ocean). Muñoz-Chápuli and Ramos, 1989: 6, 11, 18, 19 (diagnosis, illustrated, Eastern Atlantic). Compagno et al., 1989 (in part): 22 (account, illustrated). Compagno and Niem, 1998 (in part): 1230 (cited; South Africa to Mozambique). Ebert et al., 2013 (in part): 91 (general account on *S. megalops*).

Squalus cf. *megalops*. Naylor et al. 2012a (in part): 58, 148, fig. 42 (cited, molecular systematic analysis; South Africa, Indian Ocean). Naylor et al. 2012b (in part): fig. 2.7 (molecular systematic analysis; South Africa).

Lectotype: BMNH 1905.6.8.8, juvenile female, 578 mm TL from Kwazulu-Natal, South Africa, Western Indian Ocean; donated by Dr. E. Warren. Designated by Krefft (1968).

Paralectotypes (3 specimens): BMNH 1859.5.7.68 (not *Squalus acutipinnis*), neonate female, 190 mm TL, Cape of Good Hope, South Africa, Southeastern Atlantic Ocean, donated by Sir Andrew Smith; BMNH 1881.3.11.2, adult female, 852 mm TL, Mauritius, Western Indian Ocean, stuffed specimen; donated by M. De Robillard; BMNH 1900.11.6.14 (not *Squalus acutipinnis*), adult female, 565 mm TL, Table Bay, South Africa, Southeastern Atlantic Ocean, donated by Dr. J.D.F. Gilchrist.

Non-type material (29 specimens): SAIAB 7829, adult female, 575 mm TL, Port Elizabeth, South Africa, 33.96°S, 25.60°E; SAIAB 10443, three neonate females, 200 mm TL each; neonate male, 200 mm TL; adult male, 410 mm TL, Cape Town, South Africa, 33.91°S, 18.41°E; SAIAB 19863, adult female, 570 mm TL, Port Alfred, South Africa, 34.26°S, 27.58°E; SAIAB 21933, juvenile female, 252 mm TL, off Gansbaai, South Africa, 35.03°S, 19.43°E; SAIAB 25360, adult female, 530 mm TL, Algoa Bay, South Africa, 34.03°S, 25.70°E; SAIAB 25361, juvenile female, 460 mm TL, Algoa Bay, South Africa, 34.03°S, 25.70°E; SAIAB 25369, juvenile female, 375 mm TL, adult female, 450 mm TL, Algoa Bay, South Africa, 34.03°S, 25.70°E; SAIAB 25390, juvenile female, 460 mm TL, Algoa Bay, South Africa, 34.03°S, 25.70°E; SAIAB 25394, adult female, 525 mm TL, Algoa Bay, South Africa, 34.03°S, 25.70°E; SAIAB 26639, adult female, 485 mm TL, unknown locality; SAIAB 34576, adult female, 550 mm TL, Bushmans River Mouth, South Africa, 33.68°S, 26.66°E; SAM 12986, neonate female, 185 mm TL, unknown precise locality, South Africa; SAM 12996, neonate male, 205 mm TL, two neonate females, 202, 205 mm TL, St. Francis Bay, South Africa, 34.06°S, 25.13°E; SAM 28638, two juvenile females, 365, 375 mm TL, False Bay, South Africa, 34.18°S, 18.61°E; SAM 32550, adult female, 695 mm TL, unspecified locality, Eastern Cape, South Africa, 34.44°S, 26.01°E; SAM 32894, neonate female, 273 mm TL; three juvenile males, 240, 310, 318 mm TL, off Mossel Bay, South Africa, 34.56°S, 22.53°E; SAM 34217, juvenile male, 395 mm TL, unspecified locality, Eastern Cape, South Africa, 34.13°S, 26.36°E; ZMB 19151, adult female, 675 mm TL, Simonstown, South Africa.

Diagnosis. A species of *Flakeus* mostly from the Western Indian Ocean diagnosed by the following combination of characters: snout rounded and short (preorbital snout length 6.3% for lectotype, 6.5%–7.1% TL for non-type material), prenarial snout length 0.8 (0.9–1.0) times inner nostril-labial furrow space; first dorsal fin upright, triangular in shape and low (8.2%, 8.0%–9.3% TL); pectoral fins markedly broad with posterior margin conspicuously greater than trunk height when adpressed on body; and caudal fin with narrow dorsal lobe and continuous caudal fork between lobes. *Flakeus acutipinnis* can be distinguished from all species of the *S. megalops-cubensis* group (except from *S. megalops, S. brevirostris* and *S.*

crassispinus) by fewer total (108, 107–111 [mode 109, n= 10] vs. 113–125), precaudal (81, 81–83 [mode 82, n= 10] vs. 84–96) and monospondylous vertebrae (41, 37–42 [mode 40-41, n= 10] vs. 41–49).

Flakeus acutipinnis differs from *F. megalops* from southern Australia by having a rounded snout (vs. pointed snout), L-shaped free rear tips of pectoral fins and pectoral fins not lobe-like (vs. evidently rounded and lobe-like pectoral fins), triangular first dorsal fin (vs. rounded first dorsal fin at tip), pectoral fins transcending trunk height when adpressed on body (vs. pectoral fins, never reaching trunk height), shorter prespiracular length (11.6%, 7.7%–12.1% TL vs. 13.5%, 11.6%–13.4% TL), more elongated first dorsal spine (3.5%–4.3% TL vs. 1.8%–3.6% TL), dermal denticles broad at crown with length equal to width (vs. dermal denticles slender at crown with length much greater than width), and margins of pectoral and caudal fins white but not uniform (vs. evident uniform white margins). *Flakeus acutipinnis* further differs from *S. brevirostris* from Japan by having pectoral fins with L-shaped free rear tips and not lobe-like, and with straight posterior margin (vs. pectoral fins triangular and with pointed free rear tips, lobe-like and with strongly concave posterior margin), length of pectoral fin anterior margin 1.8 (1.5–1.9) times greater than length of its inner margin (vs. length of pectoral fin anterior margin 1.4, 1.2–1.5 times greater than its inner margin length), and length of first dorsal fin posterior margin relatively greater 9.6%, 8.8%–10.3% TL (vs. 7.7%, 8.3%–8.8% TL). The Southern African species is also clearly distinct from *S. crassispinus* by narrower first and second dorsal spines (first dorsal spine base width 0.6%, 0.6%–0.9% of TL vs. 1.3%, 1.2%–1.3% of TL; second dorsal spine base width 0.6%, 0.7%–1.0% of TL vs. 1.5%, 1.3%–1.4% of TL).

Description. Single values are for lectotype, while ranges represent all specimens from which data were taken.

External morphology (Figs. 94–97; Tabs. 20, 23). Body fusiform, arched from posterior margin of eye to vertical through pelvic fin origin, and very deep at trunk with height 12.0% TL in lectotype (9.2%–12.7% TL for non-type specimens). Head very small, its length 23.1% (21.4%–24.3%) TL, depressed anteriorly; head width 1.2 (1.1–1.4) times trunk width, and 1.7 (1.4–1.7) times abdomen width. Snout short 4.0% (3.9%–4.4%) TL, obtuse, and rounded at tip; nasal apertures oblique and located laterally with strongly bilobed anterior margin of nostrils; prenarial length 0.8 (0.9–1.0) times eye length and one-half preoral length; prenarial length 0.8 (0.9–1.0) times distance between nostril and upper labial furrow. Eyes large (5.1%, 4.3%–5.1% TL) and horizontally oval, with concave anterior margin and acute posterior margin; eye length 3.5 (2.0–2.8) times its height, positioned nearer to snout tip than to first gill slit. Prespiracular length about one-half prepectoral length; spiracles half-moon shaped, small (1.5%, 1.2%–2.2% TL), located above and posterior to posterior eye margin. Fifth gill slit height 1.5 (1.0–1.4) times first gill slit height.

Mouth highly arched and broad, its width 8.5% (7.7%–9.0%) TL and 2.2 (1.9–2.2) times distance between nostrils; upper labial furrow elongated 2.8% (2.5%–2.9%) TL and slim. Unicuspid teeth similar in both jaws, labial-lingually flattened and alternate, broad at crown; teeth broader in lower jaw than in upper jaw; cusp robust and slightly elongated, diagonal and upwardly directed; mesial cutting edge concave; distal heel markedly rounded; slender mesial heel; apron short in upper teeth and more elongated in lower teeth; lectotype with three series of functional teeth in upper jaw and two series in lower jaw; tooth row formula 13/11.

Pre-first dorsal length 1.4 (1.3–1.5) times prepectoral length. Triangular first dorsal fin with convex anterior margin, straight posterior margin, slightly slender at apex, very low with height 8.2% (8.0%–9.3%) TL, corresponding to 1.5 (1.4–1.5) times its inner margin length; wide at its base with base length 8.3% (7.5%–8.5%) TL; first dorsal fin length 1.2 (1.1–1.3) times second dorsal fin length. First dorsal spine short (1.9%, 3.5%–4.3% TL), not reaching fin apex. Interdorsal space 1.0 (1.0–1.3) times prepectoral length, and 1.9 (1.7–2.4) times dorsal-caudal distance. Second dorsal fin also low, its height 6.1% (5.1%–6.7%) TL, corresponding to 1.2 (1.0–1.4) times its inner margin length; wide at its base (6.5%, 5.7%–7.8% TL base length); second dorsal fin with convex anterior margin and concave posterior margin, fairly falcate. Second dorsal spine slender and elongate (3.8%, 4.5%–6.3% TL), not reaching fin apex; second dorsal spine length 2.0 (1.1–1.6) times first dorsal spine length.

Pectoral fins conspicuously broad with convex anterior margin, forming an acute angle with its posterior margin; inner margin convex; posterior margin somewhat straight; both apex and free rear tip rounded, although the latter L-shaped and not lobe-like; pectoral fin apex slightly transcending its free rear tip; length of pectoral fin anterior margin 1.8 (1.5–1.9) times greater than its inner margin length; length of pectoral fin posterior margin conspicuously transcending trunk height when adpressed on body; length of pectoral fin posterior margin 1.1 (1.0–1.4) times trunk height. Pectoral-pelvic distance 0.7 (0.7–0.9) times pelvic-caudal distance; pre-pelvic length 1.5 (1.3–1.6) times distance between dorsal fins; pelvic fin located at mid-distance between first and second dorsal fins in lectotype, but in non-type specimens second dorsal fin slightly nearer to second dorsal fin than to first dorsal.

Pelvic fins pentagonal with slightly convex anterior and posterior margins, and free rear tips pointed and triangular; pelvic fin length 10.8% (9.8%–11.6%) TL; pelvic inner margin length 5.1% (4.2%–6.4%) TL. Clasper in adult males slightly transcending pelvic fin free rear tips, with clasper outer length 1.8% TL; siphon prominent, short, and located ventrally from the posterior half of the basipterygium to intermediate cartilages of pelvic fins; clasper groove longitudinal, positioned dorsally; apopyle with broad aperture, anteriorly situated in clasper groove; hypopyle with narrow aperture, posteriorly in clasper groove and anterior to rhipidion; rhipidion large, flap-like with its free edge laterally positioned, internally supported by dorsal terminal 2 cartilage, and located at posterior end of clasper (Fig. 3).

Caudal peduncle with evident lateral keels, originating behind insertion of second dorsal fin; upper and lower precaudal furrows well developed; caudal fin somewhat rectangular with elongated upper caudal lobe (20.7%, 19.7%–22.8% TL), slightly slender at tip dorsal to vertebral column; upper caudal lobe length 0.9 (0.8–1.1) times head length, and 2.0 (1.8–2.0) times lower caudal lobe length; short lower caudal lobe (10.5%, 10.3%–12.0% TL) with straight preventral margin; very discrete caudal fork between lobes, its width 7.2% (6.9%–7.5%) TL.

Dermal denticles (Fig. 97). Denticles lanceolate and unicuspid, somewhat broad at crown; denticles close together but not imbricated; denticle length slightly greater than width; median ridge elongated, extending far anteriorly from crown base; lateral ridges shorter than median ridge, asymmetrical with irregular lengths; both median and lateral ridges bifurcate distally. Juveniles differ from adults by having somewhat more slender denticles, very sparsely grouped, relatively far from each other; median ridge prominent, not bifurcated; lateral expansions inconspicuous.

Coloration. Body brownish dorsally and pale laterally from dorsal to pelvic fins to just anterior to upper caudal furrow, and extending ventrally. Dorsal fins brown, whitish at fin base, with posterior margin discretely white although not extending to apex on first dorsal fin; dorsal fin spines light brown and whitish at tips. Pectoral fins brown, pale at base, with posterior margins white but not uniform. Pelvic fins light grey, pale dorsally and ventrally at base, and whitish on inner and posterior margins. Caudal fin predominantly dark brown with post-ventral margins not uniformly white, and slightly broad white apex on ventral lobe.

Vertebral counts (Tab. 24). Precaudal vertebrae 81 for lectotype (81–83 [mode 82] for non-type specimens); caudal vertebrae 27 (25–29 [mode 27–28]); total vertebrae 108 (107–111 [mode 109]); monospondylous vertebrae 41 (37–42 [mode 40–41]); diplospondylous vertebrae 67 (66–71 [mode 68–71]).

Geographical distribution (Fig. 98). *Squalus acutipinnis* is originally described from Kwazulu-Natal, South Africa, and Mauritius. It is more common in the Western Indian Ocean, frequently occurring from Kwazulu-Natal to Algoa Bay in the Eastern Cape (South Africa). There are few records from the Atlantic side of South Africa but without occurrences to the north-northwest of Cape Town.

Etymology. The epithet *acutipinnis* is from "*acutus*" (= acute) and "*pinna*" (= fin) in Latin, and probably concerns to the acute angle between anterior and posterior margins of the pectoral fin, which was used to characterize this species (etymology not provided in original description).

Remarks. *Flakeus acutipinnis* was first described by Regan (1908a) based on four specimens from different localities in the Eastern Atlantic and Western Indian Oceans surrounding South Africa. All specimens were mentioned in the original description and again in Regan (1908b), in which he formally stated that the syntypes were deposited in the Natural History Museum in London. Later, Krefft (1968) designated a lectotype for *F. acutipinnis* that corresponds to the specimen figured in the original description and to specific information provided by Regan (1908a).

Many morphological characters provided by Regan (1908a) are congruent with our observations; for example, the short snout, large pectoral fins, and caudal fin with continuous caudal fork between upper and lower postventral margins, as well as some proportional dimensions (e.g. pectoral fin length and its distance to the fifth gill slit). However, some supposedly diagnostic characters of the species, such as prenarial length, inner nostril to labial furrow space, and length and height of first dorsal fin, are not congruent among all type specimens of *F. acutipinnis*. This discrepancy is explained by the heterogeneous nature of the type series of *F. acutipinnis* (see discussion below). The present redescription is based on the lectotype and new (non-type) material from South Africa.

Doubts also exist concerning the precise type locality of *S. acutipinnis* as Regan (1908a, p. 241) cited two different localities, one as Bird Island near Algoa Bay in South Africa and the second as Kwazulu-Natal, South Africa. Both localities are written on the label of the type specimens. Some previous authors have mentioned the type locality as being either Algoa Bay, Bird Island or Kwazulu-Natal, such as Merrett (1973) who considered the former locality as being that of the lectotype. Kwazulu-Natal is clearly the type locality of *S. acutipinnis* as indicated in the original description as well as being the locality of the lectotype later designated by Krefft (1968), whereas Bird Island should probably be considered an error.

Analysis of the type series of *F. acutipinnis* revealed relevant morphological variation between the lectotype and paralectotypes: the proportional distance between first dorsal fin origin and pectoral fin origin 1.4 times preorbital length in the lectotype vs. 0.7–1.1 times in the paralectotypes; first dorsal fin base length 1.3 times preorbital length vs. 0.9–1.2 times; fifth gill slit 1.5 times longer than first gill slit vs. 1.1–1.2 times; dermal denticles more slender at crown base, their length somewhat equal to width, and with asymmetrical lateral expansions in the lectotype vs. denticles broader at crown base with their length greater than width, and symmetrical lateral expansions; and continuous caudal fork between lobes vs. evident discontinuous caudal fork. The types are also very distinct in dentition: upper teeth wide in lectotype vs. more slender in paralectotypes; lower teeth with thick and slightly elongated cusp, directed upwardly vs. lower teeth wider and depressed, with cusp very short and somewhat oblique; concave mesial cutting edge vs. straight mesial cutting edge; pointed mesial heel vs. rounded mesial heel; apron shorter in upper teeth than in lower teeth vs. very short apron in both jaws. Vertebral counts also show variation in the types of *S. acutipinnis*, with greater disparity in the precaudal vertebrae (81 in lectotype vs. 84) and caudal vertebrae (27 vs. 25).

Our analysis of the type specimens of *F. acutipinnis*, therefore, clearly indicates that Regan (1908a) based the original description on a combination of two different species that are not sympatric and clearly separable from each other by external morphology and measurements. Morphological variation in the type series of *F. acutipinnis* has not been previously reported and has doubtlessly contributed to the taxonomic confusion concerning the identity and validity of this species. One of the species of the type series is illustrated in the original description as the representative of *F. acutipinnis*, which refers to the lectotype (BMNH 1905.6.8.8, female, 578 mm TL) from Kwazulu-Natal (South Africa) as well as to a stuffed paralectotype (BMNH 1881. 3.11.2, female, 852 mm TL) from Mauritius (previously considered missing by Krefft, 1968). The other two remaining paralectotypes of *S. acutipinnis* (Fig. 99) represents an undescribed species of *Flakeus* that is under investigation as part of a taxonomic revision of all *Squalus* species (Viana & Carvalho, *in prep.*).

Another factor that may have contributed to the confusion concerning the validity of *F. acutipinnis* is the attempt by some authors to recognize only species groups of *Squalus* in the region (e.g. Bass *et al.*, 1976; Compagno, 1984) rather than attempt to better define morphologically the species present off South Africa. This may have, unintentionally, obscured relevant diagnostic characters of *F. acutipinnis*, contributing to its status as a synonym of other nominal species that have wide geographical distribution such as *F. megalops* and *F. mitsukurii* (e.g. Chen *et al*., 1979; Compagno, 1984).

Regan (1908b) emphasized that *F. acutipinnis* was clearly separable from *F. megalops* (type locality: Port Jackson, New South Wales, Australia) from Southern Australia and Tasmania by not having acutely pointed pectoral fin free rear tips and straight pectoral posterior margin, which reaches the level of the first dorsal fin insertion, features corroborated as diagnostic in our study. These species clearly differ from each other by pectoral fin shape, which is also consistently narrower in *F. megalops* than in *F. acutipinnis*. The former has conspicuously rounded and lobe-like free rear tips, pectoral fin apex transcending its free rear tip, and pectoral fin posterior margin never transcending trunk height when adpressed on body, confirming the observation by previous authors that *S. acutipinnis* has longer pectoral fins than *F. megalops* (e.g. Krefft, 1968). *Flakeus acutipinnis* is also very distinct from the holotype of *F. megalops* by having an arched mouth (vs. relatively straight mouth), continuous caudal fork between lobes (vs. discontinuous caudal fork), and pelvic fins with pointed and triangular free rear tips (vs. pelvic fins with very rounded and lobe-like free rear tips).

Specimens of *F. acutipinnis* further differ from *F. megalops* from Southern Australia by external measurements (Table 1 [single value for *F. megalops* is from holotype]): smaller prespiracular length (11.6%, 7.7%–12.1% TL vs. 13.5%, 11.6%–13.4% TL, respectively); smaller distance between inner margin of nostril and upper labial furrow (4.7%, 4.3%–4.9% TL vs. 5.3%, 4.6%–5.3% TL); smaller interorbital space (7.8%, 7.4%–8.6% TL vs. 8.7%, 8.3%–10.0% TL); greater length of first dorsal spine (3.5%–4.3% TL vs. 1.8%–3.6% TL) corresponding to at least half of first dorsal fin height (vs. less than half of first dorsal fin height); and second dorsal spine length 0.6 (0.8–1.0) times second dorsal fin height (vs. 0.4, 0.5–0.8 in *F. megalops*). Despite slightly overlapping, morphometric characters have recently proven useful for distinguishing closely related species of *Flakeus* (Last *et al*., 2007).

Last *et al*. (2007) reported intraspecific variation in *F. megalops* from different regions of Australia based mainly on external measurements. *Flakeus acutipinnis* differs significantly from the *F. megalops* of these authors by the following characters: greater labial furrow length (2.8%, 2.5%–2.9% TL for *F. acutipinnis* vs. 2.1%–2.4% TL and 2.3%–2.5% TL for *F. megalops* from Southeastern Australia and Queensland, respectively); smaller internarial space (3.8%, 3.6%–4.3% TL vs. 4.3%–4.7% TL and 4.6%–4.9% TL for *F. megalops* from Southeastern Australia and Queensland, respectively); higher first dorsal fin (8.2%, 8.0%–9.3% TL for *F. acutipinnis* vs. 6.1%–7.4% TL, 6.2%–6.6% TL and 7.0%–7.5% TL for *S. megalops* from Southeastern Australia, Queensland, and Western Australia, respectively); greater posterior margin of first dorsal fin (9.6%, 8.8%–10.3% TL for *F. acutipinnis* vs. 7.6%–8.1% TL and 7.5%–8.1% TL for *F. megalops* from Queensland and Western Australia, respectively); higher second dorsal fin (6.1%, 5.1%–6.7% TL for *F. acutipinnis* vs. 3.6%–4.6% TL, 3.2%–4.0% TL and 3.7%–4.3% TL for *F. megalops* from Southeastern Australia, Queensland and Western Australia, respectively); greater length of pectoral anterior margin (17.7%, 15.1%–18.1% TL for *F. acutipinnis* vs. 13.6%–14.9% TL, 12.3%–12.6% TL and 13.7%–15.1% TL for *F. megalops* from Southeastern Australia, Queensland, and Western Australia, respectively), and greater length of pectoral inner margin (9.8%, 9.5%–11.8% TL for *F. acutipinnis* vs. 7.4%–9.2% TL and 7.7%–8.8% TL for *F. megalops* from Southeastern Australia and Queensland, respectively).

Measurements of the lectotype of *F. acutipinnis* are clearly distinct from those provided by Garrick (1960) for *F. megalops* from Southeastern Australia, with exception of preoral distance (8.9% TL vs. 8.5%–9.2% TL), dorsal caudal margin length (20.7% TL vs. 19.6%–22.1% TL), and precaudal distance (79.9% TL vs. 79.0%–82.0% TL). These observations are congruent with the results given for *S. megalops* by Bass *et al*. (1976) from South Africa, indicating its conspecificity with *S. acutipinnis*. These authors probably took into account their definition of the *S. megalops* group for evaluating the taxonomic status of the South African species, rather than the strong differences in measurements apparent between these two species. The synonymy of these two species proposed by Bass *et al*. (1976) is unwarranted according to our results that support the validity of *S. acutipinnis*.

The southern African species is also easily distinct from its regional congeners *S. acanthias, S. blainvillei* (*sensu* Bass *et al*., 1976) and *S. mitsukurii* (*sensu* Compagno, 1984) by: short and rounded snout (vs. elongate and pointed snout); broad pectoral fins (vs. narrow pectoral fins); lanceolate dermal denticles (vs. non-lanceolate unicuspid in *S. acanthias*, and tricuspid in specimens identified as *S. blainvillei* and *S. mitsukurii* from South Africa). Besides, *S. acutipinnis* differs from *S. acanthias* by lacking white spots dorsally on the body (vs. presence of conspicuous white spots), and greater precaudal vertebrae (81, 81–83 vs. 74–81, respectively). It is also distinct from *S. acanthias* by having anterior margin of nostrils bilobate (vs. anterior margin of nostrils unilobate), first dorsal fin origin anterior to pectoral free rear tips (vs. first dorsal fin origin posterior to pectoral free rear tips).

More recently, Naylor et al. (2012a,b), based on mitochondrial genes, indicated that a possible new species might occur in South Africa that is distinct from *S. megalops* from Australia and more closely related to *S. brevirostris* from Japan. Our current study shows that *S. acutipinnis* is clearly distinct from the Japanese species by: pectoral fin with rounded free rear tips, not lobe-like, and straight posterior margin (vs. triangular and pointed free rear tips, lobe-like, and strongly concave posterior margin); length of pectoral anterior margin 1.8, 1.5–1.9 times length of pectoral fin inner margin (vs. length of pectoral anterior margin 1.4, 1.2–1.5 times length of pectoral inner margin); pre-first branchial length 1.6, 1.5–2.5 times prespiracular length (vs. pre-first branchial length 1.5, 1.4–1.5 times prespiracular length);

and length of posterior margin of first dorsal fin greater in *S. acutipinnis* than in *S. brevirostris* (9.6%, 8.8%–10.3% TL vs. 7.7%, 8.3%–8.8% TL, respectively). The pelvic fin of the lectotype of *S. acutipinnis* is located closer to the midline between both dorsal fins whereas in the holotype of *S. brevirostris* it is closer to the first dorsal fin.

Squalus cf. *megalops* (*sensu* Naylor et al., 2012a, b) also refers to a new species of *Squalus* from South African waters that was probably also included in the analysis of Bass et al. (1976) when defining the *S. megalops* group in the region, an act that further contributed to the taxonomic confusion concerning *S. acutipinnis*. Current investigation of this apparent new species indicates it exhibits more morphological similarities with *S. megalops* from Australia and *S. brevirostris*, rather than with *S. acutipinnis*.

Concerning dentition, the middle tooth is absent in *S. acutipinnis*, contrary to what was reported by Bass *et al*. (1976) and Myagkov and Kondyurin (1986) for distinguishing Southern African species of *Squalus*. This character is rarely efficient in separating species of the genus (e.g. Chen et al., 1979; Muñoz-Chápuli and Ramos, 1989; Last et al., 2007), as presently noticed for *S. acutipinnis, S. megalops*, and *S. brevirostris*.

The clasper of the three species compared here is very conservative in relation to the number of terminal cartilages and the shapes of the beta cartilage, intermediate segment, axial cartilage, and marginal cartilages. *Squalus acutipinnis* is, however, more similar to *S. brevirostris* than to *S. megalops* concerning the terminal cartilages. The former two species have accessory terminal cartilage (spur) thicker and shorter as well as dorsal terminal cartilage (claw) thicker, shorter and conspicuously concave in its distal portion when compared to *S. megalops* from Australia. The internal morphology of the clasper may be useful for distinction at species level in *Squalus* as shown by descriptions of terminal clasper components in species from other regions (Muñoz-Chápuli and Ramos, 1989).

Vertebral counts are greatly useful for distinguishing many species of the genus (e.g. Springer and Garrick, 1964; Last *et al*., 2007). *Squalus acutipinnis*, *S. megalops* from Southern Australia, and *S. brevirostris* present overlap in numbers of vertebrae, even though the holotype of *S. megalops* has more precaudal vertebrae than the lectotype of *S. acutipinnis* and specimens of *S. brevirostris*. On the other hand, *S. acutipinnis* can be easily distinguished from other congeners such as *S. bucephalus*, *S. raoulensis*, *S. albifrons*, *S. altipinnis*, and *S. notocaudatus* by monospondylous, precaudal, and total vertebrae.

According to Last *et al*. (2007), some specimens of the *S. megalops* group can be placed in the "highfin *megalops* subgroup", characterized by tricuspid dermal denticles, small snout (6.0%–7.0% TL preoral length), high and upright first dorsal fin (7.7%–9.4% TL height), and heavy dorsal-fin spines (0.7%–1.1% TL exposed base length). These characters are present in *S. acutipinnis*, except for the shape of the dermal denticles (lanceolate as in some other species of the *Squalus megalops* group), and shape of the dorsal fins. Due to the overlap of characters between the species complexes of *Squalus*, we prefer not to allocate *S. acutipinnis* to a species group. Current investigation of the species of *Squalus* in South African waters (Viana and Carvalho, *in prep*.) indicates that the diversity of the genus in both the Atlantic and Indian Oceans is greater than previously recognized.

Comparative material: Specimens of *Flakeus megalops* and *F. brevirostris* listed in this Chapter.

***Flakeus brevirostris* (Tanaka, 1917)**

(**Japanese shortsnout spurdog; Tsumari-aizam** in Japanese)

Figs. 100–106; Tables 21, 23–24

Squalus brevirostris Tanaka, 1917: 464-467, plates CXXIX and CXXX, figs. 362-364 (original description, illustrated; type by original designation; Japan); Garrick, 1960: 537 (cited; Northwestern Pacific Ocean); Yuanding, 1960: 106, 110-112 (description; Northwest Pacific Ocean); Chen *et al*., 1979: 26, 40 (cited; Northwestern Pacific Ocean); Zhu, Meng & Li, 1984: 296 (cited; Northwestern Pacific Ocean); Siming *et al*. 1988: 1 (listed; Northwest Pacific Ocean); Compagno, 1999: 472 (listed); Nakabo, 2002: 155 (listed; Ryukyu Islands, Japan); Duffy & Last, 2007: 31, 36, 37 (cited, North and Central Western Pacific Ocean); Ward *et al*., 2007: 116 (cited; Naylor *et al*., 2012a: 58 (cited; Northwestern Pacific Ocean); Naylor *et al*., 2012a: 58 (cited; Northwestern Pacific Ocean); Naylor *et al*., 2012b: 42 (cited; Northwestern Pacific Ocean); Ebert *et al*., 2013: 78, 85 (cited, description; Northwest Pacific Ocean); Nakabo, 2013: 195 (listed; Japan); Shinohara *et al*., 2014: 233 (listed; Northwestern Pacific Ocean).

Squalus megalops: Compagno, 1984: 118-119 (cited; Northwestern Pacific Ocean); Yuanding & Qingwen, 2001: 311, 318-319 (cited, description; Northwest Pacific Ocean); Ebert *et al*., 2013 (in part): 76, 91 (cited, description; Northwest Pacific Ocean).

Holotype: ZUMT 7630, adult male, 426 mm TL, collected at Tokyo fish market. Collecting date unknown.

Paratypes: not mentioned.

Type locality: Tokyo fish market, Japan, probably from Shimonoseki, Yamagueh Prefecture.

Non-type material (27 specimens): CSIRO H 6293-29, juvenile female, 404 mm TL, Tashi fish market, near I-Lan (NE coast), Taiwan; CSIRO H 6483-02, adult male, 450 mm TL, off Kasasa, Kagoshima, Japan, East China Sea, 31°29’N,130°02’E; HUMZ 33679, juvenile male, 390 mm TL, East China Sea, 29°54’N,126°08’E; HUMZ 37664, adult female, unknown total length, off northwest Borneo, 3°07.8’N,110°45.4’E; HUMZ 95065, adult female, 465 mm TL, East China Sea, 26°14.7’N,124°42.5’E; HUMZ 189743, adult male, 387 mm TL, East China Sea; HUMZ 189745, adult female, 450 mm TL, East China Sea; HUMZ 189747, adult male, 365 mm TL, East China Sea; HUMZ 189751, adult male, 395 mm TL, East China Sea; HUMZ 189756, adult female, 402 mm TL, East China Sea; HUMZ 189757, juvenile female, 357 mm TL, East China Sea; HUMZ 189758, adult female, 475 mm TL, East China Sea; HUMZ 189761, adult male, 400 mm TL, East China Sea; HUMZ 189762, adult male, 403 mm TL, East China Sea; HUMZ 189763, adult female, 433 mm TL, East China Sea; HUMZ 189767, juvenile male, 275 mm TL, East China Sea; KAUM-I 185, adult female, 500 mm TL, off Kasasa, Kagoshima, Japan, East China Sea, 31°29’N,130°02’E;

KAUM-I 187, adult female, 578 mm TL, off Kasasa, Kagoshima, Japan, East China Sea, 31°29'N,130°02'E; KAUM-I 377, adult male, 377 mm TL, off Kasasa, Kagoshima, Japan, East China Sea, 31°29'N,130°02'E; NSMT-P 47377, adult male, 467 mm TL, Central Pacific Ocean; NSMT-P 47378, adult female, 600 mm TL, Central Pacific Ocean; NSMT P-4737, adult male, 452 mm TL, Central Pacific Ocean; NSMT-P 64979, two juvenile females, 480, 520 mm TL, East China Sea; ZUMT uncatalogued, juvenile female, 147 mm TL, juvenile male, 182 mm TL, Japan.

Diagnosis. A small Japanese species of dogfish that differs from its congeners by a combination of characters: head markedly small, its length 21.9% (20.0%–29.6%) of TL; snout conspicuously short, its prenarial length 4.0% (3.8%–4.4%) of TL; dorsal fins very low (first dorsal fin height 7.6%, 6.5%–8.6% of TL; height of second dorsal fin 6.0%, 5.2%–7.1% of TL); short dorsal spines, never reaching the fin apex (length of first dorsal spine 1.6%–4.2% of TL; length of second dorsal spine 4.6%, 4.2%–6.6% of TL); dermal denticles unicuspid and lanceolate with its length greater than its width. It also differs from its congeners by having: pectoral fins conspicuously narrow; pectoral free rear tips markedly pointed and large; pectoral posterior margin strongly concave; dermal denticles unicuspid and lanceolate, slender at crown with its length greater than its width.

It is distinguished from *F. megalops* by having body brownish grey (vs. grey for *F. megalops*), and postventral caudal margins broadly white, including posterior and ventral caudal tips (vs. narrowly white and uniform).

Description. Single values are for holotype. Range values are for non-type specimens.

External morphology (Figs. 100–105; Tabs. 21, 23). Small size species (147-578 mm TL) of Japanese dogfish with body fusiform and slender, equally deep from head to trunk (head height 0.9, 0.9-1.0 times trunk height, and 1.0, 0.8-1.2 times abdomen height). Head very short, its length 21.9% (20.0%-29.6%) of TL; head width 1.4 (1.0-1.4) times broader than trunk width, and 1.1 (1.1-1.6) times abdomen width. Snout somewhat obtuse ventrally, very short (preorbital length 6.7%, 6.5%-7.5% of TL); anterior nasal flap broad and bifurcated, nearest to the snout tip than to the mouth with prenarial length 0.8 (0.8-0.9) times distance from nostril to upper labial furrow. Eyes oval with anterior margin rounded and posterior margin notched; eyes large, its length 2.3 (1.8-2.5) times its height. Prespiracular length 0.6 (0.5-0.6) times prepectoral length, and 1.8 (1.6-1.9) times preorbital length. Spiracle crescent and narrow, its length one-fourth the eye length, nearest to posterior margin of the eye than to first gill slit. First and fifth gill slits somewhat concave and low; fifth gill slit 1.1 (0.9-1.6) times higher than first gill slit.

Preoral length somewhat equal to mouth width, corresponding to 1.1 (1.1-1.2) times the latter. Mouth markedly arched and narrow, its width 2.3 (1.8-2.3) times broader than internarial space; upper labial furrow small (its length 2.6%,2.0%-2.7% of TL) with thin fold; lower labial furrow also short with fold subdivided into three small interdigits. Teeth tiny and unicuspid, labial-lingually flattened and alternate, similar in both jaws, lower teeth slightly wider than the upper teeth; cusp short and oblique; mesial cutting edge concave; both distal and mesial heels rounded; apron elongated in upper and lower teeth; three and two series of functional teeth on upper and lower jaws for holotype (two series in non-type specimens); 12-13 (12-12) teeth rows in upper jaw; 10-10 (10-10) teeth rows in lower jaw.

Pre-first dorsal length 1.4 (1.3-1.6) times prepectoral length. First dorsal fin short and low, its length 1.7 (1.5-1.9) times its height; its height 1.3 (1.2-1.5) times greater than its inner margin length; anterior margin concave, posterior margin straight, slenderer at the fin apex. Origin of first dorsal spine anterior to vertical at free rear tips of pectoral fin; first dorsal spine apparently short (broken in the holotype), never reaching the fin apex, its length

0.3-0.6 times the fin height. Interdorsal space 1.1 (1.1-1.3) times prepectoral length, and 2.4 (2.2-2.6) times larger than dorsal-caudal space. Pre-second dorsal length 2.8 (2.7-3.3) times greater than prepectoral length, and 3.0 (2.8-3.2) times the length of dorsal caudal margin. Second dorsal fin very short (its length 11.6%, 11.2%-13.2% of TL), corresponding to 0.9 (0.8-1.0) times first dorsal fin length; second dorsal fin low, its height 1.2 (0.8-1.4) times length of its inner margin; anterior margin concave, posterior margin markedly falcate, evidently slenderer and lobulate at the apex. Second dorsal spine thick and elongated, although not reaching the apex, its length 0.8 (0.8-1.1) times the fin height; second dorsal spine 1.8 (1.3-2.6) times greater than length of first dorsal spine.

Pectoral fin conspicuously narrow with anterior margin length 1.4 (1.3-1.9) times larger than posterior margin, and 1.4 (1.1-1.5) larger than inner margin lengths; anterior and inner margins convex, posterior margin deeply concave; apex rounded and lobe-like; pectoral free rear tips markedly pointed and triangular, strongly lobe-like; free rear tips reaching the horizontal line when it is traced at the apex. Pectoral-pelvic space 0.8 (0.6-0.9) times pelvic-caudal space. Pelvic fins nearest to first dorsal fin than second dorsal fin. Pelvic fins very narrow with straight margins, and rounded at apex; pelvic free rear tips triangular and pointed, lobe-like; pelvic fin length 1.2 (0.9-1.2) times length of preventral caudal margin. Clasper flattened ventrally, small (its outer length 3.9%, 1.4%-5.1% of TL), transcending the free rear tips; clasper groove dorsal, longitudinal, and small; apopyle and hypopyle with conspicuous apertures, near each other; rhipidion, blade-like, located at the posterior end of the clasper; inner length of clasper 1.2 (0.5-1.2) times length of pelvic inner margin.

Upper and lower precaudal pits well marked. Caudal keel prominent, reaching from forward second dorsal fin insertion to behind origin of caudal fin. Caudal fin wide anteriorly and slightly slender in the dorsal lobe; both dorsal caudal margin and upper postventral caudal margin convex; rounded dorsal caudal tip; dorsal caudal margin 0.8 (0.7-1.0) times the head length, and 2.0 (1.5-2.0) times larger than preventral caudal margin; lower postventral caudal margin also convex (broken in the holotype); preventral caudal margin strongly convex and short, its length 1.7 (1.6-2.3) times greater than length of pelvic inner margin; ventral caudal tip rounded (broken in the holotype); caudal fork discontinuous between lobes, its width 6.6%, 6.6%-7.6% of TL.

Dermal denticles (Fig. 105). Dermal denticles unicuspid and lanceolate, not imbricated; cusp rounded and posterior; denticles conspicuously slender at crown, although markedly broad medial-anteriorly at its base; denticles with length much greater than its width; median ridge tall and thick, bifurcated anteriorly with profound anterior furrow; lateral ridges tall and thin, shorter than median ridge.

Coloration. Body brownish grey dorsally, white ventrally and posterior-lateraly. Pectoral fins grey with posterior and inner margins white. Pelvic fins white dorsal and ventrally. First dorsal fin brownish grey, slightly white at its posterior margin, free rear tip and at fin base; second dorsal fin light brown, whitish at the fin base, somewhat white at apex, posterior margin and freer rear tip. Dorsal spines grey, dark grey anteriorly and white at the tip. Caudal fin light brown, whitish near vertebral column; postventral caudal margins white, broadly white at dorsal caudal tip, and from ventral caudal tip to caudal fork; light black caudal stripe.

Vertebral counts. (Table XII) 80-89 precaudal vertebrae; 25-30 caudal vertebrae; 39-42 monospondylous vertebrae; 106-114 total vertebrae.

Geographical distribution (Fig. 106). It occurs in the West Pacific Ocean from North Japan to Indonesia.

Etymology. The etymology for the name "*brevirostris*" is not mentioned in the original description.

Remarks.

Type specimens of *Flakeus brevirostris.* Holotype of *F. brevirostris* is in medium preserved conditions in the fish collection. Natural color changed to dar brown in this specimen. Few damages are observed in the pectoral and caudal fins, and first dorsal fin. Dorsal fins slighty fringed at posterior margin. First dorsal spine is half-broken. Pectoral fins with posterior margin fringed, missing part of its apex in the left pectoral fin. Caudal fin somewhat fringes in the postventral caudal margins, ventral caudal tip missing or broken. Some incisions are observed laterally at the abdomen, and ventrally near the head in the holotype.

Morphological variations within *Flakeus brevirostris.* Great morphological variations are observed among specimens of *F. brevirostris* for the first time, regarding shape of pectoral and dorsal fins, dermal denticles and color of caudal fin. First dorsal fin has posterior margin somewhat straight near its apex like in the holotype, although it may show posterior margin concave in other specimens. Pectoral fins are slightly broad at posterior margin in specimens from Central Pacific Ocean (except Taiwan) while others have narrow pectoral fins like it is observed for the holotype. Pelvic fins are nearest to first dorsal fin like it is observed for the holotype, although it may be in the midline between two dorsal fins in few specimens. Caudal fin has postventral caudal margins white, although narrowly white at caudal fork in specimens from Kagoshima.

The thickness at the crown of the dermal denticles varies within *F. brevirostris* from very slender to conspicuously broad in few specimens from Kagoshima. Differences in vertebral counts are also observed for this species with large ranges for diplospondylous, precaudal and total vertebrae. These variations, however, seem not to be related to dimorphism or ontogenty in *F. brevirostris* and it is hard to recognize any other morphological pattern within the range of distribution of this species in the North to Central Pacific Ocean. No other previous studies reported them in the literature, with exception to Duffy & Last (2007) that has noticed differences in the dermal denticles due to ontogeny. Further investigations on this species are in need for comparing specimens from North Japan to Central Pacific Ocean, including Taiwan in order to better understand these variations.

Taxonomic status of *Flakeus brevirostris.* The current results are congruent with the original description of *F. brevirostris* provided by Tanaka (1917). The specimen illustrated in his study assemblages those from North to Central Japan rather than those from Southern Japan, regarding color of caudal fin and shape of dorsal fins. Despite of providing a very detailed description of this nominal species, its characteristics easily overlap in more than one species of *Flakeus*, which contributed to the difficulty on identifying it properly (e.g. Garrick, 1960; Chen *et al.*, 1979; Compagno, 1984). In the present study, *F. brevirostris* is considered a valid species and endemic to North and Central Pacific Oceans, which it is in congruence with findings of Chen *et al*. (1979), Duffy & Last (2007), Naylor *et al*. (2012a,b), Ebert *et al*. (2013a), and Shinohara *et al*. (2014).

Chen *et al*. (1979) suggested that the Japanese species could be a subspecies of the Australian *F. megalops* or even conspecificity due to intrinsic similarity betweent them, and it was followed by Compagno (1984) and Compagno *et al*. (2005). In fact, diagnostic characters for *F. brevirostris* and its distinction from *F. megalops* are quite difficult to establish through analysis of external and skeletal morphology. Great intraspecific variations within the Japanese species also contribute for separating these two nominal species as observed in the present study. Morphological similarities are also observed between *F. brevirostris* and few specimens herein identified as *F. crassispinus* from Western Australia, suggesting that *F. brevirostris* may reach southern waters of the Pacific Ocean. However, this primary hypothesis needs further investigation through analysis of additional material collected between South Japan, North Australia and Taiwan.

Despite of overlap on shape of dermal denticles, vertebral counts, external measurements and general morphology of the body, *F. brevirostris* differs from *F. megalops* from Southern Australia by having pectoral free rear tips markedly pointed (vs. rounded), first dorsal fin with posterior margin concave near the apex (vs. straight), body brownish grey (vs. grey), postventral caudal margin broadly white (vs. narrowly white). The Japanese species also differs by some morphometrics that may help to distinguish them: lower first dorsal fin (its height 7.6%, 6.5%-8.6% of TL vs. 5.3%, 7.8%-10.5% of TL for *F. megalops*); length of pectoral inner margin with greater range in *F. brevirostris* (10.3%, 9.8%-12.0% of TL vs. 10.9%, 9.4%-10.9% of TL); eye length 2.3, 1.8-2.5 times its height vs. 2.2, 1.8-3.8 times for *F. megalops*; pectoral anterior margin 1.4, 1.3-1.9 times greater than length of pectoral posterior margin vs. 1.4, 1.1-1.5 times for for *F. megalops*; first dorsal height 1.1, 0.9-1.2 times preorbital length vs. 0.7, 1.1-1.5 times; first dorsal height 1.3, 1.2-1.5 times greater than length of its inner margin vs. 0.8, 1.3-2.3 times for *F. megalops*. *Flakeus brevirostris* also exhibits more elongate dorsal spines than *F. megalops*: length of first dorsal spine 0.3-0.6 times first dorsal height vs. 0.2-0.4 times; second dorsal spine length 0.8, 0.8-1.1 times height of second dorsal fin vs. 0.4, 0.5-0.9 for *F. megalops*; length of second dorsal spine 0.7, 0.7-1.1 times base length of second dorsal fin vs. 0.4, 0.5-0.8 times.

Comparative material: Specimens of *F. megalops*, *F. cubensis*, *F. acutipinnis*, and *F. crassispinus* listed in this Chapter.

Flakeus cubensis (Howell-Rivero, 1936)

(Cuban dogfish)

Figs. 107–113; Tables 22, 23–24

Squalus specie dubia Poey,1868: 454 (description; Cuba); Howell-Rivero, 1936: 47 (cited; Cuba); Bigelow & Schroeder, 1948: 478 (cited; Cuba).
Acanthias acanthias not Linnaeus: Poey, 1875: 202–203 (listed; Cuba).
Squalus cubensis Howell-Rivero, 1936: 45–47, plates 10–11 (original description; Havana, Cuba); Bigelow & Schroeder, 1948: 473–478, figs. 89–90 (redescription; Cuba, Trinidad); Bigelow *et al*., 1953: 222 (cited; Cuba, Trinidad); Bigelow & Schroeder, 1957: 26, 36–37, fig. 4 (redescription); Garrick, 1960: 537 (cited; Cuba); Figueiredo, 1977 (in part): 8 (cited; Cuba and Venezuela); Cadenat & Blache, 1981: 52, fig. 31 (A–E) (cited; Cuba); Compagno, 1984 (in part): 116–117 (redescription; Gulf of Mexico); Kondyurin & Myagkov, 1984: 118–120, fig. 1B (redescription; West Atlantic); Myagkov & Kondyurin, 1986 (in part): 1–20, figs. 1B, 2 (redescription; Atlantic); Parin, 1988: 48–49 (listed, cited; Cuba); Compagno, 2002: 368, 381, 385 (redescription; West Central Atlantic); Compagno, *et al*., 2005: 75, pl. 3 (redescription; North to South West Atlantic); Last *et al*., 2007: 22 (cited; Cuba); Tavares & Arocha, 2008: 492 (cited; Venezuela); Naylor *et al*., 2012a: 57 (cited; Jamaica); Naylor *et al*., 2012b: 42 (cited; Jamaica); Ebert *et al*., 2013a (in part): 76, 87 (cited, description; Western North and Central Atlantic Ocean).
Squalus sp. of *megalops*-*acutipinnis*-*cubensis* group: Cadenat & Blache, 1981: 51–52, fig. 31 (F–G) (description; Cuba); Figueiredo, 1981: 16–17 (cited; Cuba).

Holotype. MCZ 1458-S, adult male, 531 mm TL, off Havana, Cuba. Collected by Poey.

Paratypes (4 specimens): MCZ 1459-S, neonate male, 210 mm TL; MCZ 1460-S, neonate female, 297 mm TL; MCZ 1461-S, adult female, 690 mm TL; MCZ 1462-S, neonate male, 277 mm TL. All collected at same locality of holotype.

Type locality: off Havana, Cuba.

Non-type material (82 specimens): AMNH 12306, juvenile female, 445 mm TL, Cuba; AMNH 33453, juvenile female, 490 mm TL, Yucatán, Mexico; AMNH 33454, adult male, 535 mm TL, Louisiana, The United States of America; AMNH 33457, juvenile male, 375 mm TL, Mexico; AMNH 33458, juvenile female, 334 mm TL, Mexico; AMNH 33459, neonate male, 278 mm TL, Mexico; CAS 60863, adult male, 510 mm TL, Puerto Rico; CAS 61162, juvenile male, 400 mm TL, Puerto Rico; CAS 230367, two juvenile males, 395–415 mm TL, South of Pensacola, Florida, The United States of America; MCZ 37398, two juvenile females, 376–420 mm TL, Gulf of Mexico; MCZ 40138, adult male, 522 mm TL, Florida, The United States of America; MCZ 40681, neonate female, 217 mm TL, Puerto Rico; SAIAB 6027, adult male, 427 mm TL, Northwestern Atlantic Ocean; SAIAB 6030, adult male, 430 mm TL, locality same as SAIAB 6027; SAIAB 6032, adult male, 415 mm TL, locality same as SAIAB 6027; SAM 38282, 315 mm TL, juvenile male, off Louisiana coast, 28.88ºN,88º52'W; SAM 39880, adult male, 595 mm TL, Northwestern Atlantic; UF 28449, juvenile female, 460 mm TL, Campeche Bank, Mexico; USNM 157843, neonate female, 205 mm TL, neonate male, 210 mm TL; neonate male, 215 mm TL, Alabama, The United States of America, 22º91'N,79º45'W; USNM 157846, adult male, 495 mm TL, Cuba, 22º91'N,79º26'W; USNM 157853, neonate female, 290 mm TL, Cuba, 22º91'N,79º45'W; USNM 158589, juvenile female, 445 mm TL, Florida, The United States of America, 28º82'N,85º75'W; USNM 160847, juvenile male, 410 mm TL, Gulf of Mexico; USNM 164247, adult female, 595 mm TL, Dominican Republic; USNM 187686, neonate male, 217 mm TL, Jamaica, 16º75'N,81º45'W; USNM 187689, neonate female, 286 mm TL, Panama, 09º30'N,80º36'W; USNM 187691, neonate male, 247 mm TL, Honduras, 16º63'N,86º56'W; USNM 187700, juvenile female, 460 mm TL, Panama, 09º07'N, 81º42'W; USNM 187711, juvenile male, 405 mm TL, Nicaragua, 16º43'N, 81º58'W; USNM 187715, adult male, 460 mm TL, Nicaragua, 12º41'N,82º25'W; USNM 187716, juvenile male, 403 mm TL; adult male, 510 mm TL, Nicaragua, 16º75'N,81º45'W; USNM 187717, adult male, 510 mm TL, Nicaragua, 16º75'N,81º45'W; USNM 187726, neonate male, 188 mm TL, Panama, 09º05'N,81º37'W; USNM 187933, neonate female, 200 mm TL; neonate male, 192 mm TL, three adult males, 405–410 mm TL, Mississipi, The United States of America, 29º18'N,88º10'W; USNM 187934, adult female, 532 mm TL, Cuba, 23º50'N,79º45'W; USNM 187935, neonate male, 225 mm TL, neonate female, 306 mm TL, Cuba, 23º86'N,79º38'W; USNM 187936, neonate female, 255 mm TL, Puerto Rico, 18º52’N,66º83’W; USNM 187937, juvenile male, 425 mm TL, Cuba, 23º66’N,79º30’W; USNM 188026, two neonate males, 210–260 mm TL, adult male, 422 mm TL, adult female, 400 mm TL, Cuba, 23º50'N,79º45’W; USNM 188027, juvenile male, 400 mm TL, Cuba, 23º98'N,79º28’W; USNM 188079, juvenile male, 415 mm TL, neonate female, 230 mm TL, Mississipi, The United States of America, 29º19’N,88º19’W; USNM 188080, juvenile male, 400 mm TL, Mississipi, The United States of America, 29º21’N,87º97’W; USNM 188081, juvenile male, 410 mm TL, adult male, 430 mm TL, Mississipi, The United States of America, 29º18’N,88º11’W; USNM 196544, adult male, 440 mm TL, Cuba, 22º98’N,79º28’W; USNM 205325, adult male, 610 mm TL, adult female, 650 mm TL, Barbados; USNM 205587, two neonate males, 273–290 mm TL, juvenile male, 410 mm TL, Louisiana, The United States of America, 28º18’N,90º13’W; USNM 206057, adult male, 540 mm TL, Saint Lucia Island, 13º68’N,60º88’W; USNM 206058, adult female, 610 mm TL, Haiti, 20º72’N,73º48’W; USNM 220519, neonate male, 215 mm TL, neonate female, 265 mm TL, Florida, The United States of America, 29º10’N,88º43’W; USNM 220520, juvenile male, 383 mm TL, Texas, The United States of America, 26º52’N,96º30’W; USNM 220521, neonate female, 275 mm TL, Texas, The United States of America, 26º50’N,96º27’W; USNM 220522, two juvenile males, 390–410 mm TL, Alabama, The United States of America, 29º17’N,88º08’W; USNM 220584, neonate female, 235 mm TL, Colombia, 11º40’N,73º78’W; USNM 220586, juvenile female, 395 mm TL, Texas, The United States of America, 27º80’N,94º61’W; USNM 220587, juvenile male, 380 mm TL, Texas, The United States of America, 27º70’N,94º43’W; USNM 220599, juvenile female, 400 mm TL, neonate male, 270 mm TL, two juvenile males, 355–450 mm TL, Texas, The United States of America, 27º43’N,96º23’W; USNM 220600, neonate female, 267 mm TL, Mississipi, The United States of America, 28º98N,88º80’W; USNM 220603, two juvenile males, 330–360 mm TL, juvenile female, 350 mm TL, Gulf of Maricaibo, Venezuela, 12º28’N,72º51’W;

USNM 220864, adult female, 460 mm TL, Louisiana, The United States of America, 27º87'N,92º48'W.

Diagnosis. Small size species of *Flakeus* that is differentiated from its congeners by having conspicuous black marking on upper half of each dorsal fin. *Flakeus cubensis* differs from *F. brevirostris* and *F. blainvillei* by broader space between nostrils, its width 3.9%–4.5% of TL in adult specimens (vs. 3.4%–3.8% of TL for adults of *F. brevirostris* vs. 3.2%–3.8% of TL for adults of *F. blainvillei*).

Flakeus cubensis is easily distinguished from *F. bucephalus, F. notocaudatus* and *F. hemipinnis* by monospondylous vertebrae (39–46 vs. 49 for *F. bucephalus* vs. 48 for for *F. notocaudatus* vs. 37 for *F. hemipinnis*). It differs from *F. acutipinnis, F. bucephalus, F. notocaudatus* and *F. hemipinnis* by precaudal vertebrae (84–92 vs. 80–83 for *F. acutipinnis* vs. 93 for *F. bucephalus* vs. 97 for *F. notocaudatus* vs. 74 for *F. hemipinnis*). It has fewer total vertebrae (111–118) than *F. bucephalus* (124) and *F. notocaudatus* (123–127), and more than *F. hemipinnis* (98 total vertebrae).

Description.

External morphology (Figs. 107–122; Tabs. 22, 23). Body fusiform and slender throughout all its extension; its greatest width at head, corresponding to 1.3 (1.2–1.7; 1.2–1.6) times trunk width and 2.0 (1.4–2.0; 1.4–2.0) times broader than abdomen width; body slightly deep at head, its height at head 1.1 (0.8–1.2; 0.9–1.1) times trunk height and 1.1 (0.9–1.3; 0.9–1.4) times abdomen height. Head flattened dorsally and arched distally; head very short, its length 23.6% (22.8%–24.6%; 20.4%–25.9%) of TL. Snout rounded at tip and conspicuously small, its preorbital length 7.3% (7.5%–8.1%; 6.4%–8.1%) of TL; anterior margin of nostrils bilobed with its distance to tip of snout 0.8 (0.7–0.9; 0.7–0.9) times distance from nostrils to upper labial furrow, and 0.5 (0.4–0.5; 0.4–0.5) times preoral length; internarial space 0.9 (0.5–1.2; 0.8–1.0) times length of eye. Eyes oval with anterior margin concave and posterior margin notched; eyes elongate, its length 2.4 (1.7–3.0; 1.6–2.6) times greater than its height. Prespiracular length 1.8 (1.7–1.9; 1.7–2.0) times larger than preorbital length and 0.6 (0.6; 0.5–0.6) times prepectoral length. Spiracles crescent, placed laterally behind the eyes; spiracles small, its length 0.4 (0.3–0.4; 0.3–0.5) times length of eyes. Prebranchial length 1.5 (1.4–1.6; 1.4–1.6) times prespiracular length. Gill slits vertical, somewhat straight, located laterally in front of origin of pectoral fins; gill slits very low with fifth gill slit 1.6 (1.2–1.4; 1.1–1.5) times higher than first gill slit.

Preoral length 1.2 (1.2–1.4; 1.0–1.4) times greater than mouth width. Mouth arched and broad, its width 1.8 (1.6–1.9; 1.5–2.5) times prenarial length and 2.1 (1.8–2.9; 1.7–2.2) times wider than internarial space; upper labial furrow short with thin fold, its length 2.4% (2.1%–2.9%; 2.2%–4.3%) of TL; lower labial furrow markedly elongate, lacking fold. Two series of functional teeth on upper and lower jaws. Upper teeth with 14–14 (12–12; 12–13) rows and lower teeth with 11–12 (11–12; 13–13) rows. Teeth unicuspid and similar in both jaws; mesial cutting edge straight to weakly convex; mesial heel notched; distal heel rounded; cusp very short and thin, oblique; apron small and thick, at midline of crown base; upper teeth slightly smaller than lower teeth.

Pre-first dorsal length 1.3 (1.2–1.4; 1.2–1.6) times prepectoral length; origin of first dorsal fin prior to vertical traced at pectoral free rear tips. First dorsal fin upright and somewhat triangular with anterior margin straight, and posterior margin convex, although weakly concave at its midline; apex of first dorsal fin conspicuously rounded and free rear tips pointed; inner margin of first dorsal fin large, its length 6.1% (5.8%–6.9%; 5.1%–6.8%) of TL; first dorsal fin short, its length 14.7% (12.5%–14.6%; 12.0%–13.7%) of TL, corresponding to 1.1 (1.1–1.2; 1.0–1.2) times length of second dorsal fin; first dorsal fin low its height 1.4 (1.2–1.4; 1.1–1.3) times its inner margin length. First dorsal spine rather thick (its base width 0.9%, 0.8%–1.1%, 0.6%–1.1% of TL) and large, its length 0.5 (0.3–0.5; 0.3–0.6) times height of first dorsal fin. Interdorsal space 1.0 (0.9–1.2; 1.0–1.1) times prepectoral length and 2.1 (2.0–2.7; 2.0–2.4) times greater than dorsal-caudal distance.

Pre-second dorsal length 2.7 (2.4–2.9; 2.5–2.9) times larger than prepectoral length. Second dorsal fin large, it slength 13.1% (11.6%–12.4%; 10.6%–12.8%) of TL; second dorsal fin with anterior margin weakly convex and posterior margin notched and falcate; second dorsal fin with apex rounded and lobe-like, and free rear tips pointed; inner margin of second dorsal fin elongate, its length 5.6% (5.5%–6.0%; 4.7%–6.1%) of TL; second dorsal fin low, its height 1.2 (1.0–1.2; 0.9–1.4) times length of inner margin. Second dorsal spine slender, its base width 1.0% (1.0%–1.2%; 0.7%–1.1%) of TL, and conspicuously elongate, almost reaching the fin apex, its length 0.9 (0.7–1.0; 0.6–1.2) times height of second dorsal fin; second dorsal spine 1.4 (1.4–2.0; 1.2–1.9) times greater in length than first dorsal spine.

Pectoral fins somewhat broad, its posterior margin length 12.1% (8.7%–10.1%; 9.2%–11.9% of TL); pectoral anterior margin almost straight, inner margin straight, and posterior margin conspicuously concave; pectoral free rear tips markedly pointed and triangular, reaching horizontal line traced at pectoral apex; the latter rounded; pectoral anterior margin length 1.3 (1.3–1.6; 1.2–1.6) times larger than its inner margin length and 1.2 (1.4–1.6; 1.2–1.4) times greater than length of pectoral posterior margin. Distance between pelvic and pectoral fins 0.7 (0.7–1.0; 0.5–0.9) times pelvic-caudal distance. Pelvic fins nearest to midline between first and second dorsal fins; pelvic fins elongate, its length 13.0% (9.4%–11.5%; 10.0%–12.9%) of TL; pelvic fins with margins weakly convex and free rear tips pointed. Claspers very short, its inner margin length 1.2 (0.5–0.7; 0.5–1.3) times length of pelvic inner margin; clasper groove small, not reach insertion of pelvic fins; apopyle and hypopyle constricted, placed proximal and distally in the clasper groove; rhipidion flap-like, slender and small, located medial-distally at clasper.

Upper and lower precaudal pits profound; caudal keel lateral and prominent, placed at midline between origin and insertion of second dorsal fin until behind origin of caudal fin. Caudal fin small, its dorsal caudal margin length 0.9 (0.8–1.0; 0.8–1.0) times head length and 1.8 (1.7–2.0; 1.8–2.0) times greater than length of preventral caudal margin; caudal fin with dorsal caudal margin straight; upper postventral caudal margin convex, although somewhat straight distally; lower postventral caudal margin convex; preventral caudal margin straight and short, its length 1.8 (1.8–2.2; 1.4–2.8) times larger than length of pelvic inner margin; dorsal and ventral caudal tips weakly pointed (rounded in neonates and juveniles); caudal fin discontinuous and slender with width at caudal fork 6.8% (6.6%–7.0%: 6.3%–7.4%) of TL.

Dermal denticles (Fig. 109). Unicuspid, lanceolate, and thin at crown, its length much greater than its width; cusp rounded distally; lateral ridges thin and symmetrical.

Coloration. Body light brown dorsally, white ventral and laterally at lower half of the body from insertion of pectoral fins to origin of caudal fin. First dorsal fins light brown and whitish at fin base; black marking conspicuous, rounded and large, placed from upper half of height of first dorsal fin to its apex; anterior margin of first dorsal fin white; posterior margin slightly white below its midline to free rear tips. First dorsal spine light grey anteriorly and white laterally to it tip. Second dorsal fin light brown and white at its base; black marking conspicuous, rounded and large from upper half of its height to the apex (more evident in neonates and juveniles); posterior margin of second dorsal fin brown (or white in young juveniles). Second dorsal spine greyish and white at its tip. Pectoral fins brown dorsal and ventrally; pectoral posterior margin uniformly white. Pelvic fins brown dorsally and light brown ventrally; pelvic anterior and posterior margins slightly white. Caudal fin brown and whitish over vertebral column; black caudal stripe evident; dorsal caudal margin white from origin to its midline with black upper caudal fringe distally; postventral caudal margins white, except at caudal fork where it is dark brown; preventral caudal margin white; lower caudal lobe mostly light brown; dorsal and ventral caudal tips broadly white.

Vertebral counts (Tab. 24). 43 (41–44; 39–43 [mode 41]) monospondylous vertebrae; 85 (87–89; 83–92 [mode 84]) precaudal vertebrae; 115 (114–117; 111–118 [mode 111–114]) total vertebrae.

Geographical distribution (Fig. 113). It occurs in the Central West Pacific Ocean from U.S.A to Venezuela.

Etymology. The name "*cubensis*" refers to its type locality, Cuba.

Remarks.

Morphological variations within *Flakeus cubensis*. Despite of the lack of natural coloration of holotype of *Flakeus cubensis*, it is possible to note a large black marking at apex of both dorsal fins. Juveniles from the Western Central Atlantic and Caribbean Sea have large black markings on first dorsal fin only while in adults have it on both dorsal fins. Specimens from the Western Central Atlantic Ocean and Caribbean Sea exhibit great range of external measurements (e.g. prepectoral length; length of upper labial furrow). No other differences on external morphology, however, were noticed among these specimens, which support their conspecificity. Further investigations on the morphology as well as molecular analysis of this species in these regions are needed in order to better characterize it and evaluate the incidence of possible cryptic species in the Atlantic Ocean.

Taxonomic status of *Flakeus cubensis*. *Flakeus cubensis* (Howell-Rivero, 1936) is originally described from Havana, Cuba and whose geographical distribution reaches also the Caribbean Sea (Cervigón & Alcalá, 1999; Compagno *et al*., 2005). Other authors also reported its occurrence in the Southwest Atlantic Ocean (e.g. Bigelow & Schroeder, 1948, 1957; Figueiredo, 1977, 1981; Kondyurin & Myagkov, 1984; Myagkov & Kondyurin, 1986; Gomes *et al*., 2010; Figueirêdo, 2011). Reanalysis of species of this region reveals that *F. cubensis* is restrict to North and Central West Atlantic Ocean and that the form observed in Brazilian waters is an undescribed species.[5] These findings are in disagreement with Ebert (2013) that did not recognize the Cuban species in the North Atlantic Ocean.

Ledoux (1970) considered *F. cubensis* as extreme subspecies of *F. blainvillei* that also occurs in the Atlantic waters. According to his observations, overlapping of external measurements, shape of pectoral fins and dermal denticles between them in which the Mediterranean species exhibit intermediate pattern between *F. cubensis* and *F. megalops*. In fact, external morphometrics are greatly congruent between these three species as well as *F. brevirostris*, as it was noticed previously by Bigelow & Schroeder (1957). However, the current analysis shows that a combination of characteristics of external morphology and number of vertebrae give support for separating them. Similar differences were reported among other recently described species of the genus worldwide (e.g. Garrick, 1960; Bass *et al*., 1976; Last *et al*., 2007). Adult specimens of *F. cubensis* is distinct from *F. blainvillei* by showing smaller first dorsal spine, its length 2.7%–4.7% of Tl (vs. 4.2%–5.6% of TL for *F. blainvillei*), smaller second dorsal fin, its anterior margin length 9.4%–10.9% of TL (vs.

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[5] This species is described later in this Chapter as *Flakeus* sp. 7

10.2%–12.1% of TL for *F. blainvillei*), and larger pectoral fins, its anterior margin length 13.2%–14.7% of TL (vs. 14.4%–17.4% of TL). *Flakeus cubensis* shows somewhat more precaudal (84–92) and total vertebrae (111–118) than *F. blainvillei* (80–84 precaudal vertebrae and 107–111 total vertebrae).

The shape of pectoral fins are often reported (e.g. Howell-Rivero, 1936a; Bigelow & Schroeder, 1957; Garrick, 1960; Bass *et al.*, 1976; Muñoz-Chápuli & Ramos, 1989) as useful for distinguishing *F. cubensis* from its congeners, including posterior margin strongly concave and free rear tips conspicuously pointed and triangular. The same pattern of pectoral fins is noticed for *F. brevirostris* from Japan and Taiwan, *F. megalops* and related forms reported from South Africa, *F. crassispinus* from Australia and *Flakeus* sp. 7 from Brazil. These species also share snout very short, dermal denticles unicuspid and lanceolate, body small and few vertebral counts. *Flakeus cubensis* is slightly distinct from *F. brevirostris* by shorter first dorsal fin, its length 12.0%–13.6% of TL in adults (vs. 13.5%–14.7% of TL for adults of *F. brevirostris*), and from *F. megalops* by shorter pectoral fins, its anterior margin length 13.2%–14.7% of TL (vs. 14.0%–17.0% of TL for adults of *F. megalops*). Body color also helps to differentiate them because *F. cubensis* bears conspicuous black markings at apex of both dorsal fins (vs. absence in other species), which it is in agreement with Bigelow & Schroeder (1948) and Compagno (1984, 2002). *Flakeus megalops* and *F. brevirostris* also have fewer total vertebrae than *F. cubensis* (100–112 for *F. megalops* vs. 105–113 for *F. brevirostris*). *Flakeus crassispinus* has body light grey with caudal fin almost pale, which it is distinct from *F. cubensis*. The former species also bears heavy dorsal spines with base width of first dorsal spine 1.1%–1.3% of TL and for second dorsal spine 1.2%–1.4% of TL (vs. base width for first dorsal spine 0.6%–1.1% of TL, and for second dorsal spine 0.7%–1.1% of TL in *F. cubensis*).

Comparative material: Specimens of *F. megalops, F. brevirostris, F. acutipinnis, F. crassispinus* and *F. blainvillei* listed in the current Chapter.

Flakeus crassispinus (Last, Edmunds & Yearsley, 2007)

(Fatspine spurdog)

Figs.114–119; Tables 25, 31–32

Squalus sp. D Last & Stevens, 1994: 48, 95 (cited, description; Eastern Indian Ocean); Compagno *et al*., 2005: 80 (description; Eastern Indian Ocean).
Squalus crassispinus Last, Edmunds & Yearsley, 2007: 11–22 (original description; illustrated; Western Australia); Ebert *et al*., 2013: 74, 87 (cited, description; Southwest Pacific Ocean).

Holotype. CSIRO H 2547-06, adult female, 576 mm TL, west of North West Cape, Western Australia, 21°37′S,113°59′E, 215 meters depth. Collected on 24 January 1991.

Paratypes (10 specimens): CSIRO CA 4074, juvenile female, 495 mm TL, North of Nickol Bay, Western Australia, 19°11′S,116°4′E; CSIRO H 1035-12, adult female, 562 mm TL, North of Dampier Archipelago, Western Australia, 19°08′S,116°54′E; CSIRO H 1035-14, adult female, 566 mm TL, locality same as CSIRO H 1035-12; CSIRO H 1035-15, adult male, 475 mm TL, locality same as CSIRO H 1035-12; CSIRO H 4031-86, adult female, 540 mm TL, North of Cape Lambert, Western Australia, 18°57′S,117°14′E; CSIRO H 4031-87, adult female, 535 mm TL, locality same as CSIRO H 4031-86; CSIRO H 4649-03, juvenile female, 400 mm TL, North of Nickol Bay, Western Australia, 19°06′S,117°01′E; CSIRO H 4649-04, adult male, 445 mm TL, locality same as CSIRO H 4649-03; WAM P 26207-005, adult male, 455 mm TL, Western Australia, 18°42′S,117°40′E; WAM P 26223-001, adult female, 487 mm TL, Western Australia, 16°32′S,120°52′E.

Type locality: West of North West Cape, Western Australia.

Non-type material (6 specimens): CSIRO H 6412-01, juvenile male, 420 mm TL, North of Monte Bello Islands, Western Australia, 19°48.46S,115°17.65E; CSIRO H 6412-02, juvenile female, 440 mm TL, North of Monte Bello Islands, Western Australia, 19°48.46S,115°17.65E; CSIRO H 6412-03, juvenile female, 404 mm TL, North of Monte Bello Islands, Western Australia, 19°48.46S,115°17.65E; CSIRO H 6412-04, adult female, 474 mm TL, North of Monte Bello Islands, Western Australia, 19°48.46S,115°17.65E; CSIRO H 6412-05, adult female, 482 mm TL, North of Monte Bello Islands, Western Australia, 19°48.46S,115°17.65E; CSIRO H 6412-06, juvenile male, 460 mm TL, North of Monte Bello Islands, Western Australia, 19°48.46S,115°17.65E.

Diagnosis. Small species of dogfish from the Eastern Indian Ocean that is clearly distinct from its congeners on having first and second dorsal spines conspicuously stout: base width of first dorsal spine 1.2% for holotype, 1.1%–1.2% of TL for paratypes (1.1%–1.3% of TL for non-type specimens); base width of second dorsal spine 1.3%, 1.2%–1.3% (1.2%–1.4%) of TL. It is also distinguished from them by (except for *F. megalops*, *F. acutipinnis*, *F. brevirostris* and *F. cubensis*): snout markedly small, its prenarial length 4.6%, 4.3%–4.8% (4.8%) of TL; pectoral fin with posterior margin concave and pointed free rear tips; dermal denticles unicuspid and lanceolate. *Flakeus crassispinus* is distinguished from *F. megalops*, *F. acutipinnis*, *F. brevirostris* and *F. cubensis* by having: dermal denticles markedly broad at anterior base and median ridge; caudal fin conspicuously pale with no uniform white postventral caudal margins; first and second dorsal fins upright and markedly slender at the apex.

Flakeus crassispinus is separated from *F. megalops* and *F. brevirostris* by having shorter inner margin of pectoral fin (its length 7.8%, 8.3%–8.6% [8.2%–8.6%] of TL vs. 10.9%, 9.4%–10.9% of TL for *F. megalops* vs. 7.8%, 8.3%–8.6% of TL for *F. brevirostris*).

It is easily separated from *F. megalops* by: more elongate first dorsal spine (its length 4.6%, 4.2%–6.0% [5.9%–6.4%] of TL vs. 1.8%–3.7% of TL for *F. megalops*); taller second dorsal fin (its height 1.4, 1.5–1.6 [1.5] times its inner margin length vs. 1.3, 1.0–1.4 times for *F. megalops*); broader first dorsal fin in *F. crassispinus* (base length 9.5%, 8.9%–9.4% [8.7%–9.8%] of TL vs. 8.5%, 7.1%–8.8% of TL for *F. megalops*). *Flakeus crassispinus* is distinct from *F. brevirostris* on having more elongate (its anterior margin length 13.2%, 13.1%–13.4% [12.6%–12.9%] of TL vs. 10.3%, 7.9%–12.0% of TL for *F. brevirostris*) and higher first dorsal fin (9.2%, 9.4%–9.8% [9.4%-10.0%] of TL vs. 7.6%, 6.5%–8.6% of TL for *F. brevirostris*). Second dorsal fin is larger in *F. crassispinus* than in *F. brevirostris*: its base length 8.2%, 8.7%–9.0% [8.3%–9.3%] of TL vs. 6.6%, 6.1%–7.9% of TL for *F. brevirostris*; its posterior margin length 5.7%, 5.4%–5.7% [5.8%–6.0%] of TL vs. 4.3%, 2.9%–5.3% of TL for *F. brevirostris*).

Description.

External morphology (Figs. 114–117; Tabs. 25, 31). Body fusiform but markedly robust, arched since the posterior margin of the eye to the pelvic fins origin; body very deep in the trunk and abdomen (trunk height 13.1%, 11.5%–12.3% [10.2%–12.4%] of TL; abdomen height 12.9%, 11.2%–12.4% [11.3%–12.0%] of TL), turning more slender to caudal fin; head height 0.9 (0.9–1.0; 0.9–1.0) times trunk and abdomen heights. Head elongate, its length 21.7%, 21.9%–22.5% [21.7%–22.2%] of TL, flattened and strongly narrow anteriorly (its width at nostrils 6.7%, 6.6%–7.2% [7.1%–7.4%] of TL). Snout rounded (obtuse in paratypes) and clearly short with preorbital length 7.2%, 6.7%–7.1% [7.3%–7.5%] of TL; anterior margin of nostril bilobate, equally near to snout tip and to upper labial furrow (prenarial length 1.0, 0.9 [0.9–1.0] times nostril-labial furrow space); prenarial length half of preoral distance and 1.2 (1.0; 0.9–1.0) times eye length; internarial space 1.0 (0.8–0.9; 0.8–0.9) times eye length. Eyes evidently rounded with convex anterior margin and notched posterior margin; eyes small, its length 1.7 (1.9–2.3; 1.8–2.4) times its height. Prespiracular length 1.6 (1.7–1.8; 1.6–1.7) times preorbital length and 0.5 (0.5–0.6; 0.6) times prepectoral length. Spiracles crescent and small, its length 0.4 (0.3–0.4; 0.3) times eye length, placed laterally just behind the eyes. Gill slits vertical, somewhat concave and low, fifth gill slit 1.4 (1.0–1.2; 1.1–1.2) higher than first gill slit, located anterior to the pectoral fin origin.

Preoral length 1.2 (1.2–1.3; 1.3) times mouth width. Mouth arched and conspicuously broad, its width 7.3% (7.2%–7.9%; 7.4%–7.5%) of TL, corresponding to 1.6 (1.6–1.8; 1.5) times prenarial length and 1.9 (1.9–2.0; 1.8–1.9) times internarial space; upper labial furrow small, its length 1.9% (2.0%–2.2%; 2.0%–2.2%) of TL, with a prominent fold; lower labial furrow inconspicuous with a large aperture anteriorly. Unicuspid teeth, similar in both jaws, flattened labial-lingually, very broad at crown; upper teeth fairly smaller than lower teeth; cusp very short, thick, oblique and clearly rounded at tip; mesial cutting edge convex (strongly convex in lower teeth); rounded both distal and mesial heels; apron short and markedly thick at its base. Two series of functional teeth on upper jaw and three on lower jaw for holotype. Upper teeth 12–11 (12–12), lower teeth 9–9 (10–10).

Pre-first dorsal fin very short, its length 26.4% (25.7%–29.2%; 26.7%–27.4%) of TL, comprising 1.2 (1.2–1.4; 1.2–1.3) times prepectoral length; its origin anterior to pectoral free rear tips. First dorsal fin upright with anterior margin convex, posterior margin straight but concave near the tip, apex somewhat pointed; free rear tips triangular and short, its length 5.5% (5.5%–6.0%; 5.4%–6.0%) of TL; first dorsal fin broad at base, turning slender to the apex, its base length 9.5% (8.9%–9.4%; 8.7%–9.8% of TL; first dorsal fin tall, its height 1.7 (1.6–1.7; 1.6–1.8) times larger than its inner margin length. First dorsal spine conspicuously wide at base, its base length 1.2% (1.1%–1.2%; 1.1%–1.3%) of TL, and elongate, although not reaching the fin apex, its length 4.6% (4.2%–6.0%; 5.9%–6.4%) of TL. Interdorsal space

1.1 (1.1–1.2; 1.0–1.2) times prepectoral length and 2.2 (2.3–2.4; 2.2–2.6) times dorsal-caudal space. Pre-second dorsal length 3.6 (3.5–3.8; 3.8–4.1) times greater than pectoral anterior margin length. Second dorsal fin also broad at base, its length 8.2% (8.7%–9.0%; 8.3%–9.3% of TL, and tall, its height 1.4 (1.5–1.6; 1.5) times its inner margin length; second dorsal fin upright with anterior margin convex, posterior margin slightly falcate; apex rounded and lobulated; free rear tip pointed and short, its length 4.5% (4.4%–4.7%; 4.5%–4.9%) of TL. Second dorsal spine also markedly wide at base, its width 1.3% (1.2%–1.3%; 1.2%–1.4%) of TL, and elongate, although not reaching the fin apex, its length 5.6% (4.3%–5.5%; 4.1%–6.6%) of TL, comprising 0.9 (0.6–0.9; 0.6–1.0) times second dorsal fin height and 1.2 (0.9–1.0; 0.6–1.1) times first dorsal spine length. Thick dorsal spines with approximate length, not reaching the fin apexes.

Pectoral fins somewhat narrow with anterior and inner margins strongly convex, posterior margin concave; inner margin very short, its length 7.8% (8.3%–8.6%; 8.2%–8.6%) of TL; anterior margin length 1.4 (1.2–1.6; 1.5–1.6) times posterior margin length and 2.1 (1.8–2.0; 1.7–1.8) times greater than inner margin length; apex and free rear tips rounded and lobulated with both reaching equally the horizontal line traced between them. Pectoral-pelvic space 0.7 (0.6–0.7; 0.6–0.7) times pelvic-caudal space; pelvic fins placed in the midline between the first and second dorsal origins. Pelvic fins with all margins straight; free rear tips triangular (rounded and lobulated in males); pelvic fin length 10.3% (10.3%–11.7%; 9.6%–12.1%) of TL.

Caudal keel inconspicuous laterally. Caudal fin with both dorsal and ventral lobes markedly narrow; all caudal margins straight (in young juveniles, upper post-ventral margin convex); dorsal caudal margin elongate, its length 1.0 (0.9–1.0; 1.0) times head length and 1.8 (1.8; 1.8) times pre-ventral caudal length; preventral caudal lobe large, its length 2.4 (2.0–2.4; 1.8–2.6) greater than pelvic inner margin length; both dorsal and ventral apex rounded;

caudal fork discontinuous between lobes and narrow, its width 7.3%(6.9%–7.7%; 6.9%–7.2%) of TL.

Dermal denticles. Unicuspid and lanceolate, slightly imbricate, its length somewhat greater than its width; cusp rounded posteriorly; median ridge conspicuously broad and tall with anterior furrow wide and profound; anterior base of median ridge rounded; lateral ridges prominent and tall, although short and symmetrical with profound anterior furrow; denticles markedly broad at the crown base and anteriorly at its median ridge.

Coloration. Body mostly whitish and light grey dorsally. First dorsal fin light grey, whitish at its base; anterior and posterior margins white on its first half; apex lightly dark grey. Second dorsal fin also light grey, slightly darker at the apex and whitish in the fin base; posterior margin broadly white. Dorsal spines grey, whitish posteriorly. Pectoral fins pale but light grey near its base; pectoral posterior margin white but not uniform; pectoral anterior margin fairly grey in young specimens. Pelvic fins also pale, slightly light grey near its base; anterior and posterior pelvic margins white, although not uniform. Caudal fin light grey (mostly white in young specimens), whitish in the vertebral column; dorsal caudal margin slightly grey posteriorly, although not extending to dorsal caudal tip; postventral caudal margins broadly white but not uniform; preventral caudal margin slightly whitish; caudal stripe dark grey.

Vertebral counts (Tab. 32). Monospondylous vertebrae 42 (41); precaudal vertebrae 86 (84–87); caudal vertebrae 26 (26–27); total vertebrae 112 (111–113).

Geographical distribution (Fig. 118). It occurs in Western Australia from North of Cape Lambert to Monte Bello Islands.

Etymology. The epithet "*crassispinus*" means *crassus* (= fat or stout) and *spinus* (= spine) in Latin, regarding to the thick dorsal fin spines as indicated in the original description.

Remarks. *Flakeus crassispinus* is known from very few specimens, collected in Western Australia. It comprises a valid species that is easily separated from its congeners by its very robust dorsal spines. These findings are in congruence with Last *et al*. (2007b), Compagno *et al*., 2005, and Ebert *et al*. (2013a). Other proportional measurements are useful for differentiating them, despite of slight overlapping as it was observed by Last *et al*. (2007b) and in the current results: longer pectoral fins for *F. crassispinus* (its anterior margin length 2.1, 1.8–2.0 times its inner margin length vs. 1.6, 1.2–1.8 times for *F. megalops*). In contrast to these authors, the current study does not support its separation through: first dorsal fin height and length of its inner margin; pre-second dorsal fin length; pectoral anterior margin length; dorsal caudal margin length and pre-ventral caudal margin length; pelvic inner margin length. The current study noticed additional characters for separating these two species: smaller distance from snout to first dorsal fin origin in *F. crassispinus* (26.4%, 25.7%–29.2% of TL vs. 34.5%, 28.7%–31.4% of TL for *F. megalops*); narrower mouth (its width 7.3%, 7.2%–7.9% of TL vs. 9.6%, 7.5%–9.4% of TL for *F. megalops*); shorter upper labial furrow (1.9%, 2.0%–2.2% of TL vs. 2.7%, 2.2%–3.0% of TL for *F. megalops*).

Besides diagnostic features to distinguish *F. crassispinus* and *F. brevirostris,* some morphometric are useful for separation even though slight overlapping may occur. The former species, for instance, shows shorter range values of pre-first dorsal fin length than the Japanese species (its length 26.4%, 25.7%–28.3% [26.7%–27.4%] of TL vs. 29.6%, 28.5%–31.7% of TL for *F. brevirostris*) and more elongate prenarial length (4.6%, 4.3%–4.8% [4.8%] of TL vs. 4.0%, 3.8%–4.4% of TL for *F. brevirostris*). *Flakeus crassispinus* further exhibits larger first dorsal spine (its length 4.6%, 4.2%–6.0% [5.9%–6.4%] of TL vs. 1.6%–4.2% of TL for *F. brevirostris*), smaller inner margin of pectoral fin (its length 4.5%, 4.4%–4.7% [4.5%–4.9%] of TL vs. 5.0%, 4.8%–6.7% of TL for *F. brevirostris*), and broader pectoral fin at base (its length 5.9%, 5.4%–6.0% [5.3%–5.6%] of TL vs. 4.7%, 3.8%–5.3% for *F. brevirostris*).

Morphological variations in *Flakeus crassispinus*. No morphological variations were observed in the Indo-West Pacific species of dogfish. However, some specimens of *Flakeus* from Western Australia exhibit intermediary characteristics from *F. crassispinus*, *F. brevirostris* and *F. megalops*. These specimens are very similar to *F. crassispinus* on body coloration light grey to pale with caudal fin often pale, and on having dorsal fin upright (Fig. 119). They differ from it by having conspicuous black caudal bar in the caudal fork (vs. caudal fin markedly pale, no caudal bar or blotch evident), dorsal spines smaller (its length 2.8%–4.0% of TL) and more slender, its base width 0.5%–0.7% of TL (vs. more elongate and stout in *F. crassispinus*), dorsal fins lower, its height 8.0%–8.9% of TL, and broad at fin web (vs. tall and slender at fin web), and pectoral fins narrower (its anterior margin length 14.1%–14.8% of TL) with markedly concave posterior margin (vs. broad pectoral fin with somewhat concave posterior margin).

Some specimens also show dermal denticles conspicuously slender at the crown, and lateral ridges very short and assymetrical (vs. very broad at the crown with more elongate lateral ridges, often symmetrical), which is similar to those of *F. brevirostris* and *F. megalops*. Specimens of *F. brevirostris* from Kagoshima and Taiwan share many of these characters with these specimens from Western Australia as well. A more accurate morphological investigation is needed between them after the variations within *F. brevirostris* be elucidated in order to establish its correct identification. These features still indicate that these specimens from Western Australia may comprise a possible undescribed species. For now, these specimens are herein identified as a variation of *F. crassispinus*.

Comparative material: Specimens of *F. megalops* and *F. brevirostris* listed previously in this chapter. *Flakeus cf. crassispinus* (14 specimens): AMS I 22807-006, juvenile male, 370 mm TL; juvenile female, 410 mm TL, North of Port Hedland, Western Australia; AMS I 31155-009, two juvenile females, 455, 520 mm TL, off Point Cloates, Western Australia; AMS I 31165-002, juvenile female, 380 mm TL; juvenile male, 405 mm TL, off Shark Bay, Western Australia; CSIRO H 2362-01, juvenile male, 435 mm TL, Northwest of Cape Naturalist, Western Australia, 33°20′S,114°30′E; CSIRO H 2565-02, juvenile male, 319 mm TL, West of Bernier Island, Western Australia, 24°51′S,112°06′E; CSIRO H 6581-19, juvenile male, 318 mm TL, Northwest of Cape Leveque, Western Australia, 14°58′S,121°42′E; CSIRO H 6581-20, juvenile female 320 mm TL, locality same as CSIRO H 6581-19; CSIRO H 6581-21, juvenile male, 319 mm TL, locality same as CSIRO H 6581-19; CSIRO H 6581-22, juvenile male, 343 mm TL, locality same as CSIRO H 6581-19; CSIRO H 6581-23, juvenile female, 345 mm TL, locality same as CSIRO H 6581-19; CSIRO H 6581-24, juvenile female, 328 mm TL, locality same as CSIRO H 6581-19; CSIRO H 6581-25, juvenile female, 286 mm TL, locality same as CSIRO H 6581-19.

Flakeus raoulensis (Duffy & Last, 2007)

(Kermadec spiny dogfish)

Figs. 120–126; Tables 26, 31–32

Squalus raoulensis Duffy & Last, 2007: 31–38 (original description; illustrated; type by original designation; Raoul Island, New Zealand); Ebert *et al*., 2013a: 78, 95 (cited, description; Southwest Pacific Ocean).

Holotype. NMNZ P 41678, adult male, 655 mm TL, off Raoul Island, Kermadec Islands, New Zealand, 29°14′S,177°53′W, 320 meters depth. Collected on 8 November 2004.

Paratypes (2 specimens): NMNZ P 34436, adult female, 725 mm TL, Kermadec Ridge, North of Raoul Island, Kermadec Islands, New Zealand, 28°41′S,177°46′W. Collected on 22 June 1997; NMNZ P 42572, adult male, 678 mm TL, collecting data same as holotype.

Type locality: off Raoul Island, Kermadec Islands, New Zealand.

Non-type material (26 specimens): AIM 655693, adult male, 696 mm TL, Northwest of Cheesman Island, Kermadec Islands, New Zealand; AIM 655697, adult female, 710 mm TL, Northwest of Cheesman Island, Kermadec Islands, New Zealand; AIM 655737, adult female, 775 mm TL, South of Curtis and Cheesman Islands, Kermadec Islands, New Zealand; NMNZ P 50419, adult female, 830 mm TL, Northwest of Cheesman Island, Kermadec Islands, New Zealand, 30°30′S,178°35′W; NMNZ P 50447, adult female, 828 mm TL, same locality as NMNZ P 50419; NMNZ P 52091, adult male, 610 mm TL, Southwest off Denham bay, Kermadec Islands, New Zealand, 29°17′S,178°01′W; NMNZ P 52092, adult male, 628 mm TL, locality same as NMNZ P 52091; NMNZ P 52093, adult male, 590 mm TL, locality same as NMNZ P 52091; NMNZ P 52094, adult male, 640 mm TL, locality same as NMNZ P 52091; NMNZ P 52095, adult male, 618 mm TL, locality same as NMNZ P 52091; NMNZ P 52096, adult male, 625 mm TL, locality same as NMNZ P 52091; NMNZ P 52097, adult male, 603 mm TL, locality same as NMNZ P 52091; NMNZ P 52098, juvenile male, 533 mm TL, locality same as NMNZ P 52091; NMNZ P 52099, adult male, 623 mm TL, locality same as NMNZ P 52091; NMNZ P 52100, adult male, 605 mm TL, locality same as NMNZ P 52091; NMNZ P 52101, adult male, 633 mm TL, West of Smith Bluff, Kermadec Islands, New Zealand, 29°17′S,178°02′W; NMNZ P 52109, juvenile male, 400 mm TL, locality same as NMNZ P 52091; NMNZ P 52110, juvenile female, 392 mm TL, locality same as NMNZ P

52091; NMNZ P 52111, juvenile male, 352 mm TL, locality same as NMNZ P 52091; NMNZ P 52112, juvenile male, 370 mm TL, locality same as NMNZ P 52091; NMNZ P 52113, juvenile male, 365 mm TL, locality same as NMNZ P 52091; NMNZ P 52114, juvenile female, 286 mm TL, locality same as NMNZ P 52091; NMNZ P 52115, adult male, 603 mm TL, locality same as NMNZ P 52091; NMNZ P 52116, juvenile female, 538 mm TL, locality same as NMNZ P 52091; NMNZ P 52117, adult male, 582 mm TL, locality same as NMNZ P 52091; NMNZ P 52118, adult male, 490 mm TL, locality same as NMNZ P 52091; NMNZ P 52119, adult male, 595 mm TL, locality same as NMNZ P 52091; MNZ P 52120, adult male, 592 mm TL, locality same as NMNZ P 52091.

Diagnosis. Small species of dogfish shark from New Zealand distinct from its congeners by body redish grey dorsally. It is also distinguished from its congeners (except *F. acutipinnis*) by having pectoral fins markedly broad, its posterior margin transcending the trunk height, its posterior margin length 1.2 (1.3, 1.0–1.4) times greater than trunk height. It is also distinct from them by (except *F. megalops, F. acutipinnis, F. brevirostris, F. cubensis,* and *F. crassispinus*): snout markedly short, its prenarial length 4.5% (4.4%–4.5%, 4.3%–6.0%) of TL; dermal denticles unicuspid and lanceolate. It differs from *F. megalops, F. acutipinnis, F. brevirostris*, and *F. crassispinus* by having greater number of total vertebrae (114–115 for *F. raoulensis* vs. 100–112 vs. 107–111 vs. 105–113 vs. 111–113). It is further separated from *F. megalops* and *F. acutipinnis* by, respectively, monospondylous (42–44 vs. 39–41) and caudal (85–86 vs. 80–83) vertebrae. *Flakeus raoulensis* still differs from *F. acutipinnis* and *F. crassispinus* by bearing dermal denticles conspicuously slender at crown (vs. very broad).

Description.

External morphology (Figs. 120–124; Tabs. 26, 31). Body slender in all its extension, slightly arched from the posterior margin of the eye to pectoral fin insertion; head height 1.0 (0.9–1.0, 0.9–1.0) times trunk height and 1.1 (0.9–1.0, 0.8–1.0) times abdomen height; widest at head with head width 1.2 (1.1, 1.0–1.3) times trunk width and 1.4 (1.5–1.6, 1.2–1.6) times abdomen width; narrower at nostril with head width 6.8% (6.7%–7.8%, 6.4%–8.1%) of TL. Conspicuously rounded and short snout, its preorbital length 7.3% (7.4%, 7.0%–9.1%) of TL; anterior margin of nostril bilobate, its distance to snout tip 0.9 (0.8, 0.8–1.2) times its distance to upper labial furrow; prenarial length corresponding to half of preoral length; internarial space 0.9 (0.8, 0.6–1.0) times eye length. Eyes oval and large, its length 4.7% (4.7%–5.0%, 4.4%–6.4%) of TL, corresponding to 2.2 (2.2–3.1, 2.1–2.6) times its height; anterior margin convex and notched posterior margin; elongate interorbital space 8.2% (8.2%–8.4%, 7.9%–9.7%) of TL. Pre-spiracular length 1.7 (1.7–1.8, 1.6–1.8) times preorbital length and 0.6 (0.6, 0.5–0.6) times prepectoral length. Half-moon shaped spiracles, very narrow (its length 1.3%, 1.2%–1.4%, 1.1%–1.8% of TL), placed lateral-dorsally behind the eyes. Vertical gill slits, very low with fifth gill slit 1.0 (0.8–1.3, 0.9–1.5) times first gill slit, located just before the pectoral fins; prebranchial length 19.0% (18.9%–19.5%, 18.3%–23.1%) of TL.

Preoral length 1.2 (1.2–1.3, 1.2–1.5) times mouth width. Mouth arched and narrow, its width 1.7 (1.6–1.8, 1.4–1.8) times greater than prenarial length and 1.9 (1.8–2.1, 1.7–2.1) times broader than internarial space; upper labial furrow elongate, its length 2.5% (2.2%–2.5%, 1.7%–3.0%) of TL, and a thin upper fold; lower labial furrow short without a fold. Teeth similar in both jaws, unicuspid, flattened labial-lingually; upper teeth a much smaller than lower teeth; cusp pointed, thick and short, directed obliquely; mesial cutting edge convex; both distal and mesial heels rounded; apron short and thick.Two series of functional rows on each jaw. 14–13 (13–13, 13–13) upper teeth, 11-11 (11–12, 10–10) lower teeth.

First dorsal fin origin just anterior to free rear tips of pectoral fin; pre-first dorsal length 1.3 (1.4, 1.3–2.2) times prepectoral length. First dorsal fin length 1.0 (1.0–1.1, 1.0–1.2) times second dorsal fin length. First dorsal fin low, its height 1.1 (1.0–1.1, 1.1–1.3) times preorbital length and 1.5 (1.2–1.4, 1.4–1.7) times inner margin length; convex anterior margin, posterior margin concave, apex markedly rounded; first dorsal fin wide, more slender at the tip with base length 1.1 (1.0, 0.9–1.2) times preorbital length; free rear tip pointed and short, its length 5.7% (6.1%–6.2%, 5.5%–6.8%) of TL. First dorsal spine thin, somewhat large but never reaching the fin apex, its length 4.9% (3.6%–3.7%, 2.1%–4.3%) of TL, corresponding to 0.6 (0.4–0.5) times first dorsal fin height.

Pre-second dorsal length 2.6 (2.7–2.8, 2.5–2.9) larger than times prepectoral length and 3.8 (3.8–4.0, 3.6–4.0) times greater than length of pectoral anterior margin. Interdorsal space 1.0 (1.0–1.1, 0.9–1.2) times prepectoral length and 2.2 (2.2–2.4, 1.9–2.6) times larger than dorsal-caudal space. Second dorsal fin also low, its height 6.5% (5.6%–6.2%, 5.5%–7.4%) of TL, corresponding to 1.2 (1.0–1.2, 1.4–1.7) times its inner margin length; anterior margin concave, posterior margin falcate, apex markedly rounded and lobate; free rear tip pointed and elongate, its length 5.2% (5.3%–5.5%, 4.4%–6.0%) of TL; second dorsal fin also wide but slender at the tip with its base length 1.1 (1.0, 0.9–1.2) times base length of first dorsal fin. Second dorsal spine slim and elongate, almost reaching the fin apex, its length 0.9 (0.9, 0.5–1.0) times second dorsal fin height, and 1.2 (1.3, 1.2–1.8) times larger than length of second dorsal spine.

Pectoral fins conspicuously wide, transcending the trunk height when adpressed laterally against the body; length of pectoral posterior margin 1.2 (1.3, 1.0–1.4) times trunk height; both anterior and inner margins convex; pectoral anterior margin length 1.6 (1.6–1.7, 1.4–1.8) times greater than inner margin length; concave pectoral posterior margin (slightly straight in the right side); rounded and lobulated apex, reaching the horizontal line traced in the pectoral tip; free rear tips somewhat triangular (left side) or rounded (right side), lobulate.

Pectoral-pelvic space 18.9% (20.1%–21.7%, 17.4%–23.1%) of TL, corresponding to 0.7 (0.8–0.9, 0.6–0.9) times pelvic-caudal space. Pelvic fins narrow with margins convex; strongly triangular and lobe-like free rear tips; pelvic fins small, its length 12.9% (10.8%–12.1%, 10.5%–15.1%) of TL; pelvic fins nearest midline between origin of first and second dorsal fins. In adults, claspers short but exceeding slightly the pelvic free rear tips with clasper inner length 1.1 (1.1, 0.5–1.2) times pelvic inner margin length; clasper groove also short, longitudinal and dorsally located; apopyle and hypopyle very narrow, placed, respectively, anterior to the clasper groove and posteriorly, just before the rhipidion; rhipidion short and thin, blade-like, attached medially to distal end the clasper.

Caudal keels prominent, placed laterally in caudal peduncle from the second dorsal fin insertion to the caudal fin origin. Caudal fin somewhat rectangular with straight dorsal caudal margin; postventral caudal margins strongly convex; preventral caudal margin convex and short, its length 11.5% (11.2%–11.4%, 10.5%–12.8%) of TL, corresponding to 1.9 (1.8–2.1, 1.5–2.3) times larger than length of pelvic inner margin; dorsal caudal margin length equal to head length and 1.9 (1.9, 1.9–2.1) times greater than length of preventral caudal margin; dorsal and ventral tips rounded; caudal fin more slender dorsally than ventrally; discontinuous caudal fork between lobes with its width 7.4% (7.2%–7.6%, 6.9%–8.2%) of TL.

Dermal denticles (Fig. 125). Unicuspid and lanceolate, not imbricate; denticles very narrow at the crown, its length much greater than its width; cusp rounded posteriorly; dermal denticles with median ridge prominent, slender and elongate with anterior furrow; lateral ridges markedly short and longitudinal.

Coloration. Body brownish grey dorsally and white ventrally. Dorsal fins brown, slightly darker at the apex; first dorsal fin brown with posterior margin somewhat white from its midline to the tip; second dorsal fin brown with posterior margin white; dorsal spines also brown, darker anteriorly, and whitish at the tips. Pectoral fins brown, although light brown ventrally; pectoral posterior margin uniformly white. Pelvic fins light brown dorsally and white ventrally with pelvic posterior margin white. Caudal fin brown with post-ventral caudal margins uniformly white, broadly whitish at the apex; dark caudal stripe evident.

Vertebral counts (Tab. 32). 42 (42–44) Monospondylous vertebrae; 85 (85–86) Precaudal vertebrae; 114 (114–115) Total vertebrae.

Geographical distribution (Fig. 126). It occurs in the Kermadec Islands from New Zealand.

Etymology. The name "*raoulensis*" is a latinized word that refers to Raoul Island, type locality if this species.

Remarks. *Flakeus raoulensis* is endemic to the North of Kermadec Islands (off Raoul Island) in New Zealand, according to the current results, which it is in congruence with Duffy & Last (2007a) and Ebert *et al*. (2013a). It comprises the third species of Squalidae occurring in New Zealand waters, together with *S. acanthias* and *F. griffini*. It has a conspicuous distinct body coloration that varies from brownish grey to redish. It is easily distinguish from similar related congeners (e.g. *F. megalops*, *F. brevirostris*, *F. cubensis*, *F. acutipinnis*, *F. crassispinus*) by pectoral free rear tips rounded (vs. pointed, including some specimens of *F. megalops*). The New Zealand species is also distinguished from *F. cubensis* by lacking black blotches on apex of dorsal fins, and from *F. crassispinus* by having postventral caudal margins uniformly white (vs. markedly pale and broad in *F. crassispinus*). *Flakeus raoulensis*, *F. megalops* and *F. acutipinnis* are very similar in general morphology, including color pattern of dorsal fins, caudal fins and pectoral fins that are uniformly white at posterior margins.

External measurements greatly overlap between the Kermadec species and *F. megalops*, which it is in disagreement with Duffy & Last (2007a). These authors stated that proportional ratio of preoral length and internarial width is useful for separating them, in contrast to the current results (2.2–2.8 for *F. raoulensis* vs. 2.0–2.7 times for *F. megalops* from Southern Australia). *Flakeus brevirostris*, *F. acutipinnis* and *F. crassispinus* have similar ratio (2.1–2.6 vs. 2.1–2.4 vs. 2.3–2.4 times, respectively) as well. Despite of some overlapping, *Flakeus raoulensis* differs from the Japanese species by having greater prespiracular length (12.4%, 12.4%–13.1% [12.0%–15.3%] of TL vs. 12.1%, 11.3%–12.9% of TL for *F. brevirostris*), greater preorbital length (7.3%, 7.4% [7.0%–9.1%] of TL vs. 6.7%, 6.5%–7.5% for *F. brevirostris*), larger prenarial length 4.5%, 4.4%–4.5% [4.3%–6.0%] of TL vs. 4.0%, 3.8%–4.4% for *F. brevirostris*), wider internarial space (4.2%, 3.9%–4.0% [3.8%–5.1%] of TL vs. 3.6%, 3.4%–4.7% of TL for *F. brevirostris*). It also distinct from *F. brevirostris* by having larger pectoral fins (its anterior margin length 15.6%, 15.0%–16.4% [14.6%–18.7%] of TL vs. 14.7%, 12.0%–15.7% of TL for *F. brevirostris*), and larger caudal fin (its dorsal caudal margin length 21.9%, 21.3%–21.4% [21.2%–25.7%] of TL vs. 20.5%, 19.2%–21.5% of TL for *F. brevirostris*). These findins are not in agreement with Duffy & Last (2007a).

Flakeus raoulensis and *F. acutipinnis* are the only species of dogfish whose pectoral fin transcends the trunk height when adpressed laterally on body. Duffy & Last (2007a) did not notice this particular shape of pectoral fin in *Flakeus raoulensis*. A third species of dogfish shark also shows pectoral fins similar to them, and it will be described and compared with these species later in this Chapter. These two species are distinct by larger prespiracular length (12.4%, 12.4%–13.1% [12.0%–15.3%] of TL vs. 11.6%, 11.2% [7.7%–12.1%] of TL for *F. acutipinnis*), larger preorbital length (7.3%, 7.4% [7.0%–9.1%] of TL vs. 6.3%, 7.1% [6.5%–7.1%] of TL for *F. acutipinnis*), more elongate prenarial length (4.5%, 4.4%–4.5% [4.3%–6.0%] of TL vs. 4.0%, 4.4% [3.9%–4.4%] of TL for *F. acutipinnis*), more elongate preoral length (9.6%, 9.4%–9.8% [9.1%-11.8%] of TL vs. 8.9%, 8.4% [8.4%–9.2%] of TL for *F. acutipinnis*), larger distance from nostrils to upper labial furrow (5.1%, 5.3% [4.8%–6.4%] of TL vs. 4.7%, 3.7% [4.3%–4.9%] of TL for *F. acutipinnis*). The Kermadec species is further separated from *F. acutipinnis* by larger length of anterior margin of first dorsal fin (11.5%, 11.0% [11.4%–13.4%] of TL vs. 11.1%, 9.9% [11.1%–11.8%] of TL for *F. acutipinnis*), and shorter second dorsal fin (its base length 8.5%, 7.3%–7.8% [6.8%–10.3%] of TL vs. 6.5%, 6.0% [5.7%–7.8%] of TL for *F. acutipinnis*).

Comparative material: Specimens of *F. megalops*, *F. cubensis*, *F. acutipinnis*, *F. brevirostris* and *F. crassispinus* listed in this Chapter.

Flakeus bucephalus **(Last, Sèret & Pogonoski, 2007)**

(**Bighead spurdog; Aiguillat à grosse tête** in French)

Figs. 127–132; Tables 27, 31–32

Squalus bucephalus Last, Sèret & Pogonoski, 2007: 23–29 (original description; illustrated; New Caledonia); Ebert *et al*., 2013: 78, 86 (cited, description; Southwest Pacific Ocean).

Holotype. MNHN 2006-1754, juvenile male, 550 mm TL, Norfolk Ridge, south of New Caledonia, 23°43′S,168°16′E, 405–411 meters depth. Collected on 28 November 1993.

Paratypes (3 specimens): MNHN 1997-3641, juvenile female, 430 mm TL, Stylaster Seamount, Norfolk Ridge, New Caledonia, 23°37′S, 167°42′E, 420–470 meters depth;

NMNZ P 34030, two adult males, 787–802 mm TL, Stylaster Seamount, Norfolk Ridge, New Caledonia, 23°35′S,167°42′E, 448–880 meters depth.

Type locality: Norfolk Ridge, off South New Caledonia.

Diagnosis. Species of *Flakeus* endemic to New Caledonia that it is distinguished from its congeners by: head conspicuously humped dorsal-posteriorly and wide, its width at mouth 13.5% (12.9%–13.4%) of TL; anterior margin of nostrils conspicuously bilobate and broad; mouth straight and broad, its width 8.7% (8.1%–8.4%) of TL; caudal fin very slender on upper and lower lobes, and elongate, its dorsal caudal margin 24.2% (22.4%–23.4%) of TL. *Flakeus bucephalus* is further distinguished by having smaller distance from pelvic fin to caudal fin (24.9%, 23.5%–24.7% of TL) and greater number of monospondylous (49), diplospondylous (75), precaudal (93), and total (124) vertebrae.

It is clearly distinct from *F. brevirostris* and *F. cubensis* by taller first dorsal fin, its height 9.8% (9.3%–9.7% of TL vs. 6.3%–8.4% of TL in adults of *F. cubensis* vs. 7.3%–8.2% of TL in adults of *F. brevirostris*), and more elongate first dorsal fin, its anterior margin length 12.3% (12.3%–13.8% of TL vs. 9.1%–11.5% of TL in adults of *F. cubensis* vs. 7.9%–12.0% of TL in adults of *F. brevirostris*). *Flakeus bucephalus* is differentiated from *F. megalops* by having smaller pre-first dorsal length (27.5%, 28.4%–28.7% of TL vs. 29.4%–31.4% of TL in adults of *F. megalops*), and smaller pectoral fins, its inner margin length 9.1%, 8.2%–8.8% of TL (vs. 9.4%–10.9% of TL in adults of *F. megalops*).

Description.

External morphology (Figs. 127–131; Tabs. 27, 31). Body fusiform and slender, conspicuously arched dorsally since the posterior margin of the eye to the first dorsal fin origin; head height 1.0 (0.9–1.0) times trunk height, and 1.0 (1.0–1.1) times abdomen height.

Head flattened anteriorly and humped posteriorly, strongly rounded dorsal-ventrally; head markedly broad in all its extension with head width 1.2 (1.1–1.2) times trunk width and 1.5 (1.3–1.6) times abdomen width; head width at nostrils 8.2% (7.6%–8.4%) of TL, and at mouth 13.5% (12.9%–13.4%) of TL. Snout conspicuously rounded at tip and short with preorbital length 8.1% (7.5%–7.9%) of TL; nostrils with anterior margin strongly broad and bilobate with lobes very prominent, its distance to the snout tip 1.1 (1.0–1.1) times its distance to the upper labial furrow, and 0.5 (0.5–0.6) times preoral distance. Eyes oval with anterior margin concave and posterior margin notched; eyes very elongate, its length 2.7 (2.2–2.9) times its height. Prespiracular length 0.6 (0.6) times prepectoral length and 1.6 (1.7–1.8) times preorbital length. Spiracles crescent, strongly constricted, placed laterally behind the eyes, its length 0.3 (0.2–0.3) times eye length. Prebranchial length 1.4 (1.4–1.5) times prespiracular length. Vertical gill slits in front of pectoral fin origin with fifth gill slit equal in length with first gill slit (2.3%, 2.1%–2.2% vs. 2.1%, 2.0%–2.2% of TL, respectively).

Preoral length 1.1 (1.1–1.3) times mouth width. Mouth straight and wide, its width 2.0 (1.6–1.7) times wider than internarial space and 1.7 (1.6) times greater than prenarial distance; upper labial furrow with fat fold, elongate with its length 2.4% (2.3%–2.6%) of TL; lower labial furrow much larger than upper one and directed laterally, although without a fold. Unicuspid teeth, similar in both jaws, flattened labial-lingually, broad at crown; upper teeth slightly smaller than lower teeth; cusp short and slim, directed obliquely; mesial cutting edge convex; rounded distal heel; pointed mesial heel; apron short and thick. Two series of functional teeth on upper and lower jaws for type specimens (a single paratype shows three series on upper jaw). Upper teeth 13–13 (13–14) rows, and lower jaw 11–11 (11–11) rows.

Pre-first dorsal length 1.3 (1.3) times prepectoral length. First dorsal fin upright and strongly slender from the half of its height to the tip; pectoral anterior margin convex, and posterior margin straight, although concave near free rear tip; free rear tip markedly slender and pointed; first dorsal fin large and tall, its length 1.4 (1.5–1.6) times larger than its height and 1.2 (1.2–1.3) times second dorsal fin length; first dorsal fin height 1.6 (1.7) times inner margin length and 1.2 (1.2) times preorbital length. First dorsal spine thin and small (its length 2.5%, 2.7%–3.8% of TL), never reaching half of fin height. Interdorsal space 2.4 (2.3–2.6) times larger than dorsal-caudal space. Pre-second dorsal length 2.8 (2.7–2.8) times greater than prepectoral length and 3.6 (3.8–4.0) times anterior margin length of pectoral fin. Second dorsal fin upright and slender at apex, lobe-like with anterior margin convex, posterior margin not falcate, although evidently concave; free rear tip slender and pointed; second dorsal fin also elongate and tall, its length 2.0 (1.8–2.1) times its height and its height 1.2 (1.2–1.4) times inner margin length. Second dorsal spine somewhat convex and wider (second spine base width 1.0, 0.9–1.4 times first spine base width), and larger than first one, although not reaching the fin apex; second spine length 1.3 (1.3) times first spine length and 0.7 (0.7) times second dorsal fin height.

Pectoral-pelvic space 0.8 (0.8–0.9) times pelvic-caudal space. Pectoral fins narrow anteriorly and wider posteriorly; anterior and inner margins somewhat convex (strongly convex in paratypes); inner margin length very small (its length 9.1%, 8.2%–8.8% of TL); anterior margin length 1.8 (1.8–1.9) much larger than inner margin length; posterior margin almost straight (strongly concave in large male paratype), often not exceeding the trunk height when adpressed laterally against the body (except on small male paratype), its length 1.1 (1.0–1.2) times trunk height; apex and free rear tips of pectoral fins rounded and slightly lobe-like, its apex transcending the free rear tip when a horizontal line is traced between them.

Prepelvic length 2.9 (2.8–2.9) times larger than distance between origins of first and second dorsal fins; pelvic fins in the midline between two dorsal fins. Pelvic fins somewhat broad with straight margins (slightly convex in adult males); pelvic apex rounded; pelvic free rear tips rounded and lobe-like; pelvic fin length 10.9% (9.8%–12.3%) of TL. Adult males with claspers stout, flattened ventrally, its tips reaching slightly beyond the pelvic fin free rear tips; clasper inner margin length 1.1–1.2 times pelvic inner margin length; clasper groove short, longitudinal and dorsal; apopyle with broad aperture, placed anteriorly in the clasper groove; hypopyle also with large aperture, located more distally and anterior to the rhipidion; rhipidion leaf-like (not free), elongate and very broad, located in the dorsal-posterior end of the clasper.

Caudal keel very discreet, placed posterior to the second dorsal fin insertion to the caudal fin origin. Caudal fin conspicuously tapered in both dorsal and ventral lobes; dorsal caudal margin straight and elongate, its length 1.1 (1.0) head length and 2.0 (1.9–2.0) times larger than preventral caudal margin length; dorsal and ventral caudal tips rounded; upper post-ventral margin also straight; lower post-ventral margin convex; preventral caudal margin rather convex and elongate, its length twice inner margin length of pelvic fin; caudal fork between lobes discontinuous and narrow, its width 7.4% (6.7%–7.3%) of TL.

Dermal denticles (description based on picture provided by Last *et al.*, 2007b). Unicuspid and lanceolate, somewhat imbricate, its length greater than its width; denticles very narrow at crown with cusp posteriorly and rounded, directed in obtuse angle with longitudinal axis of body; median ridge prominent and elongate with anterior furrow; anterior margin of median ridge convex and slightly broad; lateral ridges small and conspicuous, smaller than median ridge.

Coloration. Body dark grey dorsally and white lateral-ventrally. First and second dorsal fins dark grey, blackish at the apex; slightly white in the fin base and in the half end of the posterior margin (in paratypes, posterior margins somewhat white since the apex). Pectoral fins also dark grey dorsal and ventrally with uniform white posterior margin. Pelvic fins grey, lighter ventrally, with all margins whitish. Caudal fin also dark grey, whitish over vertebral column; postventral caudal margins uniformly white; dorsal caudal tip white; ventral caudal tip broadly white; ventral caudal lobe conspicuously white, except under vertebral column.

Vertebral counts (Tab. 32). 49 for holotype monospondylous vertebrae; 93 precaudal vertebrae; 31 caudal vertebrae; 124 total vertebrae.

Geographical distribution (Fig. 132). It is endemic to Norfolk Ridge in New Caledonia.

Etymology. The name "*bucephalus*" means *bu* (= large in Latin) and *kephalis* (= head in Greek) in relation to its huge head, according to the original description.

Remarks. The species is endemic to New Caledonia together with *F. melanurus,* which it is in agreement with Last *et al*. (2007b). *Flakeus bucephalus* exhibit very unique shape and width of the head that easily separated it from its congeners as it is shown on the diagnosis of the present study and noticed previously by Last *et al*. (2007b). It is clearly distinct from *F. melanurus* by having lower caudal lobe mostly white (vs. black), and head much broader (vs. narrow head) and smaller snout (vs. snout conspicuously elongate) than *F. melanurus*.

In contrast to Last *et al*. (2007b), the current study notices that the holotype of this species shows greater number of vertebrae than it was reported before, which it is very valuable for separating species morphologically similar to it (e.g. *F. megalops*, *F. acutipinnis*, *F. brevirostris*, *F. crassispinus*, *F. raoulensis*). *Flakeus bucephalus* is further distinct from *F. acutipinnis* and *F. raoulensis* by having pectoral fin not transcending the trunk height when adpressed on body (posterior margin length 1.1, 1.0–1.2 times trunk height vs. 1.6, 1.6–1.7 [1.4–1.8] for *F. raoulensis* vs. 1.1, 1.1 [1.0–1.4] for *F. acutipinnis*). It is clearly distinct from *F. brevirostris, F. cubensis* and *F. crassispinus* by having free rear tips of pectoral fins rounded (vs. pointed). It is also differentiated from *F. crassispinus, F. acutipinnis* and some specimens of *F. brevirostris* by having dermal denticles much more slender at crown (vs. broad).

New Caledonian species has dorsal fins upright at slender at apex, and caudal fin with ventral caudal tip broadly white that assemblage those of *F. crassispinus*. It differs from the Australian species on having lower second dorsal fin (its height 6.1%, 5.5%–6.6% of TL vs. 6.5%, 6.4%–7.3% [6.7%–7.1%] of TL for *F. crassispinus*), and narrower dorsal spines (first dorsal spine base length 0.8%, 0.7%–0.8% of TL vs. 1.2%, 1.1%–1.2% [1.1%–1.3%] of TL; second dorsal spine base length 0.8%, 0.7%–1.0% of TL vs. 1.3%, 1.2%–1.3% [1.2%–1.4%] of TL for *F. crassispinus*).

Besides differences provided in the diagnosis, *F. bucephalus* is somewhat separated from *F. cubensis* and *F. brevirostris* by having smaller precaudal length (75.3%, 76.7%–77.8% of TL vs. 77.5%–80.8% of TL in adults of *F. cubensis* vs. 78.9%–81.3% of TL in adults of *F. brevirostris*). Like it is observed the latter two species, *F. megalops* also has more elongate pre-first dorsal length (29.4%–31.4% of TL) than *F. bucephalus*. The latter species can also be separated from *F. cubensis, F. brevirostris* and *F. megalops* by more elongate snout, its prenarial length 5.0%, 5.1%–5.2% of TL (vs. 4.3%–5.0% of TL in adults of *F. cubensis* vs. 3.8%–4.3% of TL in adults of *F. brevirostris* vs. 3.9%–4.9% of TL in adults of *F. megalops*), and broader internarial space, its width 4.4%, 4.8%–5.0% of TL (vs. 3.9%–4.5% of TL in adults of *F. cubensis* vs. 3.4%–3.8% of TL in adults of *F. brevirostris* vs. 3.6%–4.6% of TL in adults of *F. megalops*).

Flakeus bucephalus is known only from its type material as it was noticed previously by Last *et al*. (2007b). Morphological variations on this species are not unknown yet, which urgently requires additional material for checking this information. Last *et al*. (2007b) stated that *F. bucephalus* has unicuspid and multicuspid dermal denticles, although the present analysis of the illustration provided in the original description does not support this variation.

Comparative material: All specimens listed in this Chapter for *F. megalops*, *F. acutipinnis*, *F. brevirostris*, *F. cubensis*, *F. raoulensis*, and *F. crassispinus*.

Flakeus albifrons (Last, White & Stevens, 2007)

(**Eastern highfin spurdog; Taiwanese highfin; Hiretaka-tsunozame** in Japanese)

Figs. 133–138; Tables 28–29, 31–32

Squalus blainvillei not Risso: Chen *et al*., 1979: 26–42 (description; off Kyushu, Shishoku and Nagasaki, Japan).
Squalus sp. Muñoz-Chápuli & Ramos, 1989: 19 (cited; Japan).
Squalus sp. B Last & Stevens, 1994: 49, 93 (cited, description; Southwest Pacific Ocean); Compagno & Niem, 1998: 1231 (cited; Southwest Pacific Ocean); Compagno *et al*., 2005.
Squalus sp. C Last & Stevens, 1994 (in part): 49, 94 (descrption; Southwest Pacific Ocean); Compagno *et al*., 2005; White, Last & Stevens, 2007: 43.
Squalus sp. 1 Nakabo, 2002: 156 (listed; Japan); Nakabo, 2013: 195 (listed; Japan).
Squalus albifrons Last, White & Stevens, 2007: 39–53 (original description; illustrated; Australia); Ebert *et al*., 2013: 74, 84 (cited, description; Southwest Pacific Ocean).
Squalus altipinnis White, Last & Stevens, 2007: 39–53 (original description; illustrated; Australia); Ebert *et al*., 2013: 74, 84 (cited, description; Southwest Pacific Ocean). New junior synonym.
Squalus formosus White & Iglésias, 2011: 1–15 (original description, illustrated; type by original designation; Northeastern Taiwan); Naylor *et al*., 2012a: 58 (cited; Taiwan); Ebert *et al*., 2013b: 285–286 (listed; Taiwan, Japan); Straube *et al*., 2013: 264 (cited, listed; Taiwan). New junior synonym.

Holotype. CSIRO H 4627-01, adult male, 615 mm TL, East of Broken Bay, New South Wales, Australia, 33°28′S,152°05′E, 386 meters depth. Collected on 18 June 1996.

Paratypes (11 specimens): CSIRO H 449, adult male, 642 mm TL, Northeast of Townsville, Queensland, Australia, 17°57′S,147°03′E; CSIRO H 644-04, adult male, 640 mm TL, South of Saumarez Reef, Queensland, Australia, 22°49′S,154°10′E; CSIRO H 2487-01, adult female, 636 mm TL, Southeast of Ballina, New South Wales, Australia, 29°03′S,153°49′E; CSIRO H 2487-02, adult female, 660 mm TL, locality same as CSIRO H 2487-01; CSIRO H 2487-03, adult female, 680 mm TL, locality same as CSIRO H 2487-01; CSIRO H 2691-01, adult male, 691 mm TL, Northeast of Byron Bay, New South Wales, Australia, 28°30′S,153°51′E; CSIRO H 3589-01, adult female, 844 mm TL, East of Newcastle, New South Wales, Australia, 32°59′S,152°14′E; CSIRO H 4704-02, adult female, 610 mm TL, East of Sydney, New South Wales, Australia, 33°37′S,151°55′E; CSIRO H 4705-01, adult female, 592 mm TL, East of Sydney, New South Wales, Australia, 33°28′S,152°00′E; QM I 38077, adult male, 608 mm TL; QM I 19327, adult male, 610 mm TL, South East Queensland, Australia, 26°20′S,153°53′E.

Type locality: East of Broken Bay, New South Wales, Australia.

Non-type material (12 specimens): AMS I 15543-001, juvenile female, 198 mm TL, New South Wales, Australia; AMS I 37736-001, adult female, 720 mm TL, New South Wales, Australia; AMS I 44907-007, two adult males, 655–700 mm TL, New South Wales, Australia; CSIRO H 6006-13, adult female, 850 mm TL, Norfolk Ridge, Tasman Sea, 29°42′S,168°02′E; CSIRO H 7226-01, juvenile female, 220 mm TL, Britannia Seamount, Queensland, Australia, 27°55′S,155°32′E; CSIRO H 7226-02, juvenile female, 225 mm TL, two juvenile males, 220 mm TL each, locality same as CSIRO H 7226-01; MZUSP uncatalogued (previously CSIRO), adult male, 760 mm TL, East of Ballina, New South Wales, Australia, 28°55′S,153°53′E; NMMB P 10902, juvenile male, 464 mm TL, Pingtung, Taiwan; NMMB P 15487, juvenile male, 440 mm TL, locality same as NMMB P 10902.

Diagnosis. A species of dogfish shark that is distinguished from its congeners by eyebrown whitish dorsally and dermal denticles with secondary cusplets. *Flakeus albifrons* is also differentiated from them (except *F. crassispinus*) by: first dorsal fin conspicuously upright and tall (its height 9.6%, 8.2%–9.4% of TL); first dorsal spine stout, its base length 1.0% (0.9%–1.2%) of TL. It is also distinguished from its congeners (except *F. megalops, F. acutipinnis, F. cubensis, F. brevirostris, F. crassispinus, F. raoulensis*) on having short snout, its prenarial length 4.5% (4.5%–4.7%) of TL, and dermal denticles unicuspid and lanceolate. It is distinguished from *F. cubensis, F. brevirostris, F. crassispinus* on having pectoral fins with its free rear tips rounded. It is further distinct from its congeners (except *F. raoulensis* and *F. bucephalus*) by having more monospondylous (43–47), diplospondylous (72–77), precaudal (90–93), and total (115–124) vertebrae.

Description.

External morphology (Figs. 133–136; Tabs. 28, 31). Body fusiform and slender, arched dorsally from posterior margin of the eye to insertion of first dorsal fin; its greatest width at head, corresponding to 1.2 (1.0–1.4, 1.1–1.3) times trunk width and 1.6 (1.2–1.7, 1.3–1.9) times abdomen width; body equally deep from head to abdomen with head height 1.0 (0.9–1.0, 0.9–1.0) times trunk and abdomen heights. Head flattened anteriorly, elongate, its length 21.8% (21.1%–23.8%, 21.3%–26.1%) of TL; head broader at mouth than at nostrils (12.0%, 11.5%–12.9%, 11.4%–13.0% of TL vs. 7.0%, 7.1%–7.9%, 6.9%–8.9% of TL, respectively). Snout conspicuously rounded and short, its preorbital length 6.7% (6.8%–7.2%, 6.6%–10.0%) of TL; anterior margin of nostrils bilobate with its distance to snout tip 1.0 (1.0–1.1, 0.7–1.3) times its distance to upper labial furrow; prenarial distance 0.5 (0.5–0.6, 0.4–0.6) times preoral length; short internarial space 4.1% (4.3%–4.6%, 4.4%–5.5%) of TL. Eyes lateral and oval with anterior margin convex and posterior margin notched; eyes small with its length 2.8 (2.4–3.0, 1.8–2.8) times greater than its height. Prespiracular length 0.6 (0.6, 0.6) times prepectoral length and 1.7 (1.7–1.8, 1.6–1.8) times larger than preorbital length.

Spiracles crescent and narrow, its length 1.4% (1.2%–1.6%, 1.4%–2.1%) of TL, placed laterally and posterior to the eyes. Pre-branchial length 1.5 (1.5–1.6, 1.4–1.6) times greater than prespiracular length. Gill slits vertical and low with fifth gill slit 1.2 (1.0–1.4, 1.1–1.3) times higher than first gill slit, located anterior to pectoral fins.

Preoral length 1.1 (1.0–1.2, 1.0–1.7) times mouth width. Mouth almost straight, very broad, its width 1.8 (1.6–1.8, 1.1–2.1) times greater than prenarial length and 2.0 (1.7–1.9, 1.4–2.1) times internarial space; upper labial furrow short with prominent fold, its length 2.4% (2.2%–2.5%, 2.1%–2.7%) of TL; lower labial furrow also short, without a fold. Unicuspid teeth, similar in both jaws, compressed labial-lingually, wide at crown; upper teeth moderately smaller than lower teeth; cusp short, thick and oblique; mesial cutting edge straight; strongly rounded distal heel; rounded mesial heel in lower jaw and pointed in upper jaw; apron elongate and thin. Three series of functional teeth on upper jaw and two series on lower jaw for holotype. Upper teeth rows 12–12 (12–12, 13–13), lower teeth rows 10–9 (10–10, 10–11).

First dorsal fin origin in front of pectoral fin free rear tips with pre-first dorsal length very short (26.7%, 26.2%–29.5%, 27.0%–31.5% of TL), corresponding to 1.3 (1.2–1.5, 1.2–1.4) times greater than prepectoral length. First dorsal fin conspicuously upright, slender and lobe-like at apex; first dorsal fin markedly high, its height 1.4 (1.2–1.3, 0.9–1.4) times greater than preorbital length and 1.6 (1.4–1.5, 1.4–1.6) times larger than its inner margin length; first dorsal anterior margin convex; posterior margin concave and very large, its length 10.8% (10.3%–11.0%, 6.7%–12.0%) of TL; free rear tip pointed and elongate, its length 6.0% (5.9%–6.6%, 5.3%–6.9%) of TL; rounded at apex; first dorsal fin 1.2 (1.2–1.3, 1.0–2.5) times greater in length than second dorsal fin. First dorsal spine robust (base width 1.0%, 0.9%–1.2%, 0.5%–1.4% of TL), elongate but not reaching the fin apex, its length 0.5 (0.5–0.6, 0.2–0.7) times first dorsal fin height. Interdorsal space 1.2 (1.2–1.5, 0.8–1.3) times larger than prepectoral length and 2.6 (2.4–2.8, 1.9–2.8) times larger than dorsal-caudal space. Pre-second dorsal length 2.9 (2.8–3.1, 2.3–3.0) times greater than prepectoral length. Second dorsal fin upright, lobe-like and thin at the apex, markedly tall, its height 1.2 (1.1–1.5, 1.2–1.5) times its inner margin length; secon dorsal anterior margin convex and posterior margin strongly falcate; apex rounded and lobe-like; free rear tip angular and short, its length 5.1% (4.0%–5.3%, 3.7%–6.0%) of TL. Second dorsal spine slim (its base length 0.8%, 0.7%–0.9%, 0.7%–1.0% of TL) and convex, large but not reaching the fin apex, its length 0.8 (0.7–0.9, 0.6–1.1) times second dorsal fin height and 1.1 (1.0–1.2, 0.7–2.3) times more elongate than first dorsal spine.

Pectoral fins somewhat narrow with anterior margin convex and inner margin almost straight, and posterior margin concave, its length 1.0 (0.9–1.0, 0.8–1.1) times trunk height; both pectoral apex and free rear tips rounded, moderately lobe-like, reaching the same level of horizontal line traced between them; pectoral anterior margin small, its length 15.9% (15.0%–15.9%, 12.6%–16.1%) of TL, corresponding to 1.9 (1.7–2.1, 1.3–2.1) times greater than inner margin length. Pectoral-pelvic space 0.7 (0.7–0.8, 0.7–0.9) times than pelvic-caudal space. Pelvic fins narrow with its margins straight; pelvic free rear tips rounded and lobe-like; pelvic fin length 11.3% (10.8%–10.9%, 9.7%–10.9%) of TL. Claspers in adults with clasper groove dorsal, longitudinal and short; apopyple and hypopyle with constricted apertures; rhipidion blade-like, small and attached medially to the distal end of the clasper; clasper small with it inner length 1.2 (1.1–1.2, 0.5–1.3) times pelvic inner margin length.

Caudal keel modest, placed laterally from behind insertion of second dorsal fin to behind origin of caudal fin. Caudal fin elongate and narrow dorsally, its dorsal caudal margin length 1.1 (0.9–1.1, 0.9–1.0) times head length; dorsal caudal margin and upper postventral margin straight; lower postventral and preventral caudal margins convex; preventral caudal margin 2.0 (1.9–2.5, 1.8–2.7) greater in length than pelvic inner margin; both dorsal and ventral caudal tips rather pointed; caudal fork between lobes discontinuous, strongly narrow, its width 6.6% (6.7%–7.2%, 6.1%–8.2%) of TL.

Dermal denticles (Fig. 136). Unicuspid, lanceolate and slightly imbricate, its length greater than its width; denticles somewhat broad at crown; median ridge elongate and thick with anterior furrow profound and rounded; median anterior margin of denticle very broad and convex; lateral ridges symmetrical, thick and prominent, shorter than median ridge, with anterior furrow conspicuous and profound; small secondary cusps rarely present posteriorly at each lateral ridge.

Coloration. Body grey dorsally, light grey laterally and white ventrally. Eyebrow markedly whitish at the dorsal margin of the eyes (less eveident in juveniles). Both dorsal fins grey, including posterior margin, whitish on its base, and blackish at the apex; free rear tips fairly whitish at the tip only. Dorsal spines greyish anteriorly and white lateral-posteriorly as well as at the tip. Pectoral fins grey dorsal and ventrally with posterior margin fairly white. Pelvic fins also grey, light grey ventrally with margins slightly white. Caudal fin grey with postventral caudal margins white and uniform; dorsal and ventral caudal tips broadly white; black caudal stripe evident.

Vertebral counts (Tab. 32). Monospondylous 46 (43–47); diplospondylous 75 (72–77); precaudal 92 (90–93); total 121 (115–124) vertebrae.

Geographical distribution (Fig. 137). It occurs in the South Pacific Ocean from Taiwan to Australia, where it is founded from Western Australia to Queensland.

Etymology. The name "*albifrons*" is a combination of two words in Latin *albi* (=white) and *frons* (=brow) in allusion to the whitish eyebrow of this species.

Remarks. The occurance of *Flakeus albifrons* in Western Australia and Tasmania is reported herein, and support that this species is sympatric with *F. megalops* and *F. crassispinus*, which it is in disagreement with Last *et al*. (2007c). *Flakeus albifrons* bears very unique characteristics such as whitish eyebrow and first dorsal spine very robust, which it is in agreement with Last *et al*. (2007c). According to these authors, this species together with other nominal species *S. altipinnis* and *F. notocaudatus* are separated from its congeners on having first dorsal fin very tall and upright. The current results, however, notice that other species also shows similar characteristics such as *F. crassispinus*. Last *et al*. (2007c) also stated that the dermal denticles of *F. albifrons* are strong to weakly tricuspidate based on analysis of two male paratypes. In contrast, the present study shows that this species has dermal denticles unicuspid and lanceolate with rarely secondary cusplets posteriorly on each lateral ridge. These findings are based on new material and analysis of its type specimens, and suggest that these authors equivocately swapped some skin samples from other species when describing it.

Squalus altipinnis (Fig. 138) was described as separated from *F. albifrons* regarding differences on length of caudal and pectoral fins, and vertebral counts. Its diagnosis is very similar to those of *F. albifrons* and with exception of few external measurements (e.g. prevent length and length of pectoral anterior margin; pre-second dorsal length and length of dorsal caudal margin, head length and mouth width, and prevent length and dorsal caudal margin length) all other diagnostic characters are overlapped between them. In fact, differences on morphometrics are shown between type material of *S. altipinnis* and those of *F. albifrons*, as noticed by Last *et al*. (2007c). However, their ranges are almost continuous and these differences are not shown when compared with non-type material of *F. albifrons*, indicating that the disparity of measurements reported by these authors is probably due to preservation.

Squalus altipinnis is known uniquely from two specimens from Western Australia that are very old and shrinked, and no other material was found for this species yet. It exhibits similar external morphology to those of *F. albifrons* related to shape of dorsal, pectoral and caudal fins, dermal denticles, dentition and color pattern, which suggest co-specificity between them. In contrast to Last *et al*. (2007c), vertebral counts also overlaps between these species, which give additional support to consider *S. altipinnis* as junior synonym of *Flakeus albifrons*. Recently, J. Pogonoski (*pers. comm*., 2012) stated that new unpublished molecular data may support this hypothesis as well.

Flakeus albifrons is distinguished from *F. crassispinus* by more elongate upper labial furrow (its length 2.4%, 2.2%–2.5%, 2.1%–2.7% of TL vs. 1.9%, 2.0%–2.2% of TL, 2.0%–2.2% of TL for *F. crassispinus*), smaller first dorsal fin (its base length 8.3%, 8.5%–8.9%, 6.8%–8.9% of TL vs. 9.5%, 8.9%–9.4%, 8.7%–9.8% of TL for *F. crassispinus*), broader head (its width at nostrils 7.0%, 7.1%–7.9%, 6.9%–8.9% of TL vs. 6.7%, 6.6%–7.2%, 7.1%–7.4% of TL for *F. crassispinus*; its width at mouth 12.0%, 11.5%–12.9%, 11.4%–13.0% of TL vs. 10.8%, 10.9%–11.6%, 11.2%–11.6% of TL for *F. crassispinus*).

It is distinct from *F. crassispinus* and *F. raoulensis* by: broader internarial space (its width 4.1%, 4.3%–4.6%, 4.4%–5.5% of TL vs. 3.9%, 3.8%–4.0%, 3.9%–4.3% of TL for *F. crassispinus* vs. 4.2%, 3.9%–4.0%, 3.8%–5.1% of TL for *F. raoulensis*), smaller space between pelvic and caudal fins (its length 26.7%, 25.4%–27.3%, 22.0%–26.7% of TL vs. 27.4%, 27.4%–28.7%, 27.2%–28.1% of TL for *F. crassispinus* vs. 26.9%, 24.1%–26.5%, 23.1%–33.9% of TL for *F. raoulensis*), smaller second dorsal fin (its base length 7.2%, 6.5%–8.1%, 6.5%–7.4% of TL vs. 8.2%, 8.7%–9.0%, 8.3%–9.3% of TL for *F. crassispinus* vs. 8.5%, 7.3%–7.8%, 6.8%–10.3% of TL for *F. raoulensis*). It is further distinguished from *F. raoulensis* by smaller pelvic fins (its length 11.3%, 10.8%–10.9%, 9.7%–10.9% of TL vs. 12.9%, 10.8%–12.1%, 10.5%–15.1% of TL for *F. raoulensis*).

The current study also reveals that morphological similarities between the nominal species *Squalus formosus* described from Taiwanese waters (Fig. 138) and *F. albifrons* are much more overlapped than previously thought. White & Iglésias (2011) discriminated these two species based exclusively on differences on CO1 gene and it was later supported by Naylor *et al*. (2012b), Ebert *et al*. (2013b), and Straube *et al*. (2013). Few differences on external measurements were observed by White & Iglésias (2011) for separating them, including height of first and second dorsal fin, length of eyes, length of first dorsal anterior margin. These characters, however, are continuous as it is noticed in the original description and in the present analysis. Other morphometrics characters are also congruent between types specimens of *Squalus formosus* and *F. albifrons* even when only adult specimens are compared, such as, prenarial length 4.5% and 4.9% of TL for *Squalus formosus* vs. 4.3%–7.2% of TL for *F. albifrons*, preoral length 8.7% and 9.6% of TL vs. 8.4%–13.0% of TL for *F. albifrons,* length of first dorsal spine 6.3% and 3.4% vs. 2.1%–6.3% of TL of TL for *F. albifrons,* and length of pectoral anterior margin 16.1% and 13.2% of TL vs. 12.6%–16.1% of TL for *F. albifrons*.

Squalus formosus is similar to *F. albifrons* in many aspects, including dorsal fins tall and upright, dorsal spines conspicuously elongate, short snout and pectoral fins with free rear tips rounded, which are consistent with White & Iglésias (2011). It also exhibits dermal denticles lanceolate and unicuspid with small cusplets posterior to each lateral ridge rather than tricuspid and rhomboid with lateral cusps weakly developed that was described in White & Iglésias (2011). This pattern is identical to those observed for *F. albifrons* from Western and Eastern Australia, suggesting co-specificity with *S. formosus*. Teeth counts are congruent between them, including upper teeth rows 13–13 for *S. formosus* (vs. 12–12 *F. albifrons*) and lower teeth rows 10–10 for both species. Vertebral counts are also overlapped in these species, including monospondylous (47 for *F. albifrons* vs. 43–47 for *F. albifrons*), caudal (30 vs. 25–32 for *F. albifrons*), and total vertebrae (125 vs. 115–124 for *F. albifrons*).

White & Iglésias (2011) further noticed that *S. formosus* bears first dorsal fin with anterior margin conspicuously whitish while it is absent in *F. albifrons* as well as that the whitish eyebrow is particular to the Australian species. In contrast, the present study notices that eyebrow vary within specimens of both species and it can be more or less prominent individually, suggesting that does not change according to sex or stage of maturity. Furthermore, the whitish anterior margin of first dorsal fin changes in *F. albifrons* with maturity, which it is evident in neonates and disappears in juveniles and adults. In specimens from Taiwan, this characteristic is prominent from neonates to adults and also may vary from less or more evident individually. It, thus, indicates that are variations in body coloration between subpopulations from Taiwan to Australia. All these results provide support to consider *Squalus formosus* as junior synonym of *F. albifrons*.

The illustrations provided in Chen *et al*. (1979) and Nakabo (2002, 2013) for a specimen from off Nagasaki in Japan clearly shows the presence of whisith anterior margin of first dorsal fin and high dorsal fins with elongate dorsal spines in front of each one. The occurrence of *F. albifrons* in Japanese waters, however, are not confirmed in the present study and needs further investigations because no specimens examined from this area have shown such characteristics.

Comparative material (4 specimens): CSIRO CA 4111 (holotype of *S. altipinnis*), adult male, 586 mm TL, East of Rowley Shoals, Western Australia, 17°18′S,120°09′E, 305 meters depth; CSIRO CA 3297 (paratype of *S. altipinnis*), adult male, 585 mm TL, Southwest of

Rowley Shoals, Western Australia, 18°10′S,118°20′E, 298 meters depth; CSIRO H 6816-01 (holotype of *S. formosus*), adult male, 720 mm TL, Tashi fish Market, Northeastern Taiwan; CSIRO H 6292-10 (paratype of *S. formosus*), juvenile female, 335 mm TL, same locality as holotype.

Flakeus notocaudatus **(Last, White & Stevens, 2007)**

(Bartail spurdog)

Figs. 139–144; Tables 30–32

Squalus sp. A Last & Stevens, 1994: 48, 91–92 (cited, description; Southwest Pacific Ocean); Compagno & Niem, 1998: 1231 (cited; Southwest Pacific Ocean); Compagno *et al*., 2005.
Squalus notocaudatus Last, White & Stevens, 2007: 39–53 (original description; illustrated; Australia); Ebert *et al*., 2013: 74, 94 (cited, description; Southwest Pacific Ocean).

Holotype: CSIRO H 1368-02, juvenile male, 615 mm TL, east of Flinders Reef, Queensland, 17°27′S,149°46′E, 348 meters depth. Collected on 3 December 1985.

Paratypes (3 specimens): CSIRO H 1321-01, juvenile female, 490 mm TL, Capricorn Channel, Queensland, Australia, 22°52′S,152°42′E; CSIRO H 1322-01, juvenile female, 390 mm TL, East of Flinders Reefs, Queensland, Australia, 17°28′S,149°41′E; CSIRO H 1323-01, juvenile male, 364 mm TL, East of Flinders Reefs, Queensland, Australia, 17°32′S,149°34′E.

Type locality: East of Flinders Reef, Queensland, Australia.

Non-type material (2 specimens): CSIRO H 1368-03, adult female, 632 mm TL, East of Flinders Reefs, Queensland, Australia, 17°27′S,149°46′E; CSIRO H 1373-01, juvenile male, 635 mm TL, South of Saumarez Reef, Queensland, Australia, 22°36′S,153°50′E.

Diagnosis. Species of *Flakeus* differentiated from its congeners by a combination of characters: caudal fin with black upper fringe proximally on its dorsal caudal margin, upper and lower lobes mostly white; first dorsal fin with apex and posterior margin blackish; pectoral fins with posterior margin conspicuously concave and falcate; short snout, its preorbital length 6.5% (7.0%–7.7%, 7.0%–7.4%) of TL; first and second dorsal fins markedly upright and tall (its height 9.2%, 8.9%–10.0%, 8.5%–9.8% of TL, and 6.4%, 6.6%–7.2%, 5.8%–6.0% of TL, respectively); dermal denticles lanceolate and unicuspid with small lateral cusplets. It is also distinct from its congeners by having anterior margin of nostrils with second lobe thinner and more elongate than first one.

Description.

External morphology (Figs. 139–143; Tabs. 30, 31). Body fusiform and conspicuously slender in all its extension, fairly arched anteriorly from posterior margin of the eye to pectoral fin insertion; head height 1.0 (0.9–1.0, 0.9–1.0) times trunk height and 1.0 (0.9, 1.0–1.2) abdomen height. Head flattened anteriorly near the snout, small and narrow, its length 19.5% (21.1%–21.7%, 22.0%–23.4%) of TL and its width at mouth 10.8% (12.2%–12.3%, 12.4%–13.3%) of TL. Snout rounded at tip and short with preorbital length 6.5% (7.0%–7.7%, 7.0%–7.4% of TL); anterior nasal flap bilobate with second lobe thin, prominent and a little larger than first lobe; prenarial length 1.0 (0.9–1.0, 1.0–1.1) times distance from nostrils to upper labial furrow, corresponding half of preoral length; internarial space 0.9 (0.8–0.9, 0.9) times eye length. Eyes oval with anterior margin concave and posterior margin fairly notched; eyes tight and small, its length 2.9 (2.4–3.9, 2.8–3.2) times greater than its height. Prespiracular length 1.7 (1.6–1.8, 1.7) times larger than preorbital length, and 0.6 (0.6, 0.6) times prepectoral length. Spiracles also tight, crescent, its length 0.3 (0.2–0.3, 0.3) times eyes length, located laterally just behind the eyes. Prebranchial length 1.5 (1.5, 1.5) times greater than prespiracular length. Gill slits vertical, placed anteriorly to pectoral fin origin, low with fifth gill slit 1.0 (1.0–1.2, 1.2) times heigher than first gill slit. Mouth arched and wide, its width 1.7 (1.6–1.8, 1.6–1.7) times greater than prenarial length and 1.8 (1.7–1.8, 1.9) times broader than internarial space; upper labial furrow prominent with a broad fold, its length 2.1% (2.0%–2.2%, 2.2%–2.3%) of TL; lower labial furrow short without a fold. Two series of functional teeth on both upper and lower jaws. Upper teeth rows 12–13 (13–13, 12–13), lower teeth rows 10–10 (10–11, 9–9).

First dorsal fin origin anterior to pectoral free rear tips; pre-first dorsal length 27.3% (27.2%–27.8%, 28.0%–28.8%) of TL, corresponding to 1.4 (1.3–1.4, 1.3–1.4) times prepectoral length. First dorsal fin somewhat equal in size to second dorsal fin (firs dorsal length 1.0, 1.0–1.1, 1.2 times length of second dorsal fin). First dorsal fin upright, narrow at apex, tall, its height 1.4 (1.3, 1.2–1.3) times preorbital length and 1.6 (1.6–1.7, 1.5) times larger than its inner margin length; anterior margin convex, posterior margin straight but concave on its midline; apex rounded; free rear tip pointed and large, its length 5.6% (5.3%–6.1%, 5.6%–6.4%) of TL. First dorsal spine thick (its base length 0.9%, 0.8%–0.9%, 0.9%–1.0%) and elongate but not reaching the fin apex, its length 0.5 (0.2–0.4) times first dorsal fin height. Interdorsal distance large, comprising 1.4 (1.1–1.2, 1.1–1.2) times prepectoral length and 2.7 (2.1–2.3, 2.3) times greater than dorsal-caudal space. Second dorsal fin slender and lobe-like at apex; anterior margin convex, posterior margin markedly falcate, and free rear tip pointed; second dorsal fin tall, its height 1.4 (1.4–1.5, 1.2–1.3) times its inner margin length. Second dorsal spine conspicuously thin and elongate, almost reaching the fin apex, its length 0.9 (0.6–0.8, 0.8) times second dorsal fin height and 1.3 (1.2–2.2) times larger than first dorsal spine.

Pectoral fins tapered with anterior margin conspicuously convex, inner margin somewhat convex, and posterior margin strongly concave; apex and free rear tips rounded and markedly lobe-like (in juveniles, free rear tips more constricted); pectoral anterior margin conspicuously large, its length 2.0 (1.9–2.0, 2.0) times greater than inner margin length and 1.6 (1.5–1.6, 1.4–1.7) times larger than posterior margin length; pectoral apex exceeding remarkably the horizontal line traced at the free rear tip (in juveniles, less prominent). Pectoral-pelvic space 0.7 (0.7–0.8, 0.7–0.8) times pelvic-caudal space. Pelvic fins also narrow with all margins straight; free rear tips rounded and lobe-like; pelvic fins placed at middline between origins of first and second dorsal fins; pelvic fins length 10.8 % (9.8%–10.4%, 11.2%–11.5%) of TL.

Caudal keel inconspicuous laterally. Caudal fin strongly narrow at upper and lower lobes; dorsal caudal margin straight and markedly elongate, its length 1.2 (1.1–1.2, 1.0) times head length and 2.0 (2.0–2.1, 1.9–2.0) times greater in length than preventral caudal margin; postventral caudal margins straight; preventral caudal margin convex and small, its length 2.2 (2.3–2.5, 1.7–2.2) times pelvic inner margin length; dorsal and ventral caudal tip rounded; caudal fork between lobes discontinuous and strongly narrow, its width 6.6% (6.7%–7.0%, 6.5%–7.3%) of TL.

Dermal denticles (Fig. 143). Lanceolate, unicuspid and imbricate; cusp pointed posteriorly; denticles broad at the crown, its length greater than its width; median ridge prominent and thick with anterior furrow profound and large; anterior margin of crown expanded and arrow-shaped; lateral ridges small and prominent with evident furrow. Dermal denticles very heterogeneous with some denticles much smaller than other ones; additional lateral cusplets may be present, although often inconspicuous.

Coloration. Body light grey dorsally and white ventrally. Dorsal fins light grey, whitish at its base and free rear tips; first dorsal fin with apex and posterior margin fairly blackish; second dorsal fin slightly dark at apex. Dorsal spines white, moderately grey anteriorly. Pectoral and pelvic fins grey with posterior margins slightly whitish. Caudal fin also grey, whitish medially; dorsal caudal lobe with dark grey blotch anterior-proximaly as a fringe; postventral caudal margins white, broadly whitish at the dorsal and ventral caudal tips; lower caudal lobe mostly white, although with dark grey basal marking under vertebral column; dark caudal stripe absent.

Vertebral counts (Tab. 32). 48 monospondylous vertebrae; 78 diplospondylous vertebrae; 97 precaudal vertebrae; 29 caudal vertebrae; 126 total vertebrae.

Geographical distribution (Fig. 144). It occurs off Queensland, Australia from Flinders Reef to Saumarez Reef.

Etymology. The name "*notocaudatus*" is a combination of two words in Latin *nota* (mark) and *cauda* (tail) in reference to the dark blotches in the caudal fin.

Remarks. *Flakeus notocaudatus* is restricted to Queensland, Australia, which it is in congruence with Last *et al*. (2007c). These authors supported it as separate species based specially on characters of body coloration (e.g. caudal fin and dorsal fins) and vertebral counts. Its diagnosis, however, are congruent to the other two species described by these authors and no other diagnostic characters were efficient for its differentiation besides coloration, according to their results. Its external morphology assemblages those of *F. albifrons* and *F. crassispinus* regarding dorsal fins vertical, upright and tall, caudal with upper and lower lobes very slender, and robust dorsal spines. It differs from the former species by having body slender and light grey in color (vs. more robust and dark grey for *F.*

albifrons); absence of eyebrow and white anterior margin of first dorsal fin (vs. presence for *F. albifrons*); pectoral fins with posterior margin conspicuously concave and falcate (vs. almost straight). *Flakeus notocaudatus* is distinct from *F. crassispinus* by narrower dorsal spines (first spine base length 0.9%, 0.8%–0.9%, 0.9%–1.0% of TL vs. 1.2%, 1.1%–1.2%, 1.1%–1.3% of TL for *F. crassispinus*; second spine base length 0.8%, 0.7%, 0.8%–1.2% of TL vs. 1.3%, 1.2%–1.3%, 1.2%–1.4% of TL for *F. crassispinus*).

The lack of mature specimens of *F. notocaudatus* for analysis contributes for the difficulty on providing efficient diagnostic characters. Despite of some overlapping, *F. notocaudatus* may also be differentiated from *F. albifrons* by: dorsal caudal margin length 1.2 (1.1–1.2, 1.0) times head length (vs. 1.1, 0.9–1.1, 0.9–1.0 in *F. albifrons*); pectoral anterior margin 0.6 (0.6–0.7, 0.6–0.8) times distance between origin of pectoral fin and prevent length (vs. 0.6, 0.6, 0.5–0.6 times in *F. albifrons*); pre-second dorsal length 3.6 (3.4–3.8, 3.1–3.9) times greater than length of pectoral anterior margin (vs. 3.8, 3.7–4.0, 3.9–4.9 for *F. albifrons*). Other characters may also help to distinct them: larger pectoral anterior margin (its length 16.6%, 15.2%–16.8%, 15.6%–18.7% of TL) with apex exceeding conspicuously the free rear tips (vs. anterior margin straight and short, its length 15.9%, 15.0%–15.9% [12.6%–16.1%] of TL, apex and free rear tips reaching equally the horizontal line in *F. albifrons*); larger second dorsal fin base length in *F. notocaudatus* (7.8%, 7.4%–8.7%, 7.5%–8.0% of TL vs. 7.2%, 6.5%–8.1% of TL for *F. albifrons*).

The morphological disparity observed between *F. notocaudatus* and *F. albifrons* support its separation. Vertebral counts are overlapped, except for precaudal and total vertebrae, according to the present results, which it is in accordance to Last *et al*. (2007c). Future investigations on additional material and combined morphological and molecular analysis are in need for better characterization of this species.

Last *et al*. (2007c) also stated that this species has tricuspid dermal denticles as well as for *F. albifrons* and the nominal species *S. altipinnis*, which it is in disagreement with the current results. The dermal denticles of these species are lanceolate rather than having rhomboid and tricuspid shape that it is also observed within the genus. It is also observed in the present analysis that cusplets are rarely present, and it is formed as a posterior extention of the lateral ridge on each side of the denticle. These cusplets are not homologous to those noticed for other species of the genus because the cusps are a posterior extension of the crown base instead.

Comparative material: Material listed in this Chapter for *F. crassispinus, F. albifrons, F. megalops, F. brevirostris, F. mitsukurii,* and the nominal species *S. altipinnis.*

Flakeus hemipinnis (White, Last & Yearsley, 2007)

(Indonesian shortsnout spurdog)

Figs. 145–149; Tables 46–48

Squalus hemipinnis White, Last & Yearsley, 2007: 101–108 (original description; illustrated; Indonesia); Ebert *et al*., 2013a: 78, 90 (cited, description; Indo-West Pacific Ocean); Ebert, 2013: 53, 57, 61–63 (listed, cited, description; Indonesia).

Holotype: MZB 15040, adult female, 630 mm TL, Kedonganan fish landing site, Bali, Indonesia, 08°45′S,115°10′E. Collected on July 2002.

Paratypes (17 specimens): CSIRO H 5631-01, adult female, 569 mm TL; CSIRO H 5631-02, adult female, 570 mm TL; CSIRO H 5631-03, adult female, 607 mm TL; CSIRO H 5631-04, adult female, 575 mm TL; CSIRO H 5631-06, adult female, 562 mm TL; CSIRO H 5692-01, juvenile male, 420 mm TL; CSIRO H 5692-02, adult male, 495 mm TL; CSIRO H 5692-03, adult male, 483 mm TL; CSIRO H 5692-06, adult female, 562 mm TL; CSIRO H 5693-06, adult female, 533 mm TL; CSIRO H 5693-07, juvenile female, 422 mm TL; CSIRO H

5857-13, adult female, 645 mm TL; CSIRO H 5857-14, adult female, 670 mm TL; CSIRO H 5887-15, adult female, 610 mm TL; CSIRO H 5889-38, three female embryos, 163-166 mm TL. All collected at same locality as holotype.

Type locality: Kedonganan fish landing site, Bali, Indonesia.

Non-type material (16 specimens): CSIRO H 5631-05, juvenile female, 552 mm TL, Jimbaran Bay (South coast of Bali), Kedonganan, Indonesia, 08°45′S,115°10′E; CSIRO H 5692-05, two neonate females, 155 mm TL, two neonate males, 155–157 mm TL, locality same as CSIRO H 5631-05; CSIRO H 5786-01, adult female, 713 mm TL, Tanjung Luar (Southeast coast of Lombok), Indonesia, 08°45′S,116°35′E; CSIRO H 5788-06, adult female, 720 mm TL, locality same as CSIRO H 5786-01; CSIRO H 5857-06, adult male, 673 mm TL, same locality as CSIRO H 5631-05; CSIRO H 5857-09, juvenile male, 435 mm TL, same locality as CSIRO H 5631-05; CSIRO H 5857-10, adult female, 690 mm TL, locality same as CSIRO H 5631-05; CSIRO H 5875-05, adult male, 560 mm TL, locality same as CSIRO H 5786-01; CSIRO H 5875-06, adult male, 585 mm TL, locality same as CSIRO H 5786-01; CSIRO H 5876-04, adult female, 630 mm TL, locality same as CSIRO H 5786-01; CSIRO H 5889-10, juvenile female, 490 mm TL, Jimbaran Bay (South coast of Bali), Kedonganan, Indonesia; CSIRO H 5889-20, adult male, 617 mm TL, locality same as CSIRO H 5631-05; CSIRO H 5889-29, adult male, 443 mm TL, locality same as CSIRO H 5631-05.

Diagnosis. *Flakeus hemipinnis* is distinguished from its congeners (except *F. lalannei*) by fewer monospondylous (37), diplospondylous (60–61), precaudal (74), and total vertebrae (97–98). It is also distinct from them (except with *F. montalbani* and *F. griffini*) by having shorter pre-first dorsal length which comprises 27.9%–28.6% of TL in adult specimens, and smaller distance from cloaca to tip of snout (except with *F. probatovi*, *F. mitsukurii*), corresponding to 43.6%–47.5% of TL in adults. It is further distinguished from congeners by having narrower mouth (except with *F. japonicus*), its width 6.7%–7.7% of TL in adult specimens. Adult specimens of *F. hemipinnis* have more elongate space between pelvic and caudal fins (26.9%–30.1% of TL) than *F. griffini* (22.9%–25.9% of TL), *F. montalbani* (23.3%–26.1% of TL), and *F. mitsukurii* (23.7%–26.8% of TL). It has larger first dorsal spine (4.8%–6.2% of TL in adults) than *F. griffini* (2.7%–3.8% of TL in adults), *F. montalbani* (2.7%–3.5% of TL in adults), *F. grahami* (2.7%–4.5% of TL in adults), and *F. japonicus* (3.0%–3.8% of TL in adults).

Flakeus hemipinnis is easily differentiated from *F. edmundsi* by: snout rounded and shorter, its prenarial length 4.4%, 4.1%–4.7% (vs. snout pointed and larger, 5.8%, 5.7%–5.9% of TL in *S. edmundsi*); narrower internarial space (3.6%, 3.3%–4.1% of TL vs. 4.5%, 4.5%–4.9% of TL); smaller pre-second dorsal length (59.4%–61.0% of TL in adults vs. 61.7%–75.5% of TL for adults of *F. edmundsi*); shorter preoral length (8.8%, 8.4%–9.4% vs. 10.4%, 10.3%–10.7% of TL).

Description.

External morphology (Figs. 145–148; Tabs. 46, 47). Body fusiform and narrow through all its extension, slightly arched dorsally from posterior margin of spiracle to origin of first dorsal fin; head height 0.9 (0.9–1.0; 0.8–1.0) times trunk height and 1.0 (0.9–1.0; 0.8–1.2) times abdomen height; body with its greatest width athead, its head width 1.2 (1.1–1.3) times trunk width and 1.4 (1.2–1.7; 1.3–1.6) times abdomen width. Head compressed anteriorly, elongate, its length 23.8% (20.6%–22.8%; 21.6%–25.9%) of TL; head broader at mouth than at nostrils, its width at mouth 11.1% (9.6%–10.9%; 10.5%–12.0%) of TL and its width at nostrils 6.7% (6.3%–7.2%; 6.4%–7.8%) of TL. Snout somewhat obtuse at tip and short, its preorbital length 6.9% (6.4%–6.9%; 6.7%–8.9%) of TL; anterior nasal flap bilobate and nearest the snout tip than the mouth with prenarial length 0.8 (0.8–1.0; 0.8–1.2) times its distance to upper labial furrow and 0.5 (0.5–0.6; 0.5) times preoral length; internarial space 0.8 (0.7–0.9; 0.7–1.0) times eye length. Eyes oval with both anterior and posterior margins slightly notched; eyes large, its length 2.2 (2.0–2.5; 1.8–4.1) times greater than its height. Prespiracular length 0.5 (0.5–0.6; 0.6) times prepectoral length and 1.7 (1.7–1.9; 1.6-1.8) times larger than preorbital length. Spiracles strongly wide and crescent, its length 0.3 (0.3–0.4) times eye length, placed lateral-dorsally behind the eyes. Prebranchial length 1.6 (1.5–1.6) times greater than prespiracular length. Gill slits vertical and very low with fifth gill slit 1.1 (0.9–1.5; 0.9–1.7) times higher than first gill slit, located just anterior to origin of pectoral fins.

Preoral length 1.2 (1.1–1.3; 1.1–1.5) times greater than mouth width. Mouth arched and broad, its width 2.1 (1.8–2.1; 1.5–2.1) times greater than internarial space and 1.8 (1.5–1.9; 1.2–1.7) times prenarial length; upper labial furrow elongate with a thin fold, its length 2.0% (1.8%–5.3%; 1.7%–2.9%) of TL; lower labial furrow large without a fold. Three series of functional teeth on upper and lower jaws in holotype (3–2 in paratypes). 12–12 (13–12; 13–13) upper teeth rows and 9–10 (11-11; 11-11) lower teeth rows.

Pre-first dorsal fin length 1.3 (1.3–1.5; 1.3-1.4) times prepectoral length; origin of first dorsal fin anterior to pectoral free rear tips. First dorsal fin upright, conspicuously narrow at apex with anterior margin convex and posterior margin strongly falcate from its midline to its free rear tip; apex fairly pointed and lobe-like; first dorsal fin low, its height 1.5 (1.5–1.8; 1.3-1.8) times its inner margin length; free rear tip pointed with inner margin small, its length 5.6% (4.6%–5.6%; 4.7%–5.9%) of TL; first dorsal fin 1.1 (1.0–1.1; 1.1–2.2) times length of second dorsal fin. First dorsal spine heavy, its base width 0.9% (0.7%–0.9%; 0.4%–1.2%) of TL; first dorsal spine elongate, although not reaching apex of first dorsal fin with its length 0.6 (0.5–0.6; 0.2–0.7) times height of the first dorsal fin height. Interdorsal space 1.1 (1.0–

1.3; 0.9–1.2) times prepectoral length and 2.2 (1.9–2.3; 2.1–2.4) times greater than dorsal caudal space. Pre-second dorsal length 2.7 (2.7–3.1; 2.5–3.0) times prepectoral length. Second dorsal fin oblique, also evidently narrow at apex with anterior margin convex and posterior margin markedly falcate; apex lobe-like and fairly pointed; free rear tips rounded with inner margin small, its length 4.0% (4.1%–5.0%; 2.7%–5.9%) of TL; second dorsal fin oblique and low, its height 1.4 (1.2–1.5; 0.7–2.0) times its inner margin length. Second dorsal spine convex and conspicuously robust, its base width 1.2% (0.9%–1.1%; 0.8%–1.1%) of TL; second dorsal spine short, never reaching the fin apex, its length 0.8 (0.8–0.9; 0.7–1.0) times height of second dorsal fin and 1.0 (1.0–1.3; 0.9–2.5) times length of first dorsal spine.

Pectoral fins conspicuously broad posteriorly with both anterior and inner margins convex, and posterior margin strongly concave and falcate; pectoral anterior margin conspicuously elongate, its length 2.0 (1.8–1.9; 1.6–2.3) times greater than length of pectoral inner margin and 1.5 (1.3–1.5; 1.3–1.7) times larger than length of pectoral posterior margin; pectoral apex rounded and lobe-like, transcending greatly the horizontal line traced at pectoral free rear tips; pectoral free rear tips rounded and lobe-like. Pectoral-pelvic space 0.7 (0.6–0.8) times pelvic-caudal space; pelvic fins placed in the midline between two dorsal fins. Pelvic fins wide and elongate, its length 10.6% (10.2%–11.8%; 9.4%–11.8%) of TL; pelvic anterior and posterior margins straight; pelvic free rear tips fairly pointed, although not lobe-like (more evidently pointed in males). Claspers in adults thin and elongate, exceeding the pelvic free rear tips its inner length 1.2–1.3 (0.6–1.5) times length of pelvic inner margin; clasper groove small, dorsal and longitudinal; apopyle with narrow aperture anteriorly; hypopyle with somewhat broad aperture, located posteriorly in the clasper groove; rhipidion blade-like, large, placed medial-distally in the clasper.

Caudal keel evident since free rear tip of first dorsal fin to origin of caudal fin; upper and lower caudal pits prominent. Caudal fin conspicuously slender on both dorsal and ventral lobes; all caudal margins markedly straight; both dorsal and ventral caudal tips pointed; dorsal caudal margin short, its length 0.9 (0.9–1.0; 0.8–1.0) times head length and 1.8 (1.7–1.9; 1.8–1.9) times larger than length of preventral caudal margin; caudal fork discontinuous and almost in right angle, its width 6.9% (6.4%–7.1%; 5.9%–6.9%) of TL; preventral caudal margin elongate, its length 2.5 (1.9–2.9; 1.9–2.6) times length of pelvic inner margin.

Dermal denticles (Fig. 148). Unicuspid and lanceolate, not imbricate, its length greater than its width; denticles thin at crown, although expanded at its base; cusp posterior and rounded; median ridge elongate and thick, turning thinner distally; anterior furrow rounded and profound at median ridge; lateral ridges slender and conspicuously short, often asymmetrical.

Coloration. Body dark grey dorsally, white ventral and laterally. First dorsal fin dark grey, whitish at its base, light grey in the free rear tip; slightly white in the first half of posterior margin; apex blackish. Second dorsal fin also dark grey, whitish at its base with posterior margin white; apex black at the tip. Dorsal spines brownish, black anteriorly and whitish at the tips. Pectoral and pelvic fins dark grey dorsal and ventrally with posterior margin uniformly white. Caudal fin dark grey, whitish over vertebral column with large dark upper caudal blotch distally; postventral caudal margins white but not uniform; inconspicuous black caudal bar in the caudal fork (more evident in young specimens); both dorsal and ventral caudal tips whitish; dark caudal stripe evident anteriorly. Some paratypes have ventral lobe broadly white.

Vertebral counts (Tab. 48). 37 (37) monospondylous vertebrae; 74 (74) precaudal vertebrae; 23 (24) caudal vertebrae; 97 (98) total vertebrae.

Geographical distribution (Fig. 149). It is endemic to Indonesia waters near Bali.

Etymology. The name "*hemipinnis*" is a combination of two words "*hemi*" (= half in Greek) and "*pinna*" (= fin in Latin) that refers to the second dorsal fin with posterior margin conspicuously notched.

Remarks. *Flakeus hemipinnis* is a species endemic to Indonesia, according to the current results and White *et al*. (2007b). It has been misidentified with *F. edmundsi* in this region due to similarities on body shape, shape of caudal fin and dorsal fins, and dermal denticles. Besides characteristics from diagnosis, *F. hemipinnis* can be distinguished from *F. edmundsi* by: head broader at nostrils in *F. hemipinnis* than in *F. edmundsi* (6.7%, 6.3%–7.2% of TL vs. 7.1%, 7.2%–7.6% of TL, respectively); length of dorsal-caudal margin 1.8 (1.7–1.9) times larger than length of pre-ventral caudal margin (vs. 2.0, 1.9–2.0 in *F. edmundsi*). It also has pectoral apex exceeding greatly the horizontal line traced at pectoral free rear tips (vs. pectoral apex reaches almost equally the horizontal line in *F. edmundsi*), and posterior margin of both dorsal fins raked (vs. posterior margin concave in *F. edmundsi*). The shape of pectoral fins assemblages those of *F. notocaudatus* as well as caudal fin with upper and lower lobes markedly slender, although *F. hemipinnis* is clearly distinct from it by having smaller length of inner margin (6.8%–7.7% of TL in adults vs. 7.9%–9.2% of TL for adults of *F. notocaudatus*), and shorter dorsal caudal margin (its length 19.4%–21.6% of TL vs. 21.7%–23.9% of TL for adults of *F. notocaudatus*), and more elongate dorsal-caudal space (10.8%–11.9% of TL vs. 10.3%–10.7% of TL for adults of *F. notocaudatus*).

According to White *et al*. (2007b), the Indonesian species also bears characteristics that are often addressed to both *S. megalops* group and *S. mitsukurii* group because it has short snout, dermal denticles tricuspid, and caudal fin with dark caudal bar. However, the current analysis reveals that *F. hemipinnis* varies greatly in these aspects. Dark caudal bar is evident in neonates to young juveniles only like it is observed for *F. mitsukurii*. Snout length vary from very short to somewhat elongate, its prenarial length 0.8 (0.8–1.0; 0.8–1.2) times distance between nostril and upper labial furrow, comprising an intermediate pattern between those noticed for *F. grahami*, *F. mitsukurii*, *F. montalbani* and those for *F. megalops*, *F. crassispinus*, *F. brevirostris* and *F. raoulensis*. Smaller juveniles and neonates still have proportional length smaller than large adults, indicating the morphology of *F. hemipinnis* is even more complex. These results give additional support for not grouping species of *Flakeus* within complex or group of species.

In contrast to White *et al*. (2007b), the current study further noticed that dermal denticles in *F. hemipinnis* is conspicuously unicuspid and lanceolate in a specimen from Indonesia, which does not overlap with information provided in the original description for this species. Future comparison between type and non-type material are needed for this purpose in order to clarify the correct morphology of the dermal denticles in this species. If it is confirmed such variation, it is possible that *F. hemipinnis* was described based on two different forms that inhabit the Indonesian waters and its correct characterization and clarification of its taxonomic status will be imperative.

Comparative material: Specimens of *F. grahami*, *F. mitsukurii*, *F. montalbani*, *F. megalops*, *F. crassispinus*, *F. brevirostris* and *F. raoulensis* listed previously in this Chapter.

Flakeus mitsukurii **(Jordan & Snyder, 1903)**

(**Horny shark; Tsunozame, Tsunoge** in Japanese)

Figs. 150–156; Tables 34, 37–38

Squalus mitsukurii Jordan & Snyder, 1901: 129 (name only); Jordan & Snyder, 1903: 629; fig. 3 (original description; illustrated; type by original designation; type locality: Misaki, Japan); Yuanding, 1960: 107, 109-110 (description; Northwest Pacific Ocean); Zhu *et al*., 1984: 284 (cited; Japan); Bass *et al*., 1986 (in part): 61-62 (cited; description; North Pacific Ocean); Parin, 1988: 48 (cited; Japan); Siming *et al*., 1988: 1 (listed; Northwest Pacific Ocean); Last & Stevens, 1994 (in part): 49, 101-102 (cited, description; Northwest Pacific Ocean); Compagno & Niem, 1998 (in part): 1230 (cited; Northwest Pacific Ocean); Compagno, 1999: 472 (listed); Yuanding & Qingwen, 2001: 311, 319-321 (cited, description; Northwest Pacific Ocean); Compagno, 2002 (in part): 381, 385 (listed, description; Central Pacific Ocean); Nakabo, 2002: 156 (listed; Tohoku District, Ryukyu Islands, Okinawa Through, South China Sea); Compagno *et al*., 2005 (in part): 78 (description; Japan to Taiwan); Ebert *et al*., 2013a (in part): 76, 92 (cited, description; Northwest Pacific Ocean); Nakabo, 2013: 196 (listed; Tohoku District, Ryukyu Islands, Okinawa Through, South China Sea); White *et al*., 2013: 229–230 (cited; Taiwan).
Squalus blainvillei (not Risso): Yuanding & Qingwen, 2001: 311, 315–316 (cited, description; Japan).

Holotype. SU 12793, adult female, 710 mm TL, Honshu Island, Misaki, Japan.

Paratypes (6 specimens): AMNH 8822, neonate female, 248 mm TL; SU 12794, adult male, 770 mm TL; SU 7184 (identified as *S. acanthias*), neonate male, 277 mm TL; SU 7748, two neonate females, 240–243 mm TL, neonate male, 247 mm TL. All embryo paratypes taken from the holotype.

Type locality: Honshu Island, Misaki, Japan

Non-type material (28 specimens): HUMZ 33680, adult female, 760 mm TL, East China Sea, 29°38’N, 134°E; HUMZ 68767, adult male, 620 mm TL, Emperor Sea Mount, Kinmei, 35°07.3’N,171°41.4’E; HUMZ 79798, adult female, 835 mm TL, Kyushu-Palau Ridge, 26°46’5”N,135°20’3”E; HUMZ 89857, adult female, 900 mm TL, off Oshima Island, Tokyo, Japan; HUMZ 89858, adult female, 705 mm TL, off Hachijo-jima Island, Tokyo, Japan; HUMZ 97463, adult female, 800 mm TL, unknown locality; HUMZ 102986, adult female, 1005 mm TL, Central Pacific Ocean, near Northern Mariana Islands, 17°39’N, 145°50’3”E; HUMZ 102987, adult female, 970 mm TL, Central Pacific Ocean, near Northern Mariana Islands, 19°09’N,142°59’E; HUMZ 102988, adult female, 1025 mm TL, Central Pacific

Ocean, near Northern Mariana Islands, 19°09'N,142°59'E; HUMZ 113586, adult female, 1120 mm TL, off Shirahama, Shimoda, Shizuoka Prefecture, Japan; HUMZ 113587, adult female, 990 mm TL, off Shirahama, Shimoda, Shizuoka Prefecture, Japan; HUMZ 113588 adult female, 960 mm TL, off Shirahama, Shimoda, Shizuoka Prefecture, Japan; NMMB P 15560, juvenile male, 656 mm TL, Pingtung county, Taiwan; NMMB P 15619, juvenile female, 700 mm TL, locality same as NMMB P 15560; NMMB P 15668, juvenile female, 760 mm TL, locality same as NMMB P 15560; NSMT-P 44097, juvenile female, 740 mm TL, unknown locality, Southern Japan; NSMT-P 44381, adult male, 770 mm TL, unknown locality, Southern Japan; NSMT-P 65518, adult female, 1119 mm TL, Southern Japan, Japan; NSMT-P 72728, two juvenile females, 414–420 mm TL, four adult females, 700–840 mm TL, Japan; NSMT-P 77187, adult male, 1000 mm TL, unknown locality; NSMT-P 97762, neonate male, 278 mm TL, Sea of Japan, Japan; ZUMT 1360, neonate female, 178 mm TL, off Atami, Kanagawa Prefecture; ZUMT 21114, neonate female, 190 mm TL, Nagasaki.

Diagnosis. Large species (760–1120 mm TL for adults) of *Flakeus* that is distinguished from its congeners by a combination of characters: body markedly robust and dark grey to black on all its extension; snout conspicuously large, its preorbital length 7.3% (7.2%–8.8%; 6.9%–10.7%) of TL; first dorsal fin elongate, its anterior margin length 12.0% (10.2%–13.2%; 9.3%–12.3%) of TL; second dorsal fin large, its anterior margin length 10.2% (9.9%–11.6%; 7.7%–11.9%) of TL; first dorsal spine elongate, although not reaching the first dorsal apex (its length 3.9% [2.1%–5.4%; 2.4%–5.0%] of TL); second dorsal spine large, its length 4.2% (3.3%–4.4%; 3.4%–5.3%) of TL. It is also distinct from congeners by having pectoral fins with posterior margin concave and free rear tips rounded, and markedly large, its anterior margin length 15.2% [12.3%–16.7%; 13.5%–17.7%] of TL, corresponding to 1.8–2.3 times length of pectoral inner margin in adults. *Flakeus mitsukurii* is further separated from its congeners by having caudal fin somewhat rectangular, although very slender distally at upper caudal lobe with dorsal caudal margin markedly elongate (its length 24.4% [21.2%–23.4%; 20.1%–22.2%] of TL). *Flakeus mitsukurii* is easily distinct from its congeners by taller fifth gill slit, its height 2.4%–2.6% of TL in adult specimens.

Flakeus mitsukurii has more total vertebrae than *F. blainvillei* and *F. probatovi* (112–117 vs. 107–111 for *F. blainvillei* vs. 118–124 for *F. probatovi*). It is distinguished from *F. japonicus*, *F. grahami* and *F. blainvillei* by monospondylous vertebrae (44–46 vs. 41–43 for *F. japonicus* vs. 41–42 for *F. grahami* vs. 40–43 for *F. blainvillei*) and from *F. montalbani*, and *F. probatovi* by diplospondyous vertebrae (68–72 vs. 73–74 for *F. montalbani* vs. 73–77 for *F. probatovi*).

Description.

External morphology (Fig. 150–155; Tabs. 34, 37). Body robust and fusiform markedly humped anteriorly from the posterior margin of the spiracle to the pelvic fin origin, slenderer posteriorly; head height 12.7% (8.3%–11.2%; 10.5%–12.5%) of TL, corresponding to 1.2 (1.0–1.4; 0.8–1.0) times larger than trunk height and 1.6 (1.2–1.7; 0.9–1.0) times greater than abdomen height. Head flattened, very large, its length 24.2% (22.7%–24.4%; 20.4%–23.5%) of TL and extremely broad, its width 1.2 (1.1–1.6; 1.0–1.3) times wider than trunk width and 1.5 (1.7–2.6; 1.1–1.6) times greater than abdomen height. Snout rounded at the tip and conspicuously elongate, its prenarial length 5.6%, (4.7%–6.4%; 4.1%–5.4%) of TL; anterior margin of nostrils wide and bilobed; prenarial length 1.3 (1.1–1.4; 1.1–1.2) times distance between nostrils to upper labial furrow and 0.5 (0.5–0.6) times preoral length; internarial space 1.3 (0.9–1.4; 0.8–1.3) times eye length. Eyes elliptical with anterior margin concave and posterior margin notched; eyes large, its length 3.6% (3.1%–4.6%; 3.4%–5.2%) of TL, corresponding to 4.1 (1.8–3.0; 1.6–2.8) times greater than its height. Prespiracular length 0.5

(0.6–1.0; 0.5–0.8) times prepectoral length and 1.8 (1.6–2.8; 1.5–1.7) times preorbital length. Spiracles crescent, located laterally and behind the eyes; spiracles large, its length 1.6% (1.3%–1.5%; 0.8%–1.9%) of TL and corresponding to 0.4 (0.3–0.4; 0.2–0.4) times eye length. Prebranchial length 1.6 (1.0–1.6; 1.0–1.8) times prespiracular length. Gill slits vertical and concave, placed anterior to origin of pectoral fins; gill slits very tall with first gill slit height 1.7% (1.7%–2.3%; 1.5%–2.8%) of TL; fifth gill slit 1.3 (1.1–1.3; 0.7–1.7) times taller than first gill slit.

Preoral length 1.2 (1.1–1.5; 1.0–1.4) times greater than mouth width. Mouth slightly straight and broad, its width 8.6% (7.6%–8.1%; 6.6%–8.1%) of TL, corresponding to 1.8 (1.7–2.0; 1.5–2.1) times broader than internarial width and 1.5 (1.2–1.7; 1.4–1.8) times greater than prenarial length; upper labial furrow large, its length 2.5% (2.1%–2.7%) of TL, with slender fold; lower labial furrow markedly elongate, lacking fold. Paratype with teeth unicuspid, flattened labial-lingually, similar in both jaws; teeth somewhat rectangular, very broad at the crown; cusp short and oblique, although thick; mesial cutting edge slightly concave to straight; distal heel conspicuously rounded; mesial heel sharp; apron elongated and thick, directed obliquely; median teeth present on upper jaw in adult paratype and distinct from the subsequent teeth by: teeth hexagonal with cusp and apron placed more medially; both mesial and distal heels pointed. Two series of functional teeth on both jaws in type specimens; upper jaw with 13–15 (13–1–12; 13–13) teeth rows, lower jaw with 12–12 (11–11; 11–11) teeth rows.

Interdorsal space equal to 21.1% (21.9%–24.7%; 21.7%–25.9%) of TL, its length 2.0 (2.0–3.0; 1.9–2.9) times larger than dorsal-caudal space and 0.9 (0.9–1.1; 0.9–1.3) times prepectoral length. First dorsal fin elongate, its length1.1 (1.0–1.2; 1.0–1.3) times greater than length of second dorsal fin; first dorsal fin conspicuously broad at fin web; anterior margin markedly convex and elongate, its length 12.0% (10.2%–13.2%; 9.3%–13.2%) of TL;

posterior margin somewhat concave, its length 9.3% (7.0%–10.6%; 8.4%–9.8%) of TL; inner margin also large, its length 6.2% (6.1%–6.5%; 5.0%–6.6%) of TL; apex broadly rounded; first dorsal fin vertical and low, its height corresponding to 1.6 (1.1–1.6; 1.2–1.6) times greater than length of its inner margin, and 1.3 (0.8–1.4; 0.8–1.2) times greater than preorbital length. Origin of first dorsal spine just anterior to pectoral free rear tips. First dorsal spine thick at its base (its length at base 1.0% [0.5%–1.0%; 0.7%–0.9%] of TL) and large, although not reaching the fin apex (its length 3.9% [2.1%–5.4%; 2.4%–5.0%] of TL). Pre-second dorsal length 2.5 (2.4–2.7; 2.6; 3.1) times prepectoral length. Second dorsal fin also broad at fin web and oblique with apex conspicuously rounded and lobe-like; second dorsal fin low, its height 6.8% (4.8%–7.9%; 4.5%–6.6%) of TL, corresponding to 1.3 (0.8–1.3; 1.0–1.4) times length of its inner margin; anterior margin strongly convex and large, its length 10.2% (9.9%–11.6%; 7.7%–11.9%) of TL; posterior margin concave and somewhat falcate, its length 6.3% (4.5%–6.3%; 5.0%–6.2%) of TL; length of inner margin 5.3% (4.9%–5.9%; 4.1%–4.9%) of TL. Second dorsal spine elongate, although not reaching apex of second dorsal fin, its length 0.6 (0.5–0.8; 0.7–1.0) times height of second dorsal fin and 1.1 (0.8–1.8; 0.9–1.9) times greater than length of first dorsal spine; second dorsal spine heavy spine, its base length 0.9% (0.8%–1.1%; 0.7%–0.9%) of TL.

Pectoral fins markedly broad (its posterior margin length 11.7% [9.5%–12.1%; 9.2%–12.5%] of TL), although never extending up to trunk height when adpressed laterally on body; pectoral anterior margin straight; pectoral inner margin concave; pectoral posterior margin almost straight; pectoral apex rounded and lobe-like; pectoral free rear tips rounded, reaching the same length when a horizontal line is traced at apex; pectoral anterior margin very large, its length 1.6 (.14–1.8; 1.6–2.3) times greater than length of inner margin and 1.3 (1.1–1.4; 1.3–1.5) times larger than posterior margin. Pectoral-pelvic space 0.9 (0.7–0.9; 0.8–1.1) times distance between pelvic and caudal fins. Pelvic fins broad with anterior and posterior margins convex; pelvic free rear tips rounded and lobe-like; pelvic fin large, its length 11.5% (8.4%–12.6%; 9.6%–11.6%) of TL; pelvic fins nearest to second dorsal fin than to first dorsal fin. Distance between the pectoral insertion and pelvic origin 0.9 (0.7-0.9) times the pelvic-caudal space. Adult males with clasper extremely robust and thick, covering all the terminal cartilages; clasper groove medial-dorsally and longitudinal, profound and short, not extending forwardly to inner margin of the clasper; clasper inner margin length 3.4%–8.4% of TL, corresponding to 0.7–1.1 (0.7–1.3) times length of pelvic inner margin; apopyle broad, placed anteriorly in the clasper groove; hypopyle also broad and located just above the rhipidion; rhipidion blade-like and evidently thick, large and wide, located at the medial-distal end of the clasper.

Upper and lower precaudal pits conspicuous; caudal keel laterally and prominent since insertion of the second dorsal fin to behind origin of caudal fin. Caudal fin somewhat rectangular, although noticeable slender distally at posterior caudal tip; dorsal caudal margin convex but straight distally, and very elongate, its length 24.4% (21.2%–23.4%; 20.1%–22.2%) of TL and corresponding to 1.0 (0.9–1.0; 0.9–1.1) times head length and 2.0 (1.8–1.9; 1.7–2.0) times larger than length of preventral caudal margin; upper postventral caudal margin convex, although straight proximally near posterior tip; lower postventral caudal margin rather convex; preventral caudal margin convex, its length 12.1% (11.5%–12.4%; 10.7%–12.4%) of TL, corresponding to 1.9 (1.5–3.8; 2.0–2.8) times length of pelvic inner margin; both posterior and ventral caudal tips rounded; caudal fork among lobes discontinuous and conspicuously concave, its width 7.0% (6.4%–7.7%; 6.1%–7.4%) of TL.

Dermal denticles (Fig. 155). Tricuspid, rhomboid and imbricate, conspicuously broad at the crown, its length equal to its width; cusps pointed and posterior, lateral cusps often inconspicuous and much shorter than median cusp; media cusp conspicuous and wide;

median ridge prominent, tall and thick with anterior furrow oval and profound; anterior margin of the crown broad and markedly arrow-shaped with two small ridges evident; one to two lateral ridges on each side, thick and smaller than median ridge. Dermal denticles slightly larger and more imbricate in adults than juveniles.

Coloration. Holotype with body dark brown dorsally, pale ventrally and laterally since below the eyes to origin of caudal fin. Dorsal fins dark brown, blackish at its apex and light brown in the fin base near the dorsal spines; anterior margin of dorsal fins white until its midway; posterior margin of dorsal fins narrowly white. Dorsal spines brown, white at its tips. Pectoral fins dark brown with posterior margin slightly white, not uniform. Pelvic fins dark brown with its margins slightly whitish. Caudal fin mostly dark brown, somewhat whitish over vertebral column; upper caudal blotch black and large near dorsal caudal tip; dorsal caudal margin slightly white at its proximal and distal ends; postventral caudal margins white, fairly evident at caudal fork between lobes; preventral caudal margin white. Fresh specimens with body and fins mostly black in color. Neonates and young juveniles with dark caudal bar conspicuous.

Vertebral counts (Tab. 38). 42–46 [mode 44] monospondylous vertebrae; 68 holotype (72 paratype; 69–72) [mode 70] diplospondylous vertebrae; 30 (30; 26–31) [mode 29] caudal vertebrae; 112–117 [mode 116] total vertebrae.

Geographical distribution (Fig. 156). It occurs in the Northwest Pacific Ocean from Japan to Taiwan.

Etymology. The name "*mitsukurii*" is in honor to Prof. Kakichi Mitsukuri from Japan.

Remarks.

Taxonomic status of *Flakeus mitsukurii*. *Flakeus mitsukurii* is a valid species and endemic to the Northwest and Central Pacific Oceans. These findings are in disagreement with Bigelow & Schroeder (1948, 1957), Bass *et al*. (1976), Compagno *et al*. (2005), Last *et al*. (2007), and White & Iglésias (2011) because they consider it as a species complex, the *S. mitsukurii* group, with worldwide distribution due to its similarities with other species.

Besides the characteristics provided in the current diagnosis, *F. mitsukurii* is easily distinguished from its closed related species (e.g. *F. japonicus, F. grahami, F. montalbani*, and *F. blainvillei*) and species within this subgroup by many morphological characters: shorter prenarial length in *F. mitsukurii* (4.1%–5.2% of TL for adults of *F. mitsukurii* vs. 5.2%–5.5% of TL for adults of *F. montalbani* vs. 5.0%–6.1% of TL for adults of *F. grahami*); shorter preoral length in *F. mitsukurii* (7.6%–9.9% of TL for adults of *F. mitsukurii* vs. 9.5%–11.0% of TL for adults of *F. montalbani* vs. 9.7%–11.2% of TL for adults of *F. grahami*); dorsal spines heavy in *F. mitsukurii,* base width of first dorsal spine 0.7%–0.9% of TL for adults of *F. mitsukurii* vs. 0.5%–0.7% of TL for adults of *F. japonicus* vs. 0.5%–0.8% of TL for adults of *F. grahami* and base width of second dorsal spine 0.7%–0.9% of TL for adults of *F. mitsukurii* vs. 0.7%–0.8% of TL for adults of *F. japonicus* vs. 0.6%–0.8% of TL for adults of *F. montalbani* vs. 0.6%–0.8% of TL for adults of *F. grahami*); smaller pelvic fins in *F. mitsukurii,* its inner margin length 4.2%–5.4% of TL vs. 5.2%–7.3% of TL for adults of *F. japonicus* vs. 5.2%–6.8% of TL for adults of *F. grahami*); narrower caudal fin, its caudal fork width 6.1%–6.8% of TL vs. 6.7%–7.7% of TL for adults of *F. montalbani* vs. 6.4%–7.4% of TL for adults of *F. grahami*). *Flakeus mitsukurii* also has deepest body at head and trunk than *F. japonicus* and *F. grahami,* its head height 10.5%–12.5% of TL (vs. 8.5%–10.5% of TL for adults of *F. japonicus* vs. 9.2%–10.8% of TL for adults of *F. grahami*) and its trunk height 11.4%–14.1% of TL (vs. 8.3%–11.6% of TL for adults of *F. japonicus* vs. 9.0%–11.4% of TL for adults of *F. grahami*).

Squalus montalbani and *S. chloroculus* Last, White & Motomura, 2007 were recently recognized from the Indo-West Pacific Ocean and distinct from *F. mitsukurii* based on molecular analysis and few morphological characters (Last *et al.*, 2007d). The present analysis show new characters for differentiating them, including first and second dorsal spines larger in *F. mitsukurii*, length of first dorsal spine 3.1%–5.0% of TL (vs. 2.7%–3.5% of TL for adults of *F. montalbani* vs. 2.4%–3.4% of TL for *F. chloroculus*), length of second dorsal spine 3.4%–5.3% of TL (vs. 3.0%–3.9% of TL for adults of *F. montalbani* vs. 2.7%–4.0% of TL for *F. chloroculus*). Other proportional measurements are also useful for separating them: mouth width 1.4–1.8 times greater than prenarial length (vs. 1.3–1.5 times for adults of *F. montalbani*); height of second dorsal fin 1.0–1.3 times length of second dorsal inner margin (vs. 0.9–1.1 for adults of *F. montalbani*); second dorsal spine 0.9–1.1 times length of first dorsal spine (vs. 1.1–1.3 for adults of *F. montalbani* vs. 1.1–1.4 times for *F. chloroculus*); length of pectoral anterior margin 1.8–2.3 times larger than length of pectoral inner margin (vs. 1.5–1.8 times for adults of *F. montalbani*).

Furthermore, the present study reveals that characteristics often addressed to the *S. mitsukurii* group may also be applied to other species of *Flakeus* that are not recognized within this complex, including *F. bucephalus* and *F. raoulensis* for large total length, *F. megalops*, *F. brevirostris* and *F. acutipinnis* for short dorsal spines and small dorsal fin. *Flakeus mitsukurii* has dark caudal bar prominent in neonates and young juveniles while in adults it is hardly noticed because body color and caudal fin turn dark grey to blackish with maturity, which it is in contrast to Last *et al*. (2007). All these results support the hypothesis of considering the Japanese species as a separate and valid species, endemic to the Northwestern and Central Pacific Oceans rather than a species widespread in different geographical regions and well beyond its type locality such as in the Eastern and Western Atlantic Oceans, West Indo-Pacific Ocean and Southeastern Pacific Ocean. These findings are in contrast to Compagno (1984), Compagno *et al*. (2005), Last *et al*. (2007), Sáez *et al*. (2010), and Ebert *et al*. (2013a). Species often misidentified with *F. mitsukurii* in these regions are recognized herein as separated and possibly undescribed species[1].

Another nominal species, *Squalus acutirostris* Zhu, Meng & Li, 1984, is often recognized in the North and Central West Pacific Oceans (e.g Muñoz-Chápuli & Ramos, 1989; Yuanding & Qingwen, 2001). Recently, this species was considered junior synonym of *F. mitsukurii* based on comparisons of the external measurements despite of some differentiation were noticed between them regarding interdorsal space, length of anterior margin of second dorsal fin and its base length, and length of dorsal caudal margin (White & Last, 2013). These authors suggested that difficulty on determining the origin of second dorsal fin would contribute to these variations. These variations are also supported in the present analysis and new morphometrics variations are also observed between them, such as: pre-second dorsal length (64.6% of TL for holotype and 63.9% of TL for paratype of *S. acutirostris* vs. 61.0%, 58.4%–60.5% and 59.4%–63.9% of TL for *S. mitsukurii*); pre-first dorsal length (32.3%, 31.8% of the TL vs. 32.4%, 30.2%–31.3% and 28.3%–31.8% of TL for *S. mitsukurii*); inner nostril-labial furrow space (6.9%, 8.6% of TL vs. 4.3%, 4.4%–5.3% and 3.9%–4.9% of TL for *S. mitsukurii*); internarial space (3.6%, 3.7% of TL vs. 4.7%, 4.0%–4.5% and 3.6%–5.1% of TL for *S. mitsukurii*); first dorsal height (6.0%, 5.6% of TL vs. 9.8%, 7.0%–9.8% and 6.9%–8.8% of TL for *S. mitsukurii*); second dorsal fin height (3.3%, 3.6% of TL vs. 6.8%, 4.8%–7.9% and 4.5%–6.6% of TL for *S. mitsukurii*); second dorsal spine length (2.8%, 1.9% of TL vs. 4.2%, 3.3%–4.4% and 3.4%–5.3% of TL for *S.*

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[1] These species are described and discussed later in this Chapter.

mitsukurii); head width at nostrils (6.8%, 5.2% of TL vs. 7.3%, 6.9%–7.7% and 6.6%–8.2% of TL for *S. mitsukurii*).

Squalus acutirostris is further distinct from *F. mitsukurii* by having shorter snout with nostrils clearly nearest to the snout tip than to the mouth, its prenarial length 0.6–0.7 times nostril-labial space (vs. larger snout with nostrils nearest to the mouth, its prenarial length 1.3, 1.1–1.4 and 1.1–1.2 times nostril-labial space) and narrower pectoral and pelvic fins (vs. conspicuously broad pectoral and pelvic fins). These characteristics are congruent to the observations of Zhu *et al*. (1984) and Yuanding & Qingwen (2001), and it supports the distinction between these two nominal species, which is in contrary to White & Last (2013).

Characteristics such as short snout and dermal denticles conspicuously tricuspid and rhomboid of *S. acutirostris* are intriguing because no other species of *Flakeus* show similar combined morphology (except *F. blainvillei*, *F. albifrons* and *F. notocaudatus* that has short snout and denticles weakly tricuspid but still lanceolate). Besides, no forms similar to *S. acutirostris* besides its type specimens were found in the present study, indicating that this species should be considered a *nomen dubium*. Investigations on other morphological aspects of *S. acutirostris* (e.g. vertebral counts, dentition, shape of dermal denticles) need to be achieved and new material collected from near its type locality, the South China Sea, are imperative in order to clarify its taxonomic status.

Other species that are often reported in the Northwest Pacific Ocean are *F. brevirostris*, *F. blainvillei* and *F. japonicus*. *Flakeus mitsukurii* is clearly distinct from the first two species by having more elongate snout (its prenarial length 4.1%–5.2% of TL vs.3.6%–4.2% of TL for adults of *F. blainvillei* vs. 3.8%–4.3% of TL for adults of *F. brevirostris*), although it is shorter than in *F. japonicus* (its prenarial length 5.9%–6.8% of TL for adults of *F. japonicus*). It also separated from *F. brevirostris* and *F. blainvillei* by having body much more robust (vs. slender body), and dermal denticles tricuspid and rhomboid (vs.

lanceolate and unicuspid). *Flakeus mitsukurii* is further distinguished from *F. japonicus* by smaller head (its length 20.4%–23.2% of TL vs. 23.0%–24.2% of TL for adults of *F. japonicus*), shorter prepectoral length (20.0%–22.7% of TL vs. 22.5%–23.6% of TL for adults of *F. japonicus*), and more elongate dorsal caudal margin (its length 20.1%–22.2% of TL vs. 19.6%–20.4% of TL for adults of *F. japonicus*).

Comparative material (2 specimens). SCSFRI D01562 (holotype of *S. acutirostris*), adult male, 635 mm TL, South China Sea, 18°51’N,112°41'E; SCSFRI D01548 (paratype of *S. acutirostris*), adult female, 975 mm TL, South China Sea. Specimens of *F. montalbani*, *F. grahami*, *F. japonicus*, *F. blainvillei*, *F. probatovi* listed in this Chapter.

Flakeus japonicus (Ishikawa, 1908)

(Japanese spurdog; Togari-tsunozame in Japanese)

Figs. 157–163; Tables 35, 37–38

Squalus japonicus Ishikawa, 1908: 71–73 (original description; not illustrated; type locality: Sagami Bay and Kagoshima, Japan); Chen *et al*., 1979: 26–42 (redescription; Japan); Parin, 1988: 48–49 (cited; Japan); Compagno & Niem, 1998: 1222, 1229 (listed, cited; Western North and Central Pacific Ocean); Compagno, 1999: 472 (listed); Yuanding & Qingwen, 2001: 311, 316–317 (cited, description; Northwest Pacific Ocean); nakabo, 2002: 155 (listed; Ryukyu Islands, Okinawa Trough, Southern Japan); Compagno *et al*., 2005: 75–76 (description; Northwest Pacific Ocean); Ward *et al*., 2007: 118, 123, 129, 130 (cited; Taiwan); Naylor *et al*., 2012a: 58 (cited; Taiwan); Naylor *et al*., 2012b: 42 (cited); Ebert *et al*., 2013a: 76, 90 (cited, description; Northwest Pacific Ocean); Nakabo, 2013: 194 (listed; Ryukyu Islands, Okinawa Trough, Southern Japan); Straube *et al*., 2013: 264–265 (cited; Taiwan); Shinohara *et al*., 2014: 233 (cited; Japan).

Squalus suckleyi not Girard: Fowler, 1941: 259 (listed; Japan).

Squalus sp. E Last & Stevens, 1994: 49, 96 (cited, description; Western Australia); Compagno *et al*., 2005: 80–81 (description; Western Australia).

Squalus nasutus Last, Marshall & White, 2007: 83–90 (original description, illustrated; type by original designation; Western Australia); Ward *et al*., 2007: 118, 123, 129, 130 (cited; Indonesia); Naylor *et al*., 2012a: 59 (cited; Western Australia); Naylor *et al*., 2012b: 42 (cited; Western Australia); Ebert, 2013: 53, 57 (listed, cited; Indo-Pacific Ocean); Ebert *et al*., 2013a: 74, 93 (cited, description; Indo-Pacific, Central Pacific Ocean); Ebert *et al*., 2013b: 286 (listed; Taiwan). New junior synonym.

Syntypes (3 specimens): ZUMT uncatalogued, juvenile male, unknown TL, adult male, 700 mm TL, female, unknown TL. All specimens cited by Ishikawa (1908) were deposited in the Imperial Museum of Tokyo. Syntypes are lost.

Type locality: Sagami Bay (through Tokyo Fish Market) and Kagoshima, Japan.

Non-type material (62 specimens): AMS I 22817-008, juvenile male, 362 mm TL, Northwest Shelf, 240 km north of Port Hedland, Western Australia; CSIRO H 2556-20, neonate female, 114 mm TL; six neonate males, 108-117 mm TL, West of Point Alison, Western Australia; CSIRO H 4132-02, adult male, 465 mm TL, Bolinao evening market, Philippines; CSIRO H 4132-03, juvenile female, 475 mm TL, Bolinao evening market, Philippines; CSIRO H 4132-04, adult female, 540 mm TL, Bolinao evening market, Philippines; CSIRO H 5860-01, adult female, 540 mm TL, Cilacap (South coast, central Java), Indonesia; CSIRO H 5860-02, adult female, 570 mm TL, Cilacap (South coast, central Java), Indonesia; CSIRO H 5860-03, adult female, 545 mm TL, Cilacap (South coast, central Java), Indonesia; CSIRO H 5860-13, neonate male, 155 mm TL, neonate female, 147 mm TL, Cilacap (South coast, central Java), Indonesia; CSIRO H 6125-04, adult male, 465 mm TL, Kedonganan, Jimbaran Bay (South coast of Bali), Indonesia; CSIRO H 6294-26, juvenile male, 440 mm TL, Tashi fish market, near I-Lan (NE coast), Taiwan; CSIRO H 6294-27, juvenile female, 360 mm TL, Tashi fish market, near I-Lan (NE coast), Taiwan; CSIRO H 6294-31, juvenile female, 540 mm TL, Tashi fish market, near I-Lan (NE coast), Taiwan; CSIRO H 6413-01, adult female, 580 mm TL, West of Shark Bay, Western Australia; CSIRO H 6484-01, adult female, 575 mm TL, Cilacap (South coast, central Java), Indonesia; HUMZ 40026, juvenile male, 215 mm TL, unknown locality; HUMZ 80223, adult male, unknown TL, near Okinawa, Japan, 25°33.8’N,126°25.2’E; HUMZ 95213, unknown sex and TL, East China Sea, 27°46’N,126°15.3’E; HUMZ 189642, adult male, 530 mm TL, East China Sea; HUMZ 189673, juvenile female, 430 mm TL, East China Sea; HUMZ 189675, juvenile female, 277 mm TL, East China Sea; HUMZ 189676, juvenile male, 288 mm TL, East China Sea; HUMZ 189678, adult male, 545 mm TL, East China Sea; HUMZ 189682, juvenile male, 365 mm TL, East China Sea; HUMZ 189685, adult female, 512 mm TL, East China Sea; HUMZ 189687, juvenile male, 380 mm TL, East China Sea; HUMZ 189689, juvenile male, 276 mm TL, East China Sea; HUMZ 189693, juvenile female, 380 mm TL, East China Sea; HUMZ 189695, juvenile female, 290 mm TL, East China Sea; HUMZ 189696, juvenile male, 291 mm TL, East China Sea; HUMZ 189701, juvenile male, 287 mm TL, East China Sea; HUMZ 189705, juvenile male, 282 mm TL, East China Sea; HUMZ 189735, adult male, 518 mm TL, East China Sea; HUMZ 189737, adult male, 560 mm TL, East China Sea; HUMZ 189738, adult male, 535 mm TL, East China Sea; HUMZ 189739, adult male, 530 mm TL, East China Sea; HUMZ 191688, juvenile female, 340 mm TL, Okinawa, Japan; HUMZ 191689, juvenile male, 281 mm TL, Okinawa, Japan; HUMZ 191691, juvenile male, 338 mm TL, Okinawa, Japan; HUMZ 191693, juvenile female, 410 mm TL, Okinawa, Japan; HUMZ 191694, juvenile female, 440 mm TL, Okinawa, Japan; HUMZ 191695, juvenile male, 338 mm TL, Okinawa, Japan; HUMZ 191697, juvenile female, 330 mm TL, Okinawa, Japan; HUMZ 191698, juvenile male, 388 mm TL, Okinawa, Japan; HUMZ 191699, juvenile female, 410 mm TL, Okinawa, Japan; NMMB P 15491, adult male, 593 mm TL, Pingtung county, Taiwan; NMMB P 15691, adult male, 540 mm TL, locality same as NMMB P 15491; NMMB P 15696, adult male, 580 mm TL, locality same as NMMB P 15491; NMMB P 15698, juvenile female, 448 mm TL, locality same as NMMB P 15491; NMMB P 15699, adult male, 513 mm TL, locality same as NMMB P 15491; NMMB P 15700, juvenile female, 443 mm TL, locality same as NMMB P 15491; NSMT-P 44380, adult male, 645 mm TL, Southern Japan, Japan; NSMT-P 47384, juvenile female, 433 mm TL, Central Pacific Ocean; NSMT-P 67530, adult female, 560 mm TL, Southern Japan, Japan; NSMT-P 91127, juvenile female, 410 mm TL, Southern Japan, Japan.

Diagnosis. Specimen of *Flakeus* clearly distinct from its congeners by snout conspicuously conical, obtuse at the tip and elongate (its length 5.8%–7.2% of TL); mouth markedly narrow, its width 5.3%–6.7% of TL in adult specimens; pectoral fins very narrow, its posterior margin length 6.8%–10.1% of TL, and its base length 4.0%–4.6% of TL in adults; caudal fin markedly slender on upper and lower lobes, and elongate (its dorsal caudal lobe 19.6%–21.8% of TL). It also differentiated from them by having pre-first dorsal length very large (31.8%–32.7% of TL in adult specimens), low gill slits (fifth gill slit height 1.5%–2.1% of TL for adults), and head very tapered its width at mouth 9.7%–10.5% of TL and its width at fifth gill slit 11.5%–12.3% of TL in adults.

Description. Description and range values are for specimens from Japanese waters.

External morphology (Figs. 157–161; Tabs. 35, 37). Body fusiform and skinny, somewhat arched from trunk to abdomen, turning slim to caudal fin; head height 0.8–1.1 times both trunk and abdomen heights. Head large (its length 23.0%–24.5% of TL), compressed and very narrow, its width 1.1–1.2 times trunk width and 1.0–1.6 times broader than abdomen width. Snout conspicuously conical and obtuse at the tip, very elongate (preorbital length 8.3%–10.1% of TL); anterior margin of nostrils slightly bilobed with first lobe larger than second lobe; nostrils much closer to the mouth than to the tip of the snout, its prenarial length 1.2–1.6 times the distance from nostril to upper labial furrow. Eyes oval with anterior margin convex and posterior margin notched; eyes elongate, its length 2.0–3.5 times greater than its height. Prespiracular length 0.6–0.7 times prepectoral length. Spiracles crescent, placed laterally just posterior the eyes; spiracles small, its length 0.2–0.4 times eye length. Prebranchial length 1.4–1.5 times larger than prespiracular length. Gill slits convex, located anteriorly to origin of pectoral fins; gill slits vertical and low with height of fifth gill slit 0.9-1.6 times height of first gill slit.

Preoral length 1.4–2.3 times greater than mouth width. Mouth markedly arched and narrow, its width 1.3–1.6 times broader than internarial width and 0.8–1.3 times prenarial length; upper labial furrow elongate (its length 1.9%–2.4% of TL) with fold very thin; lower labial furrow also elongate, although without fold. Teeth unicuspid and tiny on both jaws, although upper teeth smaller than lower teeth; cusp short and oblique, thicker on lower teeth than upper teeth; mesial cutting edge convex; mesial heel markedly notched; distal heel rounded; apron thick and short, somewhat conical in lower teeth. Two series of functional teeth on each jaws; 13–13 teeth rows in upper jaw; 11–11 teeth rows in lower jaw.

Pre-first dorsal length 1.3–1.4 times larger than prepectoral length. First dorsal fin evidently slender at fin web (broader in young juveniles) with anterior margin convex, posterior margin almost straight, although falcate distally, apex markedly rounded; first dorsal fin short, its length 1.5–1.9 times its height and 0.8–1.1 times length of second dorsal fin; first dorsal fin low, its height 1.1–1.6 times greater than length of inner margin; first dorsal inner margin elongate, its length 5.1%–6.1% of TL. First dorsal spine narrow (its base length 0.5%–0.7% of TL) and very short (its length 2.0%–3.8% of TL), reaching one-third to two-thirds the height of first dorsal fin. Interdorsal space 0.8–1.1 times prepectoral length and 1.8–2.4 times larger than dorsal caudal space. Pre-second dorsal length 2.6–2.8 times prepectoral length. Second dorsal fin slender at fin web with anterior margin concave, posterior margin concave and deeply falcate, fin apex rounded and lobe-like; second dorsal fin short, its length 1.8–2.5 times its height; second dorsal inner margin large, its length4.3%–5.5% of TL. Second dorsal spine slim (its base width 0.7%-1.0% of TL) and small (its length 4.1%–5.6% of TL), corresponding to 0.6–1.0 times height of second dorsal fin, almost reaching its apex; second dorsal spine 1.3–2.2 times larger than first dorsal spine.

Pectoral fin extremely narrow, its posterior margin length 6.8%–10.1% of TL; both anterior and inner margins convex, posterior margin concave (deeply concave in juveniles);

anterior margin length 1.4–1.7 times larger than length of posterior margin and length of inner margin; pectoral apex and free rear tip rounded, the latter lobe-like and reaching the horizontal line traced at pectoral apex (in juveniles, free rear tips transcend the fin apex). Pectoral-pelvic space 0.7–0.8 times pelvic-caudal space and 1.1–1.4 times larger than interdorsal space; pelvic fins in the midline between two dorsal fins, slightly nearest to first dorsal fin. Pelvic fins narrow with margins straight and free rear tips pointed; pelvic fins short, its length 9.6%–12.4% of TL. Clasper thin and small, transcending slightly the pelvic free rear tips, its inner margin length 0.5–1.3 times length of pelvic inner margin; clasper groove dorsal and longitudinal, elongate and open; apopyle rounded, anteriorly in the clasper groove; hypopyle constricted, located posteriorly in the clasper groove; rhipidion very thin and soft, flap-like, placed medially at distal end of the clasper.

Upper and lower caudal pits strongly marked; caudal keel prominent and lateral since insertion of second dorsal fin to behind origin of caudal fin. Caudal fin small, its length 0.8–0.9 times head length and 1.8–3.1 times length of preventral caudal margin; dorsal and ventral caudal lobes slender (dorsal lobe rectangular in juveniles); dorsal caudal tip pointed; dorsal caudal margin convex; upper postventral caudal margin markedly convex; lower postventral caudal margin straight; preventral caudal margin straight and short, its length 1.2–2.4 times greater than length of pelvic inner margin; ventral caudal tip rounded; caudal fork discontinuous markedly concave, and narrow, its width 6.0%–7.4% of TL.

Dermal denticles (Fig. 161). Tricuspid and markedly imbricated, its length slightly greater than its width; denticles conspicuously broad at the crown base; cusps posterior, prominent and pointed; lateral cusps shorter than median cusp, forming well marked concavity with median cusp; median ridge elongate anteriorly with anterior furrow shallow; anterior margin of the crown arrow-shaped (tapered in young juveniles); lateral ridges very thin, almost equal in length to median ridge.

Coloration. Body greyish brown dorsally; white laterally from insertion of pectoral fins to origin of caudal fin. Dorsal fins also greyish brown darker at its apex to half of the posterior margin, whitish at fin base and free rear tips; dorsal spine brown anteriorly, white posteriorly and at the tips. Pectoral fins grey, slightly darker near the anterior margin, posterior margin strongly white and uniform. Pelvic fins grey dorsally with white posterior margin; completely pale on ventral side. Caudal fin mostly greyish, light grey over vertebral column and dark grey near caudal origin; dorsal caudal margin somewhat white on its proximal end; upper postventral caudal margin not uniformly white, lower postventral caudal margin broadly white; preventral caudal margin grey; conspicuous black caudal stripe; upper caudal blotch very large and black, nearest to dorsal caudal tip; black caudal bar evident from caudal fork to midline of upper postventral caudal margin.

Vertebral counts (Tab. 38). 41–43 [mode 42] monospondylous vertebrae; 65–75 [mode 73] diplospondylous vertebrae; 84–88 [mode 87] precaudal vertebrae; 107–116 [mode 116] total vertebrae.

Geographical distribution (Fig. 162). It occurs in the Indo-Pacific Ocean from Southern Japan to Taiwan, and from Philippines to Western Australia.

Etymology. The name "*japonicus*" refers to its type locality, Japan.

Remarks. *Flakeus japonicus* is endemic to the Western Pacific Ocean from Japan and Taiwan to Philippines, Indonesia and Western Australian waters. Its occurrence in the East Pacific Ocean, East coast of Australia, waters off New Zealand, New Caledonia and Vanuatu are not observed. These findings are in congruence with Compagno (1984), Compagno & Niem (1998) but in contrast to Compagno *et al*. (2005), Last *et al*. (2007e), and Ebert *et al.* (2013a) that restricted its occurrences to the Japanese waters. These authors recognized *Squalus nasutus* Last, Marshall & White, 2007 (Fig. 163) recently described from Western Australia as a species separated from *F. japonicus*. The differentiation between these two species was supported on variations of precaudal and total vertebrae, and CO1 gene (Last *et al*., 2007e; Ward *et al*., 2007) even though differences on haplotypes suggested paraphyly on specimens from Taiwan. Other characteristics provided by these authors for separating *S. nasutus* from *F. japonicus* (e.g. pectoral-fin inner margin length; trunk height and width) are not noticed in the present study.

Many characteristics of the external morphology are intrinsically coincident between specimens from North Pacific and Central Indo-Pacific Ocean (Indonesia, Philippines and Australia) waters, including body coloration, shape of dermal denticles, dentition, and shape of dorsal, pectoral, pelvic and caudal fins, which indicates conspecificity. Morphometrics are also equivalent among them, except for: second dorsal fin height 5.3% of TL for holotype of *S. nasutus* (4.8%–5.4% of TL for paratypes of *S. nasutus*; 5.1%–5.4% of TL for specimens from Central Indo-Pacific Ocean) vs. 5.4%–7.3% of TL for *F. japonicus* from Japan; second dorsal length 10.9% (11.5%–13.0%; 10.1%–12.7%) of TL vs. 12.4%–16.1% of TL for *F. japonicus* from Japan; length of second dorsal anterior margin 8.6% (9.2%–11.2%; 8.1%–10.8%) of TL vs. 10.5%–14.5% of TL for *F. japonicus* from Japan; length of dorsal caudal margin 18.5% (19.4%–19.8%; 18.1%–19.4%) of TL vs. 19.6%–21.8% of TL *F. japonicus* from Japan. Variations on the length of second dorsal and caudal fins are also noticed when adult specimens are compared. Other differences in the precaudal length (79.7%–80.7% of TL vs. 81.4%–81.5% of TL for specimens from Central Indo-Pacific), pre-second dorsal length (61.3%–62.0% of TL vs. 62.4%–62.9% of TL for specimens from Central Indo-Pacific), prebranchial length (18.7%–20.4% of TL vs. 20.7%–21.7% of TL for specimens from Central Indo-Pacific), length of second dorsal spine (4.8%–5.6% of TL vs. 4.0%–4.4% of TL), and outer (4.3%–4.8% of TL vs. 5.6% of TL) and inner (7.2%–7.9% of TL vs. 9.1% of TL) length of clasper are also observed herein among adults.

Intraspecific variations in external measurements (e.g. interorbital space, interdorsal space, length of first dorsal fin, length of pectoral anterior margin, and width of head at nostrils) and vertebral counts are often reported between specimens from Indonesia, Philippines and Australia (Last *et al*., 2007e). However, these findings are not noticed in the current analysis. In fact, a specimen from the Philippines shows intermediate values between those of specimens from Japan and those from Western Australia. The present study further reveals that the range of values is continuous and uniform when compared all together (e.g. prepectoral length 22.5%–23.6% of TL vs. 23.6%–23.7% of TL for Central Indo-Pacific specimens; prenarial length 5.9%–6.8% of TL vs. 6.8%–6.9% of TL; mouth width 5.3%–6.7% of TL vs. 6.7%–6.8% of TL), which provides additional support for not recognizing *S. nasutus* as a separated species. Thus, the present study proposes *Squalus nasutus* as junior synonymy of *Flakeus japonicus*. The variations in morphometrics within this species are probably due to populational differentiation within the North Pacific and Central Indo-Pacific Oceans where is the expected range of its geographic distribution.

The current redescription of *F. japonicus* is in congruence with Ishikawa (1908) and Chen *et al*. (1979) with exception to the presence of two hooks in the clasper stated by Ishikawa (1908). These cartilages of the clasper probably concerns to the accessory terminal 3 cartilage (spur) and dorsal terminal cartilage (claw) that are observed for species of

Squaliformes. The data provided by Ishikawa (1908) of one of its syntype shows great differences with those of the present analysis, which indicate that the methodology for taking external measurements used by him are completely distinct from the methodology employed in this study. Last *et al*. (2007e) stated that *F. japonicus* are separated from the Central Indo-Pacific specimens by preoral length and eye length and that these values are corroborated when the syntype is compared, which it is in disagreement with the present analysis (preoral length (10.7%–12.5% of TL for Japanese specimens vs. 12.8%, 11.8%–13.0% of TL for types of *S. nasutus*; eye length 3.8%–5.2% of TL vs. 4.2%, 4.2%–5.3% of TL for types of *S. nasutus*). Besides, many other measurements present in Ishikawa (1908) are overlapped or greatly distinct to both type and specimens from North Pacific and Central Indo-Pacific Oceans, which indicates Last *et al*. (2007e) did not take it into account.

The present results also supports that grouping the Japanese spurdog together with *F. melanurus* and *F. rancureli* into a separate subgroup (*S. japonicus* subgroup) is unnecessary, which it is in contrast to findings of Last *et al*. (2007e). *Flakeus japonicus* bears exclusive morphological characteristics (external and skeletal) and no other species within the family Squalidae show similar pattern, including snout markedly elongate and body conspicuously slender from head to caudal fin, which are characteristics previously proposed to assemblage these three species together. Furthermore, new diagnostic characters proposed herein for separating this species from its congeners give additional support for this hypothesis. Potential type specimens of *S. japonicus* that could be still deposited at Zoological University Museum of Tokyo (previously Imperial Museum of Tokyo) are considered lost (Dr. M. Nakae from NSMT, *pers. comm*., 2014), which call up for future designation of a neotype of this species in order to better support its taxonomic status. No specimen collected from the same location of its type locality or nearby areas was analyzed in the current study, which makes harder to indicate any specimen as potential neotype. Future acquisition of material from Sagami Bay will be imperative for this purpose.

Comparative material (19 specimens): CSIRO H 2590-12, adult female, 503 mm TL, West of Leander Point, Western Australia, 29°15′S,113°56′E (holotype of *Squalus nasutus*). Paratypes of *Squalus nasutus* (18 specimens): CSIRO CA 3290, adult female, 550 mm TL, Southwest of Rowley Shoals, Western Australia, 18°10′S,118°18′E; CSIRO CA 4055, adult female, 525 mm TL, Southwest of Rowley Shoals, Western Australia, 18°11′S,118°14′E; CSIRO CA 4110, adult male, 493 mm TL, East of Rowley Shoals, Western Australia, 17°18′S,120°11′E; CSIRO H 1207-7, adult female, 532 mm TL, Northwest of Port Hedland, Western Australia, 18°20′S,117°50′E; CSIRO H 1207-8, adult female, 492 mm TL, Northwest of Port Hedland, Western Australia, 18°20′S,117°50′E; CSIRO H 1652-1, juvenile female, 316 mm TL, Northwest of Port Hedland, Western Australia, 18°25′S,117°48′E; CSIRO H 1652-2, juvenile female, 460 mm TL, Northwest of Port Hedland, Western Australia, 18°25′S,117°48′E; CSIRO H 1693-1, juvenile male, 360 mm TL, Rowley Shoals, Western Australia, 17°02′S,120°05′E; CSIRO H 1693-2, juvenile female, 307 mm TL, Rowley Shoals, Western Australia, 17°02′S,120°05′E; CSIRO H 1694-1, juvenile female, 420 mm TL, Rowley Shoals, Western Australia, 16°57′S,120°05′E; CSIRO H 2032-01, adult male, 460 mm TL, Rowley Shoals, Western Australia, 16°54′S,120°25′E; CSIRO H 2032-2, juvenile female, 404 mm TL, Rowley Shoals, Western Australia, 16°54′S,120°25′E; CSIRO H 2567-08, adult male, 467 mm TL, West of Dorre Island, Western Australia, 25°07′S,112°09′E; CSIRO H 2598-07, juvenile female, 463 mm TL, West of Green Head, Western Australia, 30°00′S,114°27′E; CSIRO H 2608-15, juvenile female, 413 mm TL, Rottnest Canyon, Western Australia, 31°55′S,115°10′E; CSIRO H 2898-07, juvenile male, 449 mm TL, Southwest of Rowley Shoals, Western Australia, 18°03′S,118°16′E; WAM P

28086-006, juvenile male, 380 mm TL; juvenile female, 450 mm TL, Rowley Shoals, Western Australia, 17°49′S,118°41′E.

Flakeus montalbani (Whitley, 1931)

(Philippine spurdog; Green-eyed dogfish)

Figs. 164–171; Tables 36–38

Squalus philippinus Smith & Radcliffe, 1912: 677, fig. 1 (original description; illustrated; Australia; junior homonym and preoccupied by *Squalus philippinus* Shaw, 1804, a synonym of *Heterodontus portusjacksoni* (Meyer, 1793)).
Squalus montalbani Whitley, 1931: 310 (cited only; Australia; replacement name for *S. philippinus* Smith & Radcliffe, 1912); Last, White & Motomura, 2007: 55–69 (resurrection, redescription; Australia); Ward *et al*., 2007: 117–130 (cited; Australia); Naylor *et al*., 2012a: 57 (cited; Australia); Naylor *et al*., 2012b: 42 (cited; Australia); Ebert, 2013: 53, 57, 63–64 (listed, cited, description; Philippines, Indonesia, Western Australia to New South Wales); Ebert *et al*., 2013a: 78, 93 (cited, description; Indo-West Pacific, Southwest Pacific Ocean); Ebert *et al*., 2013b: 286–287 (listed; Philippines to Westerm Australia); Straube *et al*., 2013: 265 (cited; Australia).
Squalus fernandinus not Molina: Fowler, 1941 (in part): 260–262 (cited, description; New South Wales to Southern Australia).
Squalus mitsukurii not Jordan & Snyder: Last & Stevens, 1994 (in part): 49, 101–102 (cited, description; Southwest pacific Ocean); Compagno *et al*., 2005 (in part): 77–78 (description; Philippines, Indonesia to South Australia).
Squalus chloroculus Last, White & Motomura, 2007: 55-69 (original description; illustrated; Australia); Ward *et al*., 2007: 117–130 (cited; Australia); Naylor *et al*., 2012a: 57 (cited; Australia); Naylor *et al*., 2012b: 42 (cited; Australia); Ebert, 2013: 53, 57, 59–60 (listed, cited, description; Southern Australia); Ebert *et al*., 2013a: 78, 86 (cited, description; Southwest Pacific Ocean). New junior synonym.

Holotype: USNM 70256, juvenile male, 311 mm TL, off Sombrero Island, west coast of Luzon Island, Philippines, 13°45′N,120°46′E, 425 meters depth; designated by Smith & Radcliffe (1912) as *Squalus philippinus* Smith & Radcliffe, 1912.

Paratypes: Not mentioned.

Type locality: Luzon Island, Philippines.

Non-type material (35 specimens): AMS I 43982-001, juvenile male, 565 mm TL, Jimbaran Bay, Bali, Indonesia; AMS I 45654-001, two adult females, 840–885 mm TL, Recorder Seamount, Queensland, Australia; CSIRO H 1203-2, juvenile female, 210 mm TL, North of Sahul Banks, Timor Sea, Western Australia, 11°33’S,124°58’E; CSIRO H 1290-2, juvenile male, 590 mm TL, East of Flinders Reefs, Queensland, Australia, 17°38'S,149°23'E; CSIRO H 1348-1, juvenile female, 374 mm TL, Northwest of Saumarez Reef, Queensland, Australia, 21°17'S,153°32'E; CSIRO H 2564-01, juvenile female, 405 mm TL, West of Bernier Island, Western Australia, 24°51'S,112°07'E; CSIRO H 2564-24, juvenile male, 415 mm TL, West of Bernier Island, Western Australia, 24°51'S,112°07'E; CSIRO H 2564-25, juvenile male, 325 mm TL, West of Bernier Island, Western Australia, 24°51'S,112°07'E; CSIRO H 2564-26, juvenile male, 370 mm TL, West of Bernier Island, Western Australia, 24°51'S,112°07'E; CSIRO H 2564-27, juvenile male, 390 mm TL, West of Bernier Island, Western Australia, 24°51'S,112°07'E; CSIRO H 2566-04, juvenile male, 415 mm TL, West of Bernier Island, Western Australia, 24°5'S,112°11'E; CSIRO H 2574-04, juvenile female, 222 mm TL, West of Freycinet Estuary, Western Australia, 26°35'S,112°29'E; CSIRO H 2606-02, juvenile female, 550 mm TL, West of Rottnest Island, Western Australia, 32°02'S,114°54'E; CSIRO H 2606-05, juvenile female, 605 mm TL, West of Rottnest Island, Western Australia, 32°02'S,114°54'E; CSIRO H 2606-06, adult male, 575 mm TL, West of Rottnest Island, Western Australia, 32°02'S,114°54'E; CSIRO H 2609-07, adult male, 620 mm TL, West of Rottnest Island, Western Australia, 32°07'S,115°06'E; CSIRO H 4623-01, juvenile female, 506 mm TL, East of Terrigal, New South Wales, Australia, 33°26'S,152°04'E; CSIRO H 4623-02, juvenile female, 482 mm TL, East of Terrigal, New South Wales, Australia, 33°26'S,152°04'E; CSIRO H 7054-01, neonate female, 105 mm TL, East of Sydney (Browns Mountain site), New South Wales, Australia, 34°02'S,151°39'E; CSIRO H 7054-02, neonate female, 105 mm TL, East of Sydney (Browns Mountain site), New South Wales, Australia, 34°02'S,151°39'E; CSIRO H 7054-03, six neonate female, 105–110 mm TL, neonate male, 105 mm TL, East of Sydney (Browns Mountain site), New South Wales, Australia, 34°02'S,151°39'E; CSIRO H 7066-01, juvenile female, 457 mm TL, SE of Coffs Harbour, New South Wales, Australia, 30°25'S,153°26'E; CSIRO H 7066-02, juvenile male, 456 mm TL, SE of Coffs Harbour, New South Wales, Australia, 30°25'S,153°26'E; CSIRO H 7143-08, juvenile female, 208 mm TL, juvenile male, 223 mm TL, NW of Cape Leveque, Western Australia, 15°54'S,120°45'E; MZUSP uncatalogued (previous CSIRO), adult male, 713 mm TL, East of Ballina, New South Wales, Australia; WAM P 28111-002, neonate female, 202 mm TL, Rowley Shoals, Western Australia, 18°00'S,118°20'E; WAM P 33377-001, juvenile female, 241 mm TL, Joseph Boneparte Gulf, Western Australia, 13°43'S,128°38'E.

Diagnosis. Large species of *Flakeus* that can be distinguished from its congeners by a combination of characters: snout rounded at tip and large, its preorbital length 7.1% (7.4%–10.2%) of TL; dorsal fins markedly broad at fin web and elongate (first dorsal fin length 14.2%, 12.2%–14.8% of TL; second dorsal fin length 13.4%, 10.8%–13.0% of TL); first dorsal spine very small, its length 2.1% (1.1%–3.5% of TL), not reaching half of fin height (its length 0.3, 0.1–0.4 times height of second dorsal fin); caudal fin rectangular with dorsal caudal margin elongate, its length 22.6% (20.0%–23.4%) of TL. It is also distinguished by having dermal denticles tricuspid with cusp conspicuously elongate and pointed, and caudal fin with black upper caudal blotch in the dorsal caudal margin and black caudal bar in the postventral caudal margin.

It clearly distinct from *F. mitsukurii* by body grey dorsally (vs. blackish to dark brown in *F. mitsukurii*) and caudal fin with black caudal bar at caudal fork in adults (vs. absent in adults). *Flakeus montalbani* is also differentiated from the Japanese species by having larger eyes (its length 4.1%–4.9% of TL for adult specimens of *F. montalbani* vs. 3.4%–4.0% of TL for adult specimens of *F. mitsukurii*) and lower fifth gill slit (its height 2.0%–2.3% of TL vs. 2.4%–2.6% adult specimens of *F. montalbani*).

Description. Measurements for holotype were taken from Last *et al*. (2007). Values for non-type material are given between brackets.

External morphology (Figs. 164–169; Tabs. 36, 37). Body robust, strongly arched from spiracles to pelvic fin insertion, equally deep from head to abdomen with head height 0.8 (0.9–1.0) times trunk height and 0.7 (0.8–1.0) times abdomen height. Head compressed anteriorly and elongate with its length 23.2% (22.6%–25.3%) of TL, comprising 1.0 (1.0–1.2) times dorsal-caudal margin length; head width 1.1 (1.0–1.3) times broader than trunk width and 1.5 (1.2–1.8) times wider than abdomen width. Snout rounded at tip (obtuse in young juveniles), and elongate with preorbital length 7.1% (7.4%–10.2%) of TL; anterior margin of nostrils bilobate, nearest to the mouth than to snout tip with prenarial length 0.9 (1.0–1.4) times the distance from nostrils to upper labial furrow; prenarial length 0.5 (0.5–0.6) times preoral length; internarial space 1.2 (0.5–1.2) times eye length. Eyes oval with anterior margin convex and posterior margin notched; eyes constricted and large, its length 4.3% (4.1%–6.6%) of TL and comprising 2.7 (2.0–3.5) times greater than its height. Prespiracular length 0.6 (0.5–0.6) times prepectoral length and 1.9 (1.3–1.8) times greater than preorbital length. Spiracles crescent and rather narrow, its length 0.3 (0.2–0.4) times eye length, placed more dorsally behind the eyes. Prebranchial length 1.5 (1.4–1.7) times greater than prespiracular length. Gill slits vertical and low with fifth gill slit 1.3 (1.0–1.5) times higher than first gill slit, placed anterior to origin of pectoral fins.

Preoral length 1.6 (1.2–1.4) times greater than mouth width. Mouth slightly arched and broad, its width 1.3 (1.5–2.2) times wider than internarial space and 1.4 (1.3–1.7) times greater than prenarial length; upper labial furrow large with a slim fold, its length 2.5% (2.0%–3.4%) of TL; lower labial furrow also elongate but without a fold. Teeth unicuspid, compressed labial-lingually, alike in both jaws with lower teeth larger than upper teeth; cusp very short, thick and oblique; mesial cutting edge straight; distal heel rounded and mesial heel moderately pointed; apron short and thick, placed in the middle of the crown base. Two series of functional teeth on upper and lower jaws; upper teeth 13–13 rows and lower teeth 11–11 rows.

Origin of first dorsal fin anterior to pectoral free rear tips; pre-first dorsal fin length 1.3 (1.2–1.4) times prepectoral length. First dorsal fin slightly triangular, wide at the fin web, and elongate, its length 14.2% (12.2%–14.8%) of TL; first dorsal fin low, its height 1.0 (1.1–1.5) times greater than its inner margin length; anterior margin convex, posterior margin concave and apex moderately rounded; free rear tip triangular; inner margin short, its length 6.2% (5.1%–6.6%) of TL. First dorsal spine slender and markedly short, not reaching half of fin height, its length 2.1% (1.1%–3.5%) of TL and corresponding to 0.3 (0.1–0.4) times height of first dorsal fin; first dorsal fin 1.1 (1.1–1.3) times larger than second dorsal fin. Interdorsal space 1.0 (0.9–1.2) times prepectoral length and 1.9 (2.0–2.8) times greater than dorsal-caudal space. Pre-second dorsal fin length 2.5 (2.5–2.8) times greater than prepectoral length and 2.5 (2.5–3.0) times larger than dorsal-caudal margin length. Second dorsal fin triangular with anterior margin convex and posterior margin concave, not falcate; inner margin also short, its length 5.9% (4.3%–5.5%) of TL; rounded and lobe-like at apex; free rear tip triangular; second dorsal fin low, its height 0.7 (0.9–1.3) times its inner margin length. Second dorsal spine convex, very slender and small, never reaching the fin apex with its length 0.9 (0.5–0.8) times height of second dorsal fin and 1.7 (1.1–3.2) times greater in length than first dorsal spine.

Pectoral fins with anterior and inner margins convex, posterior margin markedly concave; pectoral apex rounded and broad, slightly exceeding the horizontal line traced in the free rear tip; pectoral free rear tips rounded and strongly lobe-like; pectoral fins elongate, its anterior margin 1.5 (1.4–1.8) times greater in length than its inner margin and 1.4 (1.2–1.8) times larger than posterior margin length. Pectoral-pelvic space 0.7 (0.8–1.0) pelvic-caudal space; pelvic fins placed in the midline between the two dorsal fins. Pelvic fins with convex margins; pelvic free rear tips rounded and lobe-like; pelvic fins elongate, its length 10.1% (9.3%–12.1%) of TL. Claspers in adults exceeding slightly the pelvic fin, its inner length 1.5 (0.5–1.3) times length of pelvic inner margin; clasper groove dorsal, longitudinal and elongate; apopyle constricted, placed well anteriorly in the clasper groove; hypopyle rounded, located distally in the clasper groove; rhipidion flap-like, slender and elongate, placed medial-distally in the clasper.

Caudal keel inconspicuous (more evident in adults larger than 700 mm TL), placed from behind insertion of second dorsal fin to behind origin of caudal fin; upper and lower caudal pits prominent. Caudal fin rectangular, although slender distally in the dorsal caudal tip; dorsal caudal margin straight, upper postventral caudal margin markedly convex and straight distally, lower postventral caudal margin straight; preventral caudal margin somewhat straight and elongate, its length 3.3 (1.7–2.9) times greater than pelvic inner margin length; dorsal and ventral tips rather pointed; caudal fork discontinuous and relatively wide, its width 6.7% (6.7%–7.8%) of TL; dorsal caudal margin large, its length 1.0 (0.9–1.0) times head length and 1.9 (1.7–2.0) times greater than length of preventral caudal margin.

Dermal denticles (Fig. 169). Tricuspid and markedly imbricate, its length greater than its width, very broad at crown; cusps posterior and markedly pointed; median cusp larger than lateral cusps; median ridge conspicuous, thicker anteriorly than posteriorly, and elongate; anterior margin of crown arrow-shaped with anterior furrow shallow and two small ridges on each side; lateral ridges prominent, thin and shorter than median ridge.

Coloration. Body light grey and slightly darker anteriorly in the head dorsally, greyish ventrally. Dorsal fins dark grey, whitish on its base and blackish in the apex tip. Dorsal spines grey, somewhat black anteriorly and whitish at the tips. Pectoral fins grey, lighter ventrally with posterior margin white but not uniform. Pelvic fins light grey dorsally and white ventrally with margins moderately white. Caudal fin grey, whitish over vertebral column; postventral caudal margins broadly white except at caudal fork where it is a large and oblique black caudal bar; upper caudal blotch black and evident at dorsal caudal margin; black caudal stripe short (more prominent in adults); black basal marking ventrally near the lower precaudal pit (more evident in juveniles).

Vertebral counts (Tab. 38). Monospondylous vertebrae 38–45; precaudal vertebrae 84–85; total vertebrae 112–118.

Geographical distribution (Fig. 170). It occurs in the Indo-Pacific Ocean from Philippines to Australia, including New South Wales, Tasmania and Western Australia.

Etymology. The meaning of the name "*montalbani*" was not indicated by Whitley (1931).

Remarks. The nominal species *Squalus montalbani* was resurrected by Last *et al*. (2007d) as valid and endemic to Central Indo-Pacific Ocean based on material from Philippines, Indonesia and Australia (from Western Australia to New South Wales). Recently, the species was also recognized in Taiwan even though it formed a small separated cluster from the Australian specimens (Straube *et al*., 2013). Both studies analyzed very few specimens from its type locality (two specimens from Philippines only), which left open questions to the morphological characterization of this species. The same difficulty on analyzing material from this region is faced in the present study.

The current results show that specimens from Australia and Indonesia are very similar to the characteristics described and illustrated in the original description of this species provided by Smith and Radcliffe (1912) under the name *Squalus philippinus*. These results are also consistent with recent redescriptions of *F. montalbani* provided by Last *et al.* (2007d), Ebert (2013) and Ebert *et al.* (2013a). Thus, this species is considered valid and distributed in the Central Indo-Pacific Ocean where it is more abundant in all Australian territory from Western Australia to Tasmania. However, its recognition in Taiwanese waters is not supported herein and needs to be reinvestigated based on additional material.

A species recently described from Southern Australia, *S. chloroculus* (Fig. 171) shares great similarities with *F. montalbani* on its external and skeletal morphology such as particular coloration of the caudal fin, shapes of pectoral, dorsal and caudal fins, snout shape and dermal denticles, suggesting co-specificity between them. According to Last *et al.* (2007d), the differentiation between these two species are restricted to CO1 gene only and few variations on proportional measurements of the pre-first dorsal length and length of second dorsal fin, and pre-second dorsal length and second dorsal fin length. The present analysis, however, reveal that these differences are greatly overlapped between types of *S. chloroculus* and specimens of *F. montalbani*. In contrast to Last *et al.* (2007d), the current analysis further did not notice any differences in the length of first and second dorsal fins, width of first and second dorsal spines, and outer length of clasper between them. These measurements are also congruent when adult specimens of *F. montalbani* are compared to types of *S. chloroculus*. Vertebral counts are also overlapped between them, which give additional support to consider the latter species as its junior synonym. These findings are in disagreement with Ward *et al.* (2007), Straube *et al.* (2013), Ebert *et al.* (2013b), and Naylor *et al.* (2012a,b).

Intraspecific variations are noticed within *F. montalbani*, which it is consistent with results of Last *et al*. (2007f). Specimens from Indonesia are much darker in color than those from Australia, but no variations in the morphometrics and vertebral counts were noticed in the present analysis. Monospondylous, caudal and total vertebrae vary greatly in this species but its range is still within those expected for *F. montalbani* provided by Last *et al*. (2007d). Further comparisons between specimens from Philippines and those from Australia and Indonesia are needed in order to better characterize morphologically this species. All available redescriptions cited herein for *F. montalbani*, including the present one, were based on material from outside its type locality, which can hide important characteristics from its local form. Besides, the original description of *F. montalbani* was based in a juvenile male that possibly contributed to misidentifications because most of its characteristics may change with growth.

Flakeus mitsukurii is a Japanese species often considered synonym of *F. montalbani*. Besides the characteristics in the current diagnosis, the current results also support the validity of *F. montalbani* and its distinction from the former species based on larger preoral length in *F. montalbani* (9.5%–11.0% of TL vs. 7.6%–9.9% of TL for adult specimens of *F. mitsukurii*), smaller dorsal spines in *F. montalbani* (first dorsal spine length 2.7%–3.5% of TL vs. 3.1%–5.0% of TL for adult specimens of *F. mitsukurii* and 3.0%–3.9% of TL vs. 3.4%–5.3% of TL for adult specimens of *F. mitsukurii*), and wider caudal fin (its width at caudal fork 6.7%–7.7% of TL vs. 6.1%–6.8% of TL for adult specimens of *F. mitsukurii*). Some proportional measurements give additional support for their separation. Mouth width 1.3–1.5 times larger than prenarial length in *F. montalbani* (vs. 1.4–1.8 times in *F. mitsukurii*), height of second dorsal fin 0.9–1.1 times length of second dorsal inner margin (vs. 1.0–1.3 times in *F. mitsukurii*), and pre-second dorsal length 2.6–2.8 times larger than prepectoral length (vs. 2.7–3.1 times in *F. mitsukurii*).

Comparative material (15 specimens): CSIRO H 4775-01, adult male, 752 mm TL, off Portland, Victoria, Australia, 38°S,141°E (holotype of *Squalus chloroculus*). Paratypes of *Squalus chloroculus* (14 specimens): CSIRO CA 121, adult female, 725 mm TL, East of Ulladulla, New South Wales, Australia, 35°27'S,150°51'E; CSIRO H 1350-2, juvenile males, 220–227 mm TL; juvenile females, 217–225 mm TL, Northwest Macquarie Island, Tasmania, Australia, 41°52'S,144°23'E; CSIRO H 1405-1, adult male, 760 mm TL, South of King Island, Tasmania, Australia, 40°46'S,143°42'E; CSIRO H 1662-1, adult male, 720 mm TL, East of Maria Island, Tasmania, Australia, 42°42'S,148°24'E; CSIRO H 2867-02, adult male, 732 mm TL, Great Australian Bight, Southern Australia, 33°25'S,129°54'E; CSIRO H 2867-03, adult male, 678 mm TL, Great Australian Bight, Southern Australia, 33°25'S,129°54'E; CSIRO H 2867-04, adult female, 786 mm TL, Great Australian Bight, Southern Australia, 33°25'S,129°54'E; CSIRO H 2867-05, adult female, 782 mm TL, Great Australian Bight, Southern Australia, 33°25'S,129°54'E; CSIRO H 2966-01, adult female, 825 mm TL Great Australian Bight, Southern Australia, 33°47'S,131°27'E; CSIRO H 5941-01, adult male, 760 mm TL, West of Cape Sorell, Tasmania, Australia, 42°10'S,144°45'E; NMV A 29563-001, adult male, 856 mm TL.

Flakeus griffini **(Phillipps, 1931)**

(Griffin's dogfish)

Figs. 172–177; Tables 39, 42–43

Squalus griffini Phillipps, 1931: 360–361 (original description; off Hauraki Gulf, North Island, New Zealand; lectotype designated posteriorly in Whitley, 1940); Whitley, 1940: 138 (description, illustration, designation of lectotype by specimen illustrated; off Hauraki Gulf, New Zealand); Phillipps, 1946: 1516 (description, illustration; Auckland, New Zealand).

Lectotype. DM uncatalogued, juvenile female, 508 mm TL (about 20 inch long), off Hauraki Gulf, North Island, New Zealand.

Paralectotype: NMNZ P 662 (not *F. griffini*), adult female, 975 mm TL, North of Auckland, New Zealand. Collected by Stanford and Co. in September 1930.

Type locality: off Hauraki Gulf, North Island, New Zealand.

Non-type material (87 specimens): NMNZ P 2246, neonate female, 215 mm TL, neonate male, 220 mm TL, off Cape Egmont, Taranaki, North Island, New Zealand, 39°17’S,173°40’E; NMNZ P 2760, juvenile female, 456 mm TL, Lottin Point, Gisborne, North Island, New Zealand, 37°32’S,178°10’E; NMNZ P 22550, neonate male, 260 mm TL each, three neonate females, 206–262 mm TL, Louisville Ridge, 32°0’S,172°0’W; NMNZ P 23709, juvenile female, 426 mm TL, Chatham Islands, New Zealand, 43°48.6’S,177°25.6’W; NMNZ P 31821, two neonate male, 268–303 mm TL, neonate female, 288 mm TL, Southeast of Cape Runaway, Gisborne, North Island, New Zealand, 37°26’S,178°11.2’E; NMNZ P 34245, neonate male, 233 mm TL, Kermadec Islands, New Zealand, 30°2’S,178°42.8’E; NMNZ P 38327, juvenile male, 622 mm TL, unknown locality; NMNZ P 39441, juvenile female, 637 mm TL, Reinga Ridge, New Zealand, 33°23.57’S,170°12.30’E; NMNZ P 39886, adult male, 774 mm TL, off White Islands, Bay of Plenty, North Island, New Zealand, 37°28.4’S,177°8.8’E; NMNZ P 39890, two adult females, 862 mm TL, locality same as NMNZ P 39886; NMNZ P 39891, adult female, 788 mm TL, locality same as NMNZ P 39886; NMNZ P 39892, adult female, 755 mm TL, locality same as NMNZ P 39886; NMNZ P 39898, adult male, 780 mm TL, locality same as NMNZ P 39886; NMNZ P 39899, three neonate males, 224–226 mm TL, five neonate females, 202–223 mm TL, locality same as NMNZ P 39886; NMNZ P 39900, two neonate males, 230 mm TL each, four neonate females, 217–227 mm TL, locality same as NMNZ P 39886; NMNZ P 39903, juvenile male, 608 mm TL, Chatham Islands, New Zealand, 43°51.7'S,175°28.6'W; NMNZ P 39906, juvenile female, 593 mm TL, Chatham Islands, New Zealand, 43°54.1'S,179°9.2'W; NMNZ P 40274, two juvenile males, 545–702 mm TL, adult male, 605 mm TL, juvenile female, 602 mm TL, Chatham Islands, New Zealand, 43°33.4'S,177°22.9'W; NMNZ P 40346, adult male, 813 mm TL, off Tolaga Bay, Gisborne, North Island, New Zealand, 38°13.3'S,178°19.7'E; NMNZ P 41224, juvenile female, 540 mm TL, Chatham Islands, New Zealand, 43°56.1'S,177°25.1'W; NMNZ P 41225, juvenile female, 572 mm TL, adult male, 693 mm TL, Chatham Islands, New Zealand, 43°31.4'S,177°25'W; NMNZ P 41226, adult male, 792 mm TL, Chatham Islands, New Zealand, 43°33.5'S,177°39.9'W; NMNZ P 41336, juvenile female, 634 mm TL, adult female, 885 mm TL, Hawke's Bay, North Island, New Zealand, 39°39'S,177°48.3'E; NMNZ P 41775, juvenile female, 412 mm TL, Hawke's Bay, North Island, New Zealand, 40°15.8'S,177°1.5'E; NMNZ P 42761, juvenile male, 533 mm TL, West off Kahurangi Point, Nelson, South Island, New Zealand, 40°56.7'S,171°18.5'E; NMNZ P 43049, neonate male, 225 mm TL, four neonate females, 218–226 mm TL, off White Island, Bay of Plenty, North Island, New Zealand, 37°28.4'S,177°8.8'E; NMNZ P 43051, four male, 196–254 mm TL, five neonate females, 193–260 mm TL, Louisville Ridge, 32°0'S,172°0'W; NMNZ P 46540, neonate male, 257 mm TL, four neonate females, 250–255 mm TL, Three King Islands, New Zealand, 34°5.5'S,172°4.7'E; NMNZ P 46541, neonate female, 254 mm TL, four neonate males, 254 mm TL each, locality same as NMNZ P 46540; NMNZ P 52102, adult male, 835 mm TL, Kermadec Islands, New Zealand, 29°17.6'S,178°2.1'W; NMNZ P 52103, adult male, 770 mm TL, locality same as NMNZ P 52102; NMNZ P 52104, adult male, 890 mm TL, locality same as NMNZ P 52102; NMNZ P 52105, adult female, 880 mm TL, locality same as NMNZ P 52102; NMNZ P 52106, adult female, 692 mm TL, locality same as NMNZ P 52102; NMNZ P 52108, adult male, 840 mm TL, locality same as NMNZ P 52102; NMNZ P 52121, adult female, 909 mm TL, Kermadec

Islands, New Zealand, 29°19.1’S,178°3.3’W; NMNZ P 52226, three neonate females, 198–205 mm TL, three neonate males, 192–199 mm TL, Kermadec Islands, New Zealand, 29°17.9’S,177°54.4’W; TPM 10388, adult female, 1000 mm TL, locality same as NMNZ P 46540.

Diagnosis. Species of *Flakeus* that differs from its congeners by having pelvic fins nearest to second dorsal fin than first dorsal fin, caudal fin light grey with conspicuous white caudal bar from up to caudal fork.

Flakeus griffini has more monospondylous vertebrae (47, 46–49) than *F. edmundsi* (43–45), *F. hemipinnis* (37), *F. montalbani* (38–45), *F. japonicus* (37–43), and *F. grahami* (41–42), and *F. raoulensis* (42–44). It is also distinct from *F. raoulensis* by more total vertebrae (117–121 vs. 114–115 for *F. raoulensis*).

Description. Single values are for paralectotype. Range values are for non-type specimens.

External morphology (Figs. 172–176; Tabs, 39, 42). Body slender and fusiform, slightly arched dorsally from posterior margin of the eye to origin of first dorsal fin; equally deep from head to trunk, its head height 1.2 (0.9–1.1) times trunk height and 1.5 (0.8–1.2) times abdomen height; body with greatest width at head, its width 1.0 (1.1–1.4) times trunk width and 1.1 (1.1–1.9) times abdomen width. Head markedly elongate, its length 22.8% (21.7%–25.0%) of TL, and flattened dorsal-anteriorly; head broader at mouth than at nostrils, it width at mouth 11.0% (10.5%–12.8%) of TL and its width at nostrils 6.7% (6.9%–8.3%) of TL. Snout obtuse at tip and elongate, its preorbital length 7.6% (7.7%–9.0%) of TL; anterior margin of nostrils bilobed, nearest to mouth than to tip of snout; prenarial length 1.2 (1.1–1.3) times larger than distance from nostrils to upper labial furrow, and 0.6 (0.5–0.6) times preoral length; internarial space 1.1 (0.6–1.2) times length of eye. Eyes oval with anterior margin concave and posterior margin notched; eyes very large, its length 2.9 (2.2–4.4) times its height. Prespiracular length 0.5 (0.6) times prepectoral length and 1.6 (1.5–1.7) times greater than preorbital length. Spiracles crescent and small, its length 0.3 (0.2–0.4) times eye length, placed laterally just behind the eyes. Prebranchial length 1.6 (1.4–1.5) larger than prespiracular length. Gill slits vertical, somewhat straight and low, located laterally in front of pectoral fins; fifth gill slit 1.2 (0.9–1.4) times greater in height than first gill slit.

Preoral length 1.2 (1.2–1.6) times mouth width; mouth arched and conspicuously broad, its width 1.7 (1.5–2.0) times broader than internarial space and 1.5 (1.2–1.5) times prenarial length; upper labial furrow large with thick fold, its length 2.2% (2.0%–2.7%) of TL; lower labial furrow much larger than upper one, lacking fold. Teeth unicuspid and similar in both jaws; upper teeth much smaller than lower teeth and slightly different in shape; mesial cutting edge convex on upper teeth and straight on lower teeth; mesial heel notched and distal heel rounded; cusp small, thick and oblique; apron thinner and more elongate on upper teeth than lower teeth, and somewhat convex while it is straight on lower teeth. Two series of functional teeth on upper and lower jaws. Upper teeth 13–13 rows and lower teeth 10–10 rows.

Pre-first dorsal length 1.3 (1.2–1.5) times prepectoral length; origin of first dorsal fin over midline between origin of pectoral fins and pectoral free rear tips. First dorsal fin slender at apex with anterior margin convex and posterior straight, although slightly concave near free rear tips; first dorsal apex pointed; first dorsal fin elongate, its anterior margin length 9.9 (10.7%–14.9%) of TL; first dorsal fin upright and somewhat tall, its height 1.4 (1.2–1.8) times length of its inner margin; inner margin of first dorsal large, its length 5.3% (4.9%–7.0%) of TL. First dorsal spine thin, its base width 0.6% (0.5%–0.7%) of TL, and small, its length 0.4 (0.2–0.5) times height of first dorsal fin. Interdorsal space 2.7 (1.9–2.8) greater than dorsal-caudal space and 1.1 (0.9–1.2) times prepectoral length. First dorsal fin

1.1 (1.0–1.2) times greater in length than second dorsal fin. Pre-second dorsal length 2.8 (2.4–3.2) times greater than prepectoral length; origin of second dorsal fin over pelvic free rear tips. Second dorsal fin slender at apex, large, its length 11.6% (11.8%–13.5%) of TL, oblique and somewhat tall, its height 1.2 (1.1–1.6) times length of its inner margin; second dorsal fin with anterior margin convex, and posterior margin notched and markedly falcate; apex rounded and lobe-like (pointed in young juveniles). Second dorsal spine thin, its base width 0.7% (0.6%–1.0%) of TL, and short with its tip rarely reaching the apex of second dorsal fin, its length 0.6 (0.5–1.0) times height of second dorsal fin; second dorsal spine 1.0 (1.2–2.2) times larger than first dorsal spine.

Pectoral fin broad, its posterior margin length 10.0% (8.0%–12.6%) of TL; pectoral anterior and inner margins convex, and posterior margin straight; pectoral anterior margin 2.0 (1.5–2.2) times larger than inner margin and 1.4 (1.2–1.6) times greater than length of posterior margin; pectoral apex and free rear tips rounded. Pectoral-pelvic distance 1.1 (0.8–1.1) times distance from pelvic to caudal fin; pelvic fins conspicuously nearest to second dorsal fin than to first dorsal fin. Pelvic fins with margins slightly convex and free rear tips pointed and lobe-like; pelvic fins small, its length 10.7% (9.3%–12.7%) of TL. Claspers heavy and short, slightly transcending tips of pelvic fins, its inner margin length 0.5–1.3 times length of pelvic inner margin; clasper groove dorsal, horizontal and short; apopyle constricted, placed anteriorly in the clasper groove; hypopyle also constricted, placed distally in the clasper groove; rhipidion flap-like, thin and short, located medial-distally on clasper.

Upper and lower precaudal pits profound; caudal keel lateral and conspicuous, located from insertion of second dorsal fin to origin of caudal fin. Caudal fin elongate, its dorsal caudal margin 0.9 (0.8–1.1) times head length and 2.0 (1.7–2.1) times larger than length of preventral caudal margin; caudal fin somewhat rectangular with dorsal caudal margin straight, upper postventral caudal margin conspicuously convex, and lower postventral caudal margin straight; preventral caudal margin markedly convex and short, its length 2.2 (1.8–2.6) times larger than length if pelvic inner margin; caudal fin somewhat broad at caudal fork, its width 6.6% (6.6%–7.9%) of TL; dorsal and ventral caudal tips rounded.

Dermal denticles (Fig. 175). Tricuspid and rather imbricate, broad at crown with its length almost equal to its width; median cusp prominent, thick, posterior and pointed; lateral cusps weakly pointed, although thick, smaller than median cusp; median ridge markedly thick; lateral ridges thick and much shorter than median one; anterior margin of crown conspicuously elongate and broad, arrow-shaped with two small ridges.

Coloration. Body light grey to grey dorsally, white ventrally and laterally on lower half of the body since vertical at insertion of first dorsal fin to origin of caudal fin. Dorsal fins light grey with apex narrowly dark grey; dorsal fins with free rear tips and fin base whitish; first dorsal fin with lower half of its anterior margin rather whitish. First dorsal spine white, somewhat brownish anteriorly, and second dorsal spine light brown anteriorly and white from its upper half to the tip. Pectoral fins grey dorsally and white ventrally; pectoral posterior margin uniformly white. Pelvic fins light grey dorsally and white ventrally; anterior and posterior pelvic margins broadly white. Claspers with black and rounded spot medially and prior to rhipidion; large and oval black spot anterior-laterally. Caudal fin mostly light grey with upper caudal lobe grey and lower caudal lobe white; dorsal caudal margin somewhat dark grey; postventral caudal margins white; conspicuous white caudal bar from caudal fork up to upper postventral caudal margin till level of vertebral column; preventral caudal margin grey; black caudal stripe evident. Neonates and young juveniles differ from adults by having pectoral and pelvic fins mostly white, except at fin base where it its grey. It also shows: first dorsal fin with its anterior margin conspicuously white from down its lower half; first and second dorsal fins with apex blackish; second dorsal fin with posterior margin white; caudal fin with two upper black caudal blotches over tip of vertebral column (small and rounded) and distally at dorsal caudal margin (large and oval); oblique black caudal bar evident on lower lobe and black caudal marking at origin of lower lobe.

Vertebral counts (Tab. 43). 47 (46–49 [mode 47]) monospondylous vertebrae; 91 (86–92 [mode 90]) precaudal vertebrae; 121 (117–120 [mode 118]) total vertebrae.

Geographical distribution (Fig. 176). It occurs in waters from North to South New Zealand, including Kermadec Islands in the Southwest Pacific Ocean.

Etymology. The name "*griffini*" is honor to Louis T. Griffin, an ichthyologist from Auckland Museum.

Remarks.

Morphological variations within *Flakeus griffini*. Some specimens from New Zealand show great variations in morphology, which it is in agreement with Duffy & Last (2007b). The origin of dorsal fins is over or behind the vertical traced at pectoral free rear tips as well as the second dorsal fin has its origin far behind the pelvic free rear tips in the paralectotype and new analyzed material (vs. origin of first dorsal fin prior to pectoral free rear tips, origin of second dorsal fin over pelvic fins in the lectotype and specimens of *F. griffini*). Dorsal fins are somewhat tall, upright and slender at apex in most specimens, although dorsal fins more triangular and low are also noticed. Variation in the dorsal fins was reported earlier by Duffy & Last (2007b) for this species.

Caudal fin in some specimens are more much slender at upper lobe with dorsal caudal margin straight while others, including lectotype, show caudal fin with dorsal caudal margin convex and upper caudal lobe broad. Its color also varies between specimens from mostly light grey with lower caudal lobe whitish to caudal fin grey or brown with postventral caudal margins narrowly white, except above caudal fork where it is broadly white, which it is in agreement with Duffy & Last (2007b).

Dermal denticles are conspicuously tricuspid and imbricate, very broad at crown with its length greater than its width, cusps pointed, and anterior margin arrow-shaped, short and wide. Besides, two lateral ridges are markedly evident on each side of the dermal denticle in these specimens. These characteristics are similar to those noticed in the paralectotype and those observed for *F. griffini* in Duffy & Last (2007b). In contrast, the dermal denticles described herein for this species has lateral cusps weak and short, anterior margin of crown well elongate and wide, and a single lateral ridge is observed on each side. These results are in congruence with Duffy & Last (2007b) that reported variations in the shape of dermal denticles in *F. griffini*.

Morphological variations on these specimens are very consistent and easily to separate from each other into two different forms. One of these forms that was previously identified as *F. griffini* (e.g. Duffy & Last, 2007b) possible comprises an undescribed species. It is preferred for nomenclatural stability to retain it as a variation within *F. griffini* until further investigation on the vertebral counts and skeletal morphology.

Taxonomic status of *Flakeus griffini*. Phillipps (1931) cited *Squalus griffini* on his paper about new species from New Zealand but retained his effort to describe the nominal species *S. kirki*. This author distinguished the former species from *S. acanthias* by lacking white spots on body, less prominent cusp on teeth, and heavy second dorsal spine. No further information regarding *Squalus griffini* was given in the original description with exception to two syntypes collected off Hauraki Gulf. Later, Whitley (1940) provided a better description and designated its lectotype by means of specimen illustrated that was given by Phillipps (Article 74, ICZN). The illustration was reproduced by Phillipps (1946) but with more accuracy regarding its body coloration. In both, the lectotype of *F. griffini* exhibits dorsal fin upright, slender at apex and tall preceded by short spines, body robust, first dorsal fin with its origin over insertion of pectoral fins, and origin of second dorsal fin just prior to vertical traced at pelvic free rear tips. Dorsal fins, pectoral and caudal fins are mostly whitish or light grey in the illustration of the lectotype, and body is dark dorsally and markedly whitish laterally from a vertical traced at insertion of first dorsal fin to behind caudal fin origin. Whitley (1940), however, described its body as greyish while Phillipps (1946) stated to be brown. The second specimen deposited at Dominion Museum (today NMNZ P 662) is the paralectotype (Fig. 177), which Phillipps retained as "type" for purpose of collection management in that time (as it is noticed in the old tag attached to the specimen) but never designated it as such on posterior publications, indicating that Duffy & Last (2007b) equivocality consider it as the holotype of *Flakeus griffini*.

The current analysis of the paralectotype reveals that dorsal fins are triangular and somewhat low, origin of first dorsal fin is just behind vertical at pectoral free rear tips, second dorsal fin with its origin far behind pelvic fins, and caudal fin is more slender at upper lobe. Body color is dark brown and no evidence of white fins or white margins of the fins are noticed. These morphological differences between the specimen illustrated (lectotype) and the paralectotype are clearly contrasting, indicating that the description and illustration of Phillipps are based on two distinct forms. Recently, Duffy & Last (2007b) redescribed *F. griffini* and reported great morphological variations among its specimens that are also supported in the present study. However, these authors still considered the specimen deposited at Te Papa Museum as the holotype of this nominal species. These findings give additional support for the current hypothesis regarding the taxonomic confusion of *F. griffini*. Morphological characteristics observed in the paralectotype and other specimens from New Zealand (herein identified as *Flakeus* cf. *griffin*; Fig. 177) belongs to a possible undescribed species, and it needs further investigation. Furthermore, it is important to notice that the lectotype no longer exists, which requires the designation of a neotype for *F. griffini*.

Flakeus griffini is sympatric with *F. raoulensis* in New Zealand waters. It differs easily from this species by having dermal denticles tricuspid and rhomboid (vs. unicuspid and lanceolate in *F. raoulensis*), larger pectoral inner margin, its length 7.4%–8.7% of TL (vs. 9.0%–11.0% of TL for adults of *F. raoulensis*). Species in the West Pacific Ocean that are similar to *F. griffini* are *F. grahami*, *F. japonicus*, *F. mitsukurii*, and *F. montalbani*. *Flakeus griffini* differs from *F. grahami*, *F. japonicus* and *F. lalannei* by having wider mouth, its width 7.7%–8.0% of TL in adult specimens (vs. 7.0%–7.6% of TL for adults of *F. grahami* vs. 5.3%–6.8% of TL for adults of *F. japonicus* vs. 6.8%–7.0% for *F. lalannei*). It is further distinguished from *F. japonicus* by shorter pre-first dorsal length 28.2%–31.1% of TL in adults (vs. 31.2%–32.8% of TL for adults of *F. japonicus*) and shorter pelvic-caudal space 22.9%–25.9% of TL in adults (vs. 26.2%–28.7% of TL for adults of *F. japonicus*). The pelvic-caudal space is also distinct from those of *F. probatovi* that comprises 15.3%–20.3% of TL in adult specimens.

Flakeus griffini also has more slender first dorsal spine than *F. probatovi*, its base width 0.6%–0.7% of TL in adults (vs. 0.9%–1.1% of TL for adults of *F. probatovi*). It is distinct from *F. mitsukurii* by more elongate snout, its prenarial length 5.2%–5.9% of TL for adults (vs. 4.1%–5.2% of TL for adults of *F. mitsukurii*), and from *F. montalbani* by showing more elongate second dorsal fin, its anterior margin length 10.0%–11.3% of TL for adults (vs.

5.3%–10.0% of TL for adults of *F. montalbani*) and smaller preventral caudal margin, its length 10.3%–11.7% of TL for adults (vs. 11.7%–12.6% of TL for adults of *F. montalbani*).

Comparative material: *Flakeus* cf. *griffini* (25 specimens): NMNZ P 20982, adult male, 778 mm TL, Chatham Islands, New Zealand, 43°43.9’S,175°49.5’W; NMNZ P 39886, adult male, 775 mm TL, adult female, 915 mm TL, off White Island, Bay of Plenty, North Island, New Zealand, 37°28.4’S,177°8.8’E; NMNZ P 39887, adult female, 910 mm TL, locality same as NMNZ P 39886; NMNZ P 39888, two adult females, 911–965 mm TL, locality same as NMNZ P 39886; NMNZ P 39893, two adult females, 860–995 mm TL, locality same as NMNZ P 39886; NMNZ P 39894, adult female, 935 mm TL, locality same as NMNZ P 39886; NMNZ P 39895, two adult females, 968–970 mm TL, locality same as NMNZ P 39886; NMNZ P 39897, two adult females, 810–830 mm TL, locality same as NMNZ P 39886; NMNZ P 39898, adult female, 862 mm TL, locality same as NMNZ P 39886; NMNZ P 39901, adult male, 875 mm TL, Chatham Islands, New Zealand, 43°12.5’S,177°31.9’W; NMNZ P 39908, adult female, 820 mm TL, East Chatham Rise, 43°56.3’S,175°33.1’W; NMNZ P 39910, adult male, 836 mm TL, Hawke’s Bay, North Island, New Zealand, 40°2.5’S,177°19.5’E; NMNZ P 40346, adult male, 798 mm TL, off Tolaga Bay, Gisborne, North Island, New Zealand, 38°13.3’S,178°19.7’E; NMNZ P 40347, adult female, 915 mm TL, locality same as NMNZ P 40346; NMNZ P 40348, adult female, 882 mm TL, locality same as NMNZ P 40346; NMNZ P 44165, adult male, 735 mm TL, North Auckland, North Island, New Zealand, 35°38.8’S,175°29’E; NMNZ P 47743, adult female, 903 mm TL, off Mercury Island, South Auckland, North Island, New Zealand, 36°33’S,175°46’E; NMNZ P 52107, adult male, 940 mm TL, Kermadec Islands, New Zealand, 29°17.6’S,178°2.1’W; NMNZ P 52122, adult female, 1570 mm TL, Kermadec

Islands, New Zealand, 29°18.9’S,178°2.6’W; NMNZ P 52223, adult female, 1350 mm TL, Kermadec Islands, New Zealand, 29°17.9’S,177°54.4’W.

Flakeus melanurus (Fourmanoir & Rivaton, 1979)

(**Blacktailed spurdog; Aiguillat à queue noire** in French)

Figs. 178–184; Tables 40, 42–43

Squalus melanurus Fourmanoir & Rivaton, 1979: 438–439, figs. 27 (original description, illustrated; Uatio and Bulari, New Caledonia; type by original designation); Compagno, 1984: 120 (description; Uation and Bulari, New Caledonia); Compagno & Niem, 1998: 1215, 1230 (cited; New Caledonia); Baranes, 2003: 45, 49 (cited; New Caledonia); Compagno *et al*., 2005: 77 (description; Noumea); Fricke *et al*., 2011: 346 (cited; Southwestern Grande Terre, New Caledonia).

Squalus rancureli Fourmanoir & Rivaton, 1979: 437–438, figs. 25–26 (original description, illustrated; Vate, New Caledonia and Espiritu Santo, Vanuatu; type by original designation); Compagno, 1984: 122–123 (description; Vate, Vanuatu); Compagno & Niem, 1998: 1215, 1231 (cited; Vanuatu); Baranes, 2003: 45, 49 (cited; Vanuatu); Compagno *et al*., 2005: 78 (description; Vanuatu); Fricke *et al*., 2011: 346 (cited; New Caledonia). New junior synonym.

Holotype. MNHN 1980-0460, adult male, 670 mm TL, New Caledonia, collected between 320–340 meters depth. Collected by ORSTOM on 10 April 1978.

Paratypes: not mentioned.

Type locality: New Caledonia

Non-type material (15 specimens): MNHN 1987-1203, adult female, 640 mm TL, Vate, Vanuatu, 17°30'S,167°30'E; MNHN 1987-1204, adult female, 675 mm TL, Vate, Vanuatu, 17°55'1”S,128°19'59”E; MNHN 1997-3606, adult female, 730 mm TL, unknown locality; MNHN 1997-3607, adult female, 750 mm TL, unknown locality; MNHN 1997-3617, adult male, 680 mm TL, New Caledonia, 23°43'1”S,168°15'0”E; MNHN 1997-3619, juvenile female, 527 mm TL, New Caledonia, 23°43'1”S,168°15'0”E; MNHN 1997-3621, adult male, 647 mm TL, Norfolk Island, 17°30'S,167°30'E; MNHN 1997-3622, adult male, 662 mm TL, Norfolk Island, 17°30'S,167°30'E; MNHN 1997-3624, adult male, 650 mm TL, Norfolk

Island, 17°30'S,167°30'E; MNHN 1997-3625, adult male, 645 mm TL, Norfolk Island, 17°30'S,167°30'E; MNHN 1997-3627, adult female, 690 mm TL, Norfolk Island, 17°30'S,167°30'E; MNHN 1997-3628, adult female, 695 mm TL, Norfolk Island, 17°30'S,167°30'E; MNHN 2002-1196, adult male, 655 mm TL, New Caledonia; MNHN 2002-1197, adult male, 680 mm TL, New Caledonia; MNHN 2002-1392, adult female, 665 mm TL, New Caledonia, 23°1'1”S,166°55'1”E.

Diagnosis. *Flakeus melanurus* is distinguished from its congeners by: conspicuous black ventral caudal lobe; snout obtuse and markedly elongate, its preorbital length 9.6% (10.0%–10.9%) of TL; more elongate distance from nostrils to tip of snout, comprising 6.9% (7.2%–8.4% of TL; larger preoral length, corresponding to 12.6% (12.7%–14.3%) of TL; more elongate distance from spiracle to tip of snout, its length 14.7% (15.3%–16.8%) of TL. It is further distinct from its congeners by having broader internarial space, its width 5.1% (5.1%–6.1%) of TL, and more elongate second dorsal spine, its length 6.2% (5.7%–6.7%) of TL. Adult specimens of *F. melanurus* has taller first dorsal fin than *F. japonicus*, its height 8.2%–10.3% of TL (vs. 6.6%–7.5% of TL for *F. japonicus*).

The New Caledonian species differs from *F. mitsukurii*, *F. edmundsi*, *F. hemipinnis*, *F. griffini* and *F. probatovi* by monospondylous vertebrae (41 vs. 42–46 for *F. mitsukurii* vs. 43–44 for *F. edmundsi* vs. 37 for *F. hemipinnis* vs. 46–49 for *F. griffini* vs. 45–48 for *F. probatovi*).

Description. Single values are for holotype. Range values are for non-type specimens.

External morphology (Figs. 178–182; Tabs. 40, 42). Body fusiform and markedly thin throughout all its extension; body with its greatest width at head, its width1.3 (1.0–1.3) times trunk width and 1.8 (1.1–1.4) times abdomen width. Head flattened dorsally and conspicuously tapered, its height 0.8 (0.8–1.0) times trunk and abdomen height; head very large, its length 23.6% (22.4%–26.8%º of TL. Snout obtuse at the tip and conspicuously elongate, its preorbital length 9.6% (10.0%–10.9%) of TL; anterior margin of nostrils bilobed with second lobe pointed, larger and thinner than first lobe; nostrils much closer to mouth than tip of snout, its prenarial length 1.4 (1.4–1.7) times distance from nostril to upper labial furrow and 0.5 (0.6) times preoral length; internarial width 1.2 (1.1–1.3) times larger than length of eye. Eyes narrowly oval with anterior margin pointed; posterior margin pointed to somewhat notched; eyes large, its length 2.7 (2.3–3.1) times greater than its height. Prespiracular length 0.6 (0.6–0.7) times prepectoral length and 1.5 (1.5–1.6) times preorbital length. Spiracles crescent and markedly constricted, its length 0.2 (0.2–0.3) times eye length, placed laterally behind the eyes. Prebranchial length 1.4 (1.3–1.4) times prespiracular length. Gill slits straight to slightly concave, very low with fifth gill slit 1.2 (1.0–1.6) times greater in height than first gill slits.

Preoral length conspicuously large, comprising 2.0 (1.9–2.2) times greater than mouth width. Mouth somewhat arched and very narrow, its width 0.9 (0.8–0.9) times prenarial length and 1.3 (1.1–1.3) times larger than internarial space; upper labial furrow short with slender fold, its length 2.1% (1.9%–2.6%) of TL; lower labial furrow also short, not reaching the head laterally and lacking a fold. Teeth unicuspid and similar in both jaws; upper teeth smaller than lower teeth; mesial cutting edge convex; mesial heel notched on upper teeth and weakly notched on lower teeth; distal heel rounded; cusp short and thick, pointed obliquely; apron very short and heavy, placed at midline of the crown base. Three series of functional teeth on upper jaw and two series on lower jaw. Upper teeth rows 12–13 (13–1–13); lower teeth rows 11–11 (11–1–11).

Pre-first dorsal length 1.4 (1.2–1.4) times prepectoral length; origin of first dorsal fin prior to vertical traced at pectoral free rear tips. First dorsal fin upright and slender at apex with anterior margin convex and posterior margin straight to weakly concave near free rear tips; first dorsal apex very narrow and rounded; free rear tips pointed; inner margin short, its length 5.8% (5.0%–5.8%) of TL; first dorsal fin elongate, its length 13.8% (12.9%–14.1%) of TL, and tall with its 1.6 (1.5–1.8) times greater than length of inner margin. First dorsal fin 1.0 (1.0–1.2) times length of second dorsal fin. First dorsal spine short, its length 0.4 (0.3–0.4) times height of first dorsal fin, and slender its base width 0.8% (0.7%–1.0%) of TL. Interdorsal space 1.0 (0.9–1.1) times prepectoral length and 2.4 (2.3–3.0) times dorsal caudal distance. Pre-second dorsal length 2.7 (2.4–2.8) times prepectoral length. Second dorsal fin conspicuously slender with apex rounded and lobe-like; anterior margin convex and posterior margin concave; free rear tips pointed and inner margin very short, its length 4.7% (4.1%–4.8%) of TL; second dorsal fin tall, its height 1.5 (1.3–1.9) times length of its inner margin. Second dorsal spine very thin, its base width 0.7% (0.7%–0.9%) of TL, and elongate, its length 0.9 (0.7–0.9) times height of second dorsal fin, almost reaching second dorsal fin apex; second dorsal spine 1.6 (1.1–2.0) times larger than first dorsal spine.

Pectoral fins somewhat narrow, its posterior margin length 1.1% (9.3%–12.0%) of TL; pectoral anterior margin straight, although convex distally; pectoral inner margin convex; posterior margin straight to weakly concave; pectoral apex rounded and lobe-like; pectoral free rear tips rounded; pectoral anterior margin elongate, its length 1.7 (1.7–2.0) times larger than pectoral inner margin and 1.3 (1.2–1.5) times greater than length of pectoral posterior margin. Pectoral-pelvic space 0.6 (0.6–0.9) times pelvic-caudal distance. Pelvic fins small, its length 12.7% (10.4%–12.0%) of TL; pelvic margins convex; pelvic free rear tips rounded and lobe-like; pelvic fins placed at midline between first and second dorsal fins, slightly nearest to first dorsal fin. Claspers rather thick and short, its inner length 1.1 (1.1–1.3) times larger than length of pelvic inner margin; clasper groove longitudinal, dorsal and small; apopyle and hypopyle constricted, placed anterior and posteriorly in the clasper groove, respectively; rhipidion flap-like, short, and conspicuously thin, located medial-distally at the clasper.

Upper and lower precaudal pits profound; caudal keel prominent, located laterally in the caudal peduncle from vertical at insertion of second dorsal fin to behind origin of caudal fin. Caudal fin small, its dorsal caudal margin length 0.9 (0.7–0.9) times smaller than length of head and 2.2 (1.8–4.2) times larger than preventral caudal margin; dorsal caudal margin straight; upper postventral caudal margin somewhat convex to straight; lower postventral caudal margin straight; preventral caudal margin convex; dorsal caudal tip pointed; ventral caudal tip pointed to weakly rounded; caudal fin very thin on upper and lower lobes, its width at caudal fork 6.3% (5.7%–6.7%) of TL.

Dermal denticles (Fig. 182). Tricuspid and imbricate, very broad at crown with its length slightly greater than its width; cusps pointed and posterior; lateral cusps smaller than media cusp, although almost reaching its tip; median ridge elongate and thick, turning thin distally; lateral ridges thin and as large as median ridge; anterior margin of the crown arrow-shaped with anterior furrow oval and shallow; small lateral ridges at aside anterior furrow may be present in some denticles.

Coloration. Body greyish brown dorsally and whitish grey ventrally; both dorsal fins grey, light grey at fin base, and narrowly dark grey at the apex; dorsal free rear tips slightly white. Dorsal spine light brown, dark brown anteriorly and white at the tips. Pectoral fins dark grey with posterior margin somewhat whitish, although not uniform; pectoral fins light grey ventrally and white at its base. Pelvic fins dark grey dorsally and whitish grey ventrally; pelvic posterior margins slightly white. Caudal fin mostly grey, light grey over vertebral column; dorsal caudal margin with black upper caudal fringe small and distally, although not reaching dorsal caudal tip; upper postventral caudal margin broadly white till caudal fork; lower postventral caudal margin black; lower caudal lobe black with large white basal marking at preventral caudal margin; black caudal stripe absent.

Vertebral counts (Tab. 43). 41 (41) monospondylous vertebrae; 85 (90) precaudal vertebrae; 29 (28) caudal vertebrae; 114 (118) total vertebrae.

Geographical distribution (Fig. 183). It occurs in the Southwest Pacific Ocean from New Caledonia and Vanuatu to Norfolk Islands.

Etymology. The name "*melanurus*" refers to the black caudal marking on the lower caudal lobe of this species.

Remarks. *Flakeus melanurus* is endemic to New Caledonia and Vanuatu, which it is in agreement with previous studies of Fourmanoir & Rivaton (1979), Compagno (1984), Compagno *et al*. (2005), and Fricke *et al*. (2011). Its occurrence in Norfolk Island in the South Pacific Ocean is herein recorded for the first time where it is sympatric with *F. raoulensis*. It is distinct from the latter species by having dermal denticles tricuspid and rhomboid (vs. unicuspid and lanceolate in *F. raoulensis*), nostrils nearest to mouth than snout tip (its prenarial length 1.4, 1.4–1.7 times distance nostril-upper labial furrow vs. nostrils nearest to snout tip, its prenarial length 0.8–1.2 times in *F. raoulensis*), narrower mouth, its width 6.2%–7.4% of TL (vs. 7.5%–9.8% of TL for adults of *F. raoulensis*). A second nominal species, *Squalus rancureli* Fourmanoir & Rivaton (1979), was described from Vanuatu and it is known only from its holotype (Fig. 184). The main differences provided by Fourmanoir & Rivaton (1979) to distinguish it from *F. melanurus* were ventral caudal lobe grey (vs. conspicuously black in *F. melanurus*), absence of intermediate tooth (vs. presence of a single tooth on upper and lower jaws in *F. melanurus*), second dorsal fin lower and caudal fin shorter in *S. rancureli* than in *F. melanurus*.

Analysis of new material reveals that specimens from Vanuatu also have black ventral caudal lobe as well as all specimens from New Caledonia and Norfolk Island, which indicates its absence in the holotype of *S. rancureli* is probably due to abnormally on melanin pigmentation. Intermediate tooth is noticed in a single specimen from New Caledonia while it is exclusively evident at upper jaw of the holotype of *S. rancureli*. These findings are in contrast to Fourmanoir & Rivaton (1979). Few differences on external measurements are noticed between the holotype of *S. rancureli* and specimens of *F. melanurus*, including pectoral pelvic space 13.7% of TL for *S. rancureli* (vs. 15.2%, 14.8%–22.0% of TL for *F. melanurus*), and pelvic-caudal distance 28.2% of TL for *S. rancureli* (vs. 25.7%, 24.3%–26.9% of for *F. melanurus*). Other variations are observed for mouth width, length of second dorsal spine, length of pelvic fins, width of head at mouth and at nostrils. However, these values are strongly continuous and the variation may be due to preservation matters. Shape of dermal denticles, and teeth counts are overlapped between specimens of *F. melanurus* and *S. rancureli*. These results suggest conspecificity between these nominal species and *S. rancureli* is considered new junior synonym of *F. melanurus*.

Last *et al*. (2007e) suggested that *F. melanurus* together with *F. japonicus* and *Squalus nasutus* comprise a group of species characterized by conspicuously elongate snout and slender body, the *S. japonicus* group. In fact, *F. melanurus* assemblages *F. japonicus* in having: body very slender throughout all its extension; snout obtuse and markedly elongate, its preorbital length 9.6%, 10.0%–10.9% of TL for *F. melanurus* (vs. 8.3%–10.1% of TL for *F. japonicus*); mouth markedly narrow, its width 6.4% (6.2%–7.4%) of TL (vs. 5.3%–7.8% of TL for *F. japonicus*); pectoral fins tapered, its base length 4.2% (4.4%–5.0%) of TL (vs.

3.8%–4.7% of TL for *F. japonicus*). However, *F. melanurus* has larger snout than *F. japonicus*, its prenarial length 6.9%, 7.2%–8.4% of TL (vs. 5.8%–7.2% of TL for *F. japonicus*), first dorsal spine heavy, its base width 0.8% (0.7%–1.0%) of TL (vs. 0.5%–0.7%) of TL for *F. japonicus*). The New Caledonian species also exhibits shorter prebranchial length 20.2%–23.2% of TL than adults of *F. japonicus* (18.7%–20.4% of TL), and larger pectoral fins with its posterior margin length 11.1% (9.3%–12.0%) of TL (vs. 8.3%–9.2% of TL for adults of *F. japonicus*) and its anterior margin length 13.5%–15.3% of TL (vs. 12.9%–13.3% of TL in adults of *F. japonicus*). These current results support that the separation of the three nominal species into group of species is unnecessary. Furthermore, *Flakeus melanurus* exhibits particular morphological characteristics that it is distinguished from all its congeners (see diagnosis above). It is also characterized by dorsal fins upright and slender at apex with first dorsal fin height 9.5% (8.2%–10.3%) of TL; second dorsal spine much larger than first one, its length 1.6 (1.1–2.0) times length of first dorsal spine. It also bears caudal fin very slender on upper and lower lobes, and short with dorsal caudal margin 0.9 (0.7–0.9) times shorter than head length.

Other similar species that occurs in the West Pacific Ocean are *F. mitsukurii, F. griffini, F. montalbani, F. grahami, F. edmundsi* and *F. hemipinnis. Flakeus melanurus* is also distinguished from them by showing shorter caudal fin (except with *F. grahami, F. hemipinnis*), its dorsal caudal margin length 21.7% (19.2%–20.8%) of TL (vs. 20.1%–22.2% of TL for adults of *F. mitsukurii* vs. 20.0%–23.2% of TL for adults of *F. montalbani* vs. 22.5%–23.7% of TL for adults of *F. edmundsi* vs. 20.4%–22.3% of TL for adults of *F. griffini*). It can be separated from *F. hemipinnis* by having shorter dorsal-caudal space (9.3%, 8.2%–10.5% of TL vs. 10.8%–11.9% of TL for adults of *F. hemipinnis*) and from *F. grahami* by broader head, its width at nostrils 7.7% (7.8%–8.8%) of TL (vs. 6.6%–7.7% of TL for adults of *F. grahami*).

Comparative material (1 specimen): MNHN 1978-0693 (holotype of *Squalus rancureli*), adult male, 680 mm TL, Vate, Vanuatu, 17°30'S,167°30'E. Specimens of *F. japonicus, F. mitsukurii, F. griffini, F. montalbani, F. grahami, F. edmundsi* and *F. hemipinnis* listed in this Chapter.

Flakeus probatovi (Myagkov & Kondyurin, 1986)

(Southern dogfish)

Figs. 185–190; Tables 49, 57–58

Squalus fernandinus not Molina: Fowler, 1941 (in part): 260–262 (description; South Africa, Mauritius); Smith, 1961: 60 (description; Indo-Pacific Ocean).
Squalus blainvillei not Risso: Merrett, 1973: 93–110 (cited, description; Madagascar, Seychelles); Bass *et al.*, 1976: 15–16 (description; from Beira, Mozambique to Algoa Bay, South Africa); Compagno, 1984 (in part): 110, 115–116 (cited, description; Senegal, Namibia, South Africa, Mozambique and Madagascar); Ebert *et al.*, 2002: 355–357 cited; Kwazulu-Natal); Compagno *et al.*, 2005 (in part): 74–75 (description; Eastern Atlantic to Indian Ocean); Ebert *et al.*, 2013a (in part): 76, 85 (cited, description; Eastern Atlantic Ocean).
Squalus probatovi Myagkov & Kondyurin, 1986: 10–11 (original description, not illustrated; type by original designation; Angola).
Squalus mitsukurii not Jordan & Synder: Bass *et al.*, 1986 (in part): 61–62 (cited; South Africa, Mozambique, Namibia).

Holotype: ZMMU P-15991, neonate male, 220 mm TL, mouth of Kunene River, Angola.

Paratypes: not mentioned.

Type locality: Mouth of Kunene River, Angola.

Non-type material (20 specimens): BMNH 1972.10.10.99, adult male, 656 mm TL, Castor Bank, Madagascar; BMNH 1972.10.10.100, adult female, 670 mm TL, East of Diego Suarez, Madagascar; BMNH 1972.10.10.101, adult male, 677 mm TL, Castor Bank, Madagascar; MNHN 1969-0260, two neonate females, 276–285 mm TL, juvenile male, 325 mm TL, Ghana, 4°15'0"N,1°24'0"W; MNHN 1969-0261, juvenile female, 395 mm TL, two neonate males, 255–325 mm TL, adult male, 520 mm TL, Ivory Coast, 4°43'48"N,2°45'50"W;

MNHN 1969-0262, two juvenile females, 415–455 mm TL, Congo, 4°25'1"N,10°43'1"W; MNHN 1971-0048, juvenile male, 320 mm TL, Gulf of Guinea, 0°0'0"N,5°0'0"W; SAIAB 6021, adult male, 670 mm TL, off Durban, South Africa, 29.85°S,31°E; SAIAB 6022, adult male, 615 mm TL, same locality as SAIAB 6021; SAIAB 6024, adult female, 790 mm TL, Ponta da Barra Falsa, Mozambique, 22.91°S,35.61°E; ZMH 102298, adult male, 635 mm TL, Guinea, 8°59'N,14°41'W; ZMH 102693, adult female, 550 mm TL, Senegal, 14°28'N,17°22'W; ZMH 102865, adult female, 610 mm TL, adult male, 603 mm TL, Senegal, 14°20'N,17°17'W.

Diagnosis. An African species that differs from its congeners by origin of first dorsal fin just behind origin of pectoral fins. *Flakeus probatovi* is also separated from its congeners by: caudal fin with upper and lower lobes very slender, its caudal fork width 6.4%–7.4% of TL; dorsal fins conspicuously upright and tall (first dorsal fin height 8.2%–10.4% of TL; second dorsal fin height 5.3%–7.6% of TL); dorsal spines thick and elongate (first dorsal spine length 3.6%–5.3% of TL; second dorsal spine length 4.4%–5.6% of TL). Adults of *F. probatovi* differ from those of *F. blainvillei* on having larger internarial space (its width 4.2%–5.2% of TL vs. 3.2%–3.8% of TL), larger spiracles (its length 1.4%–1.9% of TL vs. 1.1%–1.3% of TL), more elongate first dorsal fin (its length 13.9%–15.9% of TL vs. 13.0%–13.8% of TL), thicker first dorsal spine (its base length 0.9%–1.1% of TL vs. 0.6%–0.8% of TL), and head at nostrils broader in *F. probatovi* (its width 7.2%–8.0% of TL vs. 5.9%–7.1% of TL).

Flakeus probatovi is distinguished from *F. blainvillei*, *F. acutipinnis*, *F. crassispinus*, *F. albifrons* and *F. notocaudatus* on having dermal denticles broad and conspicuously tricuspid (vs. unicuspid or weakly tricuspid in *F. blainvillei*). It also has narrower second dorsal spine than *F. crassispinus* (its base length 0.7%–0.9% of TL vs. 1.3%, 1.2%–1.4% of

TL for *F. crassispinus*). It has larger eyes than *F. notocaudatus* (its height 1.8%–2.2% of TL vs. 1.5%–1.7% of TL for *F. notocaudatus*). *Flakeus probatovi* is differentiated from *F. albifrons* on showing smaller distance between dorsal fins (21.9%–24.8% of TL vs. 25.5%–26.4% of TL for *F. albifrons*) and larger dorsal-caudal space (10.2%–11.0% of TL vs. 9.3%–10.0% of TL).

Flakeus probatovi has more monospondylous vertebrae (45–48) than *F. japonicus* (37–43), *F. grahami* (41–42), *F. hemipinnis* (37), and *F. melanurus* (41). It has more precaudal vertebrae (87–96) than *F. lalannei* (67–69), *F. montalbani* (84–85), and *F. hemipinnis* (74). It shows more total vertebrae (118–124) than *F. japonicus* (104–116), *F. grahami* (110–117), *F. mitsukurii* (112–117), *F. hemipinnis* (97–98), and *F. lalannei* (93–95).

Description. Range values are for non-type specimens.

External morphology (Figs. 185–189; Tabs. 49, 57). Body slender on all its extension, equally deep from head to abdomen (head height 0.9–1.0 times trunk height and 0.9–1.2 times abdomen height); body with greatest width at head, its width 1.1–1.4 times broader than trunk width and 1.3–1.6 times greater than abdomen width. Head flattened dorsally, slightly arched posteriorly behind spiracles, and elongate (its length 20.6%–25.2% of TL). Snout rounded at the tip (weakly obtuse in adults) and large (preorbital length 6.6%–8.6% of TL); anterior margin of nostrils bilobed; prenarial length 0.9–1.3 times distance from nostrils to upper labial furrow, and 0.4–0.6 times preoral length; distance between nostrils 4.1%–5.2% of TL. Eyes oval with anterior margin convex and posterior margin notched; eyes large, its length 2.1–4.6 times greater than its height. Prespiracular length 0.5–0.6 times prepectoral length. Spiracles crescent and elongate, its length 0.2–0.4 times eye length, placed laterally behind the eyes. Prebranchial length 1.5–1.6 times prespiracular length. Gill slits vertical, straight and tall with fifth gill slit 1.0–1.6 times higher than first gill slit.

Preoral distance 1.1–1.4 times mouth width. Mouth arched and very narrow, its width 1.3–2.0 times greater than prenarial length and 1.5–2.0 times broader than internarial space; upper labial furrow elongate (its length 1.9%–2.7% of TL) with thin fold; lower labial furrow short, lacking fold. Teeth unicuspid with cusp thick, oblique and short; teeth similar and equal in length in both jaws; mesial cutting edge straight; mesial heel notched; distal heel rounded; apron markedly thin and short, placed more medially at crown. Two series of functional teeth on upper and lower jaws. Upper jaw with 13–13 teeth rows; lower jaw with 12–12 teeth rows.

Pre-first dorsal length 1.1–1.5 times prepectoral length; origin of first dorsal fin just behing the vertical traced at origin of pectoral fins. First dorsal fin slender with anterior margin straight and posterior margin straight, although concave below its midline, and apex markedly rounded; first dorsal fin conspicuously upright and tall, its height 0.6–1.4 times its inner margin length and 1.0–1.4 times preorbital length. First dorsal spine thick (its base length 0.7%–1.1% of TL) and markedly elongate, its length 3.6%–5.3% of TL and corresponding to 0.4–0.6 times height of first dorsal fin, almost reaching the apex of first dorsal fin. First dorsal fin 1.1–1.2 times greater in length than second dorsal fin. Interdorsal space 0.9–1.2 times prepectoral length and 2.0–2.4 times greater than dorsal-caudal space. Second dorsal fin lobe-like and slender with anterior margin slightly convex, posterior margin straight, although concave on its midline, and apex somewhat pointed; second dorsal fin upright and tall, its height 0.7–1.2 times its inner margin length. Second dorsal spine thick (its base length 0.7%–0.9% of TL) and large, its length 4.4%–5.6% of TL and corresponding to 0.7–0.9 times height of second dorsal fin, not reaching its apex.

Pectoral fins with anterior and inner margins weakly convex, posterior margin straight; pectoral apex somewhat pointed and free rear tips rounded; pectoral fins very narrow with posterior margin length between 9.3%–12.0% of TL; pectoral anterior margin large, its length 1.6–2.0 times greater than length of pectoral inner margin and 1.3–1.5 times more elongate than 1.3–1.5 times length of pectoral posterior margin. Pectoral-pelvic space 0.5–0.8 times distance between pelvic and caudal fins. Pelvic fins nearest to the midline between two dorsal fins; pelvic fins rhomboid with its margins straight and free rear tips pinted; pectoral fins very tapered, its length 9.9%–12.1% of TL. Claspers elongate, its inner length 0.5–1.4 times length of pelvic inner margin; clasper groove dorsal, longitudinal and elongate; apopyle and hypopyle constricted, placed anterior and posteriorly at the clasper groove; rhipidion flap-like, thin and elongate, placed distally in the clasper.

Upper and lower precaudal pits profound; caudal keel conspicuous laterally in the caudal peduncle from anterior the vertical traced at free rear tip of second dorsal fin to origin of caudal fin. Caudal fin markedly slender on upper and lower lobes; dorsal caudal margin straight, its length 0.8–1.1 times head length and 1.7–2.0 times larger than preventral caudal margin; postventral caudal margins straight; dorsal and ventral caudal tips pointed; preventral caudal margin somewhat convex and elongate, its length 1.8–2.3 times larger than pelvic inner margin length; caudal fork markedly discontinuous with its width 6.4%–7.4% of TL.

Dermal denticles (Fig. 189). Tricuspid, rhomboid and imbricate; denticles conspicuously broad at crown, its length almost equal to its width; cusps posterior and pointed, although lateral cusps may be weakly pointed as well; median cusp broader and more elongate than lateral cusps; median ridge broad anteriorly and thin posteriorly; anterior furrow profound and oval with two small ridges; anterior margin of the crown wide and markedly arrow-shaped; lateral ridges thick and smaller than median ridge.

Coloration. Body bluish brown on all its extension; pale ventrally, and slightly white laterally from insertion of pelvic fins to caudal fin. First dorsal fin dark brown and light brown at its base and near free rear tips. Second dorsal fin brown and light brown at its base and at its posterior margin. Dorsal spines light brown. Pectoral fins brown with its posterior margin weakly whitish. Pelvic fins brown dorsal and ventrally, and slightly white at its free rear tips. Caudal fin dark brown on all its extension, although weakly white at postventral caudal margins; black caudal stripe present.

Vertebral counts (Tab. 58). 45–48 monospondylous vertebrae; 73–77 diplospondylous vertebrae; 87–96 precaudal vertebrae; 118–124 total vertebrae.

Geographical distribution (Fig. 190). It occurs in the East Atlantic and West Indian Oceans from Ghana to Madagascar.

Etymology. The name "*probatovi*" is in honor to A. N. Probatov who was a Russian ichthyologist.

Remarks. *Flakeus probatovi* is resurrected as valid and re-described based on new material. It is characterized by having body bluish brown with dorsal fins conspicuously upright and tall with a large spine in front of each fin, and caudal fin with very narrow lobes. The validity of *F. probatovi* was always an open question because its original description is very vague, based on a neonate specimen that was not illustrated. Morphometrics for this species from Myagkov & Kondyurin (1986) are not useful for comparisons with congeners and other data because these authors did not provide definitions of the measurements in the original description or anywhere else in the literature, which contributed to the difficulty on understanding the morphological definition of *F. probatovi*. Consequently, many authors considered it a synonym of other nominal species occurring in the Eastern Atlantic Ocean (e.g. Muñoz-Chápuli & Ramos, 1986; Compagno, 1984). *Flakeus probatovi* is regularly considered junior synonym of *F. blainvillei* (e.g. Compagno, 1984; Compagno *et al*., 2005; Ebert *et al*., 2013) because its specimens show elongate snout, tricuspid dermal denticles and long dorsal spines, all characteristic of the latter species, according to these authors.

Merrett (1973) and Bass *et al*. (1976, 1986) also recognized *F. blainvillei* in the Indo-Pacific Ocean. However, the present examination of specimens analysed by these authors clearly demonstrates that it is another species that is different from *F. blainvillei* from Mediterranean waters. *Flakeus probatovi* is distinguished in having the pelvic fins placed in the midline between two dorsal fins (nearest to first dorsal fin in *F. blainvillei*). Despite of overlapping on external measurements, adult specimens of *F. probatovi* are differentiated from *F. blainvillei* by: broader interorbital space (its width 8.0%–8.6% of TL vs. 7.2%–8.1% of TL for *F. blainvillei*); eyes taller in *F. probatovi* (its height 1.8%–2.2% of TL vs. 1.0%–1.8% of TL); more elongate first dorsal fin (base length 7.8%–9.6% of TL vs. 7.5%–7.9% of TL in *F. blainvillei*); smaller second dorsal spine, never reaching fin apex (its length 4.5%–5.1% of TL vs. 5.0%–7.3% of TL in *F. blainvillei*); head broad at mouth in *F. probatovi* (its width 11.2%–13.0% of TL vs. 9.2%–11.3% of TL in *F. blainvillei*). *Flakeus probatovi* is further distinct from *F. blainvillei* on having more elongate dorsal caudal margin (its length 21.0%–23.4% of TL vs. 19.5%–21.9% of TL in *F. blainvillei*).

More recently, Ebert (2015) considered this species a synonym of *F. acutipinnis,* although no explanations were provided to support this hypothesis. *Flakeus probatovi* is differentiated from *F. acutipinnis* on having dermal denticles tricuspid (vs. unicuspid) and pectoral fins small, never reaching the trunk height (vs. large pectoral fins, transcending greatly the trunk height). Adult specimens of *F. probatovi* are still separated from those of *F. acutipinnis* by: larger prespiracular length (11.3%–13.9% of TL vs. 7.7%–11.8% of TL); more elongate snout (its prenarial length 4.0%–6.1% of TL vs. 3.9%–4.8% of TL); wider internarial space (its width 4.2%–5.2% of TL vs. 3.6%–4.2% of TL for *F. acutipinnis*); more elongate eyes (its length 4.4%–5.5% of TL vs. 4.3%–4.5% of TL); smaller distance between pectoral and pelvic fins 15.3%–20.3% of TL vs. 20.1%–22.6% of TL); broader first dorsal spine (its base length 0.9%–1.1% of TL vs. 0.6%–0.9% of TL).

Other senior synonyms often applied to *Flakeus probatovi* are *Squalus fernandinus* (e.g. Fowler, 1941; Smith, 1961) and *Flakeus megalops* (e.g Heemstra & Heemstra, 2004). The present study noticed that *F. probatovi* is easily distinct from its congeners by having the origin of its first dorsal fin right behind origin of pectoral fins (vs. just in front of pectoral free rear tips in other species of *Flakeus*), which it is in accordance to Fowler (1941).

In the African waters, which includes Southern Africa, Western and Central Africa, and Eastern Africa, there is no other available nominal species other than *Flakeus probatovi* described from this region that can be applied to the current species. Despite of information regarding vertebral and teeth counts from Myagkov & Kondyurin (1986) for this species were compiled from previous studies (e.g. Bass *et al*., 1976), these values are congruent with the current results, suggesting co-specificity between them. Bass *et al*. (1976) further provided illustrations of specimens from Kwazulu-Natal whose main characteristics of pectoral fins, snout and dermal denticles clearly point to *F. probatovi*. Comparison between specimens of *Flakeus* from North to South Eastern Atlantic and Indian Oceans examined herein, with the holotype of *F. probatovi* gave additional support to correctly apply this species-name in the region. Neonates and young juveniles of this species exhibit dorsal fins upright and tall, pectoral fins narrow with rounded free rear tips, and snout obtuse and elongate that are also observed in the holotype. However, morphometric analysis and vertebrae counts of the holotype still need to be taken for better comparisons. The body coloration and number of vertebrae provided in Myagkov & Kondyurin (1986) and Bass *et al*. (1976) are key characters for recognizing this species because no other African species of

Flakeus exhibit similar characteristics (except *Flakeus* sp. 2 whose vertebral counts somewhat overlap).

The geographical distribution of *F. probatovi* along both Atlantic and Indian coasts of Africa are congruent with findings of Myagkov & Kondyurin (1986), Merrett (1973) and Bass *et al*. (1976), although the latter authors stated not to be able to determine its occurrences in the West African coast. The present results also notice for the first time that *F. probatovi* occurs in higher latitudes of the Eastern Atlantic Ocean beyond its type locality, Angola, where it inhabits waters from Congo to Senegal as well.

Flakeus probatovi differs from *F. blainvillei*, *F. megalops*, *F. acutipinnis* and *F. crassispinus* on having larger number of monospondylous (45–48 vs. 40–43 for *F. blainvillei* vs. 39–41 for *F. megalops* vs. 37–42 for *F. acutipinnis* vs. 41–42 for *F. crassispinus*), diplospondylous (73–77 vs. 67–69 for *F. blainvillei* vs. 63–67 for *F. megalops* vs. 66–71 for *F. acutipinnis* vs. 70–72 for *F. crassispinus*), precaudal (87–96 vs. 80–84 for *F. blainvillei* vs. 79–86 for *F. megalops* vs. 80–83 for *F. acutipinnis* vs. 84–87 for *F. crassispinus*), and total vertebrae (118–124 vs. 107–111 for *F. blainvillei* vs. 105–112 for *F. megalops* vs. 107–111 for *F. acutipinnis* vs. 111–113 for *F. crassispinus*).

Flakeus probatovi is further separated from *F. crassispinus* by having narrower first dorsal spine (its base length 0.7%–1.1% of TL vs. 1.2%, 1.1%–1.3% of TL for *F. crassispinus*). The African species also shows larger upper labial furrow than adult specimens of *F. notocaudatus* (its length 2.1%–2.7% of TL vs. 2.2%–2.3% of TL for *F. notocaudatus*), more elongate inner margin of second dorsal fin (4.8%–5.6% of TL vs. 4.3%–4.9% of TL for *F. notocaudatus*), thinner second dorsal spine (its base length 0.7%–0.9% of TL vs. 0.8%–1.2% of TL for *F. notocaudatus*), and larger pectoral fins (its posterior margin length 11.2%–12.0% of TL vs. 9.7%–11.1% of TL).

Flakeus mitsukurii, F. montalbani, F. griffini, F. grahami, F. edmundsi, F. hemipinnis and *F. japonicus* are similar to *F. probatovi* regarding the tricuspid dermal denticles and elongate snout. The latter species, however, differs from *F. grahami, F. edmundsi, F. hemipinnis*, and *F. japonicus* by mouth width (7.6%–8.1% of TL in adults vs. 7.0%–7.6% of TL for adults of *F. grahami* vs. 8.2%–9.4% of TL in adults of *F. edmundsi* vs. 6.7%–7.7% of TL for adults of *F. hemipinnis* vs. 5.3%–6.8% of TL for adults of *F. japonicus*). *Flakeus probatovi* also shows shorter pelvic-caudal space (15.3%–20.3% of TL in adults) than *F. montalbani* (20.3%–22.0% of TL), *F. griffini* (21.0%–26.3% of TL), *F. grahami* (20.1%–22.5% of TL) and *F. edmundsi* (21.1%–24.1% of TL). It is distinguished from *F. mitsukurii* by more elongate inner nostril-labial furrow space (4.4%–5.0% of TL in adults vs. 3.9%–4.5% of TL in adults of *F. mitsukurii*), and higher first dorsal fin, its length 8.2%–10.4% of TL in adults (vs. 6.9%–8.3% of TL in adults of *F. mitsukurii*).

Comparative material. Specimens of *F. blainvillei*, *F. megalops*, *F. acutipinnis* and *F. crassispinus, F. mitsukurii*, *F. albifrons*, and *F. notocaudatus* listed in this Chapter.

Flakeus lalannei (Baranes, 2003)

(Seychelles spurdog)

Figs. 191–194; Tables 41–42

Squalus lalannei Baranes, 2003: 33, 42–49 (cited, original description, illustration; type by original designation; off Alphonse Island, Seychelles); White *et al.*, 2007: 106 (cited; Seychelles); Ebert, 2013: 53, 56 (listed, cited; Seychelles); Ebert & Mostarda, 2013: 22, 24 (cited; Seychelles).

Holotype. HUJ 18445, adult female, 788 mm L, Alphonse Island, Seychelles, 1000 meters depth. Collected on 20 December 1998 by Interuniversity Institute for Marines Sciences of Elat, Israel.

Paratypes (1 specimen): TAU 12131, adult male, 615 mm TL, same locality as holotype.

Type locality: Alphonse Island, Seychelles.

Non-type material (1 specimen): MNHN 2005-1012, adult female, 810 mm TL, Seychelles.

Diagnosis. Species of *Flakeus* from Seychelles that clearly differs from its congeners by having: caudal fin with upper and lower lobes conspicuously symmetrical; lower caudal lobe elongate with dorsal caudal margin 1.5 times larger than preventral caudal margin; dorsal and ventral caudal tips pointed; dorsal caudal lobe distally white till dorsal caudal tip. It is also distinct from congeners by showing fewer precaudal (67–69) and total (93–95) vertebrae.

Flakeus lalannei is further distinguished from its congeners by: larger precaudal length (except with *F. japonicus, F. 366raham, F. edmundsi*), comprising 80.5% (82.1%) of TL; more elongate pre-second dorsal length, 63.5% (66.0%) of TL (except with *F. mitsukurii* and *F. edmundsi*); shorter prespiracular length, corresponding to 11.7% of TL (except with *F. mitsukurii* and *F. probatovi*); narrower space between nostrils, its distance 3.9% of TL (except with *F. mitsukurii* and *F. hemipinnis*); more elongate distance between first and second dorsal fins 26.6% (28.4%) of TL (except with *F. edmundsi*); and shorter dorsal caudal margin, its length 17.6% of TL.

Description. Single values are for holotype followed by non-type specimen between brackets.

External morphology (Figs. 191–193; Tabs. 41–42). Body fusiform and slender throughout all its extension, its head height 0.9 (0.9) times trunk and abdomen heights; body with its greatest width at head, comprising 1.3 (1.4) times broader than abdomen width and 1.3 (1.6) times trunk width. Head flattened dorsally and large, its length 21.8% (21.6%) of TL; head narrower at nostrils (its width 5.9%, 7.3% of TL) than at mouth (its width 8.4%, 10.3% of TL). Snout rounded at tip and somewhat large, its preorbital length 6.7% (7.2%) of TL;

anterior margin of nostrils bilobed with first lobe thicker than second one; nostrils equally distant to snout and to upper labial furrow, its prenarial length 1.0 (1.0) times distance from nostril to upper labial furrow; prenarial length one-half preoral length and 0.9 (1.2) times length of eyes; internarial space 0.8 (0.9) times length of eyes. Eyes oval with anterior margin concave and posterior margin notched, placed laterally; eyes large, its length 3.0 (2.2) times greater than its height. Prespiracular length 0.5 (0.6) times prepectoral length and 1.8 (1.6) times preorbital length. Spiracles crescent and markedly broad, placed laterally behind the eyes; spiracles elongate, its length 0.2 (0.3) times length of eyes. Prebranchial length 1.5 (1.5) times prespiracular length. Gill slits vertical and weakly concave, placed in front of origin of pectoral fins; gill slits tall with height of fifth gill slit 0.9 (1.3) times height of first gill slit.

Preoral length large, comprising 1.3 (1.4) times mouth width. Mouth arched and broad, its width 1.4 (1.5) times greater than prenarial length and 1.8 (1.8) times broader than internarial space; upper labial furrow elongate with fold somewhat thick, its length 2.5% (2.1%) of TL; lower labial furrow much larger than upper one, lacking a fold. Teeth unicuspid and similar in both jaws; upper and lower teeth almost equal in size; teeth small with mesial cutting edge markedly convex; mesial heel somewhat rounded; distal heel rounded; cusp very short, thick and oblique; apron very small and rather thick, placed in the midline of the crown base. Two series of functional teeth on upper jaw and three series on lower jaw; 14–13 (14–14) upper teeth rows and 12–10 (12–12) lower teeth rows.

Pre-first dorsal length 1.3 (1.5) times prepectoral length; origin of first dorsal fin prior to vertical traced at pectoral free rear tips. First dorsal fin broad at fin web with anterior margin slightly convex, posterior margin straight and apex rounded; first dorsal free rear tip pointed and inner margin elongate, its length 4.8% (5.0%) of TL; first dorsal fin low, its height 1.3 (1.3) times greater than length of inner margin; first dorsal fin 1.3 (1.3) times larger than second dorsal fin. First dorsal spine thick, its base width 0.8% (0.7%) of TL, and small, its length 0.6 (0.4) times height of first dorsal fin, never transcending apex of first dorsal fin. Interdorsal space 1.2 (1.4) times prepectoral length and 2.5 (2.7) times greater than space between second dorsal fin and caudal fin. Pre-second dorsal length 2.9 (3.1) times larger than prepctoral length and 3.8 times greater than length of dorsal caudal margin. Second dorsal fin broad with anterior margin convex, posterior margin concave, although not falcate, and apex rounded; second dorsal fin free tip pointed and inner margin large, its length 3.8% (4.1%) of TL; second dorsal fin low, its height 0.8 (1.1) times length of its inner margin. Second dorsal spines heavy, its base width 0.8% (0.8%) of TL, and elongate, its length 1.0 times height of second dorsal fin, almost reaching fin apex; length of second dorsal spine 1.0 times length of first dorsal spine.

Pectoral fins conspicuously broad, its posterior margin length 11.2% (12.1%) of TL; pectoral anterior, inner and posterior margin straight; pectoral anterior margin 2.1 (2.0) times larger than length of pectoral inner margin and 1.3 (1.2) times length of pectoral posterior margin; pectoral apex and free rear tips rounded; pectoral fin narrow at base, its base length 5.3% (4.5%) of TL. Pectoral-pelvic distance 1.0 (0.7) times pelvic-caudal space; pelvic fins at midline between first and second dorsal fins. Pelvic fins with margins straight, broad and elongate, its length 9.9% (10.8%) of TL; pelvic free rear tips weakly pointed.

Upper and lower precaudal pits profound; caudal keel prominent, placed laterally from insertion of second dorsal fin to behind origin of caudal fin. Caudal fin with upper and lower lobes symmetrical; dorsal caudal margin straight; upper and lower postventral caudal margins somewhat straight; preventral caudal margin straight; dorsal and ventral caudal tips conspicuously pointed; lower lobe markedly elongate with length of preventral caudal margin 1.9 times larger than length of pelvic inner margin; dorsal caudal margin length 1.5 times length of preventral caudal margin and 0.8 times head length; caudal fin broad at caudal fork, its width 5.8% (6.5%) of TL.

Dermal denticles. Based on picture of skin sample taken from holotype and provided in Baranes (2003). Tricuspid, markedly imbricate, and broad at crown; lateral cusps weak, short, and somewhat pointed; median cusp posterior, pointed and as large as lateral cusps; median ridge thick and small, although more elongate than lateral ridges; the latter thin and short.

Coloration. Body brown, light brown laterally from insertion of first dorsal fin to origin of caudal fin, and light brown ventrally. Dorsal fin dark brown and light brown at fin base. Dorsal spines light brown, blackish anteriorly and white at the tips. Pectoral fins dark brown and weakly whitish at pectoral posterior margin. Pelvic fins brown dorsally and light brown ventrally with pelvic posterior margin weakly white. Caudal fin dark brown and light brown over vertebral column; upper caudal lobe broadly white distally, including dorsal caudal tip; upper postventral caudal margin brown proximally; lower postventral caudal margin light brown; preventral caudal margin brown; absence of caudal stripe.

Vertebral counts. 69 (67) precaudal vertebrae; 26 caudal vertebrae; 95 (93–94) total vertebrae (Baranes, 2003).

Geographical distribution (Fig. 194). It is endemic from Seychelles.

Etymology. The name "*lalannei*" is in honour to Maurice Lousteau-Lalanne, the Minister for the Protection of the Environment of Seychelles.

Remarks. *Flakeus lalannei* is a species endemic from Seychelles and the second representative of the genus *Flakeus* in these waters besides *F. probatovi*. It has very unique morphological characteristics and it is easily distinguished from its congeners by shape and color of caudal fin, and vertebral counts. The particular shape of caudal fin in *F. lalannei* is described herein for the first time and comprises a character of high taxonomic value for separating from other species of *Flakeus*. This species is known from two specimens only that were described in the original description as holotype and paratype. A third specimen was analyzed at MNHN in the current study and gave additional support for considering *F. lalannei* as valid. The holotype of *F. lalannei* is very damaged with its head somewhat shrink and most of its body color natural color lost. Caudal fin of the holotype is broken on upper caudal lobe as well. The paratype of *F. lalannei*, however, is considered lost.

Flakeus lalannei bears very few precaudal and total vertebrae that differentiate it from all species within the family Squalidae, including *S. acanthias*. This assumption is based on observations from Baranes (2003) because no radiograph was taken from its specimens during the present study. This characteristic is similar to those observed for *F. hemipinnis* which it also has very few vertebrae. *Flakeus lalannei* is distinct from *F. hemipinnis* by showing fewer precaudal (67–69 vs. 74 for *F. hemipinnis*) and total vertebrae (93–95 vs. 97–98 for *F. hemipinnis*). These results are in congruence with White *et al*. (2007b) and in disagreement with Baranes (2003) because this author stated that *F. lalannei* assemblages *S. acanthias* regarding number of vertebrae (75–88 precaudal and 101–117 total vertebrae for *S. acanthias*).

The Seychelles species assemblages *F. mitsukurii, F. montalbani, F. 370raham370* and *F. probatovi, F. edmundsi, F. hemipinnis, F. japonicus, F. 370raham* in having snout markedly elongate and dermal denticles tricuspid and rhomboid. Besides the characteristics provided in the diagnosis, *F. lalannei* is further distinguished from these species (except *F. mitsukurii, F. hemipinnis* and *F. probatovi*) by having shorter snout, its preorbital length 6.7% (7.2%) of TL (vs. 8.3%–10.1% of TL for *F. japonicus* vs. 7.4%–10.2% of TL for *F.*

montalbani vs. 7.6%–9.5% of TL for *F. 371raham* vs. 7.9%–9.6% of TL for *F. edmundsi* vs. 7.7%–9.0% of TL for *F. 371raham371*). It is also distinct from these species (except *F. montalbani*) by: lower first and second dorsal fins, height of first dorsal fin 6.2% (6.5%) of TL (vs. 6.9%–8.8% of TL for *F. mitsukurii* vs. 6.6%–10.0% of TL for *F. japonicus* vs. 6.8%–9.9% of TL for *F. 371raham* vs. 8.7%–9.7% of TL for *F. edmundsi* vs. 7.8%–9.8% of TL for *F. hemipinnis* vs. 7.3%–11.0% of TL for *F. 371raham371* vs. 8.2%–10.4% of TL for *F. probatovi*), and height of second dorsal fin 3.2% (4.6%) of TL (vs. 4.5%–6.6% of TL for *F. mitsukurii* vs. 5.4%–7.3% of TL for *F. japonicus* vs. 4.7%–7.4% of TL for *F. 371raham* vs. 6.0%–7.1% of TL for *F. edmundsi* vs. 5.6%–6.6% of TL in adults of *F. hemipinnis* vs. 5.3%–7.3% of TL for *F. probatovi* vs. 5.5%–8.7% of TL for *F. 371raham371*). *Flakeus lalannei* is further differentiated from *F. mitsukurii* by having shorter pectoral inner margin, its length 7.0% (7.2%) of TL (vs. 7.7%–9.5% of TL for *F. mitsukurii*).

The occurrence of *F. lalannei* into waters from Madagascar, Mozambique and South Africa is unknown, which it is in contrast to *F. probatovi*. The latter species further is distinguished from *F. lalannei* by more elongate dorsal spines with first dorsal spine length 3.6%–5.3% of TL in adults of *F. probatovi* (vs. 3.4%, 2.5% of TL in *F. lalannei*), length of second dorsal spines 4.5%–5.1% of TL in adults of *F. probatovi* (vs. 3.1% of TL in *F. lalannei*). Additional material of *F. lalannei* is needed in order to better understand its geographical distribution in the Indian Ocean.

Comparative material: Specimens of *F. mitsukurii, F. montalbani, F. 371raham371* and *F. probatovi, F. edmundsi, F. hemipinnis, F. japonicus, F. 371raham* listed in this Chapter, and specimens of *Squalus acanthias* listed in the previous Chapter.

Flakeus grahami **(White, Last & Stevens, 2007)**

(Eastern longnose spurdog)

Figs. 195–202; Tables 44, 47–48

Squalus sp. F: Last & Stevens, 1994: 49, 97 (cited, description; Australia); Compagno & Niem, 1998: 1222, 1232 (listed, cited; East Australia); Compagno *et al*., 2005: 81 (description; East Australia).

Squalus grahami White, Last & Stevens, 2007: 71–81 (original description; illustrated; Australia); Ward *et al*., 2007: 117–130 (cited; Northeast Australia); Last & Stevens, 2009: 46, 54–55 (cited, description; Northeast Australia); Naylor *et al*., 2012a: 57 (cited; Australia); Naylor *et al*., 2012b: 42 (cited; Australia); Ebert *et al*., 2013a: 74, 89 (cited, description; Northeast Australia); Straube *et al*., 2013: 264 (cited; Australia).

Holotype: CSIRO H 4476-01, adult male, 602 mm TL, Northeast of Batemans Bay, New South Wales, 35°29′S,150°46′E. 234 meters depth. Collected on 4 December 1996.

Paratypes (30 specimens): CSIRO H 452, adult female, 625 mm TL, Southwest of Saumarez Reef, Queensland, Australia, 22°52′S,152°42′E; CSIRO H 453, adult male, 526 mm TL, Northeast of Hinchinbrook Island, Queensland, Australia, 17°57′S,147°03′E; CSIRO H 454, adult male, 550 mm TL, Northeast of Hinchinbrook Island, Queensland, Australia, 17°58′S,147°00′E; CSIRO H 455, adult female, 626 mm TL, locality same as CSIRO H 454; CSIRO H 456, adult male, 552 mm TL, locality same as CSIRO H 454; CSIRO H 457-01, adult female, 624 mm TL, locality same as CSIRO H 453; CSIRO H 602-2, juvenile female, 370 mm TL, South of Saumarez Reef, Queensland, Australia, 22°42′S,154°05′E; CSIRO H 644-3, adult male, 522 mm TL, South of Saumarez Reef, Queensland, Australia, 22°49′S,154°10′E; CSIRO H 644-5, adult male, 531 mm TL, locality same as CSIRO H 644-3; CSIRO H 644-6, adult male, 523 mm TL, locality same as CSIRO H 644-3; CSIRO H 1311-3, adult female, 652 mm TL, East of Whitsunday Group, Queensland, Australia, 19°29′S,150°17′E; CSIRO H 1312-6, juvenile female, 287 mm TL, locality same as CSIRO H 602-2; CSIRO H 1312-7, juvenile female, 342 mm TL, locality same as CSIRO H 602-2; CSIRO H 1312-8, juvenile female, 282 mm TL, locality same as CSIRO H 602-2; CSIRO H 1312-9, juvenile male, 278 mm TL, locality same as CSIRO H 602-2 locality same as CSIRO H 644-5; CSIRO H 1344-01, juvenile female, 232 mm TL, locality same as CSIRO H 644-5; CSIRO H 1344-2, juvenile male, 238 mm TL, locality same as CSIRO H 644-5; CSIRO H 1344-3, juvenile male, 325 mm TL, locality same as CSIRO H 644-5; CSIRO H 1346-01, juvenile male, 294 mm TL, Northeast slope, Queensland, Australia; CSIRO H 1347-1, juvenile female, 371 mm TL, East of Flinders Reef, Queensland, Australia, 17°29′S,149°32′E; CSIRO H 1406-1, juvenile female, 221 mm TL, Queensland Trough, Australia, 17°55′S,147°06′E; CSIRO H 2468-02, adult female, 658 mm TL, Northeast of Hinchinbrook Island, Queensland, Australia, 17°57′S,147°02′E; CSIRO H 2469-04, adult female, 650 mm TL, Northeast of Hinchinbrook Island, Queensland, Australia, 17°58′S,147°01′E; CSIRO H 2469-05, adult female, 630 mm TL, locality same as CSIRO H 2469-04; CSIRO H 2688-02, adult male, 565 mm TL, East of Coffs Harbour, New South Wales, Australia, 30°24′S,153°23′E; CSIRO H 4476-08, adult female, 576 mm TL, locality same as holotype; CSIRO H 4682-01, adult male, 553 mm TL, east of Broken Bay, New South Wales, Australia, 33°32′S,152°00′E; CSIRO H 4682-02, adult female, 685 mm TL, locality same as CSIRO H 4682-01; CSIRO H 4682-03, adult female, 697 mm TL, locality same as CSIRO H 4682-01; CSIRO H 4682-04, adult male, 570 mm TL, locality same as CSIRO H 4682-01.

Type locality: Northeast of Batemans Bay, New South Wales, Australia.

Non-type material (33 specimens): AMS I 15526-002, juvenile female, 307 mm TL, off Brisbane, Queensland, Australia; AMS I 15527-002, juvenile female, 325 mm TL, off Brisbane, Queensland, Australia; AMS I 37735-001, adult female, 685 mm TL, off Terrigal, New South Wales, Australia; AMS I 37735-002, adult male, 730 mm TL, off Terrigal, New South Wales, Australia; AMS I 46063-001, three adult males, 920–935 mm TL, Gascoyne Seamount, New South Wales, Australia; CSIRO H 602-13, juvenile female, 353 mm TL, South of Saumarez Reef, Queensland, Australia, 22°42′S,154°05′E; CSIRO H 4476-03, adult male, 520 mm TL, Northeast of Batemans Bay, New South Wales, Australia, 35°29′S,150°46′E; CSIRO H 4476-04, adult male, 523 mm TL, Northeast of Batemans Bay, New South Wales, Australia, locality same as CSIRO H 4476-03; CSIRO H 4476-05, juvenile female, 576 mm TL, locality same as CSIRO H 4476-03; CSIRO H 4476-09, juvenile female, 577 mm TL, locality same as CSIRO H 4476-03; CSIRO H 4471-01, juvenile male, 515 mm TL, East of Brush Island, New South Wales, Australia, 35°30′S,150°45′E; CSIRO H 4708-01, juvenile male, 545 mm TL, Northeast of Batemans Bay, New South Wales, Australia, 35°45′S,150°36′E; CSIRO H 7043-03, neonate female, 192 mm TL, two neonate males, 192–194 mm TL, East of Ballina (Byron Banks site), New South Wales, Australia, 28°59′S,153°53′E; CSIRO H 7043-04, two neonate females, 170–175 mm TL, two neonate males, 173–183 mm TL, East of Ballina (Byron Banks site), New South Wales, Australia, locality same as CSIRO H 7043-03; CSIRO H 7043-05, juvenile male, 433 mm TL, locality same as CSIRO H 7043-03; CSIRO H 7043-06, juvenile male, 417 mm TL, locality same as CSIRO H 7043-03; CSIRO H 7055-01, neonate female, 193 m TL, East of Ballina (Byron Banks site), New South Wales, Australia, 28°57′S,153°53′E; CSIRO H 7055-02, neonate male, 195 m TL, locality same as CSIRO H 7055-01; MZUSP uncatalogued (previously CSIRO), adult male, 560 mm TL, East of Wooli, New South Wales, Australia, 29°56′S,153°40′E; MZUSP uncatalogued (previously CSIRO), adult male, 565 mm TL, East of Ballina, New South Wales, Australia, 28°57′S,153°53′E; QM I 31433, adult female, 630 mm TL, Northeast of Leopard Reef, Queensland, Australia, 18°55′S,148°50′E; QM I 31572, adult male, 498 mm TL, Northeast of Leopard Reef, Queensland, Australia; QM I 31573, adult male, 523 mm TL, Northeast of Leopard Reef, Queensland, Australia, 18°54′S,148°47′E; QM I 31574, adult male, 572 mm TL, Northeast of Leopard Reef, Queensland, Australia, 18°56′S,148°50′E; QM I 31575, adult male, 570 mm TL, locality same as QM I 31574.

Diagnosis. Species of *Flakeus* that is differentiated from its congeners by a combination of characters: snout markedly obtuse and elongate, its prenarial length 5.7% (5.7%–6.8%; 5.0%–6.4%) of TL; mouth very narrow, its width 6.3% (7.0%–7.9%; 7.0%–8.3%) of TL; pectoral fins somewhat narrow, its posterior margin length 10.5% (8.7%–11.5%) of TL; low dorsal fins (height of first dorsal fin 7.0%, 6.5%–8.0%; 6.8%–9.9% of TL; height of second dorsal fin 6.1%, 4.8%–6.3%; 4.7%–7.4% of TL); dermal denticles tricuspid with anterior margin of crown conspicuously oval and arrow-shaped; caudal fin rather rectangular with black caudal bar and upper caudal blotch prominent.

Adult specimens of *Flakeus grahami* is distinct from those of *F. japonicus* by shorter pre-first dorsal length (28.8%–31.5% of TL vs. 31.8%–32.7% of TL for *F. japonicus*), wider mouth (its width 7.0%–7.6% of TL vs. 5.3%–6.7% of TL for *F. japonicus*), broader pectoral fin (its base length 4.7%–5.3% vs. 4.0%–4.6% of TL for *F. japonicus*), wider head (its width at mouth 10.6%–11.8% of TL vs. 9.7%–10.5% of TL for *F. japonicus*). *Flakeus grahami* differs clearly from *F. mitsukurii* and *F. montalbani* by showing body slender (vs. robust), snout tip obtuse (vs. rounded) and pectoral fins with posterior margin more concave (vs. straight). It is further distinct from *F. mitsukurii* by having body greyish with conspicuous upper black caudal blotch and black caudal bar over caudal fork (vs. body blackish to dark grey, lacking any black markings on caudal fin), and lower fifth gill slit (its height 1.8%–2.3% of TL vs. 2.4%–2.6% of TL in adults of *F. mitsukurii*). It is distinct from *F. probatovi* by having fewer monospondylous (41–42 vs. 45–48 for *F. probatovi*) and total vertebrae (110–117 vs. 118–124 for *F. probatovi*).

Description.

External morphology (Figs. 195–201; Tabs. 44, 47). Body fusiform and narrow for all its extension, slightly arched from posterior margin of spiracles to first dorsal fin origin; head height 1.0 (0.9–1.0; 0.8–1.0) times trunk height and 0.9 (0.8–1.0; 0.8–1.2) times abdomen height. In female paratypes, body is much more humped and deep in trunk and abdomen than males. Head flattened anteriorly, elongate, its length 22.8% (22.3%–24.1%; 21.9%–25.9%) of TL; head narrower at nostrils than at mouth with its width at nostrils 7.2% (6.5%–8.8%; 6.6%–8.9%) of TL; head width 1.1 (1.1–1.2; 1.1–1.4) times trunk width and 1.4 (1.1–1.4; 1.3–2.4) times abdomen width. Snout extremely pointed at tip and large, its preorbital length 8.5% (8.4%–9.3%; 7.6%–9.5%) of TL; anterior margin of nostrils bilobate, located ventral-laterally in the snout, nearest to the mouth than to the snout tip with prenarial length 1.2 (1.1–1.4; 0.9–1.4) times the distance of nostrils to upper labial furrow; prenarial length 0.5 (0.5–0.6) times preoral length; internarial space 1.0 (0.9–1.2; 0.8–1.1) times eye length. Eyes oval with convex anterior margin and notched posterior margin, elongate, its length 2.3 (2.0–2.8; 1.8–3.2) times its height. Prespiracular length 0.6 (0.6–0.7; 0.5–0.7) times prepectoral length and 1.5 (1.5–1.6; 1.5–1.7) times greater than preorbital length. Spiracles crescent and wide, its length 0.3 (0.2–0.3; 0.2–0.4) times smaller than eyes, placed laterally behind the eyes. Prebranchial length 1.5 (1.4–1.5; 1.4–1.6) times greater than prespiracular length. Gill slits vertical and low with fifth gill slit 1.3 (1.0–1.5; 1.0–1.6) times higher than first gill slit, placed anteriorly to the pectoral fin origin.

Preoral length large, corresponding to 1.7 (1.4–1.6; 1.3-1.7) times mouth width. Mouth somewhat straight and conspicuously narrow, its width 1.1 (1.1–1.2; 1.1–1.5) times prenarial length and 1.4 (1.3–1.6; 1.5–1.8) times broader than internarial space; upper labial furrow elongate with fold thin, its length 2.3% (1.8%–2.6%; 1.9%–3.0%) of TL; lower labial furrow much larger than first one but without a fold. Teeth uniscupid, flattened labial-lingually, similar in both jaws, although lower teeth larger and thinner than lower teeth; cusp short and thick, placed more obliquely; mesial cutting straight (slightly convex in upper teeth); distal heel rounded and mesial heel moderately pointed; apron short, broader and placed more medially in lower teeth than upper teeth. Two series of functional teeth on both upper and lower jaws. Upper teeth 12–13 (13–13; 13–12) rows; lower teeth 10–9 (9–10; 11–10) rows.

Origin of first dorsal fin anterior to pectoral free rear tips; pre-first dorsal fin length 1.4 (1.3–1.5) times prepectoral length. First dorsal fin vertical with anterior margin straight and posterior margin conspicuously concave on its midline; apex markedly rounded; free rear tip pointed with large inner margin, its length 6.2% (5.0%–6.6%; 5.5%–6.7%) of TL; first dorsal fin broad at fin web and low, its height 1.1 (1.1–1.5; 1.2–1.6) times its inner margin length; first dorsal fin 1.0 (1.0–1.2) times greater in length than second dorsal fin. First dorsal spine slender, its base width 0.6% (0.6%–0.7%, 0.5%–0.8%) of TL; first dorsal spine large but not reaching the fin apex, its length 0.6 (0.3–0.6; 0.2–0.5) times height of first dorsal fin. Interdorsal space 1.1 (1.0–1.2; 0.8–1.2) times prepectoral length and 2.2 (2.0–2.5; 1.9–2.6) times larger than dorsal caudal space. Pre-second dorsal length 2.9 (2.6–3.0; 2.3–3.0) times prepectoral length and 2.7 (2.7–3.3; 2.3–3.4) times greater than length of dorsal caudal margin. Second dorsal fin oblique, broad at fin web and low, its height 1.2 (1.0–1.2; 1.0–1.3) times its inner margin length; anterior margin convex, posterior margin strongly concave but not falcate; apex moderately pointed and lobe-like; free rear tip pointed; inner margin length somewhat elongate 5.3% (3.9%–5.6%; 4.3%–6.4%) of TL. Second dorsal spine markedly slender, its base width 0.7% (0.7%–0.8%; 0.6%–1.1%) of TL; second dorsal spine large, although not reaching the apex of second dorsal fin, its length 0.8 (0.7–0.9; 0.6–0.9) times height of second dorsal fin and 1.2 (1.1–2.3; 0.9–2.7) times larger than length of first dorsal spine.

Pectoral fins narrow, its posterior margin length 10.5% (8.7%–11.5%; 8.1%–11.7%) of TL, and elongate with its anterior margin length 15.1% (12.8%–15.3%; 12.6%–15.3%) of TL; pectoral anterior margin 1.9 (1.4–1.9; 1.3–2.0) times greater in length than pectoral inner margin and 1.4 (1.3–1.5; 1.2–1.6) times larger than length of pectoral posterior margin;

pectoral anterior margin straight, inner margin convex, and posterior margin concave; pectoral apex rounded and lobe-like, reaching equally the horizontal line traced at pectoral free rear tip; pectoral free rear tips somewhat rounded and broad (in juveniles, evidently rounded, lobe-like and more elongate with apex not reaching the horizontal line traced at free rear tips). Pectoral-pelvic space 0.7 (0.7–0.9; 0.6–0.9) times pelvic-caudal space; pelvic fins placed in the midline between two dorsal fins. Pelvic fins narrow with its margins convex; pelvic free rear tips slightly triangular (in adult males, markedly rounded and lobe-like); pelvic fins large, its length 12.2% (10.9%–12.9%; 10.4%–12.8%) of TL. Clasper with clasper groove very large, longitudinal and placed dorsally; apopyle with constricted aperture and hypopyle with wide aperture, located, respectively, more anteriorly and posteriorly in the clasper groove; rhipidion flattened and thin, blade-like and somewhat elongate, placed distally in the clasper; clasper elongate, exceeding the pelvic free rear tips, its inner length 1.2 (0.6–1.3; 0.5–1.4) times length of pelvic inner margin.

Caudal keel prominent laterally from anterior to insertion of the second dorsal fin to caudal fin origin; upper and lower precaudal pits conspicuous. Caudal fin narrow on upper and lower lobes to weakly rectangular; dorsal caudal margin straight; upper postventral caudal margin markedly convex proximally and straight distally; both lower postventral caudal margin and preventral caudal margin slightly convex; both dorsal and ventral caudal tips rounded and narrow; caudal fork between lobes discontinuous and tapered, its width 6.8% (6.4%–7.4%; 6.4%–7.9%) of TL; dorsal caudal margin large, its length 1.0 (0.8–1.0; 0.7–1.0) times head length and 1.9 (1.7–2.1) times greater than length of preventral caudal margin; preventral caudal margin also large, its length 1.9 (1.6–2.3; 1.5–2.2) times greater than length of pelvic inner margin. In juveniles, caudal fin conspicuously rectangular.

Dermal denticles (Fig. 201). Tricuspid and markedly wide at crown, imbricate, its length greater than its width; median cusp posterior and pointed; lateral cusps weakly pointed and posterior, much smaller than median cusp, and forming a weak concavity with median cusp on each side; median ridge prominent, tall, large and thick on all its extension with anterior furrow profound; anterior margin of the crown arrow-shaped and conspicuously oval with two small secondary ridges; lateral ridges thin and smaller than median ridge. In juveniles: dermal denticles rarely imbricate and conspicuously slender at crown; median ridge and cusp much longer than lateral ridges; lateral cusps somewhat pointed or inconspicuous.

Coloration. Body dark grey dorsally, white ventrally and lateral-posteriorly. Dorsal fins entirely grey but slightly whitish on its base and in the free rear tips, blackish at the apex. Dorsal spines light grey, somewhat blackish anteriorly and white at the tips. Pectoral fins dark grey dorsal and ventrally with both inner and posterior margins slightly whitish but not uniform. Pelvic fins grey dorsally and white ventrally with margins whitish. Caudal fin grey and whitish over vertebral column; postventral caudal margins white, broadly whitish in the dorsal caudal tip; large black upper caudal blotch (narrower in juveniles); black caudal stripe conspicuous; black caudal bar in the caudal fork well prominent; ventral caudal lobe mostly white, greyish medially; black basal marking prominent (more evident in juveniles).

Vertebral counts (Tabs. 48). 41 (41; 42) monospondylous vertebrae; 73 (69; 70–75) diplospondylous vertebrae; 88 (83; 83–86) precaudal vertebrae; 114 (110; 112–117) total vertebrae.

Geographical distribution (Fig. 202). It occurs in the East coast of Australia from New South Wales to Queensland.

Etymology. The name "*grahami*" is a latinized word in honor to an Australian ichthyologist, Ken Graham (NSW Department of Primary Industries, Cronulla).

Remarks. *Flakeus grahami* is a species endemic to Eastern Australia, occurring exclusively between New South Wales and Queensland. It is characterized by having snout well elongate, low dorsal fins and dermal denticles tricuspid. These findings are in agreement with Compagno *et al*. (2005), White *et al*. (2007c), Naylor *et al*. (2012a,b), and Ebert *et al*. (2013a). The current study shows that dermal denticles in this species vary in shape with growth, turning much wider and imbricate in adult specimens than in juveniles. Cusps are very prominent and anterior margin of the crown is conspicuously arrow-shaped and oval, which it is in contrast to the description of White *et al*. (2007c).

It shares with *F. montalbani*, *F. japonicus* and *F. edmundsi* the particular coloration of the caudal fin that exhibits black caudal bar prominent. Apart of the characteristics in the diagnosis presented herein, *F. grahami* and *F. montalbani* show overlapping of external measurements and vertebral counts. Types of *F. grahami* is slightly differentiated from *F. montalbani* by: larger pelvic-caudal space in *F. grahami* (27.6%, 26.1%–29.0% vs. 26.3% for holotype, 22.0%–26.1% of TL in *F. montalbani*); larger preoral distance 1.7 (1.4–1.6) times mouth width vs. 1.6 (1.2–1.4) times in *F. montalbani*; narrower mouth width 1.1 (1.1–1.2) times prenarial length vs. 1.4 (1.3–1.7) times in *F. montalbani*; length of first dorsal spine 0.6 (0.3–0.6) times height of first dorsal fin vs. 0.3 (0.1–0.4) times in *F. montalbani*. Adult specimens of *F. grahami* still differ from those of *F. montalbani* by having narrower head, its width at nostrils 6.6%–7.7% of TL vs. 7.2%–8.1% of TL and its width at mouth 10.6%–11.8% of TL vs. 11.1%–12.6% of TL.

Flakeus grahami also assemblages *F. japonicus* and *F. edmundsi* by having snout conspicuously obtuse at the tip and very elongate as well as slender body. Adult specimens can further be distinguished from those of *F. japonicus* by smaller preorbital length (7.6%–8.7% of TL vs. 8.7%–9.3% of TL for *F. japonicus*), shorter second dorsal spine (3.2%–4.9% of TL vs. 4.8%–5.6% of TL for *F. japonicus*), and wider pectoral fins (its posterior margin length 9.2%–11.7% of TL vs. 8.3%–9.2% of TL for *F. japonicus*). *Flakeus grahami* has body wider at head and trunk than in *F. japonicus*, its head width 12.1%–13.9% of TL vs. 11.5%–12.3% of TL for adults of *F. japonicus*, and its trunk width 10.4%–12.4% of TL vs. 9.7%–10.8% of TL for adults of *F. japonicus*. Types of *F. grahami* are distinct from those of the nominal species *Squalus nasutus* by: obtuse snout (vs. acute snout in *S. nasutus*); shorter pre-first dorsal length (29.2%, 29.5%–31.6% vs. 32.4%, 31.2%–32.9% of TL in *S. nasutus*); preorbital length (8.5%, 8.4%–9.3% vs. 10.3%, 9.3%–10.0% of TL in *S. nasutus*); prenarial length 5.7%, 5.7%–6.8% vs. 7.5%, 6.6%–7.3% of TL in *S. nasutus*); preoral length 10.6% (10.8%–11.8%) of TL vs. 12.8% (11.8%–13.0%) of TL in *S. nasutus*; broader pectoral fins with posterior margin length 10.5%, 8.7%–11.5% of TL (vs. narrower pectoral fins with posterior margin length 8.2%, 7.2%–8.3% of TL).

Common synonym applied to this species is *F. mitsukurii* like it was also considered for many other species within Australian and New Zealand waters, including *F. montalbani* and *F. griffini* (e.g. Whitley, 1940; Compagno, 1984). In contrast to the Japanese species, adult specimens of *F. grahami* shows larger prenarial length (5.0%–6.1% of TL vs. 4.1%–5.2% of TL in adults of *F. mitsukurii*), more elongate preoral length (9.7%–11.2% of TL vs. 7.6%–9.9% of TL in adults of *F. mitsukurii*), larger distance from nostril to upper labial furrow (4.3%–5.1% of TL vs. 3.9%–4.5% of TL in adults of *F. mitsukurii*) and more elongate eyes (its length 3.9%–5.0% vs. 3.4%–4.0% of TL in adults of *F. mitsukurii*). *Flakeus grahami* also exhibits thinner dorsal spines (base width of first dorsal spine 0.5%–0.8% of TL vs. 0.7%–0.9% of TL in adults of *F. mitsukurii*; base width of second dorsal spine 0.6%–0.8% of TL vs. 0.7%–0.9% of TL in adults of *F. mitsukurii*). It also shows lower body with its head height 9.2%–10.8% of TL (vs. 10.5%–12.5% of TL in adults of *F. mitsukurii*) and trunk height 9.0%–11.4% (vs. 11.4%–14.1% of TL in adults of *F. mitsukurii*).

Comparative material: Specimens of *F. mitsukurii*, *F. japonicus*, *F. montalbani*, *F. probatovi* and types of *S. nasutus* listed in this Chapter.

Flakeus edmundsi (White, Last & Stevens, 2007)

(Edmund's spurdog)

Figs. 203–208; Tables 45, 47–48

Squalus sp. C Last & Stevens, 1994 (in part): 49, 94 (cited, description; Southwest Pacific Ocean); Compagno *et al*., 2005 (in part): 79–80 (description; Western Australia); White *et al*., 2007: 72 (synonymy of *S. edmundsi*).

Squalus edmundsi White, Last & Stevens, 2007: 71–81 (original description; illustrated; Western Australia); Ward *et al*., 2007: 117–130 (cited; Australia); Naylor *et al*., 2012a: 57 (cited; Western Australia, Indonesia); Naylor *et al*., 2012b: 42 (cited; Western Australia); Ebert, 2013: 53, 57, 59–61 (listed, cited, description; Indonesia, Western Australia); Ebert *et al*., 2013a: 78, 88 (cited, description; Indo-West Pacific Ocean); Straube *et al*., 2013: 264 (cited; Australia).

Holotype: CSIRO H 2566-01, adult male, 610 mm TL, West of Bernier Island, Western Australia, 24°55′S,112°11′E, 344 meters depth. Collected on 28 January 1991.

Paratypes (11 specimens): CSIRO H 822-16, juvenile male, 543 mm TL, Southwest of Shark Bay, Western Australia, 27°03′S,112°40′E; CSIRO H 1207-06, neonate female, 299 mm TL, Northwest of Port Hedland, Western Australia, 18°20′S,117°50′E; CSIRO H 2567-10, juvenile female, 448 mm TL, West of Dorre Island, 25°09′S,112°09′E; CSIRO H 2575-18, juvenile female, 495 mm TL, West of Freycinet Estuary, Western Australia, 26°42′S,112°33′E; CSIRO H 2590-11, adult male, 618 mm TL West of Leander Point, Western Australia, 29°15′S,113°56′E; CSIRO H 2599-01, adult male, 581 mm TL, West of Green Head, Western Australia, 29°58′S,114°26′E; CSIRO H 2605-05, adult female, 647 mm

TL, Northwest of Rottnest Island, Western Australia, 31°43′S,114°58′E; CSIRO H 2605-06, juvenile female, 557 mm TL, locality same as CSIRO H 2605-05; CSIRO H 2605-07, juvenile female, 510 mm TL, locality same as CSIRO H 2605-05; CSIRO H 2608-16, adult female, 737 mm TL, Rottenest Canyon, Western Australia, 31°57′S,115°08′E; CSIRO H 6410-03, juvenile male, 457 mm TL, West of Shark Bay, Western Australia, 25°31′S,112°10′E.

Type locality: West of Bernier Island, Western Australia.

Non-type material (8 specimens): AMS I 31165-003, juvenile female, 468 mm TL, juvenile male, 435 mm TL, off Shark Bay, Western Australia; CSIRO CA 4071, juvenile male, 280 mm TL, Southwest of Rowley Shoals, Western Australia, 18°45′S,117°09′E; CSIRO H 2014-1, adult male, 595 mm TL, North of Abrolhos Islands, Western Australia, 28°11′S,113°15′E; CSIRO H 2264-3, adult male, 604 mm TL, West of Geraldton, Western Australia, 28°30′S,113°27′E; CSIRO H 2591-17, adult male, 621 mm TL, West of Leander Point, Western Australia, 29°18′S,113°56′E; CSIRO H 2619-10, adult female, 665 mm TL, West of Bunbury, Western Australia, 32°22′S,114°31′E; CSIRO H 3969-15, adult female, 598 mm TL, Southwest of Fremantle, Western Australia, 32°20′S,115°00′E.

Diagnosis. Species of *Flakeus* distinguished from its congeners by: more elongate prepectoral length, comprising 23.5%–27.8% of TL in adults; head large, its length 25.6%–28.8% of TL in adults; mouth conspicuously wide, its width 8.2%–9.4% of TL in adults; more elongate first and second dorsal spines (first dorsal spine length 5.5%–6.5% of TL; second dorsal spine length 6.1% of TL); first dorsal spine very robust with base width of first dorsal spine 1.0%–1.1% of TL (except *F. crassispinus, F. hemipinnis, F. probatovi* and *F. melanurus*). It also distinct from its congeners (except *F. mitsukurii*) by having more elongate prespiracular length (14.0%–16.7% of TL) and distance from first gill slit to snout tip (21.7%–24.7% of TL in adults of *F. edmundsi*).

Adult specimens of *Flakeus edmundsi* has upper labial furrow more elongate, its length 2.7%–3.2% of TL than those of its congeners (except *F. montalbani*). It further differs from *F. mitsukurii*, *F. japonicus*, and *F. montalbani* by upright and higher first dorsal fin, its height 8.7%–9.7% of TL (vs. 6.9%–8.3% of TL for *F. mitsukurii* vs. 6.6%–7.5% of TL for *F. japonicus* vs. 7.0%–8.6% of TL for *F. montalbani*). *Flakeus edmundsi* also has more elongate dorsal caudal margin (its length 22.5%–23.7% of TL in adults) than *F. mitsukurii* (its length 20.1%–22.2% of TL), *F. japonicus* (its length 18.1%–20.4% of TL), *F. hemipinnis* (its length 19.4%–21.6% of TL) and *F. griffini* (its length 20.4%–22.3% of TL).

Description.

External morphology (Figs. 203–207; Tabs. 45, 47). Body fusiform and slender through all its extension, somewhat arched dorsally from posterior margin of spiracle to insertion of first dorsal fin; head height 1.0 (0.9–1.0) times trunk and abdomen heights; body wider at head than in the rest of the body with head width 1.1 (1.1–1.2) times trunk width and 1.4 (1.4–1.5; 1.3–1.6) times broader than abdomen height. Head flattened anteriorly, very elongate, its length 23.3% (22.6%–25.1%; 24.0%–28.8%) of TL; head narrower at nostrils than at mouth, its width at nostril 7.1% (7.2%–7.6%; 7.5%–8.8%) of TL vs. its width at mouth 11.2% (10.7%–12.1%; 11.9%–14.1%) of TL. Snout markedly obtuse at tip and elongate, its preorbital length 8.3%, (7.9%–8.5%; 7.9%–9.6% of TL; anterior margin of nostrils bilobate with first lobe thicker than second one; nostrils nearest the mouth than snout tip, its prenarial length 1.2 (1.2–1.3; 1.1–1.2) times nostril-labial furrow space and 0.5 (0.5–0.6; 0.5) times preoral length; internarial space 1.0 (0.9–1.0; 0.8–0.9) times eye length. Eyes oval and narrow with both anterior and posterior margins convex, very elongate, its length 2.9 (2.1–

2.5; 2.2–3.4) times greater than its height. Prespiracular length 0.6 (0.6; 0.6) times prepectoral length and 1.6 (1.5–1.7; 1.7) times greater than preorbital length. Spiracles crescent and broad, its length 0.3 (0.3; 0.2) times eye length, placed behind the eyes. Prebranchial length 1.4 (1.4–1.5; 1.4–1.5) prespiracular length. Gill slits vertical and low with fifth gill slit 1.3 (1.3–1.4; 1.2–1.4) times higher than first gill slit, placed anteriorly to origin of pectoral fins.

Preoral length 1.4 (1.3–1.7; 1.3–1.4) times greater than mouth width. Mouth evidently arched and wide, its width 1.7 (1.4–1.7; 1.6–1.8) times greater than internarial space and 1.3 (1.1–1.4; 1.6–1.8) times prenarial length; upper labial furrow large with fold thin, its length 2.2% (2.1%–2.4%; 2.7%–3.2%) of TL; lower labial furrow also elongate but without a fold. Teeth unicuspid and similar in both jaws; upper teeth slightly larger than lower teeth; cusp short and thinner in upper teeth than lower teeth, oblique, although more lateral in lower teeth; mesial cutting edge convex; distal heel rounded and mesial heel somewhat notched; apron very small and thick, placed more medially. Two series of functional teeth on upper and lower jaw of holotype (2–3 in paratypes). 13–12 (13–12; 12–13) upper teeth rows and 9–10 (11–10; 10–10) lower teeth rows.

Pre-first dorsal length 1.3 (1.3–1.4; 1.3) times prepectoral length; origin of first dorsal fin anterior to pectoral free rear tips. First dorsal fin vertical and fairly tall, its height 1.5 (1.1–1.6; 1.4–1.7) times greater than its inner margin length; first dorsal fin with anterior margin convex, posterior margin straight but slightly concave near the tip, somewhat pointed and more slender at the apex; free rear tip rounded with inner margin short, its length 5.4% (5.2%–6.2%; 5.3%–6.9%) of TL; first dorsal fin 1.1 (1.0–1.3; 1.1–1.3) times greater in length than second dorsal fin. First dorsal spine thick on its base, its base width 1.0% (0.6%–1.0%; 0.8%–1.1%) of TL; first dorsal fin elongate but not reaching the fin apex, its length 0.6 (0.6–0.7; 0.4–0.7) times the fin height. Interdorsal space 2.5 (2.2–2.6; 2.3–2.8) times greater than dorsal-caudal space and 1.1 (1.1–1.2; 1.0–1.1) times prepectoral length. Pre-second dorsal length 2.7 (2.7–2.9; 2.6–2.7) times prepectoral length. Second dorsal fin oblique and tall, its height 1.3 (1.2–1.4; 1.3–1.4) times its inner margin length; second dorsal fin with anterior margin convex, posterior margin strongly falcate, and apex rounded and lobe-like; free rear tip pointed and elongate with inner margin length 4.6% (4.2%–5.3%; 4.4%–5.3%) of TL. Second dorsal spine thin, its base width 0.7% (0.6%–0.8%; 0.9%) of TL; second dorsal spine large, almost reaching the fin apex, its length 0.9 (0.8–0.9; 0.7–1.0) times height of second dorsal fin and 1.0 (0.9–1.2; 1.1–1.2) times length of first dorsal spine.

Pectoral fins with both anterior and inner margins convex, and posterior margin concave; pectoral fins conspicuously broad with anterior margin comprising 1.9 (1.9–2.1; 1.7–2.0) times greater in length than pectoral inner margin, and 1.9 (1.4–1.5; 1.4–1.7) times greater than length of pectoral inner margin; pectoral apex rounded and lobe-like, exceeding the horizontal line traced at pectoral free rear tips; pectoral free rear tips rounded and lobe-like. Pectoral-pelvic space 0.7 (0.7–0.9; 0.7–0.8) times pelvic-caudal space; pelvic fins located right in the midline between dorsal fins. Pelvic fins narrow with straight margins; pelvic fin length 11.7% (9.5%–12.2%; 9.6%–11.9%) of TL; pelvic free rear tips rounded and lobe-like. Claspers in adults flattened ventrally, thin and short but transcending the pelvic free rear tips, its inner length 1.2 (1.1–1.2; 0.5–1.0) times length of pelvic inner margin; clasper groove small, dorsal and longitudinal; apopyle with very narrow aperture, located anteriorly in the clasper groove; hypopyle also narrow, placed more posteriorly; rhipidion flattened, flap-like and short, located medially at distal end of clasper.

Caudal keel prominent, placed laterally in the caudal peduncle since anterior the insertion of second dorsal fin to behind origin of caudal fin; upper and lower precaudal pits prominent. Caudal fin slender in both dorsal and ventral lobes (slightly rectangular in juveniles); dorsal caudal margin straight, postventral caudal margin convex, and straight preventral caudal margin; dorsal and ventral caudal tips conspicuously pointed (rounded in juveniles); caudal fork discontinuous and narrow, its width 6.5% (6.5%–6.9%; 6.7%–8.2%) of TL; dorsal caudal margin short, its length 0.9 (0.9–1.0; 0.8–0.9) times head length and 2.0 (1.9–2.0; 1.9) times larger than length of preventral caudal margin; preventral caudal margin elongate, its length 1.8 (1.8–2.5; 2.0–2.2) times larger than length of pelvic inner margin.

Dermal denticles (Fig. 207). Unicuspid, lanceolate, and imbricate; denticles markedly wide at crown, its length greater than its width; median cusp posterior, very broad and pointed, oblique to the longitudinal axis of body; lateral cusps inconspicuous posteriorly, not forming a marked concavity with the median cusp; median ridge slender and elongate with anterior furrow shallow; median ridge with its anterior margin arrow-shaped; lateral ridges markedly small and thin, much smaller than median ridge.

Coloration. Body light grey and white lateral-ventrally. First dorsal fin grey, whitish on its base and darker at the apex; anterior margin whitish till its midline; posterior margin white from its midline to the free rear tips. Second dorsal fin also grey, whitish on its base and darker at the apex; posterior margin white. Dorsal spines dark brown (first dorsal spine light brown) and whitish at the tips. Pectoral fins grey with posterior margin somewhat white. Pelvic fins also grey and light grey ventrally with posterior margin whitish. Caudal fin grey with upper lobe partially dark grey, its dorsal caudal margin blackish; postventral caudal margins white, except in the caudal fork where it is black caudal bar; dorsal caudal tip broadly white; lower lobe mainly white, including its ventral caudal tip but partially dark grey in the remaining areas; preventral caudal margin whitish from its midline to the tip.

Vertebral counts (Tab. 48). 45 (43; 44) Monospondylous vertebrae; 89 (86; 90) precaudal vertebrae; 115 (115; 118) total vertebrae.

Geographical distribution (Fig. 208). It occurs in the Western Australia from Port Hedland to Bunbury.

Etymology. The name "*edmundsi*" is lazitinized word in honor to the ichthyologist Matt Edmunds (CSIRO).

Remarks. *Flakeus edmundsi* is endemic to Western Australia and does not occur in Indonesian waters. These results are in contrast to White *et al*. (2007c). Specimens from Indonesia were misidentified previously by these authors and belong to another species, *F. hemipinnis*. *Flakeus edmundsi*, then, is sympatric with *F. crassispinus*, *F. grahami* and *F. japonicus* in this region. It is similar to *F. japonicus* on having very slender body throughout all its extensions but it is easily distinct from it by larger prepelvic length (46.5%–55.6% of TL in adults vs. 43.7%–45.9% of TL for adults of *F. japonicus*), and more elongate interdorsal space (25.3%–31.0% of TL in adults vs. 22.5%–25.2% of TL for adults of *F. japonicus*).

It shares with *F. albifrons* and *F. crassispinus* dorsal fins markedly tall and upright with dorsal spines elongate, although it easily differs from these species by more elongate snout, its preorbital length 8.3% (7.9%–8.5%; 7.9%–9.6%) of TL vs. 7.2% (6.7%–7.1%; 7.3%–7.5%) of TL for *F. crassispinus* and 8.8% (8.3%–9.6%; 8.4%–10.3%) of TL for *F. albifrons*. *Flakeus edmundsi* further is distinguished from *F. albifrons* by lower first dorsal fin (its height 5.4%, 5.2%–6.2%; 5.3%–6.9% of TL vs. 9.6%, 8.2%–9.4%; 7.9%–10.2% of TL for *F. albifrons*) and from *F. crassipinus* by thinner dorsal spines (its base width 1.0%, 0.6%–1.0%;

0.8%–1.1% of TL vs. 1.2%, 1.1%–1.2%; 1.1%–1.3% of TL for *F. crassispinus*). It also differs from these species by monospondylous vertebrae 43–45 vs. 41-42 for *F. crassispinus* vs. 43–47 for *F. albifrons*.

Flakeus edmundsi is similar to *F. grahami* in having snout elongate and obtuse, and pectoral fins broad with anterior margin conspicuously large, posterior margin concave and pectoral free rear tips rounded. These species also share dorsal spines thin and elongate, and caudal fin slender on upper and lower lobes. Besides the characteristics on the diagnosis, *Flakeus edmundsi* clearly differs from *S. grahami* by having more elongate base length of first dorsal fin (8.5%–10.1% of TL vs. 6.6%–8.0% of TL for adults of *F. grahami*), and larger pectoral fins, its anterior margin length 16.0%–18.0% of TL in adults (vs. 12.6%–15.3% of TL for adults of *F. grahami*).

Black caudal bar at postventral caudal margins is conspicuous in *F. edmundsi* as well as in *F. grahami*, *F. montalbani* and *F. japonicus*. White *et al*. (2007c) stated that the caudal bar is oblique and from anterior margin of lower lobe to caudal fork in *F. edmundsi* rather than vertical along caudal fork in other species. The current analysis, however, reveals that this pattern is more evident in neonates to young juveniles of *F. edmundsi* and it turns restrict to the caudal fork when maturing, which it is similar to those observed for *F. grahami*, *F. montalbani* and *F. japonicus*. The caudal bar in these three species run up to upper postventral caudal margin till it meets the tip of vertebral column while it is smaller in *F. edmundsi*. Adult specimens of *Flakeus edmundsi* is distinguished from *F. montalbani* by having more elongate distance from pelvic to caudal fin (26.3%–33.5% of TL in adults vs. 23.3%–26.1% of TL for adults of *F. montalbani*), and larger prenarial length (5.9%–6.6% of TL for adults vs. 5.2%–5.5% of TL for adults of *F. montalbani*).

Comparative material: Specimens of *F. grahami*, *F. montalbani*, *F. mitsukurii* and *F. japonicus, F. albifrons* and *F. crassispinus* listed in this Chapter.

Flakeus sp. 1

(Proposed vernacular: Smith's dogfish shark)

Figs. 209–213; Tables 50, 57–58

Squalus acutipinnis. Regan, 1908: 248 (in part) (original description of *S. acutipinnis*; Table Bay, Cape of Good Hope); Regan, 1921: 412 (cited); Krefft, 1968: 34, 51–54, pl. III A (in part) (cited, description; Eastern Atlantic); Myagkov & Kondyurin, 1986: 8–10, 15 (description; Southern Africa); Last *et al*., 2011: 11 (cited; Western Indian); Ebert *et al*., 2010: 22–23 (cited; Southern Africa); Ebert, 2013: 66 (catalogued; North Atlantic).

Squalus megalops not Macleay: Bass *et al*., 1976 (in part): 10–12, 16–18, 60 (revision; Southearn Africa); Bass *et al*., 1977: 9–18; 59, 60,64, figs. 6b, 7b, 8 (C,D), 11 (in part) (revision; Southern Africa); Compagno, 1984 (in part): 118–119 (listed, described; Southern Africa).

Holotype: SAIAB 25389, adult male, 543 mm TL, off West Coast, South Africa, 30.43°S,15.44°E.

Paratypes (10 specimens): MNHN 1987-2092, adult male, 430 mm TL, Namibia, 20°22'59"S,12°31'1"E; SAIAB 20560, juvenile female, 350 mm TL; juvenile male, 312 mm TL, Walvis Bay, Namibia, 22.91°S,14.46°E; SAIAB 21856, adult male, 452 mm TL, off Cape Columbine, South Africa, 32.71°S,17.33°E; SAIAB 21858, adult male, 455 mm TL, Jakkalsbaai, South Africa, 29.85°S,15.18°E; SAIAB 21859, juvenile female, 440 mm TL, Cape Point, South Africa, 34.91°S,18.64°E; SAIAB 21939, juvenile female, 360 mm TL, off Cape Columbine, South Africa, 32.61°S,17.36°E; SAIAB 25362, adult female, 475 mm TL, Algoa Bay, South Africa, 34.03°S,25.70°E; SAIAB 25366, adult male, 460 mm TL, off West Coast, South Africa, 29.86°S,15.54°E; SAIAB 25377, adult male, 445 mm TL, off West Coast, South Africa, 35.59°S,19.88°E.

Type locality: off West coast. South Africa.

Non-type specimens (24 specimens): BMNH 1912.12.10.45-46, two juvenile males, 243–263 mm TL, juvenile female, 441 mm TL, adult female 575 mm TL, South Africa; BMNH 1922.1.13.4, adult female, 665 mm TL, Knysna, South Africa; BMNH 1935.5.2.45-46, adult female, 600 mm TL, South Africa; BMNH 1935.5.2.47-48, juvenile male, 415 mm TL, juvenile female, 415 mm TL, South Africa; BMNH 1986.5.9.3, juvenile male, 307 mm TL, Cape Province, South Africa; MNHN 1987-2093, adult male, 420 mm TL, Namibia, 20°40'59''S,13°45'0''E; NMW 61060, three neonate males, 150–179 mm TL, six neonate females, 178–215 mm TL, Morrocco; NMW 86153, adult male, 517 mm TL, Morrocco; SAIAB 25372, adult male, 450 mm TL, off West Coast, South Africa, 29.91°S,15.51°E; SAIAB 25382, adult male, 460 mm TL, off West Coast, South Africa, 35.56°S,19.60°E; SAIAB 38255, four neonate male, 230–280 mm TL, Hangklip Cape, South Africa, 34.75°S,18.76°E; SAIAB 40765, four neonate female, 215–220 mm TL, South Africa, 34.40°S,24.28°E; SAM 12992, adult male, 535 mm TL, unspecified locality, South Africa; SAM 18210, adult male, 520 mm TL, Kalk Bay, South Africa, 34.11°S,18.43°E; SAM 34646, neonate male, 380 mm TL; two adult males 460–500 mm TL, Western Cape, South Africa, 34.24°S,19.5°E; ZMA 112.257, juvenile female, 425 mm TL, adult female, 492 mm TL, three juvenile males, 393–420 mm TL, Table Bay, Cape Town, South Africa; ZMB 21984, juvenile male, 369 mm TL, Southeastern Atlantic Ocean; ZMB 21985, adult male, 445 mm TL, Southeastern Atlantic Ocean; ZMB 22990, adult male, 470 mm TL, Southeastern Atlantic Ocean; ZMB 22991, adult male, 445mm TL, Southeastern Atlantic Ocean; ZMB 22992, adult male, 365 mm TL, Southeastern Atlantic Ocean; ZMH 11164, two juvenile females, 300–317 mm TL, Lüderitz, Namibia; ZMH 11169, two juvenile females, 347, 400 mm TL, Cape Town, South Africa; ZMH 11172, adult female, 515 mm TL, South Africa.

Type locality: off West coast, South Africa.

Diagnosis. A species of *Flakeus* from the Eastern Atlantic Ocean distinct from its congeners by the following combination of characters: first dorsal fin evidently high (8.3%, 8.6%–10.2% of TL); first dorsal fin conspicuously rounded at the apex, broad in the fin web from its lower half to fin base, and posterior margin strongly concave; pectoral fin extremely broad with posterior margin 0.9 (1.0-1.8) times trunk height; pelvic fins also wide with free rear tips triangular and very short, its length 12.1% (10.6%–13.1% of TL).

It differs from *F. acutipinnis* by having: shorter distance between tip of snout to cloaca (46.0%, 46.1%–47.8% of TL vs. 49.8% of TL in lectotype of *F. acutipinnis*); shorter distance between the tip of snout to origin of pelvic fin (42.4%, 43.7%–45.4% of TL vs. 45.8% of TL); more elongate second dorsal spine (its length 4.8%, 4.2%–6.3% of TL vs. 3.8% of TL for *F. acutipinnis*, never reaching the fin apex); shorter lower caudal lobe (length of preventral caudal margin 12.1%, 11.0%–12.8% of TL vs. 10.5% of TL); broader head (its width at nostrils 6.5%, 7.5%–8.3% of TL vs. 6.4% of TL); body lower at abdomen in *Flakeus* sp. 1 (its height 11.5%, 6.7%–10.3% of TL vs. 11.9% of TL).

Description.

External morphology (Figs. 209–212; Tabs. 50, 57). Body fusiform, arched dorsally from posterior margin of spiracle until origin of pelvic fin; body narrow with head width 1.2 times trunk width in holotype (1.0–1.3 in paratypes) and 1.2 (1.2–1.6) times broader than abdomen width; head height 0.8 (0.9–1.1) times trunk height and 0.8 (0.9–1.4) times abdomen height. Snout obtuse and short, its prenarial length 4.0% (3.5%–4.5%) of TL; anterior margin of the nostrils bilobed; prenarial length 0.7 (0.6–1.0) times eye length and half the preoral length in holotype; prenarial length 0.9 (0.7–1.0) times the distance between nostril to upper labial furrow. Eyes rounded with anterior margin concave and posterior margin slightly notched; eyes large, its length 4.0% (4.4%–5.9%) of TL, corresponding to 2.9 (1.9–3.5) times its height. Prespiracular length corresponding to one-half the prepectoral length. Spiracles half-moon shaped and small, its length 1.6% (1.5%–2.3%) of TL, located behind posterior margin of the eyes and more dorsally. Gill slits vertical, concave and low, fifth gill slit 1.2 (1.1–1.3) times higher than first gill slit.

Mouth arched and very wide, its width 7.6% (7.5%–9.0%) of TL and corresponding to 1.9 (1.8–2.2) times larger than prenarial length and 2.3 (1.9–2.5) times broader than internarial space; upper labial furrow slim and elongate, its length 2.5% (2.0%–2.9%) of TL; lower labial furrow also large, lacking fold. Teeth similar in both jaws, labial-lingually flattened, unicuspid; upper teeth smaller than lower teeth; cusp very short and somewhat oblique; mesial cutting edge straight; mesial and distal heels rounded; apron very small and thick. Two series of functional teeth on both upper and lower jaws; teeth rows ranging from 13–13 in upper jaw and 11–11 rows in lower jaw for holotype.

Pre-first dorsal length 1.3 (1.2–1.4) times larger than prepectoral length; origin of first dorsal fin prior to vertical line traced at pectoral free reae tips. First dorsal fin conspicuously elongate and high, its length 14.6% (12.2%–14.5%) of TL and its height 8.3% (8.6%–10.2%) of TL; first dorsal fin height 1.3 (0.8–1.7) times the inner margin length; first dorsal fin broad at its base (its base length 8.1%, 6.4%–8.4%) of TL, and slender from midway posterior margin to its apex; apex conspicuously rounded; anterior margin convex, posterior margin markedly concave; first dorsal spine thick (its base width 0.6%, 0.6%–1.0% of TL) and very short 4.2% (2.2%–5.4%) of TL, not extending above one-half the height of first dorsal fin. Interdorsal space equal to prepectoral length and 1.9 (1.9–2.2) times larger than dorsal-caudal distance. Pre-second dorsal length 2.6 (2.4–2.8) times greater than length of dorsal caudal margin. Second dorsal fin very elongate and high, its length 13.1% (11.1%–13.1%) of TL and its height 6.2% (5.9%–9.1%) of TL; second dorsal fin very broad at the fin web and at its base, its base length 8.0% (6.5%–7.8%) of TL; anterior margin convex and posterior margin concave, although not falcate; second dorsal height 1.2 (0.8–1.5) times its inner margin length; second dorsal spine elongate, its length 4.8% (4.2%–6.3%) of TL, although never reaching the fin apex; second dorsal spine 1.1 (1.0-1.9) times greater in length than first dorsal spine.

Pectoral fins with both anterior and inner margins convex, posterior margin somewhat straight and fringe-like; apex and free rear tips rounded, lobe-like; its apex not transcending the free rear tip; pectoral fins very wide with its posterior margin much greater in length than trunk height when adpressed laterally on body; pectoral posterior margin length 11.3% (10.1%–14.5%) of TL and corresponding to 0.9 (1.0–1.8) times trunk height; pectoral anterior margin 1.7 (1.4–1.8) times greater in length than pectoral inner margin, and 1.5 (1.2-1.6) times larger than pectoral posterior margin.

Pectoral-pelvic distance 0.6 (0.7–0.8) times pelvic-caudal distance, pelvic fins at the midline between first and second dorsal fins. Pelvic fins strongly broad and elongate, its length 12.1% (10.6%–13.1%) of TL; pelvic margins slightly convex, and free rear tips triangular; pelvic inner margin length 5.6% (5.3%–6.8%) of TL. Claspers in adult males transcending the free rear tips of pelvic fins; clasper outer lengths 3.8%, 1.3%–4.8% of TL; siphon prominent, broad and large, located medial-ventrally since anterior margin of the pelvic girdle to the proximal portion of axial cartilage; clasper groove longitudinal and elongate, located dorsally in the midline of the clasper axis; apopyle with wide aperture, placed anteriorly in the clasper groove; hypopyle with broad aperture, located distally to the clasper groove and anterior to the rhipidion; rhipidion narrow, leaf or blade-like, placed more dorsal-mesially and distally in the clasper; clasper inner length 1.3 (0.5–1.4) times greater than pelvic inner margin length.

Upper and lower caudal pits prominent; caudal keel conspicuous laterally, from insertion of second dorsal fin to caudal origin. Caudal fin slender at upper lobe with dorsal caudal margin large straight and large, its length 22.0% (21.3%–23.3%) of TL, corresponding to 1.0 (0.9–1.0) times head length, and 1.8 (1.8–2.0) times larger than length of preventral caudal margin; preventral caudal margin convex and very short, its length 12.1% (11.0%–12.8%) of TL, corresponding to 2.2 (1.7–2.4) times length of pelvic fin inner margin; caudal fork discontinuous and broad, its width 7.4% (7.0%–8.0%) of TL.

Dermal denticles (Fig. 212). Lanceolate and unicuspid, strongly broad at crown base, not imbricated, situated near to each other and aligned vertically to the body line; denticle length greater than its width; cusps prominent and pointed posteriorly; median ridge thick and tall, bifurcated, extending far in front of crown base; lateral ridges short, thin and symmetrical.

Coloration. Body brown dorsally, and pale lateral and ventrally, particularly from insertion of pectoral fins to caudal peduncle. Both dorsal fins brown, whitish at fin base; posterior margin irregularly white from apex; free rear tips whitish; dorsal fin spines white on all its extension. Pectoral fins also brown, whitish dorsally and ventrally at pectoral fin origin; pectoral posterior margin inconspicuously white. Pelvic fins light brown dorsally and ventrally with inner and posterior margins unevenly whitish. Caudal fin brown with postventral caudal margins not uniformly white; dorsal and ventral caudal tips whitish.

Vertebral counts (Tab. 58). 38–43 Monospondylous vertebrae; 69–73 diplospondylous vertebrae; 80–85 precaudal vertebrae; 107–115 total vertebrae.

Geographical distribution (Fig. 13). Found in the Eastern Atlantic Ocean with regular occurrences between Namibia and Cape Town, South Africa. Several specimens were collected in Morocco, but none in Northwestern Africa.

Remarks. Viana & Carvalho (*in press*) notices that *F. acutipinnis* was described based on more than two forms, of which the second one is herein identified as *Flakeus* sp. 1. Many studies showed a large morphological variation when describing the former species, indicating that the characteristics of *Flakeus* sp. 1 were hidden (e.g. Regan, 1908; Krefft, 1968; Bass *et al*., 1976). The wide range of precaudal and total vertebrae provided by Bass *et al*. (1976) for describing the nominal species *S. megalops* in South Africa clearly shows that the authors used specimens of both *F. acutipinnis* and *Flakeus* sp. 1 for their counts.

The current results verify that *Flakeus* sp. 1 is distinct from *F. acutipinnis*. In addition to the characteristics provided in the Diagnosis above, *Flakeus* sp. 1 is distinguished by: longer prespiracular distance (11.5%, 11.7%–13.1% TL vs. 11.6% TL for *F. acutipinnis*); space between origin of first dorsal fin and the vertical traced at origin of pectoral fin 1.0 (0.6–1.2) preorbital length (vs. 1.4); base length of first dorsal fin 1.3 (0.9–1.2) in preorbital length (vs. 1.3); fifth gill slit 1.2 (1.1–1.3) times higher than the first gill slit (vs. 1.5). *Flakeus* sp. 1 is further distinguished from *F. acutipinnis* by: dermal denticles wide at crown base, its length greater than its width with symmetrical lateral expansions (vs. slender at the crown base; somewhat equal in length and width; asymmetrical lateral expansions); teeth slimmer at the crown base on upper teeth, broad and depressed on lower teeth, cusp very short and somewhat oblique, straight mesial cutting edge, rounded mesial and distal heels, and apron very short (vs. teeth wider on lower jaw only with cusp thick, elongate and directed upwardly, concave mesial cutting edge, slender mesial heel; apron shorter in the upper teeth only); caudal fork between lobes discontinuous (vs. continuous).

Small differences are observed between adult specimens of *Flakeus* sp. 1 and *F. acutipinnis* regarding length of spiracles (1.7%–2.0% of TL vs. 1.2%–1.7% of TL for *F. acutipinnis*), interdorsal space (21.2%–24.7% of TL vs. 24.5%–25.4% of TL), length of pelvic fins (11.0%–13.1% of TL vs. 9.8%–11.5% of TL). *Flakeus* sp. 1 differs from it by having pre-second dorsal length 2.6–2.9 times length of dorsal caudal margin (vs. 2.8–3.2 times for *F. acutipinnis*), dorsal caudal margin 0.9–1.2 times head length (vs. 0.8–0.9 times for *F. acutipinnis*). Meristic data are not helpful in separating these two species. They differ from each other by only a few vertebrae such as total (109 for *Flakeus* sp. 1 vs. 108 for *F. acutipinnis*, respectively) and monospondylous vertebrae (42 vs. 41, respectively). Greater differences are noticed for precaudal (84 vs. 81, respectively) and caudal vertebrae (25 vs. 27, respectively).

Flakeus sp. 1 and *F. acutipinnis* have no occurrences in the Northwestern Africa, which it is in contrast to the assumptions of Ebert & Stehmann (2013). *Flakeus* sp. 1 apparently does not reach Namibian waters while *F. acutipinnis* occurs in the Indian Ocean only (Viana & Carvalho *in press*). These two species are often misidentified as *F. megalops* or *F. blainvillei* from the Mediterranean. These two species share general aspects of the external morphology such as short snout, dermal denticles lanceolate and unicuspid, pectoral fins with free rear tips weakly rounded. However, comparative analysis of the external morphology in detail shows great differences that help recognize *Flakeus* sp. 1 as a separate species (e.g. pectoral fins wide, transcending the trunk height when adpressed on body; dermal denticles broader at crown; dorsal fins upright and high).

Vertebral counts and morphometrics also overlap between *Flakeus* sp. 1, *F. megalops* and *F. blainvillei*, and therefore not useful for separating them. However, slight differences are noticed when adult specimens are compared. *Flakeus* sp. 1 can be separated from *F. blainvillei* by prebranchial length (18.0%–22.4% of TL vs. 16.8%–18.4% of TL for *F. blainvillei*), prenarial length (4.1%–4.6% of TL vs. 3.6%–4.2% of TL for *F. blainvillei*), height of eyes (1.8%–2.6% of TL vs. 1.0%–1.8% of TL for *F. blainvillei*), narrow caudal fork (its width 7.0%–7.2% of TL vs. 6.4%–7.0% of TL for *F. blainvillei*). It is also distinct from *F. megalops* by more elongate first dorsal spine (its length 3.0%–5.4% of TL vs. 1.8%–3.7%

of TL for *F. megalops*), pre-second dorsal length 3.3–3.8 times larger than length of dorsal caudal margin in *Flakeus* sp. 1 (vs. 3.6–4.5 times for *F. megalops*).

Comparative material. Specimens of *Flakeus acutipinnis*, *F. megalops*, *F. probatovi* and *F. blainvillei* listed in this Chapter.

Flakeus sp. 2

(Proposed vernacular: Longnose African dogfish)

Figs 214–218.; Tables 51, 57–58

Squalus mitsukurii not Jordan & Synder: Compagno, 1984 (in part): 121–122 (description; South Africa); Bass *et al*., 1986 (in part): 61–62 (cited; South Africa, Mozambique); Compagno *et al*., 2005 (in part): 67–68 (description; Southeastern Atlantic and West Indian Oceans); Ebert, 2013: 53 (cited; Indian Ocean).
Squalus cf. *mitsukurii* Naylor *et al*., 2012a: 57 (cited; South Africa).

Holotype. SAM 33476, adult male, 683 mm TL, near Agulhas Bank, Western Cape, South Africa, 36.21°S,20.04°E. Collected on 11 June 1994. Collector South Coast Biomass Survey.

Paratypes (23 specimens): SAIAB 25341, adult female, 680 mm TL, off West coast, South Africa, 32.16°S,16.86°E; SAIAB 25923, adult male, 790 mm TL, off West coast, South Africa, 32.10ºS,16.90ºE; SAIAB 25924, adult male, 730 mm TL, locality same as SAIAB 25923; SAIAB 26419, juvenile female, 450 mm TL, off West Coast, South Africa, 30.60°S,17.17°E; SAIAB 26420, juvenile female, 485 mm TL, locality same as SAIAB 26419; SAIAB 26421, juvenile male, 450 mm TL, locality same as SAIAB 26419; SAIAB 53305, adult male, 750 mm TL, off West coast, South Africa, 34.06ºS,17.49ºE; SAIAB 186461, juvenile male, 392 mm TL, off Durban, South Africa; SAM 32611, adult male, 695 mm TL, juvenile male, 285 mm TL, off West coast, South Africa, 30.09ºS,16.69ºE; SAM 33150, adult female, 925 mm TL, off West coast, South Africa, 35.26ºS,18.92ºE; SAM 33153, adult male, 750 mm TL, off West coast, South Africa, 34.83ºS,18.40ºE; SAM 33154, two adult males, 730–740 mm TL, off West coast, South Africa, 30.93ºS,16.61ºE; SAM 33155, juvenile female, 400 mm TL, adult male, 715 mm TL, off West coast, South Africa, 29.83ºS,15.54ºE; SAM 33283, juvenile female, 390 mm TL, off West coast, South Africa, 29.83°S,15.54°E; SAM 33476, adult female, 750 mm TL, near Agulhas Bank, Western Cape, South Africa, 36.21°S,20.04°E; SAM 34004, adult male, 700 mm TL, adult female, 740 mm TL, off Saint Francis Bay, Eastern Cape, South Africa, 34.41ºS,25.91ºE; SAM 36412, adult female, 745 mm TL, off West coast, South Africa, 31.93ºS,16.38ºE; SAM 38042, juvenile male, 570 mm TL, off West coast, South Africa, 29.95°S,15°07'E; SAM 38334, two juvenile males, 282–388 mm TL, off Mozambique, 23.53°S,35°51'E.

Type locality: off Agulhas Bank, South Africa.

Non-type material (11 specimens): SAIAB 21872, adult male, 507 mm TL, off Jakkasbaai, South Africa, South Africa, 29.33°S,14.96°E; SAIAB 25339, adult male, 515 mm TL, off West coast, South Africa, 30.10°S,14.76°E; SAIAB 25340, juvenile male, 440 mm TL, off West coast, South Africa, 30.60°S,15.41°E; SAIAB 25342, adult female, 621 mm TL, off West coast, South Africa, 31.63°S,16.34°E; SAIAB 26321, juvenile male, 425 mm TL, off West coast, South Africa, 31.76°S,16.46°E; SAIAB 26322, juvenile female, 450 mm TL, locality same as SAIAB 26321; SAIAB 26418, juvenile female, 440 mm TL, off West coast, South Africa, 30.66°S,15.55°E; SAIAB 82057, juvenile male, 345 mm TL, Mozambique, 23°32'S,35°52'E; SAIAB 188839, juvenile female, 223 mm TL, Tugela Deep, Kwazulu-Natal, South Africa; SAM 32611, juvenile male, 285 mm TL, adult male, 695 mm TL, off West coast, South Africa, 30.09ºS,16.69ºE; SAM 33197, adult male, 730 mm TL, off West coast, South Africa, 30.39°S, 16.09°E.

Diagnosis. Longnose species from Southern Africa that it is distinguished from its congeners by a combination of characters: body robust, its head width 1.0–1.3 times trunk width and 1.1–1.7 times abdomen width; snout elongate, its prenarial length 5.0%–9.4% of TL and preorbital length 7.6%–9.1% of TL; dorsal fins broad at fin web and lobe-like; first and second dorsal fins tall (height of first dorsal fin 7.5%–9.5% of TL; height of second dorsal fin 4.3%–7.7% of TL); pectoral fins markedly large, its anterior margin length 14.6%–18.2% of TL; pectoral free rear tips rounded; caudal fin rectangular at upper lobe with dorsal caudal lobe large, its length 19.1%–23.0% of TL; dermal denticles tricuspid and rhomboid with large posterior cusps.

Flakeus sp. 2 has more monospondylous vertebrae (46–47) than *F. blainvillei* (40–43), *F. japonicus* (37–43), *F. grahami* (41–42), *F. montalbani* (38–45), *F. edmundsi* (43–45), *F. hemipinnis* (37), and *F. melanurus* (41). It shows fewer diplospondylous vertebrae (69–72) than *F. probatovi* (73–77), *F. montalbani* (73–74), *F. melanurus* (73–79) and more diplospondylous vertebrae than *F. hemipinnis* (60–61). It has more precaudal vertebrae (86–89) than *F. blainvillei* (80–84), *F. montalbani* (84–85), *F. hemipinnis* (74) and *F. lalannei* (67–69), and more total vertebrae (116–121) than *F. blainvillei* (107–111), *F. montalbani* (112–118), *F. hemipinnis* (97–98), and *F. lalannei* (93–95).

Description.

External morphology (Figs. 214–217; Tabs. 51, 57). Body slender, arched dorsally from posterior margin of the eye to origin of first dorsal fin; body with greatest width at head with head width 1.0–1.4 times trunk width and 1.1–1.6 times abdomen height; head height 0.8–1.1 times trunk height and 0.8–1.2 times abdomen height. Head large, its length 20.6%–26.2% of TL. Snout obtuse and elongate, its preorbital length 6.6%–9.1% of TL; anterior margin of nostrils bilobed; prenarial length 0.4–0.6 times preorbital length and 0.9–1.7 times distance from nostrils to upper labial furrow; distance between nostrils 0.7–1.2 times eye length. Eyes oval with anterior margin concave and posterior margin notched; eyes very large, its length 2.1–4.6 times greater than its height. Prespiracular length 0.5–0.7 times prepectoral length and 1.6–1.8 times larger than preorbital length. Spiracles crescent and short, its length 0.3–0.4 times eye length. Prebranchial length 17.3%–22.4% of TL. Gill slits vertical, somewhat convex and tall with height of fifth gill slit 0.9–1.5 times height of first gill slit.

Preoral length 1.1–1.5 times greater than mouth width. Mouth arched and narrow, its width 0.9–2.0 times prenarial length and 1.6–2.0 times internarial space; upper labial furrow very elongate, its length 1.9%–2.9% of TL with thin fold; lower labial furrow larger than upper one, lacking fold. Teeth similar in both jaws, upper teeth smaller than lower teeth; teeth unicuspid with cusp thick, short and oblique; mesial cutting edge straight; mesial heel rounded on lower jaw and notched on upper jaw; distal heel notched; apron conspicuously short and slender. Upper jaw with one to three series of functional teeth and two series on lower jaw. Upper teeth 13–13 rows and 11–11 rows on lower jaw.

Pre-first dorsal length 27.5%–33.6% of TL, corresponding to 1.1–1.5 times greater than prepectoral length; origin of first dorsal fin prior to vertical traced at pectoral free rear tips. First dorsal fin conspicuously lobe-like with anterior margin convex and posterior margin straight, although concave distally; apex markedly rounded; first dorsal fin tall, its height 0.8–1.4 times preorbital length and 0.6–1.8 times its inner margin length. First dorsal spine thick (its base length 0.5%–1.0% of TL) and elongate (its length 2.4%–5.3% of TL), not reaching apex of first dorsal fin; first dorsal spine 0.3–0.6 times first dorsal height. Interdorsal space 0.9–1.2 times prepectoral length and 1.9–2.7 times larger than dorsal-caudal space. First dorsal fin 1.0–1.3 times greater in length than second dorsal fin. Pre-second dorsal length 2.4–2.9 times larger than prepectoral length. Second dorsal fin lobe-like with anterior margin convex and posterior margin falcate; its apex rounded; second dorsal fin tall, its height 0.7–1.3 times its inner margin length. Second dorsal spine thin and elongate (its length 0.5–0.9 times height of second dorsal fin), although not reaching apex of second dorsal fin; second dorsal spine 0.7–2.0 times first dorsal spine.

Pectoral fins very narrow, its posterior margin length 9.2%–12.6% of TL; pectoral anterior and inner margins convex; posterior margin straight; pectoral anterior margin 1.3–1.9 times greater in length than pectoral inner margin and 1.3–1.7 times larger than pectoral posterior margin; free rear tips rounded; pectoral apex rounded. Pectoral-pelvic distance 0.6–1.1 times pelvic-caudal space. Pelvic fins narrow with its margins straight; pelvic fin length 10.0%–13.0% of TL; pelvic fins placed in the midline between dorsal fins. Claspers large, its inner length 2.6%–8.1% of TL, corresponding to 0.4–1.5 times inner margin of pelvic fins; clasper groove dorsal and longitudinal; apopyle broad, placed anteriorly in the clasper groove; hypopyle very constricted, placed distally in the clasper groove; rhipidion flap-like, very slender and elongate, placed distally at clasper.

Upper and lower precaudal pits prominent; caudal keel short, placed laterraly in the caudal penduncle. Caudal fin rather rectangular with dorsal caudal margin straight, upper postventral caudal margin almost straight, although convex distally near dorsal tip; lower postventral caudal margin convex; preventral caudal margin markedly convex; length of dorsal caudal margin 0.8–1.1 times head length and 1.6–2.1 times greater than length of preventral caudal margin; dorsal and ventral caudal tips rounded; preventral caudal margin short, its length 1.7–2.8 times length of pelvic inner margin; caudal fork discontinuous and very broad, its width 6.6%–8.4% of TL.

Dermal denticles (Fig. 217). Tricuspid and rhomboid, weakly imbricate; denticles somewhat broad at crown, its length almost equal to its width; cusps posterior and pointed, conspicuously slender and well elongate; lateral cusps forming prominent posterior concavity with median cusp on each side; median ridge large and thin with anterior furrow small, rounded and shallow; anterior margin of median ridge conspicuously narrow and rounded (weakly arrow-shaped in adult specimens); lateral ridges markedly thin, straight and short.

Coloration. Body dark grey to brownish grey dorsally, and pale ventrally and laterally from insertion of pelvic fins to caudal fin. First dorsal fin dark brown on all its extension, except distally at its posterior margin that is light brown; base fin whitish. Second dorsal fin brown, slightly darker at the tip, whitish at its base. First and second dorsal spines brown, darker anteriorly and whitish at the tip. Pectoral fins dark brown, somewhat white at its posterior margin; ventral base of pectoral fin pale. Pelvic fins brown dorsally and pale ventrally. Caudal fin dark brown, whitish over vertebral column; dorsal caudal margin white proximally; postventral caudal margins white, except at caudal fork; dorsal and ventral caudal tips broadly white; black caudal stripe evident. Juveniles differ from adults by having: body brown (light brown in neonates), although darker dorsally from insertion of first dorsal fin to caudal fin; dorsal fins brown with its apex blackish; caudal fin brown (mostly white in neonates) with postventral caudal margin broadly white. Neonates and very young juveniles also show: dorsal fins light brown and markedly black at its apex; two upper caudal blotch black, rounded and large present; lower caudal lobe mostly white with blackish basal marking very elongate.

Vertebral counts (Tab. 58). 45–47 [mode 47] monospondylous vertebrae; 69–74 [mode 70–72] displospondylous vertebrae; 86–89 precaudal vertebrae; 116–121 [mode 116–119] total vertebrae.

Geographical distribution (Fig. 218). It occurs in Southern Africa from Western Cape to Mozambique.

Remarks. *Flakeus* sp. 2 is a species that is abundant in South African waters from Western Cape to Durban, and in Mozambique. It is often misidentified with the Japanese species, *F. mitsukurii* in these regions (e.g. Compagno, 1984; Bass *et al*., 1986; Compagno *et al*., 2005). However, *Flakeus* sp. 2 is distinguished from it by having body grey (vs. body dark grey to blackish), more elongate eyes (its length 4.2%–6.2% of TL vs. 3.4%–4.0% of TL in adults of *F. mitsukurii*), and broader caudal fin, its width at caudal fork 6.6%–8.4% of TL (vs. 6.1%–6.8% of TL in adults of *F. mitsukurii*).

The longnose African species assemblages *F. montalbani*, *F. grahami*, *F. griffini*, and *F. japonicus* in body color, elongate snout, and dermal denticles tricuspid and rhomboid. *Flakeus* sp. 2 also shows great overlap of external measurements, even when only adult specimens are compared. However, it is somewhat distinct from *F. montalbani* by more elongate first dorsal spine, its length 3.1%–4.8% of TL in adult specimens (vs. 2.7%–3.5% of TL for adults of *F. montalbani*), and from *F. grahami* and *F. griffini* by larger pectoral inner margin, its length 8.5%–11.1% of TL (vs. 7.2%–8.5% of TL for adults of *F. grahami* vs. 7.4%–8.7% of TL for adults of *F. griffini*). It also has broader mouth than *F. grahami* and *F. japonicus*, its width 7.4%–8.9% of TL in adults (vs. 7.0%–7.6% of TL for adults of *F. grahami* vs. 5.3%–6.7% of TL for adults of *F. japonicus*). It is further differentiated from *F. montalbani*, *F. grahami* and *F. japonicus* by lacking dark caudal bar. *Flakeus* sp. 2 also exhibits much shorter preoral length than *F. japonicus* (9.0%–10.0% of TL in adults vs. 10.7%–12.2% of TL for adults of *F. japonicus*), and shorter pelvic-caudal space (23.2%–26.8% of TL vs. 26.5%–28.0% of TL for adults of *F. japonicus*).

Other species that surrounds the African waters are *F. probatovi* and *F. lalannei*. *Flakeus* sp. 2 differs from *F. probatovi* by having more elongate pectoral-pelvic space (19.9%–25.1% of TL in adults vs. 15.3%–20.3% of TL in adults of *F. probatovi*). It also has lower dorsal fins than *F. probatovi* with height of first dorsal fin 7.5%–9.0% of TL in adults (vs. upright first dorsal fin with its height 8.2%–10.4% of TL in adults of *F. probatovi*), and height of second dorsal fin 4.3%–5.8% of TL in adults (vs. 5.3%–7.3% of TL in adults of *F. probatovi*). *Flakeus probatovi* is separated from *F. lalannei* by having shorter interdorsal space (20.5%–15.7% of TL vs. 26.6%, 28.4% of TL for *F. lalannei*), more elongate snout, its prenarial length 5.0%–9.4% of TL (vs. 4.7%, 4.8% of TL for *F. lalannei*), more elongate head, its length 22.4%–26.2% of TL (vs. 21.8%, 21.6% of TL for *F. lalannei*), and caudal fin mostly uniformly grey (vs. caudal fin dark grey with conspicuous white upper caudal lobe).

Flakeus sp. 2 is easily differentiated from its congeners by vertebral counts (see on diagnosis). Despite of some overlapping, external morphology also helps to separate it from them. Naylor *et al*. (2012a) recognized a variation of *F. mitsukurii* in South Africa based on molecular analysis, which give additional support to recognize *Flakeus* sp. 2 as a separated species.

Comparative material. Specimens of *F. mitsukurii*, *F. montalbani*, *F. grahami*, *F. griffini*, *F. japonicus, F. probatovi* and *F. lalannei.*

***Flakeus* sp. 3**

(**Suggested common names: Madagascar's pointedfin dogfish**)

Figs. 219–223; Tables 52, 57–58

Squalus megalops not Macleay: Ebert, 2013 (in part): 53, 57 (listed, cited; Indian Ocean).

Holotype: SAIAB 189449, adult female, 590 mm TL, off Northern Madagascar.

Paratypes (11 specimens): MNHN 1987-1264, adult male, 450 mm TL, Madagascar, 23°19’59”S,43°31’1”E; SAIAB 25370, adult male, 500 mm TL, Algoa Bay, South Africa, 34.03°S,25.70°E (dissected); SAIAB 189449, juvenile female, 513 mm TL, same locality as holotype; SAIAB 189450, adult female, 550 mm TL, same locality as holotype; SAIAB 186419, juvenile female, 264 mm TL, off Richards Bay, South Africa; SAIAB 186461, two juvenile females, 363–440 mm TL, off Durban, South Africa; ZMH 26075, juvenile male, 402 mm TL, adult male, 539 mm TL off Socotra Islands, 12°14’5”N,53°06’5”E; ZMH 26076, juvenile female, 435 mm TL, adult male, 496 mm TL, off Northwest Madagascar, 12°31'5"S,48°17'1"E.

Type locality: Northern Madagascar.

Non-type specimens (2 specimens): NMW 86885, two juvenile females, 425–490 mm TL, Sokotra Islands.

Diagnosis. Shortsnout dogfish different from its congeners by a combination of characters: snout short, its prenarial length 4.4% (4.2%–5.0%) of TL; first dorsal fin conspicuously upright, slender at fin web, and tall, its height 7.8% (7.4%–9.2%) of TL; second dorsal fin upright, slender, and tall, its height 5.9% (4.2%–6.9%) of TL; pectoral fins markedly narrow, its posterior margin length 10.8% (8.9%–12.5%) of TL; pectoral free rear tips conspicuously pointed. It is also distinguished from its congeners by having caudal fin thin and short with length of dorsal caudal 19.7% (20.2%–21.9%) of TL, dermal denticles unicuspid, markedly slender and lanceolate. It is distinct from *F. brevirostris*, *F. crassispinus*, *F. albifrons*, and *F. notocaudatus* by having larger dorsal caudal distance 10.9%–13.0% of TL vs. 10.0%–10.6% of TL for *F. brevirostris* vs. 9.9%–10.0% of TL for *F. crassispinus* vs. 9.3%–10.0% of TL for *F. albifrons* vs. 10.3%–10.7% of TL for *F. notocaudatus*). It differs from *F. megalops* on having more elongate first dorsal fin, its length 4.2%–4.9% of TL and corresponding to 0.5–0.7 times height of first dorsal fin in adult specimens (vs. 1.8%–3.7% of TL and corresponding to 0.2–0.4 times in adults of *F. megalops*).

Adult specimens of *Flakeus* sp. 3 differ from those of *F. brevirostris* on having larger snout (its prenarial length 4.4%–4.9% of TL vs. 3.8%–4.3% of TL), and thicker first dorsal spine (its base length 0.8%–1.0% of TL vs. 0.5%–0.7% of TL). *Flakeus* sp. 3 is distinguished from *F. crassispinus* by having larger pre-first dorsal length (28.6%–32.0% of TL vs. 26.7%–27.4% of TL for adults of *F. crassispinus*), smaller first dorsal fin (its anterior margin length 10.5%–12.1% of TL vs. 12.6%–12.9% of TL; its posterior margin length 8.0%–9.0% of TL vs. 9.9%–10.9% of TL), and thinner dorsal spines (base length of first dorsal spine 0.8%–1.0% of TL vs. 1.1%–1.3% of TL; base length of second dorsal spine 0.7%–1.0% of TL vs. 1.2%–1.4% of TL for *F. crassispinus*). It is differentiated from *F. crassispinus* and *F. notocaudatus* by more elongate upper labial furrow (its length 2.5%–2.7% of TL vs. 2.0%–2.2% of TL for *F. crassispinus* vs. 2.2%–2.3% of TL for *F. notocaudatus*). *Flakeus* sp. 3 is further distinct from *F. albifrons* and *F. notocaudatus* by having large preoral length (9.5%–11.1% of TL vs. 8.4%–9.2% of TL for *F. albifrons* vs. 9.2%–9.4% of TL for *F. notocaudatus*). It is distinguished from adult specimens of *Flakeus* sp. 1 by larger prespiracular length (12.4%–13.7% of TL vs. 11.7%–12.2% of TL), narrow spiracles (its length 1.2%–1.6% of TL vs. 1.7%–2.0% of TL), smaller pectoral fins (its anterior margin length 13.0%–15.7% of TL vs. 16.2%–17.9% of TL, its posterior margin length 8.9%–12.0% of TL vs. 12.4%–14.5% of TL).

Flakeus sp. 3 is distinct from *F. probatovi*, *F. bucephalus*, *F. albifrons*, *F. notocaudatus*, and *Flakeus* sp. 2 on having fewer monospondylous (40–42 vs. 45–48 for *F. probatovi* vs. 49 for *F. bucephalus* vs. 43–47 for *F. albifrons* vs. 48 for *F. notocaudatus* vs. 46–47 for *Flakeus* sp. 2). It also has fewer diplospondylous vertebrae than *F. probatovi*, *F.*

bucephalus, *F. albifrons*, *F. notocaudatus* (65–71 vs. 73–77 for *F. probatovi* vs. 75 for *F. bucephalus* vs. 72–77 for *F. albifrons* vs. 78 for *F. notocaudatus*) and fewer precaudal vertebrae than *F. probatovi*, *F. bucephalus*, *F. albifrons*, *F. notocaudatus*, and *Flakeus* sp. 2 (80–84 vs. 87–96 for *F. probatovi* vs. 93 for *F. bucephalus* vs. 90–93 for *F. albifrons* vs. 97 for *F. notocaudatus* vs. 86–89 for *Flakeus* sp. 2).

Description.

External morphology (Figs. 219–222; Tabs. 52, 57). Body slender and fusiform, somewhat arched dorsally behind posterior margin of spiracle, and equally deep from head to abdomen (head height 1.0, 0.8–1.0 times trunk height and 1.0, 0.8–1.2 times abdomen height; body with greatest width at head, its width 1.2, 1.1–1.4 times trunk width and 1.5, 1.1–1.5 times broader than abdomen width. Head flattened anterior-dorsally and elongate, its length 21.2%, 21.0%–25.8% of TL. Snout slightly obtuse at tip and short, its preorbital length 7.2%, 6.9%–7.9% of TL; anterior margin of nostrils bilobed; prenarial length 0.4, 0.4–0.5 times preoral length and 0.9, 0.6–1.1 times distance from nostrils to upper labial furrow; internarial space 0.8, 0.7–1.0 times length of eye. Eyes oval with anterior margin convex and posterior margin pointed; eyes elongate, its length 2.3, 1.6–3.2 times greater than its height. Prespiracular length 0.6, 0.5–0.7 times prepectoral length and 1.7, 1.7–1.8 times greater than preorbital length. Spiracles crescent and small, its length 0.3, 0.2–0.4 times eye length, placed laterally behind the eyes. Prebranchial length 1.5, 1.4–1.8 times larger than prespiracular length. Gill slits straight, vertical and low with fifth gill slit 1.3, 1.0–1.5 times higher than first gill slit.

Preoral length short, its length 9.8%, 9.5%–11.1% of TL and corresponding to 1.3, 1.2–1.4 times width of mouth. Mouth arched and narrow, its width 1.7, 1.6–1.9 times greater than prenarial length and 2.0, 1.6–2.1 times broader than internarial space. Teeth similar in both jaws with upper teeth smaller than lower one; teeth unicuspid. Upper teeth with 12–13 rows and lower teeth with 10–11 rows. Two series of functional teeth in upper jaws and 2–3 series in lower jaw.

Pre-first dorsal length 1.4, 1.2–1.6 times larger than prepectoral length; origin of first dorsal fin close behind origin of pectoral fins. First dorsal fin elongate, its length 13.8%, 13.1%–14.7% of TL and corresponding to 1.2, 1.0–1.4 times larger than second dorsal fin; first dorsal fin slender and upright with anterior margin convex, posterior margin concave; apex somewhat pointed; free rear tip pointed; first dorsal anterior margin of first dorsal fin large, its length 10.9%, 10.5%–13.4% of TL; first dorsal posterior margin also large, it length 8.9%, 8.0%–9.6% of TL; first dorsal fin tall, its height 1.2, 1.2–1.6 times greater than length of its inner margin and 1.1, 1.0–1.3 times preorbital length. First dorsal spine thin (its base length 0.8%, 0.8%–1.5% of TL) and elongate, transcending one-half height of first dorsal fin but not reaching its apex, its length 0.6, 0.5–0.7 times height of first dorsal fin. Interdorsal space 1.2, 0.9–1.3 times distance between pectoral and pelvic fins, and 2.2, 1.9–2.9 times larger than dorsal-caudal space. Pre-second dorsal length 3.1, 2.4–3.2 times larger than prepectoral length. Second dorsal fin upright and slender with anterior margin convex, posterior margin conspicuously concave and raked; second dorsal anterior margin large, its length 9.7%, 8.5%–11.6% of TL; apex pointed; free rear tips pointed. Second dorsal spine markedly thin and large, reaching apex of second dorsal fin, its length 1.0, 0.8–1.3 times height of second dorsal fin; second dorsal spine 1.2, 0.9–1.5 times larger than first dorsal fin.

Pectoral fins narrow, its anterior margin convex, inner margin markedly convex, and posterior margin conspicuously concave; pectoral apex rounded; pectoral free rear tips conspicuously pointed, reaching horizontal line traced at pectoral apex; pectoral anterior margin 1.5, 1.3–1.9 times larger than its inner margin and 1.3, 1.1–1.5 times greater than its posterior margin. Pectoral-pelvic space 0.8, 0.6–0.8 times pelvic-caudal distance. Pelvic fins placed in the midline between two dorsal fins; pelvic fins with its margin convex and free rear tips pointed; pelvic fins short, its length 10.4%, 10.0%–13.4% of TL. Claspers small, its inner length 0.9–2.8 times length of pelvic inner margin; clasper groove dorsal, longitudinal and short; apopyle and hypopyle very constricted, placed anterior and posteriorly in the clasper groove, respectively; rhipidion flap-like and thin, placed distally in the clasper.

Upper and lower precaudal pits prominent; caudal keel discreet from insertion of second dorsal fin to behind origin of caudal fin. Caudal fin slender with dorsal caudal margin straight and short, its length 0.9 (0.8–1.0) times head length and 1.8 (1.8–2.1) times larger than preventral caudal margin; upper postventral caudal margin convex; lower postventral caudal margin straight; dorsal and ventral caudal tips pointed; preventral caudal margin straight and elongate, its length 1.9, 1.5–4.2 times larger than pelvic inner margin; caudal fork discontinuous and concave, its width 6.8%, 6.3%–7.4% of TL.

Dermal denticles (Fig. 222). Unicuspid, lanceolate, and not imbricate; cusp posterior and rounded; denticles slender at crown, although somewhat expanded at its anterior margin; its length much greater than its width; median and lateral ridges prominent and thin; lateral ridges smaller than median one, and assymetrical.

Coloration. Body grey dorsally (light brown in preserved specimens), white ventrally and laterally from pelvic fins to origin of caudal fin. First dorsal fin dark grey, whitish at its base and blackish at apex; first dorsal free rear tip slightly white. Second dorsal fin grey, light grey at its base, and blackish at its apex; posterior margin of second dorsal fin somewhat white. Dorsal spines grey and white at its tips; black mark at dorsal fin ventral to each dorsal spine. Pectoral fins dark grey with its posterior margin white, broader at apex than to its free rear tips. Pelvic fins light grey dorsally and lighter ventrally with posterior and inner margins white. Caudal fin grey with postventral caudal margins broadly white, except at the caudal fork where it is black; black caudal bar evident from tip of vertebral column to ventral caudal lobe; the latter mostly white with black caudal blotch near its origin; upper caudal blotch black and evident distally near upper postventral caudal margin; black caudal strip dorsally.

Vertebral counts (Tab. 58). 40–42 [mode 41] monospondylous vertebrae; 65–71 [mode 69] diplospondylous vertebrae; 80–84 [mode 82] precaudal; 107–112 [mode 110] total vertebrae.

Geographical distribution (Fig. 223). It occurs in the Western Indian Ocean from Northern Madagascar and Sokotra Islands to Richards Bay in South Africa.

Remarks. *Flakeus* sp. 3 is a small species (adults between 450–550 mm TL) from the Western Indian Ocean that assemblages *F. megalops*, *F. brevirostris, F. cubensis, F. crassispinus*, *F. acutipinnis*, *F. notocaudatus*, and *F. raoulensis* in having snout small and dermal denticles unicuspid and lanceolate. It shows pectoral fins with posterior margin concave conspicuously and free rear tips pointed like it is observed for *F. brevirostris, F. cubensis, F. crassispinus* and *F. megalops*. Due to these similarities, many authors often consider it co-specific with *F. megalops* from Australian waters. (e.g. Heemstra & Heemstra, 2004; Ebert, 2013). However, the current results support that *Flakeus* sp. 3 is likely to be a separated and undescribed species from the Western Indian Ocean.

Great variations on morphometrics and vertebral counts help to support the present hypothesis. Morphological differences between these similar species are more evident when adult specimens are compared, as it is noticed in the diagnosis provided herein. Adult specimens of *Flakeus* sp. 3 differ from those of *F. brevirostris* on having smaller pre-second dorsal length (60.0%–61.2% of TL vs. 61.1%–63.8% of TL), more elongate prespiracular length (12.4%–13.7% of TL vs. 11.3%–12.8% of TL), greater distance between nostrils

(3.7%–5.1% of TL vs. 3.4%–3.8% of TL), and more elongate first dorsal spine (its length 4.2%–4.9% of TL vs. 3.1%–4.2% of TL). *Flakeus* sp. 3 shows thicker first dorsal spine than *F. megalops* from the Southeastern Australia (its base length 0.8%–1.0% of TL vs. 0.5%–0.8% of TL), mouth width 1.6–2.1 times broader than internarial space for *Flakeus* sp. 3 vs. 2.0–2.2 times for *F. megalops*, length of second dorsal spine 0.8–1.2 times height of second dorsal fin (vs. 0.7–0.9 times for *F. megalops*) and 0.9–1.3 times greater in length the first dorsal spine for *Flakeus* sp. 3 (vs. 1.1–2.9 times for *F. megalops*).

Flakeus sp. 3 also shows pectoral and caudal fins with coloration similar to those of *F. crassispinus*. However, these species further differ by: lower second dorsal fin (its height 4.2%–6.9% of TL vs. 6.7%–7.1% of TL for *F. crassispinus*); smaller caudal fin (its dorsal caudal margin length 20.2%–21.9% of TL vs. 21.4%–22.6% of TL for *F. crassispinus*; its preventral caudal margin 10.9%–12.2% of TL vs. 12.0%–12.4% of TL). The Madagascan dogfish is also distinct from *F. brevirostris*, *F. crassispinus* and *Flakeus* sp. 1 by larger preoral length (9.5%–11.1% of TL vs. 8.4%–9.5% of TL for *F. brevirostris* vs. 9.3%–9.8% of TL for *F. crassispinus* vs. 8.2%–9.6% of TL for *Flakeus* sp. 1). *Flakeus* sp. 3 exhibits larger snout (its preorbital length 6.9%%–7.7% of TL vs. 6.5%–7.0% of TL; its prenarial length 4.4%–4.9% of TL vs. 4.1%–4.6% of TL) and larger distance between nostrils and upper labial furrow than adult specimens of *Flakeus* sp. 1 (4.8%–5.4% of TL vs. 4.3%–4.9% of TL).

Flakeus sp. 3 shows dorsal fins markedly upright and slender at apex, and high that assemblage those of *F. albifrons*, *F. notocaudatus*, and *F. probatovi*. However, this species can be further separated from *F. albifrons* by smaller dorsal fins (length of posterior margin of first dorsal fin 8.0%–9.6% of TL in adults of *Flakeus* sp. 3 vs. 9.5%–12.0% of TL for *F. albifrons*), more elongate prebranchial length (18.2%–22.0% of TL vs. 18.0%–18.6% of TL for *F. albifrons*), and smaller prespiracular length (vs. 11.5%–12.4% of TL for *F. albifrons*), upper labial furrow (4.5%–4.8% of TL for *F. albifrons*). It is also differentiated from *F. notocaudatus* by lower first dorsal fin (its height 7.4%–8.5% of TL vs. 8.5%–9.8% of TL for *F. notocaudatus*).

The Madagascan dogfish is probably endemic to the Indian Ocean from South Africa to Madagascar. Its occurrences in the Western coast of South Africa are not reported in the literature and it is not observed in the current study. Further analysis on specimens from this region may improve to understand its geographical distribution.

Comparative material. Specimens of *F. megalops*, *F. brevirostris, F. cubensis, F. crassispinus*, *F. acutipinnis*, *F. notocaudatus*, and *F. raoulensis*, *F. albifrons*, *F. bucephalus*, *F. probatovi*, *Flakeus* sp. 1 and *Flakeus* sp. 2 listed in the current Chapter.

Flakeus sp. 4[1]

(**Suggested common names: Lobed-fin Atlantic dogfish; Cação-bagre-de-nadadeiras-lobadas do Atlântico** in Portuguese)

Figs. 224–228; Tables 53, 57–58

Squalus cubensis (not Howel-Rivero): Figueiredo, 1977: 8, fig. 7 (description; Southern Brazil and Uruguay).
Squalus sp. of the *blainvillei* group: Figueiredo, 1981: 17 (listed; Brazil); Gomes *et al*., 1997: 94-95 (listed; Brazil); Marques, 1999 (description; Brazil).
Squalus mitsukurii (not Jordan & Snyder): Calderón, 1994: 1-43, fig. 5b (cited; Brazil); Lessa *et al*., 1999: 61, 150 (cited, listed; South Brazil); FIP, 2005: 57 (cited; Chile); Lamilla & Bustamante, 2005: 9, 26 (listed; Chile); Compagno, 2002: 385 (description; Northeast Brazil and Argentina); Compagno *et al*., 2005: 77-78, plate 3 (cited; Southeast Brazil).
Squalus of the *blainvillei*/*mitsukurii* group: Gadig, 2001: 29, 36, 54-55, fig. 29 (in part) (cited; Brazil).
Squalus sp. B: Soto, 2001: 96 (listed; Brazil); Soto & Mincarone, 2004: 79-82 (listed; Brazil).
Squalus sp.1: Gomes *et al*., 2010: 44 e 45 (cited; Brazil).

Holotype: HUMZ 91806, juvenile female, 557 mm TL, off Patagonia, Argentina, 39°30’S, 58°28’W. Unknown collector. Collecting date: 16 January 1979.

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1 Description taken from Viana *et al*. (*in prep*.).

Paratypes (9 specimens): HUMZ 30026, adult female, 725 mm TL, off Patagonia, Argentina, 42°35’S, 63°11’W; HUMZ 30032, adult female, 675 mm TL, off Patagonia, Argentina, 42°35’S, 63°11’W; HUMZ 91801, adult female, 650 mm TL, off Patagonia, Argentina, 39°30’S, 58°28’W; HUMZ 91804, juvenile female, 545 mm TL, off Patagonia, Argentina, 39°30’S, 58°28’W; HUMZ 91807, juvenile female, 605 mm TL, off Patagonia, Argentina, 39°30’S, 58°28’W; UERJ 1661, adult male, 640 mm TL, unknown locality (dissected), Brazil; UERJ 2024, juvenile female, 530 mm TL, off Espírito Santo (segundo Magenta), Brazil; UERJ 2025, adult female, 600 mm TL; same locality as UERJ 2024. UERJ 2026, adult female, 675 mm TL, same locality as UERJ 2024.

Non-type material (32 specimens): FURG 80.0607, juvenile female, 510 mm TL, off Rio Grande do Sul coast, Brazil, 32°19'S, 51°52'W; FURG 80.0609, adult male, 630 mm TL, South of Mar del Plata, Argentina, 38°S, 51°W; FURG 98.0031, two juvenile males, 380-450 mm TL, off Rio Grande do Sul coast, Brazil, 32°19'S, 51°52'W; MZUSP 37351, neonate female, 240 mm TL, juvenile male, 340 mm TL, Uruguay, 35°50'S, 53°06'W; MZUSP 37355, two juvenile female, 335-340 mm TL; three juvenile male, 335-360 mm TL, Uruguay, 35°44'S, 53°22'W; UERJ 1112, adult male, 635 mm TL, Rio Grande do Sul, Brazil (dissected); ZMH 104558, adult male, 600 mm TL, Argentina, 38°0'S, 56°33'W; ZMH 104707, juvenile male, 247 mm TL, Argentina, 36°49'S, 54°37'W; ZMH 104945, neonate female, 235 mm TL, Argentina, 42°16'S, 61°53'W; ZMH 107897, adult male, 605 mm TL, Argentina, 40°0'S, 59°0'W.

Diagnosis. Species of *Flakeus* from SWAO that differs from its congeners by a combination of characters: dorsal fins markedly broad and lobe-like; clasper groove short, not reaching the rhipidion. *Flakeus* sp. 4 is also clearly distinguished from *F. mitsukurii*, its morphologically closest congener, by having a slender body (vs. highly robust body in *F. mitsukurii*), pectoral posterior margin concave (vs. pectoral posterior margin straight in *F. mitsukurii*), narrower interorbital space (8.8%, 6.8%–8.5% TL vs. 9.3%, 9.1%–9.8% TL in *F. mitsukurii*); inner clasper length 1.4 times pelvic fin inner margin length (vs. 0.7–1.1 times in *F. mitsukurii*).

Flakeus sp. 4 can be distinguished from *F. edmundsi*, *F. grahami* and types of *S. nasutus* by much smaller snout (prenarial length 5.4%, 4.5%–5.3% of TL for *Flakeus* sp. 4; 5.8%, 5.6%–5.8% of TL for *F. edmundsi*; 5.6%, 5.7%–6.3% for *F. grahami*; and 7.3%, 6.4%–6.7% of TL for *S. nasutus*). It also differs from *S. acanthias* from SWAO, *F. montalbani*, *S. nasutus*, *F. hemipinnis*, *F. crassispinus*, *F. megalops*, and *F. raoulensis* by greater total and precaudal vertebrae. *Flakeus* sp. 4 is distinct from *F. grahami*, *F. griffini*, *S. nasutus*, *F. hemipinnis*, *F. crassispinus*, *F. megalops*, *F. bucephalus*, *F. raoulensis*, *F. japonicus*, and *F. notocaudatus* by monospondylous vertebrae. It further differs from all its congeners from SWAO by much larger pectoral inner margin length, except from *Squalus acanthias* (10.5%, 9.2%–11.0% of TL in *Flakeus* sp. 4 vs. 10.9%, 8.1%–8.8% of TL for *Flakeus* sp. 5 vs. 8.1%, 8.4%–8.9% of TL for *Flakeus* sp. 6).

Description.

External morphology (Figs. 224–227; Tabs. 53, 57). Body fusiform, slender and depressed through all its extension with head height 0.9 (0.8–1.3) times trunk height and 1.0 (0.8–1.2) times abdomen height; body more expanded in the head than in the abdomen with head width 1.3 (1.0–1.3) times trunk width and 1.6 (1.2–1.7) times abdomen width. Head flattened dorsally and elongate, its length 22.7% (21.5%–24.3%) of TL; head broader at mouth than at nostrils (its width at mouth 12.2%, 9.7%–12.2% of TL vs. 7.5%, 6.3%–7.4% of TL its width at nostrils). Snout very large (preorbital length 7.9%, 7.0%–7.9% of TL), obtuse and rounded at tip; anterior margin of nostrils strongly bilobate, placed more laterally; prenarial length 1.2

(1.0–1.2) times distance from nostril to upper labial furrow; prenarial length 1.3 (1.1–1.4) times eye length; internarial space 1.1 (0.9–1.5) times eye length. Eyes oval, placed laterally nearest the snout tip than the first gill slit, with convex anterior margin and notched posterior margin; eyes enlarged, its length 2.3 (1.7–2.9) times its height. Prespiracular length 1.6 (1.6–1.7) times preorbital length. Spiracles subtriangular and conspicuously broad, its length 1.2% (1.0%–1.6%) of TL, corresponding to 0.3 (0.3–0.4) times eyes length. Prebranchial length 1.5 (1.5–1.7) times prespiracular length. Gill slits vertical and tall, with fifth gill slit 1.2 (1.0–1.6) times higher than first gill slit.

Preoral length 9.7% (8.6%–9.9%) of TL, corresponding to 1.3 (1.1–1.4) times mouth width. Mouth somewhat arched, markedly broad, its width 1.7 (1.5–2.0) times internarial width and 1.4 (1.4–1.7) prenarial length; upper labial furrow large, its length 2.4% (2.0%–2.6%) of TL, with a slender fold; lower labial furrow conspicuously deep and elongate, reaching laterally the head, without a fold. Unicuspid teeth, similar in both jaws, markedly broad at the crown, flattened labial-lingually and alternate; upper teeth smaller and narrower than lower teeth; cusp thick and short, oblique and directed laterally; mesial cutting edge conspicuously convex; mesial heel pointed; distal heel markedly rounded; apron thick, although larger on lower teeth than upper teeth; two series of functional teeth on upper and lower jaws; teeth rows varying from 13–13 (13–13 paratypes) on upper jaw and 11–10 (12–11 paratypes) on lower jaw (Fig. 16).

Pre-first dorsal length 1.4 (1.3–1.5) times prepectoral length; distance from first dorsal fin origin to pectoral fin origin 1.2 (0.8–1.4) times preorbital length. Origin of first dorsal fin prior to pectoral free rear tips. First dorsal fin markedly broad on fin web, lobe-like, and elongate (its length 1.9, 1.6–2.0 times its height); first dorsal fin tall, its height 7.6%, 6.5%–8.1% of TL, corresponding to 1.0 (0.9–1.1) times preorbital length and 1.1 (1.0–2.2) times its inner margin length; first dorsal anterior margin evidently convex and elongate, its length 11.1% (10.3%–11.9%) of TL; its posterior margin almost straight, its length 9.6% (6.7%–9.2%) of TL; first dorsal apex strongly rounded and its free rear tip triangular; large inner margin, its length 6.6% (3.3%–7.1%) of TL. First dorsal spine somewhat broad at base (width at base 0.7%, 0.6%–0.9% of TL) and short (its length 3.8%, 2.2%–4.0% of TL), reaching half of the fin height. First dorsal fin 1.1 (1.0–1.2) times larger than second dorsal fin. Interdorsal space short, its length 24.6% (21.9%–24.1%) of TL, corresponding to 1.1 (1.0–1.2) times prepectoral length and 2.4 (2.1–2.3) times dorsal-caudal space. Second dorsal fin also broad on the fin web, lobe-like, and low with its height 1.0 (0.6–1.4) times its inner margin length; anterior margin markedly convex and elongate (its length 11.1%, 9.2%–11.6% of TL); its posterior margin conspicuously falcate, its length 5.5% (4.1%–6.4%) of TL; second dorsal apex rounded and free rear tip triangular; its inner margin very large, its length 5.8% (2.8%–6.1%) of TL. Second dorsal spine slender and conspicuously elongate, reaching the fin apex, its length 0.9 (0.7–1.4) times second dorsal height and 1.4 (1.0–1.6) times larger than first dorsal spine.

Pre-pectoral length 0.7 (0.7-0.8 paratypes) times pre-first dorsal length and 0.4 (0.4–0.5 paratypes) times pre-vent length. Pectoral fin markedly broad posteriorly (posterior margin length 11.2%, 9.7%–11.7% of TL) and elongate, its anterior margin length 16.0%, 13.8%–17.2% of TL; anterior margin length 1.5 (1.5–1.8) times inner margin length; posterior margin length 0.9 (0.9–1.8) times the trunk height; anterior and inner margins rather straight, posterior margin concave; apex strongly rounded and lobate; free rear tips also rounded and lobate reaching the horizontal line traced in the pectoral fin apex.

Pelvic fins somewhat wide with anterior margin slightly concave; inner and posterior margins straight; free rear tips and apex rounded, the former conspicuously lobate; pelvic fin length 10.4% (9.9%–11.6%) of TL; origin of pelvic fins 3.0 (2.9–3.2) times the distance between the origins of the two dorsal fins, nearest to first dorsal fin than to second dorsal fin (although nearest to midline between the origins of two dorsal fins in paratypes); pectoral-pelvic space 0.7 (0.8–0.9) times pelvic-caudal space. Claspers in male paratype rather cylindrical, markedly thick or fat and compressed dorsal-ventrally throughout all its extension, transcending free rear tips of the pelvic fin, its outer length among 4.3% of TL; elongate and wide siphon, placed medial-ventrally from middline of basipterygium until origin of ventral marginal cartilage; clasper groove longitudinal, short (not reaching the rhipidion) and very constricted, dorsally located; apopyle narrow anteriorly in the clasper groove; hypopyle also narrow, located posteriorly in the clasper groove; rhipidion conspicuously large, blade-like and thin, placed medially at the distal end of the clasper (Fig. 18).

Lateral keels well marked on each side of caudal peduncle with its origin behind the insertion of second dorsal fin; upper and lower precaudal furrows profound. Caudal fin subrectangular with dorsal caudal margin straight and large, its length 21.7% (19.7%–22.0%) of TL; dorsal caudal margin length 1.0 (0.8–1.0) times head length and 1.8 (1.7–2.0) times greater than preventral caudal margin length; posterior caudal tip rounded; both postventral caudal margins convex; upper caudal lobe narrow, its width at caudal fork 6.9% (6.3%–7.4%) of TL; caudal fork between lobes strongly concave; preventral caudal margin convex and elongate, its length 11.8% (10.6%–12.2%) of TL and corresponding to 2.2 (2.0–2.7) times pelvic inner margin length; ventral caudal tip rounded.

Dermal denticles (Fig. 227). Dermal denticles tricuspid with cusps conspicuous and pointed; median projection anteriorly at the crown well prominent and rounded with small expansions posterior-laterally on each side, and crown furrow medially; lateral cusps much shorter than median cusp; lateral ridges prominent and bifurcate, reaching the tips of lateral cusps; median ridge conspicuous and tall with its origin far anteriorly at crown base and reaching the tip of median cusp distally; dermal denticles markedly broad at the crown, although its length slightly greater than its width; dermal denticles rather imbricated and near each other. Dermal denticles also tricuspid in juveniles, although much smaller than in adults and not imbricated; its cusps markedly slender and pointed with lateral cusps forming a prominent concavity with median cusp on each side.

Coloration. Body darkish grey dorsally and pale ventrally. Dorsal fins also dark gray, whitish at dorsal fin base; first dorsal fin slightly white at posterior margin and free rear tip, darker at its apex and first half of posterior margin; second dorsal fin also dark grey with posterior margin rather white and apex slightly blackish; dorsal spines grey, blackish anteriorly, white posteriorly and at its tips. Pectoral fins dark gray dorsal-ventrally and pale under pectoral radials; pectoral posterior margin markedly white; pectoral apex broadly white; pectoral inner margin light grey. Pelvic fins grey dorsally and light grey ventrally; both pelvic anterior and posterior margin white. Caudal fin dark grey and whitish at the vertebral column; dorsal caudal margin somewhat whitish, although not uniform; posterior caudal tip white; upper postventral caudal margin rather white, except in the caudal fork which it is grey; lower postventral caudal margin also white; ventral caudal tip slightly white; preventral caudal margin whitish; conspicuous black caudal stripe in the dorsal lobe. Juveniles with body much darker than in adults.

Vertebral counts (Tab. 58). Monospondylous vertebrae 45 (44–48 paratypes); precaudal vertebrae 88 (80–89); caudal vertebrae 30 (28–31); total vertebrae 118 (110–119).

Geographical distribution (Fig. 228). *Flakeus* sp. 4 occurs from southern Brazil to Uruguay and Patagonia in Argentina, where it seems to be more common. Its occurance in the coast of

Espírito Santo, Brazil (Dr. C. Magenta, *pers. comm.*), is still doubtful due to lack of precise locality information.

Remarks. *Flakeus* sp. 4 is often misidentified as *Flakeus mitsukurii* from Japan, or as a member of the *Squalus mitsukurii* group at least in the SWAO (e.g. Figueiredo, 1981; Lucifora *et al*., 1999; Marques, 1999; Gomes *et al*., 1997, 2010). Calderón (1994) recognized *F. mitsukurii* off the Southern Brazilian coast based on morphological characteristics provided by Compagno (1984) specifically proportional measurements of the head, pectoral and dorsal fins base length and pelvic fin length. These characters occur, however, in more than one species of *Squalus*, which may have led to the misidentification *F. mitsukurii* in this region.

Flakeus sp. 4 shares with *F. mitsukurii* few morphological characteristics such as (Table V): moderately elongate body; snout obtuse and markedly elongate (preorbital length 7.3%, 7.0%–7.4% of TL for *Flakeus* sp. 4 vs. 7.3%, 7.2%–8.8% of TL for *F. mitsukurii*); nostrils closer to snout tip than to the mouth (prenarial length 1.0, 1.1–1.2 times inner nostril-labial length vs. 1.3, 1.1–1.4 times for *F. mitsukurii*); pectoral fins broad and smaller than its head length; tricuspid dermal denticles; dark caudal bar. However, this species can be easily distinguished from it by the characteristics provided in its diagnosis. Despite some overlapping, distance from nostrils to upper labial furrow may be useful for separating them: (4.5%, 3.6%–4.4% of TL for *Flakeus* sp. 4 vs. 4.3%, 4.4%–5.3% of TL for *F. mitsukurii*). *Flakeus* sp. 4 also has shorter prespiracular length in (12.6% of TL, 11.5%–12.7% of TL vs. 12.8% of TL, 12.7%–21.5% of TL for *F. mitsukurii*).

Chen *et al*. (1979) provided vertebral counts for *F. mitsukurii* in Japan that are much higher than those for *Flakeus* sp. 4 despite of some overlapping, respectively: total vertebrae (118, 110–119 vs. 118–127). According to Last *et al*. (2007), members of this group share a relatively great total length, presence of dark caudal bar, dorsal spines small, first dorsal fin short and falcate, tricuspid dermal denticles, pectoral fin not falcate with rounded free rear tips, and high number of vertebrae. *Flakeus* sp. 4 differs from members of this group by having robust and elongate dorsal spines (first dorsal spine length 3.8% for holotype, 2.2%–4.0% of TL for paratypes; second dorsal spine length 5.3%, 3.4%–5.3% of TL), as well as first dorsal fin conspicuously broad and lobate, not falcate.

A paratype of *F. mitsukurii* (SU 7184) was not taken into account in our morphometric comparisons because it corresponds to a specimen of *Squalus acanthias* clearly identified by presence of white spots dorsally and first dorsal spine located posterior to pectoral fins, as previously noticed by Bigelow & Schroeder (1957) and Muñoz-Chápuli & Ramos (1989). This type specimen was illustrated on the original description of *F. mitsukurii* and posteriorly reproduced by Tanaka (1912) but it does not agree with the diagnosis of the Japanese species. Recently, investigations concerning the taxonomy and geographical distribution of *F. mitsukurii* (e.g. Last *et al*., 2007) have strongly demonstrated that it might be a complex of species rather than a single valid species (e.g. Bigelow & Schroeder, 1957; Chen *et al*., 1979; White & Iglésias, 2011).

Flakeus sp. 4 is also distinguished from *F. edmundsi*, *F. grahami* and *S. nasutus* (Last *et al*., 2007) by much smaller snout (prenarial length 5.4%, 4.5%–5.3% of TL for *Flakeus* sp. 4; 5.8%, 5.6%–5.8% of TL for *F. edmundsi*; 5.6%, 5.7%–6.3% for *F. grahami*; and 7.3%, 6.4%–6.7% of TL for *S. nasutus*). It also differs from *S. acanthias* from SWAO, *F. montalbani*, *S. nasutus*, *F. hemipinnis*, *F. crassispinus*, *F. megalops*, and *F. raoulensis* by greater total and precaudal vertebrae. It also differs from *F. grahami*, *F. griffini*, *S. nasutus*, *F. hemipinnis*, *F. crassispinus, F. megalops, F. bucephalus*, *F. raoulensis*, *F. japonicus*, and *F. notocaudatus* by number of monospondylous vertebrae (taken from Last *et al*., 2007).

The recognition of *Flakeus* sp. 4 as new species supports that the current acceptance of *F. mitsukurii* as a comospolitan species may possibly be a mistake propagated when using the general descriptive literature (e.g. Compagno, 1984) for identifying species regionally, as they usually lack informative taxonomic data. Further analysis of material identified as *F. mitsukurii* from other localities where it is reported to occur, such as in the Southeastern Atlantic and Western Indian Oceans, and Northeastern Pacific Ocean, is needed to check if this species is indeed widespread or more restricted (e.g. Compagno *et al*., 2005).

Comparative material: Types of *Flakeus mitsukurii*.

***Flakeus* sp. 5**[2]

(Suggested common names: Northeastern-Brazilian dogfish shark; Cação-bagre-da-Bahia in Portuguese)

Figs. 229–235; Tables 54, 57–58

Squalus fernandinus (not Molina): Fowler, 1936: 71 (description; South Atlantic); Bigelow & Schroeder, 1948: 480; Bigelow & Schroeder, 1957 (in part): 24-37 (revision; Argentina).
Squalus blainvillei (not Risso): Lucena & Lucena, 1981: 2, 4, 5, fig. 3 (listed; Brazil); Menni *et al*., 1984: 84 (listed; Argentina and Uruguay); Muñoz-Chápuli, 1985: 397, 398, fig. 1 (cited); Muñoz-Chápuli & Ramos, 1989: 21, figs. 1, 2B, 3B (revision; Eastern Atlantic); Canizarro *et al*., 1994: 113 (cited); Szpilman, 2000: 75 (listed); Nion *et al*., 2002: 4 (listed); Meneses & Paesch, 2003: 8, 25 (cited); FIP, 2005: 53, 54 (cited; Chile); Saéz *et al*., 2010: 623 (identification key; Chile).
Squalus cubensis (not Howell-Rivero): Kondyurin & Myagkov, 1984: 118-120, fig. 1B (revision; Western Atlantic); Nunan & Senna, 2007: 169, 170 (cited; Brazil).
Squalus mitsukurii (not Jordan & Snyder): Calderón, 1994: fig. 5B (cited); Lessa *et al*., 1999: 61, 150 (cited, listed; Northeast Brazil); Compagno, 2002: 385 (description; Northeast Brazil and Argentina); Haimovici *et al*., 2003: 38, 39 (cited); Jablonski *et al*., 2006: 177 (cited); Louro & Rossi-Wongtschowski, 2007: 18, 27, 28, 30, 49 (cited); Menni & Lucifora, 2007: 3 (listed). Fischer *et al*., 2006: 495-501 (cited; Northeastern Brazil);
Squalus sp. of the *blainvillei* group: Gomes *et al*., 1997: 93-95, 109 (listed; Brazil); Marques, 1999 (cited; Brazil).
Squalus of the *blainvillei*/*mitsukurii* group: Gadig, 2001: 29, 36, 54, 55, 57, 58, fig. 29 (in part) (listed; Brazil).
Squalus sp. B: Soto, 2001: 96 (listed; Brazil); Soto & Mincarone, 2004: 79-82 (listed; Brazil).
Squalus sp.1: Gomes *et al*., 2010: 44, 45 (cited; Brazil).

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[2] Description taken from Viana *et al*. (*in prep*).

Holotype: MNRJ 30180, adult male, 590 mm TL, Bahia coast, Brazil, 15°48'30"S 38°35'16"W, 599 meters depth. Collected on 12 June 2000, Station 0510, Thalassa cruise, Revizee program.

Paratypes (2 specimens): MNRJ 30178, adult male, 615 mm TL, 599 meters depth; MNRJ 30179, adult male, 690 mm TL. 599 meters depth. Same locality as holotype.

Diagnosis. *Flakeus* sp. 5 is distinct from all species of the *Squalus megalops* group by having pectoral fins with free rear tips rounded (vs. pointed free rear tips), snout blunt and elongate (vs. snout rounded and short), and dermal denticle tricuspid and rhomboid (vs. unicuspid and lanceolate dermal denticles).

Flakeus sp. 5 is distinct from *F. mitsukurii* by having a narrower interorbital space (8.2%, 7.9%–8.3% of TL vs. 9.3%, 9.1%–9.8% of TL in *F. mitsukurii*); and shorter lower caudal lobe (preventral caudal margin 11.4%, 10.9%–11.3% of TL vs. 12.1%, 11.5%–12.4% of TL). *Flakeus* sp. 5 can be easily distinguished from *F. blainvillei* from the Mediterranean Sea by having lower dorsal fins in *Flakeus* sp. 5 (first dorsal fin height 6.9%, 7.0%–7.1% of TL vs. 8.2%, 7.3%–8.7% of TL for *F. blainvillei*; second dorsal fin height 5.3%, 4.2%–4.4% of TL vs. 7.2%, 6.6%–7.5% of TL for *F. blainvillei*); shorter upper labial furrow (its length 2.3%, 2.2%–2.2% of TL vs. 2.5%, 2.4%–2.7% of TL for *F. blainvillei*).

Flakeus sp. 5 can be easily distinct from *Flakeus* sp. 4 by: caudal fin somewhat slender vs. rectangular upper caudal lobe in *Flakeus* sp. 4; second dorsal spine not reaching dorsal fin apex vs. reaching dorsal fin apex for *Flakeus* sp. 4; shorter pectoral fin inner margin (its length 8.1%, 8.4%–8.9% of TL in *Flakeus* sp. 5 vs. 10.5%, 9.2%–11.0% of TL in *Flakeus* sp. 4); clasper outer length greater in *Flakeus* sp. 5 (5.0%, 4.6%–5.1% of TL vs. 4.3% of TL in *Flakeus* sp. 4).

Description.

External morphology (Figs. 229–234; Tabs. 54, 57). Body slender and fusiform, arched dorsally and somewhat flattened ventrally; its greatest depth in head and abdomen (head height 9.3%, 9.6%–10.0% of TL; abdomen height 10.1%, 9.6%–10.5% of TL) with head height corresponding to 0.9 (1.0–1.0) times trunk height and 0.9 (1.1–1.1) times abdomen height. Head rather elongate (its length 21.4%, 22.8%–22.9% of TL), narrower at nostrils (its width 7.0%, 7.0%–7.1% of TL), turning much broader at gills (11.9%, 12.4%–12.6% of TL). Snout markedly blunt and broad at tip (not obtuse) and well elongate (preorbital length 7.3%, 7.4%–7.9% of TL); anterior margin of nostrils bilobate, placed laterally and nearer to the mouth than to snout tip (prenarial length 1.1, 1.0–1.2 times inner nostril-labial length); prenarial length 1.4 (1.4–1.4) times eye length; internarial space 1.2 (1.3–1.4) times eye length. Eyes oval and horizontal, placed nearest to snout tip than to gill slits; its anterior margin convex and posterior margin notched; eyes large, its length 2.0 (1.9–2.7) times its height. Prespiracular length 12.2% (12.2%–12.9%) of TL, corresponding to 0.6 (0.5–0.6) times prepectoral length. Spiracles crescent, located more dorsally behind the eyes; spiracles length 0.4 (0.3–0.5) times eye length. Prebranchial length 17.9% (18.4%–18.8%) of TL, corresponding to 1.5 (1.4–1.5) times prespiracular length. Gill slits vertical and low, fifth gill slit height 1.0 (1.1–1.2) times greater than first gill slit height; gill slits placed laterally just anterior to pectoral fins.

Preoral length 9.9% (10.2%–10.5%) of TL, corresponding to at least 1.4 times mouth width. Mouth arched and somewhat broad, its width 1.7 (1.5–1.6) times internarial space and 1.4 (1.4–1.5) times prenarial length; upper labial furrow long, its length 2.3% (2.2%–2.2%) of TL with a slender fold; lower labial furrow also elongate, although without a fold. Unicuspid teeth, similar in both jaws, broad and compressed labial-lingually at crown, imbricate laterally; upper teeth smaller and narrower than lower teeth; cusp small and heavy, markedly oblique and upturned, directed laterally; mesial cutting edge conspicuously convex; mesial heel notched; distal heel strongly rounded; apron thick; two series of functional teeth on upper jaws for holotype and three series for paratypes; two series of functional teeth on lower jaws; teeth rows varying from 13–14 (13–14 paratypes) on upper jaw and 11–12 (11–11 paratypes) on lower jaw (Fig. 27).

Pre-first dorsal length 29.9% (29.7%–30.9%) of TL, corresponding to 1.4 (1.3–1.4) times prepectoral length. Origin of first dorsal fin preceding pectoral free rear tips. First dorsal fin wide at fin web and rather large (Fig. 28), its length 12.8% (13.8%–13.8%) of TL, corresponding to 1.8 (1.9–2.0) times its height; anterior margin convex and well elongate, its length 10.5% (10.3%–10.6%) of TL; posterior margin markedly concave and large, its length 7.9% (9.2%–9.6%) of TL; first dorsal apex strongly rounded and slender; first dorsal free rear tip triangular; first dorsal inner margin length 5.7% (6.4%–6.9%) of TL; first dorsal fin low, its height 6.9% (7.0%–7.1%) of TL and corresponding to 1.2 (1.0–1.1) times its inner margin length and 0.9 times preorbital length. First dorsal spine slender and small, its length 2.8% (2.9%–3.0%) of TL and corresponding to 0.4 times first dorsal height, not reaching first dorsal apex. First dorsal fin length 1.1 times second dorsal fin length. Interdorsal space 1.2 (1.1–1.2) times prepectoral length and 2.4 (2.0–2.4) times dorsal-caudal space. Pre-second dorsal fin 2.8 times prepectoral length and 4.3 (4.2–4.4) times pectoral anterior margin length. Second dorsal fin slender, small, its length 11.6% (12.1%–12.6%) of TL and 2.2 (2.8–2.9) times its height; anterior margin convex and short, its length 9.4% (9.3%–9.7%) of TL; posterior margin conspicuously concave and falcate, its length 5.0% (5.7%–5.7%) of TL; second dorsal apex rounded and lobe-like; second dorsal free rear tip triangular; second dorsal inner margin somewhat elongate, its length 5.3% (5.6%–5.6%) of TL; second dorsal fin also low, its height 1.0 (0.8–0.8) times its inner margin length. Second dorsal spine thin and short, its length 0.8 (0.8–1.0) times second dorsal height and 1.5 (1.2–1.5) times greater than first dorsal spine; second dorsal spine not reaching second dorsal fin apex (Fig. 28).

Prepectoral length 21.7% (22.0%–22.8%) of TL. Pectoral fins markedly narrow and small (anterior margin length 14.3%, 14.4%–14.5% of TL); anterior margin 1.8 (1.6–1.7) times greater in length than inner margin length and 1.4 (1.3–1.4) times posterior margin length; pectoral anterior margin straight and posterior margin convex; inner margin markedly concave, its length 8.1% (8.4%–8.9%) of TL; pectoral fin apex rounded and lobulated; pectoral free rear tips also rounded and lobate, reaching the horizontal line traced from pectoral fin apex (Fig. 26).

Prepelvic length 44.4% (45.5%–48.6%) of TL. Pectoral-pelvic space 0.7 (0.8–0.9) times pelvic-caudal space. Pelvic fins also narrow, its anterior and posterior margins straight; pelvic free rear tips slightly pointed, triangular and elongate, its length 5.8% (5.1%–5.4%) of TL. Origin of pelvic fins 2.8 (2.9–3.0) times the distance between the origins of the two dorsal fins, nearest to the first dorsal fin than to second dorsal fin in holotype (somewhat nearest to midline between the origins of two dorsal fins in paratypes); pectoral-pelvic space short, its length 19.7% (19.5%–20.3% of TL) and corresponding to 0.7 (0.7–0.8) times pelvic-caudal space. Claspers cylindrical and slender, compressed dorsal-ventrally; claspers large, transcending far posteriorly pelvic free rear tips, its outer length among 5.0% (4.6%–5.1% of TL); clasper inner margin 1.3 (1.3–1.4) times greater in length than pelvic fin inner margin; clasper groove longitudinal and very elongate, placed dorsally; apopyle very narrow, located anteriorly in clasper groove; hypopyle also narrow, located posteriorly in clasper groove; rhipidion markedly large, blade-like and slender, placed medially at the distal end of the clasper (Fig. 29).

Caudal peduncle with soft lateral caudal keels from opposite second dorsal free rear tip until caudal fin origin; upper and lower caudal furrows profound. Caudal fin with straight dorsal-caudal margin, its length 21.9% (20.0%–21.4%) of TL and corresponding to 1.0 (0.9 in paratypes) times head length and 1.9 (1.8–1.9) times preventral caudal margin length; upper post-ventral caudal margins strongly convex; lower post-ventral caudal margin convex; posterior caudal tip rounded; preventral caudal margin straight and short, its length 2.0 (2.1 times in paratypes) pelvic inner margin length; ventral caudal ip also rounded; caudal fin narrow at lobes and conspicuously concave on caudal fork , its width 6.7% (6.4%–7.1%) of TL.

Dermal denticles. (Fig. 234) Description based on paratype MNRJ 30178. Tricuspid and imbricate dermal denticles, very broad at the crown, its length somewhat equal to its width; cusps triangular and wide with median cusp larger than lateral cusps; lateral cusps forming a right angle with the median cusp; median anterior projection conspicuous and rounded with small posterior-lateral expansions on each side; median ridge conspicuous and bifurcate, forming a superficial furrow anteriorly, reaching the median cusp tip; two lateral ridges on each side of the denticle, thick and prominent, reaching the lateral cusp tips; lateral most ridge often shorter than the medial most one. In holotype, dermal denticles are more slender and not imbricate; cusps strongly thin and cylindrical; lateral cusps forming a prominent concavity with the median cusp on each side.

Coloration. Body grey dorsally, white ventrally and on its second half. First dorsal fin grey, darker at its apex and whitish at its base; anterior margin slightly white on its first half; posterior margin white. Second dorsal fin also grey and darker at its apex; posterior margin slightly white. First and second dorsal spines white, slightly grey anteriorly. Pectoral fins grey dorsal and ventrally, whitish at its ventra base; pectoral posterior margin uniformly white. Pelvic fins light grey dorsally and ventrally; pelvic posterior margin white. Caudal fin dark grey, whitish over the vertebral column; dorsal caudal margin white; upper and lower postventral caudal margins whitish; posterior caudal tip broadly white; ventral caudal tip also white; preventral caudal margin somewhat whitish caudal stripe; small and grey.

Vertebral counts (Tab. 58). 87 (87) precaudal vertebrae; 43 (43–45) monospondylous vertebrae; total vertebrae 117 (115–116).

Geographical distribution (Fig. 235). *Flakeus* sp. 5 is apparently endemic from the Brazilian northeast coast near Salvador, Bahia. However, it probably reaches more equatorial areas within this region as it was reported previously as *F. mitsukurii* (e.g. Fischer *et al*., 2006).

Remarks. *Flakeus mitsukurii* and the Mediterranean species *F. blainvillei* (Risso, 1826) are often registered in the literature from the Northern Brazilian coast to the Southern Argentina (e.g. Miranda-Ribeiro, 1907; Compagno, 1984; Calderón, 1994; Compagno *et al*., 2005; Fischer *et al*., 2006; Figueirêdo, 2011). These two species were probably misidentified in these regions for sharing characteristics of species of the *Squalus mitsukurii* group such as elongate snout, tricuspid dermal denticles, and low dorsal fins that are also observed for both *Flakeus* sp. 5 and *Flakeus* sp. 4. *Flakeus* sp. 5, however, can be easily distinct from all species of this group by absence of black caudal blotch in the caudal fin. *Flakeus* sp. 5 further differs from *Flakeus* sp. 4 by shorter first dorsal anterior margin in *Flakeus* sp. 5 than in *Flakeus* sp. 4 (its length 10.5%, 10.3%–10.6% of TL vs. 11.1%, 10.3%–11.9% of TL), and much greater interdorsal space (its length 26.5%, 24.4%–26.8% of TL vs. 24.6%, 21.9%–24.1% of TL).

Flakeus sp. 5 can also be easily distinguished from the Japanese *F. mitsukurii* by more elongate precaudal length (79.5%, 79.2%–81.2% of TL vs. 77.5%, 76.9%–78.6% of TL in *F. mitsukurii*) and pre-second dorsal length (61.5%, 61.0%–63.8% of TL vs. 61.0%, 58.4%–60.5% of TL in *F. mitsukurii*); first gill slit nearest to snout tip in *Flakeus* sp. 5 than in *F. mitsukurii* (prebranchial length 17.9%, 18.4%–18.8% of TL vs. 20.4%, 19.9%–20.0% of TL in *F. mitsukurii*). *Flakeus* sp. 5 has body depth almost equally from the head to the abdomen (head height 0.9, 1.1–1.1 times trunk height and 0.9, 1.0–1.0 times abdomen height) while *F. mitsukurii* has its greatest depth in head (head height 1.2, 1.0–1.4 times trunk height and 1.6, 1.2–1.7 times abdomen height). It is also easily distinct from *F. montalbani* by having more slender deep body (vs. markedly robust body), shorter ventral caudal lobe (its length 11.4%, 10.9%–11.3% of TL vs. 11.5%–13.2% of TL for *F. montalbani*).

Flakeus blainvillei was originally described from the temperate and tropical waters from the Eastern Atlantic Ocean and the Mediterranean Sea (Risso, 1826). It is also known from the West coast of Africa, Gulf of Mexico, Caribbean Sea and, possibly, in the Pacific Ocean (Bigelow & Schroeder, 1948, 1957; Garrick, 1960; Bass *et al.*, 1976, 1986; Muñoz-Chápuli & Ramos, 1989), and it is believed to have more wide geographical distribution throughout the Atlantic Ocean (both sides). Type specimens of *F. blainvillei* are unknown and its original illustration does not specifiy any specimens used by Risso (1826) that could suggest a possible syntype, which makes it difficult to comparatively analyze this species with congeners. However, the new species can be further distinguished from specimens of *F. blainvillei* from the Mediterranean Sea (Table X) by having wider internarial space (its width 4.2%, 4.7%–4.8% of TL vs. 3.8%, 3.5%–4.2% of TL for *F. blainvillei*), preoral length 1.4, 1.4–1.4 times mouth width (vs. 1.2, 1.0–1.3 times for *F. blainvillei*), mouth width 1.4, 1.5–1.5 times prenarial length and 1.7 (1.5–1.6) times internarial space (vs. 1.9, 1.6–2.2 times and 2.0, 1.9–2.2 times, respectively for *F. blainvillei*). *Flakeus* sp. 5 also has much larger snout than in *F. blainvillei* (its prenarial length 5.0%, 4.9%–5.1% of TL vs. 4.1%, 3.3%–4.9% of TL for *F. blainvillei*).

No morphological similarities, including morphometric and meristic data, were found between *Flakeus* sp. 5 and specimens of *F. blainvillei* from the Southeastern Atlantic, Western Central Atlantic and Northeastern Atlantic Oceans, indicating that the former species may not reach northward areas of the Atlantic Ocean besides the Southwestern Atlantic Ocean. Despite of overlapping in external measurements in *F. blainvillei* from different regions, a broad range of values is apparent that may indicate certain variability. Variations in the vertebrae counts are also noticed within this species that require further scrutiny as was pointed out by previous authors (e.g. Macleay, 1881 for Australia; Garrick, 1960 for New Zealand; Springer & Garrick, 1964; Chen *et al*., 1978 for Japan; Cadenat & Blache, 1981 for New Caledonia). A better morphological characterization of the nominal species *F. blainvillei* and designation of its neotype are also urgent in order to distinguish it from its congeners.

Comparative material. Specimens of *Flakeus mitsukurii* listed at *Flakeus* sp. 4, and of *Flakeus blainvillei* listed in Figueirêdo (2011).

***Flakeus* sp. 6**[3]

(**Suggested common names: Humpback Western dogfish shark; cação-bagre-do-corpo-arqueado-do-Ocidente** in Portuguese)

Figs 236–242; Tables 55, 57–58

Squalus blainvillei (not Risso): Regan, 1908: 45, 47 (identification key, listed); Bigelow & Schroeder, 1948: 454, 455 (cited, identification key); Garrick, 1960: 533-537, figs. 1 (D-F), 2, 3 (A-F), 6 (revision; New

[3] Description taken from Viana *et al*. (2015 *in prep*.).

Zealand); Garrick, 1961: 843 (cited); Ledoux, 1970: 65-69, figs. 1, 2 (A, B), 3 (C-F) (revision; Mediterranean Sea); Lucena & Lucena, 1981: 2, 4, 5, fig. 3 (listed; Brazil); Compagno, 1984: 110, 115, 116 (revision); Menni *et al*., 1984: 84 (listed; Argentina and Uruguay); Muñoz-Chápuli, 1985: 397, 398, fig. 1 (cited); Muñoz-Chápuli & Ramos, 1989: 21, figs. 1, 2B, 3B (revision; Eastern Atlantic); Canizarro *et al*., 1994: 113 (cited); Fricke, 1999: 27 (listed; Mascarene Island); Szpilman, 2000: 75 (listed); Nion *et al*., 2002: 4 (listed); Meneses & Paesch, 2003: 8, 25 (cited); Compagno *et al*., 2005, 74, 75, pl. 3 (revision); Lamilla & Bustamante, 2005: 9, 26 (listed; Chile); Saéz *et al*., 2010: 623 (identification key; Chile); Rosa & Gadig, 2014: 92 (listed; Brazil).

Squalus fernandinus (not Molina): Garman, 1913: 195 (description); Fowler, 1936: 71 (description; South Atlantic); Bigelow & Schroeder, 1948: 478-480 (revision; Northwestern Atlantic); Bigelow, Schroeder & Springer, 1953: 220-222 (cited; Western Atlantic); Bigelow & Schroeder, 1957: 32-36 (description); Menni *et al*., 1984: 62 (identification key; Argentina and Uruguay); Myagkov & Kondyurin, 1986: 13, 14 (revision; Atlantic); FIP, 2005: 55, 56 (cited).

Squalus lebruni: Myagkov & Kondyurin, 1986: 1-20, fig. 2 (revision; Atlantic).

Squalus mitsukurii (not Jordan & Snyder): Calderón, 1994: fig. 5B (cited); Lessa *et al*., 1999: 61, 150 (cited, listed; South Brazil); Haimovici *et al*., 2003: 38, 39 (cited); Compagno *et al*., 2005: 77-78, pl. 3 (revision; Southeast Brazil); Jablonski *et al*., 2006: 177 (cited); Louro & Rossi-Wongtschowski, 2007: 18, 27, 28, 30, 49 (cited); Menni & Lucifora, 2007: 3 (listed).

Squalus sp. of the *blainvillei* group: Gomes *et al*., 1997: 93-95, 109 (listed; Brazil); Marques, 1999 (cited; Brazil).

Squalus of the *blainvillei*/*mitsukurii* group: Gadig, 2001: 29, 36, 54, 55, 57, 58, fig. 29 (in part) (listed; Brazil).

Squalus sp. B: Soto, 2001: 96 (listed; Brazil); Soto & Mincarone, 2004: 79-82 (listed; Brazil).

Squalus sp.1: Gomes *et al*., 2010: 44, 45 (cited; Brazil).

Holotype: UERJ 1111, adult female, 700 mm TL, off coast of Rio Grande do Sul, Brazil.

Paratypes (3 specimens): UERJ 1741, adult female, 850 mm TL, REVIZEE 6089 (nearest station 6088, 89.8W, 33S), Brazil; UERJ 1819, adult female, 740 mm TL, REVIZEE 6104 (nearest station 6102, 62W, 20.8S), Brazil; MCP 773, juvenile female, 660 mm TL, between coast of Rio Grande do Sul State, Brazil and Uruguay.

Type locality: off Rio Grande do Sul coast, Brazil.

Diagnosis. A species of *Flakeus* from the Southwestern Atlantic Ocean that can be distinguished from its congeners through a combination of characters: body conspicuously robust and humped dorsally; second dorsal fin upright and markedly tall (its height 4.0%, 4.7%–5.3% of TL); first and second dorsal spines elongate (first dorsal spine length 4.3%, 3.3%–4.3% of TL; second dorsal spine length 4.4%, 3.9%–4.3% of TL) and heavy (first spine base length 0.9%, 0.7%–1.0% of TL; second spine base length 1.0%, 0.8%–0.9% of TL); caudal fin with conspicuous rectangular dorsal lobe; dermal denticles tricuspid, markedly imbricate and broad at the crown.

Flakeus sp. 6 differentiates from *Flakeus* sp. 5 by having a larger pectoral anterior margin length (15.9%, 15.5%–16.0% of TL vs. 14.3%, 14.4%–14.5% of TL for *Flakeus* sp. 5) and more elongate first dorsal spine (its length 4.3%, 3.3%–4.3% of TL vs. 2.8%, 2.9%–3.0% of TL for *Flakeus* sp. 5). *Flakeus* sp. 6 has larger first dorsal fin than *Flakeus* sp. 5 with greater length on its anterior margin (11.2%, 10.8%–11.4% of TL vs. 10.5%, 10.3%–10.6% of TL for *Flakeus* sp. 5) and fin base (its length 8.2%, 7.7%–8.5% of TL vs. 7.5%, 7.2%–7.3% of TL for *Flakeus* sp. 5). *Flakeus* sp. 6 is clearly distinct from *Flakeus* sp. 4 by larger interdorsal space (its length 26.4%, 24.0%–25.8% of TL vs. 22.3%, 21.9%–23.6% of TL for *Flakeus* sp. 4).

Description.

External morphology (Figs. 236–241; Tabs. 55, 57). Body markedly robust and humped dorsally, turning more slender from the pelvic fins to caudal fin; body extremely deep from head to tail (head width 1.0, 0.8–1.0 times trunk height and 0.9, 0.7–1.2 times abdomen height), strongly wide at head (head width 1.2, 1.2–1.4 times greater than trunk width and 1.7, 1.3–1.9 times greater than abdomen width). Head flattened dorsally from snout to spiracle and well elongate, its length 24.7% (22.2%–23.0%) of TL, corresponding to 1.3 (1.0–1.1) times dorsal caudal margin length. Snout strongly pointed at the tip and large (preorbital length 7.9%, 6.8%–7.7% of TL); anterior margin of nostrils broad and bilobate, placed ventral-laterally in the snout; prenarial length 1.0 (1.0–1.1) times distance from nostrils to upper labial furrow and 1.4 (1.0–1.4) times larger than eye length; width between nostrils narrow (its length 5.0%, 3.9%–4.1% of TL), corresponding to 1.4 (0.8–1.2) times eye length. Eyes oval with anterior margin convex and posterior notched, placed laterally nearest the snout tip than first gill slit, very large, its length 3.5%, 3.1%–4.9% of TL and corresponding to 2.6 (2.2–3.3) times its height. Prebranchial length 20.7%, 17.4%–19.2% of

TL. Gill slits vertical, markedly tall (fifth gill slit height 1.1, 1.1–1.2 times first gill slit), placed laterally just before the pectoral fins. Prespiracular length 12.8% (11.5%–12.6%) of TL, corresponding to 1.6 (1.6–1.7) times preorbital length. Spiracles crescentic, located posterior-dorsally to the eyes, very wide, its length 1.3% (1.1%–1.4%) of TL.

Preoral length 1.3 (1.2–1.4) times mouth width. Mouth straight and strongly broad, its width 1.6 (1.8–2.0) times greater than internarial space; upper labial furrow elongate, its length 2.6% (2.2%–2.5%) of TL with a prominent and fin fold on each side of the mouth; lower labial furrow also large, although not supporting a fold. Unicuspid teeth, similar in both jaws, alternate, compressed and wide labial-lingually at crown; lower teeth markedly larger and taller than upper teeth; cusp pointed, somewhat elongate and thick, oblique, directed laterally; mesial cutting edge conspicuously convex (straight on lateral lower teeth); mesial heel notched; distal heel rounded; apron short and heavy; two series of functional teeth on upper and lower jaw; teeth rows varying from 14–14 (14–14 paratypes) in upper jaw and 11–11 (11–11 paratypes) in lower jaw (Fig. 36).

Pre-first dorsal length 32.9% (28.4%–31.8%) of TL, its origin well before the vertical line traced on pectoral free rear tips. First dorsal fin very large (its length 2.2, 1.9–1.9 times greater than its height), and upright with anterior margin convex, posterior margin straight, although convex from its midline to the apex where it is more slender (Fig. 37); conspicuously rounded and slender at apex, free rear tip rounded; first dorsal anterior margin length 11.2% (10.8%–11.4%) of TL; posterior margin length 9.4% (7.7%–8.4%) of TL; and tall, its height; first dorsal fin markedly tall, its height 0.8 (0.9–1.0) times preorbital length and 1.1 (1.1–1.3) times its inner margin length. First dorsal spine stout and large, its length 4.3% (3.3%–4.3%) of TL, corresponding to 0.7 (0.5–0.6) times first dorsal fin height (not reaching the fin apex). Interdorsal space 1.1 (1.1–1.2) times prepectoral length and 2.2 (2.1–2.3) times greater than dorsal-caudal space. Pre-second dorsal length 4.0 (3.9–3.9) times pectoral anterior margin length and 3.2 (2.8–3.1) times dorsal-caudal margin length. Second dorsal fin also upright with anterior margin convex, posterior margin straight but convex and falcate from its midline to the apex (Fig. 37); apex slightly rounded; free rear tip pointed; second dorsal fin also large (its length 12.0%, 11.1%–12.5% of TL) and tall, its height 4.0% (4.7%–5.3%) of TL, corresponding to 0.9 (1.0–1.1) times its inner margin length. Second dorsal spine heavy and large, its length 4.4% (3.9%–4.3%) of TL, corresponding to 1.1 (0.8–0.9) times second dorsal fin height (almost reaching the fin apex); second dorsal spine 1.0 (1.0–1.2) times greater than first dorsal spine.

Pectoral fins with anterior margin straight, inner margin convex and posterior margin concave and fringed; apex and free rear tips rounded and lobe-like (Fig. 35); apex exceeding the horizontal line traced in the free rear tip (or reaching the line in paratypes); pectoral fins conspicuously broad, its posterior margin length 12.3%, 10.2%–12.5% of TL and corresponding to 1.1 (0.9–1.3) times trunk height; pectoral fin also very large, its anterior margin length 15.9% (15.5%–16.0%) of TL or 1.5 (1.8–2.0) times greater than its inner margin length. Pectoral-pelvic space 0.8 (0.8–0.9) times pelvic-caudal space. Pelvic fins nearest to second dorsal fin than first dorsal fin, although it is nearest the first dorsal fin in young paratypes. Pelvic fins very broad and elongate, its length 11.3% (9.9%–11.2%) of TL; all margins straight, although posterior margin fringed; free rear tips markedly pointed.

Caudal keels very strong, placed laterally in the caudal peduncle from second dorsal fin insertion until the upper caudal furrow; upper and lower caudal furrows profound. Caudal fin well elongate, its dorsal-caudal margin 19.7% (20.2%–21.3%) of TL, corresponding to 0.8 (0.9–1.0) times head length and 1.8 (1.7–1.8) times greater than preventral caudal margin length; upper caudal lobe conspicuously rectangular with dorsal caudal margin straight, upper post-ventral caudal margin convex, turning markedly convex to the tip; posterior caudal tip slightly rounded (Fig. 38); preventral caudal margin convex, its length 2.3 (2.3–2.6) times larger than pelvic inner margin length; lower post-ventral caudal margin straight; ventral caudal tip rounded; caudal fin strongly broad at fin web, its caudal fork width 7.2% (6.6%–7.1%) of TL; caudal fork between lobes strongly notched.

Dermal denticles (Fig. 241). Triscupid and markedly imbricate dermal denticles with pointed cusps with lateral cusps much shorter than median cusp; denticles very broad at the crown, its length greater than its width; median projection prominent and rounded, located anteriorly at the crown with small lateral-posterior expansions on each side; two prominent lateral ridges on each side, reaching the lateral cusp; a single median ridge conspicuous and elongate, bifurcate anteriorly, forming a profound groove between them.

Coloration. Body dark brown dorsally and pale ventrally. First and second dorsal fins also dark brown, whitish near each fin base and slightly blackish at the apex; first and second dorsal spines light brown, white at the tip and dark brown anteriorly. Pectoral fins dark brown with posterior margin white, not uniform. Pelvic fins also brownish, lighter ventrally; pelvic posterior and inner margins white. Caudal fin dark brown, whitish near the vertebral column; dorsal caudal margin white; upper and lower post-ventral margins slightly white; prominent black caudal stripe.

Vertebral counts (Tab. 58). Monospondylous vertebrae 45 holotype (46 paratypes); diplospondylous vertebrae 71 (74–75); precaudal vertebrae 87 (91–92); caudal vertebrae 29 (29 paratypes); total vertebrae 116 (120–121).

Geographical distribution (Fig. 242). *Flakeus* sp. 6 is so far known as an endemic species in southern Brazil.

Remarks. *Squalus fernandinus* Molina, 1782 is a nominal species described from Juan Fernandez, Chile that it was commonly reported to occur in the Atlantic waters (e.g. Miranda-Ribeiro, 1907; Fowler, 1936, 1941). It is often considered junior synonym as either of *Squalus acanthias* or senior synonym of *F. blainvillei* (e.g. Bigelow & Schroeder, 1948; Garman, 1960; Compagno, 1984). The taxonomic confusion regarding this species is due to the concise original description, and inexistence of type specimens and/or illustration in the literature that could contribute for clarifying its status. Guichenot (1846) synonymised it with a second nominal species from Chilenean waters, *Squalus fernandezianus* Guichenot (1846), that is characterized by brownish and robust body, first dorsal fin placed above the pectoral free rear tips, triangular dorsal fins and pelvic fins located in the midline between the two dorsal fins. These features are not applied to the present species with exception to body color and depth, indicating that both synonyms *Squalus fernandezianus* and *Squalus fernandinus* cannot be applied to the Atlantic form. A more precise investigation on specimens from Chile are urgently needed for elucidating the taxonomic status of *Squalus fernandezianus* and *Squalus fernandinus* in this region.

Flakeus griffini is another species from the South Pacific Ocean, apparently endemic to the coast of New Zealand (Duffy & Last, 2007). *Flakeus* sp. 6 is very similar morphologically to this species, sharing characteristics such as tricuspid and imbricate dermal denticles, strongly broad at the crown, and absence of dark caudal bar, as well as overlapping in a variety of external measurements and vertebral counts. It differs from it on lacking black spots dorsally on body, caudal fin without broadly white posterior margin and more slender first dorsal fin. *Flakeus* sp. 6 is further distinct from *Flakeus* cf. *griffini* by: shorter prenarial length (4.8%, 4.5%–4.9% of TL vs. 5.2%, 5.0%–5.9% of TL for *Flakeus* cf. *griffini*); more elongate pectoral inner margin (its length 10.9%, 8.1%–8.8% of TL vs. 6.5%, 5.4%–7.7% of TL for *Flakeus* cf. *griffini*).

Flakeus sp. 6 is distinct the Japanese species *F. mitsukurii* (Table V) by lacking dark caudal bar and narrower interorbital space (8.8%, 7.7%–8.0% of TL vs. 9.3%, 9.1%–9.8% of TL for *F. mitsukurii*). It can be also differentiated from *F. blainvillei* of the Mediterranean Sea by robust and markedly arched body (vs. slender and straight body) and triscuspid dermal denticles (vs. lanceolate denticles).

Flakeus sp. 6 can also be distinct from *Flakeus* sp. 4 by: shorter second dorsal spine in *Flakeus* sp. 6 (its length 4.4%, 3.9%–4.3% of TL vs. 5.3%, 3.4%–5.3% of TL for *Flakeus* sp. 4); second dorsal spine length 1.0 (1.0–1.2) times greater than first dorsal spine length in *Flakeus* sp. 6 (vs. 1.4, 1.0–1.6 times for *Flakeus* sp. 4). *Flakeus* sp. 6 also has shorter prenarial and preoral lengths than *Flakeus* sp. 5 (prenarial length 4.8%, 4.5%–4.9% of TL vs. 5.0%, 4.9%–5.1% of TL for *Flakeus* sp. 5 and preoral length 10.2%, 9.5%–10.0% of TL for *Flakeus* sp. 5).

Flakeus sp. 6 has larger number of monospondylous vertebrae than *Flakeus crassispinus*, *F. megalops*, *F. raoulensis*, *F. grahami*, *Squalus nasutus* and *F. hemipinnis* provided by Last *et al*. (2007) (45, 46–46 vs. 41, 39–42 for *F. crassispinus* vs. 37–40 for *F. megalops* vs. 41, 41–43 for *F. raoulensis* vs. 40, 38–42 for *F. grahami* vs. 39, 36–39 for *F. nasutus* vs. 36, 35–38 for *F. hemipinnis*). It is also distinguished from *F. mitsukurii*, the Mediterranean *F. blainvillei*, and *S. chloroculus*, *F. montalbani* and *F. notocaudatus* from Last *et al*. (2007) by total vertebrae (116, 120–121 for *Flakeus* sp. 6 vs. 112–113 for *F. mitsukurii* vs. 111 for *F. blainvillei* vs. 114, 111–115 for *S. chloroculus* vs. 105–114 for *F. montalbani* vs. 127, 123–125 for *F. notocaudatus*). It is easily distinct from *F. albifrons*, *Squalus altipinnis* and *F. notocaudatus* (Last *et al*., 2007) by lower first dorsal fin: its height

4.0%, 4.7%º–5.3% of TL for *Flakeus* sp. 6 vs. 8.6%, 7.7%–8.9% of TL for *F. albifrons* vs. 7.8%, 7.9% of TL for *S. altipinnis* vs. 8.2%, 8.3%–9.4% of TL for *F. notocaudatus*).

Analysis of the claspers of *Flakeus* sp. 6 is still needed for better characterizing the species as no adult males were founded in the fish collections. More specimens are required for comparisons of skeletal anatomy, including neurocranium, with its congeners.

Comparative material. Same material listed for *Flakeus* sp. 5.

***Flakeus* sp. 7**[4]

(Suggested common names: White-caudal dogfish shark; Cação-bagre-de-cauda-branca in Portuguese)

Figures 243–247; Tables 56–58

Squalus megalops (not Macleay): Regan, 1908: 45, 47 (identification key, listed); Bigelow & Schroeder, 1948: 454 (cited); Bigelow & Schroeder, 1957: 29, 36, 37, figs. 3C, 4 (revision; Northwestern Atlantic); Garrick, 1960: 537, 538, figs. 1(G-I), 3(O-T) (revision; New Zealand); Ledoux, 1970: 66, 67, fig. 3A (revision; Mediterranean Sea); Bass *et al*., 1976: 11-13, 16-18, figs. 6B, 7B, 8 (C, D), 11, PL. 3 (revision; Eastern South Africa); Fourmanoir & Rivaton, 1979: 436, fig. 24 (revision; New Caledonia); Cadenat & Blache, 1981: 51, 52 (revision; Mediterranean Sea); Compagno, 1984: 118, 119 (revision); Muñoz-Chápuli, 1985: 397, 398, fig. 1 (cited); Muñoz-Chápuli & Ramos, 1989: 1-21, figs. 1, 2 (E, F), 3 (D, E) (revision; Eastern Atlantic); Calderón, 1994: 1-104, fig. 5A (cited); Compagno & Niem, 1999: 1230 (revision; Western Central Pacific); Fricke, 1999: 27 (listed; Mascarene Islands); Szpilman, 2000: 75 (listed); Nion *et al*., 2002: 4 (listed); Haimovici *et al*., 2003: 38, 39 (cited); Meneses & Paesch, 2003: 8, 25, 45 (cited); Smith & Heemstra, 2003: 61, 62, fig. 5.26 (identification key; description); Heemstra & Heemstra, 2004 (cited, Southern Africa): 49, 53, fig. 28; Bernades *et al*., 2005: 49, 70 (cited); Compagno *et al*., 2005: 74 (revision); Braccini, 2006: 1-209 (cited); Hazin *et al*., 2006 (cited); Jablonski *et al*., 2006: 110, 177, 178 (cited); Louro & Rossi-Wongtschowski, 2007: 18, 27-30, 49, figs. 15, 16 (cited); Carrier *et al*., 2010: 44 (cited); Rosa & Gadig, 2014: 92 (listed; Brazil).

Squalus cubensis (not Howell-Rivero): Figueiredo, 1977: 8 (in part) (description; Southern Brazil); Lucena & Lucena, 1981: 4 (catalogued; Brazil); Myagkov & Kondyurin, 1986: 1-20, fig. 1 (A,E,F,H) (revision; Atlantic); Lessa *et al*., 1999: 14, 61, 150 (cited, listed; Northeast Brazil); Compagno, 2002: 384 (description; Northern and Southern Brazil, Argentina, and Uruguay); Compagno *et al*., 2005: 75, pl. 3 (catalogued; Southwest Atlantic Ocean); Last *et al*., 2007: 21-22, figs.10A, 11A (cited; Southeast Brazil); Nunan & Senna, 2007: 169, 170 (in part) (cited; Brazil).

Squalus sp. of the *megalops* group: Marques, 1994 (cited; Brazil); Gomes *et al*., 1997: 95, 98-109 (listed; Brazil); Marques, 1999 (cited; Brazil).

Squalus sp. of the *megalops-acutipinnis-cubensis* group Cadenat & Blache, 1981: 51, 52, fig. 31 (F, G) (revision; Mediterranean Sea); Figueiredo, 1981: 17 (listed; Brazil).

Squalus sp.: Gomes *et al*., 1997: 98 (listed; Brazil); Tomás *et al*., 2010 (cited; Southeast Brazil).

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[4] Description taken from Viana *et al*. (*in prep*.).

Squalus of the *megalops/cubensis* group: Gadig, 2001: 29, 36, 54, 58-60 (listed; Brazil).
Squalus sp. A: Soto, 2001: 95, 96 (listed; Brazil); Soto & Mincarone, 2004: 74-79 (listed; Brazil).
Squalus blainvillei (not Risso): FIP, 2005: 53 (cited; Chile).
Squalus sp. 2: Gomes *et al*. 2010: 44-46 (cited; Brazil).

Holotype: MNRJ 30188, adult male, 525 mm TL, north coast of Espírito Santo state, Brazil, 19°42'54"S, 39°25'57"W. 195 meters depth. Collected on 30 June 2000, Station 0531, Thalassa cruise, Revizee program.

Paratypes (11 specimens): MNRJ 30173, adult female, 590 mm TL, south coast of Bahia state, between Itacaré and Ilhéus, Brazil, 14°28'58"S, 38°54'0"W, 278 meters depth; MNRJ 30174, adult female, 580 mm TL, south coast of Bahia state, between Itacaré and Ilhéus, Brazil, 14°28'58"S, 38°54'0"W, 278 meters depth; MNRJ 30175, adult female, 560 mm TL, south coast of Bahia state, between Itacaré and Ilhéus, Brazil, 14°28'58"S, 38°54'0"W, 278 meters depth; MNRJ 30176, adult female, 540 mm TL, south coast of Bahia state, between Itacaré and Ilhéus, Brazil, 14°28'58"S, 38°54'0"W, 278 meters depth; MNRJ 30177, adult male, 450 mm TL, Morro de São Paulo, Bahia, Brazil, 13°21'51"S, 38°40'49"W, 421 meters depth; MNRJ 30181, adult male, 482 mm TL, Canavieiras, Bahia, Brazil, 15°42'41"S, 38°37'18"W, 251 meters depth; MNRJ 30183, juvenile female, 425 mm TL, Salvador, Bahia, Brazil, 13°8'54"S, 38°28'41"W, 334 meters depth; MNRJ 30184, adult male, 480 mm TL, Salvador, Bahia, Brazil, 13°8'54"S, 38°28'41"W, 334 meters depth; MNRJ 30185, adult male, 440 mm TL, Salvador, Bahia, Brazil, 13°8'54"S, 38°28'41"W, 334 meters depth; MNRJ 30186, adult female, 590 mm TL, north coast of Espírito Santo state, Brazil, 19°42'54"S, 39°25'54"W, 202 meters depth; MNRJ 30187, adult female, 610 mm TL, north coast of Espírito Santo state, Brazil, 19°42'54"S, 39°25'57"W, 195 meters depth.

Type locality: north coast of Espírito Santo state, Brazil.

Non-type material (9 specimens): MZUFBA uncatalogued, juvenile female, 420 mm TL; adult male, 502 mm TL, Praia do Forte, Mata de São João, Bahia, Brazil; NUPEC 96, adult male, 460 mm TL, South of Barra de Santos, São Paulo, Brazil; NUPEC 1354, neonate female, 285 mm TL; juvenile female, 355 mm TL, Ilha Vitória, São Paulo, Brazil; TAMAR 10.38, adult male, 490 mm TL, locality same as MZUFBA; TAMAR 10.39, juvenile female, 459 mm TL, locality same as MZUFBA; TAMAR 10.41, juvenile female, 445 mm TL, locality same as MZUFBA; TAMAR 10.42, juvenile female, 410 mm TL, locality same as MZUFBA.

Diagnosis. *Flakeus* sp. 7 can be distinguished from its congeners by a combination of characteristics: caudal fin with a mostly white ventral caudal lobe, dorsal caudal margin white at midline, and postventral caudal margins broadly white; pectoral posterior margin broadly white; first dorsal fin with anterior margin also conspicuously white on its lower half. *Flakeus* sp. 7 differs from all species of the *Squalus mitsukurii* group by: snout short vs. snout large; pectoral free rear tips pointed vs. pectoral free rear tips rounded; dermal denticles lanceolate and unicuspid vs. dermal denticles rhomboid and tricuspid.

Flakeus sp. 7 is clearly distinct from *F. cubensis* by: snout strongly pointed (vs. snout somewhat rounded); second dorsal spine not reaching the second dorsal apex (vs. reaching the second dorsal apex); first dorsal fin with dark apex, although not as black marking (vs. conspicuous black markings on both dorsal fins); pectoral fins with posterior margin broadly white (vs. narrowly white). These two species also differ in external measurements such as: narrower mouth (its width 7.9%, 6.9%–7.7% of TL vs. 7.5%, 7.8%–8.5% of TL for *F. cubensis*); shorter first dorsal fin (its anterior margin length 10.9%, 9.7%–11.2% of TL vs. 11.6%, 11.6%–12.7% of TL for *F. cubensis*); shorter second dorsal fin (its anterior margin length 9.2%, 8.8%–10.8% of TL vs. 12.3%, 11.2%–11.6% of TL for *F. cubensis*; its inner margin length 5.0%, 4.1%–5.2% of TL vs. 5.6%, 5.5%–6.0% of TL for *F. cubensis*); more slender second dorsal spine (its width at base 0.9%, 0.6%–0.9% of TL vs. 1.0%, 1.0%–1.2%

of TL for *F. cubensis*); clasper much more elongate in *Flakeus* sp. 7, its inner margin length 7.1%, 6.9%–7.7% of TL (vs. 8.0%, 3.3%–3.8% of TL for *F. cubensis*). Adults of *Flakeus* sp. 7 are differentiated from those of *F. brevirostris* by larger dorsal-caudal space (10.7%–14.1% of TL vs. 10.0%–10.6% of TL in *F. brevirostris*).

Description.

External morphology (Figs. 243–246; Tabs. 56–57). Body fusiform and thin through all its extension, slightly arched dorsally, equally deep from head to trunk (head height 1.0, 0.8–1.0 times trunk height and abdomen height), and broader at the head than at the trunk (head width 1.2, 1.0–1.4 times trunk height and 1.4, 1.2–1.4 times abdomen height). Head very short and narrow (its length 21.8%, 18.7%–24.7% of TL; its greatest width at mouth (its width 11.1%, 10.9%–12.0% of TL). Snout pointed at tip, conspicuously short (its length 7.1%, 6.8%–7.8% of TL); anterior margin of nostrils bifurcate and wide, equally near the snout tip and mouth; prenarial length 1.0, 0.8–1.0 times distance from nostrils to upper labial furrow and 0.5, 0.4–0.5 times preoral length; internarial space 1.1, 0.8–1.0 times eye length. Eyes oval and markedly large (its length 4.0%, 4.2%–5.3% of TL, corresponding to 1.5, 1.8–2.1 times its height), placed laterally; anterior margin of eyes convex and posterior margin notched; interorbital space 8.4%, 8.2%–8.9% of TL. Prespiracular length 12.5%, 11.7%–13.8% of TL, corresponding to 0.5 (0.6–0.7) times prepectoral length and 1.7 (1.7–1.9) times preorbital length. Spiracles crescent and wide, its length 1.5% (1.3%–2.0%) of TL, corresponding to 0.4, 0.3–0.4 times eye length. Prebranchial length 1.5 (1.3–1.5) times prespiracular length. Gill slits vertical and low, with fifth gill slit 1.1 (1.0–1.4) higher than first gill slit.

Preoral length 9.8%, 9.2%–11.2% of TL and equal to 1.2, 1.3–1.5 times mouth width. Mouth arched and strongly broad, its width 1.5, 1.5–1.8 times prenarial length and 1.9, 1.9–2.0 times internarial space; upper labial furrow with thin fold, very large (its length 2.3%, 2.1%–2.5% of TL); lower labial furrow also large, although without a fold. Teeth unicuspid and similar im both jaws, wide and flattened labial-lingually at crown, imbricate laterally; upper teeth much smaller than lower teeth; cusp oblique, somewhat elongate and heavy, directed laterally; mesial heel slightly notched; distal heel rounded; mesial cutting edge somewhat straight; apron thick and rather elongate. Three series of teeth on upper jaw and two series of teeth on lower jaw for holotype (paratypes 2–3 for both jaws); teeth rows ranging from 12–12 (13–14 paratypes) on upper jaw and 11–11 (11–12 paratypes) on lower jaw (Fig. 42).

Pre-first dorsal length 1.1 (1.2–1.8) times prepectoral length. Origin of first dorsal fin previous to pectoral free rear tips. First dorsal fin with anterior margin markedly convex and posterior margin straight, although concave on its first half; first dorsal apex rather rounded at tip; first dorsal free rear tip rounded (Fig. 43); first dorsal inner margin very short, its length 5.6% (4.9%–6.1%) of TL; first dorsal fin short (its length 1.7, 1.6–2.0 times its height) and low (its height 7.9%, 6.8%–8.0% of TL and corresponding to 1.4, 1.2–1.6 times first dorsal inner margin length and 1.1, 0.9–1.1 times preorbital length). First dorsal spine slender, thick (its base width 1.0%, 0.7%–1.1% of TL) and elongate (its length 4.2%, 2.3%–4.1% of TL), reaching half of first dorsal height (0.3–0.5 times first dorsal height in paratypes). First dorsal fin length 1.3 (1.0–1.3) times larger than second dorsal fin length. Interdorsal space 1.1 (1.0–1.3) times prepectoral length and 2.2 (1.7–2.6) times dorsal-caudal space. Pre-second dorsal length 2.8, 2.5–3.1 times prepectoral length and 3.2, 2.8–3.3 times dorsal-caudal margin length. Second dorsal fin also short (its length 2.0, 1.9–2.3 times its height) and somewhat tall (its height 5.4%, 4.9%–6.2% of TL, corresponding to 1.1, 0.9–1.3 times second dorsal inner margin length); first dorsal anterior margin convex and posterior margin markledy concave; first dorsal apex rounded and pointed at free rear tip (Fig. 43); second dorsal inner margin short, its length 5.0% (4.1%–5.2%) of TL. Second dorsal spine conspicuously thin and large, almost reaching the second dorsal fin height, its length 5.1% (3.4%–5.0%) of TL, corresponding to 0.9 (0.7–0.9) times second dorsal height and 1.2 (1.0–1.8) times first dorsal spine length.

Pectoral fins small but also broad with anterior margin length 13.4% (11.8%–14.4%) of TL, corresponding to 1.2 (1.2–1.4) times posterior margin length and 1.5 (1.3–1.5) times inner margin length; pectoral posterior margin 10.7% (9.7%–11.8%) of TL; pectoral anterior margin straight, inner margin convex and posterior margin concave; pectoral apex rounded and lobate (Fig. 41); pectoral free rear tips markedly pointed, transcending the horizontal line traced from pectoral apex; posterior margin length 1.1 (0.8–1.0) times trunk height. Pectoral-pelvic space 0.7 (0.5–0.9) times pelvic-caudal space. Pelvic fins nearest the first dorsal fin than the second dorsal fin in holotype and young paratypes (or nearest second dorsal fin in adult paratypes). Pelvic fin anterior margin convex and posterior margin straight; pelvic apex rounded and narrow; pelvic free rear tips rounded and lobate; pelvic fins elongate, its inner margin length 6.3% (4.2%–6.3%) of TL. Claspers cylindrical, thin, and flattened dorsal-ventrally; claspers short, slightly transcending pelvic free rear tips, its inner length among 7.1% (6.9%–7.7% of TL) and corresponding to 1.1 (1.2–1.4) times larger than pelvic inner margin length; clasper groove longitudinal and small, located dorsally; apopyle narrow, placed in the proximal end of clasper groove; hypopyle constricted at the distal end of the clasper groove; rhipidion narrow and short, blade-like and somewhat thick, placed medially at the distal end of the clasper (Fig. 44).

Caudal peduncle slender with soft caudal keel on each side; upper and lower caudal furrows markedly profound. Caudal fin slender and short, its dorsal caudal margin length 19.8% (19.3%–21.2%) of TL, corresponding to 0.9 (0.8–1.1) times head length and 1.7 (1.7–1.9) times preventral caudal margin; dorsal caudal margin straight, post-ventral caudal margin (upper and lower) convex (Fig. 45); posterior tip pointed; caudal fork between lobes with conspicuous concavity and very narrow (its width 6.5%, 6.2%–7.2% of TL); ventral tip rounded; preventral caudal margin also convex and short, its length 11.4% (10.5%–11.9%) of TL and corresponding to 1.8 (1.7–2.6) times pelvic inner margin length.

Dermal denticles. (Fig. 246) Unicuspid, lanceolate and markedly slender dermal denticles, its length much greater than its width; dermal denticles moderately assymetrical and near each other but not imbricate; median and lateral ridges well prominent, bifurcate anteriorly; crown conspicuously expanded anteriorly and rather expanded laterally; cusp rounded and elongate posteriorly.

Coloration. Body brownish grey dorsally and white ventrally, grey laterally from between the pectoral and pelvic fins, turning whitish to the caudal fin origin. First dorsal fin brownish, darker at the fin web to the apex; anterior margin broadly white on its first half and dark brown to the apex; posterior margin slightly white on its first half and brown to the apex; first dorsal spine grey, darker anteriorly, white laterally and at its tip. Second dorsal fin brown throught all its exception (few paratypes with apex white); second dorsal posterior margin white; second dorsal spine also grey, darker anteriorly and white at its tip. Pectoral fins brown dorsal and ventrally (except near its base) with posterior and inner margins conspicuously broad white, including apex and free rear tips. Pelvic fins light brown dorsally and white ventrally; pelvic posterior margin broadly white. Caudal fin mostly dark brown with dorsal caudal margin markedly white on its midline; upper caudal blotch dark grey distally in thedorsal caudal margin; post-ventral caudal margins conspicuously broad white, except in the caudal fork where it is light grey (caudal bar); posterior caudal tip also broadly white; preventral caudal margin dark grey on its first half; ventral caudal lobe conspicuous broadly white, including the ventral caudal tip; caudal stripe blackish, thick and short.

Vertebral counts (Tab. 58). 110 (110–116) total vertebrae; 39 (40–41) monospondyous vertebrae; 82 (81–89) precaudal vertebrae.

Geographical distribution (Fig. 247). *Flakeus* sp. 6 occurs in warm tropical waters between Northeastern and Southeastern Brazilian coast and it is often registered between the states of Bahia and Espírito Santo. Its distribution to Southern Brazil is unknown.

Remarks. The present study recognizes a small and undescribed species of *Flakeus* in Brazilian waters that has been misidentified with *F. cubensis*. Till recently, occurrences of *F. cubensis* in this region were reported (e.g. Compagno, 1984; Compagno *et al*., 2005; Nunan & Senna, 2007; Gomes *et al*., 2010). These two species are very similar in general morphology and share the following characteristics: dermal denticles unicuspid, slender and lanceolate, its length much greater than its width; postventral caudal margins white; snout very short; pectoral fins short but wide. The majority of external measurements are overlapped between *Flakeus* sp. 7 and specimens of the Cuban dogfish. No great differences on vertebral counts are noticed between them, even when types of *F. cubensis* are also compared. Information on variations of vertebral counts taken from the literature (e.g. Muñoz-Chápuli & Ramos, 1989) is also congruent with those of *Flakeus* sp. 7, which contributes to the complexity regarding the taxonomic separation between *Flakeus* sp. 7 and *F. cubensis*.

However, differences on shape of snout, color of dorsal fins and pectoral fins as well as variations on external measurements (e.g. mouth width; length of dorsal fins; thickness of second dorsal spines) support the separation between them. *Flakeus* sp. 7 has the apex of first dorsal fin darker but not as black markings as it is noticed for *Flakeus cubensis*. The former species also shows second dorsal fin with whitish apex, which it is not noticed for the latter. In neonates and small juveniles of *Flakeus* sp. 7, a small black marking is observed in the first dorsal fin, located below lower half of the fin web while its apex is white. Dorsal fins of young specimens of the genus are often blackish at the apex in other species as well (e.g. *F.montalbani*, *F. grahami*, *F. megalops*), indicating that this characteristic is not exclusive for *Flakeus* sp. 7.

Bigelow & Schroeder (1948, 1957) pointed out that *F. cubensis* possibly occurs in the Northeast region of South America, according to observations on pectoral fins described for *Flakeus blainvillei* from Rio de Janeiro waters in Miranda-Ribeiro (1907, 1923). Morphological characteristics provided by this author do not incide exclusively in a single species of *Flakeus,* indicating that the author probably analyzed more than one form from this region that is different from *F. cubensis*. The current study verified this when comparing specimens studied by A. de Miranda-Ribeiro in the MNRJ, from Rasa Island (Rio de Janeiro, Brazil) collected by vessel "Annie" in which Miranda-Ribeiro (1907) based his description include two different species: *Flakeus* sp. 7 and *S. acanthias*.

Subsequent authors (e.g. Ledoux, 1970; Figueiredo, 1977; Sadowsky & Moreira, 1981; Myagkov & Kondyurin, 1986) also recognized the Cuban dogfish in the Southeastern Brazil. Figueiredo (1977) provided an illustration based probably on a juvenile male from Uruguay, but which does not represent *F. cubensis* or *Flakeus* sp. 7 due to differences on shape of pectoral fins and coloration. Figueiredo (1981) also stated that two other species of *Flakeus* may occur between Uruguay and Southern Brazil in adition to *F. cubensis*. *Flakeus* sp. 7 is not recorded in this area, however, indicating that Figueiredo (1981) was probably referring to other species of *Flakeus* that has a more Southern distribution. Great variations on vertebral counts in Sadowsky & Moreira (1981) and Myagkov & Kondyurin (1986) also supported that more than one species of *Flakeus* rather than *F. cubensis* may be recognized in the SWAO.

Pelvic fins are nearest to second dorsal fin in adults of *Flakeus* sp. 7 while it is placed at midline between dorsal fins in juveniles, as previously noticied for Sadowsky & Moreira (1981). In contrast, *F. cubensis* has pelvic fins at midline between the origins of two dorsal fins in adults and nearest to first dorsal fin in juveniles, which supports the findings of Howell-Rivero (1936) and Bigelow & Schroeder (1948). Similar ontogenetical variability are observed wihtin the genus, suggesting the position of the pelvic fins related to the dorsal fins is not to a good taxonomic character for separating species. Howell-Rivero (1936) also observed variations on the length of snout and first dorsal spine that are smaller in juveniles than in adults of the Cuban species. These findings are not supported in the current results and it is not observed for *Flakeus* sp. 7 as well. No other ontogenetical differences on external measurements were noticed for *Flakeus* sp. 7.

Adult specimens of *Flakeus* sp. 7 show some differences on external morphometrics with adults of *F. brevirostirs* and *F. megalops*. The former species has larger snout than *F. brevirostris*, its prenarial length 4.3%–5.0% of TL (vs. 3.8%–4.3% of TL in adults of *F. brevirostris*), large preoral length (9.2%–11.2% of TL vs. 8.4%–9.5% of TL in adults of *F. brevirostris*), heavier first dorsal spine, its base width 0.7%–1.1% of TL (vs. 0.5%–0.7% of TL in adults of *F. brevirostris*), and smaller second dorsal spine (its length 3.4%–5.0% of TL vs. 4.7%–6.6% of TL in adults of *F. brevirostris*). *Flakeus* sp. 7 is separated from *F. megalops* by narrower mouth its width 6.9%–7.7% of TL (vs. 7.5%–9.4% of TL in adults of *F. megalops*), lower first dorsal fin, its height 6.8%–8.0% of TL (vs. 7.8%–10.5% of TL in adults of *F. megalops*), smaller pectoral fins, its anterior margin length 11.8%–14.4% of TL (vs. 14.0%–17.0% of TL of TL in adults of *F. megalops*).

Flakeus sp. 7 is clearly different from *F. crassispinus* by having more slender dorsal spines (base width of first dorsal spine 1.0%, 0.7%–1.1% of TL vs. 1.3%, 1.2%–1.3% of TL for *F. crassispinus*; base width of second dorsal spine 0.9%, 0.6%–0.9% of TL vs. 1.5%, 1.3%–1.4% of TL). It can be distinct from *F. bucephalus* by having much narrower head (its width at mouth 11.1%, 10.9%–12.0% of TL vs. 13.0%, 12.1%–13.5% of TL for *F. bucephalus*). It is also distinct from *F. bucephalus* and *F. notocaudatus* by lower first dorsal fin (its height 7.9%, 6.8%–8.0% of TL vs. 8.5%, 8.1%–8.4% of TL for *F. bucephalus* vs. 8.2%, 8.3%–9.4% of TL for *F. notocaudatus*). It is distinct from *F. raoulensis* by smaller pectoral fins (pectoral anterior margin length 13.4%, 11.8%–14.4% of TL vs. 15.3%, 15.0–16.9% of TL for *F. raoulensis*). *Flakeus* sp. 7 differentiates from *F. albifrons* by shorter first dorsal spine (its height 4.2%, 2.3%–4.1% of TL vs. 4.8%, 4.4–5.4% of TL for *F. albifrons*).

Additional material from northward Northeast Brazil is needed in order to improve the knowledge on its geographical distribution of *Flakeus* sp. 7 in the Southwestern Atlantic Ocean.

Comparative material. Specimens of *Flakeus cubensis, Flakeus megalops* and *Flakeus brevirostris* listed in this Chapter.

Discussion.

Classification of the family Squalidae. The hypothesis of subdivision of the genus *Squalus* into “groups of species” proposed previously by Bigelow & Schroeder (1948, 1953) is refuted in the present study and it is in agreement with Myagkov & Kondyurin (1986). A combination of external characteristics (e.g. shape of fins, coloration, dermal denticles), meristic data and morphometrics provide support for morphological differentiation and taxonomic separation between species within and between each group, indicating that the subdivision into groups of species is unnecessary. The current study notices that morphological diversity for *Squalus* is greater than previously emphasized on literature and that similarity of characteristics is an exception in this context in which few possible cryptic species are noticed for the group (e.g. *Flakeus acutipinnis* and *Flakeus* sp. 1). These findings are in disagreement with previous studies (e.g. Cadenat & Blache, 1981; Compagno, 1984; Compagno *et al*., 2005; Gomes *et al*., 2010) that had predisposition on identifying group of species for Squalidae rather than discussing the variations of characteristics between different forms in regional and global contexts.

Two groups of species, *S. megalops* and *S. mitsukurii* groups, share morphological characteristics regarding position of pelvic fins related to dorsal fins, coloration, and position of origin of first dorsal fin related to pectoral fins as described by Bigelow & Schroeder (1948, 1957) and followed by Garrick (1960), Bass *et al*. (1976), Compagno *et al*. (2005), and Last *et al*. (2007). The congruence of these features also gives support for not recognizing group of species for Squalidae because species might be addressed to more than one morphological group. These characteristics comprise a generic definition, indicating that these two groups of species together may represent a single taxonomic category. A third group, the *S. acanthias* group, bears exclusive characteristics that it is clearly differentiated from the latter groups (e.g. presence of white spots on body, first dorsal fin placed behind pectoral free rear tips, dermal denticles unicuspid with single ridge) and also represents a more generic definition rather than a group of species. Two separated and morphologically distinct morpho-groups are recognized: a group that comprises species previously inserted into *S. acanthias* group, and a second group that merges species of the *S. megalops* and *S. mitsukurii* groups. Based on these interpretations on the concept of “group of species” in *Squalus*, a new taxonomic classification is proposed in which a second genus is recognized for Squalidae. Thus, the genus-name *Squalus* is restricted to the “group of species” of Bigelow & Schroeder (1948) that includes its type species, *Squalus acanthias,* and more two species of spotted dogfish sharks recognized in the present study. The second genus comprises all remaining species previously included in *Squalus*.

Recent molecular studies revealed clear clades within the crown-group *Squalus* that are congruent with the current hypothesis of classification. Species of *Squalus acanthias* group are always recognized as a consistent cluster in molecular analysis and separated from remaining species of *Squalus* (e.g. Ward *et al*., 2005, 2007; Naylor *et al*., 2012a,b). Ward *et al*. (2005, 2007) recognized different species from Australian waters through analysis of COI gene and pointed out three major and consistent clusters in the genus. These clusters are coincident to morphological groups in which each cluster represents a “group of species” of Bigelow & Schroder (1948): *Squalus acanthias* group (cluster C), *Squalus megalops* group (cluster B) and *Squalus mitsukurii*/*Squalus* sp. B-F group (cluster A). Ebert *et al*. (2010) and Naylor *et al*. (2012b) made associations between these clusters and groups of species of the genus as well. However, no previous studies suggested that these clusters would represent more inner taxa within the family.

Squalus megalops and *S. mitsukurii* groups are paraphyletic in Naylor *et al*. (2012a,b) but these two groups together comprise a single and monophyletic group, suggesting that it may represent a taxonomic category separated from a smaller group that comprises the type species *S. acanthias*. Despite of DNA barcoding by itself does not help to support phylogenetic relationships among species, it is likely helpful to identify species new or not to Science and existence of possible cryptic species (Ward *et al*., 2007). Molecular studies might also be helpful for classification purposes because it permits to recognize assemblages of species through arrangement of clusters, which it is assumed to represent potential taxonomic categories above species-level.

Naylor *et al*. (2012a) indicated four major clusters in Squalidae when incorporating specimens of *Cirrhigaleus asper* and *C. australis* in the analysis. *Cirrhigaleus* comprises the fourth cluster that is sister-group to all species of *Squalu*s in this study, which corroborates previous assumptions of Bass *et al*. (1976) in recognizing a fourth morphological group of species within Squalidae, the *Squalus asper* group. Naylor *et al*. (2012b) further investigated phylogenetic relationships among species of Squalidae based on NADH2 mitochondrial gene and suggested paraphyly for *Squalus*. *Cirrhigaleus asper* and *C. australis* together are sister-group of *Squalus acanthias* and *Squalus suckleyi* and this small crown group together are sister-group to all remaining *Squalus* species (Naylor *et al*., 2012b). The authors then suggested incorporating the two species of *Cirrhigaleus* into *Squalus* in order to support monophyly of the latter genus. Investigations on species of *Cirrhigaleus* show great morphological differences with species of *Squalus* that clearly support it as a separated and valid genus[5], which it is in contrast to results of Naylor *et al*. (2012b) and in agreement with Shirai (1992). The latter author, however, did not analyzed inner interrelationships within *Squalus* for comparisons with the present study and molecular analysis.

New characters raised here separate Squalidae into two different genera such as shape and number of ridges of dermal denticles, shape of anterior margin of nostrils, and length of dorsal spines. Similar characters have been used recently to separate other genera in Squaliformes, for instance, *Zameus* and *Scymnodon* (e.g. White *et al*., 2014). Definition of genera in Squaliformes is still mostly restricted to dentition and/or comprised by a combination of characteristics related to definition at family level in which these genera are inserted. This is still the case of *Squalus* and *Cirrhigaleus*, *Aculeola* and *Centroscyllium*, *Euprotomicrus* and *Euprotomicroides* (e.g. Compagno, 1984; Compagno *et al*., 2005; Ebert *et al*., 2013a) that lack comparative morphological definition. The taxonomic classification of

[5] Taxonomy of *Cirrhigaleus* is discussed and treated separately in Chapter 3.

these genera have not accompanied recent phylogenetic studies in Squaliformes as noticed by White *et al*. (2014) for Somniosidae and in the current study for Squalidae, which contributed to constant discussions on reallocating its nominal species into different genera. These observations call attention for the necessity on redefining morphologically each genus in Squaliformes in order to avoid nomenclatural instability of its species.

The characteristics for the redefinitions of *Squalus* and *Flakeus* proposed herein were not originally provided in Linnaeus (1758) and Whitley (1939). The first author described *Squalus* in a broader context to integrate all species of sharks rather than at lower taxonomic category such as genus level, providing characteristics that nowadays are addressed to all species of Squalidae. The latter author raised *Flakeus* from subgenus to genus level without clear explanations, and characterized its species by possessing eye length four times in head length, origin of first dorsal fin over or just posterior to vertical at pectoral free rear tips, and nearest to snout tip than second dorsal fin, and body with uniform color. These characteristics are supported in the present study with exception to eye length and position of first dorsal fin related to snout tip that can be applied for both *Flakeus* and *Squalus*. Despite of it, *Flakeus* was considered junior synonym of *Squalus* by subsequent studies that also failed on comparisons and discussions on its taxonomic status (e.g. Bigelow & Schroeder, 1948, 1957; Garrick, 1960; Compagno, 1984).

The new classification for Squalidae proposed in the current study reflects recent progresses in studying taxonomy and Systematics of elasmobranch fishes in the past 60 years of research. Group of species of *Squalus* from Bigelow & Schroeder (1948) represents a first tentative on understanding the morphological complexity of its species in a context that had limited access to representatives of the genus. Studies that followed this arrangement to date (e.g. Bass *et al*., 1976; Compagno, 1984; Gomes *et al*., 1997; Compagno *et al*., 2005; Last *et al*., 2007; Ebert *et al*., 2010) attempted to the diversity of the genus globally even though the similarities between species were more emphasized that its particularities. Recent tools on modern taxonomy have contributed to accelerate these goals. However, exhaustive taxonomic and morphological revisions are still imperative, particularly on groups with extensive and complex Systematic history like *Squalus*.

New taxonomic challenges and cryptic species. Some species of *Flakeus* exhibit intraspecific variations (e.g. *F. megalops* that surrounds the Australian waters; *F. brevirostris* between North Japanese waters and Taiwan) that make difficult to provide morphological characteristics for its identification. These variations are often related to shape of pectoral fins, body coloration, shape of dermal denticles, and some proportional external measurements while teeth and vertebral counts are intrinsically overlapped among its specimens. Each species is still recognized as valid because at least one subpopulation within its range of geographical distribution bears all diagnostic characteristics that recognize originally the species. In these cases, the morphological variability might indicate incidences of possible cryptic species or a process of speciation in progress. *Flakeus* sp. 1 exhibits intrinsic morphological similarities with *Flakeus acutipinnis*, although clear differences on shape of fins and body, dentition and few external measurements are noticed between them, indicating that these species are possibly cryptic. These results are not supported on recent molecular analysis (e.g. Ward *et al.*, 2007; Naylor *et al.*, 2012a) for *F. brevirostris* and *Flakeus* sp. 1, although for *F. megalops* differences on pairwise were noticed among its subpopulations. Studies on biological aspects and molecular analysis of dogfish in African waters are still poorly investigated, which call for need in verifying these taxonomic assumptions.

Squalus acanthias is often considered a complex of cryptic species (e.g. Ward *et al.*, 2007; Veríssimo *et al.*, 2010; Last & White, 2011; White & Last, 2012) because specimens from North Pacific and those from remaining areas of the world exhibit intrinsic external morphology but distinct genotypes (Veríssimo *et al*., 2010) and biological patterns of feeding and reproduction (Gallucci *et al*., 2009). Taxonomic status of the North Pacific subpopulations are elucidated in Ebert *et al*. (2010) and in the present study. However, specimens of *S. acanthias* from North and South Atlantic Oceans, South Pacific and Indian Oceans still show overlapping of external and skeletal morphology with variations regarding vertebral counts, dermal denticles and dentition, suggesting that other cryptic species might be recognized in these areas. Veríssimo *et al*. (2010) noticed small differences on nuclear gene NADH2 between specimens from South Atlantic and South Pacific Oceans with those of North Atlantic Ocean, which gives additional support for this hypothesis.

Similar situation is noticed for *Flakeus japonicus* between Japan, Taiwan and Australia that also have variations on vertebrae and few external measurements. Ward *et al*. (2007) recognized the Australian subpopulation as a separated species, *Squalus nasutus*, and considered the Japanese species as paraphyletic due to specimens from Taiwan bear two different haplotypes. A smaller group of *F. japonicus* from Taiwan is sister-group of specimens from Australia and Indonesia in analysis of Ward *et al*. (2007) and this group together comprises a consistent subcluster, suggesting that all specimens should be conspecific. The current study shows that the morphological variations in *F. japonicus* form North and Central Pacific Oceans are not sufficient for recognition of cryptic species in this case because continuous values between them are observed. These findings demonstrate that the decision on recognizing a separate species based on DNA barcoding must first consider morphological and molecular variations in a broader context of analysis rather than considering a narrower scope in which consistency on bootstrap values of subclusters are considered more relevant data for supporting hypothesis of new species.

Other species exhibit inner variations that permit clearly to recognize two distinct morphological groups, indicating that one of it might be an undescribed species. This is the case of *F. griffini* between North and South Islands in New Zealand and *F. crassispinus* from Western Australia. However, due to difficulty on obtaining extra data or more representatives for these species it is preferable to consider them as conspecific till further investigations. The diversity on species of Squalidae shows to be much greater and complex than previously thought and that studies on the taxonomy of its species underestimated its variations in different regions of the world.

Geographical distribution of species of *Squalus* and *Flakeus*. Species of *Squalus* and *Flakeus* have occurrences in Oceans from all over the world, including tropical (e.g. *F. probatovi, Flakeus* sp. 2, *Flakeus* sp. 3), antitropical (e.g. *S. acanthias, S. wakiyae, F. mitsukurii, F. montalbani, F. brevirostris*) and antiequatorial (e.g. *F. blainvillei, F. melanurus, F. albifrons, F. crassispinus, F. grahami*) waters as well as but less evident in equatorial regions (e.g. *F. cubensis, F. hemipinnis*).

Four nominal species are considered to have wide geographical distribution in areas outside and far from its type locality: *Squalus acanthias*, *S. mitsukurii*, *S. megalops* and *S. blainvillei* (Bigelow & Schroeder, 1957; Garrick, 1960; Bass *et al*., 1976; Compagno, 1984; Compagno & Niem, 1998; Compagno, 2002; Compagno *et al*., 2005; Figueirêdo, 2011). In contrast, the current study points out that these species exhibit certain degree of endemism, with exception to *S. acanthias*. Last *et al*. (2007), Naylor *et al*. (2012a) supported *F. megalops* as endemic to Australian waters, which it is in agreement with the current results. Specimens from coast off Southern Africa and Brazil, and Mediterranean Sea are addressed to be different species. The occurrence of *F. mitsukurii* in South Atlantic, Central Atlantic and Western Indian Oceans (e.g. Compagno, 1984; Compagno, 2002; Compagno *et al*., 2005;

Sáez *et al*., 2010; Ebert *et al*., 2013a) are equivocated. *Flakeus* sp. 2, *Flakeus* sp. 4, and *Flakeus* sp. 5 are species that occurs in these areas and distinct from *F. mitsukurii*, indicating that the Japanese species have a more confined geographical distribution than previously reported in the literature. Last *et al*. (2007) and Duffy *& Last* (2007b) made similar observations when recognizing *F. montalbani, F. grahami,* and *F. griffini* in Southwestern Pacific Ocean instead of *F. mitsukurii* as it is also supported in the present analysis. *Flakeus blainvillei* have distribution restrict to the Mediterranean Sea and its occurrence in other regions of the Atlantic Ocean are refuted by recognizing *F. probatovi* and *Flakeus* sp. 6 in the present study in Northeast coast off Africa and West Indian Ocean, and South Brazilian coast.

Flakeus hemipinnis, F. melanurus, F. bucephalus, and *F. lalannei* are species with remote distributions, indicating high degree of endemism in Squalidae. *Squalus suckleyi, S. wakiyae, Flakeus griffini, F. montalbani*, *F. raoulensis*, *F. grahami*, *F. notocaudatus*, *F. acutipinnis, Flakeus* sp. 1, *Flakeus* sp. 2, *Flakeus* sp. 3, *Flakeus* sp. 4, *Flakeus* sp. 5, *Flakeus* sp. 6, and *Flakeus* sp. 7 present geographical distribution more restrict to an area or country. However, these species are mostly sympatric in the Southeast Pacific, Indo-Pacific and South Atlantic Oceans. Only three species, *S. acanthias*, *F. japonicus and F. albifrons* have distributions on both antitropical and antiequatorial areas. Disrupted geographical distributions of fishes in the Indo-Pacific region are often under discussion on literature and still intriguing for many scientists (e.g. Randall, 1981; Humphries & Parenti, 2001; Last & White, 2011). Comparative biogeographical studies in species of Squalidae are imperative to understand these patterns of distribution.

Phylogenetic studies. Despite of the diversity of species of Squalidae have advanced considerably in the past eight years of research, studies on the phylogeny of Squalidae have not accompanied the same rhythm. Shirai (1992) and Naylor *et al*. (2012b) are few examples for understanding interrelationships for *Squalus* and *Cirrhigaleus*. Inner relationships among its species were analyzed only recently with Naylor *et al*. (2012b) and comprises a modest and tentative phylogenetic arrangement of the family because only 14 species were included in the molecular analysis. *Flakeus megalops, F. brevirostris, F. acutipinnis* and *Flakeus* sp. 3 comprise a monophyletic group and sister-group of all remaining species of *Flakeus (*Naylor *et al*., 2012b). The current study supports this arrangement because these species share many characteristics of the external and skeletal morphology. *Flakeus cubensis*, similar morphologically to these four species as well, comprises a small polytomy with *Flakeus* sp. 2 and *Flakeus* sp. 4. These latter species are share characteristics with *F. montalbani* instead, indicating that the relationship between *F. cubensis* and its congeners needs to be reevaluated. *Flakeus japonicus* is monophyletic and sister-group to other species of *Flakeus*, which it is in agreement with the current taxonomic results that notices very particular morphological characteristics on this species.

Squalus wakiyae and many species of *Flakeus* such as *F. mitsukurii, F. blainvillei, F. melanurus, F. bucephalus, F. hemipinnis* were not yet incorporated in previous investigations. Future cladistics analyses on species of *Squalus* and *Flakeus* through molecular and/or morphological characters are urgent in order to elucidate the taxonomic classification of Squalidae at genera level and understand the natural history of the group.

Literature cited

Al-Badri, M. & Lawson, R. (1985) Contribution on the taxonomy of the spiny dogfish *Squalus acanthias* L. *Cybium*, 9 (4), 385–399.

Applegate, S.P. (1967) A survey of shark hard parts. *In:* Gilbert, P.W. & Mathewson, R.F. & Rall, D.P. (Eds.). *Sharks, skates and rays.* John Hopkins Press, Baltimore, pp. 37–67.

Artedi, P. (1738) *Genera Piscium. In quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis. Speciebus 242 ad Genera 52.* Ichthyologiæ pars III. Lugduni Batavorum, Apud Conradum Wishoff, 723 pp.

Avsar, D. (2001) Age, Size, reproduction and feeding of the spurdog (*Squalus acanthias* Linnaeus, 1758) in the South-eastern Black Sea. *Estuarine, Coastal and Shelf Science*, 52 (2), 269–278.

Baranes, A. (2003) Sharks from the Amirantes Islands, Seychelles, with a description of two new species of squaloids from the deep sea. *Israel Journal of Zoology*, 49, 33–65.

Bass, A.J., D'Aubrey, J.D. & Kistnasamy, N. (1976) Sharks of the east coast of southearn Africa. VI The families Oxynotidae, Squalidae, Dalatiidae and Echinorhinidae. *Investigational Report*, 45, Oceanographic Research Institute, Durban, 1–103.

Bass, A.J., Compagno, L.J.V. & Heemstra, P.C. (1986) Squaliformes. *In*: Smith, M.M. & Heemstra, P.C. (Eds.), *Smith's Sea Fishes*. Macmillan, Johannesburg, pp. 49–62.

Bigelow, H.B. & Schroeder, W.C. (1948) Sharks. *In*: J.Tee-Van *et al*. (Eds.), *Fishes of the Western North Atlantic. Part 1*. Memoir Sears Foundation for Marine Research, Yale University, New Haven, pp. 1–576.

Bigelow, H.B. & Schroeder, W.C. (1957) A study of the sharks of the suborder Squaloidea. *Bulletin of the Museum of Comparative Zoology at Harvard College in Cambridge*, 117 (1), 1–150.

Blainville, H. de (1816) *Prodrome d'une nouvelle distribution systématique du règne animal*. Bulletin de la Société Philomathique de Paris, 8, 121–124.

Bonaparte, C.L. (1832) *Saggio di una distribuzione metodica degli animali vertebrati a sangue freddo*. Giornale Arcadico di Scienze Lettere ed Arti, Roma, 86 pp.

Cadenat, J. & Blache, J. (1981) *Requins de Méditerranée et d'Atlantique (plus particulierment de La Côte Ocidentale d'Afrique)*. Fauna Tropicale ORSTOM, 330 pp.

Cervigón, F. & Alcalá, A. (1999) *Los peces marinos de Venezuela. Volume V*. Fundación Museo del Mar, Carracas, 230 pp.

Chen, C., Taniuchi, T. & Nose, Y. (1979) Blainville's dogfish, *Squalus blainville*, from Japan, with notes on *S. mitsukurii* and *S. japonicus*. *Japanese Journal of Ichthyology*, 26 (1), 26–42.

Compagno, L.J.V. (1984) *FAO Species Catalogue. Vo. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes*. FAO Fisheries Synopsis, Rome, 4 (125), 249 pp.

Compagno, L.J.V. (2002) Sharks. *In*: Carpenter, K.E. (Ed.), *The living marine resources of the Western Central Atlantic. Vol. 1. Introduction, molluscs, crustaceans, hagfishes, sharks, batoid fishes and chimaeras.* FAO Species identification guide for fishery purposes and American Society of Ichthyologists Special Publication, FAO, Rome, 5, pp. 357–505.

Compagno, L.J.V., Dando, M. & Fowler, S. (2005) *Sharks of the World – Princeton Field Guides*. Harper Collins Publishers Ltd., London, 368 pp.

Compagno, L.J.V., Ebert, D.A. & Smale, M.J. (1989) *Guide to the Sharks and Rays of Southern Africa*. Struik, Cape Town.

Compagno, L.J.V. & Niem, V.H. (1998) Several family accounts. *In*: Carpenter, K.E. & Niem, V.H. (Eds.). *Fao species identification guide for fishery purposes. The living marine resources of the western central pacific. Cephalopods, crustaceans, holothurans and sharks.* FAO, Senckenbergiana Biologica, Rome, 2, pp. 687–1396.

D'Aubray, J.D. (1964) Preliminary guide to the sharks found off the east coast of South Africa. *Oceanographic Research Institute, Investigational Report*, Durban 8, 1–95.

Demirhan, S.A. & Seyhan, K. (2007) Life history of spiny dogfish, *Squalus acanthias* (L. 1758), in the southern Black Sea. *Fisheries Research,* 85 (2007), 210–216.

Duffy, C.A.J. & Last, P.R. (2007a) Part 4 - *Squalus raoulensis* sp. nov., a new spurdog of the *megalops-cubensis* group from the Kermadec Ridge. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Dogfishes of the Genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, Hobart, 31–38.

Duffy, C.A.J. & Last, P.R. (2007b) Redescription of the Northern Spiny Dogfish *Squalus griffini* Phillipps, 1931 from New Zealand. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Dogfishes of the Genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, Hobart, pp. 91–100.

Duméril, A.H.A. (1865) Histoire naturelle des poissons ou ichthyologie générale. Tome Premier. I. Elasmobranches. Plagiostomes et Holocéphales ou Chimères. *Tableau élémentaire de l'histoire naturelle des animaux*, 1, 1–720.

Ebert, D.A. (2013) *Deep-sea cartilaginous fishes of the Indian Ocean*. Vol 1 – Sharks. FAO Species Catalogue for Fisheries Purposes No.8, Rome, FAO. 256 pp.

Ebert, D.A. (2015) Deep–Sea Cartilaginous Fishes of the Southeastern Atlantic Ocean. *FAO Species Catalogue for Fishery Purposes,* 9, 264 pp.

Ebert, D.A., Fowler, S. & Compagno, L.J.V. (2013a) *Sharks of the World: A Fully Illustrated Guide*. Wild Nature Press, London, 528 pp.

Ebert, D.A., HO, H.-C., White, W.T. & Carvalho, M.R. (2013b) Introduction to the systematics and biodiversity of sharks, rays, and chimaeras (Chondrichthyes) of Taiwan. *Zootaxa*, 3752, 5–19.

Ebert, D.A. & Stehmann, M.F.W. (2013) *Sharks, batoids and chimaeras from the North Atlantic*. FAO Species Catalogue for Fisheries Purposes No.7, Rome: FAO, 523 pp.

Ebert, D.A., White, W.T., Goldmann, K.J., Compagno, L.J.V., Daly-Engel, T.S. & Ward, R.D. (2010) Resurrection and redescriptions of *Squalus suckleyi* (Girard, 1854) from the North Pacific, with comments on the *Squalus acanthias* subgroup (Squaliformes: Squalidae). *Zootaxa*, 2612, 22–40.

Eschmeyer, W. N. & R. Fricke (Eds.) (2015) Catalog of fishes: genera, species, references. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp. Electronic version accessed on 20 June 2015.

Fernholm, B. & Wheeler, A. (1983) Linnaean fish specimens in the Swedish Museum of Natural History, Stockholm. *Zoological Journal of the Linnean Society*, 78, 199–286.

Figueiredo, J.L. (1977) *Manual de peixes marinhos do sudeste do Brasil. I. Introdução, Cações, raias e quimeras*. Museu de Zoologia da Universidade de São Paulo, São Paulo, 104 pp.

Figueiredo, J.L. (1981) Estudo das distribuições endêmicas de peixes da Província Zoogeográfica Marinha Argentina. Unpublished PhD Thesis. Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, 121 pp.

Figueirêdo, S.T.V. (2011) Revisão taxonômica e morfológica do gênero *Squalus* Linnaeus, 1758 do oceano Atlântico Sul Ocidental (Chondrichthyes: Squaliformes: Squalidae). Unpublished MSc Thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo, 348 pp.

Fourmanoir, P. & Rivaton, I. (1979) Poissons de la pente récifale externe de Nouvelle-Calédonie et des Nouvelles-Hébrides. *Cahiers de l'Indo–Pacifique*, 1(4), 405–443.

Fowler, H.W. (1941) Contributions to the biology of the Philippine archipelago and adjacent regions. The fishes of the groups Elasmocephalii, Holocephali, Isospondyli, and Ostariophysi obtained by the United States Fisheries Steamer "Albatross" in 1907 to 1910, chiefly in the Philippine islands and adjacent seas. *Bulletin of the United States National Museum*, 100, 1–879.

Fricke, R., Kulbicki, M. & Wantiez, L. (2011) Checklist of the fishes of New Caledonia, and their distribution in the Southwest Pacific Ocean (Pisces). *Stuttgarter Beiträge zur Naturkunde A*, Neue Serie 4, 341–463.

Gallucci, V.F., McFarlane & Bargmann, G.G. (2009) *Biology and management of dogfish sharks*. American Fisheries Society, Bethesda, Maryland, 435 pp.

Garman, S. (1913) *The Plagiostoma (sharks, skates and rays)*. Memoirs of the Museum of Comparative Zoology at Harvard College, 36, Cambridge, 515 pp.

Garrick, J.A.F. (1960) Studies on New Zealand Elasmobranchii. Part XII. The species of *Squalus* from New Zealand and Australia; and a general account and key to the New Zealand Squaloidea. *Transactions of the Royal Society of the New Zealand*, 88 (3), 519–557.

Garrick, J.A.F. (1961) A note on the spelling of the specific name of immaculate spiny dogfish *Squalus blainvillei* (Risso, 1826). *Transactions of the Royal Society of the New Zealand*, 88(4), 843.

Gomes, U.L., Lima, M.C., Paragó, C. & Quitans, A.P. (1997) *Catálogo das coleções ictiológicas do Departamento de Biologia Animal e Vegetal*. Instituto de Biologia da Universidade Estadual do Rio de Janeiro, Rio de Janeiro, Gráfica UERJ, 185 pp.

Gomes, U.L., Signori, C.N., Gadig, O.B.F. & Santos, H.R.S. (2010) *Guia para Identificação de Tubarões e Raias do Rio de Janeiro*. Technical Books, Rio de Janeiro, 234 pp.

Gracan, R., Lazar, B., Posavec, I., Gregorovic, G. & Lackovic, G. (2013) Maturation, fecundity and reproductive cycle of spiny dogfish, *Squalus acanthias*, in the Adriatic Sea. *Marine Biology Research*, 9 (2), 198–207.

Heemstra, P.C. & Heemstra, E. (2004) Coastal fishes of Southern Africa. National Inquiry Service Centre (NISC) and South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa. 420 pp.

Howell-Rivero, L. (1936a) Some new, rare and little-known fishes from Cuba. *Proceedings of Boston Society of Natural History*, 41, 41–76.

Howell-Rivero, L. (1936b) A new shark from Tasmania. *Occasional Papers of the Boston Society of Natural History*, 8, 267–268.

Humphries, C.J. & Parenti, L. (2001). *Cladistic biogeography: interpreting patterns of plant and animal distributions*, 2nd ed. Oxford University Press, Oxford, 188 pp.

Iglésias, S. P. (2012) *Chondrichthyans from the North-eastern Atlantic and the Mediterranean (A natural classification based on collection specimens, with DNA barcodes and standardized photographs).* Volume I, Provisional version 06, 83 pp.

Ishikawa, C. (1908) Description of a new species of squaloid shark from Japan. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 60, 71–73.

Jones, B.C. & Geen, G.H. (1976) Taxonomic Reevaluation of the Spiny Dogfish (*Squalus acanthias* L.) in the Northeastern Pacific Ocean. *Journal of the Fisheries Research Board of Canada*, 33 (11), 2500–2506.

Jordan, D.S. (1891) Relations of temperature to vertebrae among fishes. *Proceedings of The United States National Museum,* 14, 107–120.

Jordan, D.S. & Evermann, B.W. (1896) The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. *Bulletin of the United States National Museum*, 47, 1–1240.

Jordan, D.S. & Snyder, J.O. (1903) *Squalus*. *In*: Jordan, D.S. & Fowler, H.W. (Eds) A review of the Elasmobranchiate fishes of Japan. *Proceedings of the United States National Museum,* 26 (1324), 593–674.

Kondyurin, V.V. & Myagkov, N.A. (1979) Status of spiny dogfish, *Squalus acutipinnis* Regan, 1908 (Squalidae, Squaliformes), from the South African Waters. *Zoological Zhurnal,* 58 (10), 1604–1606.

Kondyurin, V.V. & Myagkov, N.A. (1984) Sharks of the genus *Squalus* of the western Atlantic ocean. *Journal of Ichthyology*, 24 (3), 118–121.

Krefft, G. (1968) Knorpelfische (Chondrichthyes) aus dem tropischen Ostatlantik. *Atlantide Reports,* 10, 33–81.

Last, P.R., Edmunds, M. & Yearsley, G.K. (2007a) Part 2 - *Squalus crassispinus* sp nov., a new spurdog of the *megalops-cubensis* group from the eastern Indian Ocean. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Dogfishes of the Genus Squalus (Squaloidea: Squalidae).* CSIRO Marine and Atmospheric Research Paper, 14, Hobart, pp. 11–22.

Last, P.R., Marshall , L.J. & White, W.T. (2007e) Part 8 - *Squalus nasutus* sp. nov, a new long-snouted spurdog of the *S. japonicus* group from the Indian Ocean. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Dogfishes of the Genus Squalus (Squaloidea: Squalidae).* CSIRO Marine and Atmospheric Research Paper, 14, Hobart, 83–90.

Last, P.R., Sèret, B. & Pogonoski, J.J. (2007b) Part 3 - *Squalus bucephalus* sp nov., a new short-snout spurdog from New Caledonia. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Dogfishes of the Genus Squalus (Squaloidea: Squalidae).* CSIRO Marine and Atmospheric Research Paper, 14, Hobart, 23–29.

Last, P.R. & Stevens, J.D. (1994) *Sharks and Rays of Australia*, 1st edition. CSIRO Publishing, Melborne, 513 pp.

Last, P.R. & Stevens, J.D. (2009) *Sharks and Rays of Australia*, 2nd edition. Harvard University Press, Cambridge, 644 pp.

Last, P.R. & White, W.T. (2011) Biogeographic patterns in the Australian chondrichthyan fauna. *Journal of Fish Biology*, 79 (5), 1193–1213.

Last, P.R., White, W.T. & Motomura, H. (2007d). Part 6 - A description of *Squalus chloroculus* sp. nov., a new spurdog from southern Australia, and the resurrection of *S. montalbani* Whitley. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Dogfishes of the Genus Squalus (Squaloidea: Squalidae).* CSIRO Marine and Atmospheric Research Paper, 14, Hobart, 55–69.

Last, P.R., White, W.T. & Pogonoski, J.J. (2007) *Descriptions of new dogfishes of the genus Squalus (Squaloidea: Squalidae).* CSIRO Marine and Atmospheric Research Paper, 14, 130 pp.

Last, P.R., White, W.T. & Stevens, J. (2007c) Part 5 - New species of *Squalus* of the highfin *megalops* group from the Australasian region. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New*

Dogfishes of the Genus Squalus (Squaloidea: Squalidae). CSIRO Marine and Atmospheric Research Paper, 14, Hobart, 39–53.

Ledoux, J.C. (1970) Affinités et origines du *Squalus blainvillei* de Méditerranée. *Journées Ichthologique*, C.I.E.S.M., 65–69.

Lindberg, G.U. & Legeza, M.I. (1956) On two forms of spiny dogfish *Squalus acanthias* L. *Zoologicheskii Zhurnal*, 35 (11), 1685–1688 (In Russian).

Linnæus, C. (1746) *Fauna Svecica sistens animalia Sveciæ Regni: qvadrupedia, aves, amphibia, pisces, insecta, vermes, distributa per classes & ordines, genera & species. Cum differentiis specierum, synonymis autorum, nominibus incolarum, locis habitationum, descriptionibus insectorum*. Lugduni Batavorum (Wishoff), pp. 1–28, 1–411.

Linnæus, C. (1748) *Systema naturæ sistens regna tria naturæ, in classes et ordines, genera et species redacta tabulisque æneis illustrata. Editio sexta, emendata et aucta*. Stockholmiæ. (Kiesewetter). pp. [1–3], 1–224.

Linnaeus, C. (1754) *Hans Maj:ts Adolf Frideriks vår allernådigste konungs naturalie samling innehållande Saelsynte och Fraemmande djur, som bevaras på kongl. lust-slottet Ulriksdahl; beskrevne och afritade samt på nådig befallning = Museum S:æ R:æ M:itis. Adolphi Friderici (...) in quo animalia rariora imprimis, et exotica: quadrupedia, aves, amphibia, pisces, insecta, vermes*. Stockholm, (Kongl. Tryckeriet), pp. [1–4], I-XXX [= 1–30], 1–95, [1–14].

Linnaeus, C. (1758) *Systema Naturae. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decimal, reformata.*. Tomus I, Sweden, Holmiae, 824 pp.

Macleay, W. (1881) A descriptive catalogue of Australian fishes. Part IV. *Proceedings of the Linnean Society of New South Wales*, 6 (2), 202–387.

Marouani, S., Chaâba, R., Kadri, H., Saidi, B., Bouain, A., Maltagliati, F., Last., P.R., Séret, B. & Bradai, M.N. (2012) Taxonomic research on *Squalus megalops* (Macleay, 1881) and *Squalus blainvillei* (Risso, 1826) (Chondrichthyes: Squalidae) in Tunisian waters (Central Mediterranean Sea). *Scientia Marina*, 76 (1).

McCullogh, A.R. (1927) Checklist of the fishes and fish-like animals of New South Wales. *Australian Zoologist*, 2 (3), 97–170.

McDowall, R.M. (2008) Jordan's and other ecogeographical rules, and the vertebral number in fishes. *Journal of Biogeography*, 35, 501–508.

Merrett, N.F. (1973) A new shark of the genus *Squalus* (Squalidae, Squaloidea) from the equatorial western Indian Ocean, with notes on the *Squalus blainvillei*. *Journal of Zoological Society of London*, 171, 93–110.

Molina, G.I. (1782) *Saggio sulla storia naturale del Chile, del Signor Abate Giovanni Ignazio Molina*. Bologna, Saggio Chile, 306 pp.

Müller, J. & Henle, J. (1841) *Systematische Beschreibung der Plagiostomen*. Berlim, 300 pp.

Muñoz-Chápuli, R. & Ramos, F. (1989) Morphological comparisons of *Squalus blainvillei* and *S. megalops* in the Eastern Atlantic, with notes on the genus. *Japanese Journal of Ichthyology*, 36 (1), 6–21.

Myagkov, N.A. & Kondyurin, V.V. (1986) Dogfishes *Squalus* (Squalidae), of the Atlantic Ocean and comparative notes on the species of this genus from other regions. *Journal of Ichthyology,* 27 (1), 1–18.

Nakabo, T. (2002) *Fishes of Japan with pictorial keys to the species*, English edition. Tokai University Press, Tokyo Japan, 1, 866 pp.

Nakabo, T. (2013) *Fishes of Japan with pictorial keys to the species*. Tokai University Press, Tokyo Japan. 3rd Ed., 1, 864 pp.

Naylor, G.J.P., Caira, J.N., Jensen, K., Rosana, A.M., White, W. T. & Last, P.R. (2012a) A DNA sequence-based approach to the identification of shark and rays species and its implication of global elasmobranch diversity and parasitology. *Bulletin of the American Museum of Natural History*, 367, 262 pp.

Naylor, G. J. P., Caira, J.N., Jensen, K., Rosana, A.M., Straube, N. & Lakner, C. (2012b) Elasmobranch Phylogeny: A mitochondrial estimate based on 595 species. *In*: Carrier, J.C., Musick, J.A., & Heithaus, M.E. (Eds.). *Biology of Sharks and their relatives.* 2nd ed., CRC Press., pp. 31–56.

Oddone, M.C. & Paesch, L. & Norbis, W. (2015) Population structure of the piked dogfish *Squalus acanthias* (Elasmobranchii: Squalidae), with preliminary reproductive observations. *Ichthyological Research,* 62 (4), 463–473.

Orlov, A.M., Savinykh, V.F., Kulish, E.F. & Pelenev, D.V. (2012a) New data on the distribution and size composition of the North Pacific spiny dogfish *Squalus suckleyi* (Girard, 1854). *Scientia Marina,* 76 (1), 111–122.

Orlov, A.M., Shubin, O.A., Vinnikov, A.V., Mukhametov, I.N. & Kulish, E.F. (2012b) New data on the North Pacific Spiny Dogfish Squalus suckleyi (Squalidae, Chondrichthyes) from the Pacific Ocean off Kuril Islands and Kamchatka. *Problems of Fisheries*,13 (49), 41–70.

Parin, N. (1988) Species of spiny dogfish of genus *Squalus,* living on Southeastern Pacific Ocean Seamounts. *Scripta Technica Inc,* UDC 597.3.57.06, 43–50.

Phillipps, W.J. (1931) New species of piked dogfish. *New Zealand Journal of Science and Technology*, 12 (6), 360–361.

Phillipps, W.J. (1946) Sharks of New Zealand. *Dominion Museum Records*, 1 (2), 5–20.

Rafinesque, C.S. (1810) *Indice d'ittiologia siciliana; ossia, catalogo metodico dei nomi latini, italiani, e siciliani dei pesci, che si rinvengono in Sicilia disposti secondo un metodo naturale e seguito da un appendice che contiene la descrizione de alcuni nuovi pesci sicilian*. Messina, 70 pp.

Randall, J.E. (1981) Examples of Antitropical and Antiequatorial Distribution of Indo-West-Pacific Fishes. *Pacific Science*, 35 (3), 197–209.

Regan, C.T. (1908a) A synopsis of the sharks of the family Squalidae. *Op. cit,* 8 (2), 39–57.

Regan, C. T. (1908b) A collection of fishes from the coasts of Natal, Zululand, and Cape Colony. *Annals of the Natal Museum,* 1 (3), 241–255.

Regan, C. T. (1921) New fishes from deep water off the coast of Natal. *Annals and Magazine of Natural History* (Series 9), 7 (41), 412–420.

Reiss, K.L. & Bonnan, M.F. (2010) Ontogenetic Scaling of Caudal Fin Shape in *Squalus acanthias* (Chondrichthyes, Elasmobranchii): A Geometric Morphometric Analysis with Implications for Caudal Fin Functional Morphology. *The Anatomical Record*, 293, 1184–1191.

Risso, A. (1826) *Histoire Naturelle des principales productions de L' Europe Meridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes*. Tomo III, Paris, 480 pp.

Saéz, S., Pequeño, G. & Lamilla, L. (2010) Clave taxonômica cel Superordem Squalomorphi de Chile (Pisces: Elasmobranchii). *Revista de Biología Marina y Oceanografía*, 45 (1), 619–634.

Shinohara, G., Nakae, M, Ueda, Y., Kojima, S. & Matsuura, K. (2014) Annotated checklist of deep-sea fishes of the Sea of Japan. In: Fujita, T. (ed.): Deep-sea fauna of the Sea of Japan. *National Museum of Nature and Science Monographs*, 44, 225–291.

Shirai, S. (1992) *Squalean phylogeny: a new framework of "squaloid" sharks and related taxa*. Hokkaido University Press. Sapporo, 151 pp.

Smith, H.M. (1912) The squaloid sharks of the Philippine Archipelago, with descriptions of new genera and species. *Proceedings of the United States National Museum*, 41, 677–685.

Smith, J. L. B. (1961) *The Sea Fishes of Southern Africa*. 4th Edition. Central News Agency, Cape Town.

Springer, V.G. & Garrick, J.A.F. (1964) A survey of vertebral numbers in sharks. *Proceedings of the United States National Museum*, 116 (3496), 73–96.

Straube, N., White, W.T., HO, H.-C., Rochel, E., Corrigan, S., Li, C. & Naylor, G.J.P. (2013) A DNA sequence-based identification checklist for Taiwanese chondrichthyans. *Zootaxa*, 3752, 256–278.

Tanaka, S. (1917) Figures and descriptions of the fishes of Japan, including the Riukiu Islands, Bonin Islands, Formosa, Kurile Islands, Korea, and southern Sakhalin. *Figures and Descriptions of the Fishes of Japan*, 26, 455–474.

Vaillant, L.L. (1888) Poissons. *In: Mission scientifique du Cap Horn, 1882-83. Zoologie*, Gauthier-Villars et Fils, Imprimeurs-Libraires, Paris, 6, 1–35.

Veríssimo, A. & MacDowell, J.R. & Graves, J.E. (2010) Global population structure of the spiny dogfish Squalus acanthias, a temperate shark with an antitropical distribution. *Molecular Ecology*, 19 (8), 1651–1662.

Viana & Carvalho, *in press*. Redescription of *Squalus acutipinnis* Regan, 1908, a valid species of spiny dogfish from Southern Africa (Chondrichthyes: Squaliformes: Squalidae). *Copeia*.

Viana *et al*., *in prep*. Taxonomic and morphological revision of the genus *Squalus* Linnaeus, 1758 from the Southwestern Atlantic Ocean. *Zootaxa*.

Ward, R.D., Holmes, B.H., Zemlak, T.S. & Smith, P.J. (2007) DNA barcoding discriminates spurdogs of the genus *Squalus*. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.). *Descriptions of new dogfishes of the genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, pp. 117–130.

Wheeler, A. C. (1987) Peter Artedi, founder of modern ichthyology. *In*: S. O.Kullander & B. Fernholm (Eds). *Proceedings Fifth Congress of European Ichthyologists*, Stockholm, 3–10.

Wheeler, A. C. (1991) The Linnaean fish collection in the Zoological Museum of the University of Uppsala. *Zoological Journal of the Linnean Society*, 103 (2), 145–195.

White, W.T. & Iglésias, S.P. (2011) *Squalus formosus*, a new species of spurdog shark (Squaliformes: Squalidae), from the Western North Pacific Ocean. *Journal of Fish Biology*, 1–15.

White, W.T. & Last, P.R. (2012) A review of the taxonomy of chondrichthyan fishes: a modern perspective. *Journal of Fish Biology*, 80 (5), 901–917.

White, W.T. & Last, P.R. (2013) Notes on shark and ray types at the South China Sea Fisheries Research Institute (SCSFRI) in Guangzhou, China. *Zootaxa*, 3752, 228–248.

White, W.T., Last, P.R. & Stevens, J.D. (2007c). Part 7 - Two new species of *Squalus* of the *mitsukurii* group from the Indo-Pacific. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Dogfishes* *of the Genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, Hobart, 71–81.

White, W.T., Last, P.R. & Yearsley, G.K. (2007b) Part 10 - *Squalus hemipinnis* sp. nov, a new short-snouted spurdog from eastern Indonesia. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Dogfishes of the Genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, Hobart, 101–108.

White, W.T., Vaz, D.F.B., HO, H.-C., Ebert, D.A., Carvalho, M.R., Corrigan, S., Rochel, E., Carvalho, M., Tanaka, S. & Naylor, G.J.P. (2015) Redescription of Scymnodon ichiharai Yano and Tanaka 1984 (Squaliformes: Somniosidae) from the western North Pacific, with comments on the definition of somniosid genera. *Ichthyological Research*, 62 (2), 213–229.

White, W.T., Yearsley, G.K. & Last, P.R. (2007a) Clarification of the status of *Squalus tasmaniensis* and a diagnosis of *Squalus acanthias* from Australia, including a key to the Indo-Australasian species of *Squalus*. *In*: Last, P.R., White, W.T. & Pogonoski, J.J. (Eds.), *Descriptions of New Dogfishes of the Genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research Paper, 14, Hobart, 109–115.

Whitley, G.P.(1939) Taxonomic notes on sharks and rays. *Australian Zoologist*, 9 (3), 227–262.

Whitley, G.P. (1940) *The fishes of Australia. Part 1. The sharks, rays, devil fishes and other primitive fishes of Australia and New Zealand*. Royal Zoological Society of New South Wales, Sydney, 230 pp.

Whitley, G.P. (1964) A survey of Australian Ichthyology. *Proceedings of the Linnean Society of New South Wales*, 89 (1), 11–127.

Wilga, C.D. & Motta, P.J. (1998) Conservation and variation in the feeding mechanism of the spiny dogfish *Squalus acanthias*. *The Journal of Experimental Biology*, 201, 1345–1358.

Yuanding, Z. (= Chu, Y.T.), Meng, Q.W. & Li, S. (1984) Description of a new species of Squalidae of China. *Oceanologia et Limnologia Sinica*, 15 (4), 283–286. English version.

Yuanding, Z. & Qingwen, M. (2001) *Faina Sinica – Cyclostomata, Chondrichthyes*. Science Press, Beijing, 552 pp.

Table 10. External measurements of lectotype and paralectotypes of *Squalus acanthias* expressed as percentage of the total length (% TL). Total length is expressed in milimeters. Values for non-type specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	Lectotype	Paralectotypes			Baltic Sea				Northeastern Atlantic				Mediterranean Sea			
	NRM 85	UUZM 159	UUZM 160	UUZM 287	N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD
TL (mm)	177.0	346.0	380.0	700.0	7	158.0 - 715.0	400.3	209.2	31	158.0 - 875.0	442.5	225.4	7	208.0 - 620.0	390.1	165.1
PCL	75.9	78.0	73.4	85.7	7	76.1 - 80.8	78.9	1.4	31	70.4 - 80.9	77.9	2.0	7	77.8 - 79.6	78.9	0.7
PD2	59.3	59.2	56.6	70.4	7	58.5 - 65.1	60.9	2.2	31	52.9 - 63.3	59.0	2.6	7	57.9 - 61.0	59.5	1.2
PD1	34.8	31.6	30.8	37.9	7	32.9 - 34.8	33.9	0.7	31	26.4 - 52.3	34.2	4.4	7	31.8 - 33.9	33.1	0.8
SVL	49.4	51.7	52.6	59.3	7	50.5 - 54.7	52.2	1.7	31	40.9 - 53.8	50.2	2.7	7	47.3 - 52.1	50.5	1.8
PP2	47.3	48.3	48.4	54.3	7	48.2 - 52.1	43.3	16.7	31	30.7 - 50.8	47.2	3.9	7	45.9 - 49.0	47.9	1.3
PP1	22.9	20.9	19.9	19.5	7	18.2 - 22.9	21.0	1.4	31	16.5 - 23.0	20.5	1.5	7	19.8 - 22.6	21.1	1.1
HDL	23.4	21.6	21.1	19.5	7	19.2 - 23.3	21.6	1.2	31	17.1 - 23.6	21.1	1.5	7	20.6 - 23.0	21.8	1.0
PG1	20.2	18.3	16.7	15.7	7	16.1 - 19.7	18.0	1.1	31	14.5 - 21.3	17.7	1.5	7	16.9 - 18.8	17.9	0.8
PSP	13.2	11.4	12.3	10.2	7	10.0 - 13.2	11.9	1.1	31	9.7 - 14.3	11.7	1.3	7	10.7 - 13.2	11.8	1.0
POB	8.0	6.4	6.9	5.7	7	5.8 - 7.9	7.1	0.7	31	5.7 - 8.6	7.2	0.8	7	6.2 - 8.1	6.9	0.6
PRN	5.2	4.2	4.5	4.2	7	3.8 - 5.3	4.7	0.6	31	3.7 - 5.8	4.7	0.6	7	4.2 - 5.5	4.7	0.4
POR	10.4	9.4	9.0	7.0	7	7.9 - 10.9	9.7	1.1	31	7.5 - 11.9	9.6	1.3	7	8.9 - 10.5	9.8	0.6
INLF	6.0	4.7	5.2	3.3	7	3.8 - 5.2	4.6	0.5	31	2.9 - 5.9	4.6	0.7	7	4.3 - 5.4	4.9	0.4
MOW	7.6	7.5	7.4	6.2	7	6.3 - 7.3	6.9	0.3	31	6.4 - 8.0	7.1	0.4	7	5.9 - 7.7	7.0	0.6
ULA	2.8	2.4	3.3	1.6	7	2.0 - 3.3	2.4	0.5	31	1.8 - 3.0	2.4	0.3	7	1.9 - 2.3	2.2	0.2
INW	3.9	3.0	3.4	2.2	7	3.0 - 3.7	3.5	0.2	31	2.6 - 8.4	3.6	1.0	7	3.3 - 4.1	3.5	0.3
INO	9.2	7.6	6.9	5.3	7	6.5 - 9.1	7.9	0.9	31	5.3 - 10.3	7.5	1.1	7	6.8 - 9.0	7.7	0.8
EYL	5.3	5.0	3.8	3.6	7	3.5 - 6.1	4.5	0.8	31	2.8 - 5.8	4.1	0.8	7	3.5 - 5.0	4.3	0.6
EYH	3.2	2.2	0.6	1.5	7	1.7 - 4.6	2.8	1.0	31	1.4 - 4.1	2.3	0.7	7	1.2 - 3.4	2.1	0.8
SPL	1.8	1.5	1.1	1.2	7	0.9 - 2.4	1.6	0.5	31	0.9 - 2.2	1.5	0.4	7	0.9 - 1.9	1.3	0.5
GS1	1.5	1.6	1.3	1.8	7	1.5 - 2.2	1.8	0.3	31	1.2 - 2.3	1.7	0.3	7	1.2 - 2.3	1.7	0.3
GS5	2.1	2.0	1.4	2.6	7	2.0 - 2.8	2.2	0.3	31	1.7 - 2.5	2.1	0.2	7	1.9 - 2.4	2.1	0.2
IDS	17.9	19.3	21.2	26.4	7	18.0 - 23.7	19.8	2.0	31	16.1 - 23.0	19.7	1.8	7	18.5 - 20.4	19.6	0.7
DCS	11.2	11.5	11.7	10.6	7	9.8 - 11.7	10.9	0.7	31	10.0 - 13.0	11.3	0.7	7	10.0 - 12.5	11.0	0.8
PPS	22.3	22.7	27.5	28.6	7	21.3 - 27.6	24.2	2.4	31	17.9 - 28.8	23.1	2.4	7	21.4 - 24.1	22.7	1.2
PCA	20.5	23.0	22.4	24.3	7	20.4 - 23.3	22.1	0.9	31	19.6 - 24.3	22.0	1.0	7	20.9 - 23.8	22.5	1.2
D1L	12.1	12.5	12.0	9.7	7	11.0 - 13.7	12.0	1.0	31	10.2 - 13.8	11.9	0.7	7	10.6 - 12.3	11.8	0.6
D1A	9.3	10.6	9.3	6.9	7	8.2 - 10.7	9.6	0.8	31	8.1 - 11.6	9.8	0.9	7	9.3 - 10.4	9.9	0.4
D1B	6.9	7.4	7.2	6.3	7	6.5 - 7.9	7.2	0.6	31	5.6 - 8.0	6.9	0.5	7	6.5 - 7.5	6.8	0.3
D1H	6.6	6.6	7.9	4.2	7	5.9 - 7.5	6.8	0.6	31	5.5 - 7.7	6.7	0.5	7	6.5 - 7.1	6.8	0.2
D1I	5.3	5.3	6.5	4.2	7	4.7 - 5.8	5.1	0.4	31	4.5 - 5.7	5.1	0.3	7	4.1 - 5.5	5.0	0.5
D1P	5.8	5.7	4.1	4.8	7	5.2 - 7.6	6.6	0.8	31	5.1 - 8.7	6.7	0.9	7	4.7 - 7.6	6.3	1.0
D1ES	1.2	2.4	2.7	1.7	6	1.2 - 2.3	1.8	0.4	30	1.3 - 2.8	2.0	0.4	7	1.2 - 2.6	1.9	0.5
D1BS	0.5	0.5	0.7	0.5	7	0.4 - 1.1	0.7	0.3	31	0.4 - 1.1	0.6	0.2	7	0.4 - 0.8	0.5	0.2
D2L	11.8	13.5	14.4	9.5	7	10.9 - 13.6	11.7	0.9	31	10.4 - 12.9	12.0	0.6	7	11.3 - 12.9	12.3	0.6
D2A	9.8	9.8	10.5	6.8	7	8.1 - 10.5	9.2	0.9	31	7.7 - 10.8	9.4	0.7	7	8.8 - 10.5	9.8	0.6
D2B	7.1	7.8	9.8	5.8	7	6.4 - 8.6	7.0	0.7	31	6.1 - 8.3	7.2	0.6	7	6.5 - 8.3	7.5	0.7
D2H	4.7	5.3	4.3	1.7	7	4.4 - 6.5	5.5	0.7	31	4.1 - 6.0	5.1	0.6	7	4.0 - 5.6	5.1	0.6
D2I	4.6	4.5	5.6	3.9	7	4.1 - 4.9	4.5	0.2	31	4.2 - 5.6	4.9	0.3	7	4.1 - 5.4	4.7	0.4
D2P	5.9	5.4	5.4	3.6	7	4.5 - 5.6	5.2	0.4	31	4.1 - 6.1	5.0	0.5	7	4.1 - 5.5	4.9	0.5
D2ES	2.4	4.6	4.4	3.3	6	2.6 - 4.3	3.2	0.7	28	2.1 - 4.9	3.4	0.6	7	2.8 - 4.3	3.7	0.6
D2BS	0.9	1.0	0.9	0.8	6	0.5 - 1.4	0.9	0.3	31	0.5 - 1.3	0.8	0.2	7	0.7 - 1.3	0.9	0.3
P1A	11.2	13.1	16.7	11.2	7	10.9 - 15.3	13.2	1.6	31	11.5 - 16.1	13.5	1.4	7	11.3 - 14.8	13.1	1.4
P1I	7.2	7.2	8.5	5.7	7	6.9 - 8.9	7.8	0.6	31	6.8 - 9.5	7.9	0.6	7	6.8 - 8.6	7.7	0.7
P1B	4.1	4.9	4.9	4.5	7	3.5 - 4.9	4.4	0.6	31	3.0 - 5.2	4.3	0.5	7	3.7 - 5.1	4.4	0.5
P1P	6.9	8.9	9.9	5.3	7	7.1 - 11.2	8.8	1.5	31	5.4 - 11.9	8.5	1.3	7	6.3 - 9.3	8.0	1.1
P2L	9.3	10.4	9.9	9.2	7	8.5 - 11.5	9.7	1.0	31	8.0 - 11.7	9.9	0.9	7	8.3 - 11.0	9.8	1.2
P2I	4.7	4.5	4.8	4.6	7	3.9 - 5.9	4.6	0.7	31	3.4 - 6.0	4.6	0.6	7	3.7 - 5.2	4.5	0.6
CDM	21.0	20.1	25.9	16.4	7	19.3 - 21.3	19.9	0.7	31	18.8 - 23.0	20.7	1.0	7	18.8 - 21.1	20.2	0.8
CPV	11.6	10.5	13.7	7.8	7	9.9 - 11.5	10.8	0.5	31	10.0 - 12.7	11.1	0.7	7	9.7 - 10.8	10.3	0.4
CFW	8.2	6.1	6.8	5.3	7	6.1 - 8.0	7.0	0.7	31	5.9 - 7.6	6.7	0.5	7	5.5 - 7.1	6.4	0.6
HANW	7.8	6.7	6.4	4.3	7	5.9 - 7.7	6.7	0.6	31	5.2 - 7.8	6.4	0.7	7	5.8 - 7.4	6.6	0.6
HAMW	10.9	9.6	8.5	8.5	7	8.2 - 11.3	9.9	1.0	31	8.5 - 11.3	9.7	0.7	7	8.3 - 11.0	9.7	0.9
HDW	11.4	10.6	7.7	9.6	7	9.4 - 11.3	10.7	0.6	31	9.1 - 12.1	10.8	0.6	7	8.5 - 11.5	10.6	1.0
TRW	8.9	7.4	3.9	10.3	7	7.9 - 9.9	8.6	0.7	31	6.4 - 12.5	9.3	1.3	7	6.7 - 10.0	8.7	1.2
ABW	5.8	8.4	6.9	7.8	7	6.1 - 10.6	7.9	1.6	31	6.3 - 13.5	8.6	1.5	7	6.7 - 9.9	7.7	1.1
HDH	9.5	9.9	5.2	9.5	7	8.4 - 9.7	9.0	0.5	31	7.1 - 11.2	8.8	1.1	7	7.3 - 9.2	8.2	0.7
TRH	9.2	10.3	5.9	9.7	7	9.2 - 10.8	10.0	0.7	31	7.3 - 13.1	9.7	1.3	7	7.8 - 9.2	8.7	0.5
ABH	7.1	9.3	7.9	8.2	7	7.9 - 10.5	9.2	1.0	31	7.5 - 12.6	9.2	1.3	7	7.2 - 9.6	8.6	0.8
CLO	-	1.3	-	6.1	3	1.6 - 5.3	2.8	2.1	17	1.3 - 5.8	2.6	1.6	1	-	1.7	-
CLI	-	2.5	-	6.8	3	2.7 - 8.4	4.7	3.2	17	2.0 - 8.5	4.1	2.3	1	-	3.5	-

Table 11. External measurements of specimens of *S. acanthias* from other localities, including holotype of *S. barbouri* (MCZ 1463-S). Measurements are expressed as percentage of the total length (% TL) and total length in milimeters. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	Northwestern Atlantic*					Southeastern Atlantic				Southwestern Atlantic				Black Sea	
	MCZ 1463-S	N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD	N	*x*
TL (mm)	267.0	17	210.0 - 910.0	618.4	203.4	21	145.0 - 700.0	454.6	190.0	31	192.0 - 880.0	510.1	199.7	1	280.0
PCL	77.2	17	76.7 - 82.1	80.1	1.3	21	75.9 - 81.4	78.6	1.5	31	73.5 - 80.6	78.3	1.6	1	77.1
PD2	59.2	17	59.2 - 64.9	62.4	1.6	21	58.1 - 65.6	60.5	2.0	31	53.4 - 60.7	58.5	1.9	1	58.2
PD1	34.5	17	31.7 - 36.7	33.7	1.3	21	30.0 - 50.8	34.1	4.1	31	29.1 - 34.6	32.4	0.9	1	31.9
SVL	52.4	17	48.0 - 55.9	53.1	1.8	21	47.4 - 54.7	51.4	1.9	31	25.6 - 52.8	49.2	4.7	1	48.9
PP2	54.3	17	45.0 - 53.1	50.1	1.8	21	44.0 - 52.3	48.5	2.1	31	21.0 - 50.3	46.1	4.9	1	46.8
PP1	21.8	17	19.9 - 23.8	21.4	1.2	21	19.8 - 23.8	21.3	1.2	31	17.8 - 21.9	19.9	1.2	1	20.6
HDL	22.4	17	20.9 - 25.2	22.4	1.4	21	20.4 - 25.7	22.3	1.3	31	18.3 - 22.7	20.6	1.3	1	21.3
PG1	18.5	17	16.7 - 20.0	18.3	1.0	21	16.6 - 21.4	18.4	1.3	31	15.4 - 19.0	17.1	1.1	1	17.6
PSP	12.6	17	10.3 - 13.4	11.3	0.9	21	10.4 - 13.9	11.7	1.0	31	9.9 - 13.2	11.0	1.0	1	11.7
POB	7.0	17	5.8 - 8.2	6.9	0.7	21	6.4 - 8.8	7.1	0.6	31	5.8 - 7.8	6.8	0.5	1	7.4
PRN	5.1	17	3.9 - 5.2	4.6	0.4	21	4.1 - 5.4	4.6	0.3	31	3.8 - 5.2	4.4	0.4	1	4.5
POR	9.9	17	7.4 - 11.0	9.4	1.0	21	8.0 - 11.1	9.2	0.9	31	4.6 - 10.6	8.8	1.1	1	9.4
INLF	4.9	17	3.8 - 5.3	4.5	0.4	21	4.1 - 5.8	4.6	0.5	31	3.7 - 9.1	4.5	1.0	1	4.8
MOW	6.6	17	6.2 - 7.9	7.1	0.4	21	7.0 - 8.7	7.7	0.5	31	4.0 - 7.9	6.8	0.7	1	6.4
ULA	2.5	17	1.8 - 3.0	2.3	0.3	21	1.9 - 2.9	2.4	0.3	31	2.0 - 7.2	2.4	0.9	1	2.4
INW	2.8	17	3.0 - 3.7	3.4	0.2	21	2.9 - 4.6	3.6	0.5	31	2.8 - 4.1	3.3	0.3	1	3.8
INO	7.2	17	6.6 - 8.2	7.2	0.5	21	6.4 - 10.5	7.6	1.2	31	6.5 - 8.9	7.2	0.8	1	7.1
EYL	3.5	17	1.9 - 3.6	2.7	0.5	21	3.3 - 6.3	4.2	0.9	31	2.8 - 5.7	3.7	0.8	1	4.1
EYH	0.9	17	0.8 - 3.1	1.9	0.6	21	1.4 - 3.8	2.2	0.7	31	1.4 - 3.6	2.0	0.6	1	2.4
SPL	1.3	17	0.8 - 2.0	1.2	0.3	21	1.0 - 2.9	1.6	0.5	31	0.9 - 2.2	1.4	0.4	1	1.5
GS1	1.7	17	1.4 - 2.3	1.6	0.2	21	1.4 - 2.5	1.8	0.3	31	1.4 - 2.3	1.7	0.2	1	1.0
GS5	1.8	17	1.8 - 2.6	2.2	0.2	21	1.7 - 2.7	2.1	0.3	31	1.2 - 3.0	2.0	0.4	1	1.1
IDS	18.9	17	18.7 - 26.5	22.5	2.2	21	16.1 - 24.4	20.9	2.2	31	17.1 - 22.7	20.0	1.7	1	18.8
DCS	10.8	17	9.7 - 12.0	11.2	0.6	21	10.1 - 12.5	11.3	0.7	31	9.6 - 12.4	11.2	0.6	1	11.5
PPS	24.9	17	23.0 - 28.6	25.9	1.9	21	16.1 - 27.1	22.7	2.7	31	19.4 - 26.8	23.1	1.9	1	21.0
PCA	22.2	17	19.7 - 25.3	22.7	1.2	21	20.2 - 27.4	23.1	1.7	31	20.3 - 24.4	22.4	1.1	1	22.3
D1L	12.1	17	11.2 - 13.6	12.3	0.7	21	10.9 - 13.6	12.4	0.7	31	10.5 - 13.2	12.1	0.6	1	10.8
D1A	11.5	17	8.1 - 12.0	9.6	0.9	21	6.8 - 12.6	9.4	1.2	31	8.5 - 10.9	9.4	0.6	1	9.6
D1B	7.0	17	6.2 - 8.5	7.2	0.6	21	6.0 - 7.9	7.1	0.5	31	6.4 - 7.5	6.9	0.3	1	6.3
D1H	7.8	17	6.0 - 7.6	6.8	0.4	21	5.3 - 8.2	6.7	0.7	31	6.0 - 7.2	6.6	0.3	1	6.5
D1I	5.7	17	5.0 - 6.5	5.6	0.4	21	4.8 - 6.4	5.6	0.4	31	4.4 - 5.9	5.2	0.4	1	4.4
D1P	5.9	17	6.0 - 8.3	7.2	0.7	21	5.6 - 9.2	7.0	0.9	31	4.9 - 8.2	6.8	0.8	1	6.4
D1ES	2.7	15	1.6 - 3.1	2.0	0.4	18	1.2 - 3.1	2.0	0.5	25	1.5 - 6.6	2.3	1.0	1	1.6
D1BS	0.6	17	0.4 - 0.8	0.6	0.1	21	0.4 - 1.6	0.7	0.3	27	0.4 - 5.5	0.7	0.9	1	0.6
D2L	12.6	17	10.0 - 13.2	11.9	0.8	21	9.9 - 14.7	12.0	1.0	31	11.5 - 14.3	12.7	0.8	1	11.6
D2A	11.1	17	7.6 - 10.1	9.0	0.7	21	6.9 - 11.4	8.9	1.2	31	8.1 - 11.3	9.7	0.9	1	9.0
D2B	7.9	17	5.7 - 8.1	7.0	0.6	21	5.2 - 9.6	6.9	1.0	31	6.9 - 9.8	7.9	0.8	1	7.1
D2H	7.0	17	4.4 - 6.9	5.1	0.7	21	3.8 - 5.9	4.8	0.7	31	4.1 - 10.8	5.1	1.2	1	4.9
D2I	5.0	17	4.4 - 6.1	5.1	0.5	21	4.6 - 6.8	5.3	0.5	31	4.2 - 5.5	4.9	0.3	1	4.8
D2P	3.3	17	4.2 - 6.7	5.4	0.6	21	4.4 - 6.3	5.4	0.5	31	4.3 - 6.2	5.2	0.4	1	5.4
D2ES	4.3	16	2.5 - 4.1	3.4	0.5	20	3.0 - 4.9	3.7	0.7	31	1.9 - 4.3	3.4	0.5	1	3.3
D2BS	1.0	17	0.6 - 1.3	0.8	0.2	21	0.6 - 1.9	0.9	0.4	31	0.5 - 1.1	0.7	0.2	1	0.9
P1A	12.3	17	10.9 - 17.6	14.6	1.7	21	11.8 - 16.6	14.3	1.1	31	11.2 - 16.3	13.9	1.1	1	11.5
P1I	7.3	17	7.3 - 9.0	8.2	0.5	21	7.0 - 9.6	8.7	0.7	31	7.0 - 8.8	7.9	0.5	1	6.3
P1B	4.3	17	4.1 - 5.5	4.9	0.4	21	4.4 - 8.0	5.0	0.7	31	3.0 - 5.2	4.3	0.6	1	4.1
P1P	7.7	17	6.6 - 11.9	9.7	1.6	21	4.1 - 12.1	9.4	1.6	31	6.7 - 11.4	8.9	1.1	1	9.4
P2L	8.0	17	9.2 - 12.3	10.7	1.1	21	9.4 - 12.3	10.7	0.7	31	8.6 - 12.4	10.5	1.0	1	8.9
P2I	4.6	17	3.9 - 6.7	5.2	0.8	21	3.2 - 7.8	5.1	1.1	31	3.6 - 6.4	4.9	0.7	1	4.1
CDM	22.7	17	11.3 - 22.0	20.3	2.4	21	18.9 - 22.5	21.1	1.0	31	19.0 - 22.0	20.6	0.8	1	21.0
CPV	10.3	17	5.6 - 22.0	11.4	3.1	21	9.7 - 15.2	11.6	1.3	31	10.4 - 12.3	11.2	0.5	1	11.9
CFW	5.4	17	6.1 - 7.5	6.8	0.4	21	6.4 - 8.8	7.1	0.7	31	6.0 - 7.7	6.9	0.4	1	6.0
HANW	5.9	17	4.9 - 6.6	5.8	0.5	21	5.6 - 9.2	6.9	1.0	31	5.5 - 7.7	6.3	0.6	1	6.0
HAMW	7.3	17	8.1 - 10.5	9.1	0.6	21	8.7 - 12.3	10.0	1.0	31	8.1 - 10.7	9.5	0.6	1	8.9
HDW	7.8	17	9.1 - 12.5	10.8	0.8	21	10.5 - 12.6	11.4	0.7	31	8.3 - 12.6	10.6	0.8	1	9.2
TRW	7.2	17	7.1 - 11.1	8.8	1.3	21	7.8 - 11.7	9.6	1.2	31	6.6 - 11.2	8.9	1.1	1	8.0
ABW	4.1	17	5.4 - 8.8	7.0	1.0	21	5.3 - 9.9	7.5	1.3	31	5.6 - 11.1	7.9	1.2	1	6.5
HDH	6.5	17	5.7 - 10.0	8.9	1.0	21	7.3 - 10.1	8.6	0.7	31	6.7 - 10.0	8.5	0.9	1	7.0
TRH	6.4	17	6.9 - 11.3	9.3	1.2	21	7.9 - 11.8	9.2	1.0	31	6.8 - 11.1	9.3	1.1	1	7.2
ABH	4.9	17	6.1 - 10.5	8.3	1.3	21	6.9 - 11.4	8.2	1.1	31	6.4 - 11.9	9.1	1.4	1	7.2
CLO	-	9	1.3 - 6.7	4.6	2.4	13	1.2 - 6.7	3.7	1.9	17	1.1 - 6.6	3.8	2.0	1	1.5
CLI	-	9	1.4 - 9.6	6.6	3.3	13	2.7 - 9.3	5.8	2.3	17	2.2 - 9.1	5.6	2.6	1	2.4

*Data taken from Figueirêdo (2011).

Table 12. External measurements of specimens of *S. acanthias* from other localities, including holotype of *S. tasmaniensis* (MCZ 146-S), syntype of *S. kirki* (BMNH 1931.8.10.1) and types of *Acanthias lebruni*. Measurements are expressed as percentage of the total length (% TL) and TL is expressed in milimeters. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	Southwestern Pacific Ocean						Southeastern Pacific Ocean					
	MCZ 146-S	BMNH 1931.8.10.1	N	Range	*x*	SD	MNHN 1883-201	MNHN 1883-202	N	Range	*x*	SD
TL (mm)	245.0	785.0	17	217.0 - 993.0	569.6	258.6	268.0	295.0	3	190.0 - 795.0	551.7	319.4
PCL	77.6	80.5	17	71.1 - 80.4	78.4	2.2	78.0	78.6	3	76.3 - 82.1	80.1	3.2
PD2	57.1	61.9	17	55.9 - 61.9	59.6	1.5	57.1	58.6	3	55.6 - 64.8	61.3	5.0
PD1	30.6	31.3	17	30.9 - 35.9	33.0	1.2	29.6	32.1	3	32.3 - 34.3	33.5	1.1
SVL	49.0	51.6	17	50.2 - 54.4	54.7	10.2	47.9	50.8	3	48.0 - 54.5	51.1	3.2
PP2	44.9	47.4	17	47.2 - 51.4	51.9	10.2	44.3	47.5	3	45.7 - 50.7	48.3	2.5
PP1	19.6	19.7	17	18.6 - 23.3	20.9	1.3	21.1	20.8	3	20.8 - 21.8	21.4	0.6
HDL	19.9	21.3	17	19.8 - 23.7	21.6	1.2	21.0	20.7	3	22.0 - 23.1	22.5	0.6
PG1	16.4	15.8	17	16.3 - 19.8	18.0	1.1	17.7	17.2	3	17.9 - 19.3	18.6	0.7
PSP	9.8	9.7	17	9.8 - 13.4	11.5	1.1	11.9	11.4	3	10.8 - 12.2	11.4	0.7
POB	5.4	5.8	17	6.3 - 7.8	7.2	0.5	6.7	6.7	3	6.4 - 7.8	7.1	0.7
PRN	3.3	3.9	17	4.1 - 5.4	4.7	0.4	4.6	4.1	3	3.9 - 5.1	4.5	0.6
POR	7.6	7.6	17	7.8 - 11.1	9.3	1.1	9.6	9.1	3	8.3 - 10.6	9.2	1.3
INLF	3.6	4.0	17	3.8 - 5.5	4.5	0.5	5.0	4.2	3	4.0 - 5.1	4.4	0.6
MOW	5.6	6.7	17	6.6 - 8.5	7.3	0.5	7.2	6.6	3	7.0 - 7.6	7.3	0.3
ULA	2.2	2.0	17	1.8 - 2.9	2.3	0.3	2.4	2.2	3	2.0 - 7.8	4.1	3.3
INW	3.2	2.9	17	3.1 - 4.0	3.5	0.3	3.1	3.3	3	3.1 - 3.5	3.3	0.2
INO	6.2	6.3	17	6.3 - 8.7	7.5	0.8	7.6	7.5	3	6.6 - 8.5	7.4	1.0
EYL	3.1	3.4	17	2.6 - 5.8	3.7	1.0	4.8	4.3	3	2.0 - 4.6	3.0	1.4
EYH	1.6	1.1	17	1.4 - 3.5	2.0	0.6	1.5	1.4	3	1.4 - 2.9	1.9	0.8
SPL	1.8	0.9	17	0.8 - 1.9	1.3	0.4	1.6	1.3	3	0.9 - 1.7	1.3	0.4
GS1	1.0	1.8	17	1.5 - 2.1	1.8	0.2	1.6	1.6	3	1.4 - 1.8	1.6	0.2
GS5	1.6	1.7	17	1.5 - 2.8	2.2	0.3	1.6	1.7	3	2.0 - 2.3	2.1	0.1
IDS	19.9	21.1	17	18.2 - 21.7	20.2	1.1	19.0	19.4	3	17.8 - 24.6	22.3	3.9
DCS	11.9	11.6	17	9.9 - 12.8	11.2	0.7	12.1	12.8	3	11.2 - 12.5	11.7	0.7
PPS	22.2	24.5	17	18.3 - 27.6	23.5	2.4	18.8	20.8	3	19.9 - 27.6	24.2	3.9
PCA	22.4	23.2	17	20.8 - 23.3	22.0	0.8	22.5	24.2	3	22.9 - 23.3	23.1	0.2
D1L	13.2	13.0	17	11.6 - 13.9	12.6	0.6	12.8	11.8	3	12.0 - 13.6	12.7	0.8
D1A	11.2	9.6	17	9.0 - 11.4	10.0	0.7	10.5	9.6	3	8.8 - 10.4	9.8	0.9
D1B	7.9	8.6	17	6.6 - 11.1	7.5	1.0	7.8	6.9	3	7.2 - 8.7	8.0	0.8
D1H	6.9	6.3	17	5.9 - 8.0	6.9	0.6	6.8	6.8	3	5.8 - 6.9	6.4	0.6
D1I	5.8	4.7	17	4.5 - 5.7	5.3	0.3	5.0	4.8	3	4.6 - 5.2	4.9	0.3
D1P	6.2	7.3	17	5.4 - 8.8	7.2	0.8	5.1	5.7	3	6.3 - 8.4	7.0	1.2
D1ES	2.4	2.5	17	1.2 - 2.7	2.0	0.4	1.9	2.2	3	0.8 - 1.7	1.3	0.4
D1BS	0.9	0.5	17	0.4 - 0.8	0.5	0.1	0.4	0.6	3	0.4 - 0.8	0.6	0.2
D2L	13.1	12.7	17	11.3 - 13.8	12.7	0.7	13.6	13.1	3	10.8 - 11.9	11.2	0.6
D2A	10.0	8.5	17	8.2 - 10.9	9.6	0.8	10.3	9.6	3	6.8 - 8.9	8.0	1.1
D2B	7.8	8.0	17	6.7 - 9.2	7.9	0.8	9.1	8.7	3	5.8 - 7.5	6.8	0.9
D2H	5.9	3.6	17	4.2 - 6.0	4.8	0.5	4.4	5.2	3	3.7 - 5.1	4.4	0.7
D2I	5.5	4.6	17	4.1 - 5.3	4.8	0.4	4.6	4.5	3	4.3 - 4.9	4.6	0.3
D2P	5.6	5.8	17	4.7 - 6.1	5.4	0.5	5.1	4.6	3	4.7 - 5.9	5.3	0.6
D2ES	4.4	2.6	17	2.7 - 4.4	3.4	0.6	4.0	3.8	3	1.5 - 3.0	2.5	0.8
D2BS	1.1	0.6	17	0.5 - 1.2	0.7	0.2	0.6	0.6	3	0.6 - 0.9	0.7	0.2
P1A	13.1	13.9	17	12.6 - 16.8	14.8	1.0	13.2	13.6	3	11.7 - 15.3	13.7	1.9
P1I	8.7	7.4	17	5.9 - 9.8	8.1	0.9	7.4	7.5	3	7.5 - 8.4	7.9	0.4
P1B	4.2	4.6	17	3.9 - 5.3	4.7	0.4	4.3	4.6	3	3.4 - 5.4	4.4	1.0
P1P	10.0	7.9	17	6.4 - 11.0	9.0	1.3	6.3	6.8	3	7.6 - 10.8	9.7	1.9
P2L	9.4	11.9	17	9.2 - 11.9	10.7	0.7	9.8	10.4	3	8.8 - 11.4	10.3	1.3
P2I	5.3	4.8	17	3.8 - 5.7	4.8	0.7	3.4	3.7	3	4.1 - 5.5	4.9	0.7
CDM	22.7	20.6	17	18.5 - 23.2	20.7	1.1	22.2	21.8	3	16.0 - 20.9	18.8	2.5
CPV	11.9	11.2	17	9.4 - 12.2	11.0	0.7	11.5	12.4	3	10.4 - 11.4	11.0	0.5
CFW	6.5	6.6	17	6.0 - 8.4	7.0	0.6	6.0	6.0	3	6.6 - 7.3	7.0	0.3
HANW	5.9	5.7	17	5.1 - 7.7	6.2	0.7	6.5	7.1	3	4.9 - 6.8	5.8	1.0
HAMW	8.6	8.3	17	8.8 - 10.8	9.7	0.7	10.0	10.1	3	8.4 - 10.3	9.3	1.0
HDW	8.7	9.6	17	10.2 - 13.2	11.6	0.7	8.8	9.1	3	9.8 - 12.9	11.2	1.6
TRW	6.4	6.6	17	7.0 - 11.9	9.5	1.4	5.3	6.6	3	6.4 - 8.4	7.4	1.0
ABW	3.2	6.1	17	5.4 - 10.5	7.4	1.4	5.3	6.2	3	4.6 - 6.6	5.6	1.0
HDH	6.2	9.8	17	6.7 - 10.1	8.9	0.9	7.4	7.6	3	7.9 - 8.9	8.5	0.5
TRH	6.9	10.8	17	7.3 - 10.5	9.1	0.9	7.4	8.4	3	6.1 - 9.4	7.9	1.6
ABH	4.7	10.7	17	6.7 - 10.7	8.7	1.2	6.9	7.9	3	5.0 - 9.9	8.0	2.6
CLO	-	6.2	6	1.5 - 6.4	4.3	2.2	-	1.2	2	1.7 - 6.0	3.8	3.1
CLI	-	7.0	6	2.7 - 8.8	6.0	2.6	-	2.5	2	2.7 - 8.1	5.4	3.8

Table13. Tooth counts for specimens of *Squalus acanthias*. Numbers represent mean values. Dash means not ob

Character	Lectotype	Paralectotypes			*Acanthias lebruni*			Baltic Sea (N=7)	Northeast Atlantic (N=21)	Mediterranean Sea (N=4)	Northwest Atlantic (N=3)	Southeast Atlantic (N=8)	Southwest Atlantic (N=30)	Southwest Pacific (N=15)
	NRM 85	UUZM 159	UUZM 160	UUZM 287	MNHN 1883-190	MNHN 1883-201	MNHN 1883-202							
upper teeth (right)	13	14	14	12	12	12	13	13	13	14	13	12	14	13
upper teeth (left)	13	13	14	14	12	12	12	13	13	14	13	12	14	13
intermediate upper teeth	-	-	-	-	1	-	-	1	1	-	-	1	1	-
lower teeth (right)	11	11	-	10	11	10	10	11	11	12	11	10	11	11
lower teeth (left)	10	11	-	11	11	10	10	11	11	12	12	11	12	11
intermediate lower teeth	-	-	-	-	-	-	-	1	1	-	-	1	1	-
upper teeth series	2	2	2	2	3	2	2	3	2	2	2	2	2	2
lower teeth series	2	2	2	2	3	2	2	2	2	2	2	2	2	2
Source	present study													

Table 14. Tooth counts for *Squalus suckleyi* and *S. wakiyae.*

	S. suckleyi	*S. wakiyae*
	Neotype CAS 227267	**N= 16**
upper teeth (rig	15	13
upper teeth (lef	13	13
intermediate u|	-	1
lower teeth (rig	14	11
lower teeth (lef	12	11
upper teeth ser	2	1
lower teeth ser	3	2
intermediate lo	1	2
Source	Ebert *et al*. (2010	present study

Table 15. Monospondylous, diplospondylous, precaudal, caudal and total vertebrae for specimens of *Squalus acanthias*.

	Monospondylous vertebrae																	
	41	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**
UUZM 159								1										
UUZM 160								1										
BMNH 1931.8.10.1				1														
Baltic Sea						1		3	3	1								
Northeast Atlantic							1		1	1								
Mediterranean Sea											1							
Southeast Atlantic			1	1	1													
Southwest Atlantic			1	4			2											

	Diplospondylous vertebrae																	
	53	**54**	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**
UUZM 159												1						
UUZM 160										1								
BMNH 1931.8.10.1										1								
Baltic Sea											1	1	2	2		2		
Northeast Atlantic												1	1	1				
Mediterranean Sea								1										
Southeast Atlantic								1	1		1							
Southwest Atlantic					1	1		1	2	1	1							

	Precaudal vertebrae																	
	71	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**
UUZM 159											1							
UUZM 160											1							
BMNH 1931.8.10.1								1										
Baltic Sea									1					3	2	2		
Northeast Atlantic												1	1					1
Mediterranean Sea															1			
Southeast Atlantic					1		1	1										
Southwest Atlantic					2	1	1		2		1							

	Caudal vertebrae																	
	21	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**
UUZM 159											1							
UUZM 160									1									
UUZM 287								1										
BMNH 1931.8.10.1								1										
Baltic Sea								1	2	2	3							
Northeast Atlantic						1					2							
Mediterranean Sea						1												
Southeast Atlantic							1		1	1								
Southwest Atlantic						2	3		1	1								

	Total vertebrae																	
	101	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**
UUZM 159												1						
UUZM 160										1								
BMNH 1931.8.10.1						1												
Baltic Sea									1				1	3	1	1	1	
Northeast Atlantic													2	1				
Mediterranean Sea											1							
Southeast Atlantic				1	1		1											
Southwest Atlantic	2			1	1	1		1	1									

Table 16. External measurements for specimens of *Squalus suckleyi* expressed as percentage of the total length (% TL). Total length is expressed in milimeters. Values for neotype (CAS 227267) taken from Ebert *et al*. (2010). N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	Neotype	N	Range	*x*	SD
TL (mm)	674.0	18	160.0 - 710.0	327.7	123.0
PCL	80.6	18	75.0 - 81.0	77.9	1.6
PD2	64.5	18	57.9 - 65.5	60.7	1.9
PD1	34.1	18	32.3 - 37.1	35.2	1.5
SVL	54.9	18	49.1 - 53.9	51.6	1.3
PP2	51.5	18	47.4 - 51.4	49.0	1.1
PP1	22.3	18	21.1 - 25.9	23.2	1.0
HDL	23.0	18	21.3 - 24.5	23.0	0.9
PG1	18.0	18	17.4 - 23.0	19.6	1.3
PSP	11.4	18	11.1 - 22.7	13.6	2.9
POB	6.4	18	6.7 - 13.4	8.2	1.4
PRN	4.2	18	4.6 - 6.0	5.3	0.4
POR	9.1	18	8.4 - 11.7	10.5	0.9
INLF	-	18	3.2 - 5.4	4.8	0.5
MOW	6.2	18	6.9 - 9.4	8.0	0.6
ULA	2.2	18	2.1 - 3.3	2.6	0.3
INW	4.2	18	2.9 - 4.6	3.9	0.4
INO	7.0	18	0.9 - 10.1	8.1	1.9
EYL	3.6	18	2.6 - 5.9	4.0	1.0
EYH	1.5	18	1.7 - 3.7	2.5	0.6
SPL	1.5	18	1.3 - 2.3	1.7	0.3
GS1	1.9	18	1.5 - 2.1	1.8	0.2
GS5	2.1	18	1.9 - 2.5	2.2	0.2
IDS	23.6	18	17.7 - 24.1	19.9	1.8
DCS	11.4	18	9.4 - 13.8	11.6	1.0
PPS	27.3	18	16.8 - 25.5	22.4	2.6
PCA	-	18	20.4 - 25.9	22.6	1.3
D1L	11.6	18	11.3 - 12.8	11.9	0.4
D1A	8.8	18	9.0 - 12.0	9.9	0.7
D1B	6.2	18	6.3 - 7.5	6.9	0.4
D1H	6.2	18	5.8 - 8.0	6.7	0.5
D1I	7.7	18	4.8 - 5.9	5.3	0.3
D1P	5.2	18	5.3 - 8.0	6.5	0.7
D1ES	-	17	1.3 - 2.2	1.8	0.3
D1BS	-	18	0.4 - 0.8	0.6	0.1
D2L	11.1	18	9.4 - 12.6	11.1	0.8
D2A	7.9	18	6.8 - 10.9	8.3	1.0
D2B	5.9	18	4.8 - 7.8	6.3	0.8
D2H	3.0	18	4.1 - 5.5	4.8	0.4
D2I	4.9	18	4.5 - 5.4	4.9	0.3
D2P	5.6	18	4.6 - 5.8	5.3	0.3
D2ES	-	18	2.9 - 4.6	3.5	0.4
D2BS	-	18	0.6 - 3.8	1.1	0.7
P1A	12.9	18	11.0 - 15.0	12.8	1.0
P1I	6.5	18	7.3 - 10.2	8.3	0.7
P1B	6.4	18	3.8 - 5.2	4.4	0.4
P1P	11.0	18	6.6 - 10.3	8.6	1.2
P2L	11.7	18	8.9 - 11.0	10.0	0.6
P2I	-	18	3.9 - 6.9	4.9	0.7
CDM	19.4	18	20.4 - 24.6	21.8	1.1
CPV	10.4	18	10.1 - 12.9	11.5	0.8
CFW	-	18	5.6 - 7.6	6.6	0.5
HANW	-	18	5.8 - 9.1	7.2	0.8
HAMW	-	18	9.4 - 11.3	10.2	0.6
HDW	11.0	18	6.8 - 12.1	10.8	1.3
TRW	10.5	18	7.2 - 10.4	8.5	1.0
ABW	-	18	4.3 - 7.6	6.0	0.8
HDH	6.5	18	7.4 - 9.7	8.6	0.8
TRH	9.9	18	6.7 - 10.8	8.9	1.1
ABH	-	18	5.6 - 9.3	8.1	0.9
CLO	6.4	12	1.5 - 3.1	1.9	0.5
CLI	11.4	12	2.3 - 4.3	3.1	0.6

Table 17. External measurements for specimens of *Squalus wakiyae* expressed as percentage of the total length (% TL). Total length is expressed in milimeters. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	N	Range			*x*	SD
TL (mm)	10	165.0	-	952.0	631.1	257.3
PCL	10	76.4	-	80.9	78.9	1.3
PD2	10	56.2	-	62.3	60.0	1.9
PD1	10	32.6	-	35.6	33.8	1.0
SVL	10	50.1	-	53.6	51.7	1.1
PP2	10	47.2	-	50.6	49.0	1.1
PP1	10	19.8	-	23.3	21.3	1.2
HDL	10	20.0	-	24.2	21.9	1.2
PG1	10	16.2	-	20.8	18.3	1.2
PSP	10	9.5	-	13.0	11.5	1.0
POB	10	6.3	-	8.2	7.5	0.6
PRN	10	4.2	-	5.5	5.0	0.4
POR	10	8.0	-	10.7	9.5	0.8
INLF	10	3.9	-	5.6	4.4	0.6
MOW	10	6.9	-	8.2	7.4	0.4
ULA	10	1.7	-	3.2	2.3	0.4
INW	10	3.1	-	4.1	3.7	0.3
INO	10	6.9	-	9.6	7.7	0.8
EYL	10	2.7	-	5.9	3.8	1.1
EYH	10	1.4	-	2.7	1.8	0.3
SPL	10	1.0	-	1.9	1.3	0.3
GS1	10	1.3	-	2.0	1.7	0.2
GS5	10	2.0	-	2.6	2.1	0.2
IDS	10	16.2	-	22.1	19.8	1.8
DCS	10	9.9	-	11.5	10.9	0.5
PPS	10	20.7	-	25.1	23.3	1.6
PCA	10	20.4	-	22.6	21.5	0.9
D1L	10	10.6	-	12.4	11.9	0.6
D1A	10	8.8	-	10.9	9.6	0.8
D1B	10	6.4	-	7.6	7.1	0.4
D1H	10	5.9	-	6.7	6.3	0.3
D1I	10	4.4	-	5.3	4.9	0.3
D1P	10	5.0	-	7.2	6.6	0.7
D1ES	8	1.0	-	2.0	1.6	0.3
D1BS	10	0.3	-	0.6	0.4	0.1
D2L	10	9.6	-	13.7	12.0	1.1
D2A	10	7.0	-	10.5	8.7	0.9
D2B	10	5.9	-	8.7	7.5	0.8
D2H	10	3.6	-	5.0	4.4	0.5
D2I	10	3.7	-	4.8	4.4	0.4
D2P	10	4.4	-	5.8	5.0	0.4
D2ES	9	1.9	-	3.5	2.7	0.4
D2BS	10	0.4	-	1.0	0.6	0.2
P1A	10	10.7	-	15.0	13.8	1.4
P1I	10	7.3	-	8.7	7.8	0.4
P1B	10	3.5	-	4.9	4.4	0.4
P1P	10	7.0	-	9.9	9.1	0.8
P2L	10	9.3	-	12.5	10.6	1.0
P2I	10	3.5	-	5.6	4.7	0.7
CDM	10	19.3	-	21.9	21.0	0.8
CPV	10	9.9	-	20.8	11.9	3.2
CFW	10	6.3	-	11.2	7.3	1.4
HANW	10	5.6	-	8.0	6.6	0.8
HAMW	10	9.1	-	11.3	9.9	0.6
HDW	10	9.5	-	12.6	11.2	1.1
TRW	10	6.6	-	13.6	9.8	1.9
ABW	10	5.4	-	9.7	7.9	1.6
HDH	10	7.8	-	10.6	9.1	0.9
TRH	10	8.5	-	13.9	10.3	1.7
ABH	10	7.0	-	12.4	9.7	1.9
CLO	4	2.0	-	6.0	5.0	2.0
CLI	4	2.2	-	9.2	6.8	3.1

Table 18. Monospondylous, diplospondylous, precaudal, caudal and total vertebrae for *Squalus suckleyi* and *S. wakiyae*.

	Monospondylous vertebrae																						
	37	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**
CAS 227267 (neotype of *S. suckleyi*)								1															
S. suckleyi	1	2	3	3	1		2																
S. wakiyae				1	2	1																	

	Diplospondylous vertebrae																						
	54	**55**	**56**	**57**	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**
CAS 227267 (neotype of *S. suckleyi*)					1																		
S. suckleyi							1		2					3	3			1			1		1
S. wakiyae					2			1	1														

	Precaudal vertebrae																						
	68	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**
CAS 227267 (neotype of *S. suckleyi*)						1																	
S. suckleyi					1	1	1				2		1	2		1	3						
S. wakiyae				1	2	1																	

	Caudal vertebrae																						
	18	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
CAS 227267 (neotype of *S. suckleyi*)												1											
S. suckleyi							1	2		2	1	1	5										
S. wakiyae										2			1	1									

	Total vertebrae																						
	98	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**
CAS 227267 (neotype of *S. suckleyi*)					1																		
S. suckleyi					1	2		1	3		1		2				2						
S. wakiyae		2		1			1																

Table 19. External measurements expressed as percentage of the total length (% TL) for *Flakeus megalops*. Values for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	Southern Australia					Queensland	Western Australia
	Holotype	N	Range	*x*	SD	AMS I. 45622-001	CSIRO H 3969-14
TL (mm)	550.0	14	220.0 - 665.0	474.0	137.2	198.0	545.0
PCL	90.4	14	75.0 - 80.3	78.3	1.3	77.3	79.8
PD2	71.6	14	58.9 - 62.7	61.2	1.4	58.8	62.9
PD1	34.5	14	28.7 - 31.4	29.9	0.8	30.0	31.2
SVL	57.8	14	44.0 - 51.8	48.0	2.0	47.9	49.4
PP2	54.9	14	43.2 - 50.1	45.9	2.0	46.3	47.2
PP1	23.7	14	20.2 - 24.0	21.8	1.1	22.9	21.7
HDL	24.7	14	20.7 - 24.8	22.4	1.3	23.9	22.3
PG1	22.3	14	17.4 - 20.3	18.9	0.9	20.5	18.8
PSP	13.5	14	11.6 - 13.4	12.5	0.6	14.2	12.2
POB	7.5	14	6.6 - 7.7	7.1	0.3	8.2	7.0
PRN	4.2	14	3.9 - 5.4	4.4	0.4	4.9	4.2
POR	9.7	14	8.7 - 10.7	9.4	0.6	11.6	9.2
INLF	5.3	14	4.4 - 5.3	5.0	0.3	5.9	4.8
MOW	9.6	14	7.5 - 9.4	8.4	0.6	7.7	8.5
ULA	2.7	14	2.2 - 3.0	2.6	0.2	2.7	2.6
INW	4.5	14	3.6 - 4.8	4.2	0.3	4.7	3.9
INO	8.7	14	7.4 - 10.0	8.7	0.6	10.2	8.4
EYL	5.2	14	4.1 - 6.5	4.9	0.6	6.7	4.5
EYH	2.3	14	1.2 - 2.7	2.2	0.4	3.1	2.2
SPL	1.1	14	1.0 - 2.0	1.5	0.2	2.1	1.3
GS1	2.0	14	1.2 - 2.5	2.0	0.4	2.1	1.9
GS5	3.0	14	1.7 - 2.6	2.3	0.3	2.6	2.5
IDS	27.3	14	21.3 - 27.2	24.4	1.7	20.3	25.9
DCS	11.0	14	9.3 - 11.7	10.5	0.8	9.7	10.6
PPS	26.9	14	16.8 - 24.2	20.5	2.2	19.3	23.9
PCA	26.4	14	22.8 - 28.1	25.8	1.9	24.4	25.8
D1L	15.1	14	10.9 - 15.1	13.6	1.1	13.7	13.8
D1A	8.9	14	10.3 - 13.3	11.7	0.9	13.7	10.7
D1B	8.5	14	7.1 - 8.8	7.9	0.6	8.2	7.7
D1H	5.3	14	7.8 - 10.5	8.7	0.9	9.7	8.0
D1I	6.9	14	3.6 - 6.8	6.0	0.7	5.9	6.0
D1P	8.9	14	7.1 - 9.9	8.7	0.9	6.2	8.7
D1ES	-	14	1.8 - 3.7	3.0	0.5	2.1	3.3
D1BS	0.8	14	0.5 - 0.8	0.7	0.1	0.5	0.6
D2L	10.9	14	10.4 - 13.9	12.1	1.0	12.2	10.6
D2A	9.5	14	8.8 - 12.0	10.3	0.9	11.6	8.7
D2B	7.0	14	5.6 - 8.1	6.9	0.7	7.0	6.3
D2H	5.7	14	4.8 - 7.6	6.0	0.8	7.0	5.2
D2I	4.3	14	4.3 - 5.9	5.3	0.5	5.5	4.4
D2P	3.9	14	4.1 - 6.3	5.0	0.6	3.6	4.4
D2ES	2.5	14	3.6 - 6.1	4.6	0.7	5.3	4.3
D2BS	0.9	14	0.6 - 0.9	0.7	0.1	0.9	0.7
P1A	17.0	14	12.7 - 17.0	15.0	1.2	13.4	15.5
P1I	10.9	14	9.4 - 10.9	10.1	0.5	9.5	10.8
P1B	5.2	14	3.9 - 6.0	4.9	0.6	4.9	5.0
P1P	12.2	14	9.8 - 14.6	12.0	1.5	8.4	11.4
P2L	10.9	14	6.1 - 12.7	11.1	1.6	10.3	10.1
P2I	5.4	14	4.9 - 7.0	6.0	0.6	6.3	5.3
CDM	-	14	19.5 - 23.0	21.4	0.9	21.4	20.1
CPV	8.9	14	6.0 - 12.7	11.0	1.5	13.3	10.8
CFW	6.0	14	6.5 - 8.1	7.3	0.5	7.3	7.0
HANW	7.6	14	6.3 - 8.7	7.1	0.6	8.4	6.8
HAMW	12.5	14	10.6 - 13.6	12.0	0.8	12.0	11.6
HDW	14.6	14	11.2 - 15.1	13.4	1.2	11.9	14.4
TRW	11.4	14	8.7 - 13.2	11.3	1.4	9.9	11.8
ABW	7.2	14	7.1 - 11.1	9.1	1.1	9.2	10.2
HDH	11.4	14	9.5 - 11.5	10.6	0.8	8.2	10.4
TRH	11.5	14	9.6 - 12.8	11.3	1.1	9.2	10.7
ABH	11.6	14	9.0 - 13.8	11.0	1.4	9.7	11.7
CLO	-	7	1.3 - 5.4	3.9	1.5	1.3	-
CLI	-	7	3.0 - 7.6	6.2	1.8	2.7	-

Table 20. External measurements expressed as percentage of the total length (% TL) for *Flakeus acutipinnis*. Total length is expressed in millimeters. A: BMNH 1881.3.11.2; B: BMNH 1859.5.7.68; C: BMNH 1900.11.6.14; N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Flakeus acutipinnis*							
	Lectotype	A	B	C	N	Range	*x*	SD
TL (mm)	578.0	852.0	190.0	565.0	8	310.0 - 695.0	525.6	110.8
PCL	79.9	81.2	76.8	80.2	8	75.8 - 80.0	78.6	1.3
PD2	61.1	64.9	55.4	61.1	8	58.1 - 63.5	61.4	1.7
PD1	31.3	27.9	29.6	28.0	8	28.6 - 31.3	29.9	1.0
SVL	49.8	53.4	46.1	48.1	8	45.8 - 50.4	48.5	1.7
PP2	45.8	49.6	43.8	45.3	8	42.6 - 48.7	46.1	2.3
PP1	22.5	19.4	22.1	22.7	8	19.4 - 23.6	21.6	1.4
HDL	23.1	20.2	24.3	23.0	8	21.4 - 24.3	23.1	0.9
PG1	18.8	16.2	19.1	19.1	8	17.7 - 19.3	18.7	0.6
PSP	11.6	11.2	13.1	11.9	8	7.7 - 12.1	11.2	1.5
POB	6.3	7.1	6.9	7.1	8	6.5 - 7.1	6.8	0.2
PRN	4.0	4.4	3.5	4.7	8	3.9 - 4.4	4.2	0.2
POR	8.9	8.4	10.1	9.5	8	8.4 - 9.2	8.9	0.3
INLF	4.7	3.7	4.8	4.9	8	4.3 - 4.9	4.5	0.2
MOW	8.5	6.8	7.5	8.5	8	7.7 - 9.0	8.3	0.4
ULA	2.8	1.8	2.4	2.4	8	2.5 - 2.9	2.6	0.2
INW	3.8	4.5	3.7	3.8	8	3.6 - 4.3	4.0	0.2
INO	7.8	8.4	9.9	8.4	8	7.4 - 8.6	8.2	0.4
EYL	5.1	3.8	5.9	4.0	8	4.3 - 5.1	4.6	0.3
EYH	1.5	2.5	1.7	2.0	8	1.6 - 2.4	2.0	0.2
SPL	1.5	1.3	1.5	1.4	8	1.2 - 2.2	1.6	0.3
GS1	1.8	1.1	2.4	2.3	8	1.7 - 2.4	2.0	0.2
GS5	2.7	2.0	2.7	2.6	8	2.1 - 2.6	2.3	0.2
IDS	22.1	28.9	21.2	25.3	8	20.1 - 25.4	24.0	1.9
DCS	11.5	10.8	11.3	11.9	8	10.3 - 12.3	11.1	0.7
PPS	18.0	23.5	18.7	22.3	8	17.8 - 22.6	20.7	1.9
PCA	25.3	27.6	24.1	25.3	8	24.8 - 27.2	25.7	0.7
D1L	13.9	13.7	12.2	13.3	8	13.4 - 14.2	13.8	0.3
D1A	11.1	9.9	12.9	10.1	8	11.1 - 11.8	11.4	0.3
D1B	8.3	8.2	6.4	8.6	8	7.5 - 8.5	7.9	0.4
D1H	8.2	7.1	10.2	8.0	8	8.0 - 9.3	8.7	0.4
D1I	5.6	5.2	6.9	4.8	8	5.5 - 6.5	6.0	0.3
D1P	9.6	9.2	8.5	8.8	8	8.8 - 10.3	9.4	0.5
D1ES	1.9	4.9	2.2	2.4	8	3.5 - 4.3	3.8	0.3
D1BS	0.6	0.9	0.6	0.7	8	0.6 - 0.9	0.7	0.1
D2L	11.6	10.0	13.1	11.2	8	10.5 - 13.0	11.6	1.0
D2A	9.5	7.8	10.6	9.6	8	8.9 - 11.3	9.6	0.8
D2B	6.5	6.0	7.1	7.1	8	5.7 - 7.8	6.6	0.7
D2H	6.1	4.6	9.1	4.6	8	5.1 - 6.7	5.8	0.5
D2I	5.1	3.9	6.0	4.2	8	4.1 - 5.7	5.0	0.6
D2P	5.9	4.4	4.9	4.7	8	4.5 - 6.2	5.4	0.6
D2ES	3.8	4.8	4.2	5.1	7	4.5 - 6.3	5.2	0.6
D2BS	0.6	0.6	1.2	1.2	8	0.7 - 1.0	0.8	0.1
P1A	17.7	13.1	16.0	17.7	8	15.1 - 18.1	16.9	1.0
P1I	9.8	6.0	11.2	9.5	8	9.5 - 11.8	10.2	0.8
P1B	4.2	6.2	4.1	4.8	8	4.6 - 5.9	5.2	0.5
P1P	13.7	11.1	10.1	14.2	8	9.9 - 14.5	13.5	1.5
P2L	10.7	8.7	10.6	11.2	8	9.8 - 12.0	11.1	0.7
P2I	5.1	5.7	5.4	4.9	8	4.2 - 6.4	5.4	0.7
CDM	20.7	20.4	23.3	20.3	8	19.7 - 22.8	21.3	1.1
CPV	10.5	9.6	12.8	10.8	8	10.3 - 12.0	11.1	0.7
CFW	7.2	6.2	8.0	6.9	8	6.9 - 7.5	7.2	0.2
HANW	6.4	7.1	7.5	6.8	8	6.9 - 8.5	7.4	0.5
HAMW	12.3	10.2	12.2	12.1	8	10.7 - 12.0	11.4	0.4
HDW	13.1	10.7	10.9	13.3	8	11.5 - 13.5	12.7	0.6
TRW	10.6	10.3	10.1	10.3	8	9.0 - 11.5	10.1	0.9
ABW	7.6	8.6	9.1	9.6	8	7.0 - 9.7	8.3	1.0
HDH	10.7	10.2	10.4	10.8	8	9.1 - 11.2	10.1	0.7
TRH	12.0	10.1	9.6	12.2	8	9.2 - 12.7	10.5	1.1
ABH	11.9	9.5	7.3	11.4	8	8.4 - 12.4	9.9	1.2
CLO	-	-	-	-	1	-	1.8	-
CLI	-	-	-	-	1	-	4.3	-

Table 21. External measurements expressed as percentage of the total length (% TL) for *Flakeus brevirostris.*Values for other specimens are also provided. TL is expressed in milimeters. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus brevirostris***						
	Holotype	N	Range			*x*	SD
TL (mm)	426.0	14	147.0	-	578.0	406.9	104.6
PCL	79.8	14	75.1	-	81.3	79.1	1.4
PD2	61.7	14	58.4	-	63.8	61.9	1.4
PD1	29.6	14	28.5	-	31.7	30.1	1.1
SVL	47.7	14	43.1	-	49.5	46.5	1.6
PP2	43.7	14	42.4	-	46.9	44.2	1.3
PP1	21.7	14	19.0	-	22.9	21.1	1.0
HDL	21.9	14	20.0	-	29.6	22.6	2.2
PG1	17.9	14	16.8	-	21.0	18.3	1.0
PSP	12.1	14	11.3	-	12.9	12.1	0.5
POB	6.7	14	6.5	-	7.5	7.1	0.3
PRN	4.0	14	3.8	-	4.4	4.2	0.2
POR	9.1	14	8.4	-	10.0	9.1	0.5
INLF	5.0	14	4.5	-	5.5	4.9	0.3
MOW	8.1	14	7.4	-	8.6	7.8	0.3
ULA	2.6	14	2.0	-	2.7	2.4	0.2
INW	3.6	14	3.4	-	4.7	3.7	0.3
INO	8.6	14	7.8	-	10.3	8.4	0.6
EYL	5.0	14	4.2	-	6.1	4.7	0.5
EYH	2.2	14	1.8	-	2.6	2.2	0.2
SPL	1.7	14	1.4	-	2.4	1.6	0.3
GS1	2.1	14	1.5	-	2.6	2.0	0.3
GS5	2.3	14	1.7	-	2.6	2.3	0.2
IDS	24.9	14	23.3	-	27.2	24.6	1.2
DCS	10.5	14	9.9	-	10.6	10.3	0.2
PPS	21.4	14	17.2	-	22.8	19.9	2.0
PCA	28.1	14	24.6	-	29.4	27.5	1.3
D1L	13.0	14	12.6	-	14.7	13.8	0.5
D1A	10.3	14	7.9	-	12.0	10.9	1.0
D1B	7.3	14	7.4	-	9.2	7.9	0.5
D1H	7.6	14	6.5	-	8.6	7.9	0.5
D1I	5.8	14	5.2	-	6.8	6.1	0.5
D1P	7.7	14	6.6	-	9.6	8.6	0.7
D1ES	-	12	1.6	-	4.2	3.3	0.7
D1BS	0.7	14	0.5	-	0.8	0.6	0.1
D2L	11.6	14	11.2	-	13.2	12.3	0.7
D2A	9.8	14	9.7	-	12.4	10.9	0.7
D2B	6.6	14	6.1	-	7.9	7.1	0.6
D2H	6.0	14	5.2	-	7.1	6.4	0.6
D2I	5.0	14	4.8	-	6.7	5.4	0.5
D2P	4.3	14	2.9	-	5.3	4.7	0.6
D2ES	4.6	14	4.2	-	6.6	5.5	0.7
D2BS	0.8	14	0.7	-	0.9	0.8	0.1
P1A	14.7	14	12.0	-	15.7	14.3	1.0
P1I	10.3	14	9.8	-	12.0	10.7	0.6
P1B	4.7	14	3.8	-	5.3	4.5	0.5
P1P	10.4	14	6.3	-	11.5	10.4	1.3
P2L	11.7	14	10.3	-	13.6	11.7	0.8
P2I	6.1	14	4.8	-	6.7	6.0	0.5
CDM	20.5	14	19.2	-	21.5	20.5	0.6
CPV	10.1	14	10.1	-	12.4	11.0	0.6
CFW	6.6	14	6.6	-	7.6	7.0	0.3
HANW	7.7	14	6.2	-	9.1	7.0	0.7
HAMW	12.1	14	10.7	-	12.7	11.6	0.5
HDW	12.1	14	11.0	-	14.1	12.7	0.8
TRW	8.9	14	8.0	-	12.9	10.4	1.5
ABW	11.2	14	7.1	-	12.4	9.5	1.6
HDH	9.9	14	9.0	-	11.9	10.0	0.8
TRH	10.7	14	9.3	-	13.1	10.5	1.3
ABH	10.1	14	7.7	-	13.2	10.5	1.7
CLO	3.9	6	1.4	-	5.1	4.1	1.4
CLI	7.1	6	3.0	-	8.1	6.8	1.9

Table 22. External measurements for *Flakeus cubensis* expressed as percentage of the total length (% TL). N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Flakeus cubensis*												
	Holotype	Paratypes				Gulf of Mexico				Caribbean Sea			
		N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD
TL (mm)	525.0	4	210.0 - 690.0	368.5	217.5	12	275.0 - 532.0	415.3	77.9	14	205.0 - 650.0	418.2	161.9
PCL	79.0	4	74.1 - 79.7	76.9	2.4	12	77.5 - 81.6	79.3	1.3	14	76.6 - 81.5	79.4	1.4
PD2	61.9	4	58.9 - 63.8	60.4	2.2	12	60.2 - 64.6	62.3	1.3	14	58.9 - 66.3	62.1	2.3
PD1	30.5	4	28.9 - 31.0	30.0	0.9	12	28.9 - 34.5	32.0	1.7	14	29.4 - 34.4	31.1	1.4
SVL	48.6	4	45.2 - 50.7	47.9	2.4	12	43.4 - 50.8	47.7	1.9	14	41.9 - 52.5	46.7	3.1
PP2	45.7	4	42.9 - 47.8	45.7	2.2	12	43.1 - 48.9	45.2	1.7	14	40.7 - 50.8	44.2	3.1
PP1	22.9	4	21.7 - 24.1	22.8	1.3	12	21.4 - 26.3	23.4	1.6	14	19.5 - 23.4	22.4	1.0
HDL	23.6	4	22.8 - 24.6	23.7	0.8	12	20.4 - 25.9	23.0	1.4	14	19.9 - 24.0	22.9	1.0
PG1	20.0	4	19.4 - 20.5	20.1	0.5	12	17.4 - 21.6	19.5	1.0	14	17.1 - 20.5	19.5	1.1
PSP	13.0	4	12.6 - 14.2	13.8	0.8	12	11.7 - 14.1	13.1	0.6	14	10.7 - 14.8	13.1	1.0
POB	7.3	4	7.5 - 8.1	7.7	0.3	12	6.4 - 8.1	7.3	0.5	14	6.8 - 8.2	7.5	0.4
PRN	4.3	4	4.0 - 4.9	4.7	0.4	12	3.9 - 5.0	4.5	0.4	14	4.3 - 5.4	4.7	0.3
POR	9.4	4	9.6 - 11.4	10.8	0.8	12	8.8 - 11.1	10.1	0.7	14	8.7 - 11.8	10.4	0.8
INLF	5.2	4	5.1 - 6.0	5.7	0.4	12	4.7 - 5.8	5.3	0.3	14	3.8 - 5.9	5.2	0.5
MOW	7.5	4	7.8 - 8.5	8.0	0.3	12	7.0 - 9.7	8.4	0.7	14	7.2 - 9.4	8.0	0.6
ULA	2.4	4	2.1 - 2.9	2.6	0.3	12	2.2 - 4.3	2.7	0.6	14	2.3 - 2.8	2.5	0.2
INW	3.6	4	2.7 - 4.4	3.6	0.7	12	3.9 - 4.5	4.2	0.2	14	3.6 - 4.8	4.3	0.3
INO	8.5	4	8.5 - 10.1	9.3	0.7	12	7.5 - 9.7	9.0	0.6	14	7.8 - 11.1	9.0	0.8
EYL	4.2	4	3.7 - 4.9	4.3	0.6	12	3.9 - 5.1	4.6	0.4	14	3.2 - 6.0	4.4	0.7
EYH	1.8	4	1.3 - 2.9	2.1	0.6	12	1.6 - 2.9	2.3	0.4	14	1.0 - 2.7	2.0	0.4
SPL	1.6	4	1.2 - 1.8	1.5	0.2	12	1.3 - 2.0	1.7	0.3	14	1.0 - 2.1	1.6	0.3
GS1	1.4	4	1.5 - 1.9	1.7	0.2	12	1.2 - 2.2	1.7	0.3	14	1.2 - 2.4	1.8	0.3
GS5	2.3	4	1.9 - 2.5	2.2	0.3	12	1.7 - 2.5	2.1	0.2	14	1.9 - 2.7	2.3	0.3
IDS	23.8	4	22.2 - 26.1	23.6	1.7	12	22.4 - 28.4	25.1	1.8	14	20.0 - 27.7	24.1	2.4
DCS	11.5	4	9.8 - 11.6	10.9	0.7	12	9.7 - 12.3	11.2	0.9	14	10.3 - 12.0	11.0	0.5
PPS	19.0	4	17.9 - 23.6	20.6	2.6	12	14.6 - 22.9	19.2	2.7	14	14.9 - 22.7	17.7	2.5
PCA	26.7	4	22.6 - 27.6	25.0	2.2	12	24.8 - 30.6	27.1	1.9	14	26.2 - 29.2	27.7	0.9
D1L	14.7	4	12.5 - 14.6	13.8	0.9	12	12.0 - 13.7	13.0	0.5	14	12.6 - 14.5	13.6	0.6
D1A	11.6	4	11.6 - 12.7	12.3	0.5	12	9.1 - 12.0	10.5	0.9	14	9.5 - 14.2	11.2	1.2
D1B	8.8	4	6.9 - 8.9	8.3	1.0	12	6.7 - 7.9	7.4	0.4	14	6.9 - 9.3	7.8	0.6
D1H	8.6	4	7.5 - 9.0	8.4	0.7	12	6.3 - 8.4	7.3	0.8	14	6.6 - 9.6	8.0	0.8
D1I	6.1	4	5.8 - 6.9	6.3	0.5	12	5.1 - 6.8	6.1	0.6	14	5.4 - 6.7	5.9	0.4
D1P	8.4	4	6.8 - 9.9	7.9	1.4	12	7.1 - 9.7	8.4	0.8	14	7.5 - 10.1	9.2	0.8
D1ES	4.3	4	2.1 - 4.7	3.2	1.1	12	2.5 - 4.7	3.6	0.8	14	2.1 - 4.9	3.5	0.9
D1BS	0.9	4	0.8 - 1.1	1.0	0.1	12	0.6 - 1.1	0.9	0.2	14	0.6 - 1.1	0.9	0.1
D2L	13.1	4	11.6 - 12.4	12.1	0.3	12	10.6 - 12.8	11.6	0.6	14	11.0 - 12.7	12.0	0.5
D2A	12.3	4	11.2 - 11.6	11.4	0.2	12	9.4 - 11.0	10.2	0.5	14	9.1 - 11.8	10.5	0.8
D2B	7.6	4	6.6 - 6.9	6.7	0.1	12	5.5 - 7.9	6.6	0.7	14	5.9 - 7.7	6.7	0.6
D2H	6.9	4	5.9 - 7.5	6.7	0.7	12	4.7 - 6.9	5.8	0.8	14	5.3 - 7.7	6.2	0.7
D2I	5.6	4	5.5 - 6.0	5.8	0.3	12	4.7 - 6.1	5.3	0.4	14	4.8 - 6.4	5.5	0.5
D2P	5.1	4	2.8 - 5.5	4.4	1.2	12	4.3 - 5.8	5.0	0.4	14	3.5 - 6.0	5.0	0.7
D2ES	6.0	4	4.2 - 6.5	5.3	1.0	12	4.0 - 6.0	5.0	0.6	14	4.2 - 6.3	5.1	0.6
D2BS	1.0	4	1.0 - 1.2	1.1	0.1	12	0.7 - 1.1	0.9	0.1	14	0.8 - 1.1	1.0	0.1
P1A	15.2	4	13.3 - 15.8	14.2	1.2	12	13.2 - 14.7	13.9	0.5	14	11.3 - 15.1	13.6	1.2
P1I	11.5	4	8.8 - 11.0	10.1	1.0	12	8.7 - 12.1	10.2	0.9	14	8.9 - 11.9	10.3	0.7
P1B	3.9	4	4.0 - 4.4	4.2	0.2	12	3.7 - 9.8	4.7	1.6	14	3.5 - 10.4	4.9	1.6
P1P	12.1	4	8.7 - 10.1	9.3	0.6	12	9.2 - 11.9	10.6	1.0	14	8.1 - 12.6	10.4	1.2
P2L	13.0	4	9.4 - 11.5	10.7	1.0	12	10.0 - 12.3	11.1	0.8	14	10.0 - 12.9	11.2	0.9
P2I	6.9	4	5.6 - 6.7	6.1	0.6	12	4.3 - 8.1	5.7	0.9	14	4.3 - 7.0	5.7	0.7
CDM	21.6	4	20.8 - 23.8	22.0	1.4	12	20.1 - 22.9	21.3	0.9	14	19.5 - 22.9	21.5	1.0
CPV	12.3	4	10.5 - 13.5	12.0	1.3	12	10.5 - 12.0	11.1	0.5	14	10.5 - 13.9	11.8	1.0
CFW	6.8	4	6.6 - 7.0	6.8	0.2	12	6.3 - 7.4	6.8	0.3	14	5.5 - 7.7	6.7	0.6
HANW	7.0	4	6.6 - 9.0	7.6	1.0	12	6.6 - 7.6	7.1	0.3	14	6.5 - 10.6	7.3	1.0
HAMW	10.8	4	11.2 - 12.3	11.7	0.5	12	9.8 - 13.0	11.7	0.9	14	10.1 - 13.8	11.7	0.9
HDW	12.5	4	10.8 - 13.5	12.2	1.2	12	10.8 - 13.5	12.3	0.8	14	10.2 - 15.0	12.4	1.3
TRW	9.8	4	6.3 - 11.0	9.1	2.0	12	7.8 - 10.6	9.1	0.9	14	6.7 - 13.9	10.0	2.0
ABW	6.3	4	5.5 - 8.8	7.5	1.4	12	6.2 - 9.5	7.5	0.9	14	6.3 - 11.8	8.3	1.4
HDH	8.8	4	9.3 - 11.1	9.9	0.8	12	8.4 - 12.5	10.0	1.2	14	8.8 - 11.6	10.4	0.7
TRH	8.0	4	8.0 - 12.7	10.6	2.3	12	7.9 - 13.5	10.1	1.4	14	8.8 - 12.6	10.5	0.9
ABH	7.9	4	7.3 - 10.5	9.4	1.5	12	7.3 - 11.1	8.8	1.2	14	7.6 - 12.1	9.8	1.4
CLO	4.4	2	1.2 - 1.5	1.4	0.2	8	1.3 - 4.8	3.6	1.3	7	1.3 - 5.9	3.4	1.8
CLI	8.0	2	3.3 - 3.8	3.5	0.3	8	2.7 - 7.9	6.2	1.8	7	1.7 - 7.6	5.1	2.5

Table 23. Tooth counts for *Flakeus megalops*, *F. acutipinnis*, *F. brevirostris* and *F. cubensis*. N: number of specimens.

	F. megalops		***F. acutipinnis***			***F. brevirostris***		***F. cubensis***		
	Holotype	N= 7	Lectotype	Paralectotypes (N=2)	N=4	Holotype	N=10	Holotype	Paratypes N= 4	N= 11
upper teeth (right)	13	10–14	13	13–13	12–14	12	11–14	14	10–13	11–14
upper teeth (left)	13	11–13	13	12–13	11–14	13	11–13	14	11–13	12–14
lower teeth (right)	12	8–12	11	11	10–12	10	9–12	11	10–13	11–14
lower teeth (left)	12	9–12	11	11	10–13	10	9–12	12	10–12	11–14
upper teeth series	2	1–2	3	2–2	2–2	2	2–2	2	2–2	2–2
lower teeth series	2	2–2	2	2–2	2–3	2	1–2	2	2–2	2–2
Source				present study					Figueirêdo (2011)	

Table 24. Monospondylous, diplospondylous, precaudal, caudal and total vertebrae for *Flakeus megalops*, *F.acutipinnis*, *F. brevirostris.* Values for *F. cubensis* are also provided and were taken from Figueirêdo (2011) and Viana *et al*. (*in prep*).

Monospondylous vertebrae	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
F. megalops Holotype				1																								
F. megalops Southern Australia			3	2	1																							
F. megalops Western Australia				2	2																							
F. megalops Tasmania and Victoria					3																							
F. acutipinnis Lectotype					1																							
F. acutipinnis	1		1	3	3	2																						
F. brevirostris	1	1	4	3		1	1																					
F. cubensis Holotype							1																					
F. cubensis Paratypes					1		1	1																				
F. cubensis			1	2	4	3	2																					

Diplospondylous vertebrae	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
S. megalops Holotype																												
S. megalops Southern Australia															1				1	1	2			1				
S. megalops Western Australia																	1		1	1			1					
S. megalops Tasmania and Victoria																		1	1	1		1						
S. acutipinnis Lectotype																			1									
S. acutipinnis																		1		3	3		3					
S. brevirostris																		1	3	3			2	2				
F. cubensis Holotype																								1				
F. cubensis Paratypes																						1				1		1
F. cubensis																						1	5		2	2	2	

Precaudal vertebrae	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94
S. megalops Holotype																				1								
S. megalops Southern Australia													2		1		1											
S. megalops Western Australia														1	1	1		1										
S. megalops Tasmania and Victoria						1							1		2													
S. acutipinnis Lectotype															1													
S. acutipinnis Paralectotype														1														
S. acutipinnis															1	8	1											
S. brevirostris												2		2	2	1	2	1					1					
F. cubensis Holotype																			1									
F. cubensis Paratypes																					1	1	1					
F. cubensis																	3	4	2	1	1					1		

Caudal vertebrae	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
S. megalops Holotype																												
S. megalops Southern Australia							1			1	1	2		1														
S. megalops Western Australia								1			2	1																
S. megalops Tasmania and Victoria										1		2	1															
S. acutipinnis Lectotype											1																	
S. acutipinnis Paralectotype												1																
S. acutipinnis									2		3	3	2															
S. brevirostris								1	3	1	3	1		2														
F. cubensis Holotype														1														
F. cubensis Paratypes											1	1	1															
F. cubensis										1		4	5	1	1													

Total vertebrae	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124
S. megalops Holotype																												
S. megalops Southern Australia											2		1	1	1	1												
S. megalops Western Australia									1		1		1			1												
S. megalops Tasmania and Victoria				1							1	1	1															
S. acutipinnis Lectotype												1																
S. acutipinnis Paralectotype											1																	
S. acutipinnis											1	1	4	2	2													
S. brevirostris									1	4		1		3		1	1											
F. cubensis Holotype																			1									
F. cubensis Paratypes																		1			2							
F. cubensis															2	2	2	2	2	1		1						

Table 25. External measurements for holotype and three paratypes of *Flakeus crassispinus* expressed as percentage of the total length (% TL). Values for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus crassispinus***								***Flakeus* cf. *crassispinus***		
	Holotype CSIRO H 2547-06	Paratypes CSIRO H 4031-86	CSIRO H 4649-04	WAM P 26223-001	N	Range	*x*	SD	Range	*x*	SD
TL (mm)	576.0	540.0	445.0	487.0	3	404.0 - 482.0	435.3	41.2	343.0 - 435.0	374.3	52.5
PCL	78.1	79.1	78.0	77.4	3	77.4 - 78.8	78.0	0.7	78.0 - 79.3	78.6	0.7
PD2	58.3	60.2	58.9	58.5	3	58.1 - 60.0	58.8	1.1	59.7 - 62.1	60.5	1.3
PD1	26.4	28.3	29.2	25.7	3	26.7 - 27.4	27.1	0.4	28.0 - 29.6	28.8	0.8
SVL	46.9	46.1	45.8	44.6	3	45.0 - 46.0	45.5	0.5	44.6 - 47.1	45.7	1.3
PP2	44.3	43.9	42.7	41.1	3	42.6 - 42.9	42.8	0.2	42.3 - 44.1	43.0	1.0
PP1	21.2	20.9	21.7	21.7	3	21.4 - 21.8	21.5	0.3	21.9 - 23.1	22.4	0.6
HDL	21.7	22.2	22.5	21.9	3	21.7 - 22.2	22.0	0.3	22.4 - 23.4	22.8	0.5
PG1	17.8	17.7	18.7	17.6	3	18.7 - 18.9	18.8	0.1	18.9 - 19.2	19.1	0.2
PSP	11.4	11.4	12.3	12.0	3	12.3 - 12.7	12.5	0.2	12.6 - 12.8	12.7	0.1
POB	7.2	6.8	7.1	6.7	3	7.3 - 7.5	7.4	0.1	7.1 - 7.3	7.2	0.1
PRN	4.6	4.3	4.8	4.4	3	4.8 - 4.8	4.8	0.0	4.4 - 4.6	4.5	0.1
POR	8.9	8.8	9.4	9.1	3	9.3 - 9.8	9.5	0.2	9.5 - 9.7	9.6	0.1
INLF	4.6	4.9	5.2	4.8	3	4.9 - 5.2	5.1	0.2	5.2 - 5.3	5.3	0.0
MOW	7.3	7.5	7.9	7.2	3	7.4 - 7.5	7.5	0.0	7.8 - 8.4	8.1	0.3
ULA	1.9	2.0	2.1	2.2	3	2.0 - 2.2	2.1	0.1	2.3 - 2.6	2.4	0.1
INW	3.9	3.8	4.0	3.8	3	3.9 - 4.3	4.1	0.2	4.1 - 4.4	4.2	0.2
INO	8.6	8.4	8.8	8.4	3	8.6 - 9.0	8.8	0.2	8.1 - 9.0	8.6	0.5
EYL	3.9	4.3	4.8	4.6	3	4.7 - 5.2	4.9	0.3	4.8 - 5.0	4.9	0.1
EYH	2.2	2.0	2.5	2.0	3	2.0 - 2.6	2.3	0.3	1.9 - 2.2	2.1	0.2
SPL	1.4	1.7	1.8	1.5	3	1.3 - 1.7	1.5	0.2	1.3 - 1.5	1.4	0.1
GS1	1.8	1.9	2.1	1.9	3	1.9 - 2.2	2.0	0.1	1.6 - 2.1	1.8	0.3
GS5	2.5	2.4	2.1	2.2	3	2.1 - 2.5	2.3	0.2	2.2 - 2.3	2.3	0.0
IDS	24.0	24.3	23.7	23.6	3	22.3 - 26.2	23.8	2.2	23.4 - 26.9	25.1	1.7
DCS	10.8	10.5	10.5	10.0	3	9.9 - 10.0	10.0	0.1	10.5 - 11.4	11.1	0.5
PPS	20.3	20.0	16.8	17.9	3	18.1 - 19.5	18.9	0.7	17.6 - 20.5	19.0	1.5
PCA	27.4	27.4	27.7	28.7	3	27.2 - 28.1	27.7	0.5	26.5 - 29.0	28.1	1.4
D1L	14.6	14.5	14.8	15.0	3	14.3 - 15.2	14.7	0.5	13.3 - 14.3	13.8	0.5
D1A	13.2	13.4	13.1	13.4	3	12.6 - 12.9	12.8	0.2	10.8 - 12.2	11.4	0.7
D1B	9.5	8.9	9.1	9.4	3	8.7 - 9.8	9.1	0.6	7.3 - 7.9	7.6	0.3
D1H	9.2	9.4	9.9	9.8	3	9.4 - 10.0	9.6	0.3	8.0 - 8.9	8.3	0.5
D1I	5.5	5.5	5.7	6.0	3	5.4 - 6.0	5.7	0.3	5.8 - 6.9	6.4	0.5
D1P	9.2	9.3	11.0	10.5	3	9.9 - 10.9	10.3	0.5	7.7 - 9.2	8.5	0.7
D1ES	4.6	6.0	5.7	4.2	3	5.9 - 6.4	6.1	0.3	2.8 - 4.0	3.4	0.6
D1BS	1.2	1.2	1.2	1.1	3	1.1 - 1.3	1.2	0.1	0.5 - 0.7	0.6	0.1
D2L	12.5	13.2	13.4	13.2	3	12.9 - 14.0	13.6	0.6	11.2 - 13.4	12.4	1.1
D2A	11.1	12.4	12.5	12.4	3	10.1 - 12.0	11.3	1.0	9.5 - 11.4	10.7	1.0
D2B	8.2	8.7	9.0	8.7	3	8.3 - 9.3	8.9	0.6	6.3 - 7.7	7.0	0.7
D2H	6.5	6.4	7.2	7.3	3	6.7 - 7.1	6.9	0.2	5.5 - 6.3	6.0	0.5
D2I	4.5	4.4	4.7	4.6	3	4.5 - 4.9	4.7	0.2	5.1 - 5.9	5.6	0.4
D2P	5.7	5.4	5.7	5.7	3	5.8 - 6.0	5.9	0.1	4.4 - 5.2	4.7	0.4
D2ES	5.6	5.5	5.3	4.3	3	4.1 - 6.6	5.7	1.4	4.5 - 5.9	5.4	0.8
D2BS	1.3	1.2	1.3	1.3	3	1.2 - 1.4	1.3	0.1	0.7 - 0.9	0.8	0.1
P1A	16.0	16.3	15.3	16.9	3	14.6 - 15.2	15.0	0.3	14.1 - 14.8	14.4	0.3
P1I	7.8	8.6	8.4	8.3	3	8.2 - 8.6	8.5	0.2	10.0 - 10.6	10.2	0.3
P1B	5.9	6.0	5.4	5.5	3	5.3 - 5.6	5.5	0.2	4.6 - 5.1	4.8	0.3
P1P	11.2	11.1	12.5	10.7	3	9.0 - 10.3	9.6	0.7	9.7 - 13.1	11.2	1.7
P2L	10.3	10.8	11.7	10.3	3	9.6 - 12.1	10.8	1.2	11.2 - 11.5	11.4	0.1
P2I	4.9	4.9	6.0	5.2	3	4.8 - 6.7	5.6	1.0	5.9 - 6.7	6.3	0.4
CDM	21.3	20.6	21.5	22.5	3	21.4 - 22.6	22.2	0.6	20.6 - 21.9	21.3	0.7
CPV	12.0	11.2	12.1	12.6	3	12.0 - 12.4	12.3	0.3	10.7 - 12.2	11.2	0.8
CFW	7.3	6.9	7.4	7.7	3	6.9 - 7.2	7.0	0.2	7.1 - 7.7	7.3	0.3
HANW	6.7	6.6	6.9	7.2	3	7.1 - 7.4	7.2	0.2	6.8 - 7.8	7.3	0.5
HAMW	10.8	11.5	11.6	10.9	3	11.2 - 11.6	11.4	0.2	11.7 - 11.9	11.9	0.1
HDW	13.2	13.1	12.6	12.4	3	12.1 - 12.3	12.2	0.1	12.7 - 13.4	13.0	0.3
TRW	13.1	11.4	10.4	10.2	3	9.8 - 10.5	10.1	0.4	10.3 - 11.5	10.7	0.7
ABW	11.9	9.9	9.2	8.2	3	7.4 - 8.9	8.1	0.8	8.5 - 9.5	9.0	0.5
HDH	11.2	11.4	10.8	11.5	3	10.1 - 11.1	10.5	0.5	9.2 - 10.6	10.1	0.8
TRH	13.1	12.3	11.6	11.5	3	10.2 - 12.4	11.4	1.1	9.6 - 11.1	10.6	0.9
ABH	12.9	12.4	11.2	11.5	3	11.3 - 12.0	11.6	0.3	10.1 - 10.6	10.3	0.3
CLO	-	-	4.3	-	1	-	4.4	-	4.3 - 4.8	4.5	0.4
CLI	-	-	6.8	-	1	-	7.8	-	7.5 - 7.8	7.6	0.2

Table 26. External measurements expressed as percentage of the total length (% TL) for the holotype and paratypes of *Flakeus raoulensis*. Ranges for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus raoulensis***						
	Holotype	Paratypes					
	NMNZ P 41678	NMNZ P 42572	NMNZ P 34436	N	Range	*x*	SD
TL (mm)	655.0	678.0	725.0	18	286.0 - 830.0	583.8	155.3
PCL	63.1	78.6	78.9	18	76.5 - 94.5	79.5	5.0
PD2	59.2	60.5	62.1	18	57.4 - 71.8	60.2	3.3
PD1	29.0	30.4	31.4	18	28.7 - 35.3	30.4	1.9
SVL	47.5	47.6	49.7	18	35.3 - 56.5	47.4	3.9
PP2	44.0	44.4	46.8	18	34.1 - 52.7	44.5	3.5
PP1	22.4	21.8	22.6	18	20.5 - 25.3	21.9	1.2
HDL	22.9	22.7	23.4	18	21.5 - 26.6	22.8	1.1
PG1	19.0	18.9	19.5	18	18.3 - 23.1	19.4	1.0
PSP	12.4	12.4	13.1	18	12.0 - 15.3	13.0	0.9
POB	7.3	7.4	7.4	18	7.0 - 9.1	7.6	0.5
PRN	4.5	4.4	4.5	18	4.3 - 6.0	4.7	0.5
POR	9.6	9.4	9.8	18	9.1 - 11.8	10.0	0.8
INLF	5.1	5.3	5.3	18	4.8 - 6.4	5.3	0.4
MOW	7.8	8.0	7.3	18	7.5 - 9.8	8.0	0.5
ULA	2.5	2.5	2.2	18	1.7 - 3.0	2.6	0.3
INW	4.2	3.9	4.0	18	3.8 - 5.1	4.2	0.3
INO	8.2	8.2	8.4	18	7.9 - 9.7	8.6	0.5
EYL	4.7	4.7	5.0	18	4.4 - 6.4	5.0	0.6
EYH	2.1	2.2	1.6	18	1.8 - 3.1	2.1	0.3
SPL	1.3	1.4	1.2	18	1.1 - 1.8	1.3	0.2
GS1	1.7	2.0	1.6	18	1.5 - 2.1	1.8	0.2
GS5	1.7	1.7	2.2	18	1.8 - 2.7	2.2	0.2
IDS	22.9	23.0	23.4	18	21.2 - 28.6	23.3	1.7
DCS	10.4	10.4	9.7	18	9.6 - 12.8	10.6	0.7
PPS	18.9	20.1	21.7	18	17.4 - 23.1	20.0	1.7
PCA	26.9	26.5	24.1	18	23.1 - 33.9	26.4	2.3
D1L	13.5	13.8	13.8	18	13.2 - 16.3	13.8	0.7
D1A	11.5	11.0	11.0	18	11.4 - 13.4	12.0	0.6
D1B	7.9	7.7	7.6	18	7.1 - 9.2	7.8	0.5
D1H	8.4	8.4	7.7	18	7.9 - 9.8	8.8	0.6
D1I	5.7	6.1	6.2	18	5.5 - 6.8	5.9	0.3
D1P	9.0	10.1	9.2	18	7.8 - 11.2	9.2	0.8
D1ES	4.9	3.6	3.7	17	2.1 - 4.3	3.3	0.6
D1BS	0.7	0.7	0.7	18	0.6 - 0.8	0.7	0.1
D2L	13.6	13.5	12.6	18	11.3 - 16.7	13.2	1.2
D2A	11.7	10.3	10.6	18	10.5 - 14.0	11.6	0.9
D2B	8.5	7.8	7.3	18	6.8 - 10.3	8.0	0.8
D2H	6.5	5.6	6.2	18	5.5 - 7.4	6.3	0.6
D2I	5.2	5.5	5.3	18	4.4 - 6.0	5.1	0.4
D2P	5.7	6.4	6.3	18	4.4 - 6.4	5.5	0.5
D2ES	6.0	4.8	-	18	2.8 - 5.8	4.9	0.7
D2BS	0.8	0.8	0.8	18	0.6 - 0.9	0.8	0.1
P1A	15.6	15.0	16.4	18	14.6 - 18.7	15.6	1.0
P1I	9.6	9.3	9.7	18	9.0 - 11.1	9.9	0.5
P1B	5.2	4.9	5.3	18	4.4 - 5.3	4.9	0.3
P1P	12.0	12.8	13.6	18	10.6 - 14.0	12.1	1.0
P2L	12.9	12.1	10.8	18	10.5 - 15.1	11.9	1.0
P2I	6.2	6.2	5.4	18	5.1 - 7.8	6.2	0.7
CDM	21.9	21.3	21.4	18	21.2 - 25.7	22.3	1.1
CPV	11.5	11.2	11.4	18	10.5 - 12.8	11.2	0.5
CFW	7.4	7.6	7.2	18	6.9 - 8.2	7.4	0.4
HANW	6.8	6.7	7.8	18	6.4 - 8.1	7.0	0.5
HAMW	11.9	12.2	11.6	18	10.2 - 13.4	11.8	0.7
HDW	12.7	13.6	13.7	18	12.1 - 15.8	13.4	0.8
TRW	10.9	12.4	12.5	18	9.9 - 14.6	11.6	1.3
ABW	8.9	9.0	8.7	18	8.4 - 12.3	9.8	1.1
HDH	10.1	9.7	9.9	18	8.1 - 11.8	10.1	1.0
TRH	9.8	9.9	10.4	18	7.9 - 12.7	10.6	1.1
ABH	9.1	9.6	10.7	18	8.5 - 14.5	11.3	1.6
CLO	3.6	3.9	-	10	1.2 - 5.4	3.5	1.5
CLI	7.0	6.9	-	10	3.4 - 9.0	6.2	1.8

Table 27. External measurements expressed as percentage of the total length (% TL) for all type specimens of *Flakeus bucephalus*. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus bucephalus***			
	Holotype	Paratypes		
	MNHN 2006-1754	MNHN 1997-3641	NMNZ P 34030 (2)	
TL (mm)	550.0	430.0	787.0	802.0
PCL	75.3	76.7	77.5	77.8
PD2	58.5	59.3	61.4	60.7
PD1	27.5	28.4	28.6	28.7
SVL	46.7	47.0	48.7	49.5
PP2	44.5	44.4	45.1	45.5
PP1	21.1	22.1	22.1	22.2
HDL	22.7	22.7	23.0	23.3
PG1	18.7	20.2	19.1	19.3
PSP	13.2	14.0	12.8	13.0
POB	8.1	7.9	7.5	7.6
PRN	5.0	5.2	5.2	5.1
POR	9.7	10.9	9.3	9.5
INLF	4.7	5.2	4.6	4.6
MOW	8.7	8.4	8.1	8.4
ULA	2.4	2.3	2.4	2.6
INW	4.4	5.0	5.0	4.8
INO	9.5	9.8	8.8	8.8
EYL	4.9	5.6	4.6	4.9
EYH	1.8	1.9	2.1	2.1
SPL	1.3	1.4	1.4	1.2
GS1	2.1	2.0	2.2	2.1
GS5	2.3	2.1	2.2	2.2
IDS	22.7	23.6	24.3	23.4
DCS	9.5	10.2	9.4	9.5
PPS	20.5	19.6	20.7	21.4
PCA	24.9	23.5	24.7	24.4
D1L	14.1	14.8	14.5	14.8
D1A	12.3	13.8	12.5	12.3
D1B	8.0	8.9	8.9	9.0
D1H	9.8	9.7	9.3	9.5
D1I	6.1	5.8	5.3	5.7
D1P	9.9	10.2	9.7	10.1
D1ES	3.5	2.7	2.8	3.8
D1BS	0.8	0.7	0.8	0.8
D2L	12.3	12.1	11.6	11.0
D2A	10.9	11.1	9.6	10.0
D2B	7.3	7.5	7.3	6.9
D2H	6.1	6.6	5.5	5.9
D2I	5.0	4.8	4.5	4.1
D2P	5.1	6.0	5.3	4.7
D2ES	4.5	-	3.7	-
D2BS	0.8	1.0	0.7	0.8
P1A	16.4	14.9	16.3	15.7
P1I	9.1	8.2	8.7	8.8
P1B	5.4	5.3	5.6	5.4
P1P	12.4	11.5	12.0	11.8
P2L	10.9	9.8	12.3	12.0
P2I	5.9	5.7	6.1	5.9
CDM	24.2	23.4	22.9	22.4
CPV	11.9	11.7	12.0	11.9
CFW	7.4	7.3	6.7	7.3
HANW	8.2	8.4	7.7	7.6
HAMW	13.5	13.4	12.9	12.9
HDW	13.8	13.5	12.9	13.6
TRW	11.9	12.2	10.4	11.5
ABW	9.1	10.4	8.4	8.6
HDH	10.8	11.0	10.0	9.5
TRH	11.0	12.0	10.0	10.2
ABH	10.6	11.4	9.0	8.3
CLO	-	-	2.9	3.1
CLI	-	-	6.6	6.8

Table 28. External measurements expressed as percentage of the total length (% TL) for *Flakeus albifrons*. Ranges for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

	Flakeus albifrons									
Measurements	Holotype	Paratypes					N	Range	*x*	SD
	CSIRO H 4627-01	CSIRO H 2487-01	CSIRO H 2691-01	CSIRO H 4704-02	QM I 19327	QM I 38077				
TL (mm)	615.0	636.0	691.0	610.0	610.0	608.0	7	198.0 - 760.0	433.6	262.6
PCL	76.7	75.9	78.1	76.7	77.4	77.6	7	75.9 - 78.9	77.3	1.1
PD2	59.8	59.0	60.1	59.0	60.7	60.5	7	58.0 - 62.5	60.4	1.8
PD1	26.7	26.7	26.6	26.2	29.5	28.0	7	27.0 - 31.5	29.5	1.5
SVL	46.3	45.9	47.5	46.2	45.9	47.0	7	43.9 - 50.0	47.5	2.2
PP2	43.1	43.2	44.3	43.4	43.4	43.6	7	42.3 - 48.2	45.0	2.4
PP1	20.7	19.2	20.7	21.1	19.7	21.7	7	20.4 - 26.0	22.9	2.1
HDL	21.8	21.1	23.4	22.1	22.0	23.8	7	21.3 - 26.1	23.4	1.9
PG1	18.1	17.6	18.6	18.3	18.4	20.1	7	18.0 - 23.0	20.1	2.0
PSP	11.8	12.0	12.1	12.0	12.5	12.2	7	11.5 - 15.7	13.6	1.7
POB	6.7	7.2	7.0	7.1	6.8	7.1	7	6.6 - 10.0	8.2	1.3
PRN	4.5	4.7	4.5	4.7	4.6	4.6	7	4.3 - 7.2	5.4	1.2
POR	8.8	8.3	8.9	9.2	9.6	9.6	7	8.4 - 13.0	10.7	2.0
INLF	4.6	4.2	4.7	4.5	4.6	4.7	7	4.5 - 5.8	5.1	0.5
MOW	8.3	8.1	7.9	7.8	7.8	8.3	7	7.1 - 9.2	8.1	0.6
ULA	2.4	2.2	2.3	2.5	2.5	2.2	7	2.1 - 2.7	2.4	0.2
INW	4.1	4.5	4.5	4.6	4.3	4.4	7	4.4 - 5.5	4.7	0.4
INO	8.2	8.8	8.4	8.2	8.2	8.7	7	7.9 - 10.1	8.9	0.8
EYL	4.5	4.6	5.0	4.7	1.3	4.6	7	4.5 - 6.3	5.4	0.7
EYH	1.6	1.9	1.7	1.5	1.5	1.8	7	1.6 - 3.4	2.4	0.6
SPL	1.4	1.5	1.6	1.2	1.6	1.6	7	1.4 - 2.1	1.7	0.3
GS1	2.1	1.8	1.9	1.7	2.4	1.8	7	1.7 - 2.4	2.0	0.2
GS5	2.4	2.6	2.1	2.3	2.4	2.4	7	2.0 - 2.8	2.4	0.2
IDS	25.0	25.6	25.5	25.6	29.0	27.1	7	21.2 - 26.4	23.9	2.1
DCS	9.7	10.3	10.5	9.2	11.7	10.4	7	8.8 - 11.9	10.1	1.3
PPS	19.8	20.4	20.7	20.2	19.7	19.1	7	17.4 - 23.0	19.4	1.8
PCA	26.7	25.5	26.3	25.4	26.2	27.3	7	22.0 - 26.7	24.8	2.0
D1L	14.4	14.4	14.5	15.0	14.5	14.0	7	13.3 - 15.4	14.0	0.7
D1A	12.7	12.4	11.3	12.1	11.7	11.4	7	9.2 - 13.9	12.0	1.7
D1B	8.3	8.5	8.9	8.8	8.6	8.5	7	6.8 - 8.9	7.8	0.8
D1H	9.6	9.4	8.2	9.3	8.8	9.1	7	7.9 - 10.2	9.4	0.8
D1I	6.0	6.2	5.9	6.6	6.3	5.9	7	5.3 - 6.9	6.3	0.6
D1P	10.8	10.4	10.3	11.0	10.4	10.8	7	6.7 - 12.0	8.9	1.7
D1ES	4.8	4.8	-	5.3	4.4	5.5	6	2.1 - 6.3	4.1	1.9
D1BS	1.0	1.0	1.2	1.0	0.9	0.9	7	0.5 - 1.4	0.8	0.3
D2L	12.1	12.1	11.3	12.8	11.8	11.0	7	5.7 - 13.4	11.4	2.6
D2A	10.5	10.6	10.0	11.0	9.6	9.7	7	9.2 - 12.7	10.6	1.1
D2B	7.2	7.0	7.2	8.1	6.9	6.5	7	6.5 - 7.4	6.9	0.3
D2H	6.3	5.9	5.7	5.8	6.0	6.6	7	5.4 - 7.8	6.7	1.0
D2I	5.1	5.2	4.0	4.9	5.3	4.4	7	3.7 - 6.0	5.2	0.9
D2P	6.0	6.7	5.0	5.6	6.0	5.8	7	4.7 - 6.5	5.8	0.7
D2ES	5.2	4.6	4.0	5.3	5.1	5.4	6	4.5 - 6.3	5.0	0.7
D2BS	0.8	0.7	0.8	0.8	0.9	0.9	7	0.7 - 1.0	0.9	0.1
P1A	15.9	15.9	15.8	15.7	15.1	15.0	7	12.6 - 16.1	13.8	1.3
P1I	8.5	9.4	7.4	8.3	7.8	7.6	7	6.8 - 10.5	8.8	1.2
P1B	5.1	5.1	5.4	5.2	5.0	5.4	7	4.2 - 5.2	4.6	0.4
P1P	10.9	12.6	10.8	11.0	12.9	11.2	7	8.2 - 12.3	10.2	1.7
P2L	11.3	10.8	10.8	10.8	10.9	10.8	7	9.7 - 10.9	10.4	0.4
P2I	6.0	5.9	5.6	5.0	6.3	5.7	7	4.8 - 5.8	5.4	0.3
CDM	23.3	24.2	22.4	23.3	22.7	22.1	7	20.9 - 23.7	22.4	1.1
CPV	12.0	12.4	11.8	12.2	11.7	10.8	7	10.1 - 12.9	11.7	1.0
CFW	6.6	7.1	6.7	7.2	7.1	7.0	7	6.1 - 8.2	7.2	0.7
HANW	7.0	7.4	7.1	7.1	7.9	7.2	7	6.9 - 8.9	7.9	0.7
HAMW	12.0	12.1	11.5	11.7	12.5	12.9	7	11.4 - 13.0	12.3	0.6
HDW	13.4	13.4	12.4	13.1	12.1	12.7	7	11.1 - 13.0	12.4	0.7
TRW	11.6	13.0	10.4	11.1	8.6	10.8	7	8.9 - 11.3	10.4	0.9
ABW	8.2	11.6	8.1	8.4	7.3	9.1	7	6.0 - 10.0	8.3	1.3
HDH	10.9	11.9	10.4	10.7	12.0	11.0	7	8.1 - 12.6	10.3	1.3
TRH	11.5	13.1	10.9	11.4	13.8	11.5	7	9.3 - 12.7	10.6	1.1
ABH	10.9	12.8	10.3	12.2	12.9	10.8	7	7.7 - 12.7	10.6	1.7
CLO	3.7	-	3.4	-	4.0	3.8	4	1.2 - 3.9	2.3	1.3
CLI	7.4	-	6.3	-	7.5	7.0	4	3.0 - 7.0	4.7	2.0

Table 29. External measurements for types of *Squalus formosus* and *S. altipinnis* expressed as percentage of the total length (% TL).

Measurements	*Squalus altipinnis*		*S. formosus*	
	Holotype	Paratype	Holotype	Paratype
	CSIRO CA 4111	CSIRO CA 3297	CSIRO H6816-01	CSIRO H 6292-10
TL (mm)	586.0	585.0	720.0	335.0
PCL	79.7	80.3	78.3	77.6
PD2	60.6	61.5	59.7	59.4
PD1	28.2	29.6	28.1	29.0
SVL	47.8	48.2	47.6	46.6
PP2	44.7	45.6	43.1	44.8
PP1	21.7	21.5	21.9	20.4
HDL	22.7	22.6	23.9	21.9
PG1	18.2	18.5	18.6	12.8
PSP	12.0	12.0	12.0	12.7
POB	6.5	6.9	7.0	7.4
PRN	4.4	4.3	4.5	4.9
POR	9.0	9.0	8.7	9.6
INLF	4.6	4.8	4.2	4.7
MOW	7.7	7.5	7.7	7.8
ULA	2.4	2.4	2.3	2.3
INW	4.1	4.3	4.1	4.3
INO	8.4	8.6	8.0	8.8
EYL	5.2	4.7	4.6	5.2
EYH	2.0	2.1	1.8	2.3
SPL	1.6	1.7	1.5	1.9
GS1	1.8	1.7	2.0	1.9
GS5	2.2	1.8	2.3	2.3
IDS	24.4	26.0	25.1	24.3
DCS	11.0	11.1	10.1	10.5
PPS	20.5	19.7	21.3	18.9
PCA	28.5	27.5	27.4	26.4
D1L	13.6	13.2	14.2	13.0
D1A	12.2	10.4	12.9	12.9
D1B	8.1	7.6	8.1	7.4
D1H	8.2	8.8	10.0	9.0
D1I	5.5	5.7	6.0	6.0
D1P	8.8	9.4	10.2	9.5
D1ES	5.4	5.6	6.3	3.4
D1BS	1.0	1.0	1.1	0.9
D2L	12.5	11.4	12.8	13.6
D2A	11.2	9.9	11.9	12.6
D2B	8.1	6.8	7.7	8.3
D2H	6.0	6.1	6.9	7.0
D2I	4.5	4.6	5.2	5.6
D2P	4.7	5.8	5.9	5.6
D2ES	5.2	5.2	5.9	5.5
D2BS	0.8	0.8	0.9	1.0
P1A	13.9	14.6	16.1	13.2
P1I	7.5	7.1	8.1	9.3
P1B	4.8	5.2	5.7	4.5
P1P	10.4	9.4	12.3	10.1
P2L	11.0	11.4	11.1	10.5
P2I	5.2	5.2	6.5	5.6
CDM	20.1	20.0	21.5	22.5
CPV	10.6	11.2	11.5	10.8
CFW	6.7	6.8	6.8	6.2
HANW	7.0	6.9	6.8	7.6
HAMW	10.9	11.7	11.6	12.0
HDW	12.7	12.6	13.7	12.3
TRW	10.7	10.7	11.4	12.2
ABW	7.8	8.1	8.5	10.1
HDH	9.3	9.8	10.9	10.5
TRH	9.8	9.6	12.1	12.5
ABH	9.1	10.3	10.9	12.1
CLO	3.7	3.7	3.6	-
CLI	4.8	6.3	7.2	-

Table 30. External measurements expressed as percentage of the total length (% TL) for *Flakeus notocaudatus*. Ranges for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Flakeus notocaudatus*							
	Holotype	Paratypes						
	CSIRO H 1368-02	CSIRO H 1321-01	CSIRO H 1322-01	CSIRO H 1323-01	N	Range	*x*	SD
TL (mm)	615.0	490.0	390.0	364.0	2	632.0 - 635.0	633.5	2.1
PCL	76.6	75.1	75.6	75.8	2	76.4 - 78.3	77.3	1.3
PD2	59.3	57.1	57.9	58.0	2	58.7 - 60.9	59.8	1.6
PD1	27.3	27.8	27.2	27.5	2	28.0 - 28.8	28.4	0.6
SVL	45.5	44.1	45.6	45.3	2	45.1 - 47.7	46.4	1.9
PP2	42.6	41.8	43.1	42.6	2	42.7 - 44.4	43.6	1.2
PP1	18.9	20.5	21.5	21.1	2	20.9 - 22.2	21.5	0.9
HDL	19.5	21.1	21.7	21.5	2	22.0 - 23.4	22.7	1.0
PG1	17.1	18.5	18.4	18.2	2	18.4 - 19.0	18.7	0.4
PSP	11.4	12.3	12.5	12.3	2	12.2 - 12.5	12.4	0.2
POB	6.5	7.7	7.3	7.0	2	7.0 - 7.4	7.2	0.2
PRN	4.3	4.9	4.5	4.4	2	4.6 - 5.0	4.8	0.3
POR	8.6	9.5	10.1	9.5	2	9.2 - 9.4	9.3	0.2
INLF	4.5	5.0	5.0	5.0	2	4.3 - 5.0	4.6	0.5
MOW	7.2	7.7	8.1	8.0	2	7.8 - 8.3	8.0	0.3
ULA	2.1	2.2	2.1	2.0	2	2.2 - 2.3	2.3	0.1
INW	4.1	4.6	4.4	4.5	2	4.1 - 4.4	4.3	0.2
INO	8.2	9.1	9.1	8.9	2	8.5 - 8.9	8.7	0.3
EYL	4.7	5.2	4.9	5.5	2	4.8 - 4.9	4.8	0.1
EYH	1.6	2.2	1.3	1.4	2	1.5 - 1.7	1.6	0.2
SPL	1.2	1.5	1.1	1.2	2	1.2 - 1.4	1.3	0.1
GS1	1.9	2.2	1.7	1.9	2	1.7 - 1.9	1.8	0.1
GS5	1.9	2.1	2.0	2.3	2	2.0 - 2.3	2.2	0.2
IDS	26.2	21.6	23.4	24.8	2	23.7 - 25.2	24.5	1.0
DCS	9.6	10.1	10.1	10.9	2	10.3 - 10.7	10.5	0.3
PPS	19.7	18.2	20.4	20.1	2	20.3 - 20.3	20.3	0.0
PCA	26.5	27.1	26.5	26.3	2	26.9 - 27.6	27.2	0.5
D1L	13.1	13.2	13.4	12.7	2	14.2 - 15.5	14.8	0.9
D1A	11.0	12.3	13.0	12.8	2	11.2 - 13.6	12.4	1.7
D1B	7.6	7.8	7.3	7.9	2	8.4 - 9.5	8.9	0.8
D1H	9.2	10.0	9.7	8.9	2	8.5 - 9.8	9.1	0.9
D1I	5.6	5.9	6.1	5.3	2	5.6 - 6.4	6.0	0.6
D1P	9.7	11.3	10.4	8.9	2	8.6 - 10.7	9.6	1.5
D1ES	4.4	4.4	-	2.0	-	-	-	-
D1BS	0.9	0.9	0.8	0.8	2	0.9 - 1.0	1.0	0.1
D2L	12.6	11.9	13.4	13.0	2	12.3 - 12.4	12.4	0.1
D2A	10.8	10.8	12.1	12.1	2	11.1 - 11.5	11.3	0.3
D2B	7.8	7.4	8.7	8.0	2	7.5 - 8.0	7.7	0.3
D2H	6.4	6.6	7.1	7.2	2	5.8 - 6.0	5.9	0.2
D2I	4.7	4.8	4.9	4.8	2	4.3 - 4.9	4.6	0.4
D2P	5.8	5.3	5.9	4.5	2	6.0 - 6.1	6.0	0.0
D2ES	5.6	5.4	4.9	4.4	1	-	5.0	-
D2BS	0.8	0.8	0.7	0.7	2	0.8 - 1.2	1.0	0.3
P1A	16.6	16.8	15.7	15.2	2	15.6 - 18.7	17.2	2.2
P1I	8.2	8.3	7.8	8.0	2	7.9 - 9.2	8.6	0.9
P1B	5.3	5.4	5.4	5.3	2	5.0 - 5.3	5.2	0.3
P1P	10.2	11.1	10.4	9.7	2	11.3 - 11.3	11.3	0.0
P2L	10.8	9.8	10.1	10.4	2	11.2 - 11.5	11.4	0.2
P2I	5.3	4.8	5.2	5.1	2	5.9 - 6.4	6.1	0.4
CDM	23.4	24.7	24.5	23.4	2	21.7 - 23.9	22.8	1.5
CPV	11.8	12.0	12.4	11.8	2	11.1 - 12.7	11.9	1.2
CFW	6.6	6.7	7.0	6.7	2	6.5 - 7.3	6.9	0.5
HANW	7.0	7.6	7.7	7.2	2	7.0 - 7.0	7.0	0.0
HAMW	10.8	12.3	12.3	12.2	2	12.4 - 13.3	12.9	0.7
HDW	12.2	12.8	12.5	12.4	2	13.3 - 13.6	13.4	0.3
TRW	10.0	10.2	9.0	11.8	2	11.7 - 11.9	11.8	0.1
ABW	8.4	7.9	7.0	8.4	2	8.9 - 10.5	9.7	1.1
HDH	9.3	10.4	9.9	9.7	2	10.1 - 11.0	10.6	0.6
TRH	9.5	10.6	10.4	10.4	2	10.7 - 11.0	10.9	0.2
ABH	9.0	11.3	10.5	10.9	2	9.2 - 9.7	9.4	0.3
CLO	1.6	-	-	1.0	1	-	3.6	-
CLI	3.0	-	-	2.9	1	-	6.6	-

Table 31. Tooth counts for *Flakeus crassispinus, F. raoulensis, F. bucephalus, F. albifrons* and *F. notocaudatus*. Range for type specimens of *Squalus altipinnis* is also provided.

	F. crassispinus			***F. raoulensis***			***F. bucephalus***		***F. albifrons***			***Squalus altipinnis***		***Squalus formosus***		***F. notocaudatus***		
	Holotype	Paratypes (N=3)	N=3	Holotype	Paratypes (N=2)	N= 14	Holotype	Paratype (N=1)	Holotype	Paratype (N=5)	N=4	Holotype	Paratype (N=1)	Holotype	Paratype (N=1)	Holotype	Paratype (N=3)	N=2
upper teeth (right)	12	12–12	11–13	14	13–13	13–14	13	13	12	11–12	12–14	14	14	13	13	12	12–14	12–12
upper teeth (left)	11	12–12	11–12	13	13–13	12–14	13	14	12	11–12	12–13	13	13	13	12	13	12–14	13–13
lower teeth (right)	9	9–10	10–10	11	11–12	9–11	11	11	10	9–10	9–12	11	11	10	10	10	10–11	9–9
lower teeth (left)	9	9–11	9–10	11	11–12	9–12	11	11	9	9–11	10–12	11	11	10	10	10	11–11	9–9
upper teeth series	2	2–3	2–3	2	2	1–2	2	3	3	2–3	2–3	3	2	2	2	2	2–3	2–2
lower teeth series	3	2–2	2–3	2	2	1–3	2	2	2	2–2	2–3	2	2	3	2	2	2–2	2–2
Source	present study																	

Table 32. Monospondylous, diplospondylous, precaudal, caudal and total vertebrae for *Flakeus crassispinus*, *F. raoulensis*, *F. bucephalus*, *F. albifrons*, and *F. notocaudatus*. Valeus for types of *S. altipinnis* and *S. formosus* are also provided for comparisons.

	Monospondylous vertebrae																	
	41	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**
F. crassispinus Holotype		1																
F. crassispinus Paratypes	3																	
F. raoulensis Holotype		1																
F. raoulensis Paratypes		1		1														
F. bucephalus Holotype									1									
F. albifrons Holotype						1												
F. albifrons							1											
S. altipinnis Holotype			1															
S. altipinnis Paratype					1													
S. formosus Holotype							1											
F. notocaudatus Holotype								1										

	Diplospondylous vertebrae																	
	63	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**
F. crassispinus Holotype								1										
F. crassispinus Paratypes								1	1	1								
F. raoulensis Holotype										1								
F. raoulensis Paratypes								1			1							
F. bucephalus Holotype													1					
F. albifrons Holotype													1					
F. albifrons															1			
S. altipinnis Holotype										1								
S. altipinnis Paratype															1			
S. formosus Holotype																1		
F. notocaudatus Holotype															1			

	Precaudal vertebrae																	
	84	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**
F. crassispinus Holotype			1															
F. crassispinus Paratypes	1	1		1														
F. raoulensis Holotype		1																
F. raoulensis Paratypes		1	1															
F. bucephalus Holotype										1								
F. albifrons Holotype									1									
F. albifrons									1									
S. altipinnis Holotype							1											
S. altipinnis Paratype										1								
S. formosus Holotype												1						
F. notocaudatus Holotype														1				

	Caudal vertebrae																	
	21	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**
F. crassispinus Holotype						1												
F. crassispinus Paratypes						1	2											
F. raoulensis Holotype									1									
F. raoulensis Paratypes									2									
F. bucephalus Holotype											1							
F. albifrons Holotype									1									
F. albifrons												1						
S. altipinnis Holotype					1													
S. altipinnis Paratype									1									
S. formosus Holotype										1								
F. notocaudatus Holotype									1									

	Total vertebrae																	
	111	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**	**121**	**122**	**123**	**124**	**125**	**126**	**127**	**128**
F. crassispinus Holotype		1																
F. crassispinus Paratypes	1	1	1															
F. raoulensis Holotype				1														
F. raoulensis Paratypes				1	1													
F. bucephalus Holotype														1				
F. albifrons Holotype											1							
F. albifrons														1				
S. altipinnis Holotype					1													
S. altipinnis Paratype												1						
S. formosus Holotype															1			
F. notocaudatus Holotype																1		

Table 33. External measurements for specimens of *Flakeus blainvillei* expressed as percentage of the total length (% TL). Total length is expressed in milimeters. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Flakeus blainvillei*					
	N	Range			*x*	SD
TL (mm)	21	242.0	-	700.0	413.6	123.7
PCL	21	76.6	-	80.4	78.2	0.8
PD2	21	57.3	-	74.9	60.0	3.6
PD1	21	28.4	-	31.7	29.6	0.8
SVL	21	41.7	-	50.3	45.6	1.7
PP2	21	39.6	-	44.9	42.9	1.4
PP1	21	19.0	-	22.3	21.0	0.9
HDL	21	19.8	-	23.1	21.7	0.8
PG1	21	16.8	-	19.9	18.1	0.8
PSP	21	10.8	-	13.8	12.1	0.8
POB	21	6.1	-	8.4	6.9	0.6
PRN	21	3.6	-	4.8	4.2	0.4
POR	21	7.7	-	10.6	9.2	0.7
INLF	21	3.9	-	5.7	4.8	0.5
MOW	21	7.2	-	8.2	7.9	0.2
ULA	21	2.3	-	2.8	2.5	0.2
INW	21	3.1	-	4.5	3.7	0.3
INO	21	7.2	-	9.7	8.2	0.6
EYL	21	3.9	-	5.8	4.8	0.5
EYH	21	1.0	-	2.9	1.9	0.5
SPL	21	1.1	-	1.8	1.4	0.2
GS1	21	0.9	-	2.4	1.8	0.3
GS5	21	1.8	-	2.7	2.1	0.2
IDS	21	20.0	-	24.3	21.9	1.1
DCS	21	10.3	-	11.8	11.1	0.4
PPS	21	16.8	-	21.7	18.9	1.3
PCA	21	24.6	-	28.3	26.1	1.2
D1L	21	12.4	-	14.6	13.4	0.5
D1A	21	10.6	-	13.2	11.9	0.7
D1B	21	6.6	-	8.3	7.6	0.4
D1H	21	7.9	-	10.4	9.1	0.8
D1I	21	5.2	-	6.4	5.9	0.3
D1P	21	7.5	-	10.6	9.0	0.7
D1ES	21	3.5	-	5.6	4.5	0.6
D1BS	21	0.6	-	1.0	0.7	0.1
D2L	21	11.8	-	14.6	13.0	0.7
D2A	21	10.2	-	12.3	11.3	0.5
D2B	21	6.6	-	9.1	7.8	0.6
D2H	21	5.5	-	8.0	6.7	0.6
D2I	21	4.6	-	5.8	5.3	0.3
D2P	21	4.0	-	6.4	5.2	0.6
D2ES	21	5.0	-	7.3	6.3	0.5
D2BS	21	0.7	-	1.2	0.8	0.1
P1A	21	12.5	-	17.4	15.1	0.9
P1I	21	8.4	-	10.5	9.6	0.6
P1B	21	4.0	-	5.3	4.8	0.3
P1P	21	9.5	-	13.2	11.2	0.9
P2L	21	10.0	-	12.9	11.3	0.9
P2I	21	4.5	-	7.3	5.6	0.8
CDM	21	19.5	-	22.2	21.1	0.6
CPV	21	9.6	-	12.2	11.2	0.6
CFW	21	6.3	-	7.6	6.9	0.4
HANW	21	5.9	-	8.1	7.0	0.5
HAMW	21	9.2	-	12.6	11.1	0.8
HDW	21	10.4	-	13.0	12.0	0.6
TRW	21	7.8	-	11.6	9.7	1.0
ABW	21	6.2	-	9.9	8.3	1.0
HDH	21	7.5	-	11.7	9.2	1.0
TRH	21	7.7	-	12.4	10.0	1.2
ABH	21	7.9	-	12.8	10.0	1.3
CLO	11	1.3	-	4.5	2.7	1.5
CLI	11	2.6	-	8.2	5.2	2.3

Table 34. External measurements for *Flakeus mitsukurii* expressed as percentage of the total length (% TL). Values for types of *Squalus acutirostris* are also provided for comparisons. TL is expressed in milimeters. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus mitsukurii***						***Squalus acutirostris***	
	Holotype	Paratypes (5)	N	Range	*x*	SD	Holotype	Paratype
TL (mm)	710.0	240.0 - 770.0	7	278.0 - 1120.0	844.7	282.6	635.0	975.0
PCL	77.5	76.9 - 78.6	7	77.3 - 80.4	79.0	1.0	81.9	79.0
PD2	61.0	58.4 - 60.5	7	59.4 - 63.9	61.6	1.7	64.6	63.9
PD1	32.4	30.2 - 31.3	7	28.3 - 31.8	30.3	1.2	32.3	31.8
SVL	50.0	47.3 - 48.9	7	46.4 - 52.7	49.8	2.3	52.8	46.7
PP2	47.9	45.3 - 47.6	7	43.1 - 50.0	47.1	2.4	49.3	47.2
PP1	24.6	22.1 - 24.7	7	20.0 - 23.3	21.8	1.2	24.3	23.6
HDL	24.2	22.7 - 24.4	7	20.4 - 23.5	22.1	1.2	24.4	22.6
PG1	20.4	19.9 - 20.9	7	16.6 - 22.1	19.4	2.0	20.9	17.9
PSP	12.8	12.7 - 21.5	7	11.4 - 16.6	12.8	1.9	13.9	10.6
POB	7.3	7.2 - 8.8	7	6.9 - 10.7	8.0	1.2	8.2	7.3
PRN	5.6	4.7 - 6.4	7	4.1 - 5.4	4.8	0.4	4.7	5.1
POR	10.3	8.9 - 11.5	7	7.6 - 11.1	9.4	1.1	10.4	9.5
INLF	4.3	4.4 - 5.3	7	3.9 - 4.9	4.3	0.4	6.9	8.6
MOW	8.6	7.6 - 8.1	7	6.6 - 8.1	7.5	0.5	9.4	8.2
ULA	2.5	2.1 - 2.7	7	2.1 - 2.7	2.3	0.2	2.2	1.9
INW	4.7	4.0 - 4.5	7	3.6 - 5.1	4.3	0.5	3.6	3.7
INO	9.3	9.1 - 9.8	7	7.7 - 9.4	8.4	0.6	9.6	9.2
EYL	3.6	3.1 - 4.6	7	3.4 - 5.2	3.9	0.6	3.8	2.8
EYH	0.9	1.2 - 2.5	7	1.6 - 2.3	1.8	0.2	1.6	1.7
SPL	1.3	1.3 - 1.5	7	0.8 - 1.9	1.4	0.3	1.4	0.9
GS1	1.7	1.7 - 2.3	7	1.5 - 2.8	2.1	0.5	2.4	1.3
GS5	2.3	1.8 - 2.7	7	2.1 - 2.6	2.4	0.2	3.3	1.6
IDS	21.1	21.9 - 24.7	7	21.7 - 25.9	24.3	1.6	28.3	24.6
DCS	10.6	8.1 - 11.9	7	8.9 - 11.4	10.2	0.8	10.7	8.6
PPS	21.8	18.2 - 23.4	7	19.7 - 25.3	21.1	1.9	20.3	23.1
PCA	23.7	23.0 - 26.2	7	23.6 - 27.0	24.6	1.1	26.8	21.3
D1L	13.6	11.8 - 14.5	7	12.7 - 14.9	14.0	0.8	15.0	14.1
D1A	12.0	10.2 - 13.2	7	9.3 - 12.3	11.2	1.0	27.4	10.9
D1B	8.2	5.3 - 8.8	7	7.6 - 9.0	8.4	0.5	8.5	8.6
D1H	9.8	7.0 - 9.8	7	6.9 - 8.8	7.8	0.7	6.0	5.6
D1I	6.2	6.1 - 6.5	7	5.0 - 6.6	5.7	0.6	5.7	5.6
D1P	9.3	7.0 - 10.6	7	8.4 - 9.8	9.0	0.5	8.7	7.8
D1ES	3.9	2.1 - 5.4	7	2.4 - 5.0	3.8	0.9	2.8	2.7
D1BS	1.0	0.5 - 1.0	7	0.7 - 0.9	0.8	0.1	0.6	0.4
D2L	12.3	11.6 - 12.6	7	11.2 - 13.1	12.1	0.7	10.6	9.8
D2A	10.2	9.9 - 11.6	7	7.7 - 11.9	9.6	1.3	7.6	6.8
D2B	7.2	6.2 - 7.1	7	6.8 - 8.2	7.5	0.5	5.8	4.8
D2H	6.8	4.8 - 7.9	7	4.5 - 6.6	5.2	0.7	3.3	3.6
D2I	5.3	4.9 - 5.9	7	4.1 - 4.9	4.6	0.3	5.0	5.0
D2P	6.3	4.5 - 6.3	7	5.0 - 6.2	5.7	0.5	5.7	4.7
D2ES	4.2	3.3 - 4.4	5	3.4 - 5.3	4.3	0.7	2.8	1.9
D2BS	0.9	0.8 - 1.1	7	0.7 - 0.9	0.8	0.1	0.6	0.5
P1A	15.2	12.3 - 16.7	7	13.5 - 17.7	15.7	1.5	13.5	15.4
P1I	9.5	8.1 - 9.2	7	7.7 - 9.5	8.5	0.6	8.3	6.6
P1B	5.3	3.5 - 5.8	7	4.4 - 5.2	4.8	0.3	5.4	6.1
P1P	11.7	9.5 - 12.1	7	9.2 - 12.5	10.8	1.2	11.0	10.3
P2L	11.5	8.4 - 12.6	7	9.6 - 11.6	10.8	0.6	10.2	8.7
P2I	6.3	3.1 - 7.9	7	4.2 - 5.4	5.0	0.4	5.0	5.1
CDM	24.4	21.2 - 23.4	7	20.1 - 22.2	21.2	0.9	16.7	20.5
CPV	12.1	11.5 - 12.4	7	10.7 - 12.4	11.4	0.6	10.9	11.7
CFW	7.0	6.4 - 7.7	7	6.1 - 7.4	6.6	0.5	6.9	7.4
HANW	7.3	6.9 - 7.7	7	6.6 - 8.2	7.1	0.6	6.8	5.2
HAMW	12.2	10.4 - 11.9	7	10.9 - 12.8	11.6	0.7	11.3	10.7
HDW	22.5	9.4 - 15.8	7	12.1 - 14.1	13.0	0.8	11.0	13.3
TRW	18.3	5.8 - 10.1	7	9.0 - 12.6	11.3	1.3	7.9	9.4
ABW	15.5	5.4 - 6.7	7	8.7 - 11.0	9.7	1.0	8.2	12.3
HDH	12.7	8.3 - 11.2	7	10.5 - 12.5	11.4	0.7	11.0	8.7
TRH	10.3	5.7 - 10.4	7	11.4 - 14.1	12.7	1.0	13.1	9.7
ABH	7.7	4.9 - 8.5	7	11.3 - 14.3	12.6	1.1	13.2	3.3
CLO	-	2.7 - 4.5	2	1.5 - 4.9	3.2	2.4	4.3	-
CLI	-	3.4 - 8.4	2	3.7 - 6.9	5.3	2.2	7.4	-

Table 35. External measurements for *Flakeus japonicus* expressed as percentage of the total length (% TL). Values for types of *F. japonicus* (taken from Ishikawa, 1908) and *S. nasutus* are also provided for comparisons. TL is expressed in milimeters. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	Syntype	Japan				Taiwan	Central Indo-Pacific Ocean				*Squalus nasutus*				
	Ishikawa (1908)	N	Range	*x*	SD		N	Range	*x*	SD	Holotype CSIRO H 2590-12	Paratypes CSIRO H 2567-08	CSIRO H 2598-07	CSIRO H 2608-15	CSIRO H 2898-07
TL (mm)	700.0	15	281.0 - 645.0	427.1	113.8	540.0	4	362.0 - 580.0	470.5	89.1	503.0	467.0	463.0	413.0	449.0
PCL	-	15	77.3 - 80.7	79.5	0.8	79.6	4	79.6 - 81.5	80.8	0.9	81.5	80.5	79.9	79.9	80.4
PD2	-	15	59.1 - 62.4	61.3	0.9	60.7	4	60.8 - 62.9	61.8	1.0	64.6	61.2	61.8	63.0	62.4
PD1	-	15	30.0 - 33.8	32.3	0.8	33.0	4	31.2 - 32.8	31.9	0.7	32.4	31.5	32.4	32.9	31.2
SVL	-	15	47.0 - 50.4	48.2	1.0	47.2	4	46.1 - 50.0	48.0	1.6	51.7	48.6	48.4	49.6	47.9
PP2	-	15	43.7 - 47.9	45.8	1.0	44.8	4	44.5 - 47.6	46.0	1.3	48.7	45.4	46.2	47.0	45.2
PP1	-	15	22.5 - 24.0	23.1	0.5	22.0	4	22.8 - 23.7	23.4	0.4	25.2	23.0	23.6	24.5	23.3
HDL	-	15	23.0 - 24.5	23.7	0.5	23.0	4	23.8 - 24.5	24.1	0.3	26.8	23.5	24.2	25.1	24.0
PG1	17.1	15	18.7 - 21.6	20.2	0.7	20.6	4	20.3 - 21.0	20.7	0.3	21.8	20.3	21.0	22.1	20.3
PSP	-	15	12.8 - 15.4	14.3	0.7	13.9	4	13.7 - 15.0	14.6	0.6	15.1	14.3	15.1	15.6	14.4
POB	7.1	15	8.3 - 10.1	9.4	0.5	9.3	4	9.2 - 10.4	9.7	0.5	10.3	9.5	9.5	10.0	9.3
PRN	6.0	15	5.8 - 7.2	6.6	0.4	6.8	4	6.8 - 7.5	7.1	0.3	7.5	6.6	6.9	7.3	6.8
POR	10.7	15	10.7 - 12.5	11.8	0.5	11.5	4	12.0 - 12.6	12.2	0.3	12.8	11.8	12.2	13.0	11.8
INLF	4.3	15	4.4 - 5.5	4.9	0.3	4.8	4	4.9 - 5.3	5.1	0.2	5.0	5.2	5.3	5.6	4.5
MOW	-	15	5.3 - 7.8	6.8	0.6	4.3	4	6.4 - 6.8	6.6	0.2	7.3	6.7	7.1	7.3	6.9
ULA	3.4	15	1.9 - 2.4	2.1	0.2	1.9	4	1.9 - 2.4	2.1	0.2	2.2	2.0	2.0	2.3	1.9
INW	4.7	15	4.1 - 5.4	4.5	0.4	4.4	4	4.3 - 4.7	4.5	0.2	5.1	4.8	4.6	5.4	4.5
INO	-	15	7.5 - 9.1	8.3	0.5	8.0	4	8.2 - 8.5	8.3	0.2	9.2	8.5	8.9	9.1	8.2
EYL	3.7	15	3.8 - 5.2	4.5	0.4	4.1	4	4.2 - 5.0	4.5	0.4	4.2	4.2	4.7	5.3	4.3
EYH	-	15	1.4 - 2.2	1.8	0.2	1.8	4	1.8 - 2.1	2.0	0.2	2.0	2.0	2.0	2.2	2.0
SPL	-	15	1.0 - 1.8	1.4	0.2	1.3	4	1.3 - 1.5	1.4	0.1	1.5	1.3	1.3	1.1	1.4
GS1	-	15	1.3 - 2.0	1.6	0.2	1.5	4	1.4 - 1.6	1.5	0.1	1.8	1.6	1.4	1.3	1.4
GS5	-	15	1.5 - 2.1	1.8	0.2	2.1	4	1.9 - 2.2	2.0	0.1	2.2	2.0	1.8	1.8	2.1
IDS	-	15	18.4 - 24.8	22.4	1.5	23.5	4	23.5 - 25.2	24.0	0.8	24.9	23.2	23.0	24.9	25.0
DCS	-	15	9.5 - 11.4	10.4	0.6	11.0	4	10.9 - 13.2	11.7	1.1	11.2	11.4	11.6	10.9	11.0
PPS	-	15	18.6 - 22.1	19.9	1.0	22.6	4	17.8 - 20.7	19.1	1.3	23.1	18.9	19.8	18.2	18.5
PCA	-	15	23.6 - 28.0	26.0	1.3	27.0	4	26.2 - 28.8	27.7	1.2	27.0	27.7	25.6	25.0	26.4
D1L	-	15	12.0 - 14.7	12.8	0.7	13.6	4	11.8 - 12.9	12.2	0.5	12.9	12.2	13.3	12.2	13.1
D1A	-	15	9.6 - 13.3	10.8	0.9	11.3	4	9.9 - 10.6	10.1	0.3	10.7	10.5	11.2	10.3	11.5
D1B	4.3	15	6.2 - 8.6	7.2	0.6	7.3	4	7.0 - 7.3	7.1	0.2	7.4	7.3	7.7	6.8	8.0
D1H	5.6	15	6.6 - 10.0	7.5	0.8	7.4	4	7.2 - 7.6	7.4	0.1	6.9	7.4	7.7	7.2	7.1
D1I	-	15	5.1 - 6.1	5.6	0.3	6.6	4	5.0 - 5.6	5.4	0.3	5.6	5.0	5.7	5.4	5.4
D1P	-	15	5.7 - 10.0	7.5	1.0	8.1	4	7.7 - 8.0	7.8	0.2	7.4	6.9	8.8	7.2	6.8
D1ES	5.4	14	2.0 - 3.8	2.8	0.5	3.5	3	2.4 - 3.8	3.2	0.7	3.1	3.3	3.3	3.0	3.2
D1BS	-	15	0.5 - 0.7	0.6	0.1	0.8	4	0.6 - 0.8	0.7	0.1	0.7	0.7	0.8	0.6	0.7
D2L	-	15	12.4 - 16.1	13.5	0.9	12.3	4	10.1 - 12.7	11.5	1.2	10.9	12.7	13.0	11.5	12.9
D2A	-	15	10.5 - 14.5	11.7	1.0	10.8	4	8.1 - 10.8	9.6	1.2	8.6	10.4	10.8	9.2	11.2
D2B	3.4	15	7.0 - 10.6	8.5	0.9	6.9	4	5.9 - 8.4	7.2	1.3	6.1	8.3	7.9	7.1	8.3
D2H	3.6	15	5.4 - 7.3	6.3	0.5	6.1	4	5.1 - 5.4	5.2	0.1	5.3	4.9	5.0	4.8	5.4
D2I	-	15	4.3 - 5.5	5.0	0.4	5.1	4	4.0 - 4.8	4.4	0.3	4.8	4.5	4.9	4.7	4.5
D2P	-	15	4.4 - 6.1	5.2	0.5	5.1	4	4.5 - 5.5	5.0	0.4	4.9	4.6	5.3	4.6	5.0
D2ES	7.0	14	4.1 - 5.6	4.8	0.6	5.6	4	4.0 - 4.5	4.3	0.2	3.9	4.0	4.9	4.1	4.2
D2BS	-	15	0.7 - 1.0	0.8	0.1	0.8	4	0.8 - 0.9	0.9	0.0	0.9	0.9	1.1	0.7	1.1
P1A	-	15	10.9 - 14.2	12.5	0.9	5.9	4	12.4 - 13.9	13.0	0.7	14.2	13.3	14.0	12.9	13.6
P1I	-	15	7.5 - 8.9	8.3	0.4	8.8	4	7.2 - 8.3	7.7	0.5	7.8	8.1	8.5	8.2	8.3
P1B	-	15	3.8 - 4.7	4.2	0.3	4.6	4	4.1 - 4.9	4.6	0.4	5.0	4.4	5.0	4.4	4.7
P1P	-	15	6.8 - 10.1	7.9	0.9	7.8	4	6.2 - 8.9	8.1	1.3	8.2	7.2	8.3	7.4	8.2
P2L	-	15	9.6 - 12.4	10.8	0.7	10.2	4	9.3 - 11.9	10.5	1.1	10.7	12.6	10.8	11.1	12.1
P2I	-	15	4.6 - 7.3	5.3	0.7	5.7	4	4.3 - 6.8	5.6	1.1	5.1	6.4	5.7	5.4	7.0
CDM	18.9	15	19.6 - 21.8	20.3	0.7	20.4	4	18.1 - 19.4	18.9	0.6	18.5	19.4	19.8	19.7	19.5
CPV	10.3	15	6.6 - 11.7	10.6	1.2	11.5	4	10.2 - 11.5	11.0	0.6	11.5	11.7	12.4	10.3	11.0
CFW	-	15	6.0 - 7.4	6.6	0.4	6.7	4	6.2 - 6.7	6.5	0.2	6.8	6.9	7.0	6.8	7.5
HANW	-	15	6.3 - 8.1	7.4	0.5	7.3	4	6.9 - 7.6	7.2	0.3	7.7	7.5	7.8	8.3	7.5
HAMW	-	15	9.7 - 11.9	10.8	0.6	10.2	4	10.2 - 10.6	10.4	0.2	10.7	10.7	11.3	11.2	11.1
HDW	-	15	11.0 - 13.0	11.7	0.5	11.7	4	11.2 - 12.1	11.4	0.4	12.7	12.0	11.9	12.0	11.6
TRW	-	15	9.2 - 10.8	10.2	0.5	9.1	4	8.7 - 10.0	9.4	0.6	12.0	10.0	9.5	9.7	9.4
ABW	-	15	7.1 - 10.9	9.3	1.1	6.9	4	6.3 - 9.0	7.8	1.1	9.2	9.1	8.2	8.4	7.7
HDH	-	15	8.5 - 10.6	9.5	0.7	10.1	4	8.9 - 9.6	9.1	0.3	9.8	8.9	9.1	9.8	9.4
TRH	-	15	8.3 - 11.6	10.1	1.0	10.8	4	8.9 - 10.3	9.6	0.6	10.2	10.2	9.8	10.1	10.3
ABH	-	15	8.7 - 12.2	9.9	1.1	10.9	4	8.3 - 11.3	9.8	1.3	12.2	9.4	9.8	10.5	10.8
CLO	-	7	1.4 - 4.8	2.8	1.6	-	2	2.1 - 5.6	3.9	2.5	-	5.2	-	-	3.3
CLI	-	7	2.8 - 7.9	4.9	2.5	-	2	4.3 - 9.1	6.7	3.4	-	9.0	-	-	6.6

Table 36. External measurements for *Flakeus montalbani* expressed as percentage of the total length (% TL). Values for holotype of *F. montalbani* taken from Last *et al*. (2007). Measurements for types of *Squalus chloroculus* are also provided for comparisons. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus montalbani***					***Squalus chloroculus***				
	Holotype Last *et al*. (2007)	N	Range	*x*	SD	Holotype CSIRO H 4775-01	Paratypes CSIRO H 2867-02	CSIRO H 2867-05	CSIRO H 5941-01	CSIRO CA 121
TL (mm)	311.0	10	208.0 - 885.0	546.5	222.3	752.0	732.0	782.0	760.0	725.0
PCL	76.5	10	75.5 - 79.5	77.6	1.2	79.1	78.4	78.1	80.5	77.7
PD2	57.6	10	57.7 - 63.1	60.2	1.5	61.8	60.8	61.4	63.6	60.0
PD1	30.7	10	28.3 - 31.1	29.8	1.0	29.9	29.5	32.0	29.6	29.5
SVL	47.2	10	45.7 - 50.0	48.4	1.4	49.5	49.6	50.1	52.0	48.7
PP2	43.8	10	44.7 - 48.1	46.1	1.2	46.1	46.4	47.3	48.2	46.2
PP1	22.8	10	22.0 - 24.7	22.9	0.9	22.1	21.6	21.7	21.7	22.6
HDL	23.2	10	22.6 - 25.3	23.8	0.8	23.1	22.8	23.7	22.0	23.9
PG1	20.3	10	19.1 - 21.6	20.1	0.8	19.8	18.6	20.1	18.9	20.4
PSP	13.4	10	12.0 - 14.1	13.1	0.7	13.1	12.5	13.0	12.7	13.2
POB	7.1	10	7.4 - 10.2	8.2	0.8	7.9	7.8	8.1	7.7	8.4
PRN	4.6	10	4.9 - 5.9	5.4	0.3	5.4	5.0	5.4	5.2	5.9
POR	10.1	10	9.5 - 11.8	10.5	0.8	10.1	9.5	9.9	10.2	10.2
INLF	5.3	10	3.7 - 5.4	5.0	0.5	4.9	4.6	4.8	4.9	4.7
MOW	6.5	10	7.2 - 9.1	8.0	0.6	7.7	7.9	8.9	7.7	8.8
ULA	2.5	10	2.0 - 3.4	2.5	0.4	2.4	2.3	2.6	2.3	2.4
INW	5.2	10	3.6 - 5.1	4.6	0.4	4.3	4.7	5.1	4.8	4.5
INO	8.7	10	8.0 - 9.8	9.0	0.6	8.2	8.6	9.4	8.6	9.1
EYL	4.3	10	4.1 - 6.6	5.0	0.8	4.5	4.6	4.6	4.4	4.4
EYH	1.6	10	1.3 - 2.3	1.9	0.3	2.0	2.2	2.1	2.3	1.8
SPL	1.5	10	1.2 - 1.8	1.5	0.2	1.4	1.5	1.5	1.5	1.4
GS1	1.6	10	1.4 - 2.3	1.8	0.3	1.9	2.6	2.8	2.0	1.7
GS5	2.0	10	1.9 - 2.3	2.1	0.1	2.2	2.4	2.7	2.5	2.2
IDS	21.7	10	21.8 - 25.6	23.8	1.3	25.0	24.9	24.0	27.4	23.2
DCS	11.2	10	9.2 - 11.6	10.6	0.7	10.0	10.1	9.9	10.2	10.4
PPS	18.9	10	19.4 - 22.0	20.8	0.9	21.5	20.6	21.7	23.7	21.0
PCA	26.3	10	22.0 - 26.1	24.2	1.1	25.0	24.0	23.5	24.9	23.6
D1L	14.2	10	12.2 - 14.8	13.5	0.7	13.4	13.7	13.6	12.3	13.8
D1A	12.4	10	10.6 - 12.6	11.2	0.6	11.4	11.3	11.0	9.8	11.5
D1B	8.3	10	6.0 - 8.4	7.7	0.7	7.9	8.5	8.2	7.1	8.2
D1H	6.1	10	7.0 - 8.6	7.8	0.6	6.8	7.0	7.4	6.6	7.2
D1I	6.2	10	5.1 - 6.6	5.9	0.5	5.5	5.3	5.5	5.2	5.7
D1P	6.7	10	6.1 - 9.5	7.6	0.9	7.9	7.9	8.7	7.4	8.4
D1ES	2.1	9	1.1 - 3.5	2.5	0.7	3.3	3.1	3.4	2.5	2.4
D1BS	0.7	10	0.6 - 0.9	0.7	0.1	0.7	0.7	0.7	0.6	0.6
D2L	13.4	10	10.8 - 13.0	11.8	0.7	11.4	11.9	11.7	11.2	12.0
D2A	10.2	10	5.3 - 10.0	8.8	1.5	8.4	9.3	9.4	8.5	9.5
D2B	8.1	10	6.0 - 7.5	6.9	0.5	6.8	7.8	7.3	6.3	7.4
D2H	4.2	10	4.0 - 6.5	5.3	0.7	4.5	4.3	5.2	4.5	4.6
D2I	5.9	10	4.3 - 5.5	5.0	0.4	4.5	4.2	4.5	4.2	4.5
D2P	5.2	10	4.4 - 6.3	5.4	0.6	5.5	5.0	5.0	5.1	5.4
D2ES	3.6	9	3.0 - 4.2	3.6	0.5	4.0	3.5	-	2.7	3.5
D2BS	0.8	10	0.6 - 1.1	0.8	0.2	0.7	0.8	0.8	0.6	0.6
P1A	13.6	10	12.8 - 16.5	14.3	1.1	14.9	15.4	17.3	13.9	16.2
P1I	8.9	10	7.8 - 9.5	8.8	0.6	8.2	8.4	8.5	7.9	9.5
P1B	5.0	10	4.5 - 5.6	5.1	0.4	4.6	4.5	5.7	5.1	4.3
P1P	9.6	10	7.8 - 11.4	9.9	1.2	11.1	11.1	13.8	10.5	12.0
P2L	10.1	10	9.3 - 12.1	10.3	0.9	11.9	11.9	10.9	11.5	11.1
P2I	3.7	10	4.1 - 6.8	5.3	0.9	5.6	5.9	4.8	5.5	5.3
CDM	22.6	10	20.0 - 23.4	22.4	0.9	21.3	21.9	21.6	19.5	22.6
CPV	12.2	10	11.3 - 12.7	12.0	0.5	12.0	11.6	12.7	10.8	12.3
CFW	6.7	10	6.7 - 7.8	7.3	0.4	7.2	6.6	7.6	6.6	6.9
HANW	7.7	10	7.2 - 8.9	7.8	0.5	7.1	7.1	7.9	7.4	7.1
HAMW	10.6	10	11.1 - 13.3	11.9	0.7	11.5	11.8	12.6	11.1	12.3
HDW	12.1	10	9.7 - 14.0	13.0	1.2	12.8	12.8	14.3	14.3	13.2
TRW	10.9	10	9.8 - 11.9	11.1	0.8	11.6	11.5	13.6	13.8	10.6
ABW	8.2	10	7.0 - 10.7	9.3	1.2	8.9	9.1	11.9	11.1	8.6
HDH	9.1	10	6.9 - 12.3	10.2	1.4	9.8	11.0	11.8	12.1	10.4
TRH	12.0	10	7.9 - 12.8	10.9	1.3	11.1	11.4	13.2	13.1	12.2
ABH	12.6	10	7.0 - 12.9	10.8	1.7	10.1	11.1	13.1	12.5	11.4
CLO	1.4	4	1.6 - 5.0	3.2	1.7	4.4	5.4	-	4.6	-
CLI	5.4	4	2.6 - 8.7	5.1	2.9	6.8	7.7	-	7.3	-

Table 37. Tooth counts for *Flakeus blainvillei*, *F. mitsukurii*, *F. japonicus* and *F. montalbani*. Range for types of *Squalus nasutus* and *S. chloroculus* are also provided for comparisons.

	F. blainvillei	***F. mitsukurii***			***Flakeus japonicus***		***Squalus nasutus***		***F. montalbani***		***Squalus chloroculus***	
	N= 15	Holotype	Paratypes N= 1	N= 13	Japan N= 10	Australia N= 3	Holotype	Paratypes N= 2	Holotype	N= 6	Holotype	Paratypes N= 6
upper teeth (right)	13–14	13	13	12–14	12–14	12–12	13	12–12	-	12–14	13	12–14
upper teeth (left)	12–14	15	12	12–15	12–13	12–12	13	13–13	-	13–14	13	12–14
upper intermediate teeth	-	-	1	-	-	-	-	-	-	-	-	-
lower teeth (right)	10–12	12	11	10–12	10–12	9–10	11	10–11	-	10–12	10	9–12
lower teeth (left)	10–12	12	11	10–12	10–12	9–10	10	10–11	-	10–11	9	10–11
lower intermediate teeth	-	-	-	-	-	-	-	-	-	-	-	-
upper teeth series	2–3	2	2	1–3	2–2	1–3	3	2–3	2	2–2	2	2–3
lower teeth series	2–3	2	2	2–2	2–2	2–2	2	2–3	2	2–2	2	2–2
Source	present study											

Table 38. Monospondylous, diplospondylous, precaudal, caudal and total vertebrae for *Flakeus blainvillei*, *F. mitsukurii*, *F. montalbani*, and *F. japonicus*. Valeus for types of *S. nasutus* and *S. chloroculus* are also provided for comparisons.

	Monospondylous vertebrae																	
	33	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**
Flakeus blainvillei								1	5		1							
F. mitsukurii										1		2	1	1				
F. japonicus Japan									1	2	1							
S. nasutus Holotype								1										
S. nasutus Paratypes					1	1	1											
F. montalbani						1							1					
S. chloroculus Holotype												1						

	Diplospondylous vertebrae																	
	63	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**
Flakeus blainvillei					2	3	1											
F. mitsukurii Holotype						1												
F. mitsukurii Paratype										1								
F. mitsukurii							1	3		1								
F. japonicus Japan			1								2		1					
S. nasutus Holotype						1												
S. nasutus Paratypes				1		1			1									
F. montalbani											1	1						
S. chloroculus Holotype									1									

	Precaudal vertebrae																	
	78	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**
Flakeus blainvillei			1	1		4	1											
F. mitsukurii							2		1	1			1					
F. japonicus Japan							1			2	1							
S. nasutus Holotype					1													
S. nasutus Paratypes			1	1		1												
F. montalbani							1	1										
S. chloroculus Holotype								1										

	Caudal vertebrae																	
	23	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
Flakeus blainvillei				2	4													
F. mitsukurii Holotype								1										
F. mitsukurii Paratype								1										
F. mitsukurii				1		1	2	1	1									
F. japonicus Japan	1					2	1											
S. nasutus Holotype				1														
S. nasutus Paratypes		2			1													
F. montalbani					1							1						
S. chloroculus Holotype								1										

	Total vertebrae																	
	101	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**
Flakeus blainvillei							3		1	1	1							
F. mitsukurii												1	1			2	1	
F. japonicus Japan							1								1	2		
S. nasutus Holotype								1										
S. nasutus Paratypes				1	1					1								
F. montalbani												1						1
S. chloroculus Holotype															1			

Table 39. External measurements for *Flakeus griffini* expressed as percentage of the total length (% TL). Total length is expressed in milimeters. Values for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Flakeus griffini*				*Flakeus* cf. *griffini*				
	N	Range	*x*	SD	Paralectotype	N	Range	*x*	SD
TL (mm)	20	197.0 - 1000.0	605.9	257.7	975.0	10	735.0 - 995.0	865.1	90.2
PCL	20	75.7 - 80.0	77.5	1.2	80.0	10	76.8 - 79.6	78.4	0.8
PD2	20	57.5 - 71.9	60.5	3.0	62.6	10	58.9 - 62.8	60.9	1.1
PD1	20	27.2 - 31.8	29.5	1.2	29.9	10	28.2 - 39.7	30.3	3.4
SVL	20	47.1 - 52.7	49.3	1.5	51.4	10	48.4 - 61.4	51.7	3.7
PP2	20	44.9 - 83.5	49.7	9.5	49.0	10	45.2 - 58.2	52.0	13.3
PP1	20	20.6 - 24.7	22.2	1.0	22.6	10	19.9 - 22.9	21.5	0.8
HDL	20	21.7 - 25.0	22.8	0.9	22.8	10	21.0 - 23.6	22.4	0.7
PG1	20	18.4 - 21.2	19.5	0.7	19.2	10	18.5 - 19.9	19.1	0.5
PSP	20	12.2 - 14.8	13.4	0.7	12.2	10	11.9 - 18.7	13.0	2.0
POB	20	7.7 - 9.0	8.3	0.4	7.6	10	7.6 - 12.5	8.3	1.5
PRN	20	5.2 - 6.4	5.7	0.3	5.1	10	5.2 - 5.8	5.4	0.2
POR	20	9.5 - 12.3	10.6	0.7	9.2	10	9.3 - 10.1	9.8	0.3
INLF	20	4.2 - 5.7	4.8	0.4	4.4	10	4.1 - 4.5	4.4	0.1
MOW	20	6.5 - 8.1	7.7	0.4	7.5	10	7.2 - 7.8	7.5	0.2
ULA	20	2.0 - 2.7	2.4	0.2	2.2	10	2.1 - 2.5	2.3	0.1
INW	20	4.0 - 4.9	4.7	0.2	4.5	10	4.3 - 4.9	4.5	0.2
INO	20	7.7 - 9.6	8.4	0.6	7.4	10	7.6 - 8.1	7.9	0.2
EYL	20	3.8 - 6.7	5.0	0.7	4.1	10	3.8 - 4.6	4.2	0.2
EYH	20	1.3 - 2.3	1.7	0.3	1.4	10	1.5 - 2.3	1.8	0.2
SPL	20	1.1 - 1.8	1.4	0.2	1.3	10	1.0 - 1.3	1.2	0.1
GS1	20	1.3 - 2.5	1.8	0.3	1.9	10	1.4 - 2.1	1.8	0.2
GS5	20	1.7 - 2.4	2.1	0.2	2.2	10	1.8 - 2.4	2.2	0.2
IDS	20	20.9 - 25.1	23.3	1.3	24.8	10	23.8 - 25.9	24.6	0.8
DCS	20	9.0 - 11.0	10.1	0.5	9.3	10	9.4 - 10.2	9.8	0.3
PPS	20	19.1 - 26.3	21.5	1.6	25.9	10	22.4 - 24.6	23.5	0.8
PCA	20	22.9 - 25.9	24.2	0.7	23.9	10	22.8 - 25.4	23.9	0.9
D1L	20	13.1 - 15.9	14.2	0.7	12.9	10	13.0 - 14.8	13.9	0.5
D1A	20	10.7 - 14.9	12.8	1.1	9.9	10	11.0 - 12.4	11.5	0.4
D1B	20	7.2 - 9.4	8.1	0.6	7.7	10	7.2 - 9.4	8.3	0.6
D1H	20	7.3 - 11.0	8.9	1.0	7.1	10	7.7 - 9.0	8.2	0.5
D1I	20	4.9 - 7.0	6.1	0.5	5.3	10	4.9 - 6.4	5.7	0.4
D1P	20	6.0 - 10.5	8.9	1.0	8.4	10	7.3 - 9.2	8.5	0.6
D1ES	20	2.3 - 3.8	3.0	0.4	2.8	10	2.7 - 4.1	3.5	0.4
D1BS	20	0.5 - 0.7	0.6	0.0	0.6	10	0.6 - 0.7	0.6	0.0
D2L	20	11.8 - 13.5	12.6	0.6	11.6	10	11.4 - 13.1	12.2	0.6
D2A	20	10.0 - 12.4	11.0	0.7	9.5	10	9.5 - 11.8	10.5	0.6
D2B	20	6.7 - 8.4	7.5	0.5	7.2	10	6.8 - 8.9	7.5	0.6
D2H	20	5.5 - 8.7	6.7	0.8	5.2	10	5.4 - 7.6	6.1	0.6
D2I	20	3.6 - 6.2	5.1	0.7	4.2	10	4.5 - 4.8	4.6	0.1
D2P	20	4.0 - 6.3	5.5	0.6	6.0	10	5.1 - 5.9	5.6	0.2
D2ES	20	3.6 - 5.6	4.6	0.6	2.9	10	4.0 - 5.0	4.4	0.3
D2BS	20	0.6 - 1.0	0.8	0.1	0.7	10	0.6 - 0.8	0.7	0.1
P1A	20	12.6 - 17.0	14.8	1.2	14.2	10	13.6 - 16.7	15.0	1.0
P1I	20	7.4 - 9.2	8.3	0.5	7.2	10	7.2 - 9.3	7.9	0.6
P1B	20	3.7 - 5.8	4.8	0.6	5.2	10	4.4 - 5.2	4.8	0.3
P1P	20	8.0 - 12.6	10.9	1.3	10.0	10	9.3 - 12.4	10.9	0.9
P2L	20	9.3 - 12.7	10.8	0.9	10.7	10	10.2 - 12.2	11.1	0.6
P2I	20	4.6 - 6.3	5.5	0.4	4.5	10	4.6 - 6.6	5.4	0.6
CDM	20	20.4 - 24.1	22.4	1.1	19.9	10	20.4 - 22.8	21.6	0.7
CPV	20	10.3 - 13.0	11.6	0.7	9.8	10	10.0 - 11.7	10.9	0.5
CFW	20	6.6 - 7.9	7.2	0.4	6.6	10	6.4 - 7.5	6.8	0.3
HANW	20	6.9 - 8.3	7.4	0.4	6.7	10	6.6 - 7.1	6.9	0.2
HAMW	20	10.5 - 12.8	11.9	0.5	11.0	10	10.7 - 11.9	11.2	0.5
HDW	20	11.4 - 14.2	12.7	0.7	9.7	10	10.1 - 14.2	12.4	1.1
TRW	20	8.0 - 13.2	10.7	1.3	9.7	10	10.4 - 13.2	11.4	0.8
ABW	20	6.0 - 11.4	9.0	1.3	8.7	10	7.7 - 10.3	9.3	0.9
HDH	20	7.6 - 10.6	9.4	0.8	12.1	10	8.8 - 12.3	10.0	1.0
TRH	20	7.6 - 11.7	9.8	1.2	10.4	10	8.9 - 12.5	10.5	1.2
ABH	20	8.3 - 12.5	9.7	1.3	8.2	10	8.6 - 13.0	10.3	1.5
CLO	10	1.2 - 4.7	3.0	1.5	-	3	3.7 - 4.3	4.0	0.3
CLI	10	2.5 - 7.8	5.3	2.1	-	3	6.7 - 7.2	7.0	0.2

Table 40. External measurements for *Flakeus melanurus* expressed as percentage of the total length (% TL). Total length is expressed in milimeters. Values for holotype of *Squalus rancureli* is also provided for comparisons. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Flakeus melanurus* Holotype MNHN 1980-0460	*Squalus rancureli* MNHN 1978-0693	N	Range	*x*	SD
TL (mm)	670.0	680.0	9	527.0 - 695.0	651.9	50.7
PCL	77.6	80.0	9	78.6 - 80.1	79.0	0.6
PD2	60.7	61.9	9	60.2 - 63.8	61.9	1.1
PD1	30.9	31.3	9	29.6 - 34.8	31.6	1.6
SVL	48.2	47.6	9	46.7 - 50.8	48.4	1.3
PP2	44.2	44.4	9	30.2 - 47.8	44.0	5.3
PP1	22.8	25.0	9	22.2 - 25.9	23.8	1.4
HDL	23.6	25.4	9	22.4 - 26.8	24.5	1.4
PG1	20.0	22.4	9	20.2 - 23.2	21.8	1.1
PSP	14.7	15.8	9	15.3 - 16.8	15.9	0.5
POB	9.6	10.3	9	10.0 - 10.9	10.5	0.4
PRN	6.9	7.7	9	7.2 - 8.4	7.8	0.4
POR	12.6	13.6	9	12.7 - 14.3	13.2	0.5
INLF	4.8	5.0	9	4.9 - 5.9	5.3	0.3
MOW	6.4	5.8	9	6.2 - 7.4	6.7	0.4
ULA	2.1	2.1	9	1.9 - 2.6	2.2	0.2
INW	5.1	5.3	9	5.1 - 6.1	5.6	0.3
INO	8.2	7.9	9	8.0 - 8.9	8.5	0.3
EYL	4.4	4.6	9	4.3 - 5.2	4.8	0.2
EYH	1.6	1.8	9	1.5 - 2.1	1.8	0.2
SPL	0.9	1.1	9	1.1 - 1.6	1.3	0.2
GS1	1.6	1.3	9	1.3 - 2.1	1.7	0.3
GS5	1.9	2.0	9	1.8 - 2.4	2.1	0.2
IDS	22.5	25.1	9	22.8 - 25.7	23.9	0.9
DCS	9.3	10.0	9	8.2 - 10.5	9.4	0.7
PPS	15.2	13.7	9	14.8 - 22.0	19.3	2.1
PCA	25.7	28.2	9	24.3 - 26.9	25.9	0.9
D1L	13.8	13.4	9	12.9 - 14.1	13.5	0.4
D1A	11.1	10.1	9	8.3 - 12.8	11.7	1.3
D1B	7.9	8.3	9	7.6 - 9.1	8.2	0.5
D1H	9.5	8.8	9	8.2 - 10.3	9.0	0.6
D1I	5.8	5.2	9	5.0 - 5.8	5.4	0.3
D1P	10.6	9.8	9	8.4 - 9.7	9.0	0.4
D1ES	3.9	3.7	9	2.9 - 5.1	4.2	0.6
D1BS	0.8	0.8	9	0.7 - 1.0	0.8	0.1
D2L	13.6	12.6	9	11.6 - 13.0	12.3	0.5
D2A	12.5	12.2	9	10.8 - 12.3	11.6	0.6
D2B	8.6	8.4	9	7.2 - 9.0	7.9	0.5
D2H	6.9	6.7	9	6.3 - 8.0	7.2	0.5
D2I	4.7	4.3	9	4.1 - 4.8	4.4	0.3
D2P	6.6	5.8	9	3.3 - 5.8	4.8	0.8
D2ES	6.2	4.9	9	5.7 - 6.5	5.9	0.3
D2BS	0.7	0.9	9	0.7 - 0.9	0.8	0.1
P1A	14.3	14.2	9	13.5 - 15.3	14.3	0.6
P1I	8.2	7.4	9	7.0 - 8.1	7.6	0.4
P1B	4.2	3.9	9	4.4 - 5.0	4.6	0.2
P1P	11.1	10.5	9	9.3 - 12.0	10.4	1.0
P2L	12.7	12.2	9	10.4 - 12.0	11.1	0.5
P2I	7.3	5.9	9	5.3 - 6.8	6.1	0.5
CDM	21.7	20.2	9	19.2 - 20.8	20.4	0.5
CPV	10.0	10.9	9	4.9 - 11.3	10.2	2.0
CFW	6.3	6.2	9	5.7 - 6.7	6.3	0.3
HANW	7.7	7.6	9	7.8 - 8.8	8.3	0.4
HAMW	11.2	10.5	9	10.8 - 12.7	11.9	0.6
HDW	11.9	11.1	9	11.7 - 13.3	12.4	0.5
TRW	9.3	9.4	9	9.3 - 12.3	11.0	1.2
ABW	6.8	8.6	9	8.3 - 11.8	10.3	1.2
HDH	7.6	9.4	9	8.8 - 11.2	10.1	0.9
TRH	9.3	11.1	9	9.2 - 13.3	11.4	1.4
ABH	9.2	10.9	9	8.8 - 13.7	11.2	1.3
CLO	3.8	4.2	3	3.6 - 4.3	3.9	0.3
CLI	7.9	6.8	3	7.1 - 8.6	7.8	0.7

Table 41. External measurements for *Flakeus lalannei* expressed as percentage of the total length (% TL). Total length is expressed in milimeters. N: number of specimens; *x*: mean.

Measurements	*Flakeus lalannei*		
	Holotype HUJ 18445	N	*x*
TL (mm)	788.0	1	810.0
PCL	80.5	1	82.1
PD2	63.5	1	66.0
PD1	29.4	1	31.9
SVL	50.8	1	48.8
PP2	48.9	1	46.9
PP1	22.1	1	21.0
HDL	21.8	1	21.6
PG1	18.0	1	18.0
PSP	11.7	1	11.7
POB	6.7	1	7.2
PRN	4.7	1	4.8
POR	8.7	1	9.6
INLF	4.6	1	4.6
MOW	6.8	1	7.0
ULA	2.5	1	2.1
INW	3.9	1	3.9
INO	7.3	1	7.7
EYL	5.2	1	4.1
EYH	1.7	1	1.9
SPL	1.1	1	1.4
GS1	2.1	1	1.7
GS5	1.9	1	2.2
IDS	26.6	1	28.4
DCS	10.7	1	10.7
PPS	24.6	1	20.1
PCA	24.4	1	26.9
D1L	12.8	1	12.9
D1A	10.7	1	9.5
D1B	8.2	1	8.0
D1H	6.2	1	6.5
D1I	4.8	1	5.0
D1P	7.3	1	8.7
D1ES	3.4	1	2.5
D1BS	0.8	1	0.7
D2L	9.7	1	10.2
D2A	7.6	1	7.6
D2B	6.2	1	6.1
D2H	3.2	1	4.6
D2I	3.8	1	4.1
D2P	5.2	1	5.6
D2ES	3.1		-
D2BS	0.8	1	0.8
P1A	14.7	1	14.5
P1I	7.0	1	7.2
P1B	5.3	1	4.5
P1P	11.2	1	12.1
P2L	9.9	1	10.8
P2I	4.9	1	6.0
CDM	-	1	17.6
CPV	-	1	11.5
CFW	5.8	1	6.5
HANW	5.9	1	7.3
HAMW	8.4	1	10.3
HDW	12.2	1	12.7
TRW	9.3	1	9.2
ABW	9.5	1	8.1
HDH	8.9	1	9.6
TRH	9.9	1	10.3
ABH	9.9	1	10.2
CLO	-		-
CLI	-		-

Table 42. Tooth counts for *Flakeus griffini*, *F. melanurus* and *F. lalannei.* Values for *S. rancureli* are also provided for comparisons.

	F. griffini		***F. melanurus***		***S. rancureli***	***F. lalannei***	
	Paralectotype	N= 18	Holotype	N=10	Holotype	Holotype	N= 1
upper teeth (right)	-	11–14	12	12–14	13	14	14
upper teeth (left)	-	12–14	13	12–13	11	13	14
intermediate upper teeth	-	-	-	1–1	1	-	-
lower teeth (right)	-	9–12	11	11–12	11	12	12
lower teeth (left)	10	9–12	11	11–12	11	10	12
intermediate lower teeth	-	-	-	1–1	-	-	-
upper teeth series	3	2–3	3	2–3	3	2	2
lower teeth series	2	2–3	2	1–3	2	3	2
Source	present study						

Table 43. Monospondylous, diplospondylous, precaudal, caudal and total vertebrae for *Flakeus griffini* and *F. melanurus*. Value for holotype of *S. rancureli* is also provided for comparisons.

Monospondylous vertebrae

	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61
F. griffini Paralectotype																		1														
F. griffini																	2	4	3	1												
F. melanurus Holotype												1																				
F. melanurus												1																				
S. rancureli Holotype												1																				

Diplospondylous vertebrae

	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91
F. griffini Paralectotype															1																	
F. griffini										1	3	1	4	1																		
F. melanurus Holotype														1																		
F. melanurus																		1														
S. rancureli Holotype																				1												

Precaudal vertebrae

	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98
F. griffini Paralectotype																									1							
F. griffini																				1		1	2	4	1	1						
F. melanurus Holotype																			1													
F. melanurus																								1								
S. rancureli Holotype																												1				
F. lalannei Holotype			1																													
F. lalannei Paratype	1																															

Caudal vertebrae

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
F. griffini Paralectotype											1																					
F. griffini								1	2	5	1	1																				
F. melanurus Holotype										1																						
F. melanurus									1																							
S. rancureli Holotype							1																									
F. lalannei Holotype																																
F. lalannei Paratype																																

Total vertebrae

	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121
F. griffini Paralectotype																																1
F. griffini																												2	4	2	2	
F. melanurus Holotype																									1							
F. melanurus																													1			
S. rancureli Holotype																															1	
F. lalannei Holotype						1																										
F. lalannei Paratype				1	1																											

Table 44. External measurements for *Flakeus grahami* expressed as percentage of the total length (% TL). Ranges for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Flakeus grahami*							
	Holotype	Paratypes						
	CSIRO H 4476-01	N	Range	*x*	SD	N	Range	*x*	SD
TL (mm)	602.0	10	278.0 - 697.0	539.2	139.1	15	175.0 - 935.0	580.3	241.0
PCL	78.4	10	64.6 - 80.9	77.6	5.0	15	74.3 - 94.6	79.2	4.6
PD2	59.3	10	58.7 - 63.1	61.0	1.6	15	57.1 - 62.9	60.3	1.8
PD1	29.2	10	29.5 - 31.6	30.8	0.7	15	28.8 - 33.4	30.4	1.3
SVL	46.5	10	46.4 - 50.1	48.5	1.3	15	46.9 - 54.5	48.8	1.8
PP2	43.2	10	43.3 - 47.5	45.5	1.5	15	44.3 - 52.0	45.9	1.9
PP1	20.6	10	20.8 - 23.3	22.2	0.7	15	20.0 - 25.0	22.3	1.3
HDL	22.8	10	22.3 - 24.1	23.4	0.6	15	21.9 - 25.9	23.5	1.0
PG1	19.1	10	19.0 - 20.8	20.0	0.5	15	18.8 - 21.8	20.1	1.0
PSP	12.9	10	13.0 - 14.5	13.9	0.5	15	12.5 - 15.5	13.6	0.9
POB	8.5	10	8.4 - 9.3	8.9	0.4	15	7.6 - 9.5	8.5	0.5
PRN	5.7	10	5.7 - 6.8	6.1	0.3	15	5.0 - 6.4	5.8	0.3
POR	10.6	10	10.8 - 11.8	11.3	0.3	15	9.7 - 13.0	10.9	1.0
INLF	4.9	10	4.5 - 5.3	5.0	0.2	15	4.3 - 6.2	4.9	0.6
MOW	6.3	10	7.0 - 7.9	7.3	0.3	15	7.0 - 8.3	7.3	0.4
ULA	2.3	10	1.8 - 2.6	2.3	0.2	15	1.9 - 3.0	2.4	0.3
INW	4.6	10	4.6 - 5.3	4.9	0.2	15	4.3 - 5.6	4.7	0.3
INO	7.9	10	7.9 - 9.5	8.6	0.5	15	7.5 - 10.4	8.4	0.7
EYL	4.5	10	4.3 - 5.1	4.8	0.3	15	3.9 - 6.5	4.8	0.8
EYH	1.9	10	1.8 - 2.4	2.1	0.2	15	1.6 - 2.5	1.9	0.2
SPL	1.3	10	1.1 - 1.5	1.3	0.1	15	1.0 - 2.0	1.4	0.3
GS1	1.5	10	1.4 - 2.0	1.6	0.2	15	1.4 - 2.0	1.6	0.2
GS5	2.0	10	1.6 - 2.2	2.0	0.2	15	1.8 - 2.3	2.1	0.2
IDS	23.6	10	22.9 - 26.3	24.3	1.2	15	18.9 - 26.2	23.7	2.2
DCS	10.7	10	9.6 - 11.4	10.7	0.6	15	9.4 - 11.8	10.4	0.6
PPS	18.6	10	18.8 - 22.5	20.5	1.5	15	15.7 - 22.6	20.6	2.0
PCA	27.6	10	26.1 - 29.0	27.1	1.1	15	23.5 - 28.7	25.8	1.6
D1L	13.3	10	12.1 - 13.6	12.9	0.5	15	11.4 - 15.2	13.3	0.9
D1A	10.9	10	10.2 - 11.0	10.5	0.4	15	8.0 - 12.7	11.0	1.1
D1B	7.4	10	6.8 - 7.8	7.3	0.3	15	6.6 - 8.2	7.3	0.5
D1H	7.0	10	6.5 - 8.0	7.3	0.4	15	6.8 - 9.9	8.2	0.9
D1I	6.2	10	5.0 - 6.6	5.7	0.5	15	5.5 - 6.7	6.1	0.4
D1P	8.3	10	7.4 - 8.3	7.8	0.3	15	7.2 - 10.8	8.7	1.1
D1ES	3.9	10	2.1 - 4.1	3.2	0.8	15	1.5 - 4.5	3.1	0.7
D1BS	0.6	10	0.6 - 0.7	0.7	0.0	15	0.5 - 0.8	0.7	0.1
D2L	13.8	10	11.1 - 13.1	12.3	0.7	15	11.0 - 14.0	12.6	0.8
D2A	11.0	10	9.5 - 10.8	10.3	0.4	15	7.7 - 12.1	10.2	1.3
D2B	8.4	10	6.5 - 9.0	7.5	0.8	15	6.5 - 8.9	7.3	0.6
D2H	6.1	10	4.8 - 6.3	5.5	0.6	15	4.7 - 7.4	6.1	0.8
D2I	5.3	10	3.9 - 5.6	4.7	0.5	15	4.3 - 6.4	5.3	0.6
D2P	5.7	10	4.9 - 6.4	5.4	0.5	15	5.2 - 7.2	6.0	0.6
D2ES	4.8	10	3.4 - 5.3	4.4	0.8	15	3.2 - 5.2	4.3	0.6
D2BS	0.7	10	0.7 - 0.8	0.8	0.0	15	0.6 - 1.1	0.8	0.1
P1A	15.1	10	12.8 - 15.3	14.1	0.9	15	12.6 - 15.3	14.2	0.8
P1I	8.1	10	7.4 - 9.1	8.4	0.5	15	7.2 - 10.2	8.4	1.0
P1B	5.0	10	4.4 - 5.4	4.8	0.3	15	3.7 - 5.3	4.8	0.5
P1P	10.5	10	8.7 - 11.5	10.3	0.8	15	8.1 - 11.7	10.0	1.1
P2L	12.2	10	10.9 - 12.9	11.7	0.6	15	10.4 - 12.8	11.6	0.7
P2I	6.2	10	5.1 - 6.7	6.2	0.5	15	5.2 - 7.3	6.1	0.6
CDM	21.7	10	19.1 - 22.4	20.7	1.3	15	18.6 - 24.7	21.4	1.7
CPV	11.6	10	10.4 - 12.0	11.1	0.5	15	10.1 - 12.8	11.4	0.6
CFW	6.8	10	6.4 - 7.4	6.7	0.3	15	6.4 - 7.9	7.0	0.4
HANW	7.2	10	6.5 - 8.8	7.7	0.6	15	6.6 - 8.9	7.5	0.5
HAMW	10.7	10	10.9 - 12.3	11.6	0.5	15	10.6 - 12.8	11.4	0.6
HDW	11.7	10	11.7 - 13.9	12.8	0.8	15	12.1 - 13.9	12.7	0.5
TRW	10.9	10	9.8 - 12.8	11.3	1.1	15	8.8 - 12.4	10.6	1.2
ABW	8.6	10	8.3 - 11.8	9.6	1.1	15	5.4 - 10.5	8.4	1.4
HDH	9.3	10	8.7 - 11.0	9.8	0.7	15	9.2 - 11.3	9.9	0.6
TRH	9.8	10	9.2 - 12.6	10.7	1.0	15	9.0 - 11.8	10.4	0.8
ABH	10.1	10	9.5 - 12.4	10.8	1.2	15	8.2 - 12.5	10.3	1.2
CLO	4.5	10	1.4 - 4.8	3.8	1.6	10	1.8 - 6.7	4.4	1.3
CLI	7.3	10	4.1 - 8.5	7.0	2.0	10	3.5 - 8.4	6.8	1.8

Table 45. External measurements for *Flakeus edmundsi* expressed as percentage of the total length (% TL). Ranges for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus edmundsi***								
	Holotype	Paratypes				N	Range	*x*	SD
	CSIRO H 2566-01	N	Range	*x*	SD				
TL (mm)	610.0	5	510.0 - 737.0	622.8	81.9	3	280.0 - 665.0	484.0	193.5
PCL	79.0	5	78.4 - 79.8	78.8	0.6	3	77.9 - 96.4	84.3	10.5
PD2	60.7	5	59.3 - 62.8	61.1	1.3	3	60.7 - 75.5	66.0	8.3
PD1	27.9	5	27.8 - 29.9	29.0	0.8	3	29.6 - 35.1	31.6	3.0
SVL	47.2	5	46.5 - 49.8	48.0	1.2	3	48.2 - 59.2	51.9	6.3
PP2	43.8	5	43.2 - 47.1	45.3	1.4	3	45.4 - 55.6	49.1	5.6
PP1	22.1	5	20.6 - 23.0	22.0	0.9	3	23.3 - 27.8	24.9	2.6
HDL	23.3	5	22.6 - 25.1	23.3	1.0	3	24.0 - 28.8	26.1	2.4
PG1	19.3	5	19.1 - 20.1	19.6	0.5	3	19.9 - 24.7	22.1	2.4
PSP	13.4	5	12.9 - 13.8	13.4	0.3	3	13.8 - 16.7	14.8	1.6
POB	8.3	5	7.9 - 8.5	8.2	0.2	3	7.9 - 9.6	8.6	0.9
PRN	5.8	5	5.7 - 5.9	5.8	0.1	3	5.5 - 6.6	6.0	0.6
POR	10.4	5	10.3 - 10.7	10.6	0.2	3	10.9 - 13.4	11.7	1.4
INLF	4.9	5	4.5 - 5.0	4.8	0.2	3	4.8 - 6.2	5.3	0.8
MOW	7.5	5	6.3 - 7.9	7.5	0.7	3	7.7 - 9.4	8.4	0.9
ULA	2.2	5	2.1 - 2.4	2.3	0.1	3	2.7 - 3.2	2.9	0.3
INW	4.5	5	4.5 - 4.9	4.7	0.2	3	4.5 - 5.8	5.0	0.7
INO	8.2	5	7.9 - 8.7	8.4	0.3	3	8.5 - 10.2	9.3	0.8
EYL	4.7	5	4.5 - 5.4	4.9	0.3	3	4.8 - 6.4	5.8	0.8
EYH	1.6	5	1.9 - 2.3	2.2	0.1	3	1.4 - 2.9	2.2	0.7
SPL	1.3	5	1.3 - 1.5	1.4	0.1	3	1.1 - 1.6	1.3	0.2
GS1	1.6	5	1.5 - 1.7	1.6	0.1	3	1.6 - 1.8	1.7	0.1
GS5	2.1	5	2.0 - 2.3	2.2	0.1	3	2.0 - 2.4	2.2	0.2
IDS	24.8	5	23.6 - 25.5	24.7	0.9	3	24.4 - 31.0	26.9	3.6
DCS	10.1	5	9.7 - 10.7	10.3	0.4	3	9.1 - 12.4	10.7	1.7
PPS	19.7	5	18.6 - 23.1	20.6	1.6	3	21.1 - 24.1	22.1	1.7
PCA	27.9	5	25.4 - 27.6	26.7	0.8	3	26.3 - 33.5	28.8	4.1
D1L	14.0	5	13.1 - 14.5	13.6	0.6	3	12.1 - 16.5	14.2	2.2
D1A	11.2	5	10.9 - 12.0	11.4	0.5	3	11.7 - 13.9	12.5	1.2
D1B	8.6	5	7.4 - 8.9	8.0	0.6	3	6.9 - 10.1	8.5	1.6
D1H	8.1	5	7.0 - 8.3	7.8	0.5	3	8.7 - 9.7	9.1	0.5
D1I	5.4	5	5.2 - 6.2	5.6	0.4	3	5.3 - 6.9	5.9	0.9
D1P	8.9	5	8.3 - 9.0	8.8	0.3	3	8.4 - 11.2	9.9	1.4
D1ES	5.0	5	3.9 - 5.7	4.9	0.7	3	3.4 - 6.5	5.2	1.6
D1BS	1.0	5	0.6 - 1.0	0.9	0.2	3	0.8 - 1.1	1.0	0.2
D2L	12.2	5	10.9 - 13.8	11.9	1.1	3	10.8 - 14.2	12.1	1.8
D2A	10.7	5	10.4 - 11.0	10.7	0.2	3	10.3 - 11.9	10.9	0.9
D2B	7.8	5	7.1 - 8.4	7.5	0.5	3	6.2 - 8.9	7.3	1.4
D2H	5.9	5	5.5 - 6.1	5.8	0.2	3	6.0 - 7.1	6.5	0.6
D2I	4.6	5	4.2 - 5.3	4.5	0.4	3	4.4 - 5.3	4.8	0.5
D2P	5.2	5	4.7 - 5.7	5.2	0.4	3	5.0 - 6.9	5.7	1.1
D2ES	5.1	5	4.8 - 5.4	5.1	0.3	2	4.3 - 6.1	5.2	1.3
D2BS	0.7	5	0.6 - 0.8	0.7	0.1	3	0.9 - 0.9	0.9	0.0
P1A	14.5	5	14.7 - 15.5	15.1	0.3	3	13.0 - 18.0	15.7	2.5
P1I	7.7	5	7.3 - 8.1	7.6	0.4	3	7.6 - 9.4	8.4	0.9
P1B	5.0	5	5.0 - 5.6	5.2	0.3	3	4.4 - 5.8	5.1	0.7
P1P	7.8	5	10.3 - 10.9	10.6	0.2	3	7.6 - 13.1	10.5	2.8
P2L	11.7	5	9.5 - 12.2	10.5	1.1	3	9.6 - 11.9	10.6	1.2
P2I	6.0	5	4.3 - 6.2	5.2	0.8	3	4.8 - 6.4	5.6	0.8
CDM	21.0	5	20.4 - 21.7	21.1	0.5	3	20.1 - 23.7	22.1	1.9
CPV	10.8	5	10.8 - 11.6	11.0	0.3	3	10.5 - 12.8	11.7	1.1
CFW	6.4	5	6.5 - 6.9	6.7	0.1	3	6.7 - 8.2	7.2	0.8
HANW	7.1	5	7.2 - 7.6	7.4	0.2	3	7.5 - 8.8	8.2	0.7
HAMW	11.2	5	10.7 - 12.1	11.6	0.5	3	11.9 - 14.1	12.6	1.3
HDW	12.4	5	11.7 - 13.4	12.8	0.7	3	12.3 - 15.5	13.8	1.6
TRW	10.8	5	10.3 - 12.5	11.2	0.8	3	11.2 - 12.7	11.9	0.8
ABW	8.6	5	8.6 - 9.9	9.3	0.6	3	8.0 - 10.3	9.3	1.2
HDH	10.1	5	9.3 - 10.5	10.0	0.4	3	9.6 - 11.2	10.3	0.8
TRH	10.6	5	9.8 - 11.2	10.4	0.5	3	10.0 - 12.6	11.3	1.3
ABH	10.1	5	10.1 - 11.5	10.8	0.7	3	10.4 - 11.6	10.8	0.6
CLO	3.9	2	3.3 - 4.5	3.9	0.9	2	0.9 - 4.4	2.7	2.5
CLI	7.2	2	6.4 - 7.3	6.8	0.6	2	2.4 - 6.5	4.5	2.9

Table 46. External measurements for *Flakeus hemipinnis* expressed as percentage of the total length (% TL). Ranges for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Flakeus hemipinnis*								
	Holotype	Paratypes				N	Range	*x*	SD
	MZB 15040	N	Range	*x*	SD				
TL (mm)	630.0	6	422.0 - 607.0	521.8	67.3	6	157.0 - 720.0	541.3	213.8
PCL	79.4	6	78.4 - 79.6	79.2	0.4	6	78.1 - 79.9	79.0	0.7
PD2	60.3	6	59.2 - 61.3	60.3	0.7	6	59.4 - 62.4	60.6	1.1
PD1	28.6	6	27.7 - 29.7	29.0	0.7	6	27.9 - 32.6	29.0	1.8
SVL	46.7	6	46.4 - 48.9	47.3	0.9	6	43.6 - 49.3	46.2	2.0
PP2	44.0	6	42.9 - 45.7	44.1	1.0	6	42.7 - 46.8	44.1	1.6
PP1	22.1	6	19.8 - 22.4	20.9	1.0	6	20.5 - 24.7	21.5	1.6
HDL	23.8	6	20.6 - 22.8	21.7	0.7	6	21.6 - 25.9	22.8	1.6
PG1	18.7	6	17.1 - 18.7	18.1	0.5	6	17.7 - 22.0	19.2	1.5
PSP	11.7	6	11.1 - 12.5	11.8	0.5	6	11.9 - 14.3	12.7	0.9
POB	6.9	6	6.4 - 6.9	6.7	0.2	6	6.7 - 8.0	7.4	0.5
PRN	4.4	6	4.1 - 4.7	4.4	0.2	6	4.3 - 5.5	5.0	0.4
POR	8.8	6	8.4 - 9.4	9.0	0.4	6	8.7 - 11.1	9.8	0.9
INLF	5.2	5	4.7 - 5.4	5.0	0.2	6	4.2 - 5.9	4.9	0.6
MOW	7.7	6	6.9 - 7.8	7.4	0.3	6	6.7 - 9.2	7.5	1.0
ULA	2.0	6	1.8 - 5.3	2.6	1.3	6	1.7 - 2.9	2.1	0.4
INW	3.6	6	3.3 - 4.1	3.8	0.3	6	3.6 - 4.6	4.2	0.4
INO	8.1	6	7.4 - 8.2	8.0	0.3	6	7.7 - 10.1	8.4	0.9
EYL	4.7	6	4.5 - 5.3	4.8	0.3	6	4.2 - 6.5	5.0	0.8
EYH	2.1	6	2.1 - 2.4	2.2	0.1	6	1.3 - 2.7	1.8	0.5
SPL	1.5	6	1.3 - 1.6	1.5	0.1	6	1.3 - 2.0	1.5	0.3
GS1	1.7	6	1.5 - 2.2	1.8	0.2	6	1.3 - 2.4	1.7	0.4
GS5	1.9	6	1.7 - 2.3	2.2	0.2	6	1.6 - 2.4	2.1	0.3
IDS	23.8	6	22.4 - 25.4	24.4	1.0	6	22.6 - 25.9	24.7	1.3
DCS	10.7	6	10.9 - 12.6	11.4	0.6	6	10.6 - 11.9	11.3	0.5
PPS	19.5	6	18.1 - 22.4	19.7	1.6	6	17.9 - 21.3	20.1	1.1
PCA	27.9	6	27.0 - 29.5	27.9	0.9	6	26.9 - 30.1	28.6	1.0
D1L	13.4	6	12.0 - 13.8	12.7	0.6	6	12.9 - 13.6	13.2	0.3
D1A	11.9	6	11.2 - 13.3	11.9	0.8	6	10.7 - 11.6	11.2	0.3
D1B	8.0	6	6.9 - 8.6	7.6	0.6	6	7.5 - 8.7	8.1	0.5
D1H	8.4	6	8.0 - 8.5	8.2	0.2	6	7.8 - 9.8	8.8	0.8
D1I	5.6	6	4.6 - 5.6	5.2	0.4	6	4.7 - 5.9	5.4	0.4
D1P	9.0	6	7.6 - 8.7	7.9	0.5	6	5.4 - 11.3	9.2	2.3
D1ES	4.7	6	4.0 - 5.3	4.5	0.6	6	1.7 - 6.2	4.9	1.9
D1BS	0.9	6	0.7 - 0.9	0.8	0.1	6	0.4 - 1.2	0.9	0.3
D2L	12.2	6	11.7 - 12.2	11.9	0.2	6	5.9 - 12.5	10.3	2.5
D2A	11.2	6	10.6 - 11.7	11.0	0.4	6	8.5 - 11.3	10.1	1.0
D2B	8.6	6	7.1 - 7.7	7.4	0.3	6	6.1 - 8.0	7.2	0.7
D2H	5.5	6	5.6 - 6.1	5.8	0.2	6	4.3 - 6.6	5.9	0.8
D2I	4.0	6	4.1 - 5.0	4.5	0.4	6	2.7 - 5.9	4.4	1.0
D2P	4.5	6	4.1 - 4.9	4.6	0.3	6	3.1 - 6.8	5.2	1.5
D2ES	4.5	6	4.7 - 5.4	5.1	0.3	5	4.2 - 5.8	4.8	0.6
D2BS	1.2	6	0.9 - 1.1	1.0	0.1	6	0.8 - 1.1	0.9	0.1
P1A	16.9	6	14.0 - 15.8	14.6	0.7	6	12.4 - 16.7	15.0	1.6
P1I	8.3	6	7.7 - 8.2	7.9	0.2	6	6.8 - 7.8	7.4	0.4
P1B	4.9	6	4.4 - 4.9	4.6	0.2	6	4.3 - 5.6	4.9	0.5
P1P	11.4	6	9.5 - 10.8	10.1	0.5	6	7.1 - 12.8	9.9	1.8
P2L	10.6	6	10.2 - 11.8	10.8	0.6	6	9.4 - 11.8	10.7	0.9
P2I	4.4	6	4.0 - 5.7	5.0	0.6	6	4.2 - 6.0	5.2	0.6
CDM	20.4	6	19.9 - 21.2	20.4	0.5	6	19.4 - 21.6	21.0	0.8
CPV	11.2	6	10.8 - 12.0	11.4	0.4	6	11.0 - 12.2	11.6	0.4
CFW	6.9	6	6.4 - 7.1	6.7	0.3	6	5.9 - 6.9	6.5	0.3
HANW	6.7	6	6.3 - 7.2	6.7	0.3	6	6.4 - 7.8	7.1	0.6
HAMW	11.1	6	9.6 - 10.9	10.3	0.6	6	10.5 - 12.0	11.2	0.8
HDW	12.4	6	11.2 - 13.1	11.9	0.6	6	11.9 - 13.0	12.5	0.5
TRW	10.3	6	9.1 - 11.1	10.3	0.7	6	9.1 - 11.8	10.7	0.9
ABW	9.1	6	7.0 - 10.1	8.9	1.1	6	7.8 - 9.0	8.5	0.6
HDH	10.4	6	8.9 - 11.1	9.9	0.8	6	9.0 - 11.1	9.9	0.8
TRH	11.1	6	9.7 - 12.0	10.9	0.8	6	8.7 - 12.2	10.5	1.2
ABH	10.1	6	9.9 - 12.4	10.8	0.9	6	7.8 - 11.0	10.0	1.2
CLO	-	2	4.7 - 4.9	4.8	0.1	3	1.4 - 5.6	3.6	2.1
CLI	-	2	6.7 - 7.5	7.1	0.5	3	3.0 - 8.6	6.0	2.8

Table 47. Tooth counts for *Flakeus grahami, F. edmundsi* and *F. hemipinnis.*

	F. grahami			***F. edmundsi***			***F. hemipinnis***		
	Holotype	Paratypes N= 7	N= 11	Holotype	Paratypes N= 3	N= 3	Holotype	Paratypes N= 6	N= 7
upper teeth (right)	12	12–13	12–14	13	12–15	12–13	12	12–13	12–14
upper teeth (left)	13	12–13	11–14	12	12–13	12–14	12	12–13	12–14
lower teeth (right)	10	9–10	9–12	9	10–11	10–10	10	10–12	10–12
lower teeth (left)	9	9–10	10–12	10	9–11	10–10	9	10–12	10–12
upper teeth series	2	2–3	2–3	2	2–3	2–3	3	2–3	1–3
lower teeth series	2	2–3	2–3	2	2–3	2–2	3	2–3	2–3
Source	present study								

Table 48. Monospondylous, diplospondylous, precaudal, caudal and total vertebrae for *Flakeus grahami*, *F. edmundsi*, and *F. hemipinnis*.

	Monospondylous vertebrae																					
	29	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**
Flakeus grahami Holotype													1									
Flakeus grahami Paratype													1									
Flakeus grahami														2								
F. edmundsi Holotype																	1					
F. edmundsi Paratype															1							
F. edmundsi																1						
F. hemipinnis Holotype									1													
F. hemipinnis									1													

	Diplospondylous vertebrae																					
	59	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**
Flakeus grahami Holotype															1							
Flakeus grahami Paratype											1											
Flakeus grahami												1					1					
F. edmundsi Holotype												1										
F. edmundsi Paratype														1								
F. edmundsi																1						
F. hemipinnis Holotype		1																				
F. hemipinnis			1																			

	Precaudal vertebrae																					
	74	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**
Flakeus grahami Holotype															1							
Flakeus grahami Paratype										1												
Flakeus grahami										1			1									
F. edmundsi Holotype																1						
F. edmundsi Paratype													1									
F. edmundsi																	1					
F. hemipinnis Holotype	1																					
F. hemipinnis	1																					

	Caudal vertebrae																					
	19	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
Flakeus grahami Holotype								1														
Flakeus grahami Paratype									1													
Flakeus grahami											1		1									
F. edmundsi Holotype								1														
F. edmundsi Paratype											1											
F. edmundsi										1												
F. hemipinnis Holotype					1																	
F. hemipinnis						1																

	Total vertebrae																					
	97	**98**	**99**	**100**	**101**	**102**	**103**	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**
Flakeus grahami Holotype																		1				
Flakeus grahami Paratype														1								
Flakeus grahami																1					1	
F. edmundsi Holotype																			1			
F. edmundsi Paratype																			1			
F. edmundsi																						1
F. hemipinnis Holotype	1																					
F. hemipinnis		1																				

Table 49. External measurements for *Flakeus probatovi* expressed as percentage of the total length (% TL). N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus probatovi***			
	N	Range	*x*	SD
TL (mm)	10	325.0 - 677.0	570.1	119.7
PCL	10	76.6 - 79.9	77.9	1.1
PD2	10	58.2 - 61.8	59.8	1.3
PD1	10	27.5 - 29.5	28.6	0.6
SVL	10	43.1 - 50.4	46.6	2.2
PP2	10	41.6 - 47.2	43.8	1.8
PP1	10	20.1 - 24.7	22.9	1.6
HDL	10	20.6 - 25.2	23.4	1.6
PG1	10	17.3 - 21.1	19.6	1.2
PSP	10	11.3 - 13.9	12.7	0.9
POB	10	6.6 - 8.6	7.5	0.7
PRN	10	4.0 - 6.1	5.1	0.7
POR	10	8.7 - 11.0	10.0	0.8
INLF	10	4.4 - 5.0	4.7	0.2
MOW	10	7.2 - 8.4	7.9	0.3
ULA	10	1.9 - 2.7	2.4	0.3
INW	10	4.1 - 5.2	4.5	0.4
INO	10	8.0 - 9.0	8.5	0.3
EYL	10	4.4 - 5.9	5.0	0.5
EYH	10	1.3 - 2.2	1.8	0.3
SPL	10	1.4 - 2.0	1.6	0.2
GS1	10	1.3 - 2.4	1.8	0.3
GS5	10	1.7 - 2.7	2.2	0.3
IDS	10	21.5 - 24.8	23.3	1.2
DCS	10	9.9 - 11.7	10.6	0.5
PPS	10	15.3 - 20.3	17.4	1.6
PCA	10	25.2 - 27.9	26.6	0.9
D1L	10	13.9 - 15.9	14.8	0.6
D1A	10	11.0 - 13.3	12.4	0.8
D1B	10	7.6 - 9.6	8.7	0.6
D1H	10	8.2 - 10.4	9.1	0.6
D1I	10	5.4 - 6.9	6.1	0.4
D1P	10	8.2 - 11.7	9.9	1.0
D1ES	10	3.6 - 5.3	4.5	0.7
D1BS	10	0.7 - 1.1	0.9	0.1
D2L	10	12.1 - 13.5	13.0	0.4
D2A	10	9.5 - 12.1	11.0	0.7
D2B	10	7.2 - 8.6	7.8	0.5
D2H	10	5.3 - 7.6	6.5	0.7
D2I	10	4.8 - 5.6	5.1	0.3
D2P	10	4.7 - 6.4	5.6	0.6
D2ES	10	4.4 - 5.6	4.9	0.4
D2BS	10	0.7 - 0.9	0.8	0.1
P1A	10	13.5 - 17.0	15.2	1.0
P1I	10	7.6 - 9.5	8.5	0.6
P1B	10	4.5 - 5.3	4.9	0.2
P1P	10	9.3 - 12.0	11.1	0.9
P2L	10	9.9 - 12.1	11.1	0.9
P2I	10	4.6 - 6.0	5.6	0.5
CDM	10	21.0 - 23.5	22.2	0.8
CPV	10	10.8 - 13.0	11.7	0.7
CFW	10	6.4 - 7.4	7.0	0.3
HANW	10	7.2 - 8.3	7.8	0.3
HAMW	10	11.2 - 13.0	12.0	0.6
HDW	10	12.0 - 13.6	12.8	0.6
TRW	10	8.5 - 11.8	10.2	1.2
ABW	10	7.3 - 10.0	8.8	0.8
HDH	10	9.9 - 11.7	10.6	0.6
TRH	10	9.8 - 12.9	11.4	1.0
ABH	10	8.8 - 12.2	10.5	1.2
CLO	10	1.2 - 5.4	3.9	1.4
CLI	10	3.0 - 8.1	6.0	1.8

Table 50. External measurements for *Flakeus* sp.1 expressed as percentage of the total length (% TL).Total length is expressed in milimeters. N: number of specimens; Min: minimum range; Max: maximum range; *x*: mean; SD: standard deviation.

Measurements	*Flakeus* sp. 1													
	Holotype	Paratypes									Non-type material			
		SAIAB 20560	SAIAB 21856	SAIAB 21858	SAIAB 21859	SAIAB 21939	SAIAB 25362	SAIAB 25366	SAIAB 25377	MNHN 1987-2092	N	Range	*x*	SD
TL (mm)	543.0	312.0	452.0	455.0	449.0	360.0	475.0	460.0	445.0	430.0	10	215.0 - 600.0	408.2	129.6
PCL	75.0	78.5	78.5	79.8	76.2	76.1	78.3	78.3	78.9	77.7	10	75.9 - 79.8	77.8	1.1
PD2	56.7	59.3	59.7	62.4	59.9	59.4	58.9	59.8	61.6	58.6	10	55.5 - 61.2	59.3	1.7
PD1	28.2	30.4	28.8	30.1	29.2	32.2	29.5	29.3	28.1	28.1	10	28.5 - 32.3	30.3	1.2
SVL	46.0	46.5	47.6	48.8	47.9	49.4	46.7	47.8	47.6	46.5	10	46.2 - 49.2	47.5	1.2
PP2	42.4	44.9	45.4	45.5	44.1	49.2	45.3	44.6	45.3	43.7	10	43.3 - 46.7	44.8	0.9
PP1	21.8	22.3	24.3	21.6	20.9	22.5	22.7	21.7	22.1	22.4	10	20.7 - 23.5	22.3	1.0
HDL	22.9	23.4	24.8	18.1	18.2	19.0	23.2	22.8	18.4	22.7	10	21.0 - 24.6	23.0	1.2
PG1	18.5	19.1	19.0	22.4	21.4	23.1	18.0	18.2	21.9	18.9	10	17.5 - 19.9	18.8	0.8
PSP	11.5	12.3	12.0	12.0	12.0	12.2	11.7	11.8	12.2	11.7	10	11.2 - 13.6	12.5	0.7
POB	6.5	6.9	7.0	6.6	6.7	6.4	7.0	6.8	7.0	6.5	10	6.1 - 8.2	7.2	0.6
PRN	4.0	4.1	4.5	4.6	4.2	3.9	4.3	4.2	4.3	4.1	10	3.7 - 4.8	4.3	0.3
POR	8.5	9.6	8.9	8.6	8.2	9.2	8.6	8.8	8.6	9.6	10	8.3 - 11.3	9.7	0.9
INLF	4.5	4.7	4.5	4.5	4.3	4.7	4.3	4.5	4.5	4.9	10	4.3 - 5.5	4.9	0.4
MOW	7.6	9.0	9.0	7.8	8.7	8.1	7.9	8.1	8.3	8.4	10	6.8 - 9.4	8.3	0.8
ULA	2.5	2.6	2.5	2.7	3.0	2.3	2.0	2.9	2.7	2.9	10	2.6 - 3.4	2.9	0.2
INW	3.4	3.8	3.6	4.0	4.2	3.9	4.1	4.0	4.0	3.8	10	3.5 - 4.3	3.9	0.2
INO	7.8	8.0	8.1	79.6	8.4	8.4	8.5	8.3	8.7	8.8	10	8.2 - 10.1	8.8	0.6
EYL	5.5	5.2	4.6	4.6	4.2	4.9	4.4	4.8	4.3	5.0	10	4.3 - 5.7	5.1	0.5
EYH	1.9	2.3	1.8	2.2	2.2	2.4	2.0	2.2	2.2	2.6	10	1.5 - 3.1	2.3	0.6
SPL	1.6	2.3	1.9	1.8	2.0	2.0	1.7	1.8	1.8	2.0	10	1.4 - 2.2	1.8	0.3
GS1	1.9	2.7	2.0	2.2	2.3	2.2	1.7	1.9	2.1	2.0	10	1.5 - 2.6	2.0	0.4
GS5	2.2	2.9	2.3	2.3	2.4	2.7	2.4	2.2	2.4	2.5	10	2.1 - 2.8	2.4	0.2
IDS	21.4	23.7	24.3	24.6	24.7	23.7	23.2	23.9	24.7	21.2	10	20.0 - 23.3	21.6	1.4
DCS	11.1	11.4	11.3	11.6	10.8	11.4	12.2	11.4	11.8	11.3	10	10.3 - 12.2	11.1	0.6
PPS	16.0	19.0	21.0	19.8	20.0	20.9	21.1	18.5	19.1	18.8	10	16.0 - 21.4	18.8	1.8
PCA	25.1	26.4	27.0	25.3	26.3	25.1	26.3	27.2	24.9	26.1	10	24.6 - 27.3	25.6	1.0
D1L	14.6	14.0	14.2	14.1	14.5	14.0	13.2	14.5	13.7	13.3	10	13.2 - 15.1	14.1	0.7
D1A	11.7	13.1	12.0	10.8	12.5	12.8	11.6	12.6	11.5	10.9	10	10.5 - 14.8	12.1	1.5
D1B	8.1	8.4	7.8	7.5	8.0	7.6	7.4	8.3	7.8	7.3	10	7.4 - 8.7	7.9	0.4
D1H	8.3	9.8	8.6	7.3	8.6	8.3	8.8	9.1	7.6	8.6	10	7.6 - 10.5	9.0	0.9
D1I	6.2	5.9	6.5	6.6	6.5	6.5	5.4	6.3	5.9	6.6	10	5.4 - 7.1	6.4	0.5
D1P	8.6	8.8	9.0	9.6	9.8	10.0	8.8	9.0	9.9	10.0	10	8.3 - 11.1	9.4	1.0
D1ES	4.2	4.1	5.4	4.0	4.3	-	3.8	4.6	-	3.0	10	2.4 - 3.7	3.1	0.4
D1BS	0.6	1.0	0.8	0.9	0.8	0.8	0.9	0.8	1.0	0.6	10	0.6 - 1.0	0.7	0.1
D2L	13.1	12.9	11.1	10.5	10.7	11.1	11.6	12.5	11.3	12.7	10	11.6 - 13.5	12.7	0.6
D2A	11.3	11.0	10.7	8.6	9.4	9.4	10.6	10.3	9.4	10.8	10	6.7 - 11.5	10.3	1.4
D2B	8.0	7.0	7.5	5.8	5.6	5.6	6.5	7.2	6.4	7.8	10	6.6 - 8.0	7.2	0.4
D2H	6.2	5.9	6.9	4.5	5.1	5.0	6.0	6.0	4.6	6.4	10	4.9 - 7.5	6.2	0.9
D2I	5.4	5.6	5.3	4.7	5.1	5.6	5.2	5.2	4.9	5.2	10	4.7 - 6.2	5.5	0.5
D2P	4.8	5.6	5.7	5.5	6.0	6.3	5.3	5.2	5.6	4.6	10	4.6 - 6.3	5.4	0.6
D2ES	4.8	6.3	5.4	5.7	6.0	6.1	5.6	5.3	5.3	4.2	10	4.2 - 7.2	5.3	0.9
D2BS	0.7	0.9	0.9	0.9	1.0	0.8	0.8	0.7	0.9	0.6	10	0.7 - 1.2	0.9	0.2
P1A	16.5	15.9	16.7	17.8	17.4	17.8	16.9	16.8	16.2	17.9	10	14.5 - 18.2	16.7	1.3
P1I	9.7	10.0	10.4	10.0	1.0	10.1	10.2	10.6	9.2	10.1	10	9.3 - 11.2	10.1	0.6
P1B	4.3	5.0	5.7	4.6	4.7	5.9	4.9	4.7	4.6	4.8	10	4.0 - 5.4	4.9	0.4
P1P	11.3	11.8	13.0	14.1	14.3	14.5	13.7	12.4	13.0	14.5	10	10.8 - 15.3	13.6	1.3
P2L	12.1	11.3	12.8	11.1	11.0	10.9	11.3	12.8	11.9	13.1	10	10.8 - 12.9	11.9	0.7
P2I	5.6	5.9	6.3	3.2	-	6.2	5.3	6.6	3.4	6.8	10	4.4 - 7.2	6.0	0.9
CDM	22.0	21.3	21.4	22.5	22.4	22.2	22.0	21.7	21.0	22.1	10	20.6 - 23.5	22.0	0.9
CPV	12.1	12.0	11.5	10.5	10.6	10.6	11.0	11.7	10.3	11.8	10	11.1 - 12.7	11.7	0.5
CFW	7.4	7.1	7.1	7.1	7.1	7.1	7.0	7.0	7.2	7.1	10	6.8 - 8.1	7.4	0.4
HANW	6.5	7.8	7.6	7.0	7.2	7.2	7.9	7.9	6.6	8.3	10	6.8 - 9.7	7.8	1.1
HAMW	11.0	11.9	11.2	10.3	11.1	10.8	11.0	11.2	11.1	12.7	10	11.3 - 13.8	12.3	0.9
HDW	12.3	12.4	12.7	12.0	13.1	13.5	11.6	12.9	12.3	13.8	10	12.6 - 13.7	13.2	0.4
TRW	10.7	10.3	12.1	10.7	11.8	12.9	9.2	11.8	11.7	12.0	10	10.0 - 13.0	11.3	1.0
ABW	10.1	8.6	8.4	10.1	10.9	12.2	7.1	9.2	11.1	10.2	10	7.9 - 12.5	9.9	1.3
HDH	9.5	9.2	10.0	8.6	9.8	9.9	8.6	8.6	9.1	9.3	10	8.1 - 11.2	9.7	1.1
TRH	11.9	10.4	10.1	8.4	10.9	11.3	7.7	8.8	10.1	8.8	10	8.0 - 12.3	10.5	1.5
ABH	11.5	10.3	9.5	7.3	11.7	12.6	8.3	8.5	8.8	6.7	10	7.2 - 14.9	10.5	2.2
CLO	3.8	1.3	4.8	4.4	-	-	-	4.8	4.3	4.0	10	1.5 - 4.6	3.3	1.4
CLI	7.1	2.9	8.6	8.1	-	-	-	8.3	6.7	7.9	10	2.7 - 8.1	5.8	2.3

Table 51. External measurements for *Flakeus* sp. 2 expressed as percentage of the total length (% TL). N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus* sp. 2**				
	Holotype	Paratypes			
		N	Range	*x*	SD
TL (mm)	683.0	23	282.0 - 925.0	601.1	186.7
PCL	78.5	23	76.7 - 80.7	78.6	1.0
PD2	59.3	23	58.0 - 63.8	61.1	1.4
PD1	31.6	23	28.4 - 33.6	30.5	1.3
SVL	47.6	23	47.0 - 52.4	49.5	1.4
PP2	44.7	23	43.6 - 50.3	46.6	1.7
PP1	22.0	23	21.3 - 24.1	22.6	0.7
HDL	22.4	23	22.4 - 26.2	23.9	0.9
PG1	19.4	23	19.1 - 22.4	20.2	0.8
PSP	12.7	23	12.3 - 15.2	13.3	0.7
POB	8.2	23	7.6 - 9.1	8.1	0.4
PRN	5.3	23	5.0 - 9.4	5.6	0.9
POR	9.9	23	9.0 - 11.8	10.3	0.7
INLF	4.6	23	4.3 - 5.4	4.7	0.3
MOW	7.9	23	7.4 - 8.9	7.9	0.5
ULA	2.3	23	2.1 - 2.9	2.4	0.2
INW	4.3	23	4.1 - 5.0	4.6	0.2
INO	8.3	23	7.8 - 9.6	8.6	0.5
EYL	4.5	23	4.2 - 6.2	4.9	0.6
EYH	2.1	23	1.3 - 2.6	1.9	0.3
SPL	1.2	23	1.2 - 1.9	1.5	0.2
GS1	1.7	23	1.7 - 2.6	2.0	0.2
GS5	2.0	23	1.8 - 2.6	2.2	0.2
IDS	24.2	23	20.5 - 25.7	24.1	1.4
DCS	10.5	23	9.2 - 11.8	10.3	0.7
PPS	20.4	23	18.1 - 25.1	20.9	1.6
PCA	25.9	23	23.2 - 26.8	24.7	1.0
D1L	14.1	23	12.6 - 15.8	14.3	0.8
D1A	11.9	23	8.8 - 13.1	11.6	0.9
D1B	7.5	23	6.7 - 9.1	7.9	0.6
D1H	7.7	23	7.5 - 9.5	8.4	0.6
D1I	6.3	23	4.9 - 7.5	6.6	0.8
D1P	8.3	23	7.2 - 10.9	8.9	0.9
D1ES	3.7	23	2.4 - 4.8	3.6	0.7
D1BS	0.7	23	0.5 - 1.0	0.8	0.1
D2L	13.6	23	10.2 - 14.9	12.6	1.1
D2A	9.9	23	8.6 - 12.7	10.3	1.0
D2B	7.9	23	5.8 - 8.9	7.2	0.8
D2H	5.9	23	4.3 - 7.7	6.0	0.9
D2I	5.5	23	3.8 - 6.8	5.5	0.8
D2P	6.0	23	4.1 - 6.7	5.6	0.7
D2ES	4.9	23	3.1 - 5.6	4.5	0.7
D2BS	0.8	23	0.6 - 1.1	0.8	0.1
P1A	15.4	23	14.6 - 18.2	15.8	1.0
P1I	9.3	23	8.5 - 11.1	9.6	0.6
P1B	4.6	23	4.1 - 5.8	5.2	0.4
P1P	10.2	23	9.2 - 12.6	10.9	1.0
P2L	11.7	23	10.0 - 13.0	11.3	0.6
P2I	6.6	23	4.8 - 7.2	5.7	0.6
CDM	21.1	23	19.1 - 23.0	21.6	1.0
CPV	11.4	23	10.9 - 13.9	12.0	0.8
CFW	6.8	23	6.6 - 8.4	7.4	0.4
HANW	7.2	23	6.9 - 9.5	8.1	0.7
HAMW	11.8	23	11.2 - 13.7	12.2	0.7
HDW	13.1	23	11.5 - 15.0	13.4	0.9
TRW	10.9	23	9.7 - 13.8	11.5	1.1
ABW	9.9	23	7.2 - 11.9	9.5	1.3
HDH	10.2	23	8.5 - 12.5	10.5	1.1
TRH	11.6	23	8.9 - 14.2	11.3	1.6
ABH	10.9	23	8.0 - 14.8	10.6	1.7
CLO	6.0	23	1.1 - 5.1	3.5	1.7
CLI	8.4	23	2.6 - 8.1	5.7	2.2

Table 52. External measurements for *Flakeus* sp. 3 expressed as percentage of the total length (% TL). N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus* sp. 3**				
	Holotype	Paratypes		*x*	SD
		N	Range		
TL (mm)	590.0	11	264.0 - 550.0	450.2	84.4
PCL	79.3	11	76.9 - 79.1	78.2	0.8
PD2	62.4	11	58.3 - 61.2	60.2	1.0
PD1	28.8	11	28.6 - 32.0	29.7	1.0
SVL	47.5	11	44.9 - 50.1	46.9	1.4
PP2	44.2	11	41.8 - 47.3	44.3	1.7
PP1	20.1	11	18.9 - 26.0	22.1	2.0
HDL	21.2	11	21.0 - 25.8	23.0	1.6
PG1	18.2	11	18.2 - 22.0	19.7	1.2
PSP	12.4	11	12.4 - 13.7	13.1	0.5
POB	7.2	11	6.9 - 7.9	7.5	0.3
PRN	4.4	11	4.2 - 5.0	4.6	0.2
POR	9.8	11	9.5 - 11.1	10.2	0.5
INLF	4.7	11	4.7 - 7.8	5.4	0.8
MOW	7.4	11	7.4 - 8.7	7.9	0.4
ULA	2.6	11	2.2 - 2.7	2.5	0.1
INW	3.7	11	3.6 - 5.1	4.1	0.4
INO	8.3	11	6.3 - 9.0	7.8	1.1
EYL	4.8	11	4.6 - 5.5	5.0	0.3
EYH	2.1	11	1.7 - 3.0	2.4	0.4
SPL	1.3	11	1.2 - 1.9	1.5	0.2
GS1	1.7	11	1.6 - 2.6	2.0	0.3
GS5	2.2	11	1.9 - 2.9	2.4	0.3
IDS	24.1	11	19.9 - 31.7	23.9	3.2
DCS	11.2	11	10.4 - 13.0	11.3	0.8
PPS	19.4	11	16.4 - 20.9	18.8	1.3
PCA	25.6	11	25.2 - 29.2	27.2	1.2
D1L	13.8	11	13.1 - 14.7	13.8	0.6
D1A	10.9	11	10.5 - 13.4	11.7	0.7
D1B	8.6	11	7.5 - 8.3	7.9	0.2
D1H	7.8	11	7.4 - 9.2	8.2	0.5
D1I	6.3	11	5.3 - 6.4	5.9	0.3
D1P	8.9	11	8.0 - 9.6	8.8	0.6
D1ES	4.9	10	4.2 - 4.9	4.6	0.3
D1BS	0.8	10	0.8 - 1.5	0.9	0.2
D2L	11.9	11	9.6 - 13.0	11.6	1.0
D2A	9.7	11	8.5 - 11.6	10.0	1.1
D2B	7.0	11	5.8 - 7.7	6.8	0.6
D2H	5.9	11	4.2 - 6.9	5.7	1.1
D2I	4.9	11	3.2 - 5.3	4.9	0.6
D2P	5.8	11	4.3 - 6.5	5.2	0.6
D2ES	5.9	11	4.3 - 6.1	5.4	0.5
D2BS	0.8	11	0.7 - 1.0	0.8	0.1
P1A	14.4	11	12.6 - 15.2	13.9	0.7
P1I	9.6	11	7.8 - 10.8	9.3	0.9
P1B	4.0	11	3.7 - 5.0	4.4	0.5
P1P	10.8	11	8.9 - 12.5	10.9	1.1
P2L	10.4	11	10.0 - 13.4	11.4	1.1
P2I	5.7	11	2.6 - 7.2	5.2	1.5
CDM	19.7	11	20.2 - 21.9	21.3	0.6
CPV	10.8	11	10.2 - 12.2	11.2	0.6
CFW	6.8	11	6.3 - 7.4	7.0	0.4
HANW	7.3	11	6.9 - 8.1	7.3	0.4
HAMW	11.2	11	10.7 - 12.6	11.7	0.5
HDW	12.4	11	11.5 - 13.9	12.5	0.7
TRW	10.0	11	9.5 - 11.4	10.5	0.8
ABW	8.4	11	8.8 - 10.8	9.5	0.6
HDH	10.5	11	9.4 - 10.6	10.0	0.4
TRH	10.8	11	10.2 - 12.0	10.9	0.6
ABH	10.6	11	8.8 - 12.6	10.7	1.1
CLO	-	11	1.6 - 4.5	3.6	1.1
CLI	-	11	3.1 - 8.2	6.9	2.2

Table 53. External measurements expressed as percentage of the total length (% TL) for of *Flakeus* sp. 4. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus* sp. 4**				
	Holotype	Paratypes			
	HUMZ 91806	N	Range	*x*	SD
TL (mm)	557.0	8	530.0 - 725.0	637.5	59.3
PCL	78.5	8	78.3 - 80.5	79.5	0.8
PD2	61.0	8	60.0 - 64.1	61.3	1.4
PD1	31.1	8	29.8 - 31.1	30.4	0.5
SVL	47.0	8	46.9 - 51.9	49.5	1.8
PP2	44.9	8	44.6 - 48.9	46.6	1.5
PP1	22.0	8	20.5 - 23.4	21.8	0.9
HDL	22.7	8	21.5 - 24.3	22.2	0.9
PG1	19.2	8	17.7 - 20.3	18.8	0.9
PSP	12.6	8	11.5 - 12.7	12.1	0.4
POB	7.9	8	7.0 - 7.9	7.4	0.3
PRN	5.4	8	4.5 - 5.3	4.7	0.3
POR	9.7	8	8.6 - 9.9	9.4	0.4
INLF	4.5	8	3.6 - 4.4	4.1	0.3
MOW	7.4	8	7.0 - 8.1	7.6	0.3
ULA	2.4	8	2.0 - 2.6	2.4	0.2
INW	4.4	8	3.8 - 4.9	4.2	0.4
INO	8.8	8	6.8 - 8.5	8.0	0.6
EYL	4.1	8	3.1 - 4.4	3.9	0.5
EYH	1.8	8	1.4 - 2.3	1.7	0.3
SPL	1.2	8	1.0 - 1.6	1.4	0.2
GS1	1.9	8	1.4 - 1.9	1.7	0.2
GS5	2.2	8	1.9 - 2.4	2.1	0.2
IDS	24.6	8	21.9 - 24.1	23.3	0.9
DCS	10.1	8	10.4 - 11.5	10.7	0.4
PPS	18.9	8	20.3 - 24.4	22.2	1.4
PCA	26.0	8	24.8 - 28.1	26.0	1.1
D1L	14.4	8	11.8 - 14.1	13.2	0.7
D1A	11.1	8	10.3 - 11.9	11.2	0.6
D1B	7.5	8	7.1 - 8.4	7.8	0.5
D1H	7.6	8	6.5 - 8.1	7.3	0.5
D1I	6.6	8	3.3 - 7.1	5.7	1.2
D1P	9.6	8	6.7 - 9.2	8.0	0.9
D1ES	3.8	7	2.2 - 4.0	3.3	0.6
D1BS	0.7	8	0.6 - 0.9	0.8	0.1
D2L	13.7	8	11.3 - 13.0	12.3	0.7
D2A	11.1	8	9.2 - 11.6	10.0	0.8
D2B	8.2	8	6.8 - 9.2	7.5	0.8
D2H	6.0	8	3.7 - 5.6	4.7	0.8
D2I	5.8	8	2.8 - 6.1	4.8	1.1
D2P	5.5	8	4.1 - 6.4	5.4	0.9
D2ES	5.3	6	3.4 - 5.3	4.6	0.7
D2BS	0.8	8	0.7 - 1.0	0.9	0.1
P1A	16.0	8	13.8 - 17.2	15.9	1.1
P1I	10.5	8	9.2 - 11.0	9.8	0.7
P1B	4.6	8	4.3 - 5.4	4.7	0.3
P1P	11.2	8	9.7 - 11.7	10.9	0.6
P2L	10.4	8	9.9 - 11.6	10.5	0.5
P2I	5.4	8	4.2 - 5.7	4.9	0.5
CDM	21.7	8	19.7 - 22.0	20.7	0.9
CPV	11.8	8	10.6 - 12.2	11.6	0.5
CFW	6.9	8	6.3 - 7.4	7.0	0.4
HANW	7.5	8	6.3 - 7.4	6.9	0.4
HAMW	12.2	8	9.7 - 12.2	11.0	0.7
HDW	13.4	8	11.4 - 13.9	12.8	0.9
TRW	10.0	8	8.9 - 12.7	10.6	1.2
ABW	8.6	8	6.5 - 11.1	9.4	1.6
HDH	10.6	8	7.5 - 10.6	9.2	1.3
TRH	12.0	8	6.4 - 12.5	9.3	2.4
ABH	10.9	8	6.4 - 13.5	9.3	2.8
CLO	-	1	4.3 - 4.3	4.3	-
CLI	-	1	7.3 - 7.3	7.3	-

Table 54. External measurements expressed as percentage of the total length (% TL) for holotype and paratypes of *Flakeus* sp. 5. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus* sp. 5**						
	Holotype	Paratypes					
	MNRJ 30180	N	Min.		Max.	*x*	SD
TL (mm)	585.0	2	615.0	-	690.0	652.5	53.0
PCL	79.5	2	79.2	-	81.2	80.2	1.4
PD2	61.5	2	61.0	-	63.8	62.4	2.0
PD1	29.9	2	29.7	-	30.9	30.3	0.8
SVL	47.0	2	47.2	-	50.7	48.9	2.5
PP2	44.4	2	45.5	-	48.6	47.0	2.1
PP1	21.7	2	22.0	-	22.8	22.4	0.6
HDL	21.4	2	22.8	-	22.9	22.8	0.1
PG1	17.9	2	18.4	-	18.8	18.6	0.3
PSP	12.2	2	12.2	-	12.9	12.6	0.5
POB	7.3	2	7.4	-	7.9	7.7	0.3
PRN	5.0	2	4.9	-	5.1	5.0	0.1
POR	9.9	2	10.2	-	10.5	10.3	0.2
INLF	4.6	2	4.2	-	4.9	4.6	0.5
MOW	7.2	2	7.2	-	7.7	7.5	0.3
ULA	2.3	2	2.2	-	2.2	2.2	0.0
INW	4.2	2	4.7	-	4.8	4.8	0.1
INO	8.2	2	7.9	-	8.3	8.1	0.3
EYL	3.6	2	3.5	-	3.8	3.6	0.2
EYH	1.8	2	1.4	-	1.9	1.6	0.3
SPL	1.3	2	1.3	-	1.6	1.5	0.2
GS1	1.7	2	1.6	-	2.0	1.8	0.3
GS5	1.8	2	1.9	-	2.2	2.0	0.2
IDS	26.5	2	24.4	-	26.8	25.6	1.7
DCS	11.2	2	11.0	-	12.2	11.6	0.8
PPS	19.7	2	19.5	-	20.3	19.9	0.5
PCA	27.4	2	25.2	-	27.8	26.5	1.9
D1L	12.8	2	13.8	-	13.8	13.8	0.0
D1A	10.5	2	10.3	-	10.6	10.4	0.3
D1B	7.5	2	7.2	-	7.3	7.3	0.0
D1H	6.9	2	7.0	-	7.1	7.1	0.0
D1I	5.7	2	6.4	-	6.9	6.7	0.3
D1P	7.9	2	9.2	-	9.6	9.4	0.3
D1ES	2.8	2	2.9	-	3.0	2.9	0.1
D1BS	0.6	2	0.8	-	0.8	0.8	0.0
D2L	11.6	2	12.1	-	12.6	12.4	0.4
D2A	9.4	2	9.3	-	9.7	9.5	0.3
D2B	6.2	2	6.6	-	6.8	6.7	0.2
D2H	5.3	2	4.2	-	4.4	4.3	0.1
D2I	5.3	2	5.6	-	5.6	5.6	0.0
D2P	5.0	2	5.7	-	5.7	5.7	0.0
D2ES	4.1	2	3.7	-	4.3	4.0	0.4
D2BS	0.8	2	0.7	-	0.9	0.8	0.1
P1A	14.3	2	14.4	-	14.5	14.5	0.1
P1I	8.1	2	8.4	-	8.9	8.7	0.4
P1B	4.8	2	4.2	-	4.5	4.4	0.2
P1P	9.8	2	10.5	-	11.3	10.9	0.5
P2L	10.5	2	10.3	-	10.5	10.4	0.1
P2I	5.8	2	5.1	-	5.4	5.2	0.2
CDM	21.9	2	20.0	-	21.4	20.7	1.0
CPV	11.4	2	10.9	-	11.3	11.1	0.3
CFW	6.7	2	6.4	-	7.1	6.7	0.5
HANW	7.0	2	7.0	-	7.1	7.1	0.1
HAMW	10.7	2	10.6	-	10.6	10.6	0.0
HDW	11.9	2	12.4	-	12.6	12.5	0.2
TRW	9.3	2	9.9	-	11.0	10.4	0.8
ABW	7.7	2	8.4	-	8.9	8.6	0.3
HDH	9.3	2	9.6	-	10.0	9.8	0.3
TRH	9.8	2	9.1	-	9.5	9.3	0.3
ABH	10.1	2	9.6	-	10.5	10.0	0.6
CLO	5.0	2	4.6	-	5.1	4.8	0.4
CLI	7.5	2	6.6	-	7.5	7.0	0.6

Table 55. External measurements expressed as percentage of the total length (% TL) for *Flakeus* sp. 6. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus* sp. 6**				
	Holotype	N	Paratypes	*x*	SD
TL (mm)	700.0	3	660.0 - 830.0	745.0	85.0
PCL	82.9	3	78.5 - 80.1	79.4	0.8
PD2	63.6	3	60.1 - 62.3	61.5	1.2
PD1	32.9	3	28.4 - 31.8	30.3	1.7
SVL	49.7	3	47.0 - 50.6	48.4	1.9
PP2	49.3	3	44.7 - 48.0	46.2	1.6
PP1	23.7	3	21.8 - 22.6	22.2	0.4
HDL	24.7	3	22.2 - 23.0	22.6	0.4
PG1	20.7	3	17.4 - 19.2	18.5	1.0
PSP	12.8	3	11.5 - 12.6	12.2	0.6
POB	7.9	3	6.8 - 7.7	7.4	0.5
PRN	4.8	3	4.5 - 4.9	4.7	0.2
POR	10.2	3	9.5 - 10.0	9.7	0.3
INLF	4.7	3	4.0 - 4.7	4.5	0.4
MOW	7.8	3	7.3 - 7.8	7.5	0.2
ULA	2.6	3	2.2 - 2.5	2.4	0.1
INW	5.0	3	3.9 - 4.1	4.0	0.1
INO	8.8	3	7.7 - 8.0	7.9	0.2
EYL	3.5	3	3.1 - 4.9	4.2	0.9
EYH	1.3	3	1.0 - 2.1	1.5	0.5
SPL	1.3	3	1.1 - 1.4	1.3	0.1
GS1	2.0	3	1.7 - 2.0	1.8	0.2
GS5	2.3	3	2.0 - 2.2	2.1	0.1
IDS	26.4	3	24.0 - 25.8	24.9	0.9
DCS	12.1	3	10.7 - 11.4	11.1	0.4
PPS	22.1	3	20.0 - 22.9	21.6	1.5
PCA	27.1	3	25.3 - 26.2	25.6	0.5
D1L	13.7	3	13.3 - 14.3	13.7	0.5
D1A	11.2	3	10.8 - 11.4	11.1	0.3
D1B	8.2	3	7.7 - 8.5	8.2	0.4
D1H	6.4	3	6.9 - 7.6	7.2	0.3
D1I	5.6	3	5.6 - 6.1	5.9	0.3
D1P	9.4	3	7.7 - 8.4	8.1	0.3
D1ES	4.3	3	3.3 - 4.3	3.9	0.5
D1BS	0.9	3	0.7 - 1.0	0.8	0.2
D2L	12.0	3	11.1 - 12.5	12.0	0.8
D2A	9.7	3	8.1 - 10.6	9.6	1.3
D2B	7.5	3	6.7 - 8.0	7.3	0.6
D2H	4.0	3	4.7 - 5.3	5.0	0.3
D2I	4.5	3	4.6 - 4.9	4.7	0.2
D2P	5.7	3	5.1 - 5.4	5.2	0.2
D2ES	4.4	3	3.9 - 4.3	4.1	0.2
D2BS	1.0	3	0.8 - 0.9	0.8	0.1
P1A	15.9	3	15.5 - 16.0	15.9	0.3
P1I	10.9	3	8.1 - 8.8	8.5	0.4
P1B	4.6	3	4.4 - 5.2	4.8	0.4
P1P	12.3	3	10.2 - 12.5	11.2	1.2
P2L	11.3	3	9.9 - 11.2	10.6	0.6
P2I	4.8	3	4.3 - 5.3	4.7	0.5
CDM	19.7	3	20.2 - 21.3	20.6	0.6
CPV	10.9	3	11.5 - 12.2	11.8	0.4
CFW	7.2	3	6.6 - 7.1	6.9	0.3
HANW	7.6	3	6.4 - 7.2	6.7	0.4
HAMW	11.3	3	9.9 - 11.8	10.8	1.0
HDW	16.1	3	12.2 - 13.5	12.9	0.7
TRW	13.7	3	9.3 - 11.3	10.2	1.0
ABW	9.6	3	6.3 - 10.4	8.9	2.3
HDH	11.3	3	8.9 - 10.4	9.6	0.7
TRH	11.6	3	8.5 - 12.3	10.1	2.0
ABH	12.8	3	8.2 - 12.6	11.1	2.5
CLO	-	-	-	-	-
CLI	-	-	-	-	-

Table 56. External measurements expressed as percentage of the total length (% TL) for *Flakeus* sp. 7. Ranges for other specimens are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	***Flakeus* sp. 7**				
	Holotype	Paratypes			
		N	Range	*x*	SD
TL (mm)	525.0	11	425.0 - 610.0	522.5	68.4
PCL	81.5	11	78.1 - 82.5	80.0	1.3
PD2	62.9	11	57.8 - 64.4	61.0	2.2
PD1	25.1	11	27.1 - 39.9	29.7	3.5
SVL	30.5	11	42.5 - 55.9	46.4	3.5
PP2	27.6	11	39.3 - 54.2	43.7	3.9
PP1	22.9	11	20.2 - 24.0	21.6	1.0
HDL	21.8	11	18.7 - 24.7	21.7	1.4
PG1	18.1	11	17.4 - 19.6	18.3	0.6
PSP	12.5	11	11.7 - 13.8	12.7	0.6
POB	7.1	11	6.8 - 7.8	7.5	0.3
PRN	5.2	11	4.3 - 5.0	4.6	0.2
POR	9.8	11	9.2 - 11.2	10.0	0.5
INLF	5.2	11	4.6 - 5.5	5.1	0.3
MOW	7.9	11	6.9 - 7.7	7.4	0.2
ULA	2.3	11	2.1 - 2.5	2.3	0.1
INW	4.3	11	3.6 - 4.3	4.0	0.2
INO	8.4	11	8.2 - 8.9	8.5	0.2
EYL	4.0	11	4.2 - 5.3	4.8	0.4
EYH	2.6	11	2.2 - 2.8	2.4	0.2
SPL	1.5	11	1.3 - 2.0	1.5	0.2
GS1	2.2	11	1.9 - 2.3	2.1	0.2
GS5	2.4	11	2.0 - 2.8	2.4	0.3
IDS	25.9	11	22.8 - 27.5	25.0	1.2
DCS	11.7	11	10.7 - 14.1	11.6	1.0
PPS	19.0	11	15.4 - 25.4	18.8	2.6
PCA	29.0	11	25.4 - 29.4	27.3	1.0
D1L	13.6	11	12.4 - 14.5	13.1	0.6
D1A	10.9	11	9.7 - 11.2	10.6	0.5
D1B	8.2	11	7.0 - 8.7	7.6	0.5
D1H	7.9	11	6.8 - 8.0	7.4	0.3
D1I	5.6	11	4.9 - 6.1	5.5	0.3
D1P	8.8	11	8.0 - 9.4	8.8	0.4
D1ES	4.2	11	2.3 - 4.1	3.5	0.6
D1BS	1.0	11	0.7 - 1.1	0.8	0.1
D2L	10.9	11	10.4 - 12.6	11.4	0.7
D2A	9.2	11	8.8 - 10.8	9.7	0.6
D2B	6.3	11	5.7 - 7.2	6.5	0.5
D2H	5.4	11	4.9 - 6.2	5.7	0.4
D2I	5.0	11	4.1 - 5.2	4.9	0.3
D2P	4.9	11	4.5 - 6.1	5.2	0.5
D2ES	5.1	10	3.4 - 5.0	4.4	0.5
D2BS	0.9	11	0.6 - 0.9	0.8	0.1
P1A	13.4	11	11.8 - 14.4	13.6	0.7
P1I	9.0	11	8.6 - 10.2	9.5	0.5
P1B	4.0	11	3.7 - 4.7	4.2	0.3
P1P	10.7	11	9.7 - 11.8	10.6	0.6
P2L	12.1	11	9.9 - 12.2	10.9	0.7
P2I	6.3	11	4.2 - 6.3	5.2	0.7
CDM	19.8	11	19.3 - 21.2	20.1	0.8
CPV	11.4	11	10.5 - 11.9	11.2	0.4
CFW	6.5	11	6.2 - 7.2	6.7	0.2
HANW	7.1	11	6.5 - 7.4	7.0	0.3
HAMW	11.1	11	10.9 - 12.0	11.3	0.4
HDW	11.9	11	10.9 - 12.9	12.1	0.5
TRW	9.9	11	8.0 - 11.9	10.5	1.1
ABW	8.2	11	8.0 - 10.9	9.5	0.9
HDH	10.3	11	9.3 - 11.7	10.6	0.8
TRH	10.0	11	10.5 - 12.7	11.8	0.7
ABH	10.3	11	9.6 - 13.2	11.7	1.1
CLO	4.1	4	4.0 - 4.8	4.4	0.4
CLI	7.1	4	6.9 - 7.7	7.4	0.4

Table 57. Tooth counts for *Flakeus probatovi*, *Flakeus* sp. 1, *Flakeus* sp. 2, *Flakeus* sp. 3, *Flakeus* sp. 4, *Flakeus* sp. 5, *Flakeus* sp. 6 and *Flakeus* sp. 7

	Flakeus probatovi		***Flakeus sp. 1***			***Flakeus sp. 2***		***Flakeus sp. 3***			***Flakeus sp. 4***		***Flakeus sp. 5***		***Flakeus sp. 6***		***Flakeus sp. 7***	
	Holotype	N= 9	Holotype	Paratypes N=6	N=9	Holotype	Paratypes N=18	Holotype	Paratypes N=6	N=1	Holotype	Paratypes N=5	Holotype	Paratypes N=2	Holotype	Paratypes N=2	Holotype	Paratypes N=5
upper teeth (right)	13	12–14	13	11–14	12–14	-	10–14	13	12–13	13	13	13–14	13	13–14	14	14–14	12	13–14
upper teeth (left)	13	12–14	13	12–13	12–14	-	10–14	13	12–13	13	13	13–15	14	13–15	14	14–14	12	13–14
lower teeth (right)	11	11–12	11	11–12	9–12	-	10–11	10	10–11	11	11	11–12	11	10–11	11	11–11	11	10–13
lower teeth (left)	11	11–12	11	10–12	9–13	-	10–12	10	10–11	11	10	9–12	12	11–11	11	11–11	11	11–13
upper teeth series	-	2–3	2	2–2	2–3	-	1–2	2	2–3	2	2	2–2	2	3–3	2	2–2	3	2–3
lower teeth series	-	2–3	2	1–2	2–3	-	2–2	2	2–3	2	2	2–2	2	2–2	2	2–2	2	2–3
Source	present study																	

Table 58. Monospondylous, diplospondylous, precaudal, caudal and total vertebrae for *Flakeus probatovi*, *Flakeus* sp. 1, *Flakeus* sp. 2, *Flakeus* sp. 3, *Flakeus* sp. 4, *Flakeus* sp. 5, *Flakeus* sp. 6, and *Flakeus* sp. 7.

	Monospondylous vertebrae																					
	35	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**
Flakeus probatovi											1		2	1								
Flakeus sp. 1				1	1	3	4	2	1													
Flakeus sp. 2												1	5									
Flakeus sp. 3						4	6	1														
Flakeus sp. 4										4	1											
Flakeus sp. 5									2		1											
Flakeus sp. 6											1	2										
Flakeus sp. 7					1	7	3															

	Diplospondylous vertebrae																					
	65	**66**	**67**	**68**	**69**	**70**	**71**	**72**	**73**	**74**	**75**	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**
Flakeus probatovi									1	1	1		1									
Flakeus sp. 1			1		2	2	3	1	2													
Flakeus sp. 2					1	2		2		1												
Flakeus sp. 3	1			2	5		3															
Flakeus sp. 4							1		1	2	1											
Flakeus sp. 5							1	1		1												
Flakeus sp. 6							1			1	1											
Flakeus sp. 7					1	1	3			1	1											

	Precaudal vertebrae																					
	80	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**	**91**	**92**	**93**	**94**	**95**	**96**	**97**	**98**	**99**	**100**	**101**
Flakeus probatovi								1					1		1		1					
Flakeus sp. 1	2	1	2	1	4	2																
Flakeus sp. 2							2	1	1	2												
Flakeus sp. 3	2	1	4	2	2																	
Flakeus sp. 4								1	3	1												
Flakeus sp. 5								3														
Flakeus sp. 6								1				1	1									
Flakeus sp. 7		1	1	2	1		1			1												

	Caudal vertebrae																					
	25	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**
Flakeus probatovi				1	2		1															
Flakeus sp. 1			4	2	4	1																
Flakeus sp. 2						4	1	1														
Flakeus sp. 3			4	7																		
Flakeus sp. 4				1	2	1	1															
Flakeus sp. 5				1	1	1																
Flakeus sp. 6					3																	
Flakeus sp. 7		1	5	3	1																	

	Total vertebrae																					
	103	**104**	**105**	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**	**121**	**122**	**123**	**124**
Flakeus probatovi																1			1		1	1
Flakeus sp. 1					1		1	2	2	2	2		1									
Flakeus sp. 2														2	1		2		1			
Flakeus sp. 3					1	2	1	4	1	2												
Flakeus sp. 4													1			3	1					
Flakeus sp. 5													1	1	1							
Flakeus sp. 6														1				1	1			
Flakeus sp. 7								2	3			1		1								

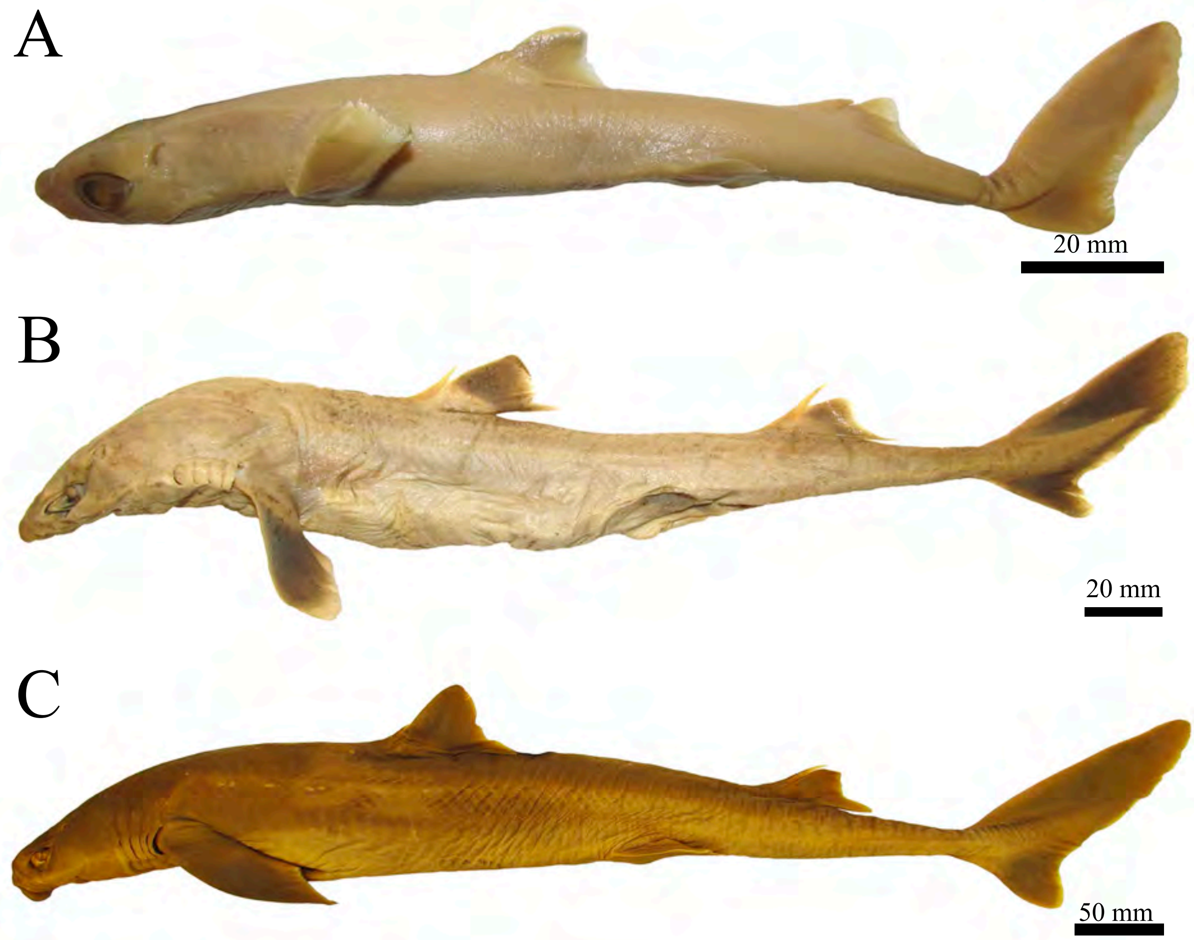

Figure 59. *Squalus acanthias* in lateral view: A: NRM 85, neonate female, 177 mm TL (lectotype); B: UUZM 159, juvenile male, 346 mm TL (paralectotype); C: NRM 21758, adult female, 715 mm TL.

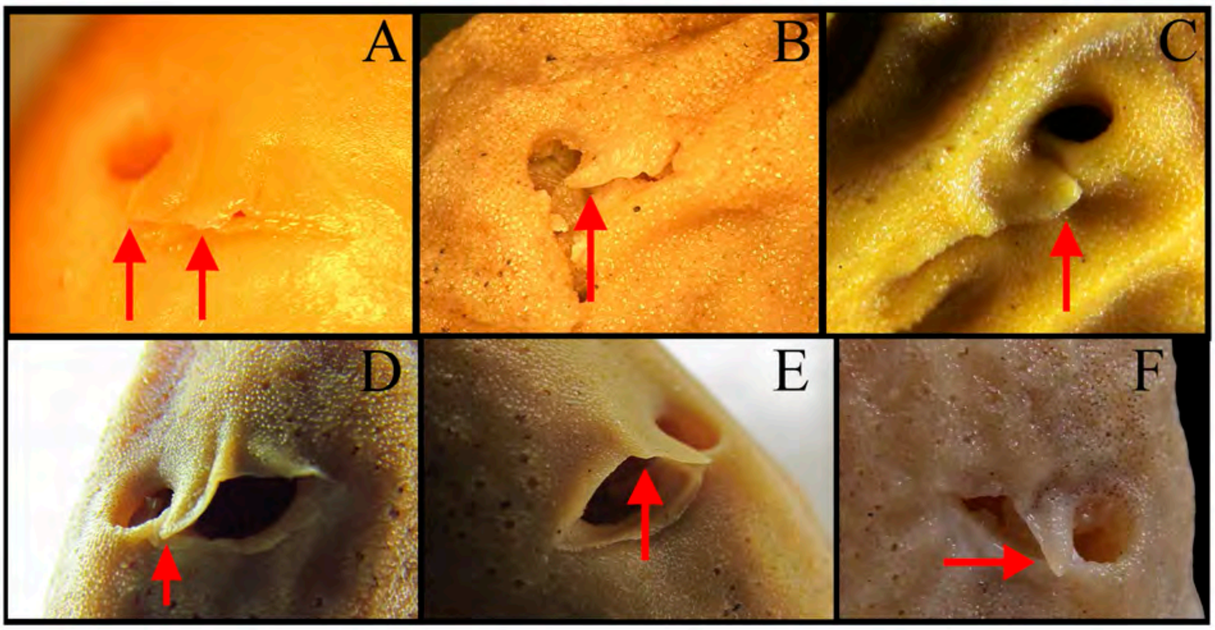

Figure 60. Anterior margin of nostrils in *Squalus acanthias*. A: lectotype, NRM 85, neonate female; B: paralectotype, UUZM 159, juvenile male; C: NRM 21758, adult female; D: HUMZ 30285, adult male; E: HUMZ 104416, adult female; F: BMNH 1999.5.4.13, juvenile female.

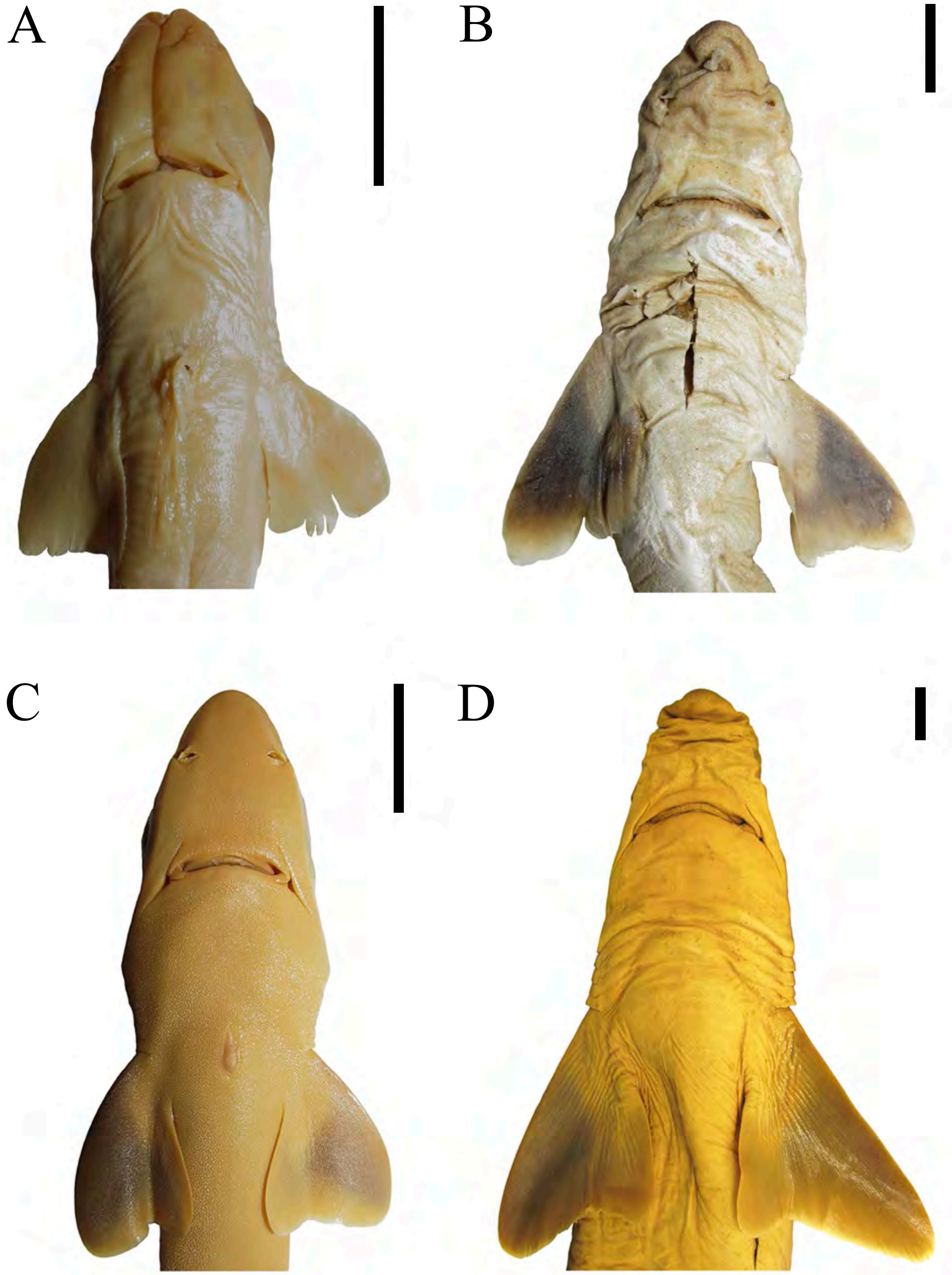

Figure 61. *Squalus acanthias* in ventral view: A: NRM 85, neonate female, 177 mm TL (lectotype); B: UUZM 159, juvenile male, 346 mm TL (paralectotype); C: NRM 21768, juvenile female, juvenile female, 256 mm TL; D: NRM 21758, adult female, 715 mm TL. Scale bar: 20 mm.

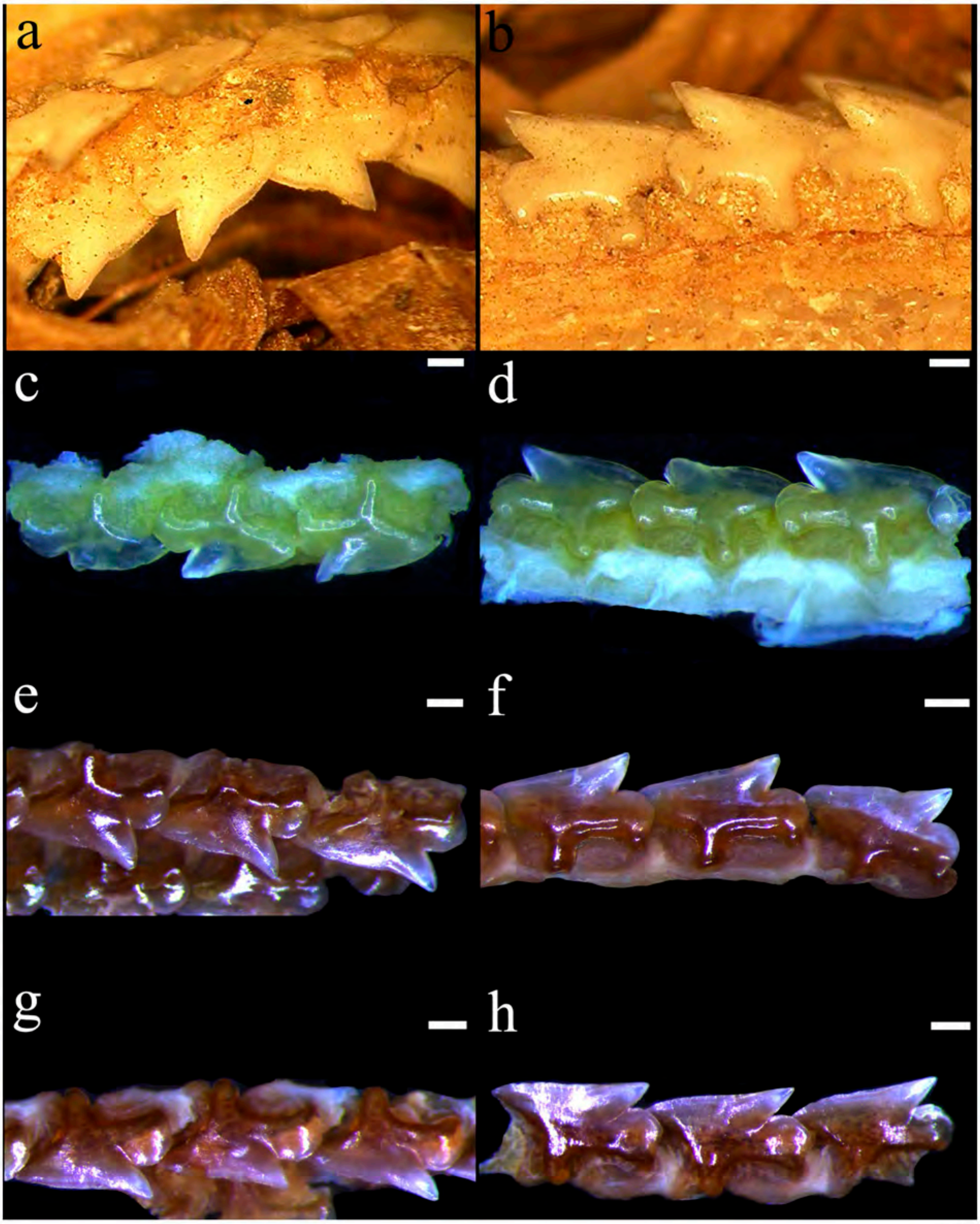

Figure 62 Upper (left) and lower (right) teeth of *Squalus acanthias*. a,b: UUZM 287, adult male, paralectotype; c,d: NMW 86034, adult male; e,f: HUMZ 30178, adult male; g.h: HUMZ 65447, adult male. Scale bar: 1 mm.

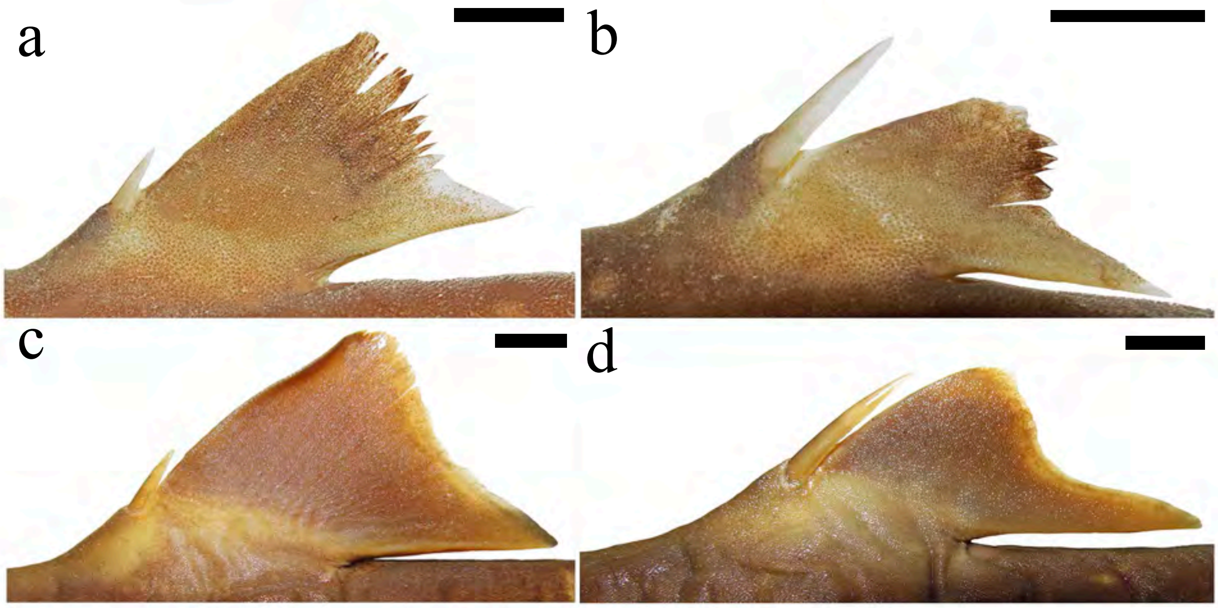

Figure 63. First (a,c) and second (b,d) dorsal fins of *Squalus acanthias*. a,b: NRM, 46764, juvenile female, 355 mm TL; c,d: ZMH 108038, adult male, 670 mm TL. Scale bar: 10 mm.

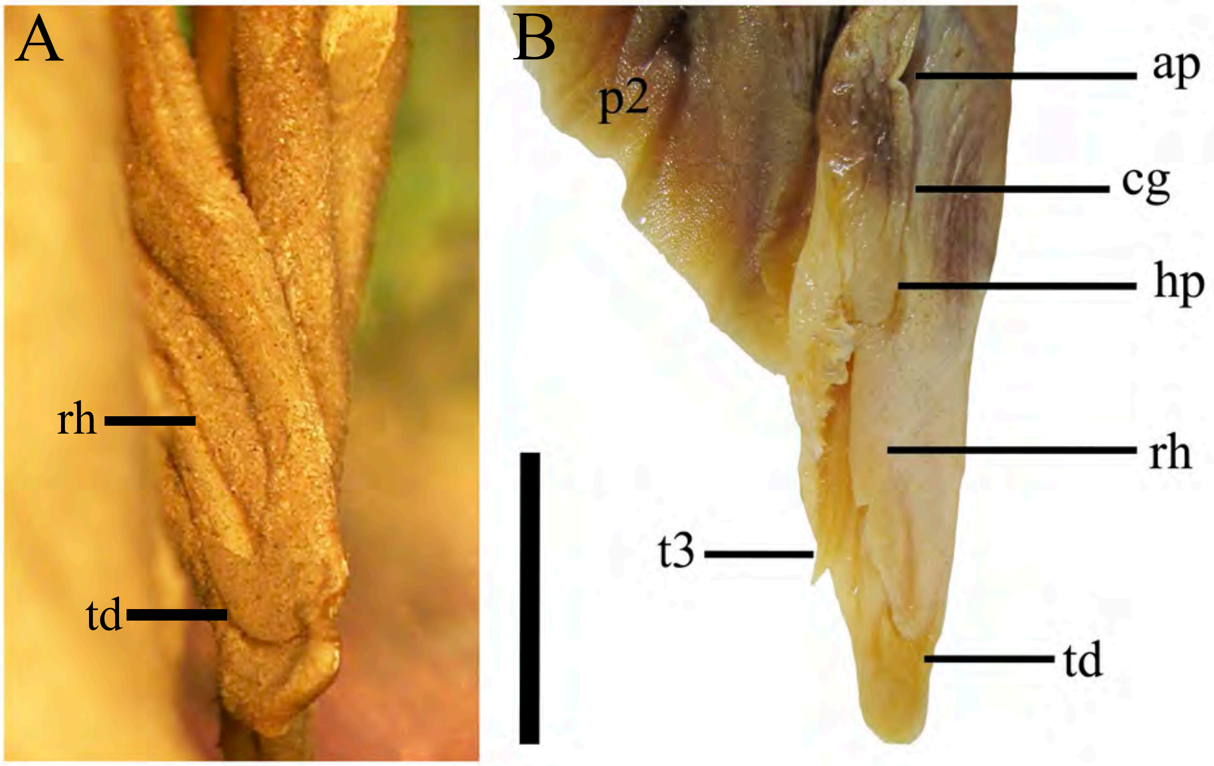

Figure 64. Clasper of *Squalus acanthias* in dorsal view. A: UUZM 287, adult male, 700 mm TL (paralectotype); B: ZMH 104951, adult male, 715 mm TL. Scale bar: 10 mm. Abbreviations: p2: pelvic fin; ap: apopyle; hp: hypopyle; cg: clasper groove; rh: rhipidion; t3: acessory terminal 3 cartilage or spur; td: dorsal terminal cartilage or claw.

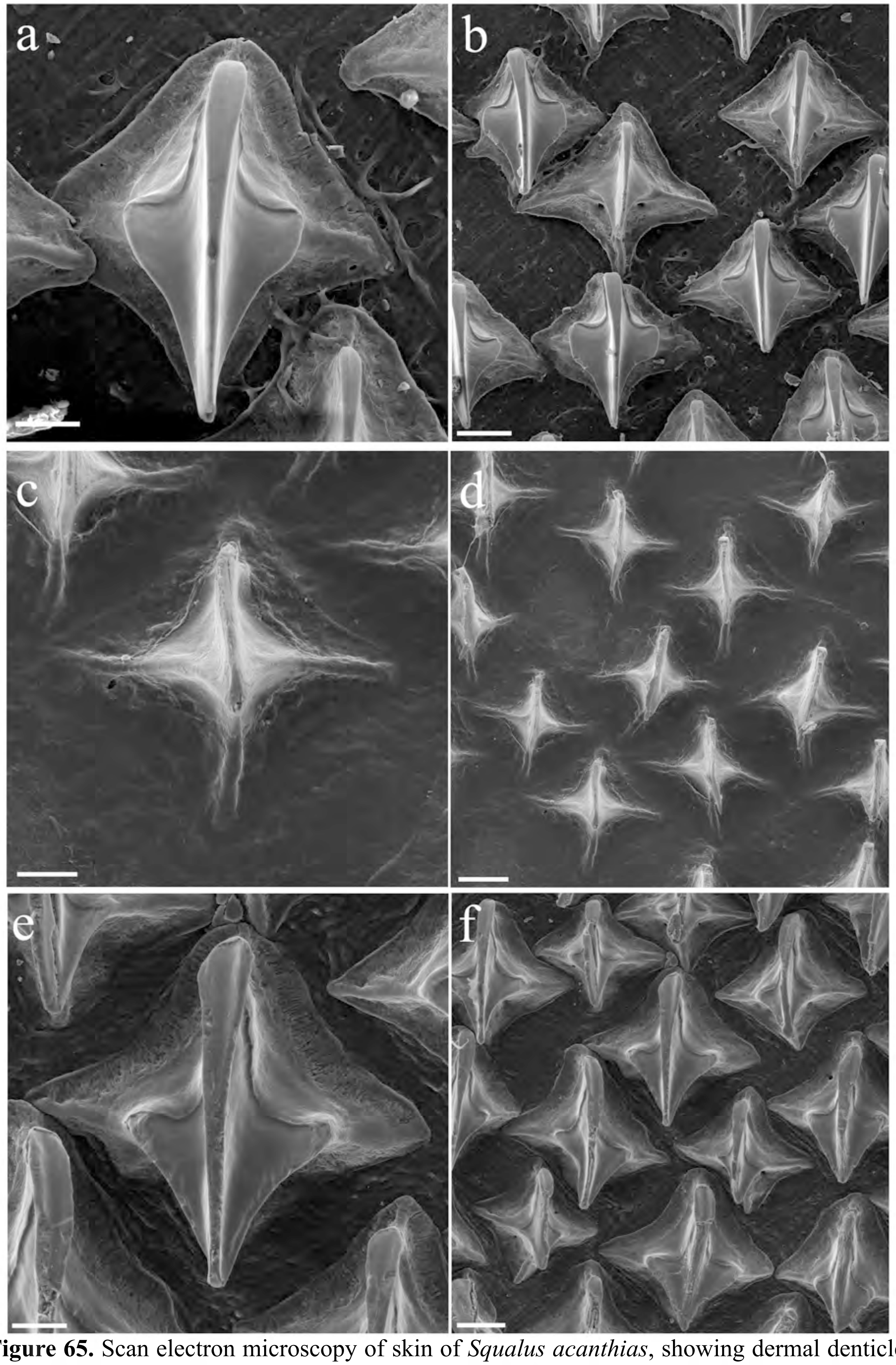

Figure 65. Scan electron microscopy of skin of *Squalus acanthias*, showing dermal denticles below first dorsal fin. a,b: BMNH 1976.7.30.20, adult female, 523 mm TL; c,d: HUMZ 30200, adult male, 655 mm TL; e,f: e,f: NMNZ 41292, adult female, 769 mm TL. Scale bars: 50 µm (a,c,e); 100 µm (b,d,f).

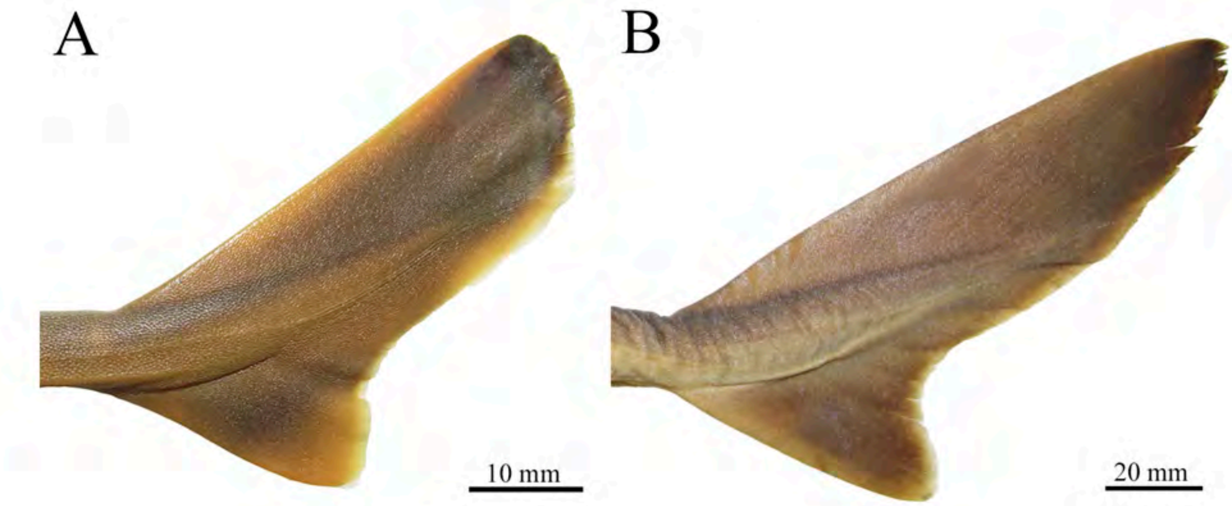

Figure 66. Caudal fin of *Squalus acanthias*: A: NRM 21768, juvenile female, 256 mm TL; B: ZMH 101886, adult female, 565 mm TL.

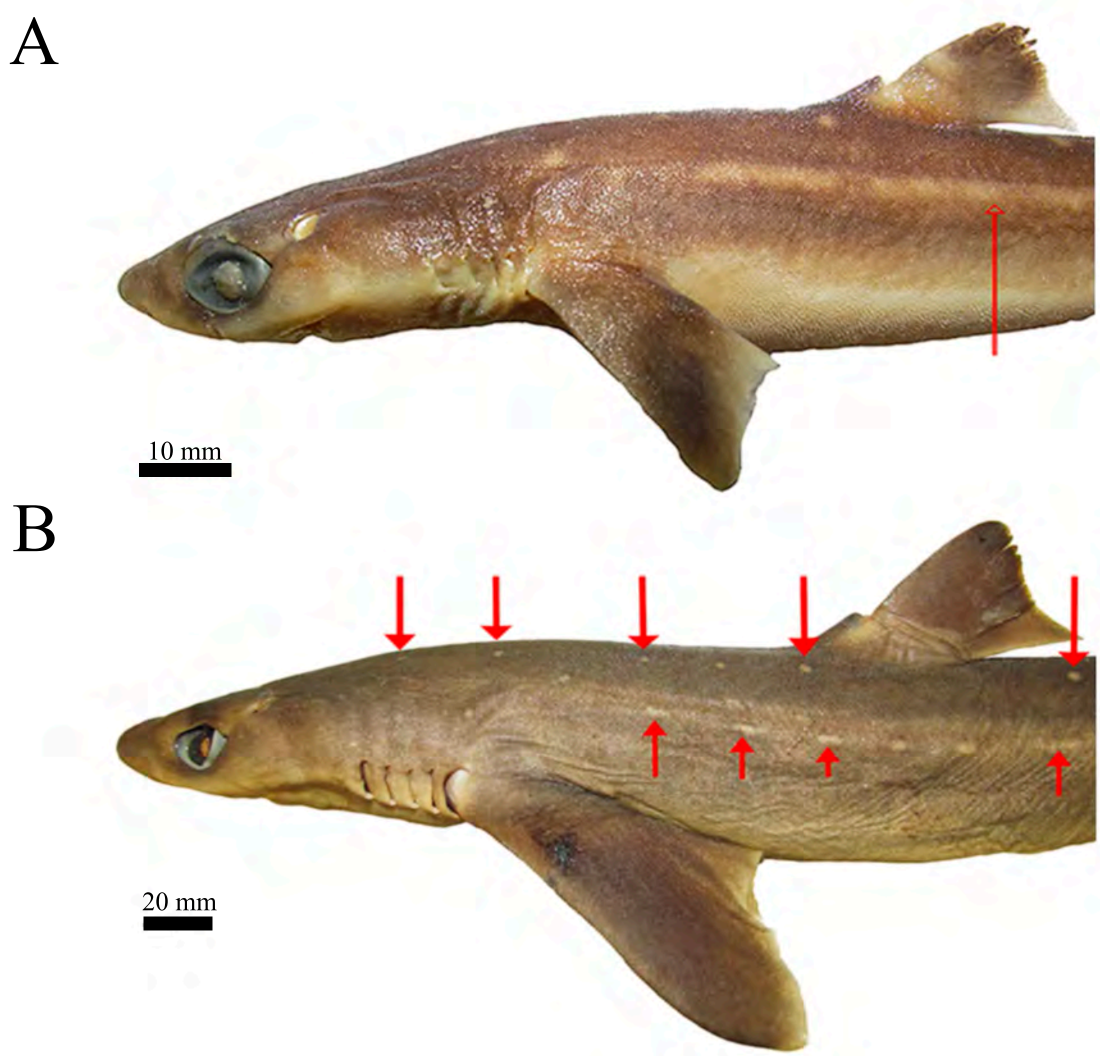

Figure 67. Color pattern of white spots in *Squalus acanthias*. A: NRM 46690, juvenile male, 255 mm TL; B: ZMH 100813, adult male, 570 mm TL. Lined red arrow: fused white spots. Full red arrow: two rows of white spots.

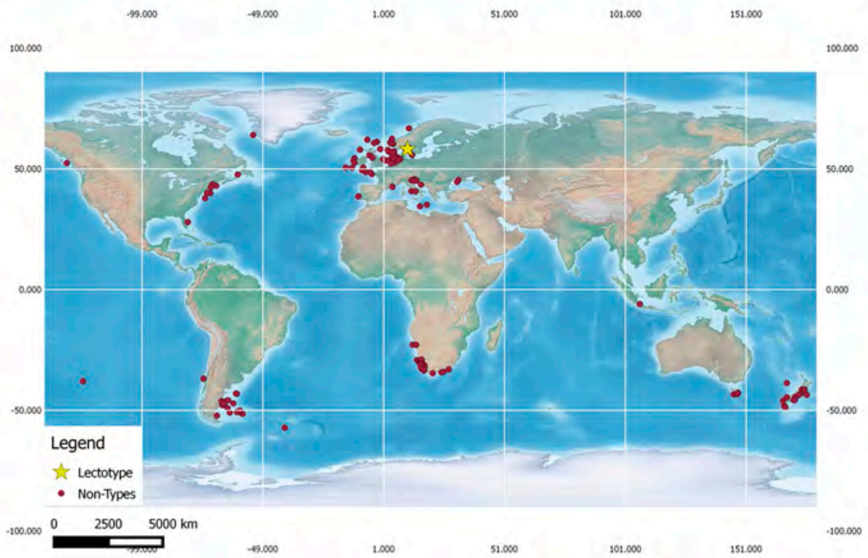

Figure 68. Map of geopgraphical distribution of *Squalus acanthias*.

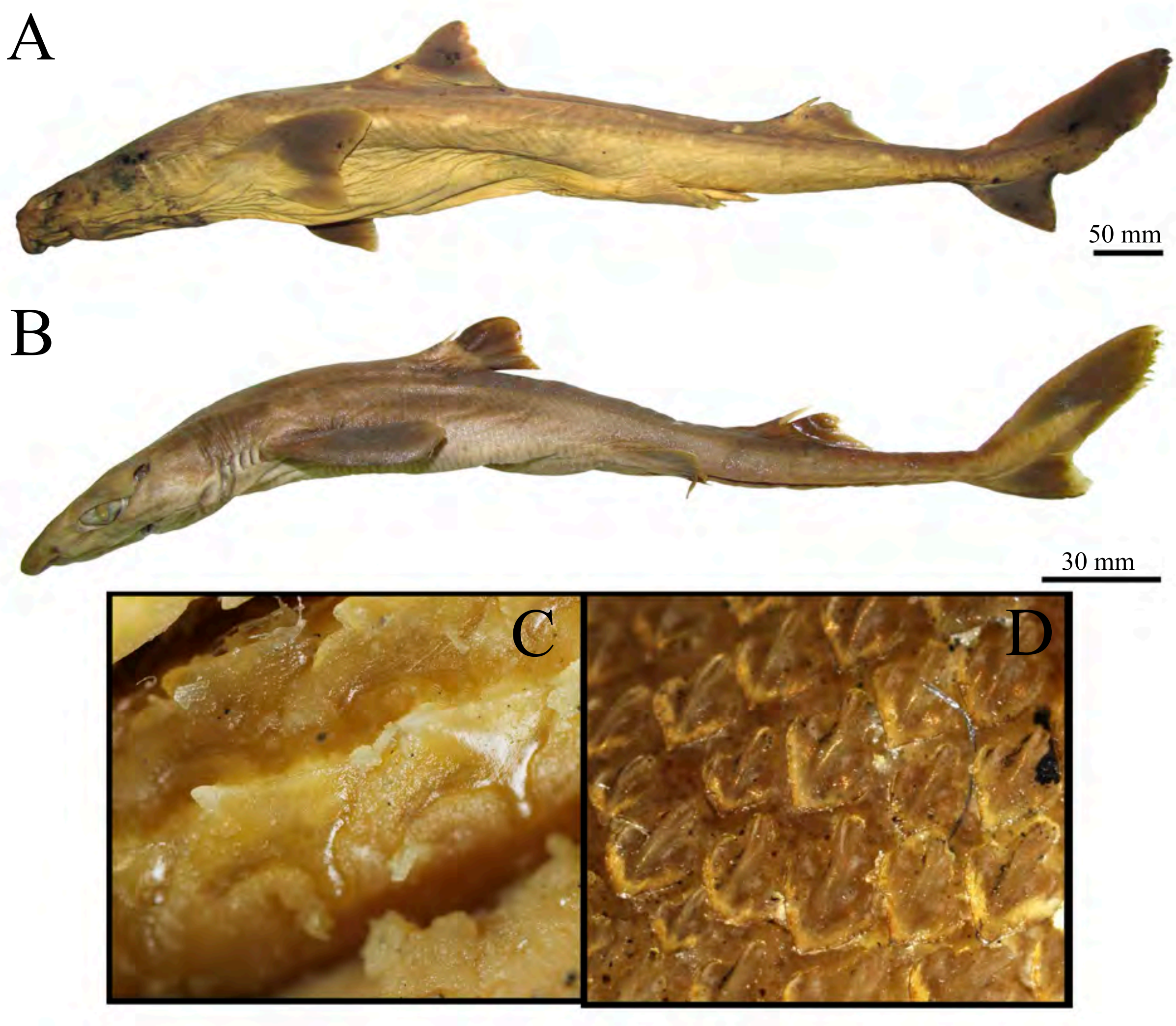

Figure 69. Syntype of *Squalus kirki* (A, C-D), BMNH 1931.8.10.1, adult male, 785 mm TL, and paratype of *Squalus lebruni* (B), MNHN 1883-202, juvenile male, 295 mm TL in lateral view. Lower teeth (C) and dermal denticles (D) of syntype of *Squalus kirki.*

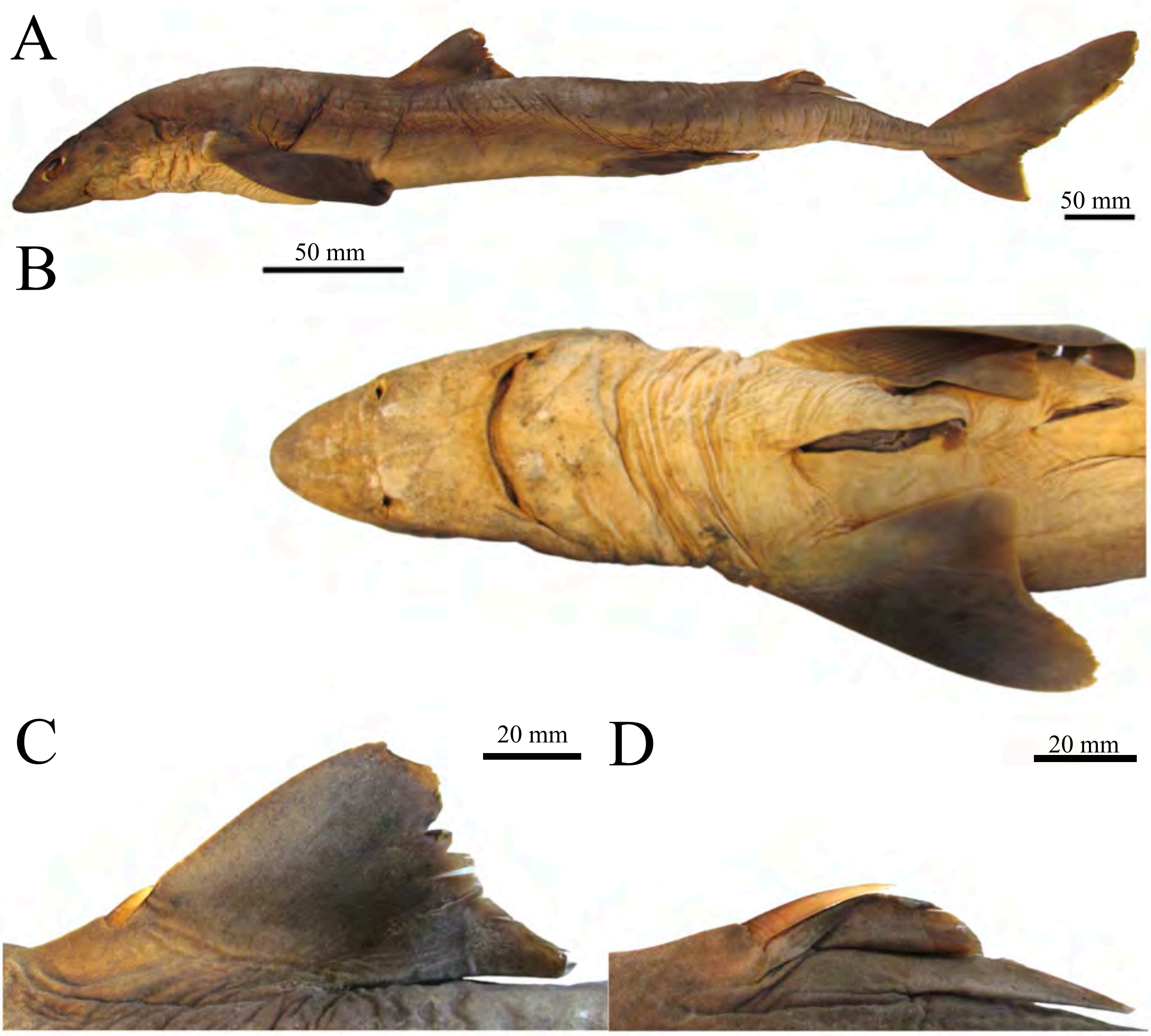

Figure 70. Specimen of *Squalus suckleyi*, BMNH 1890.11.15.365, adult male, 810 mm TL. A: lateral view; B: ventral view; C: first dorsal fin; D: second dorsal fin.

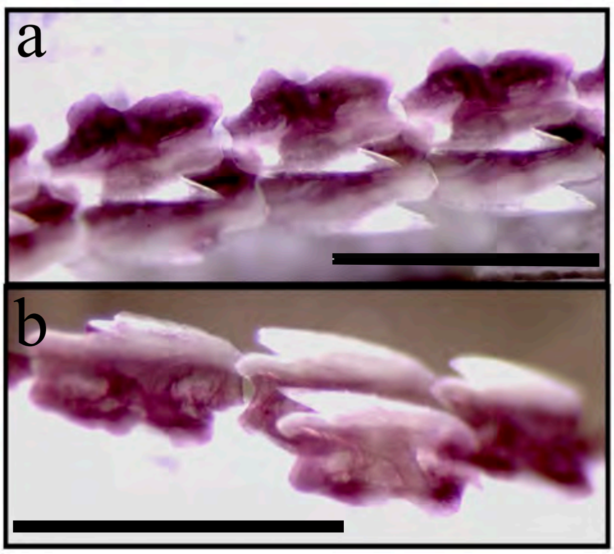

Figure 71. Upper (a) and lower (b) teeth of *Squalus suckleyi*, CAS 21971. Scale bar: 0.5 mm.

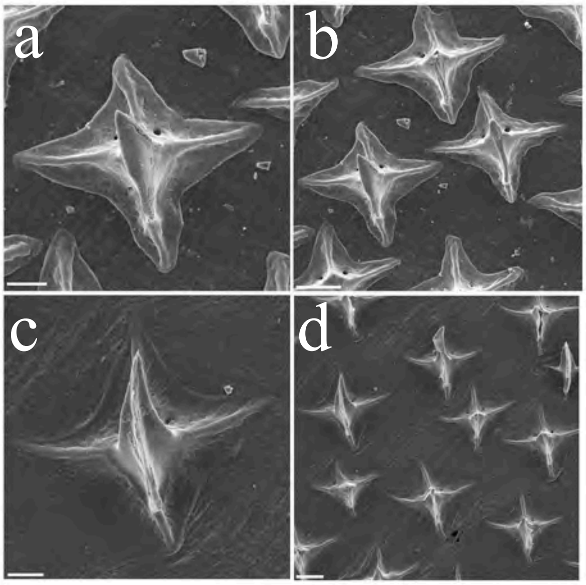

Figure 72. Scan electron microscopy of skin of *Squalus suckleyi*, showing dermal denticles: a,b: CAS 56093, neonate male, 260 mm TL; c,d: CAS 21424, juvenile male, 375 mm TL. Scale bars: 50 µm (a,c); 100 µm (b,d).

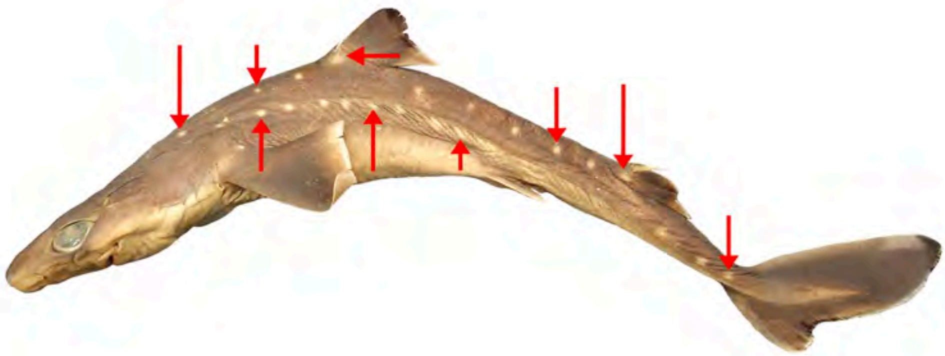

Figure 73. Color pattern of white spots in *Squalus suckleyi*, CAS 40873, juvenile male, 390 mm TL. Full red arrows: white spots laterally.

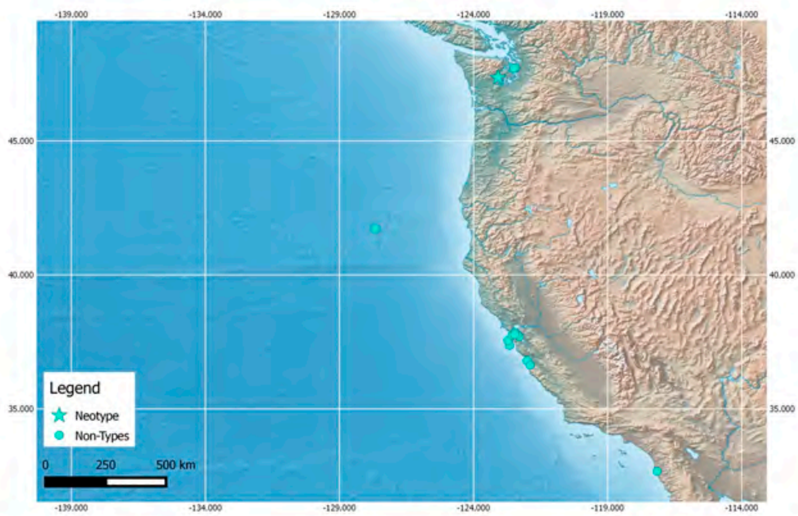

Figure 74. Map of geographical distribution of *Squalus suckleyi* in Northeast Pacific Ocean Ocean.

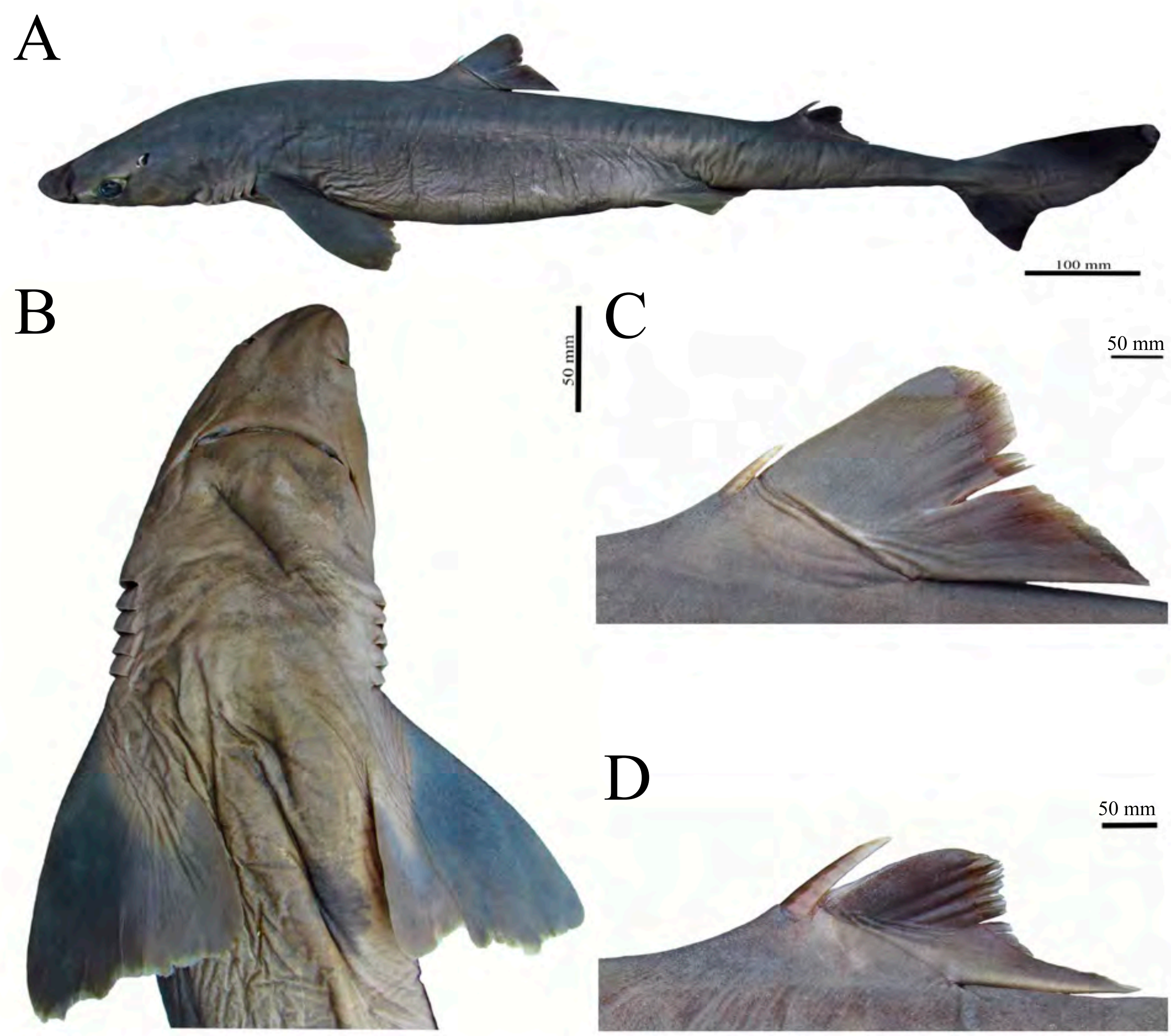

Figure 75. *Squalus wakiyae*, HUMZ 68927, adult female, 952 mm TL. A: lateral view; B: ventral view; C: first dorsal fin: D: second dor sal fin.

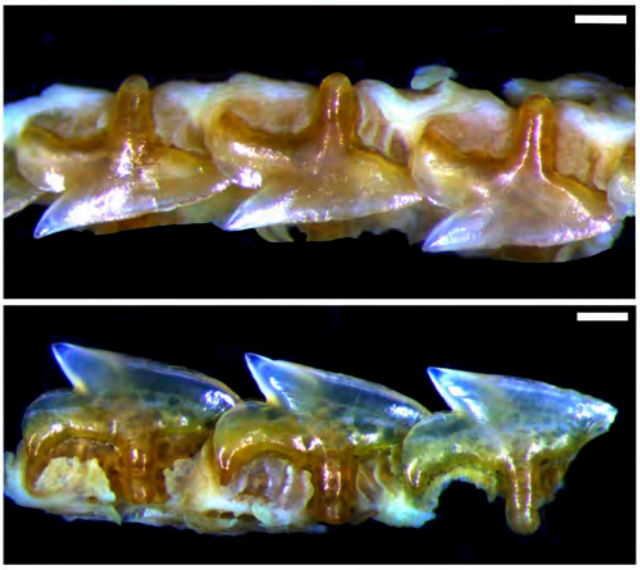

Figure 76. Upper (a) and lower (b) teeth of *Squalus wakiyae*, HUMZ 68927, adult female, 952 mm TL. Scale bar: 1 mm.

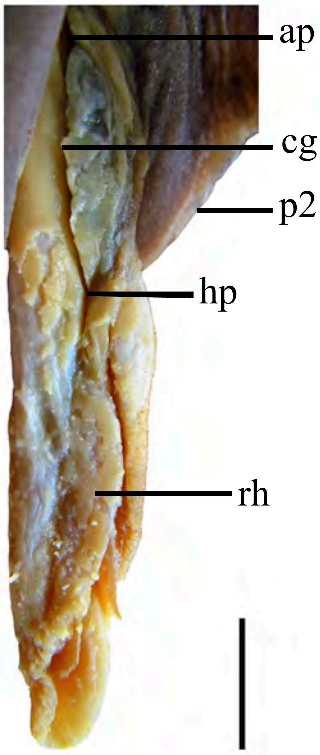

Figure 77. Clasper of *Squalus wakiyae,* HUMZ 87643, adult male, 665 mm TL in dorsal view. Scale bar: 10 mm. Abbreviations: pelvic fin (p2); apopyle (ap); hypopyle (hp); clasper groove (cg); rhipidion (rh).

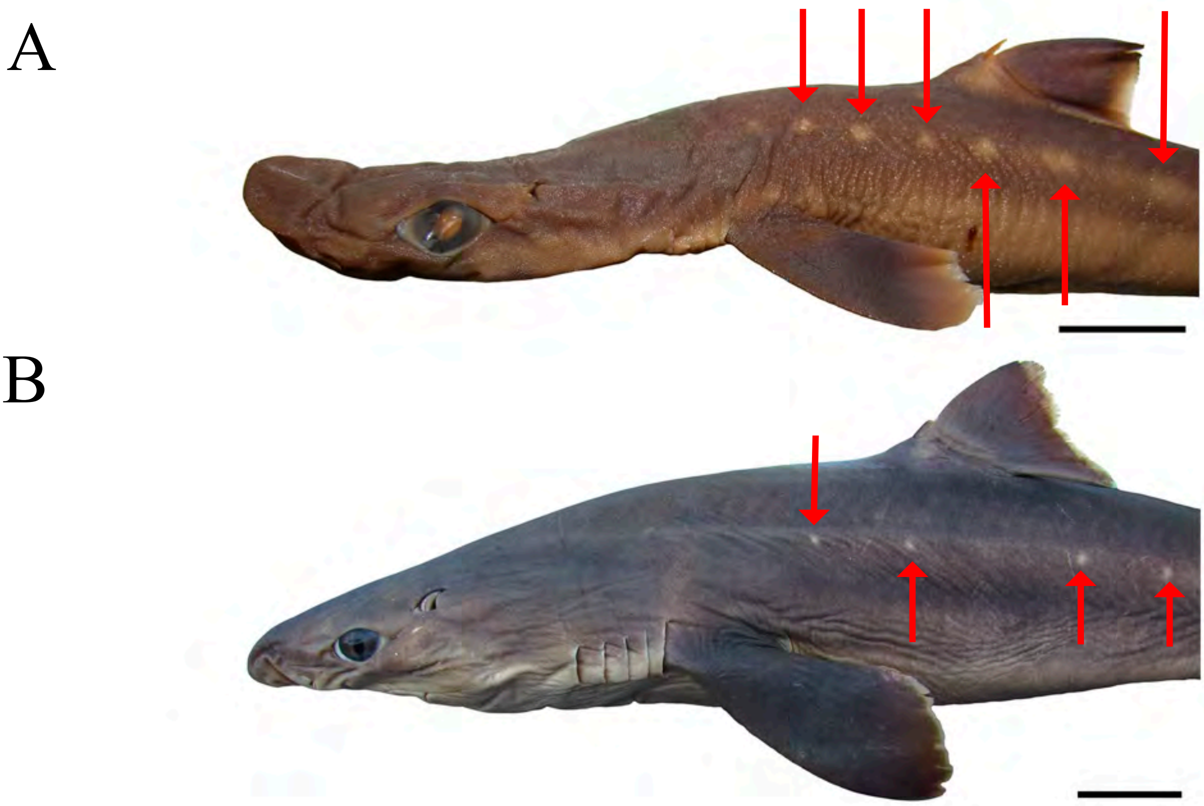

Figure 78. Pattern of white spots in S*qualus wakiyae*. A: ZUMT 46124, neonate male, 288 mm TL; B: HUMZ 90963, adult female, 784 mm TL. Red arrow: white spots.

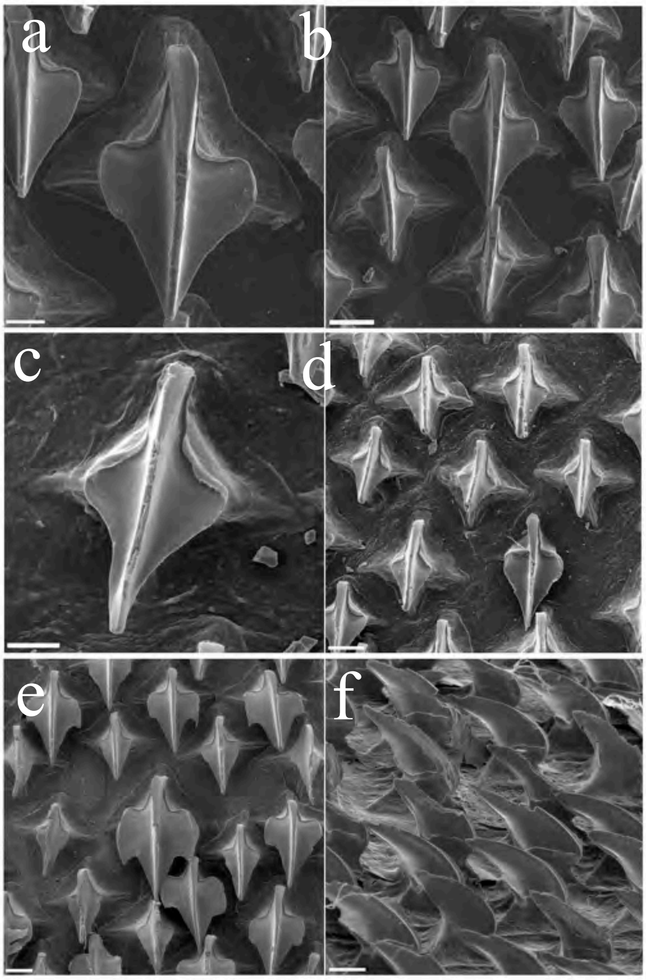

Figure 79. Scan electron microscopy of *Squalus wakiyae*, showing dermal denticles. a,b: NSMT P 92640, adult female, 740 mm TL; c,d: NSMT P 79501, adult male, 740 mm TL; e,f: HUMZ 117845, adult male, 720 mm TL. Scale bars: 50 µm (a,c); 100 µm (b,d–f).

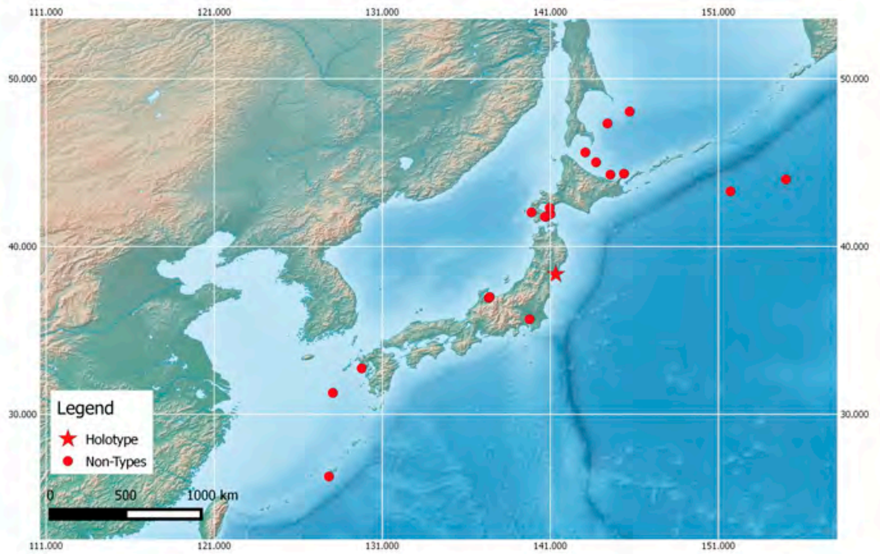

Figure 80. Map of geographical distribution of *Squalus wakiyae* in the Northwest Pacific Ocean.

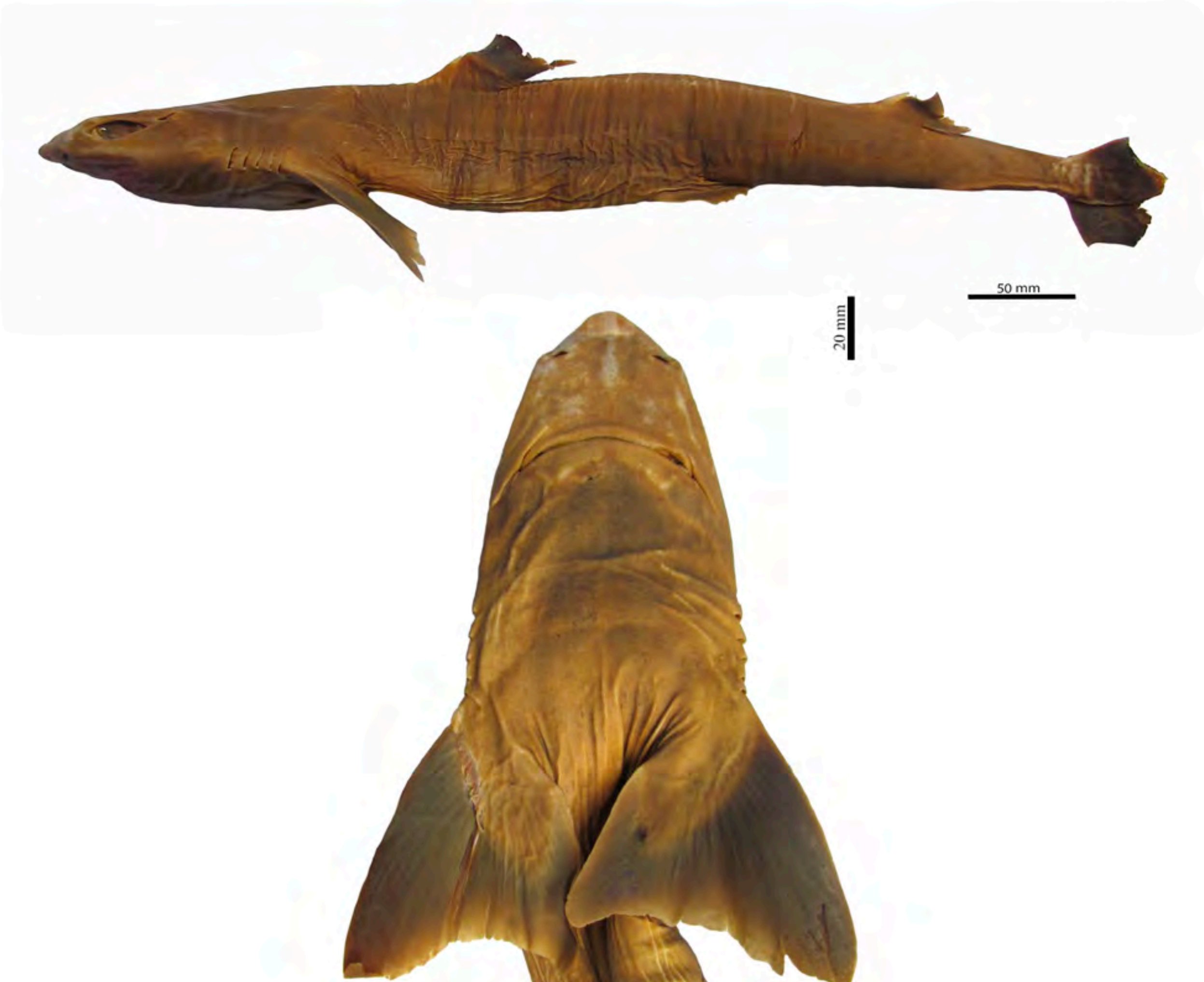

Figure 81. Holotype of *Flakeus megalops*, AMS I 16255-001, adult female, 550 mm TL. A: lateral view; B: ventral view.

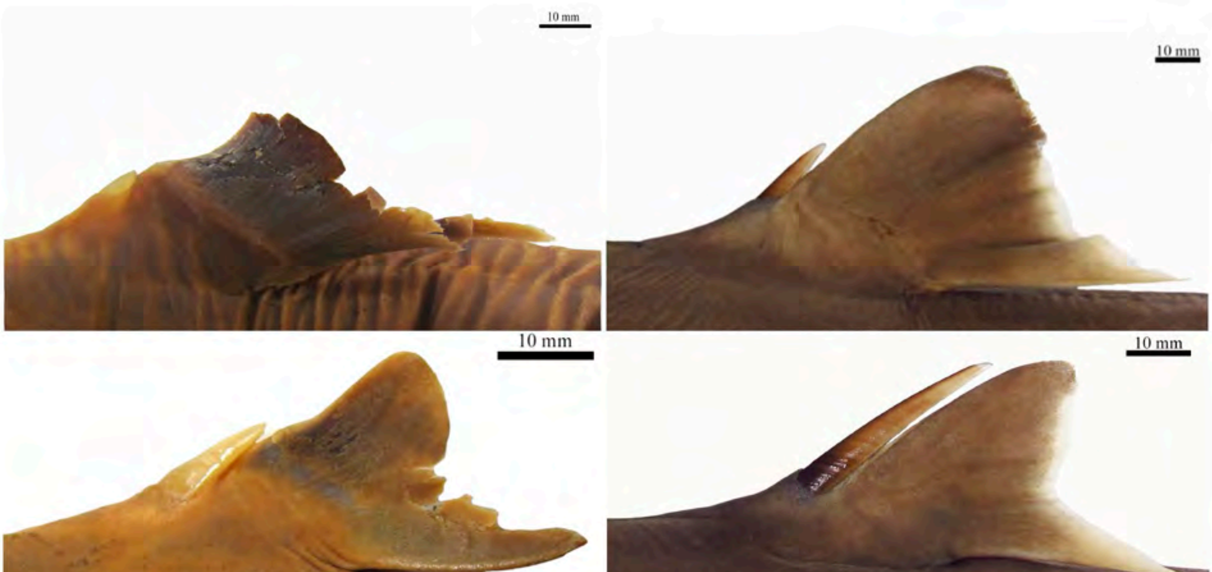

Figure 82. First (a,b) and second (c,d) dorsal fins of *Flakeus megalops*. A: AMS I 16255-001 (holotype). B: AMS I 45658-001, 625 mm TL.

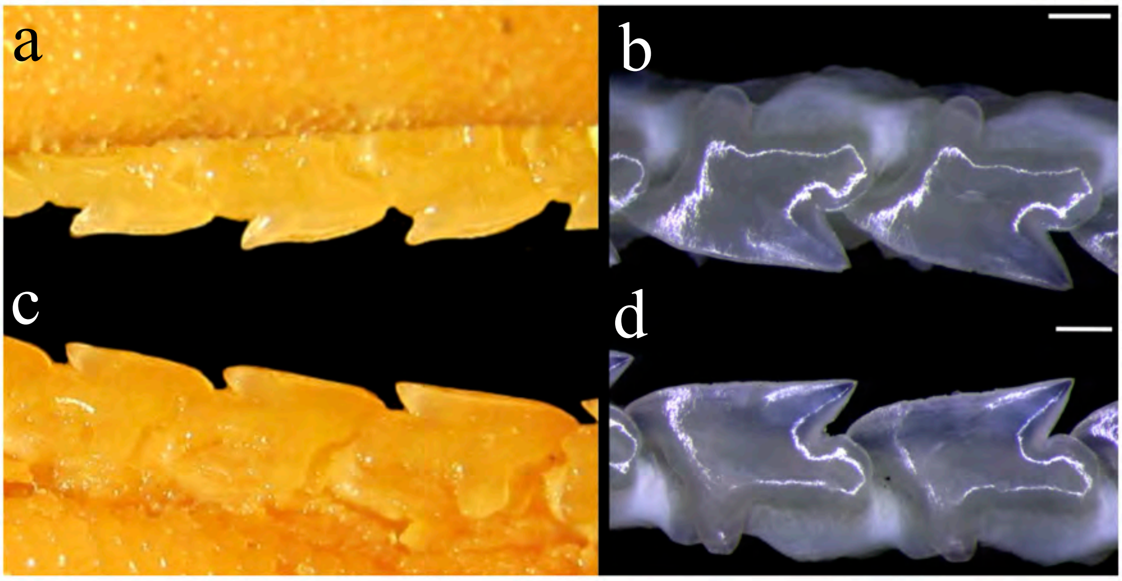

Figure 83. Upper (a,b) and lower (c,d) teeth of *Flakeus megalops*. a,c: AMS I 16255-001 (holotype). b,d: AMS I 46099-001. Scale bar: 0.5 mm.

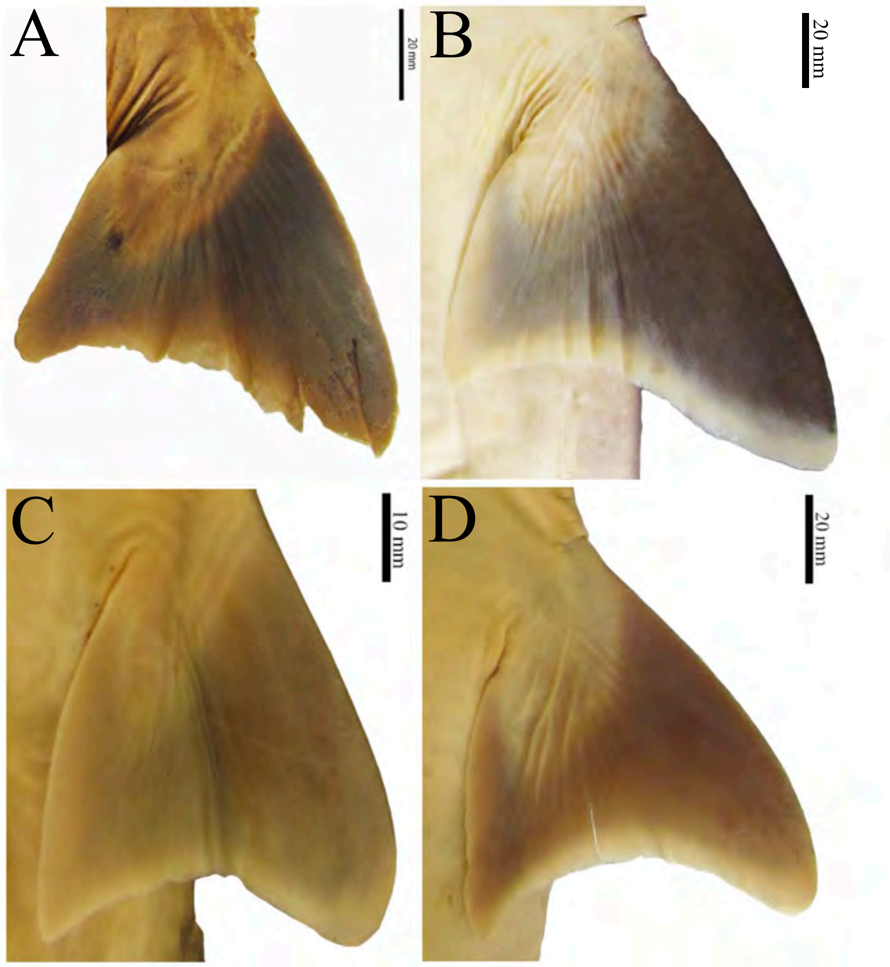

Figure 84. Variation on pectoral fins of *Flakeus megalops*. A: AMS I 16255-001 (holotype); B: AMS I 45658-001, adult female, 625 mm TL, from New South Wales. C: CSIRO H6482-01, adult male, 410 mm TL, from Tasmania; D: CSIRO H 3969-14, adult female, 545 mm TL, from Western Australia.

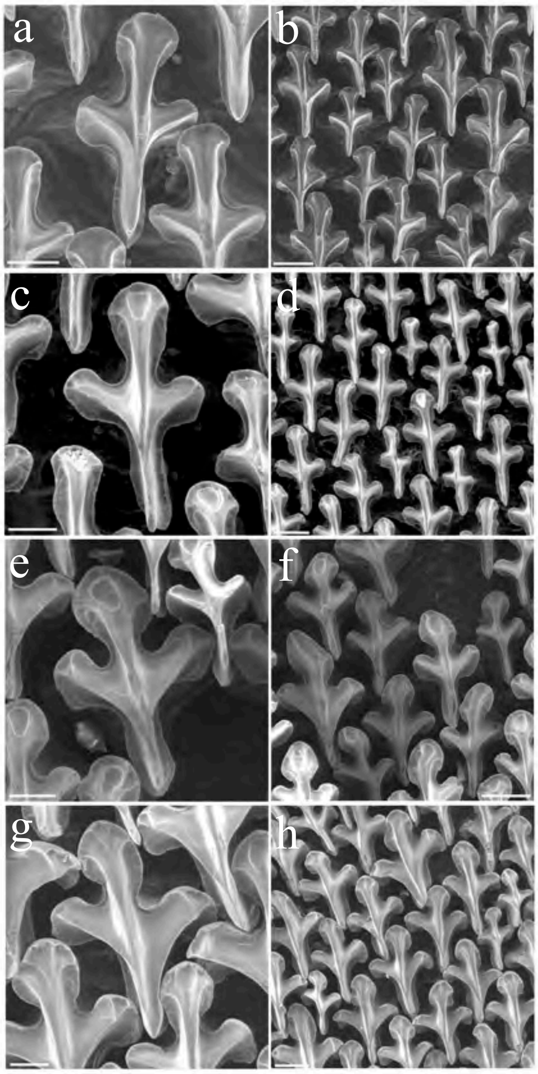

Figure 85. Dermal denticles of *Flakeus megalops*. a,b: AMS I 45658-001, adult female, 625 mm TL, New South Wales; c,d: CSIRO H 2225-01, adult male, 449 mm TL; e,f: CSIRO H 3969-14, adult female, 545 mm TL, Western Australia; g,h: CSIRO H 3762-01, adult female, 500 mm TL, Victoria. Scale bars: 50 µm (a,c,e,g); 100 µm (b,d,f,h).

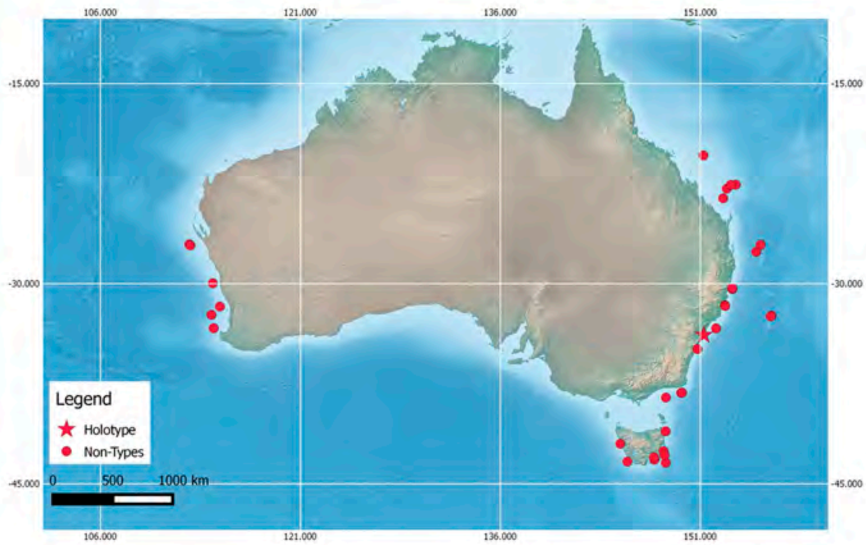

Figure 86. Map of geographical distribution of *Flakeus megalops* in the South Indo-Pacific Ocean.

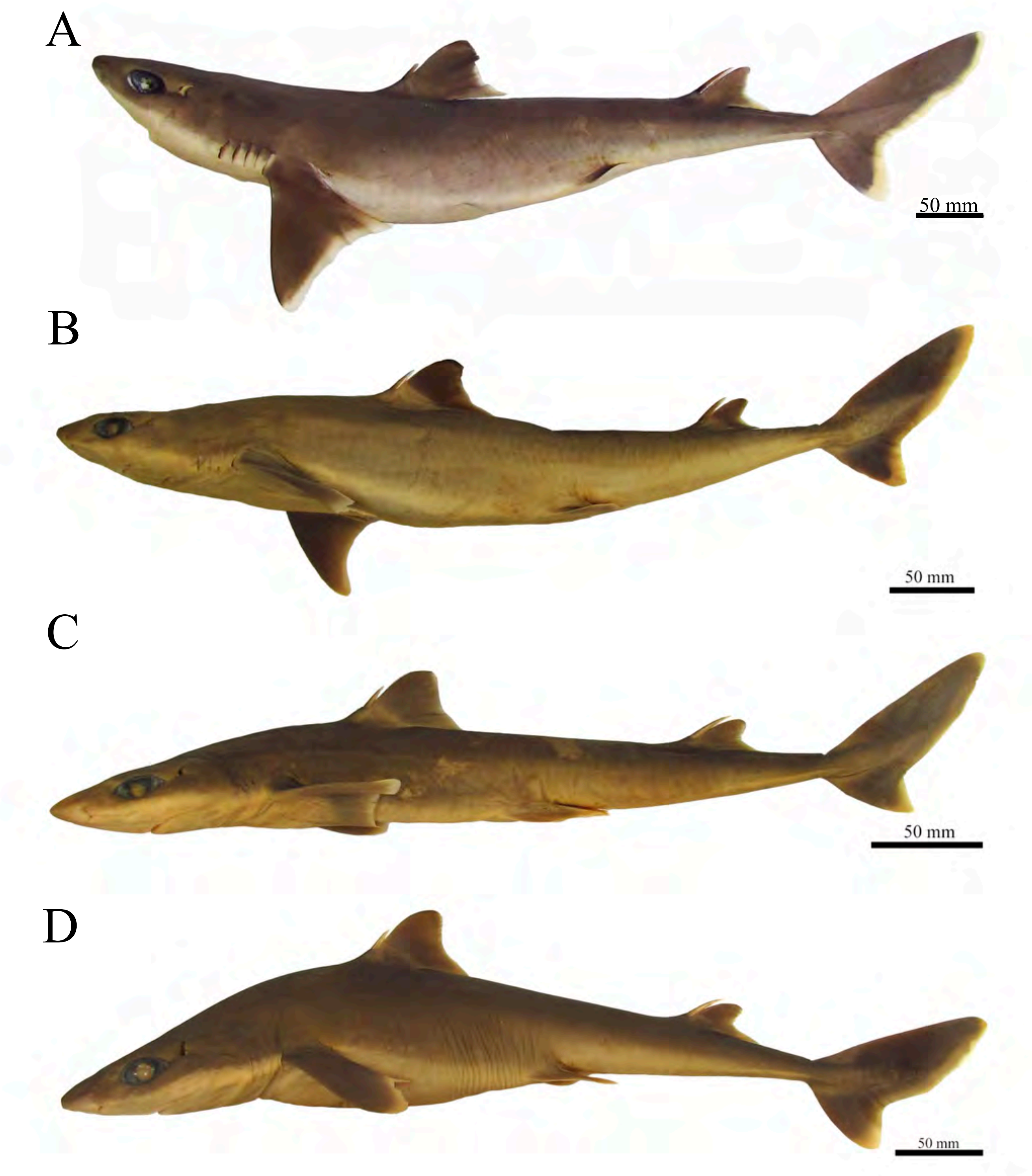

Figure 87. *Flakeus megalops* in lateral view. A: AMS I 45658-001, adult female, 625 mm TL, from New South Wales. B: CSIRO H 3969-14, adult female, 545 mm TL, from Western Australia; C: CSIRO H 6482-01, adult male, 410 mm TL, from Tasmania; D: CSIRO H 3762-01, adult female, 500 mm TL from Victoria.

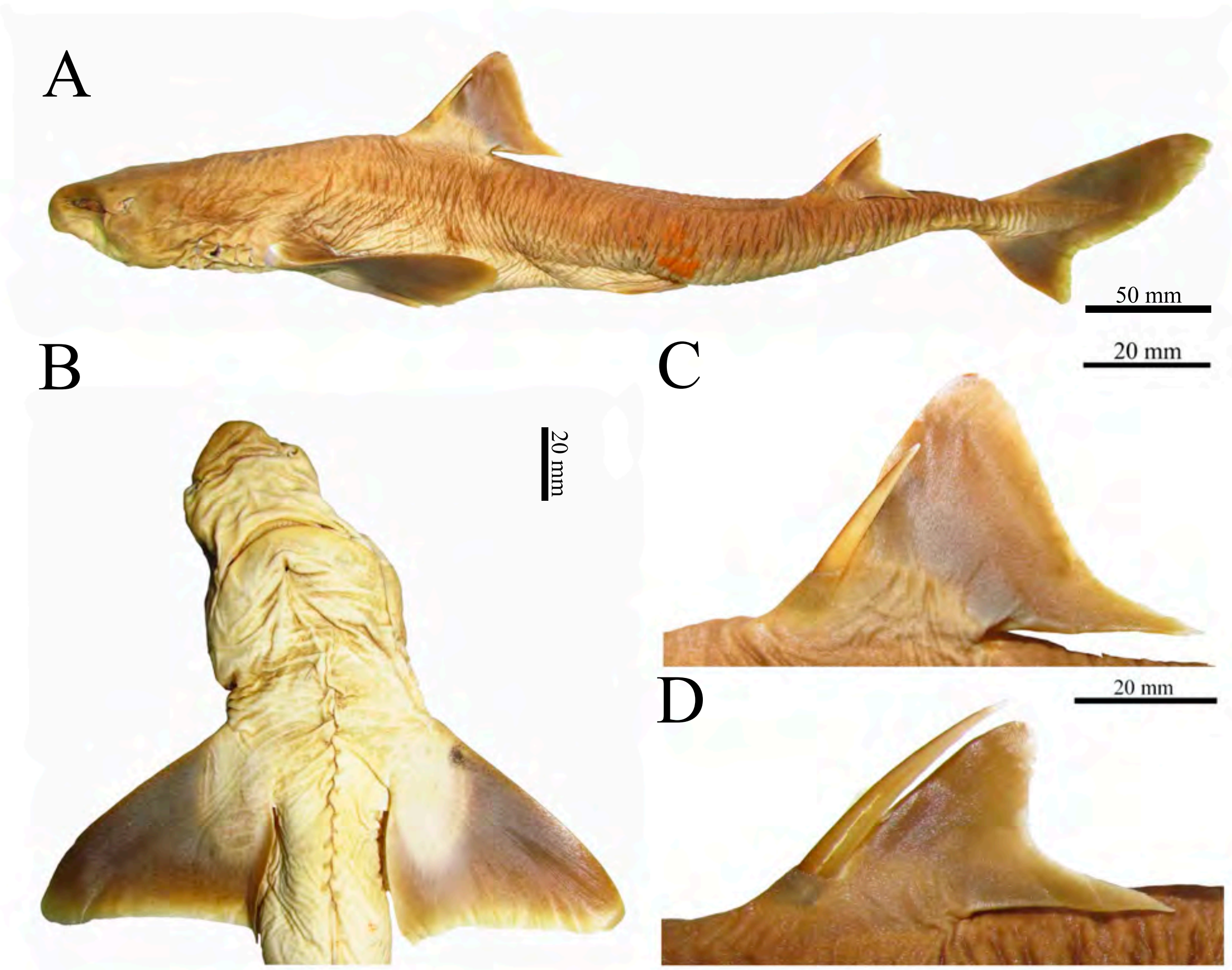

Figure 88. *Flakeus blainvillei*, MNHN 1898-1235, juvenile female, 502 mm TL. A: lateral view; B: ventral view; C: first dorsal fin; D: second dorsal fin.

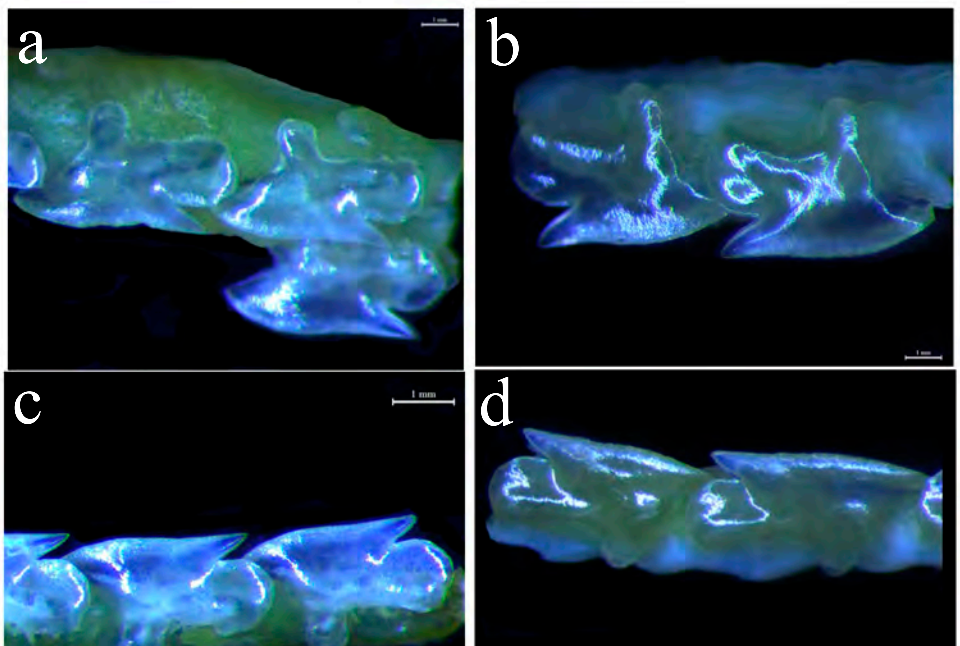

Figure 89. Upper (a,b) and lower (c,d) teeth of *Flakeus blainvillei*. a,c: BMNH 1963.5.14.13-18, juvenile male, 382 mm TL; b,c: NMW 50125, adult male, 530 mm TL. Scale bar: 1mm.

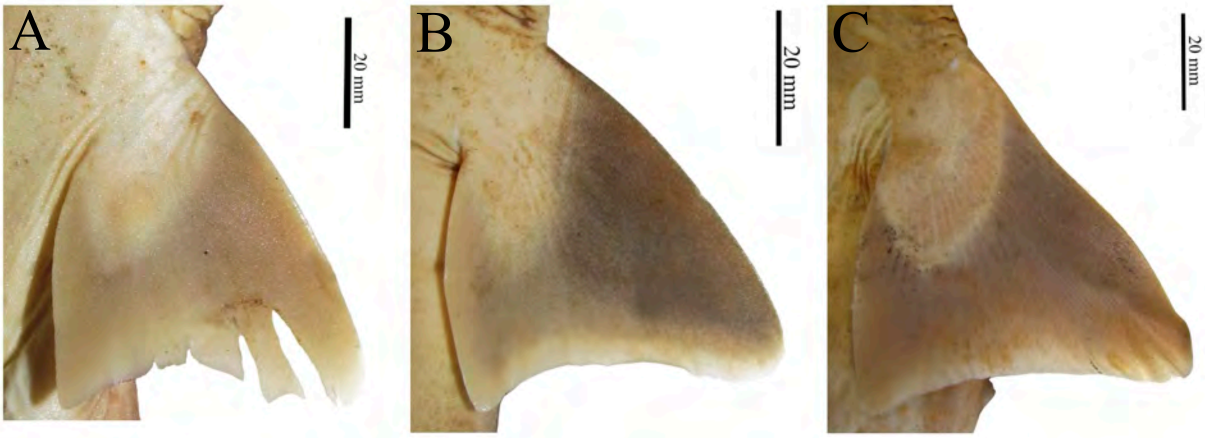

Figure 90. Pectoral fins of *Flakeus blainvillei*. A: NMW 83937, juvenile female, 262 mm TL; B: ZMA 113.606, juvenile male, 385 mm TL; C: BMNH 2013.9.3.6, adult female, 540 mm TL.

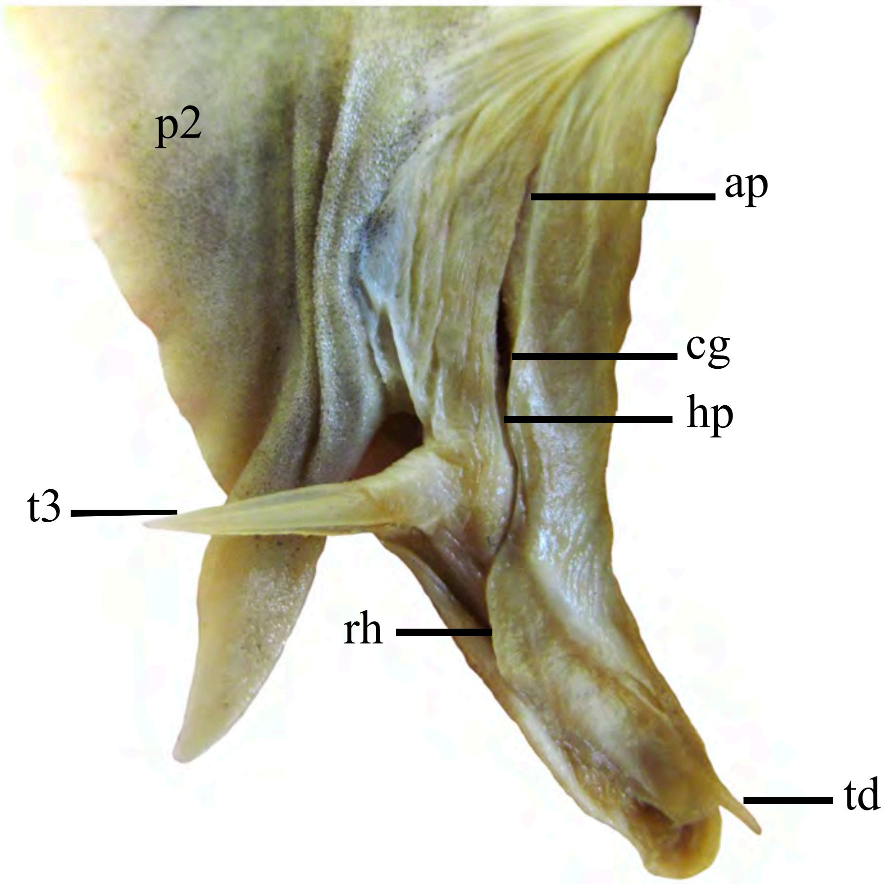

Figure 91. Clasper of *Flakeus blainvillei* in dorsal view, NMW 85903, adult male, 480 mm TL. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion; td: dorsal terminal cartilage; t3: acessory terminal 3 cartilage.

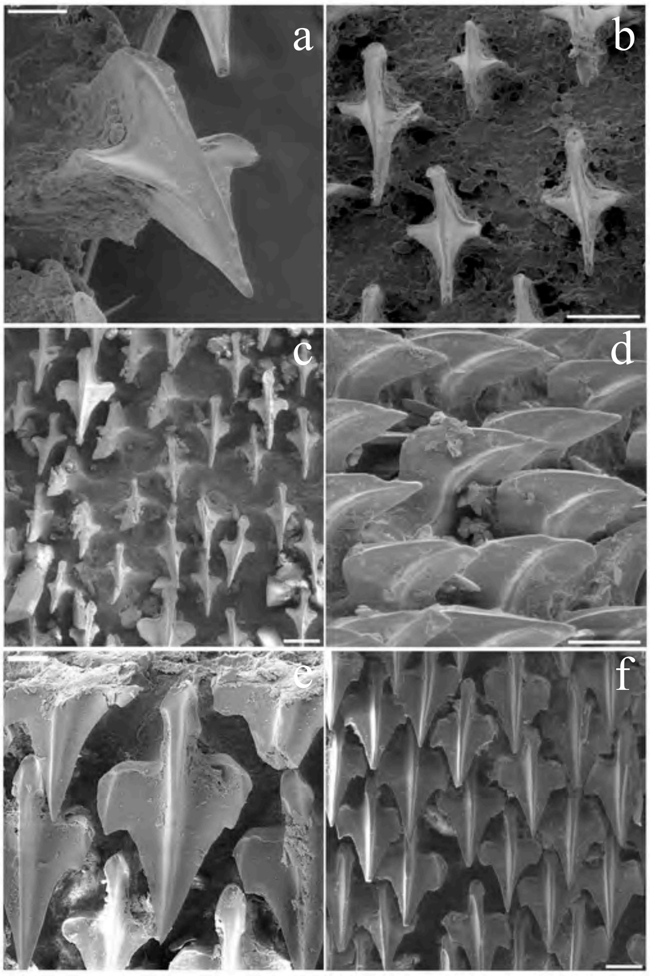

Figure 92. Dermal denticles of *Flakeus blainvillei*. a,b: BMNH 1963.5.14.13-18, juvenile male, 382 mm TL; c,d: NMW 78786, juvenile female, 436 mm TL; e,f: NMW 50125, adult male, 530 mm TL. Scale bars: 50 µm (a,e); 100 µm (b,c,d,f).

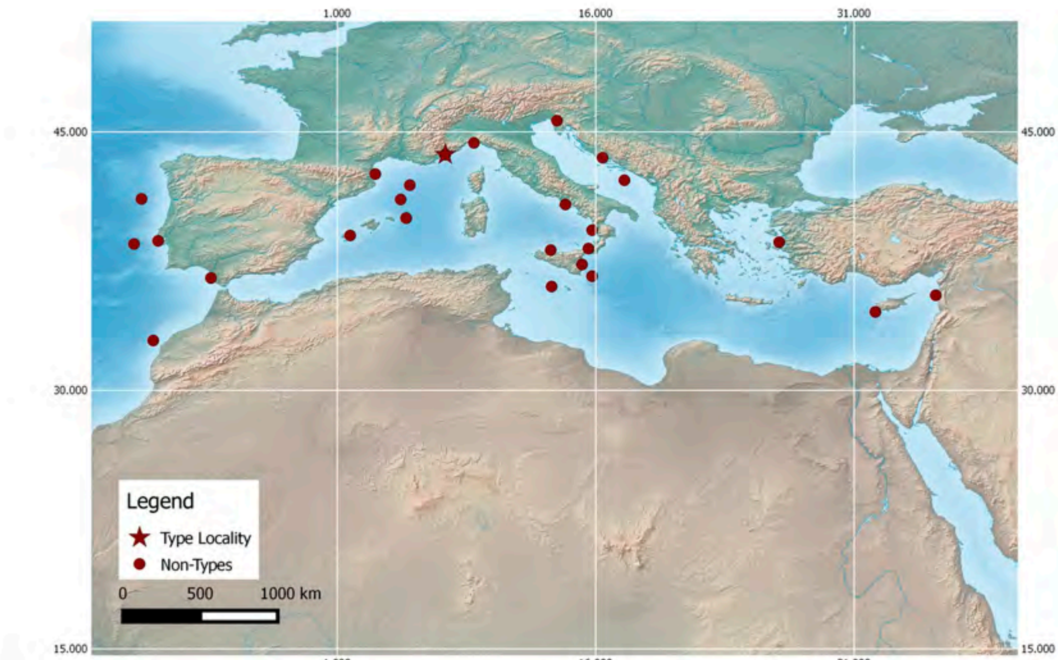

Figure 93. Map of geographical distribution of *Flakeus blainvillei* in the Mediterranean Sea and Northeast Atlantic Ocean.

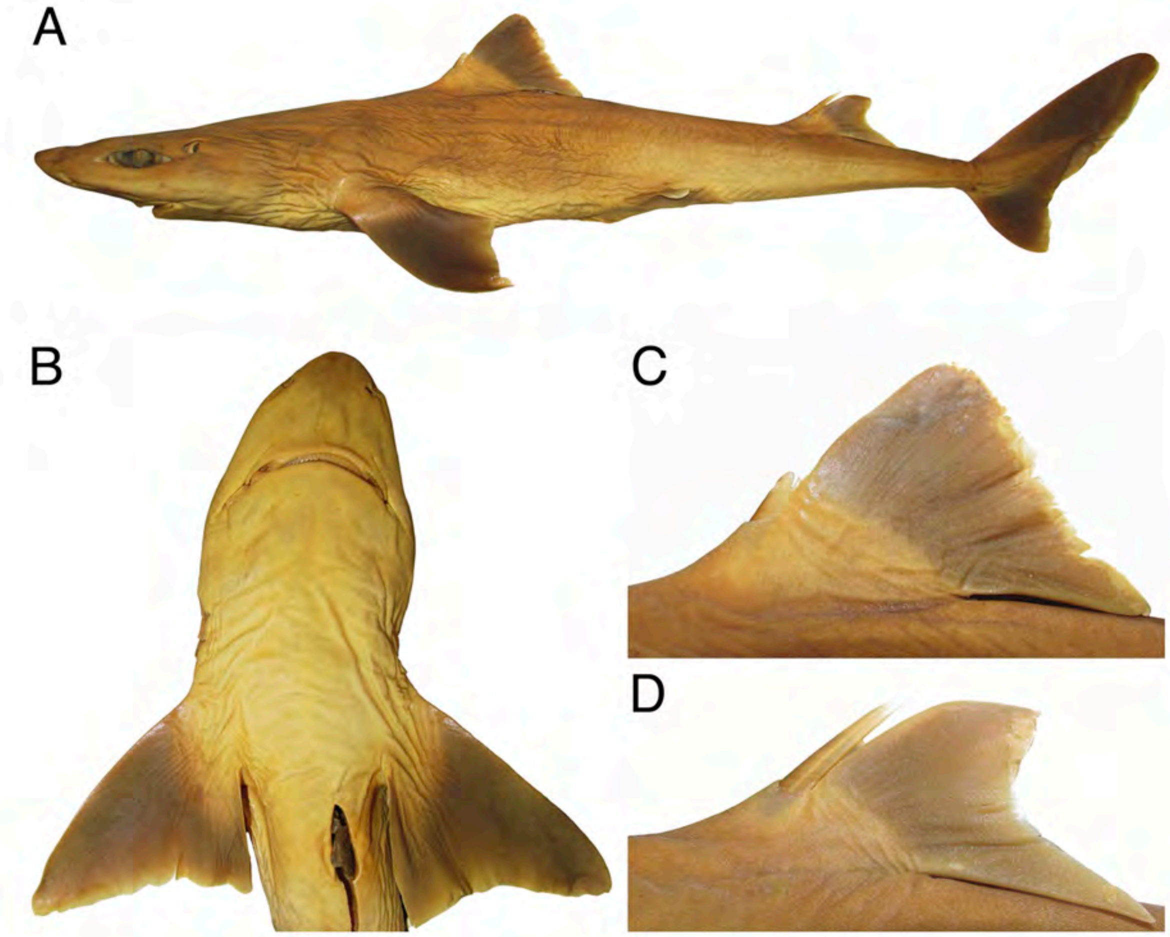

Figure 94. Lectotype of *Flakeus acutipinnis*, BMNH 1905.6.8.8, adult female, 578 mm TL from Kwazulu-Natal, South Africa: (A) lateral view; (B) ventral view; (C) first dorsal fin; (D) second dorsal fin.

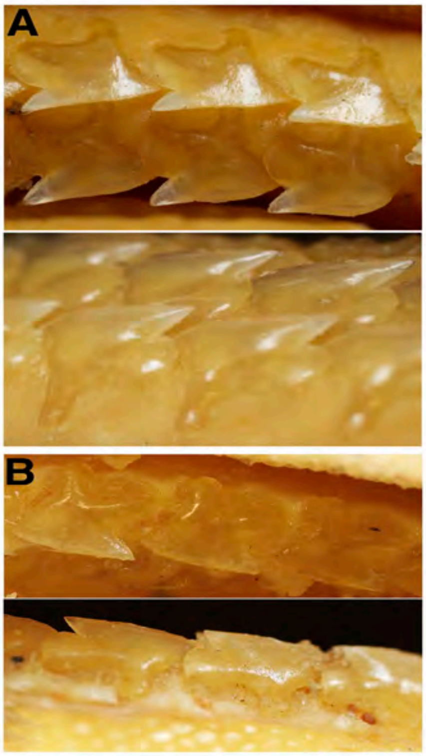

Figure 95. Detail of the upper and lower teeth. (A) *Flakeus acutipinnis*, BMNH 1905.6.8.8 (lectotype), female, 578 mm TL from Kwazulu-Natal, South Africa; (B) BMNH 1900.11.6.14 (paralectotype), female, 565 mm TL from Table Bay, South Africa.

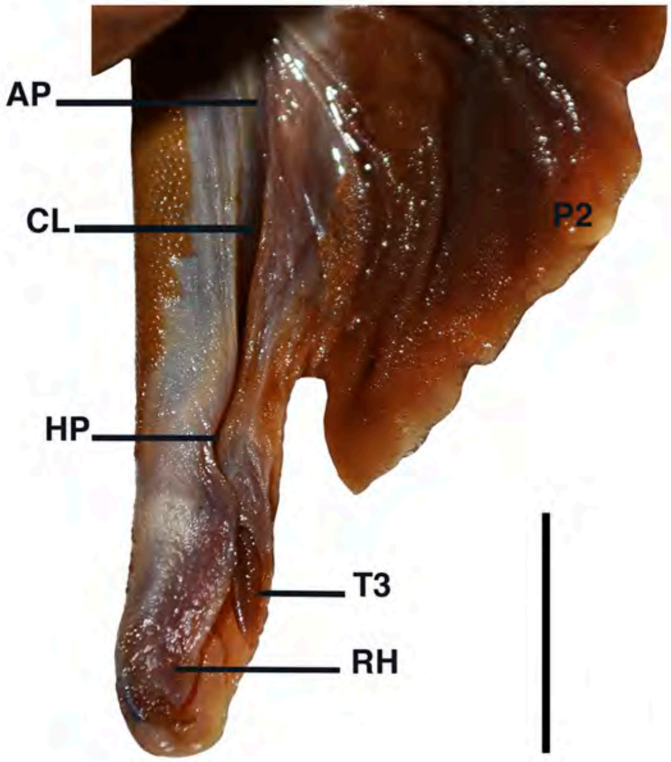

Figure 96. External morphology of clasper of *Flakeus acutipinnis* (SAIAB 10443, adult male, 410 mm TL from Cape Town, South Africa) in dorsal view. Scale bar: 10 mm. Abbreviations: accessory terminal cartilage (t3); apopyle (ap); clasper groove (cg); hypopyle (hp); pelvic fin (p2); rhipidion (rh).

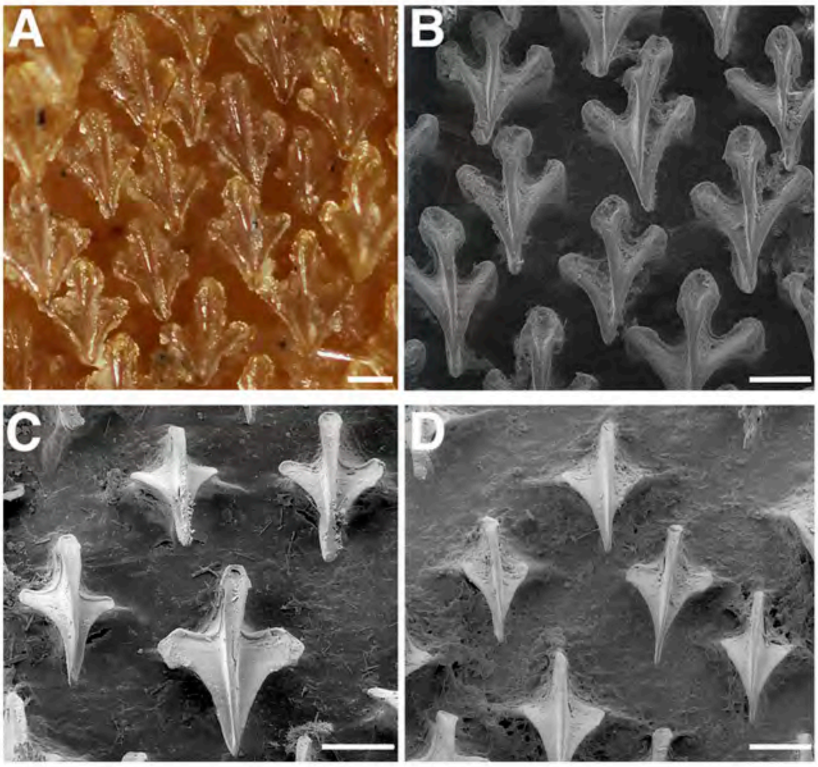

Figure 97. Dermal denticles of *Flakeus acutipinnis*. (A) BMNH 1905.6.8.8, female, 578 mm TL (photograph of lectotype). Scanning electron microscopy (SEM): (B) SAIAB 34576, female, 550 mm TL from Kwazulu-Natal, South Africa; (C) SAM 28638, female, 365 mm TL from False Bay, South Africa; (D) SAM 32894, male, 310 mm TL from Mossel Bay, South Africa. Scale bars: 100 µm.

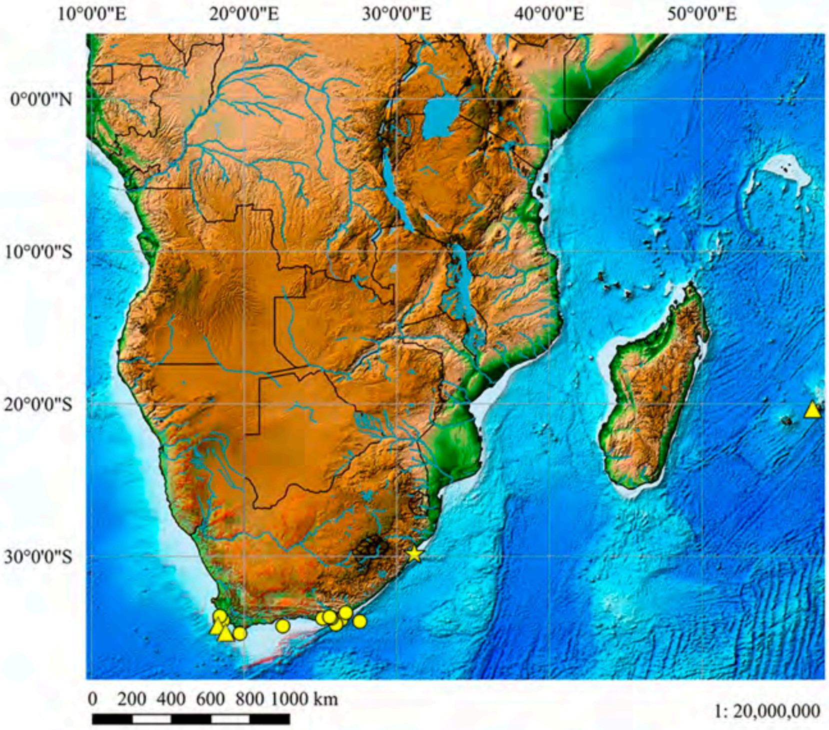

Figure 98. Map of Southern Africa, showing the distribution of *Flakeus acutipinnis*. Lectotype (yellow star); paralectotypes (yellow triangle); non-type specimens (yellow dots).

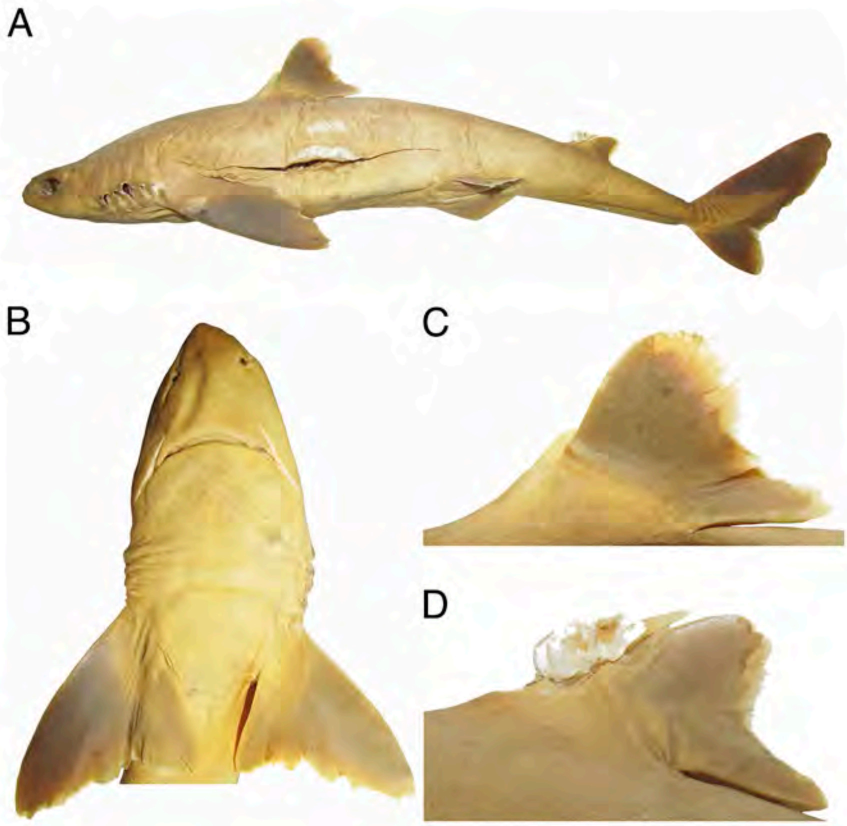

Figure 99. Paralectotype of *Flakeus acutipinnis*, BMNH 1900.11.6.14, adult female, 565 mm TL from Table Bay, South Africa: (A) lateral view; (B) ventral view; (C) first dorsal fin; (D) second dorsal fin.

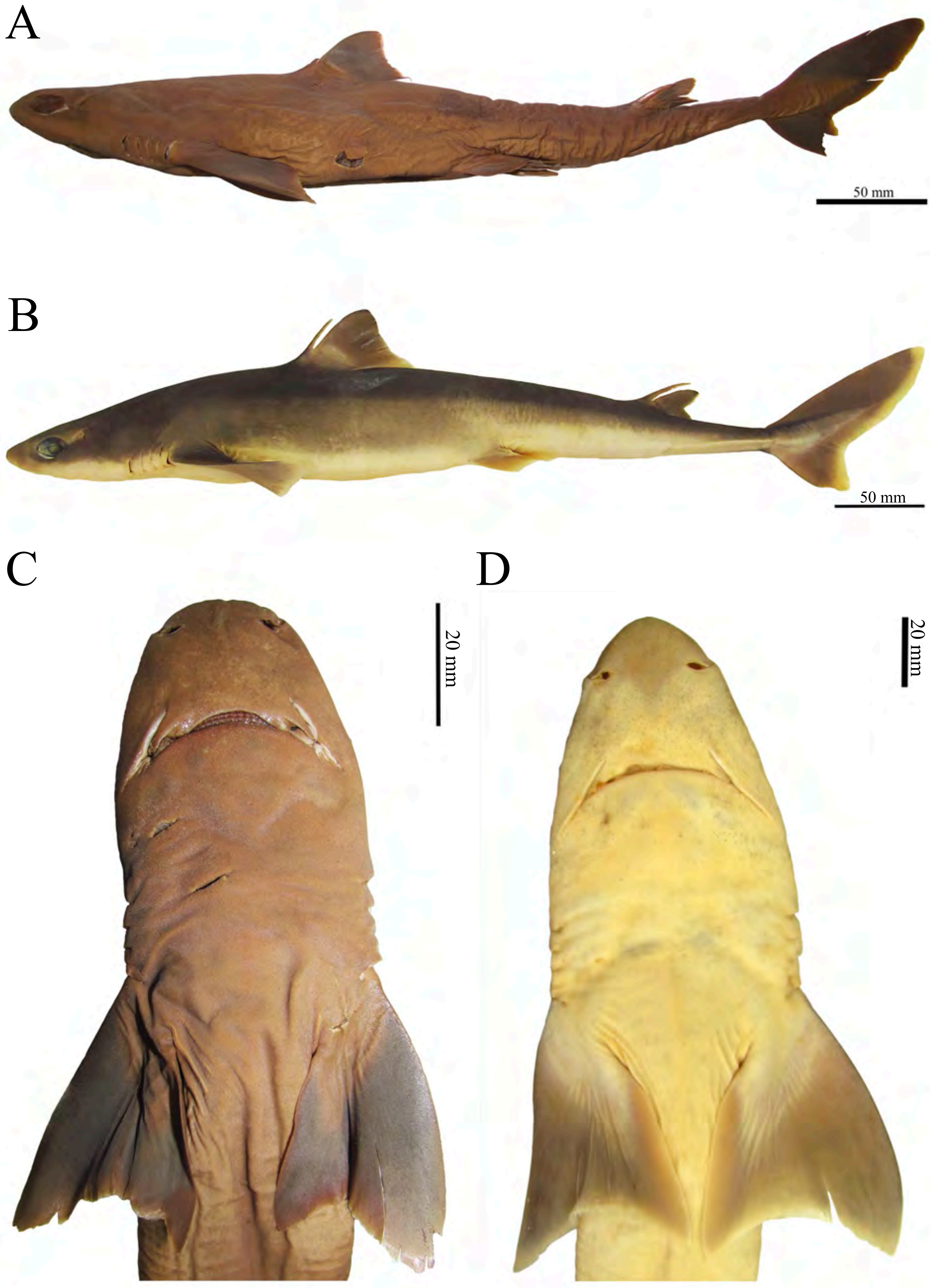

Figure 100. *Flakeus brevirostris* in lateral (A,B) and ventral (C,D) views. A,C: ZUMT 7630, adult male, 426 mm TL, holotype; B,D: KAUM-I 185, adult female, 500 mm TL.

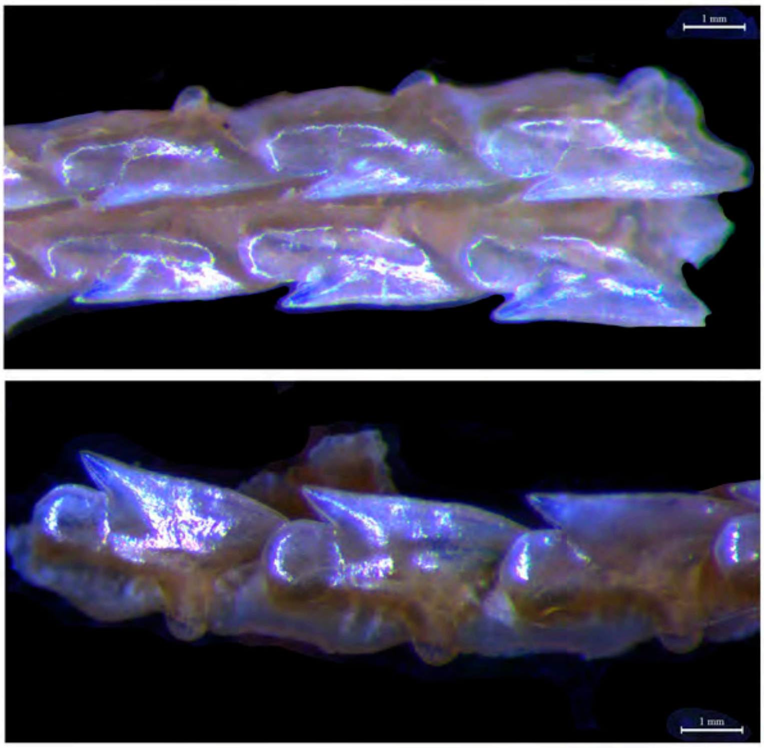

Figure 101. Upper (a) and lower (b) teeth of *Flakeus brevirostris*, HUMZ 189762, adult male, 403 mm TL.

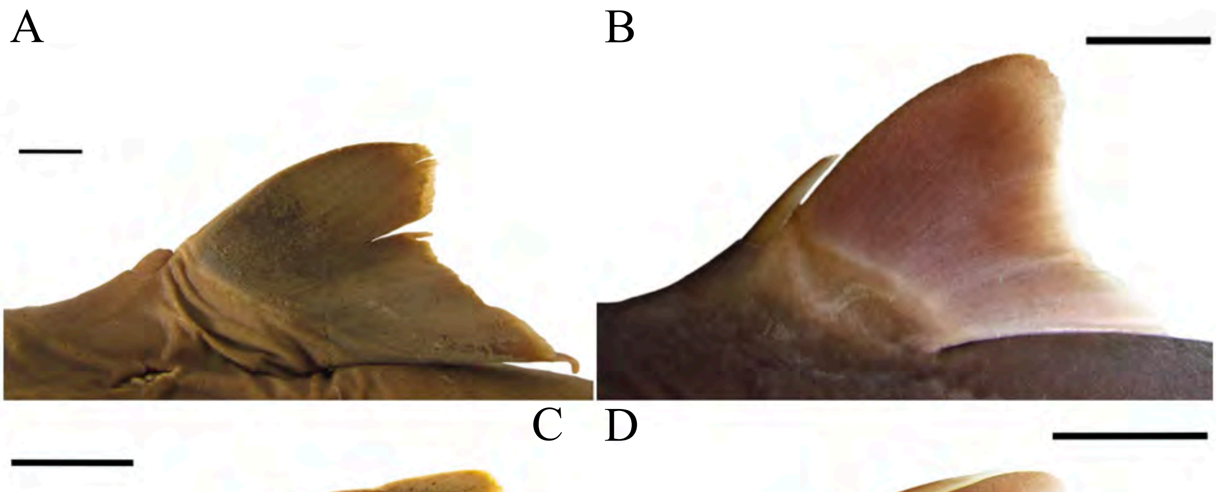

Figure 102. First (A, B) and second (C,D) dorsal fins of *Flakeus brevirostris*. A,C: ZUMT 7630, adult male, 426 mm TL, holotype; B,D: HUMZ 189762, adult male, 403 mm TL. Scale bar: 10 mm.

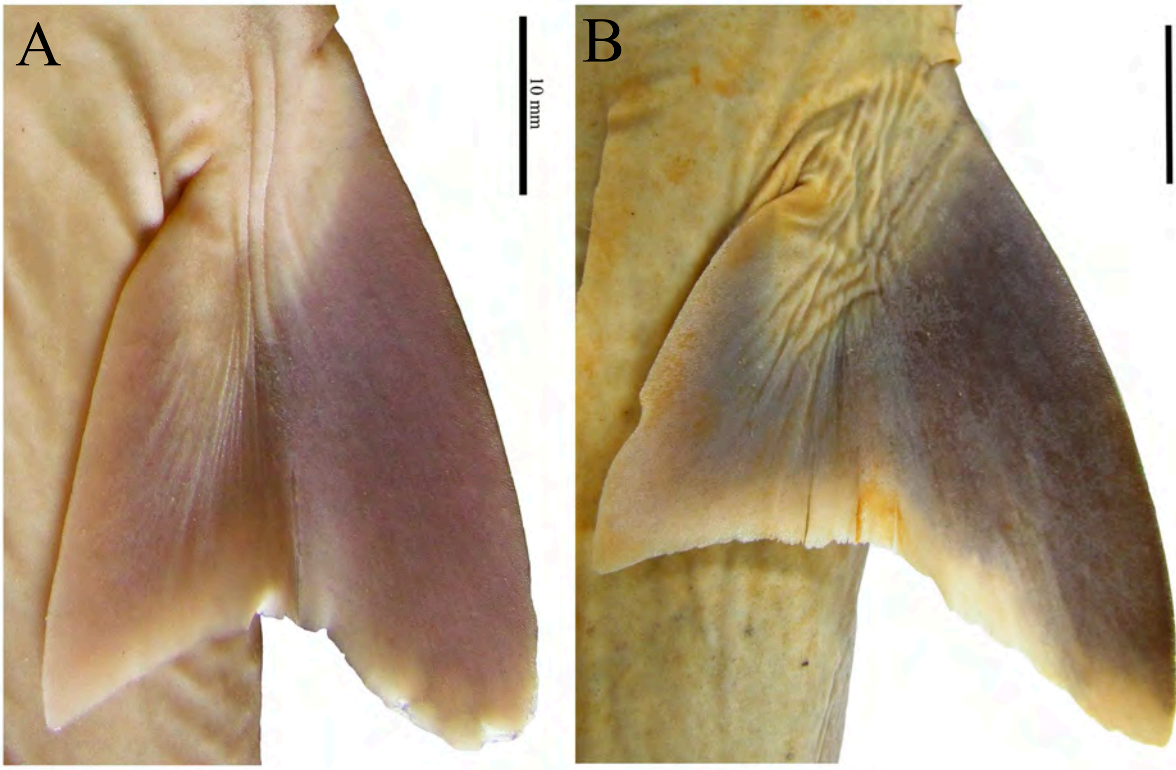

Figure 103. Pectoral fin of *Flakeus brevirostris*. A: HUMZ 189762, adult male, 403 mm TL; B: NSMT-P 47377, adult male, 467 mm TL.

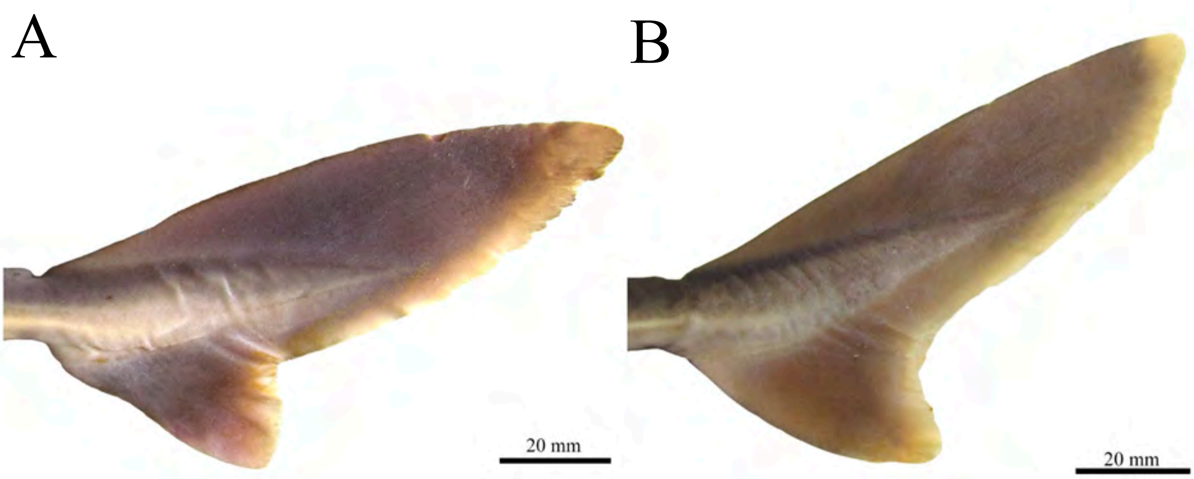

Figure 104. Caudal fin of *Flakeus brevirostris*. A: HUMZ 189745, adult female, 450 mm TL; B: KAUM-I 185, adult FEmale, 500 mm TL.

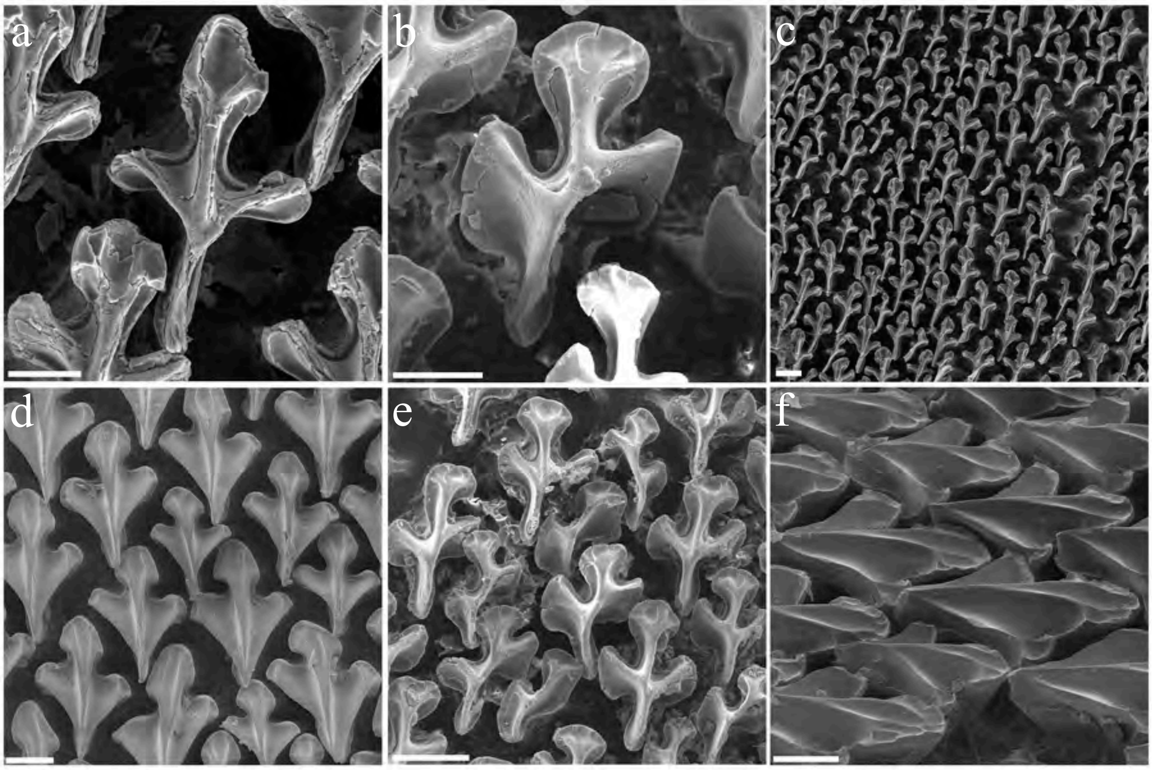

Figure 105. Scanning electron microscopy in *Flakeus brevirostris*, showing dermal denticles. a,c: 189762, adult male, 403 mm TL; b,e: NSMT-P 47378, adult female, 600 mm TL; d,f: KAUM-I 137, adult male, 377 mm TL. Scale bars: 50 µm (a,b); 100 µm (c-f).

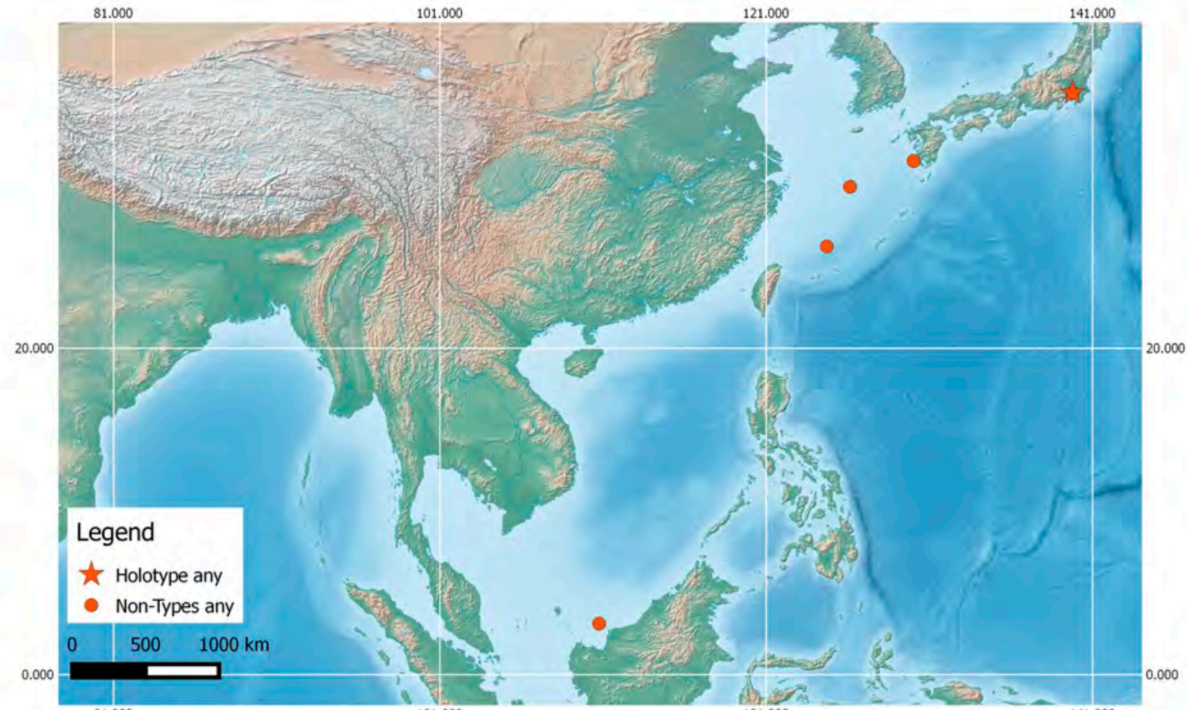

Figure 106. Map of the Northwest Pacific Ocean, showing the geographical distribution of *Flakeus brevirostris*.

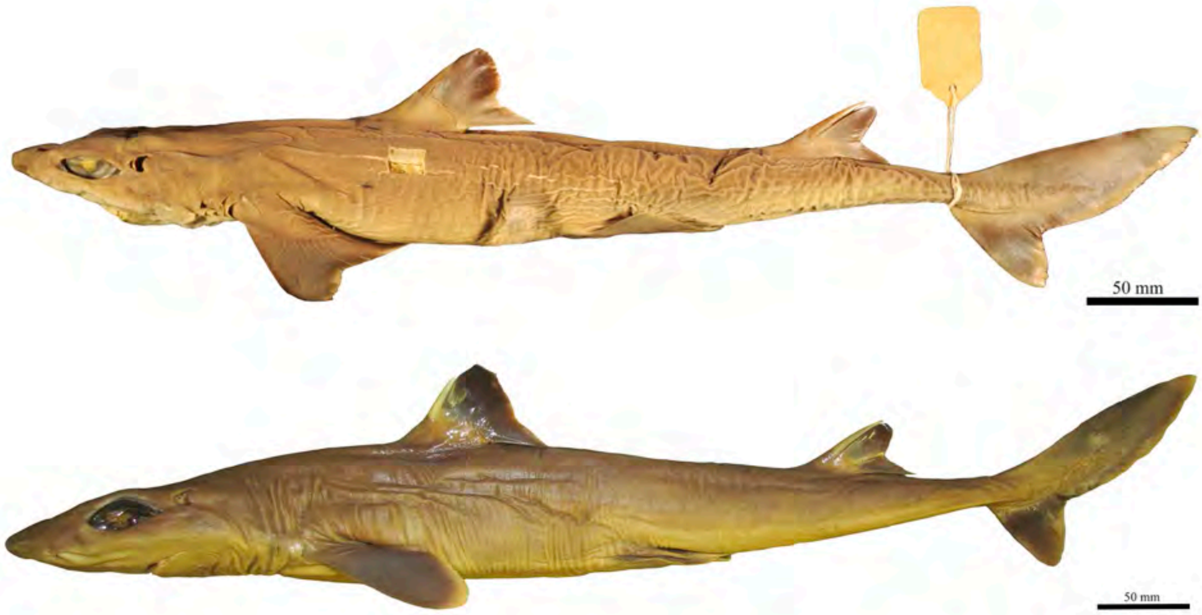

Figure 107. *Flakeus cubensis* in lateral view. A: MCZ 1458-S, adult male, 531 mm TL, holotype; B: SAM 39880, adult male, 595 mm TL.

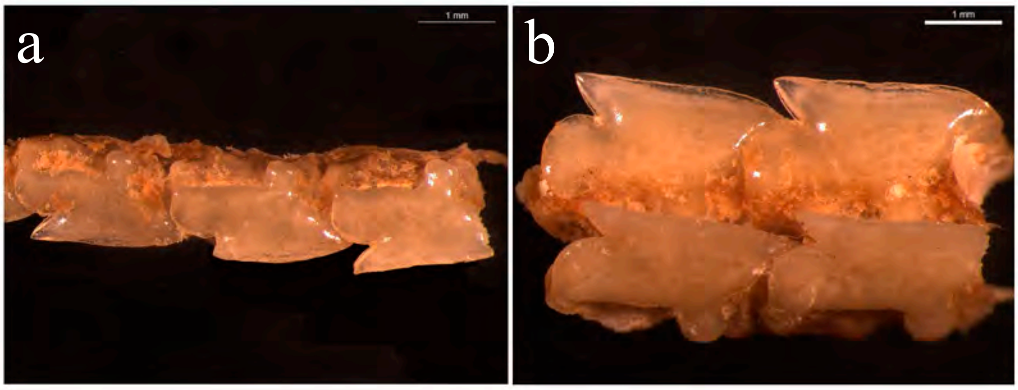

Figure 108. Upper (a) and lower (b) teeth of *Flakeus cubensis*, SAM 39880, adult male, 595 mm TL. Scale bar: 1 mm.

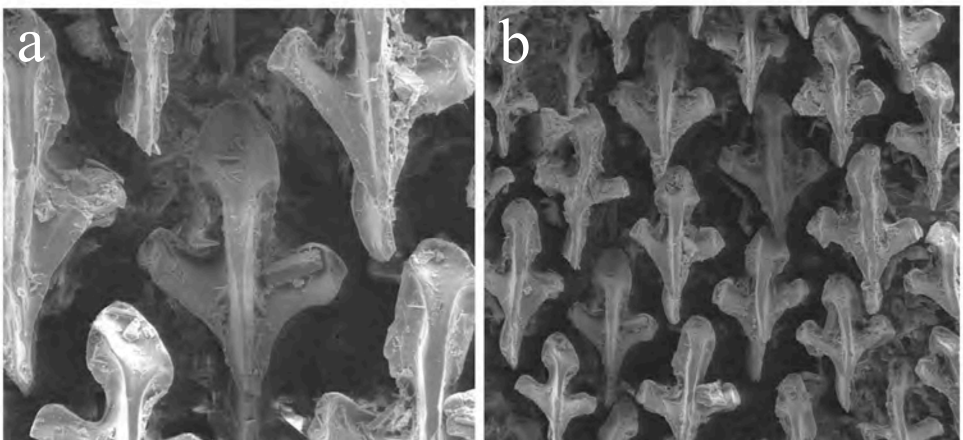

Figure 109. Dermal denticles of *Flakeus cubensis*, SAIAB 6030, adult male, 430 mm TL. Scale bar: 50 µm (a); 100 µm (c).

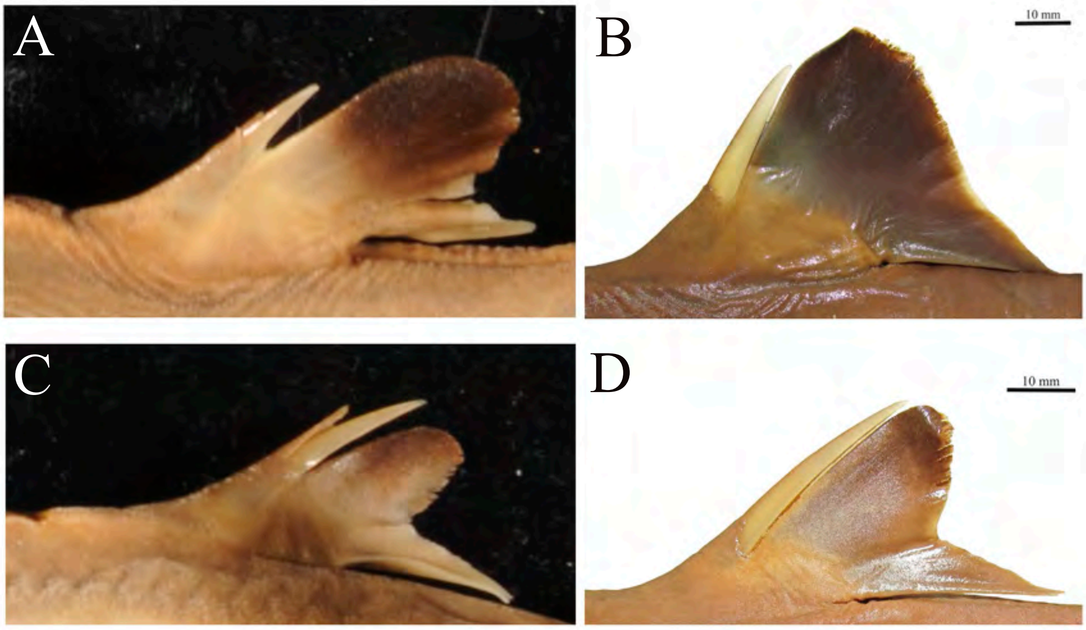

Figure 110. First (a,b) and second (c,d) dorsal fins of *Flakeus cubensis*. A: MCZ 1460-S, neonate female, 297 mm TL, paratype; B: SAM 39880, adult male, 595 mm TL.

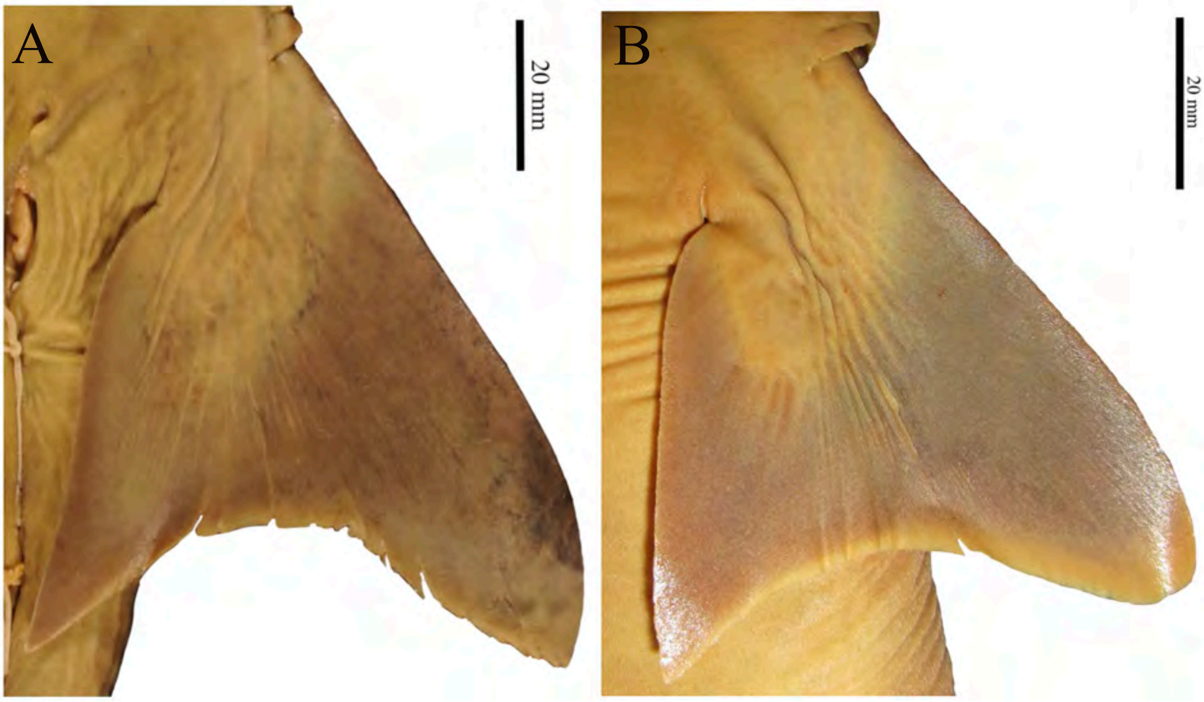

Figure111. Pectoral fin of *Flakeus cubensis*, showing free rear tips pointed. A: MCZ 1458-S, adult male, 531 mm TL, holotype; B: SAM 39880, adult male, 595 mm TL.

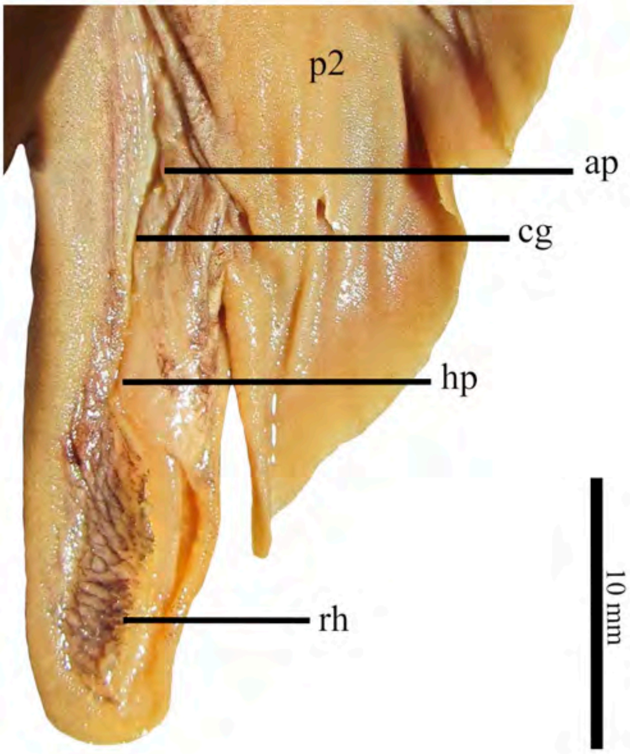

Figure 112. Clasper of *Flakeus cubensis* in dorsal view, SAM 39880, adult male, 595 mm TL. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

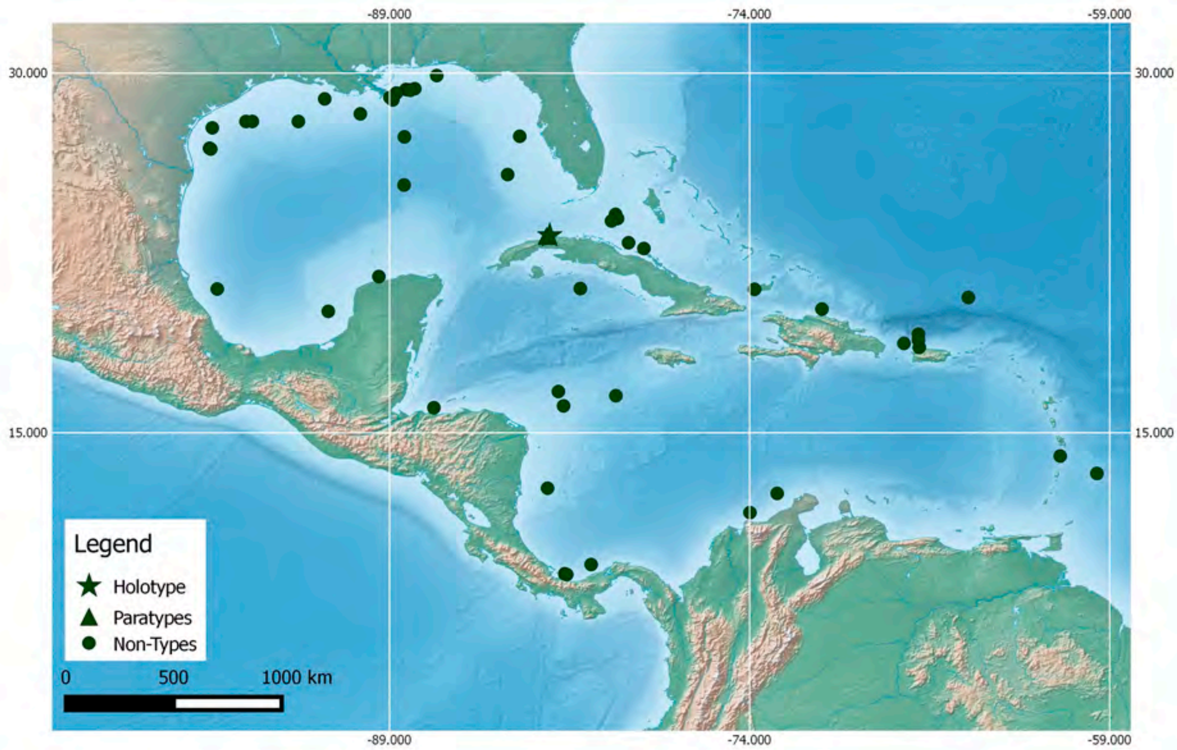

Figure 113. Map of the West Central Atlantic Ocean, showing the geographical distribution of *Flakeus cubensis*.

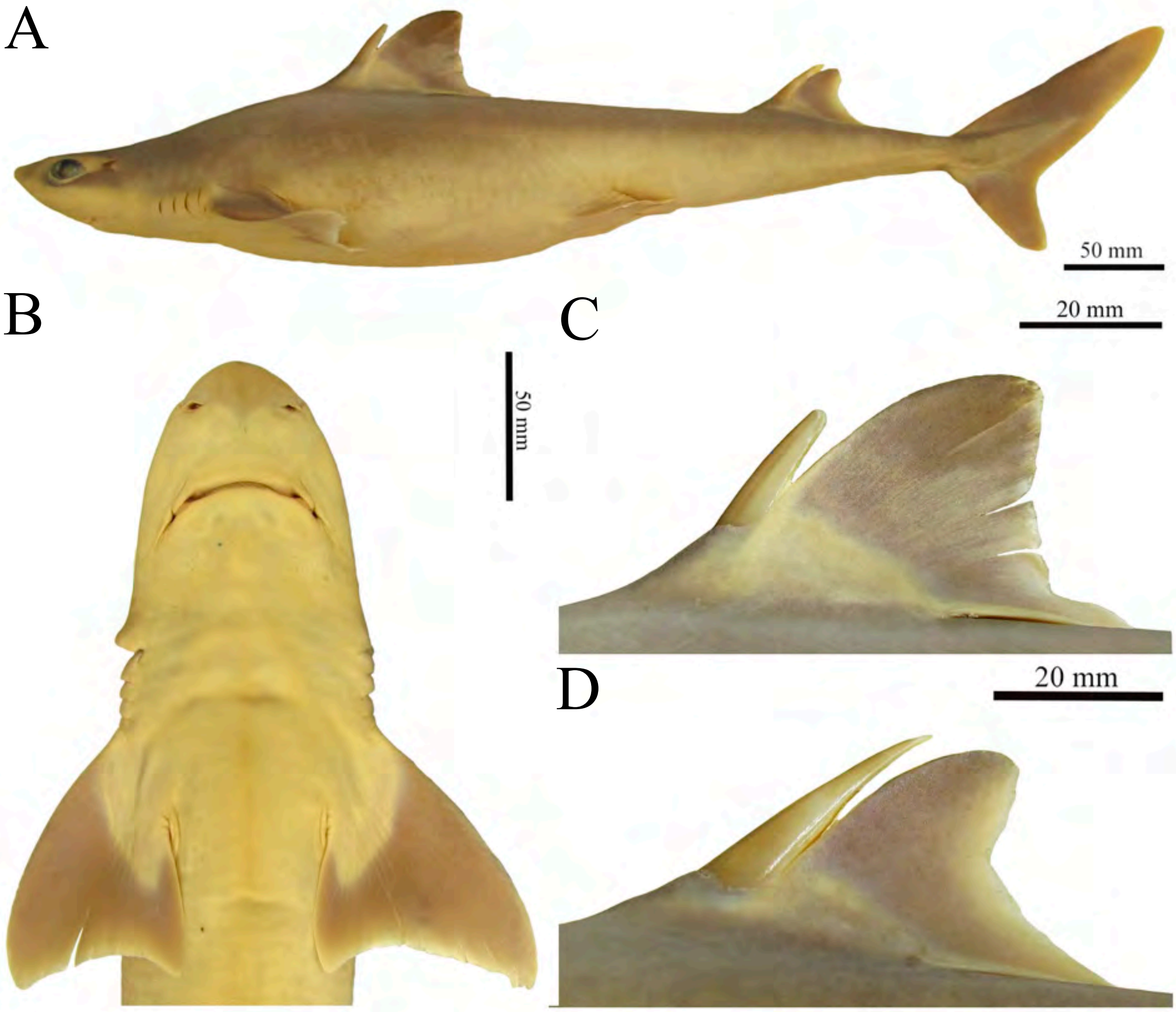

Figure 114. Holotype of *Flakeus crassispinus*, CSIRO H 2547-06, adult female, 576 mm TL. A: lateral view; B: ventral view; C: first dorsal fin: D: second dorsal fin.

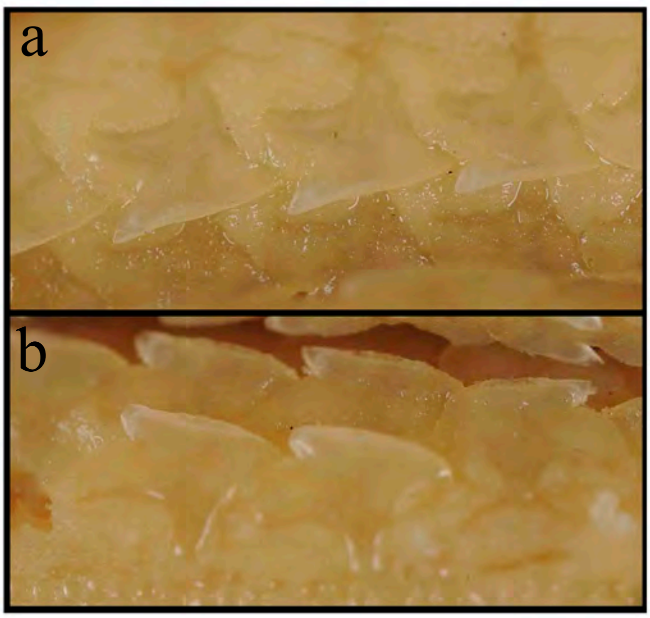

Figure 115. Upper (a) and lower (b) teeth of holotype of *Flakeus crassispinus*, CSIRO H 2547-06, adult female, 576 mm TL.

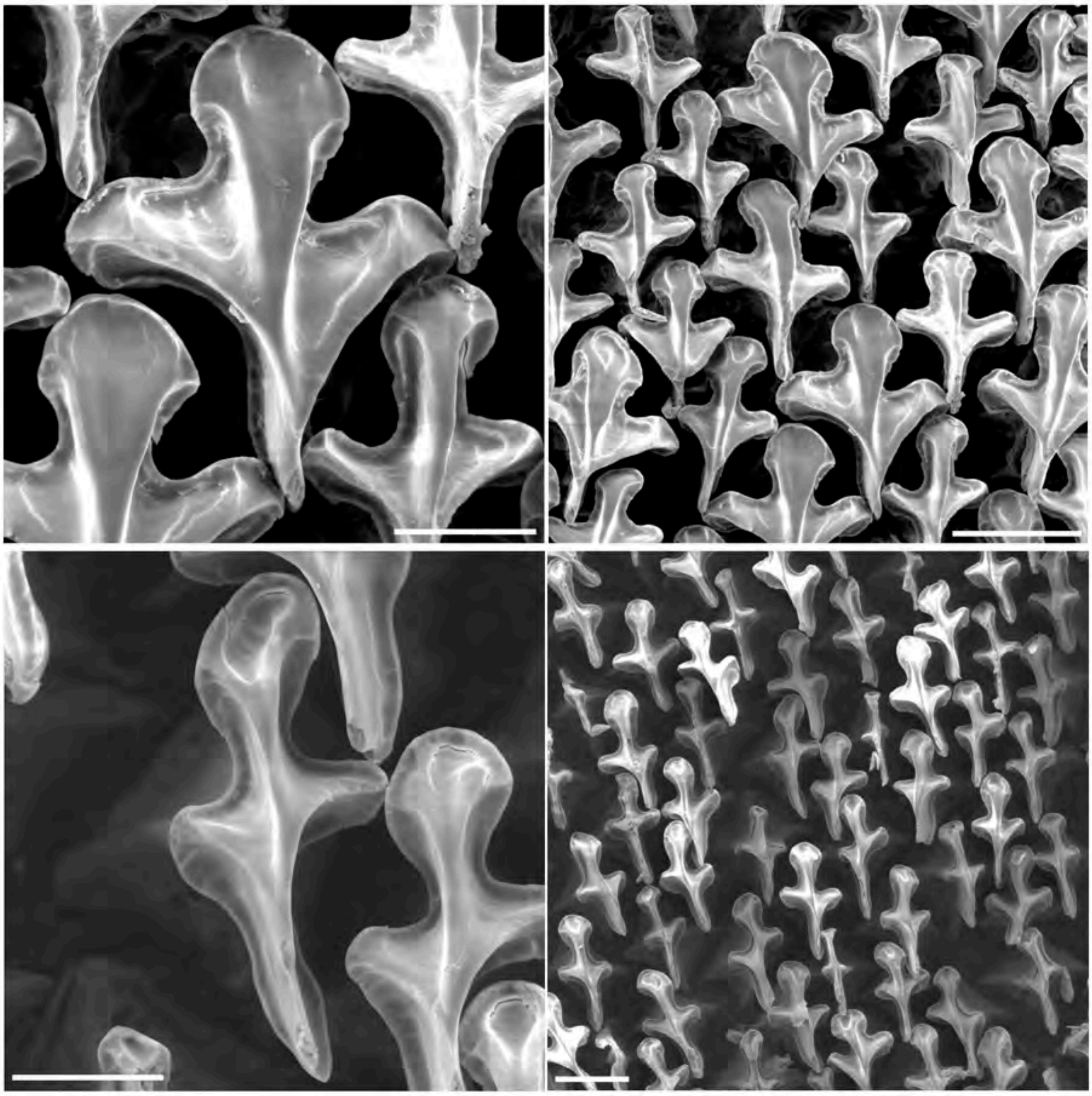

Figure 116. Scanning electron microscopy of dermal denticles and its variations in *Flakeus crassispinus*. a,b: CSIRO H6412-05, adult female, 482 mm TL; c,d: CSIRO H 6581-24, juvenile female, 328 mm TL. Scale bars: 50 µm (a,b); 100 µm (c,d).

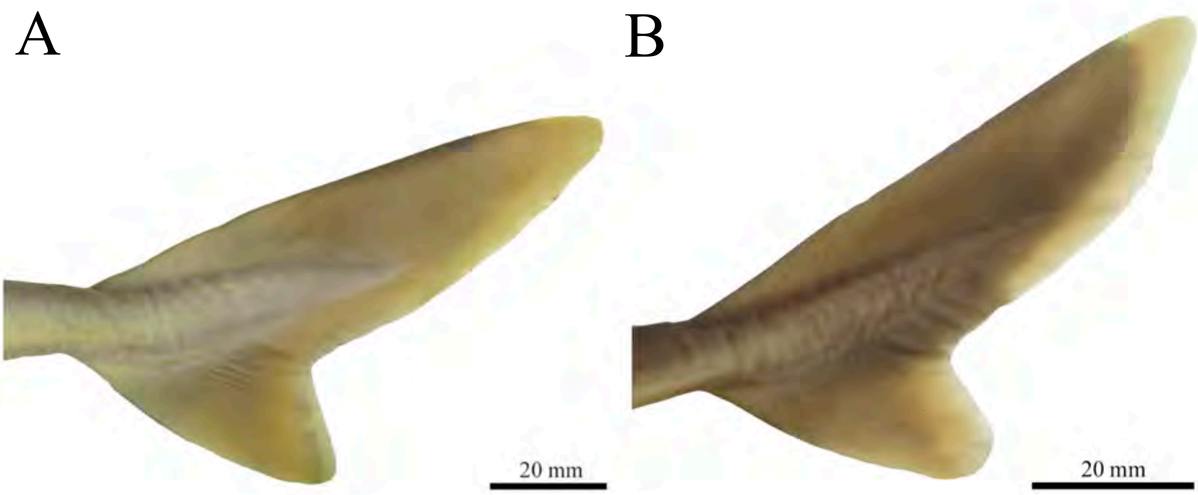

Figure 1117. Variations on caudal fin coloration of *Flakeus crassispinus*. A: CSIRO H 6412-03, juvenile female, 404 mm TL; B: CSIRO H 6581-22, juvenile male, 343 mm TL.

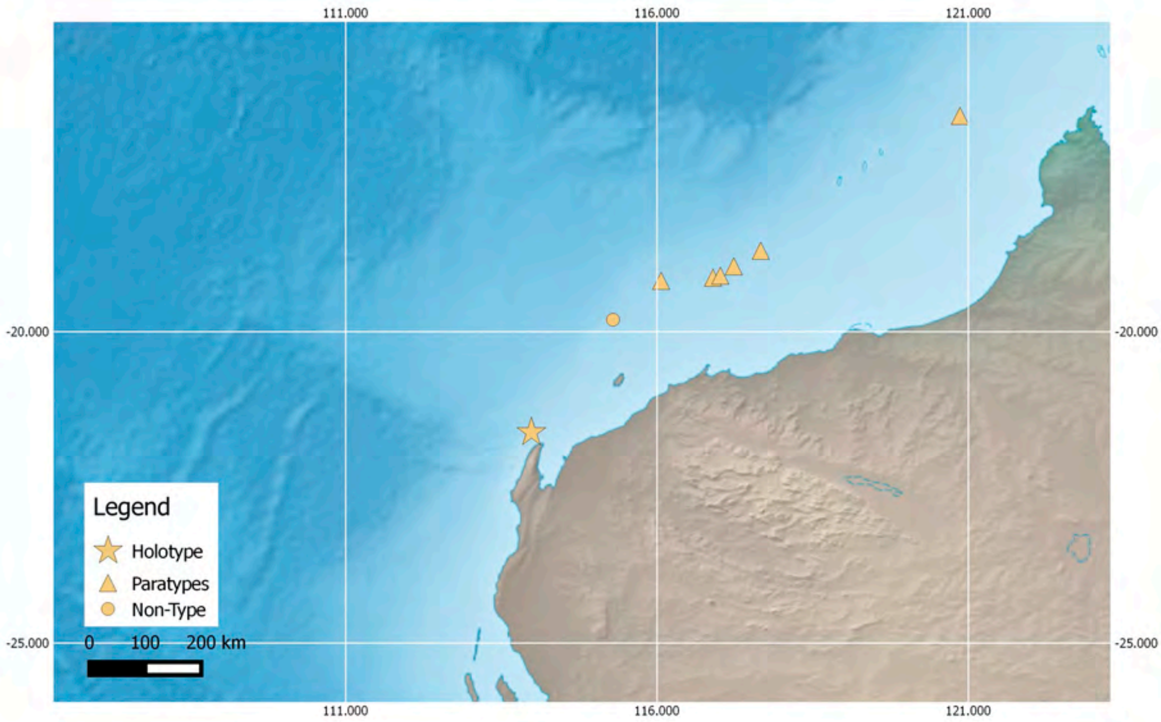

Figure 118. Map of the Western Australia, showing the geographical distribution of *Flakeus crassispinus*.

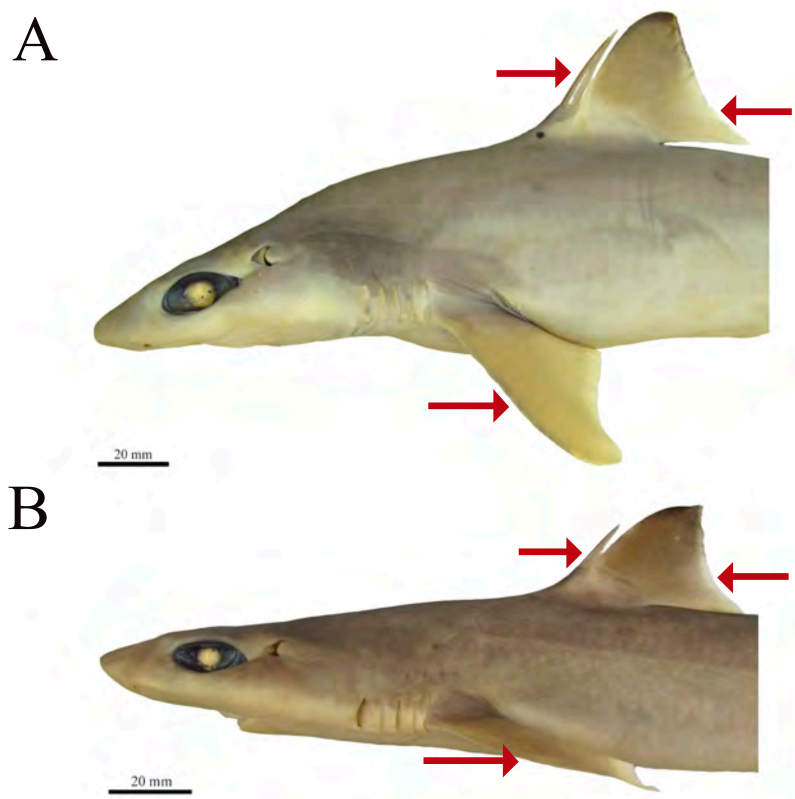

Figure 119. Specimens of *Flakeus crassispinus* in anterior-lateral view, showing variations on body color and thickness of dorsal spines. A: CSIRO H 6412-01, juvenile male, 420 mm TL; B: CSIRO H 6581-22, juvenile male, 343 mm TL.

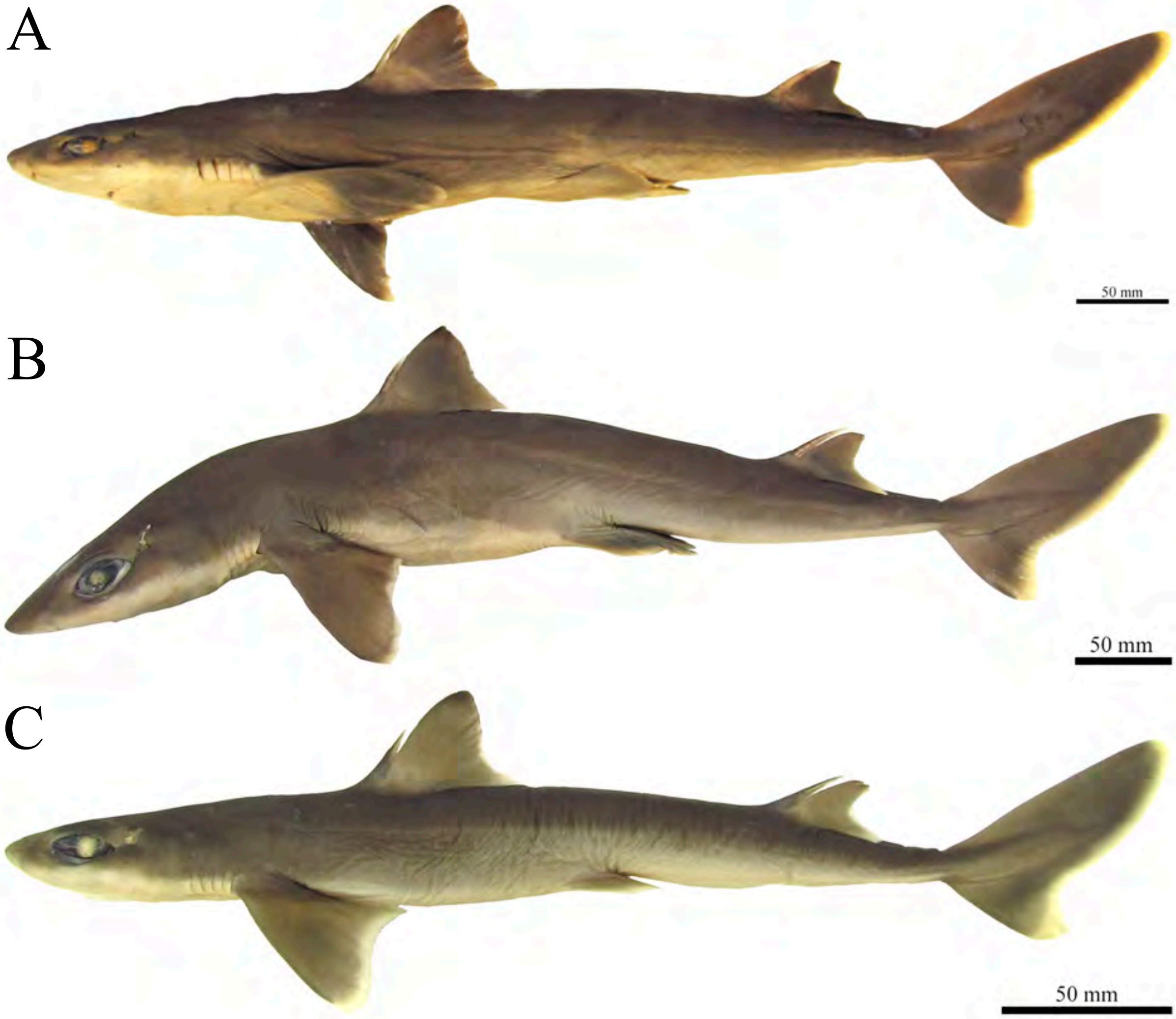

Figure 120. *Flakeus raoulensis* in lateral view. A: NMNZ P 41678, adult male, 655 mm TL, holotype; B: NMNZ P 52097, adult male, 603 mm TL; C: NMNZ P 52112, juvenile male, 370 mm TL.

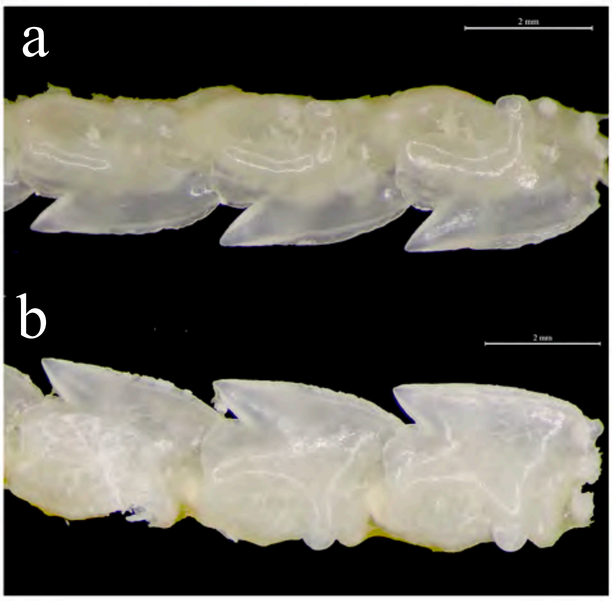

Figure 121. Upper (a) and lower (b) teeth of *Flakeus raoulensis*, AIM 655693, adult male, 696 mm TL. Scale bar: 2mm.

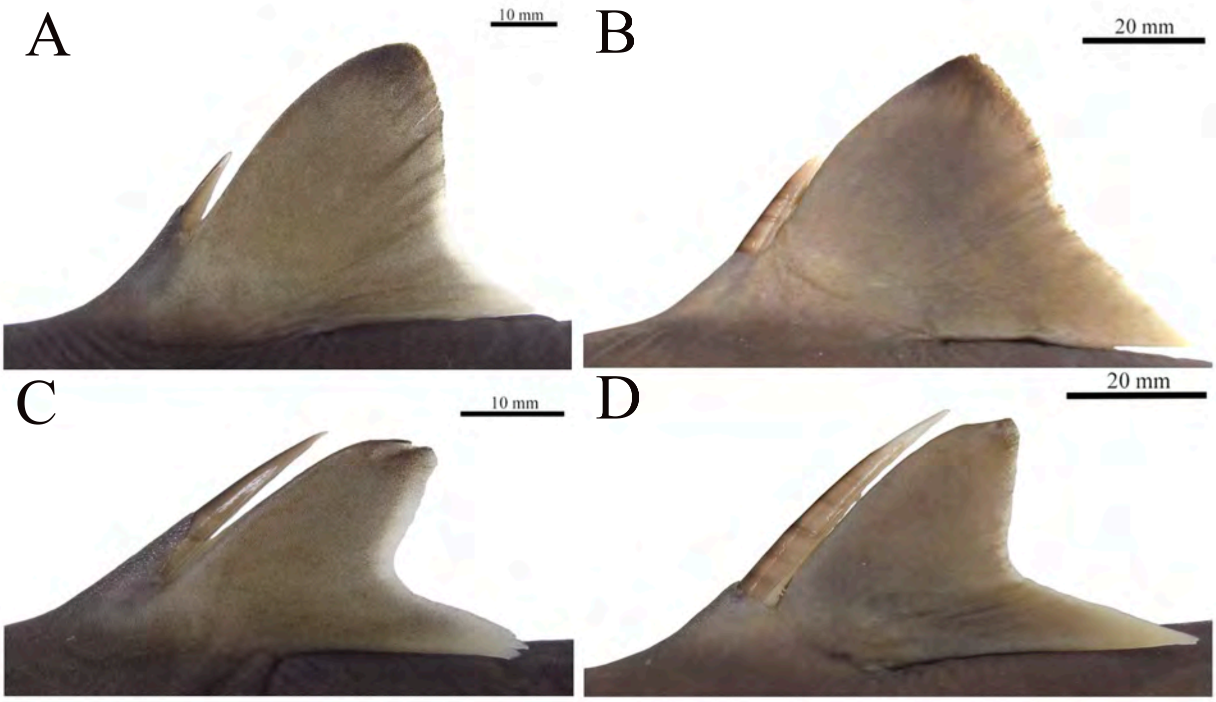

Figure 122. First (a,b) and second (c,d) dorsal fins of *Flakeus raoulensis*. A,C: NMNZ P 52112, juvenile male, 370 mm TL; B,D: NMNZ P 52097, adult male, 603 mm TL.

Figure 123. Pectoral fins of *Flakeus raoulensis* in ventral view. A: NMNZ P 52113, juvenile male, 365 mm TL; B: NMNZ P 52097, adult male, 603 mm TL.

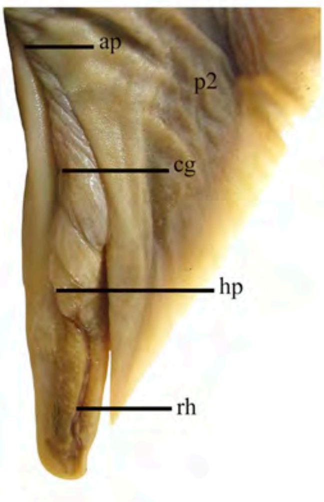

Figure 124. Clasper of holotype of *Flakeus raoulensis* in dorsal view, NMNZ P 41678, adult male, 655 mm TL. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

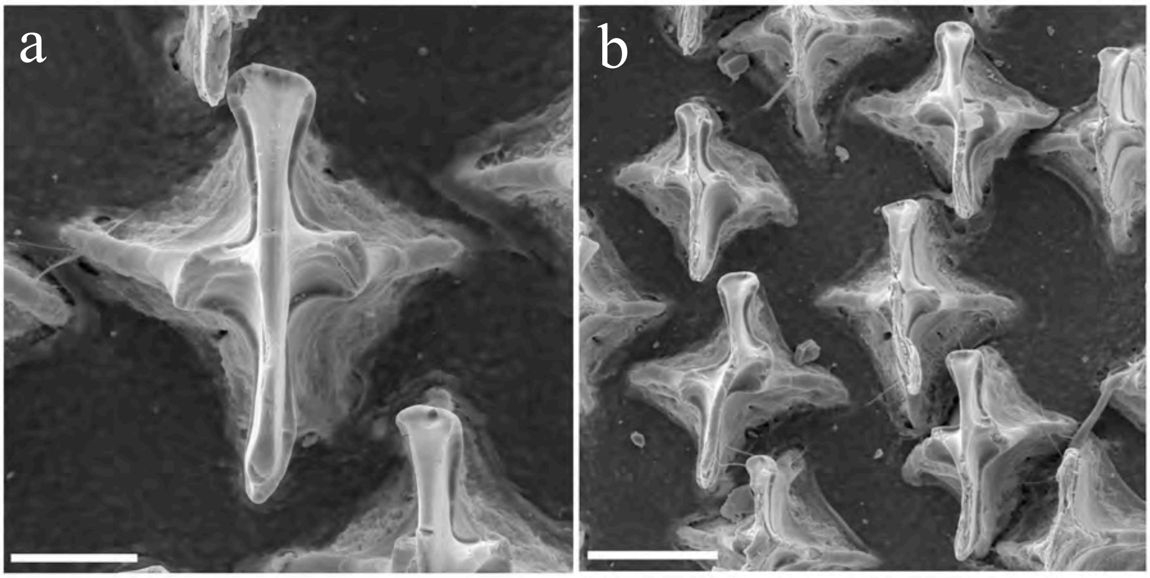

Figure 125. Scanning electron microscopy of dermal denticles of *Flakeus raoulensis*, NMNZ P 52113, juvenile male, 365 mm TL. Scale bars: 50 µm (a); 100 µm (b).

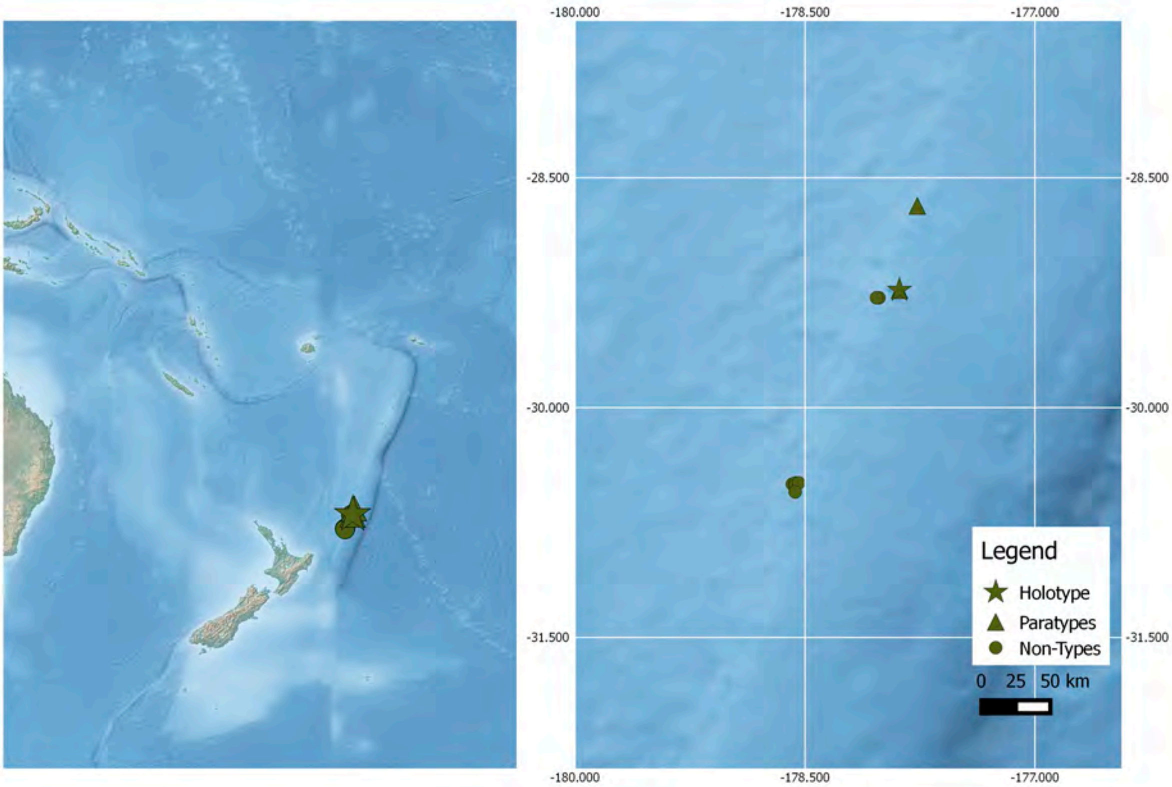

Figure 126. Map of New Zealand (left side) and amplified area (right side) showing the geographical distribution of *Flakeus raoulensis*.

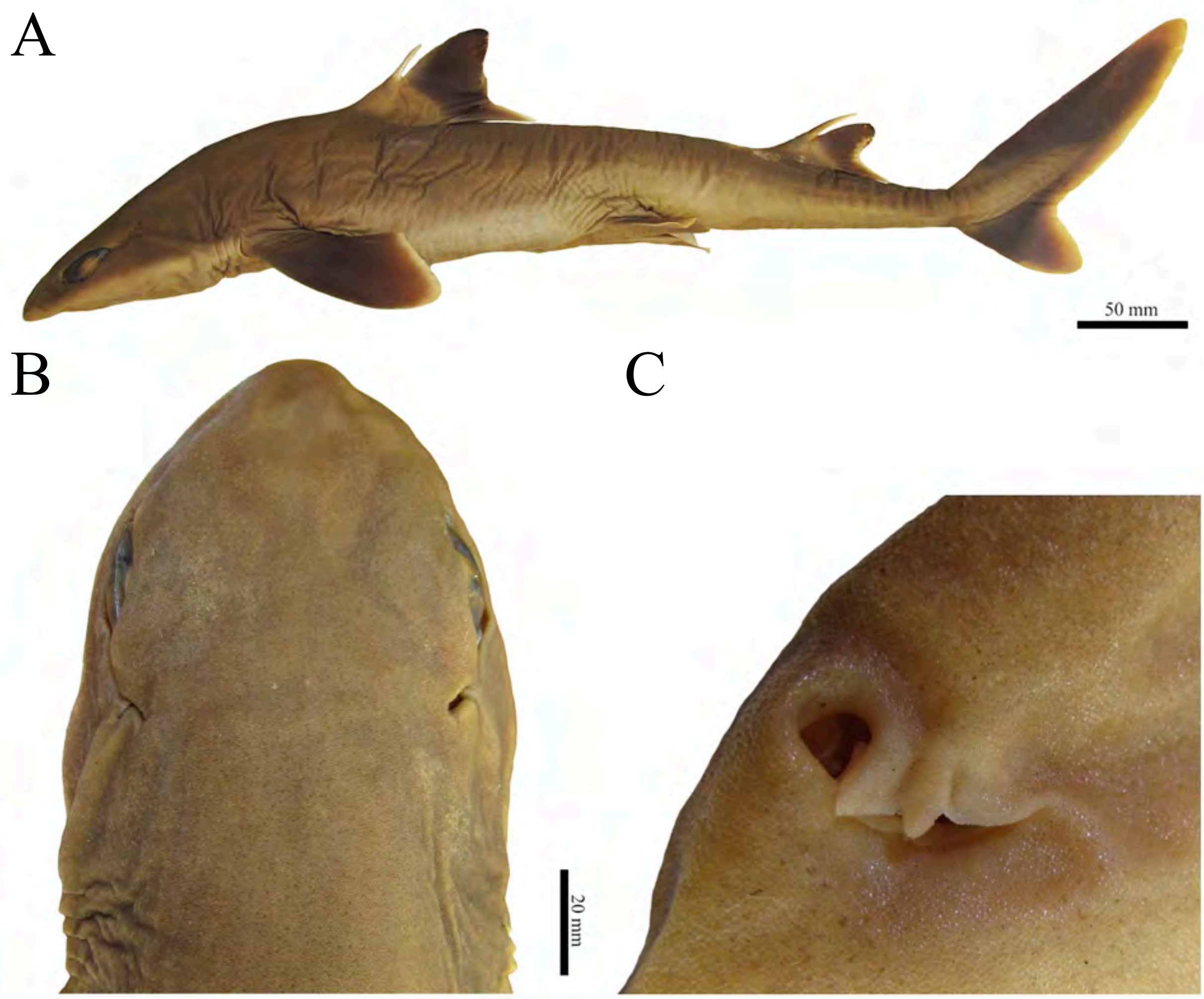

Figure 127. Holotype of *Flakeus bucephalus*, MNHN 2006-1754, juvenile male, 550 mm TL. A: lateral view; B: dorsal view of head; C: anterior margin of nostril (right side).

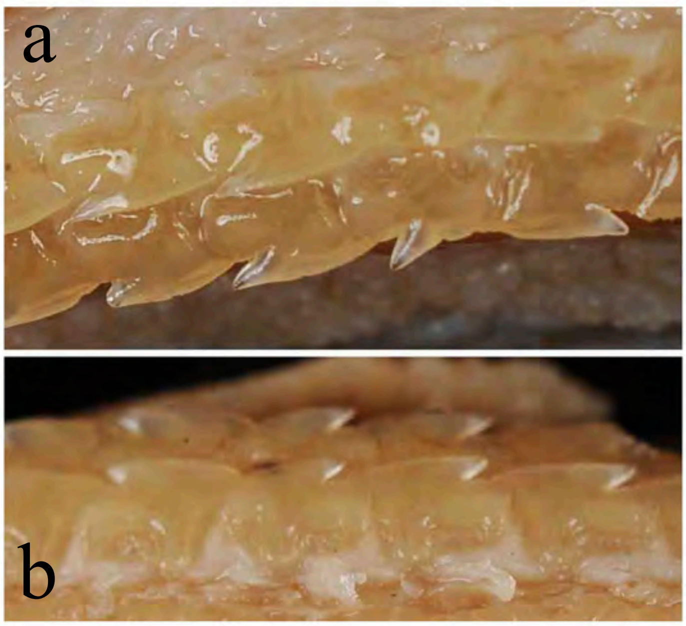

Figure 128. Upper (a) and lower (b) teeth of holotype of *Flakeus bucephalus*, MNHN 2006-1754, juvenile male, 550 mm TL.

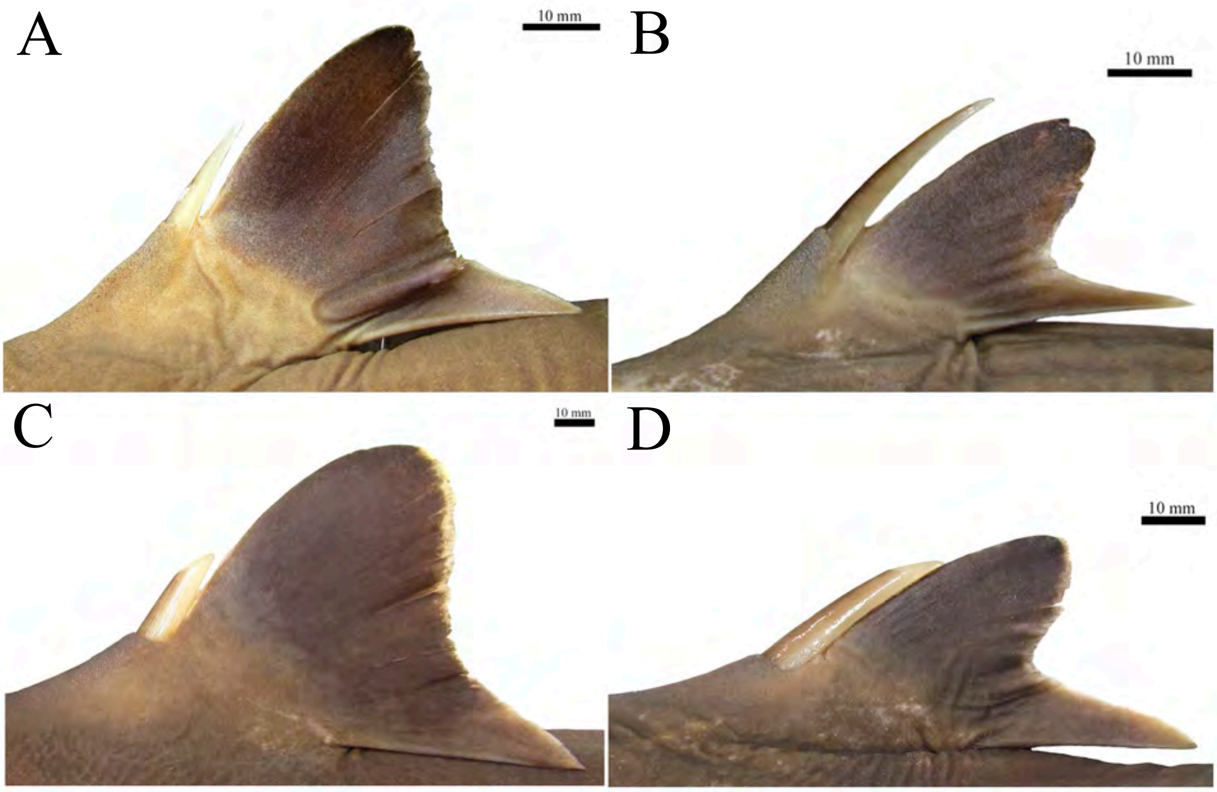

Figure 129. First (A,C) and second (D,E) dorsal fins of *Flakeus bucephalus*. A,B: holotype, MNHN 2006-1754, juvenile male, 550 mm TL; C,D: paratype, NMNZ P 34030, adult male, 787 mm TL.

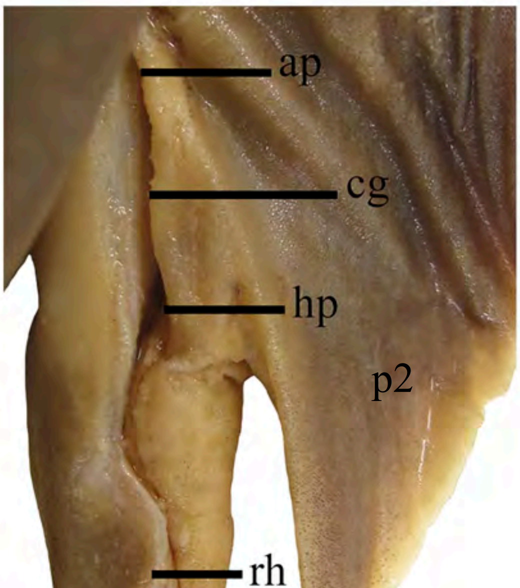

Figure 130. Clasper of paratype of *Flakeus bucephalus*, NMNZ P 34030, adult male, 787 mm TL in dorsal view. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

Figure 131. Caudal fin of paratype of *Flakeus bucephalus*, NMNZ P 34030, adult male, 787

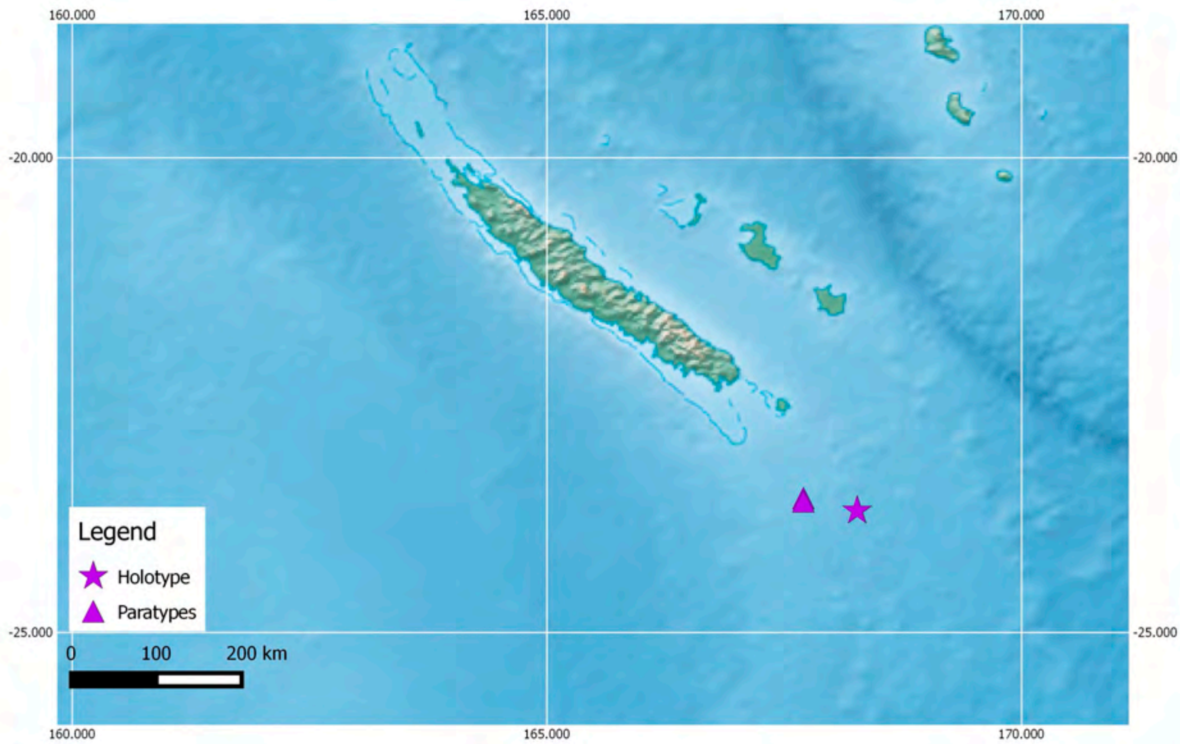

Figure 132. Map of New Caledonia, showing the geographical distribution of *Flakeus bucephalus*.

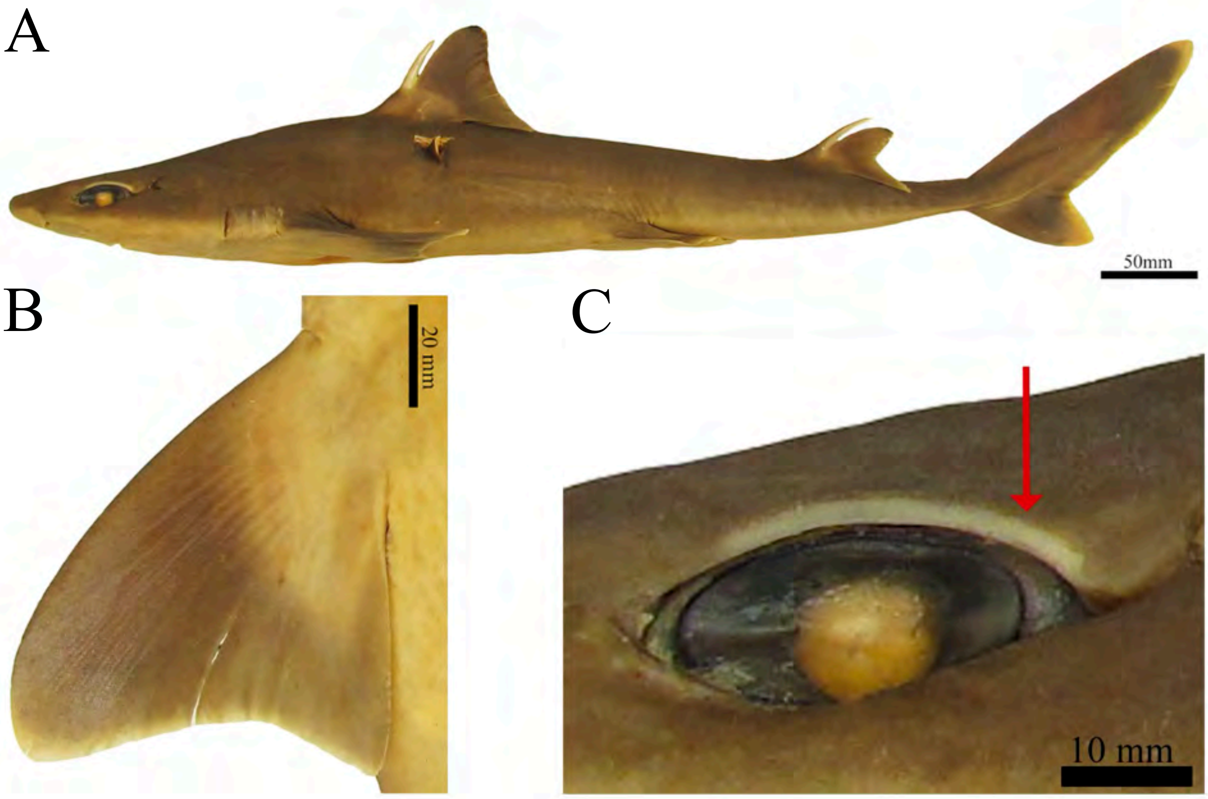

Figure 133. Holotype of *Flakeus albifrons*, CSIRO H 4627-01, adult male, 615 mm TL. A: lateral view; B: right pectoral fin; C: left eye, showing eyebrow.

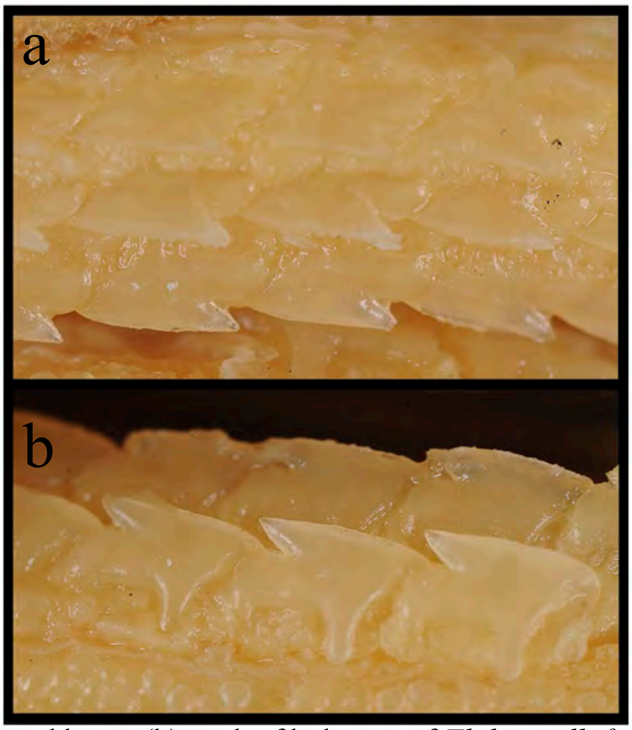

Figure 134. Upper (a) and lower (b) teeth of holotype of *Flakeus albifrons*, CSIRO H 4627-01, adult male, 615 mm TL.

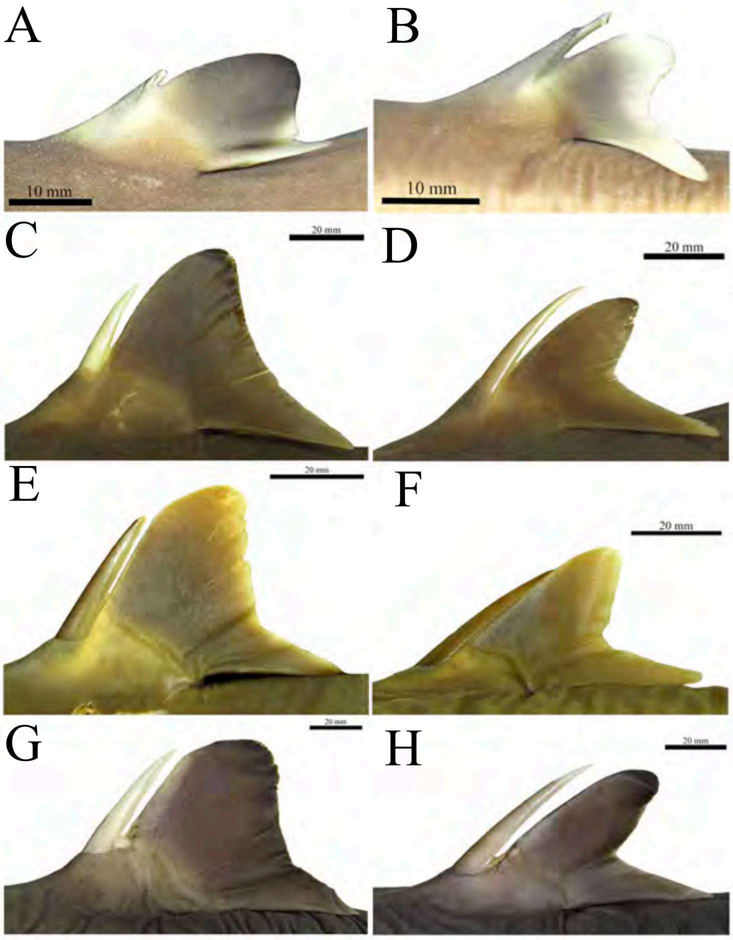

Figure 135. First (A,C,E,G) and second (B,D,F,H) dorsal fins of *Flakeus albifrons*. A,B: CSIRO H 7226-01, juvenile female, 220 mm TL; C,D: CSIRO H 4627-01, adult male, 615 mm TL, holotype of *F. albifrons*; E,F: CSIRO CA 4111, adult male, 586 mm TL, holotype of S. *altipinnis*; G,H: CSIRO H 6816-01, adult male, 720 mm TL, holotype of *S. formosus*.

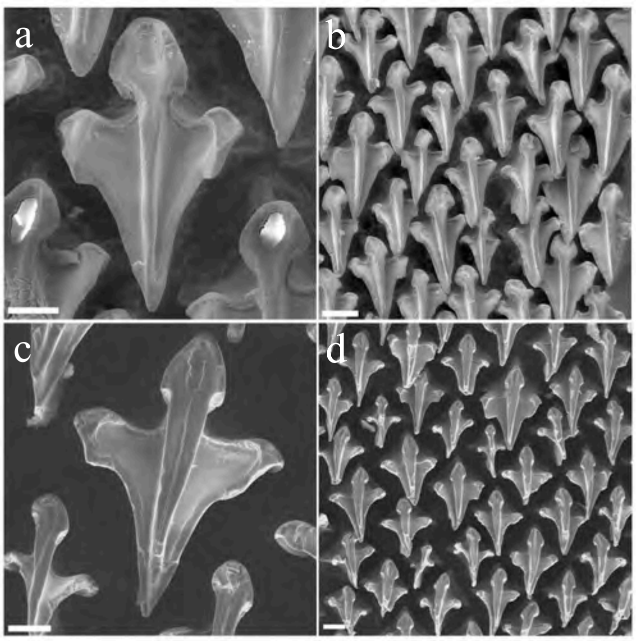

Figure 136. Scanning electron microscopy of dermal denticles of *Flakeus albifrons*. a,b: AMS I 44907-007, adult male, 655 mm TL; c,d: holotype of *S. formosus*, CSIRO H 6816-01, adult male, 720 mm TL. Scale bars: 50 µm (a,c); 100 µm (b,d).

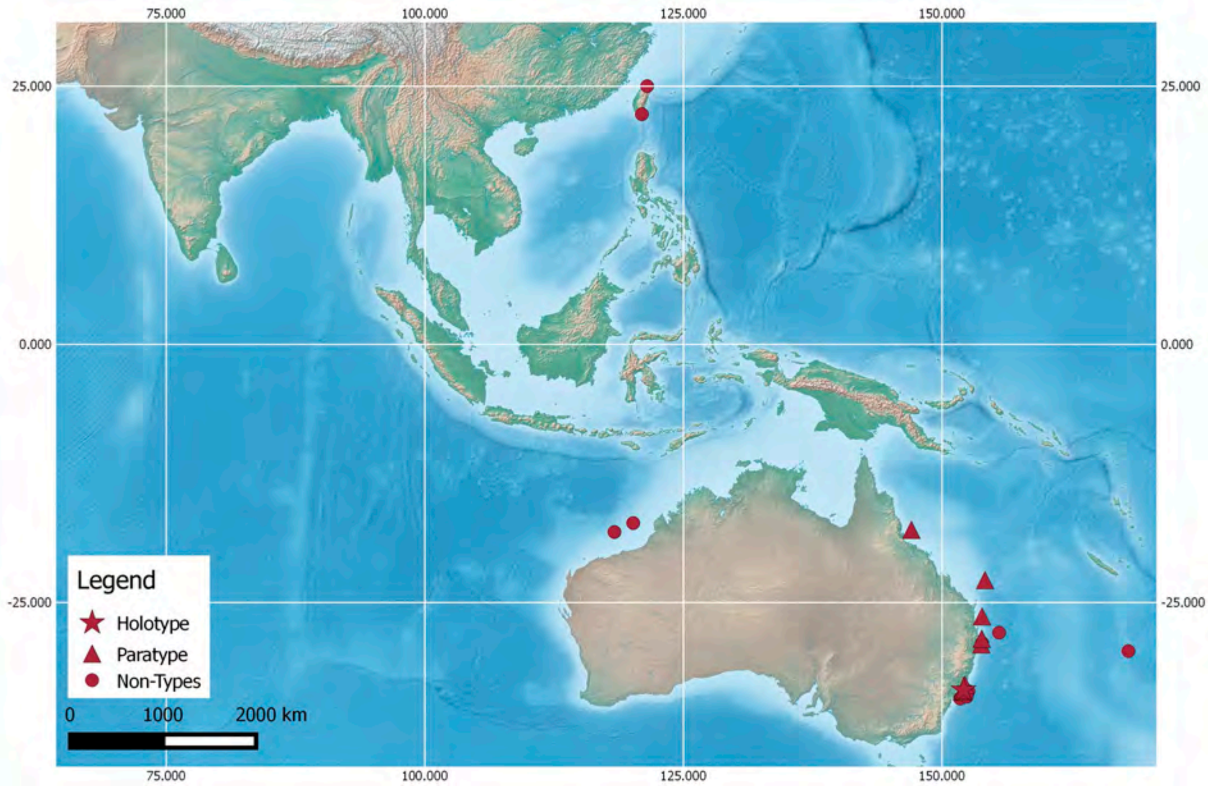

Figure 137. Map of West Pacific Ocean, showing the geographical distribution of *Flakeus albifrons*.

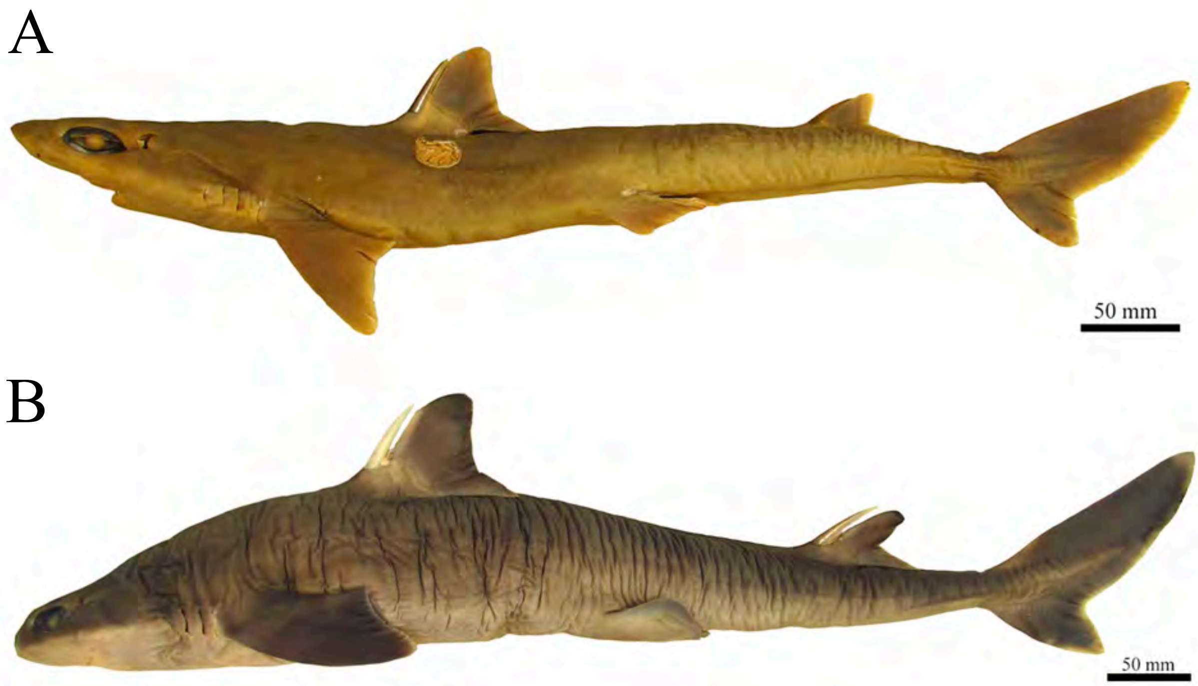

Figure 138. Holotype of *Squalus altipinnis* (A), CSIRO CA 4111, adult male, 586 mm TL, and holotype of *Squalus formosus* (B) CSIRO H 6816-01, adult male, 720 mm TL in lateral view.

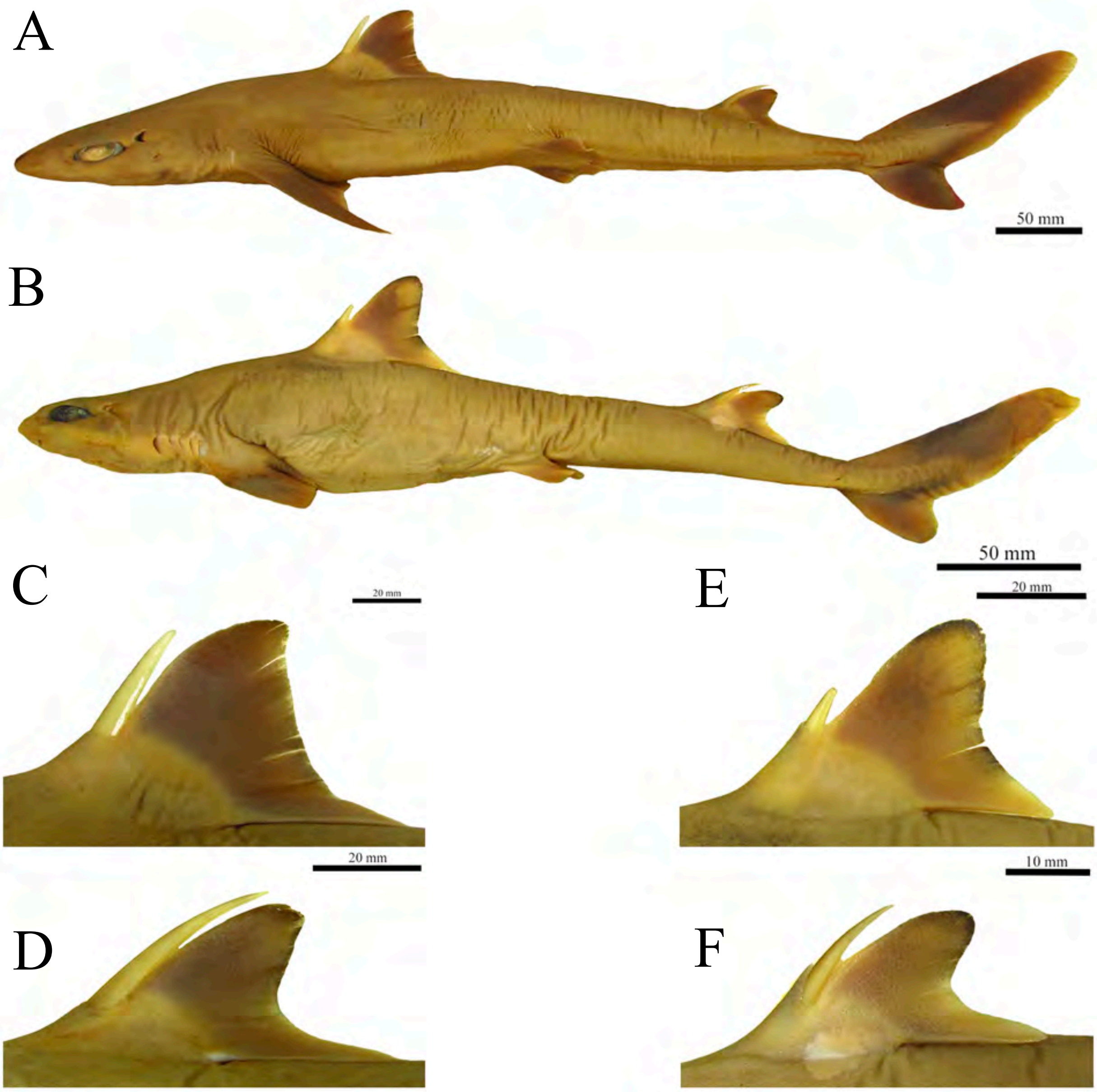

Figure 139. Specimens of *Flakeus notocaudatus* in lateral view (A,B) and detail of first (C,E) and second (D,F) dorsal fins. A,C,D: holotype, CSIRO H 1368-02, juvenile male, 615 mm TL; B,E,F: paratype, CSIRO H 1323-01, juvenile male, 364 mm TL.

Figure 140. Anterior margin of nostril of holotype of *Flakeus notocaudatus*, CSIRO H 1368-02, showing second lobe thin.

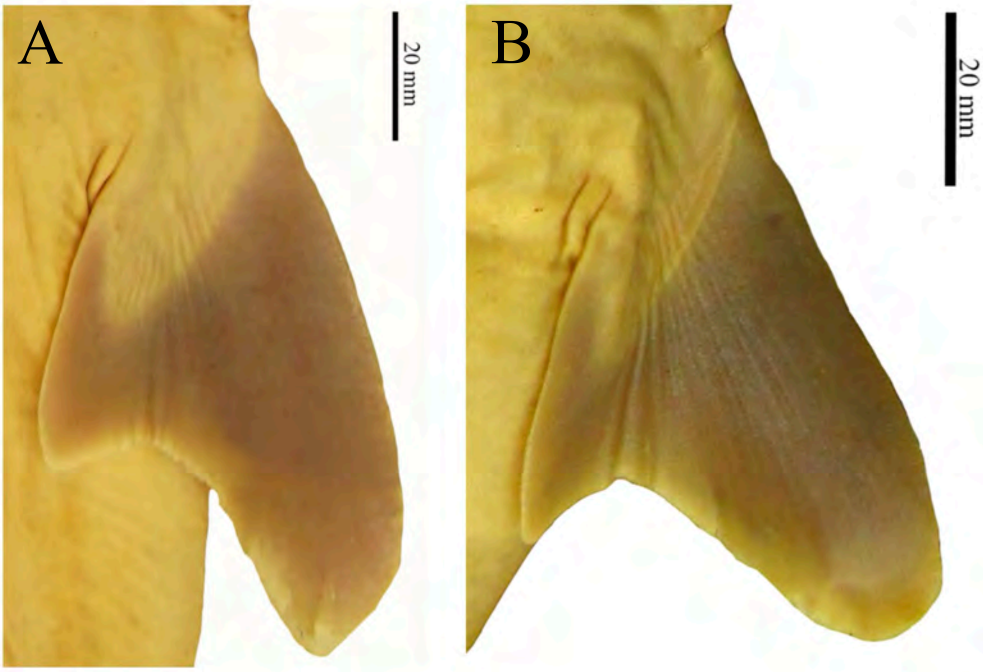

Figure 141. Pectoral fin of *Flakeus notocaudatus* in ventral view. A: holotype, CSIRO H 1368-02, juvenile male, 615 mm TL; B: paratype, CSIRO H 1323-01, juvenile male, 364 mm TL.

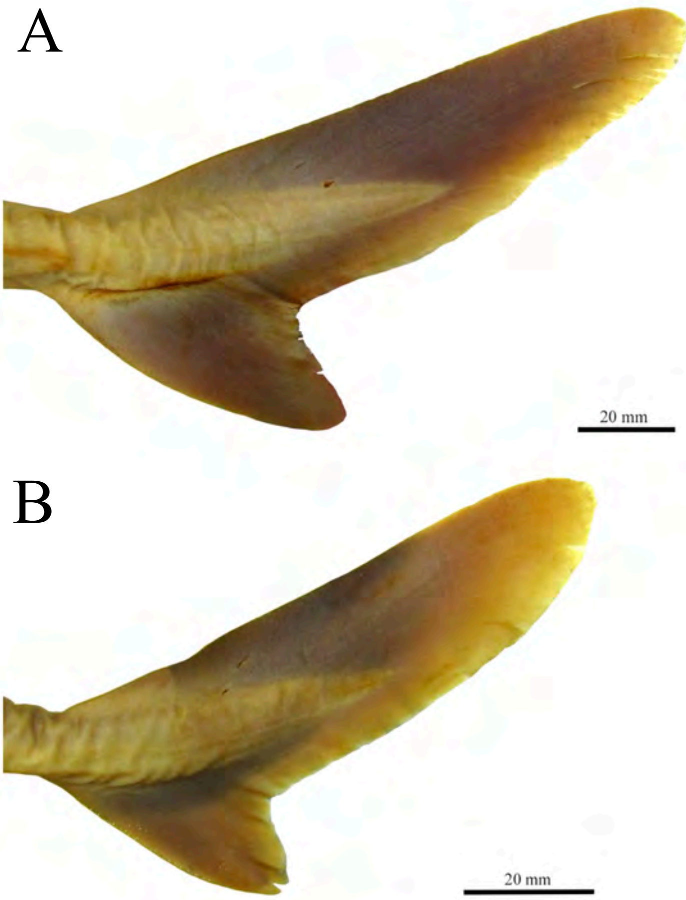

Figure 142. Caudal of *Flakeus notocaudatus*, showing black upper fringe. A: holotype, CSIRO H 1368-02, juvenile male, 615 mm TL; B: paratype, CSIRO H 1322-01, juvenile female, 390 mm TL.

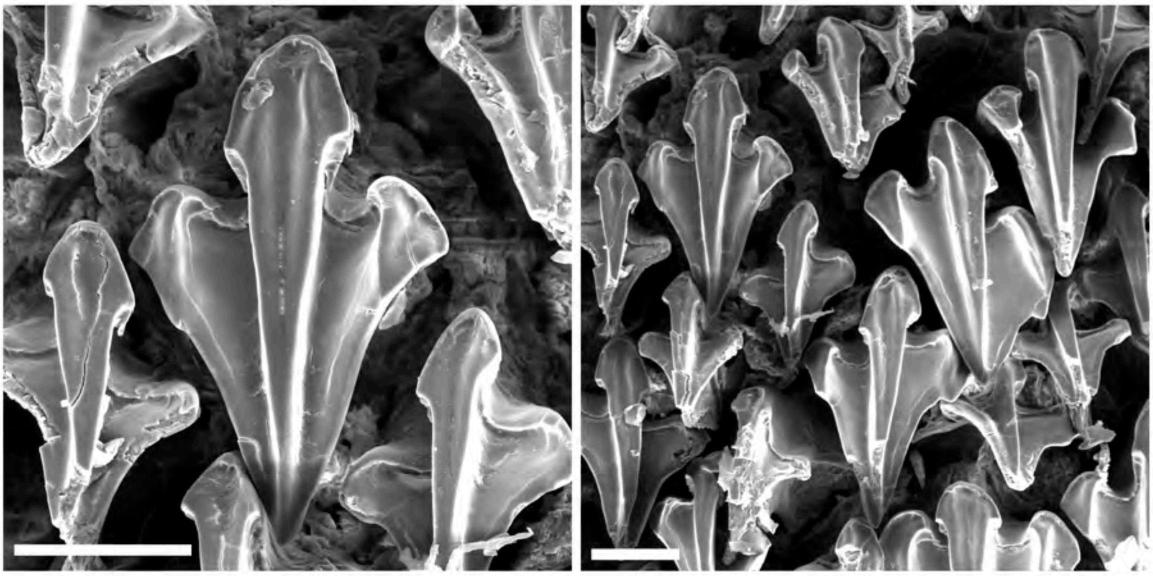

Figure 143. Scanning electron microscopy of dermal denticles of *Flakeus notocaudatus*, CSIRO H 1368-03, adult female, 632 mm TL. Scale bars: 100 µm.

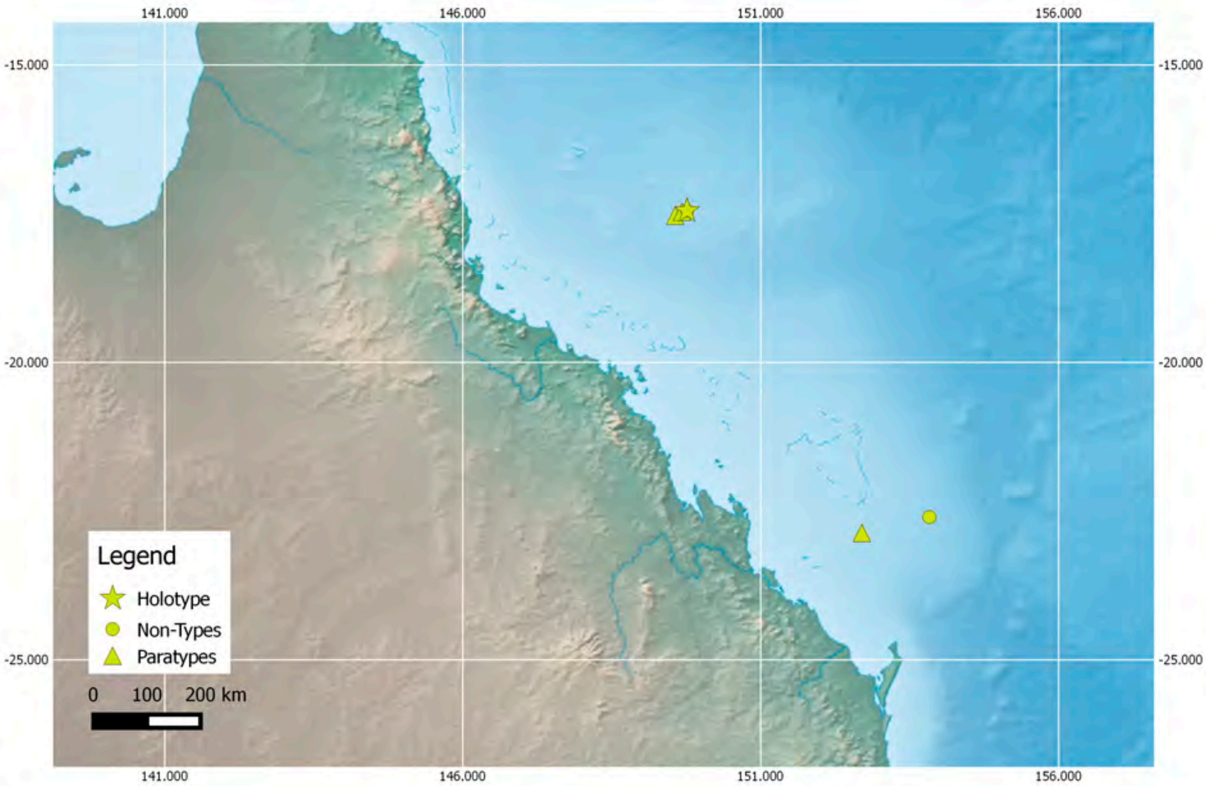

Figure 144. Map of geographical distribution of *Flakeus notocaudatus* in the South Pacific Ocean.

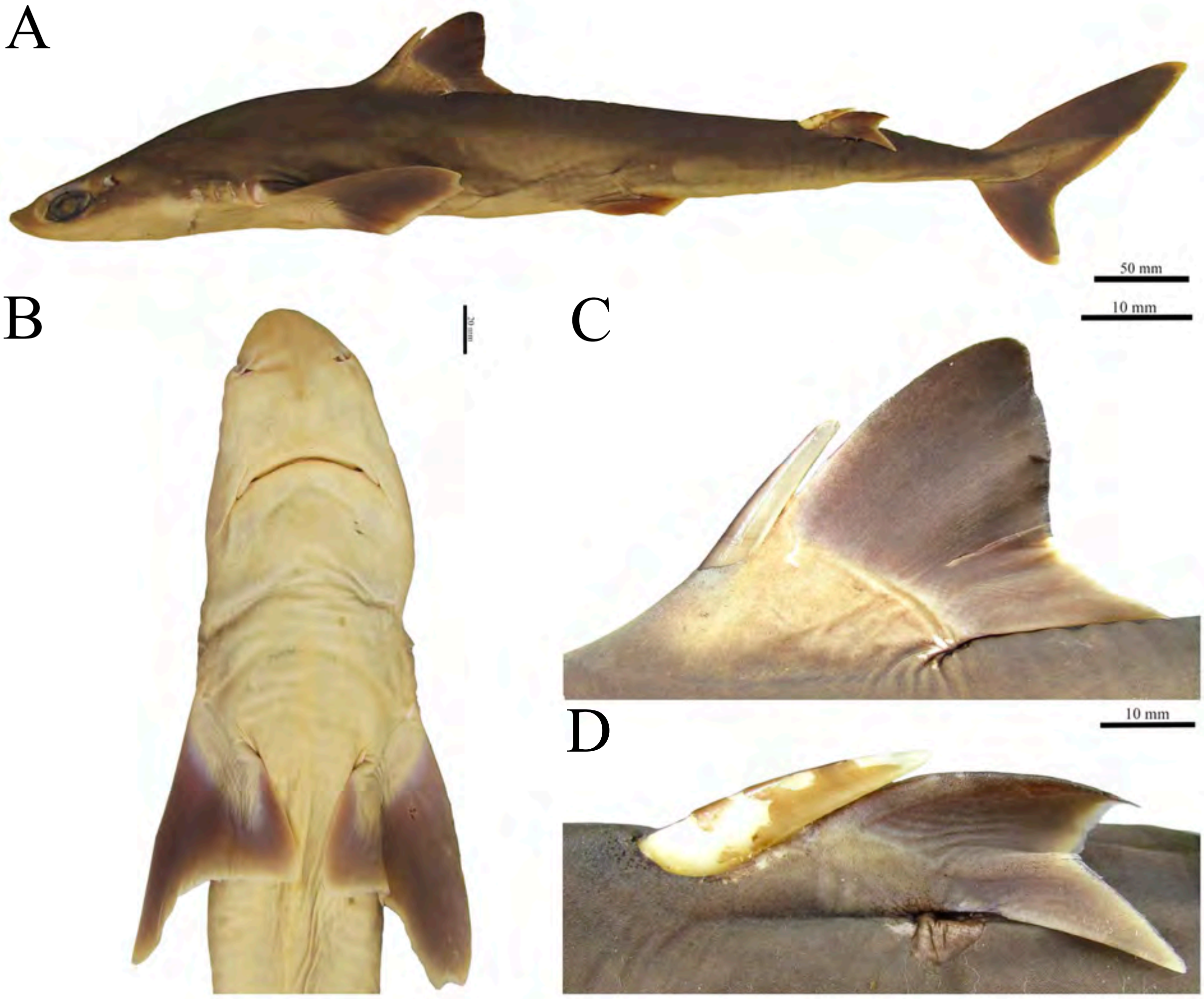

Figure 145. Holotype of *Flakeus hemipinnis*, MZB 15040, adult female, 630 mm TL. A: lateral view; B: ventral view; C: first dorsal fin; D: second dorsal fin.

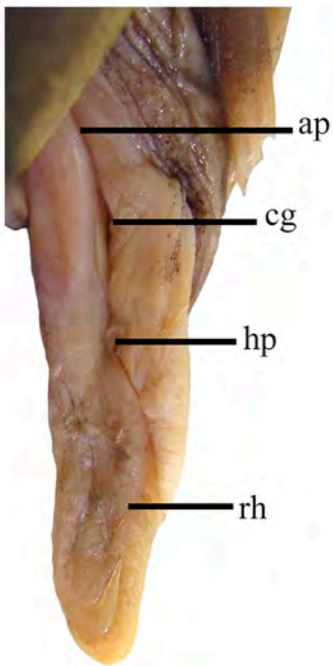

Figure 146. Clasper of paratype of *Flakeus hemipinnis*, CSIRO H 5692-03, adult male, 483 mm TL, in dorsal view. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; rh: rhipidion.

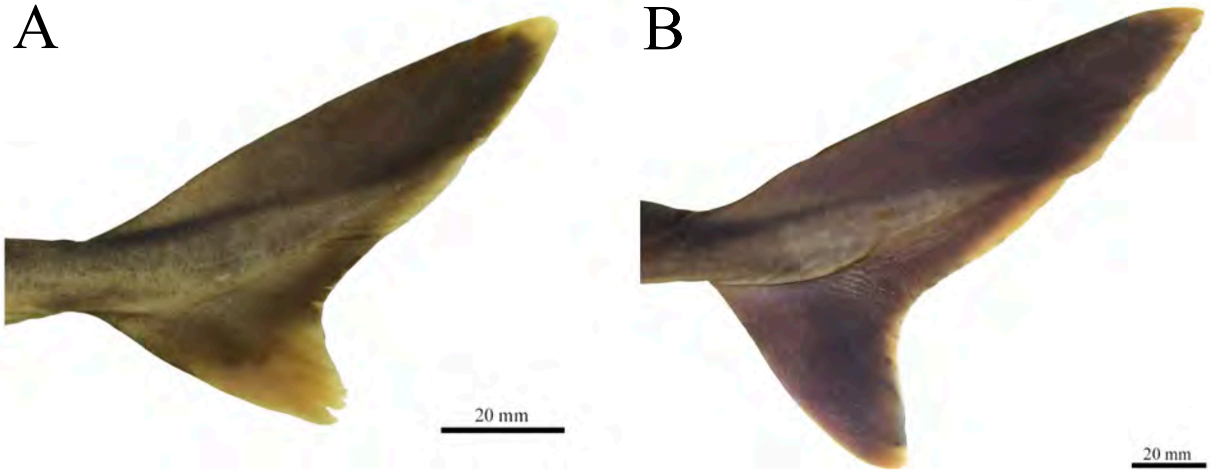

Figure 147. Caudal fin of *Flakeus hemipinnis*, showing shape and coloration. A: paratype, CSIRO H5693-07, juvenile female, 422 mm TL; B: holotype, MZB 15040, adult female, 630 mm TL.

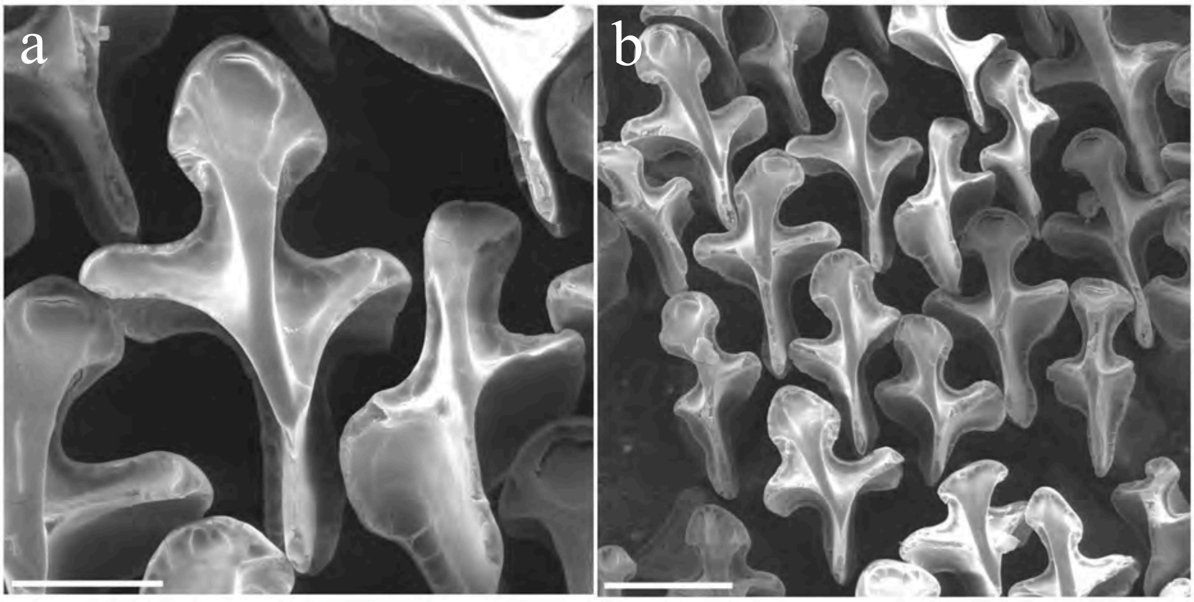

Figure 148. Scanning electron microscopy of dermal denticles of *Flakeus hemipinnis*, CSIRO H 5876-04, adult female, 630 mm TL. Scale bars: 50 μm (a); 100 μm (b).

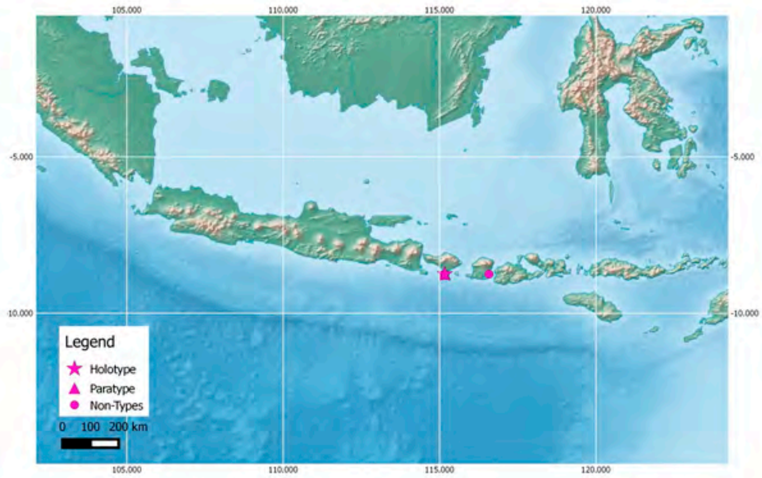

Figure 149. Map of Indonesia, showing the geographical distribution of *Flakeus hemipinnis*.

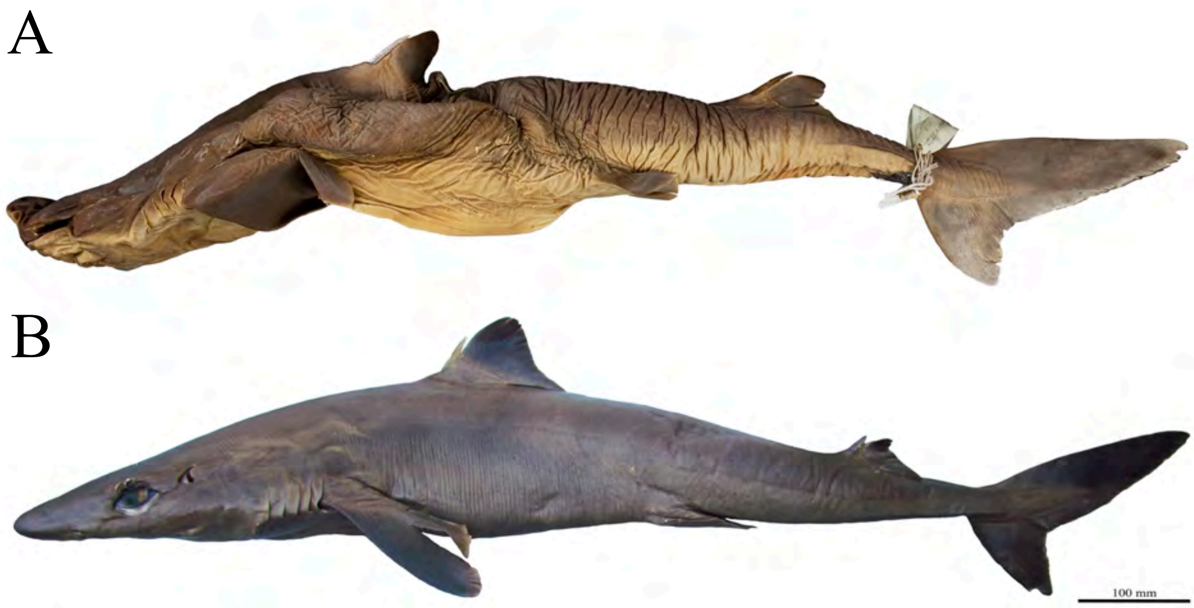

Figure 150. *Flakeus mitsukurii* in lateral view. A: holotype, SU 12793, adult female, 710 mm TL; B: HUMZ 102988, adult female, 1025 mm TL.

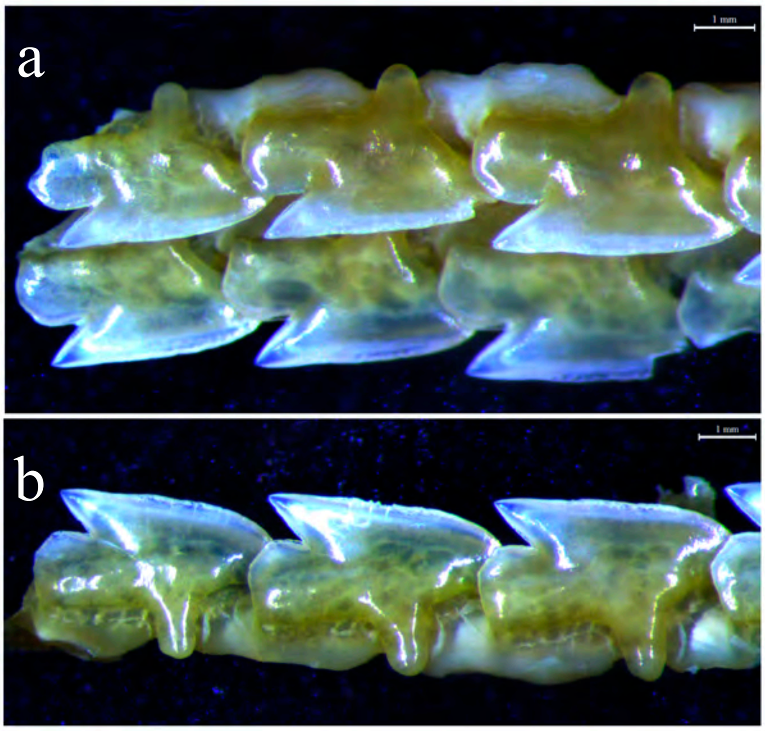

Figure 151. Upper (a) and lower (b) teeth of *Flakeus mitsukurii*, HUMZ 33680, adult female, 760 mm TL. Scale bar: 1 mm.

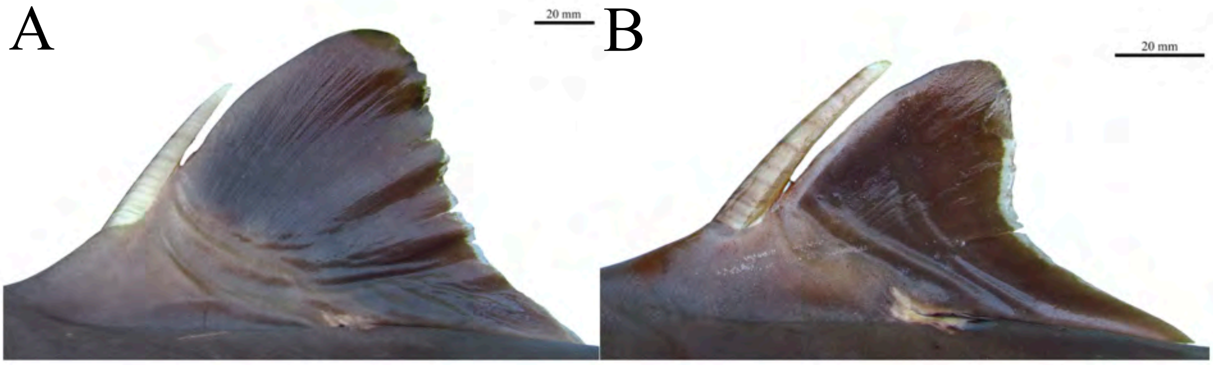

Figure 152 First (A) and second (B) dorsal fins of *Flakeus mitsukurii*, HUMZ 113587, adult female, 990 mm TL.

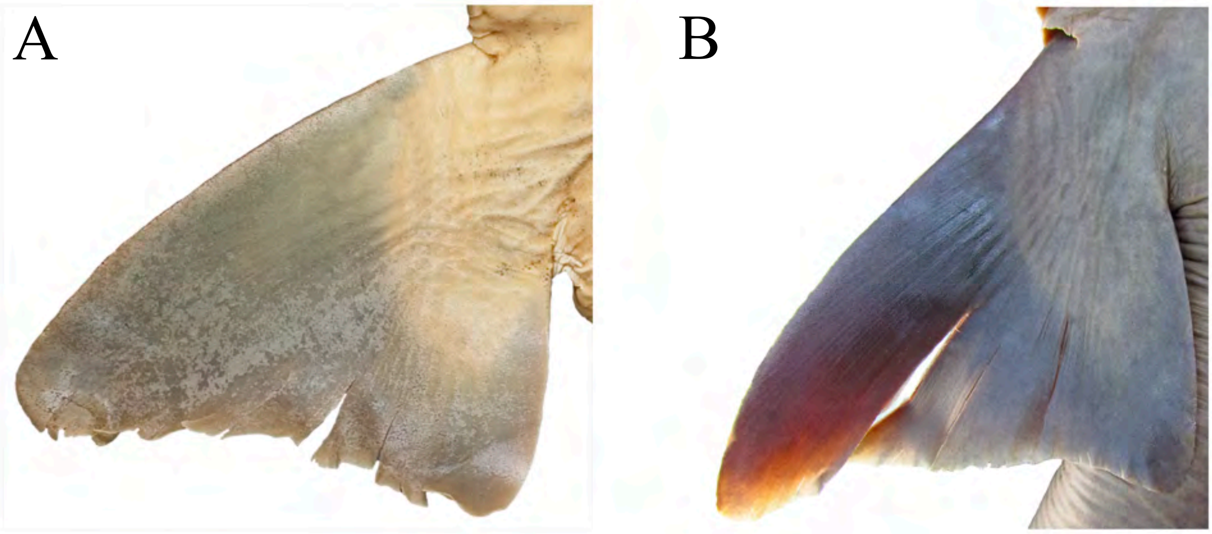

Figure 153. Pectoral fins of *Flakeus mitsukurii* in ventral view. A: paratype, SU 12794, adult male, 770 mm TL; B: HUMZ 102988, adult female, 1025 mm TL.

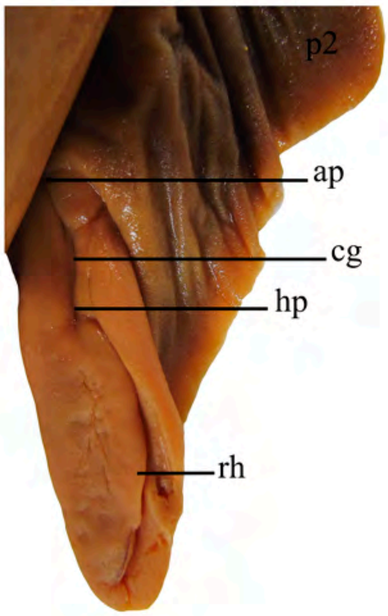

Figure 154 Clasper of *Flakeus mitsukurii*, NSMT-P 44381, adult male, 770 mm TL, in dorsal view. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

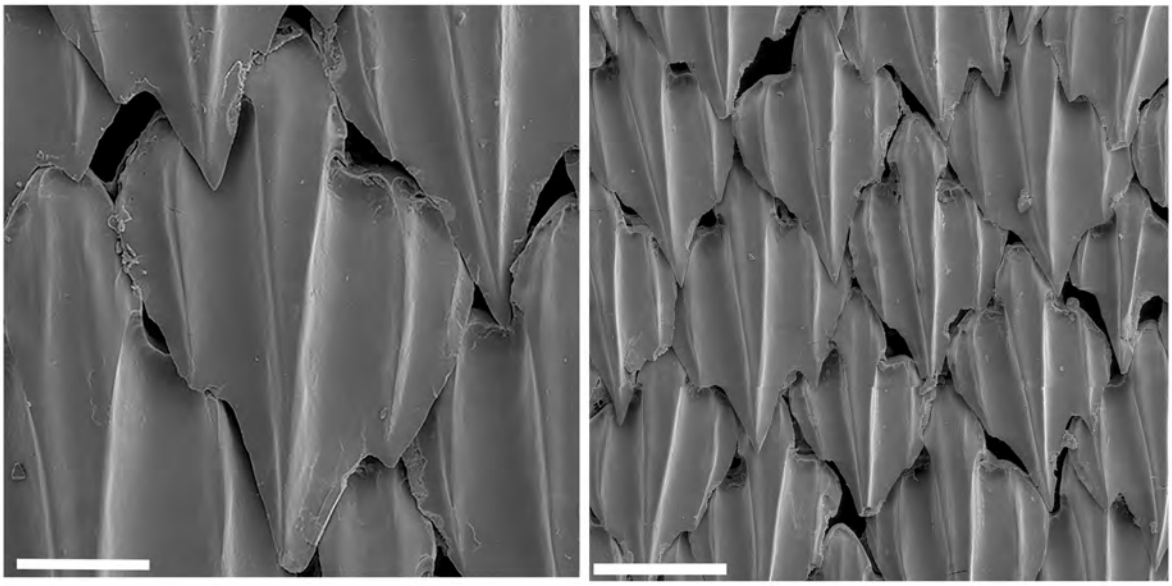

Figure 155. Scanning electron microscopy of *Flakeus mitsukurii*, HUMZ 102987, adult female, 970 mm TL, showing dermal denticles. Scale bar: 200 µm.

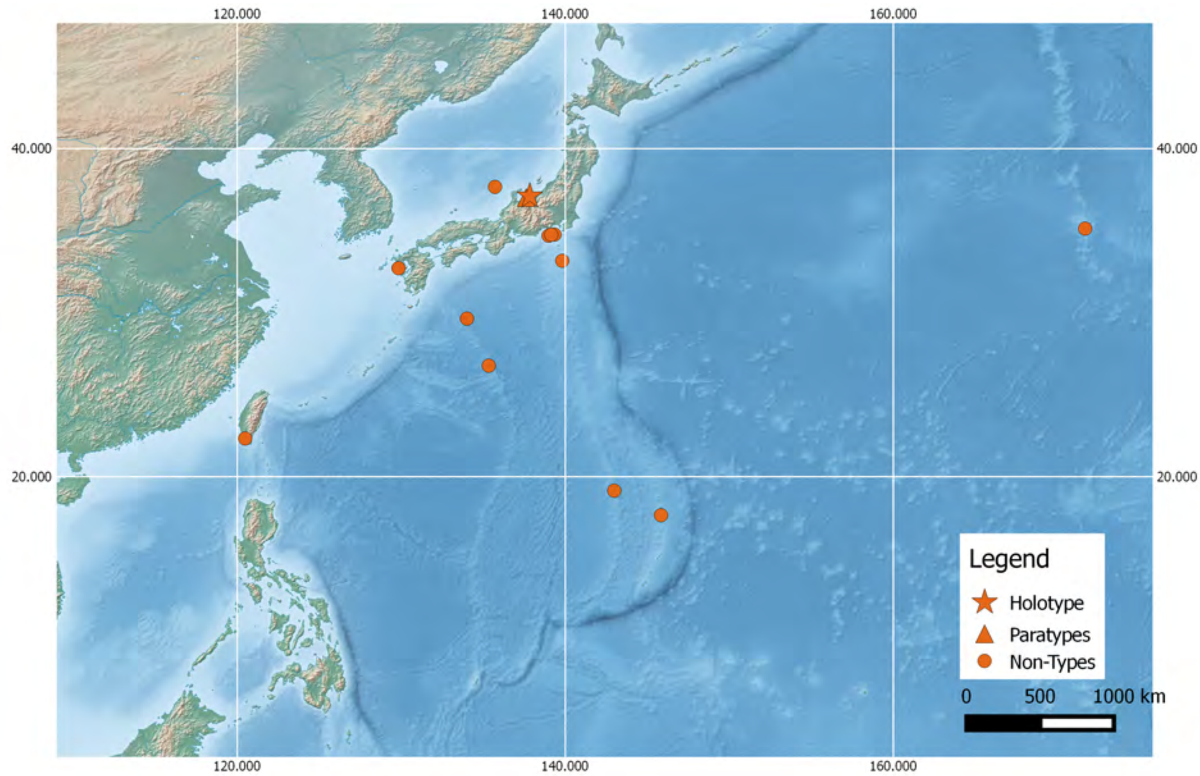

Figure 156. Map of geographical distribution of *Flakeus mitsukurii* in the Northwest Pacific Ocean.

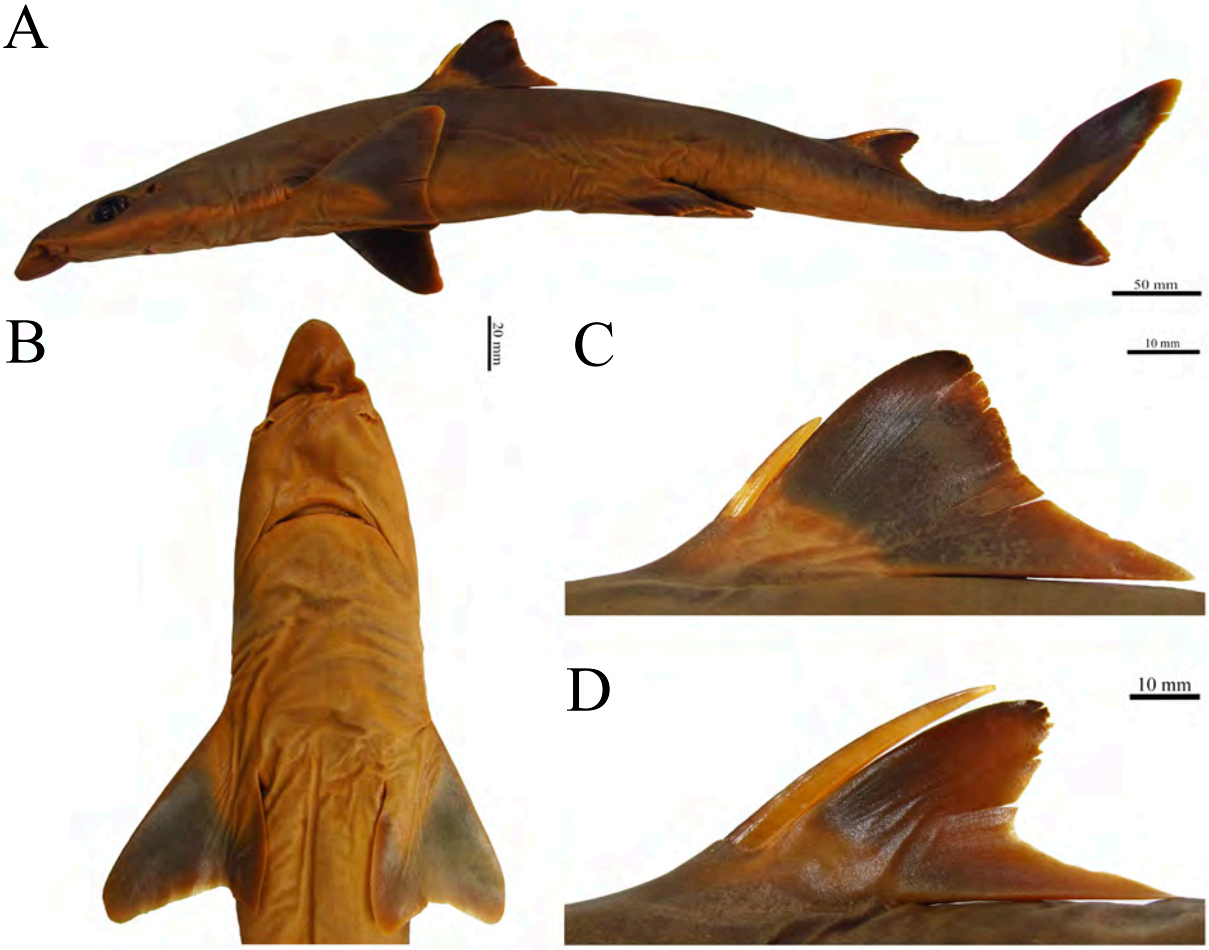

Figure 157. *Flakeus japonicus*, NSMT-P 44380, adult male, 645 mm TL, in lateral (A) and ventral (B) views, and detail of first (C) and second (D) dorsal fins.

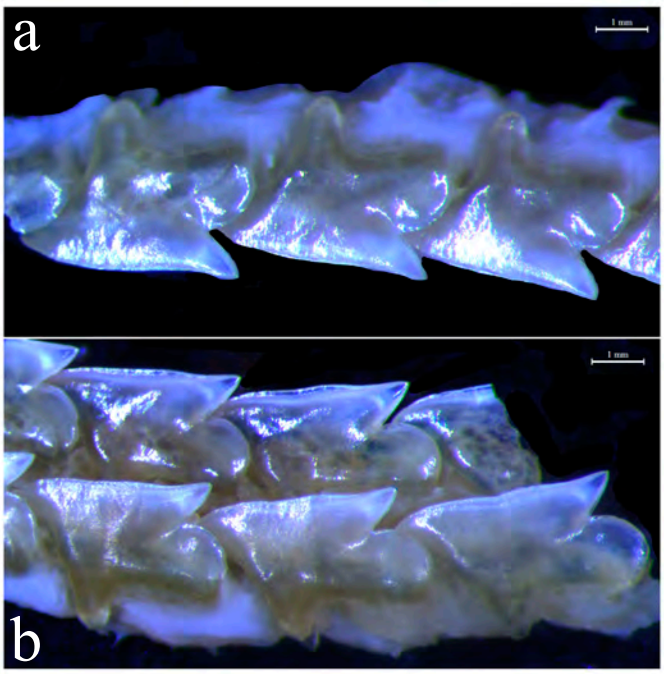

Figure 158. Upper (a) and lower (b) teeth of *Flakeus japonicus*, HUMZ 189737, adult male, 560 mm TL. Scale bar: 1 mm.

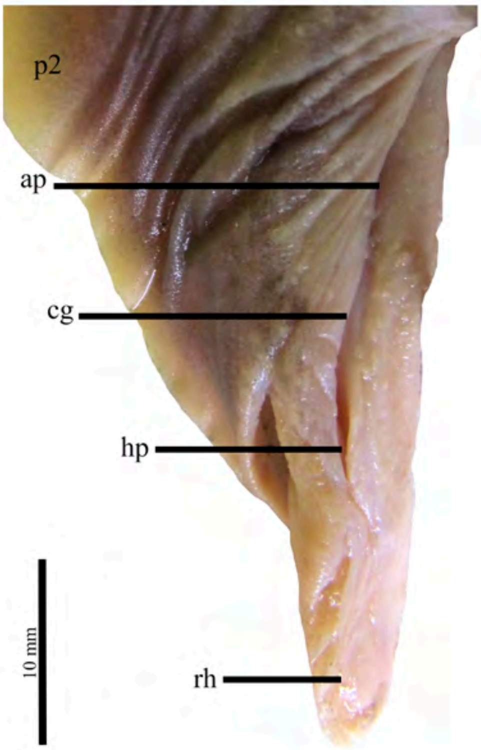

Figure 159. Clasper of *Flakeus japonicus*, HUMZ 189737, adult male, 560 mm TL, in dorsal view. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

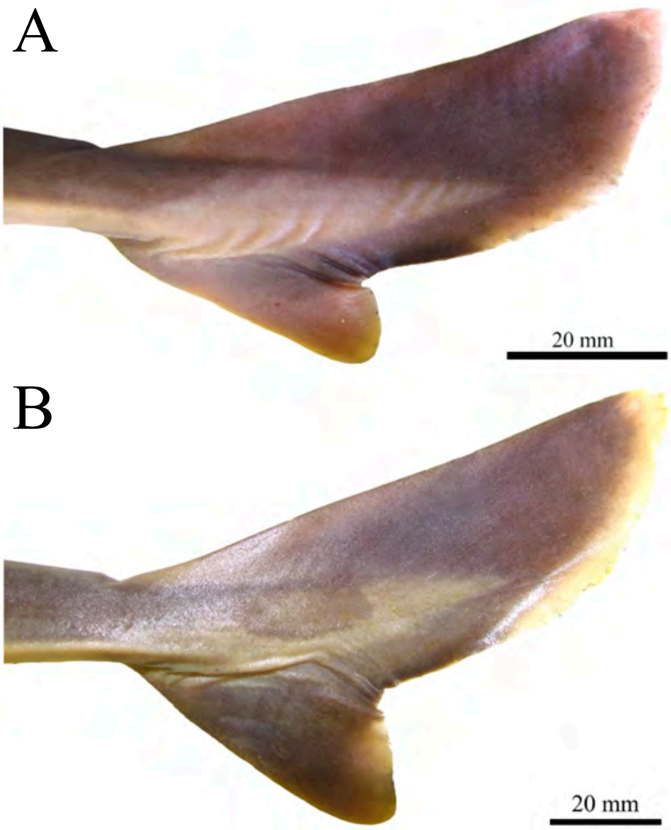

Figure 160. Caudal fin of *Flakeus japonicus*. A: HUMZ 189687, juvenile male, 380 mm TL; B: HUMZ 189738, adult male, 535 mm TL.

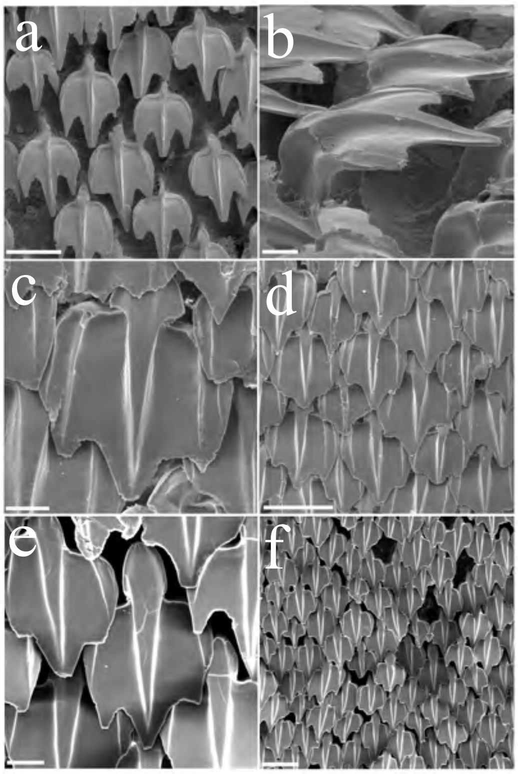

Figure 161. Scanning electron microscopy of dermal denticles of *Flakeus japonicus*. a-b: NSMT-P 91127, juvenile female, 410 mm TL; c-d: NSMT-P 44380, adult male, 645 mm TL; e-f: CSIRO H6413-01, adult female, 580 mm TL. Scale bars: 50 µm (b,c,e); 200 µm (a,d,f).

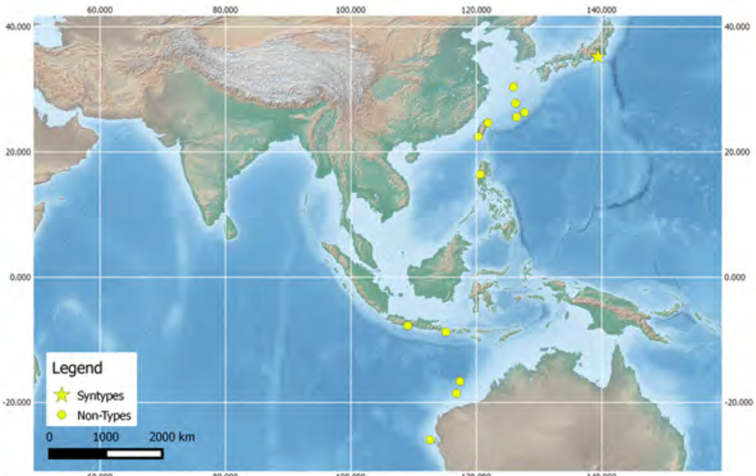

Figure 162. Map of West Pacific Ocean, showing the geographical distribution of *Flakeus japonicus*.

Figure 163. Holotype of *Squalus nasutus*, CSIRO H 2590-12, adult female, 503 mm TL in lateral view.

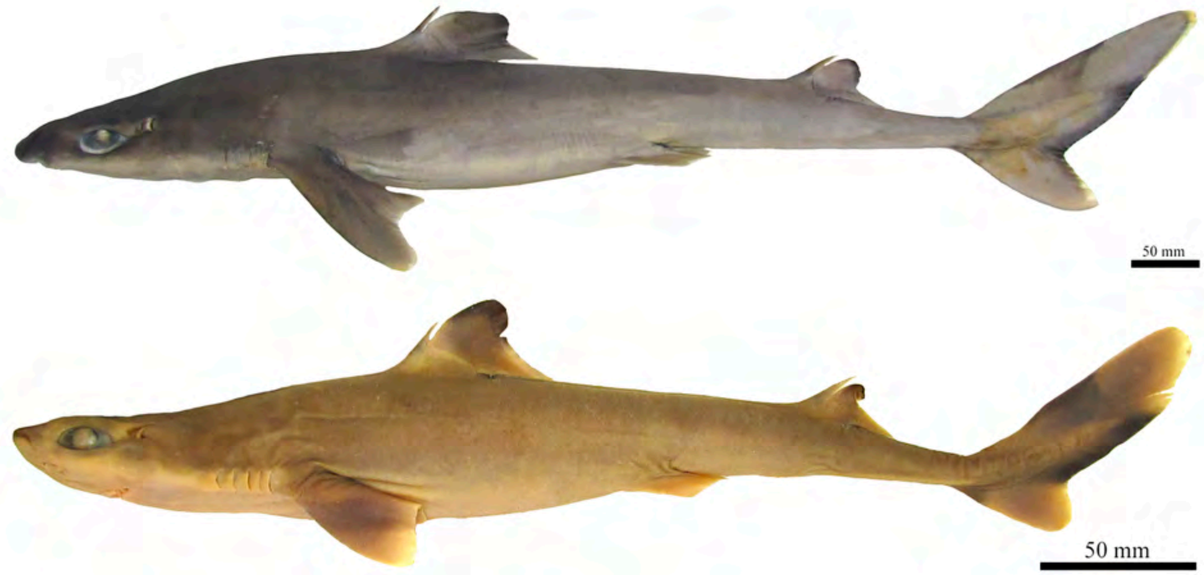

Figure 164. Specimens of *Flakeus montalbani* in lateral view. A: AMS I 45654-001, adult female, 885 mm TL; B: CSIRO H 1348-1, juvenile female, 374 mm TL.

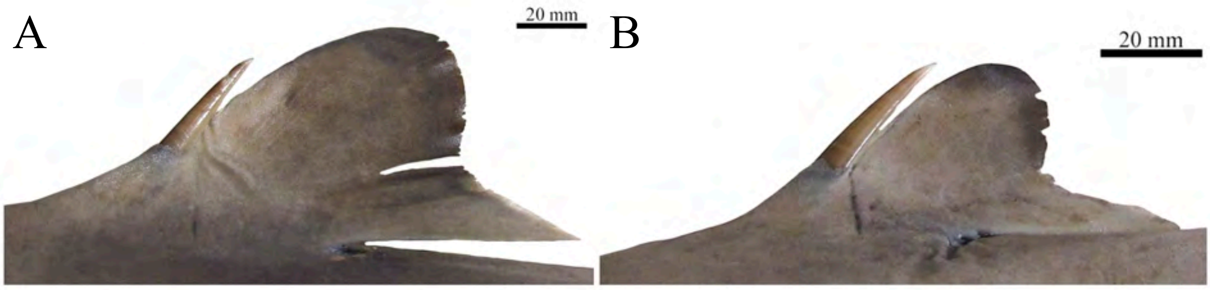

Figure 165. First (A) and second (B) dorsal fins of *Flakeus montalbani*, AMS I 45654-001, adult female, 885 mm TL.

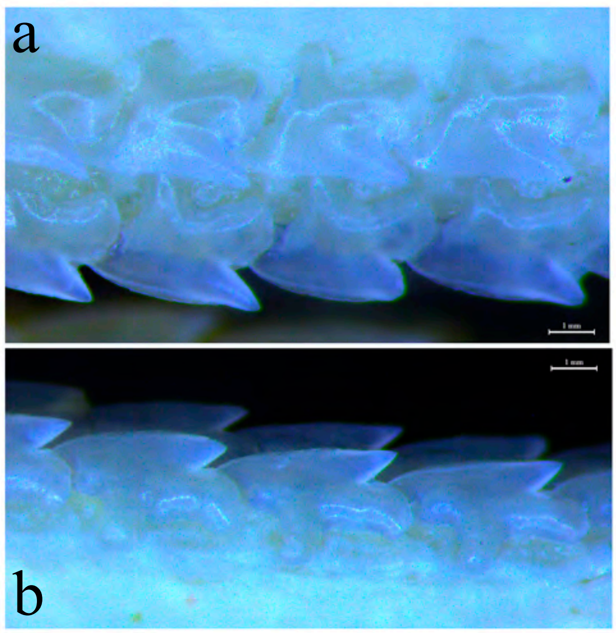

Figure 166. Upper (a) and lower (b) teeth of *Flakeus montalbani*, MZUSP not catalogued, adult male, 713 mm TL.

Figure 167. Pectoral fin of *Flakeus montalbani*, AMS I 45654-001, adult female, 885 mm TL in ventral view.

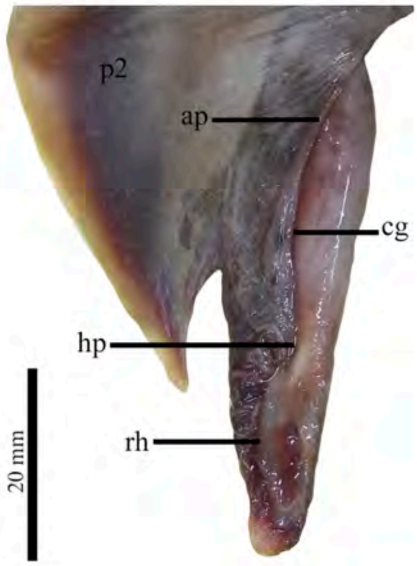

Figure 168. Clasper of *Flakeus montalbani*, MZUSP not catalogued, adult male, 713 mm TL, in dorsal view. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

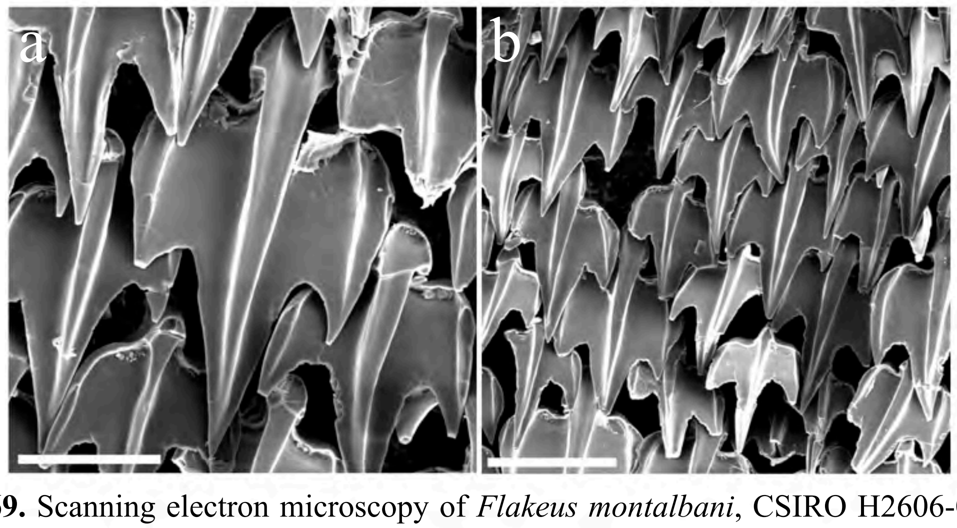

Figure 169. Scanning electron microscopy of *Flakeus montalbani*, CSIRO H2606-06, adult male, 575 mm TL, showing dermal denticles. Scale bars: 100 µm (a); 200 µm (b).

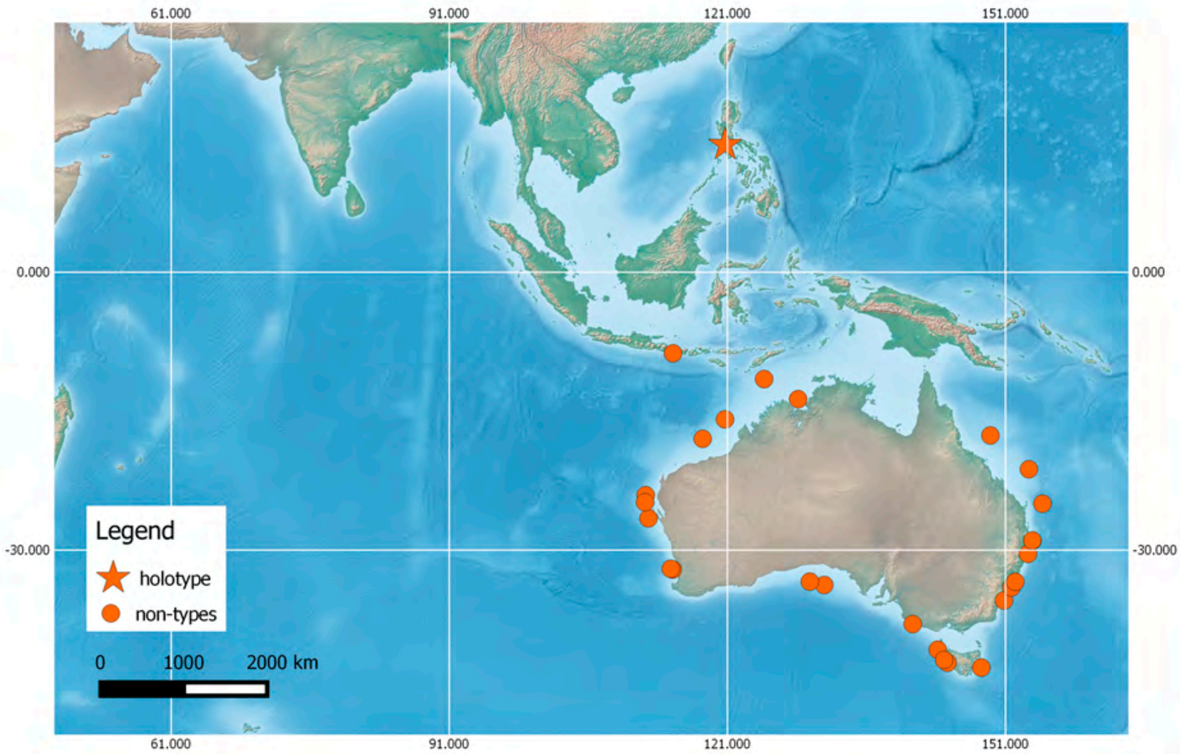

Figure 170. Map of West Central and South Pacific Ocean, showing the geographical distribution of *Flakeus montalbani*.

Figure 171. Holotype of *Squalus chloroculus*, CSIRO H 4775-01, adult male, 752 mm TL in lateral view.

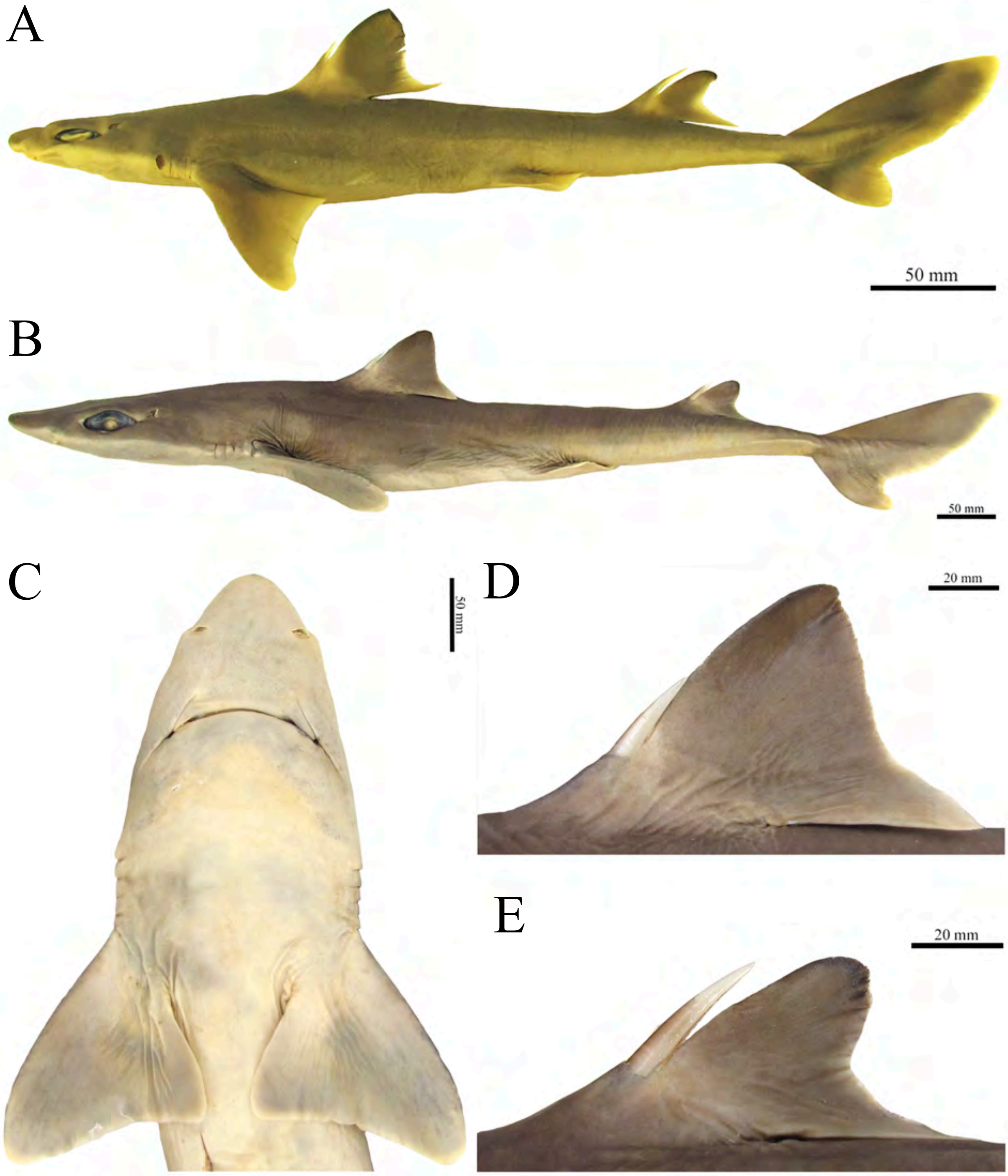

Figure 172. *Flakeus griffini* in lateral (A) and ventral (B) views, and detail of first and second dorsal fins. A: NMNZ P 41775, juvenile female, 412 mm TL; B-E: NMNZ P 52102, adult male, 835 mm TL.

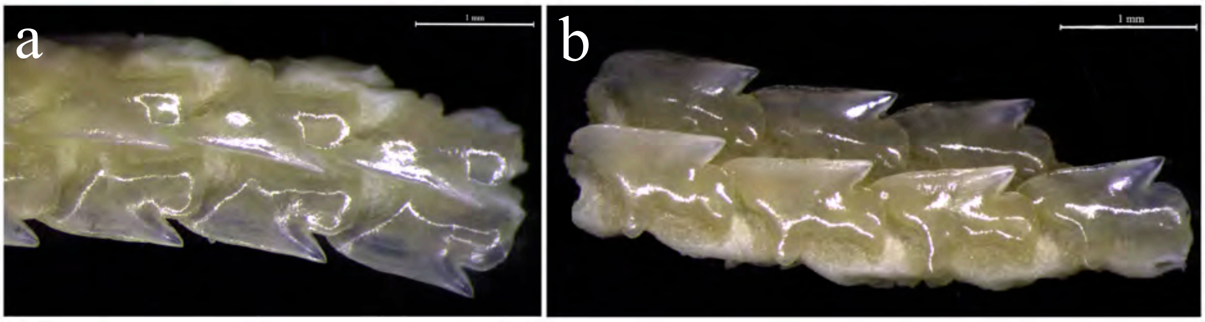

Figure 173. Upper (a) and lower (b) teeth of *Flakeus griffini*, NMNZ P 52103, adult male, 770 mm TL. Scale bar: 1 mm.

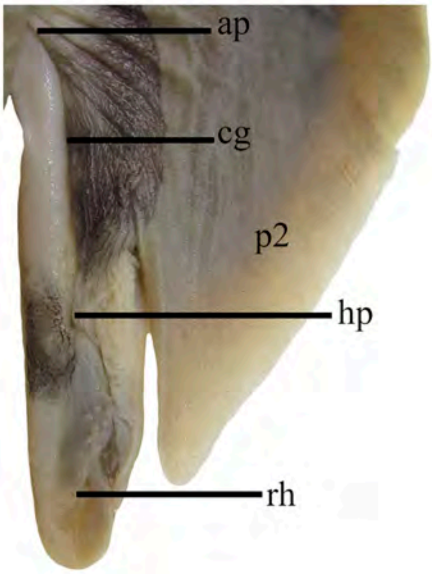

Figure 174. Clasper of *Flakeus griffini*, NMNZ P 52103, adult male, 770 mm TL in dorsal view. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

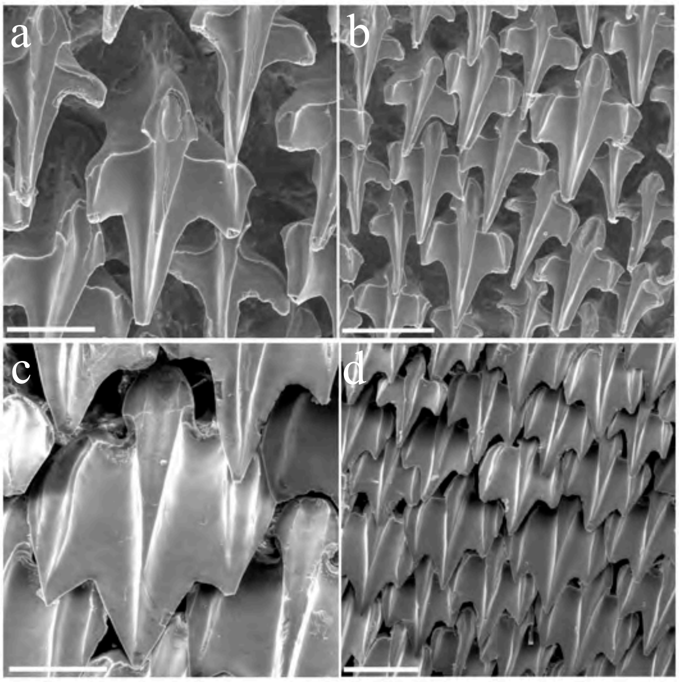

Figure 175. Variation on shape of dermal denticles of *Flakeus griffini*. a,b: NMNZ P 52103, adult male, 770 mm TL; c,d: NMNZ P40347, adult female, 915 mm TL. Scale bars: 100 µm (a,c); 200 µm (b,d).

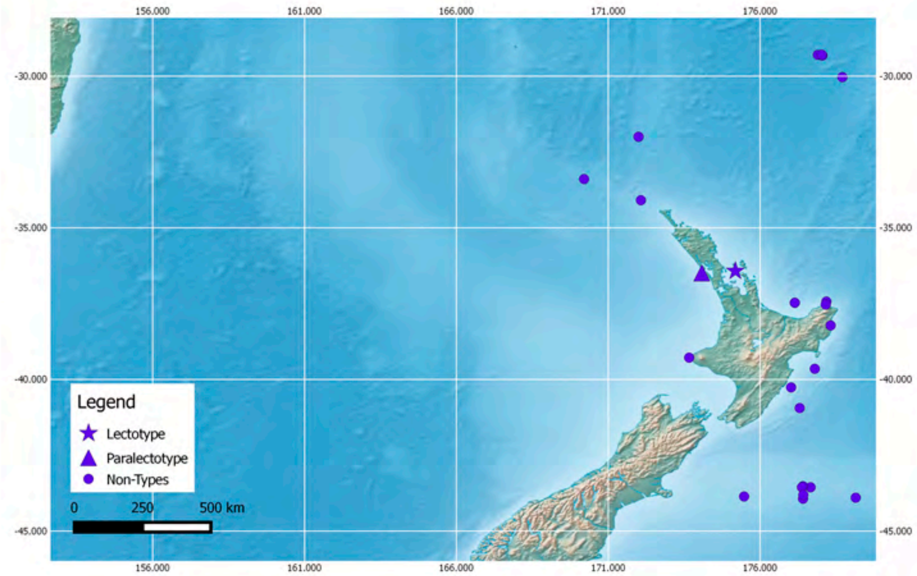

Figure 176. Map of New Zealand, showing the geographical distribution of *Flakeus griffini*.

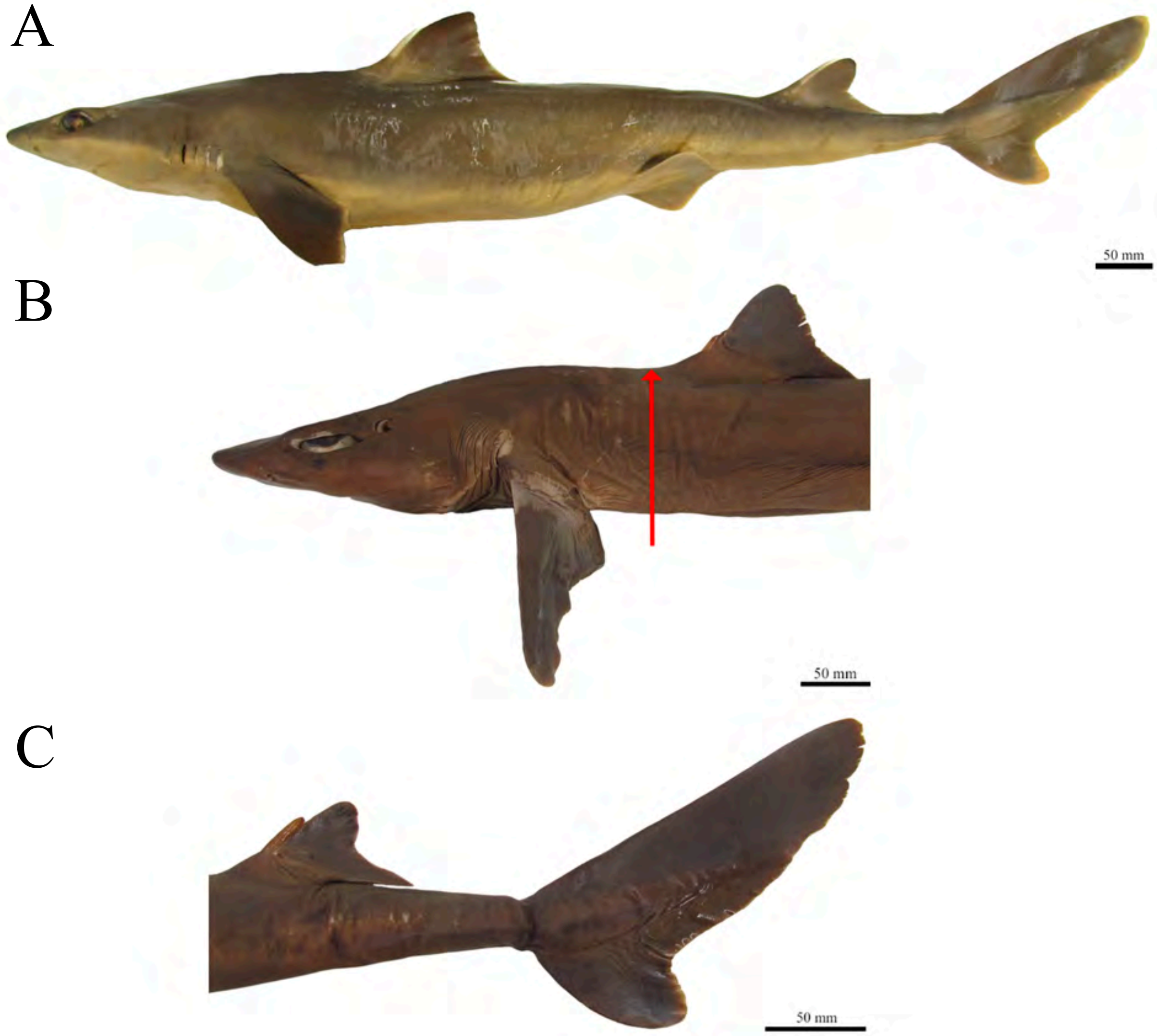

Figure 177. Specimen of *Flakeus* cf. *griffini*, NMNZ P 39895, adult female, 970 mm TL (A), and paralectotype of *F. griffini*, NMNZ P 662, adult female, 975 mm TL (B,C).

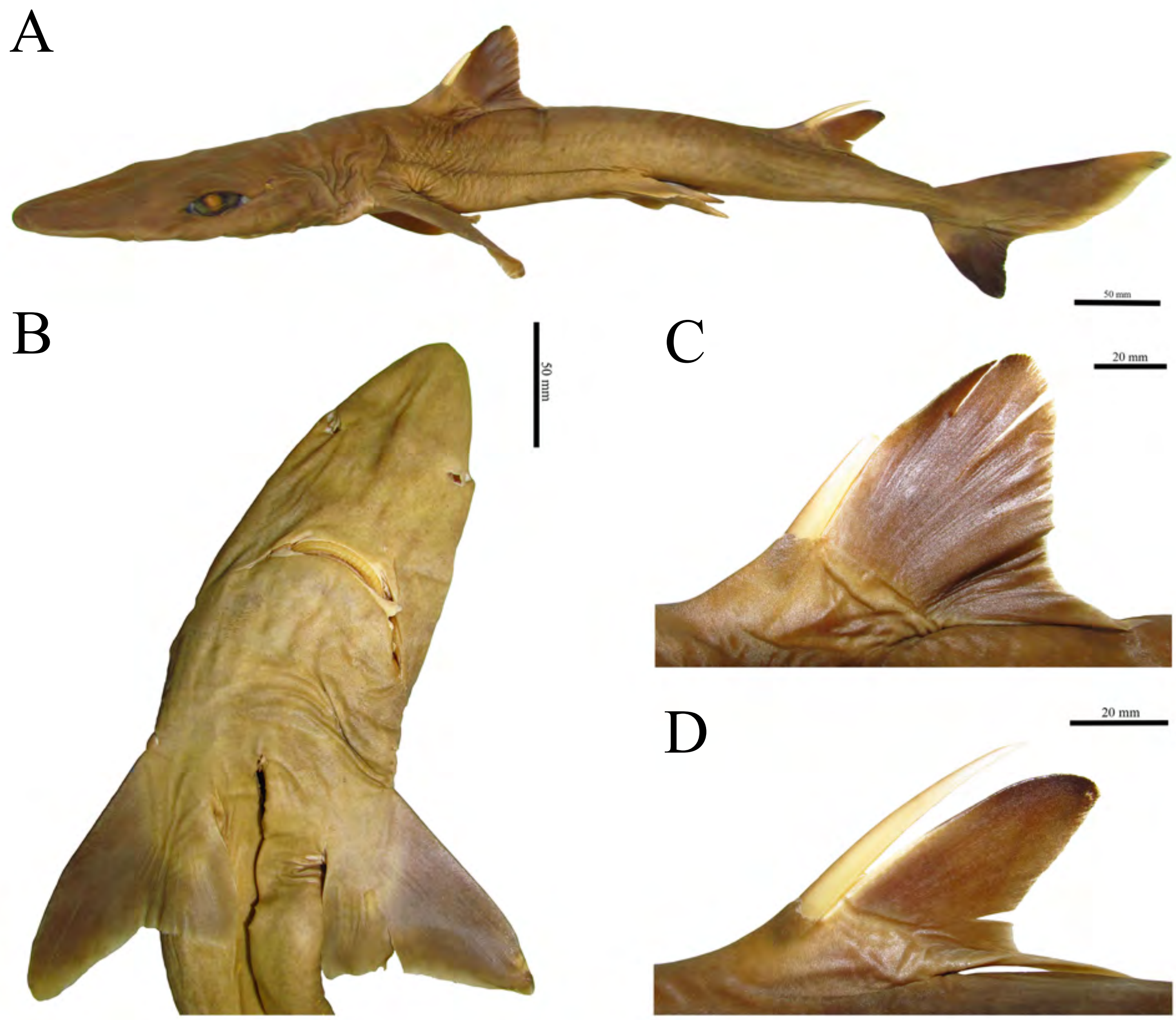

Figure 178. Holotype of *Flakeus melanurus*, MNHN 1980-0460, adult male, 670 mm TL. A: lateral view; B: ventral view; C: first dorsal fin; D: second dorsal fin.

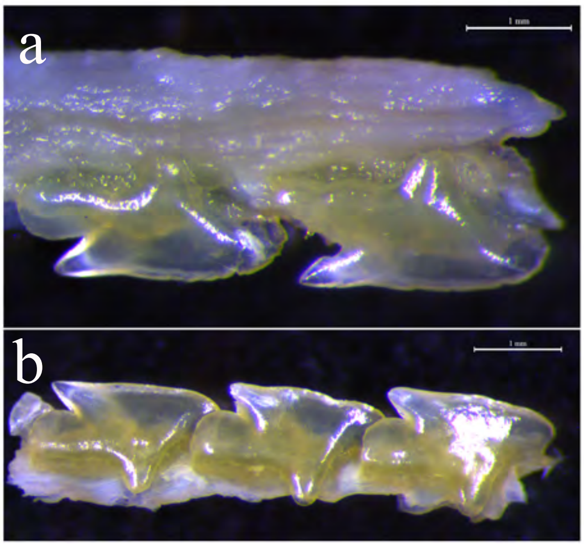

Figure 179. Upper (a) and lower teeth of *Flakeus melanurus*, MNHN 1997-3619, juvenile female, 527 mm TL. Scale bar: 1 mm.

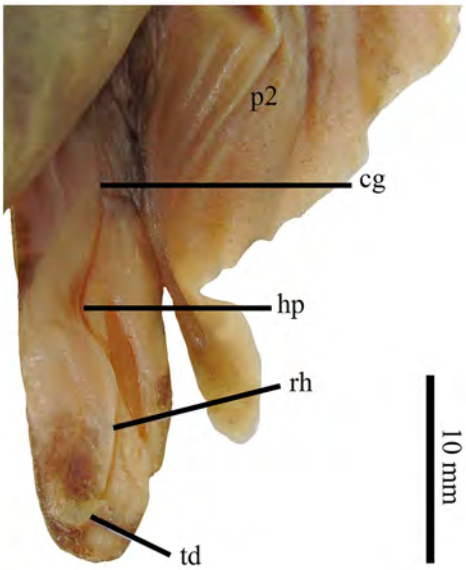

Figure 180. Clasper of holotype of *Flakeus melanurus*, MNHN 1980-0460, adult male, 670 mm TL in dorsal view. Abbreviations: cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion; td: dorsal terminal cartilage.

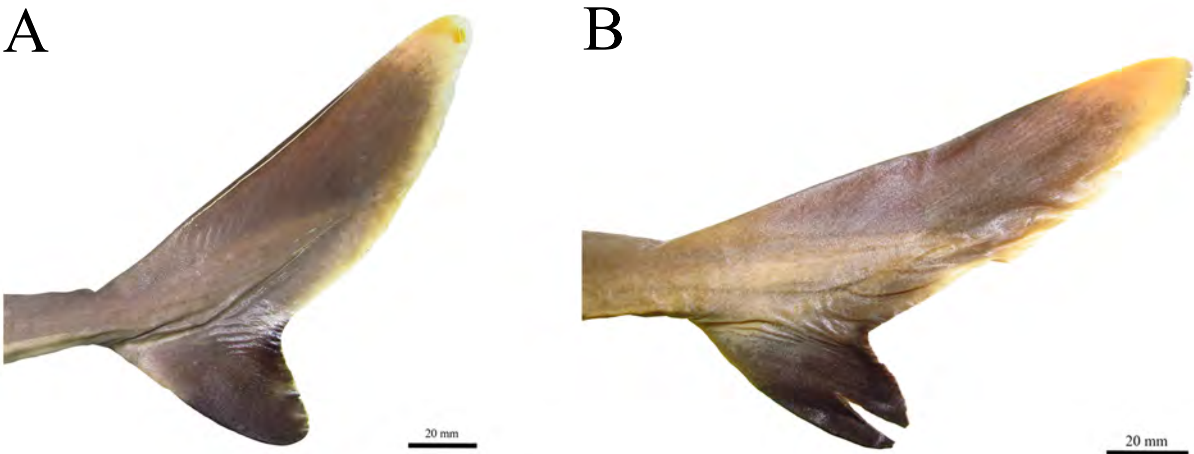

Figure 181. Caudal fin of *Flakeus melanurus*, showing black lower caudal lobe. A: MNHN 2002-1197, adult male, 680 mm TL; B: MNHN 1997-3624, adult male, 650 mm TL.

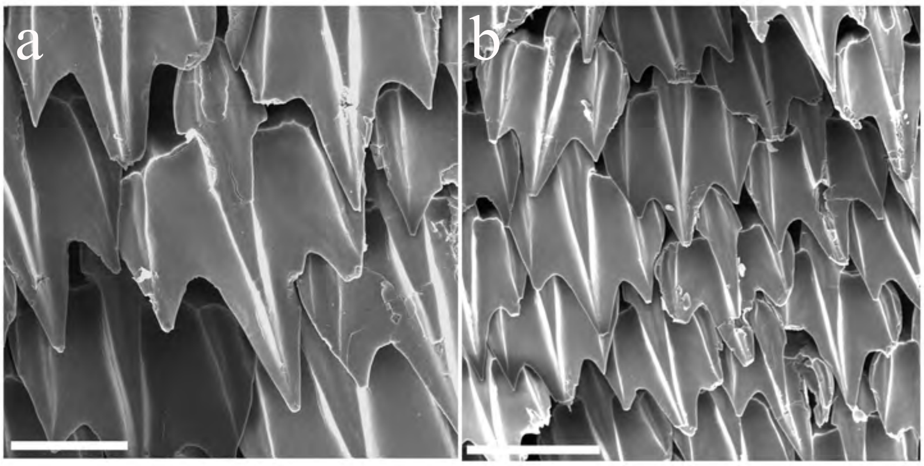

Figure 182. Dermal denticles of *Flakeus melanurus*, MNHN 1997-3627, adult female, 690 mm TL. Scale bars: 100 µm (a); 200 µm (b).

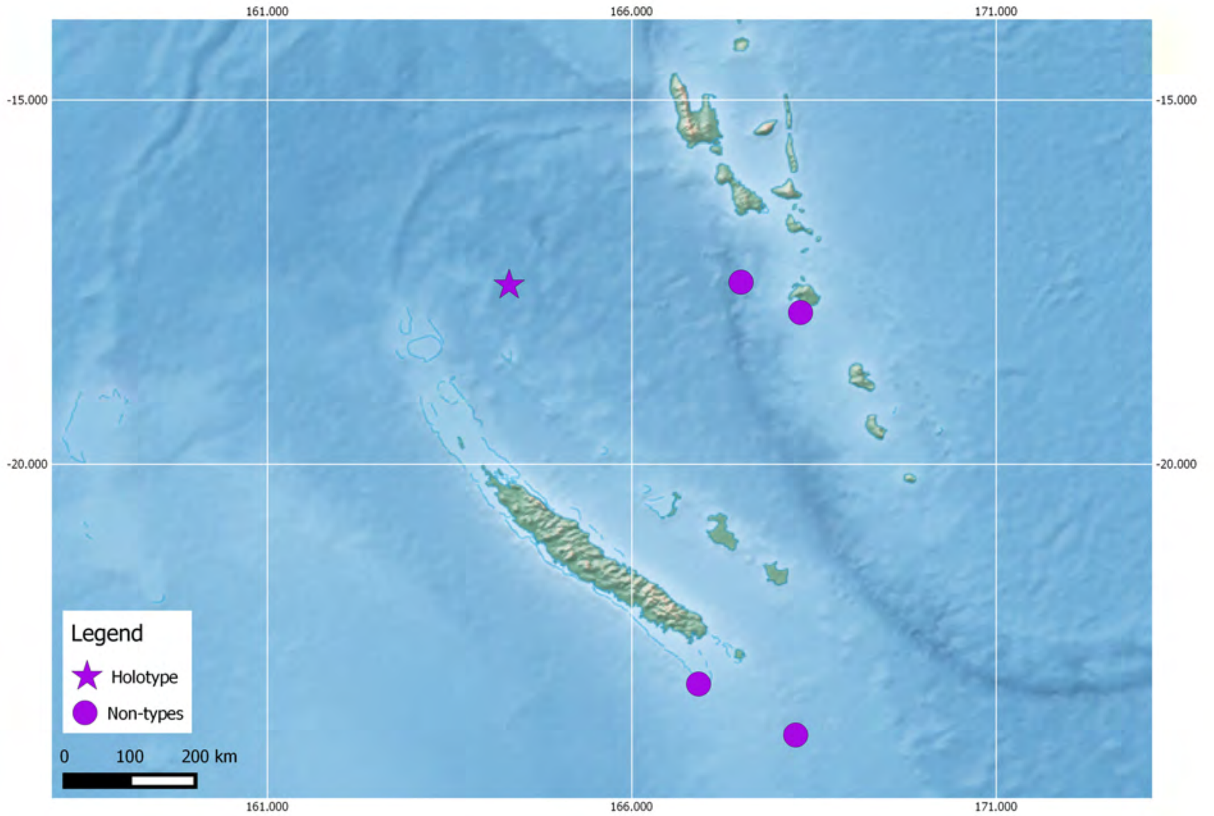

Figure 183. Geographical distribution of *Flakeus melanurus* in New Caledonia, Vanuatu, and Norfolk Island.

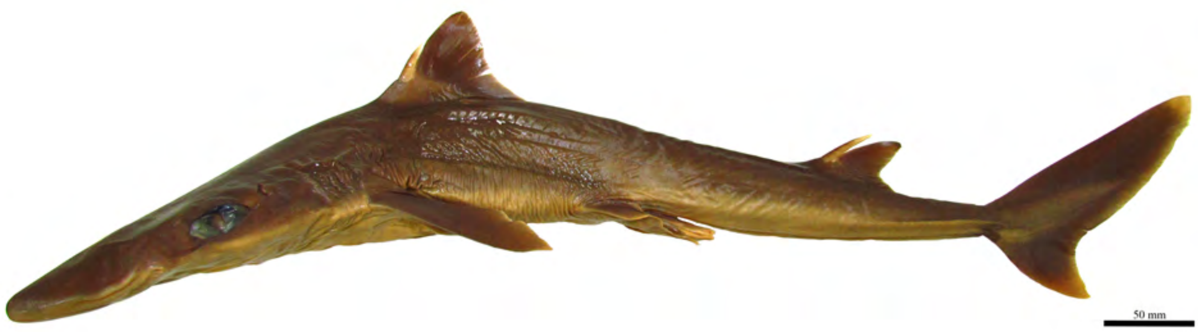

Figure 184. Holotype of *Squalus rancureli*, MNHN 1978-0693, adult male, 680 mm TL in lateral view.

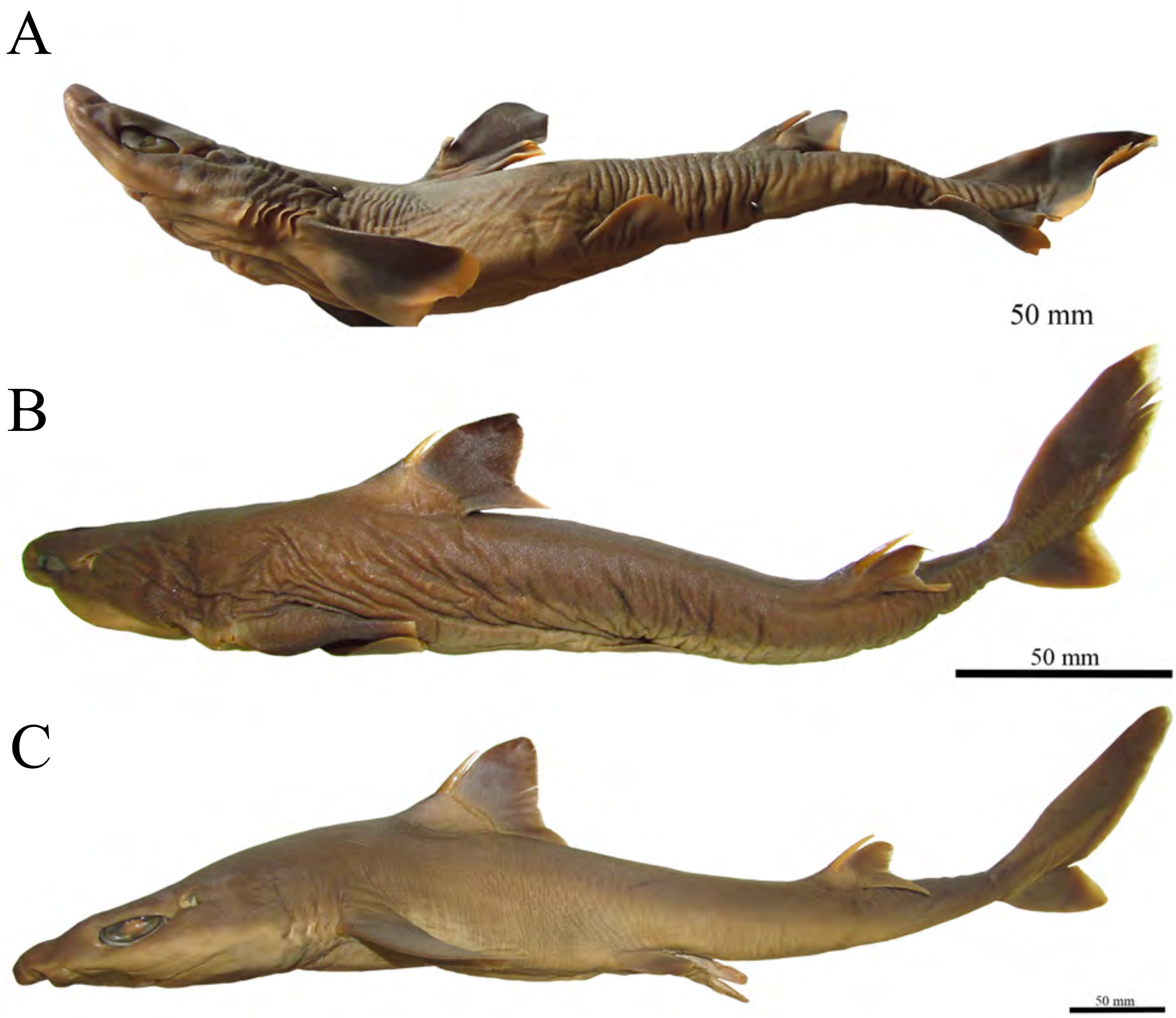

Figure 185. *Flakeus probatovi* in lateral view. A: holotype, ZMMU P-15991, neonate male, 220 mm TL. B: MNHN 1960-0260, juvenile male, 325 mm TL; C: ZMH 102865, adult male, 603 mm TL.

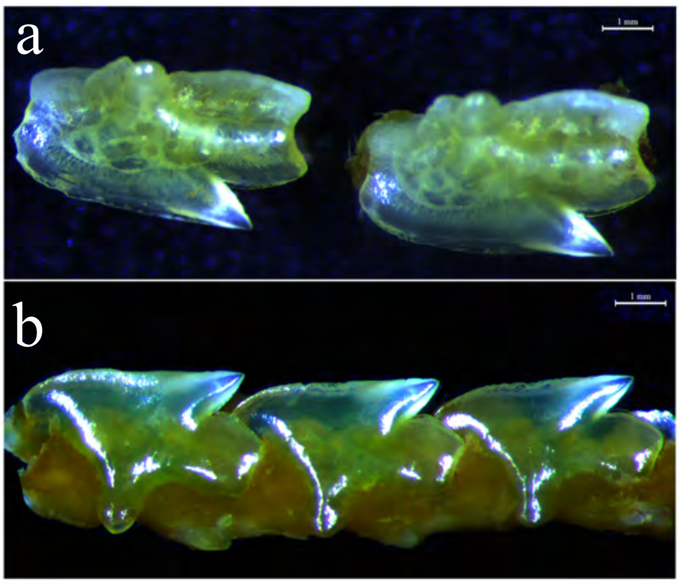

Figure 186. Upper (a) and lower (b) teeth of *Flakeus probatovi*, BMNH 1972.10.10.101, adult male, 677 mm TL. Scale bar: 1 mm.

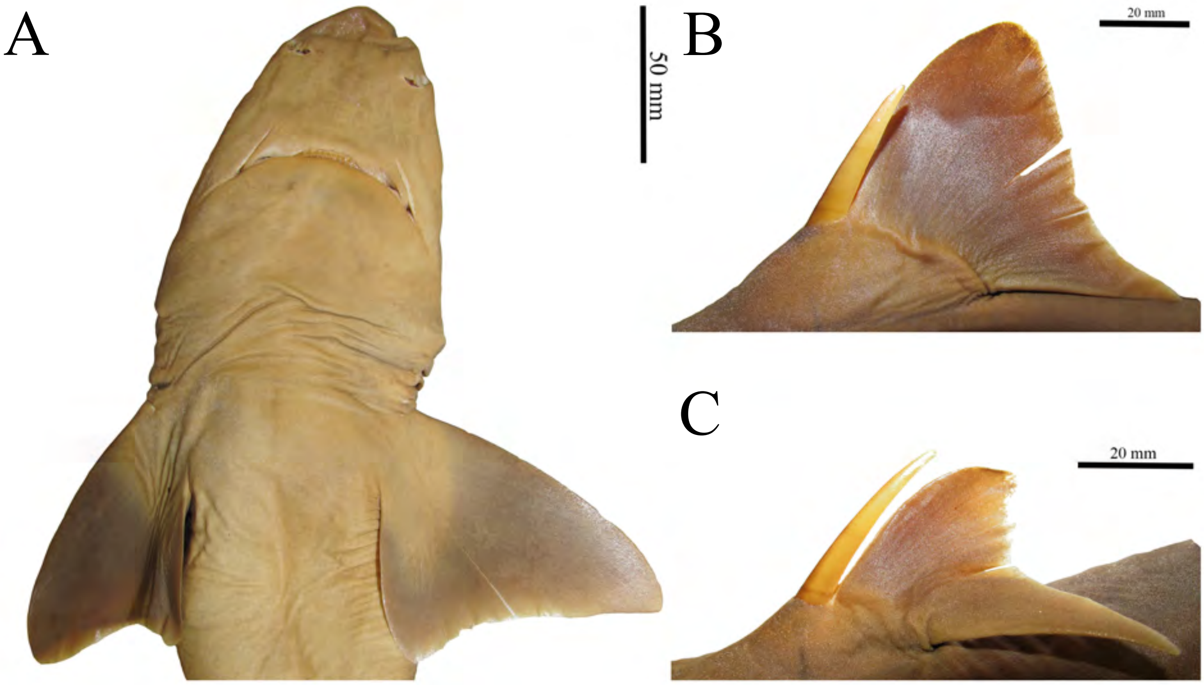

Figure 187. *Flakeus probatovi*, ZMH 102865, adult male, 603 mm TL, in ventral view (A), and detail of first (B) and second (C) dorsal fins.

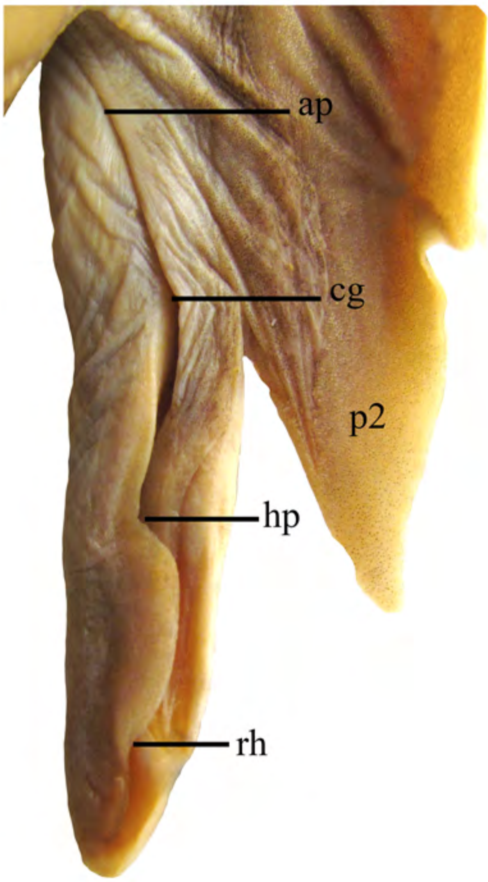

Figure 188. Clasper of *Flakeus probatovi*, ZMH 102865, adult male, 603 mm TL, in dorsal view.

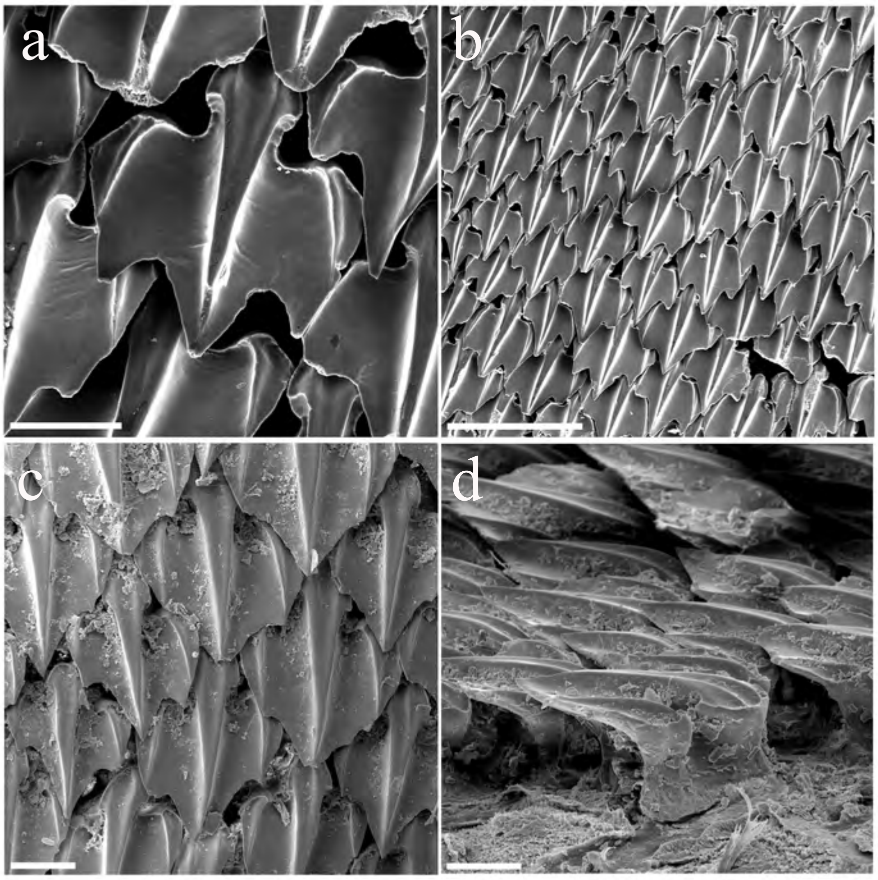

Figure 189. Scanning electron microscopy of dermal denticles of *Flakeus probatovi*. a,b: BMNH 1971.10.10.100, adult female, 670 mm TL; c,d: SAIAB 6024, adult female, 790 mm TL. Scale bars: 100 μm (a,c,d); 500 μm (b).

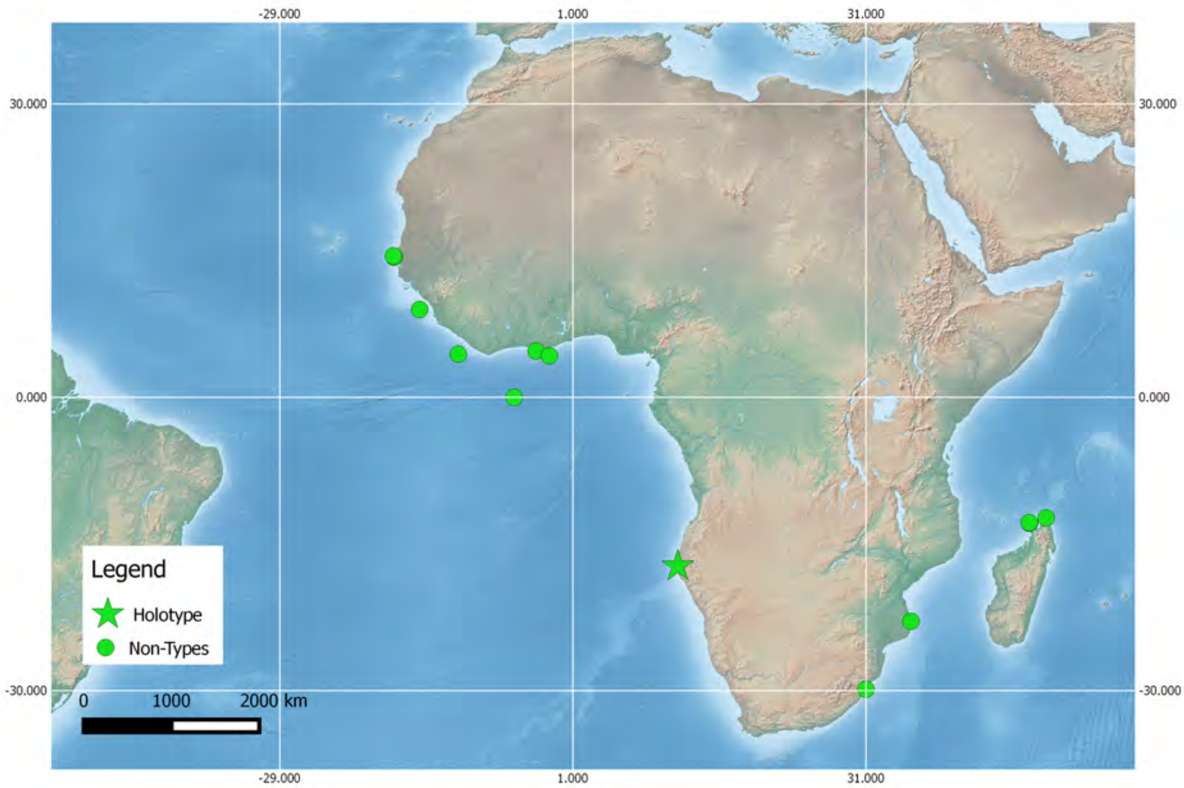

Figure 190. Geographical distribution of *Flakeus probatovi* in African waters.

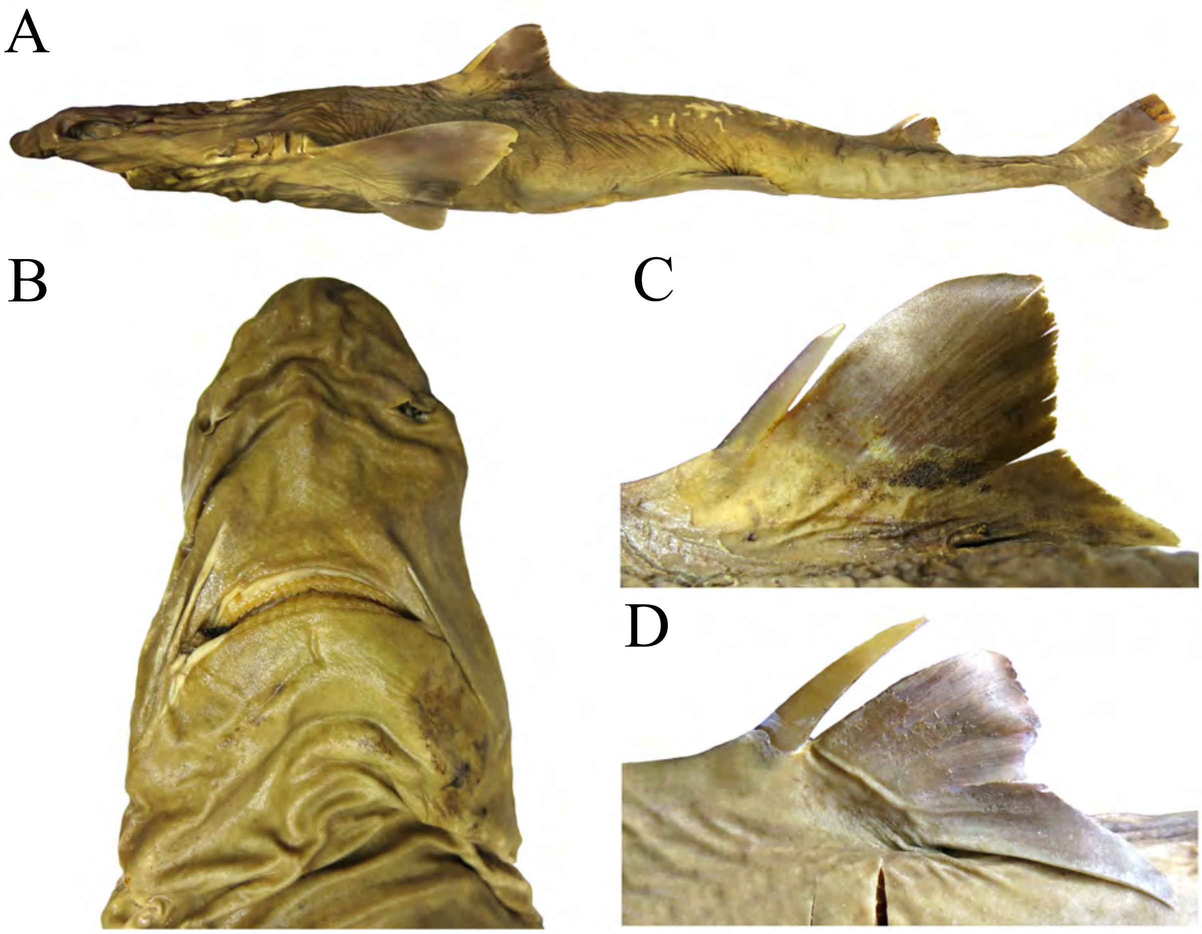

Figure 191. Holotype of *Flakeus lalannei*, HUJ 18445, adult female, 788 mm TL in lateral (A) and ventral (B) views, and detail of first (C) and second (D) dorsal fins.

Figure 192. Upper and lower teeth of holotype of *Flakeus lalannei*.

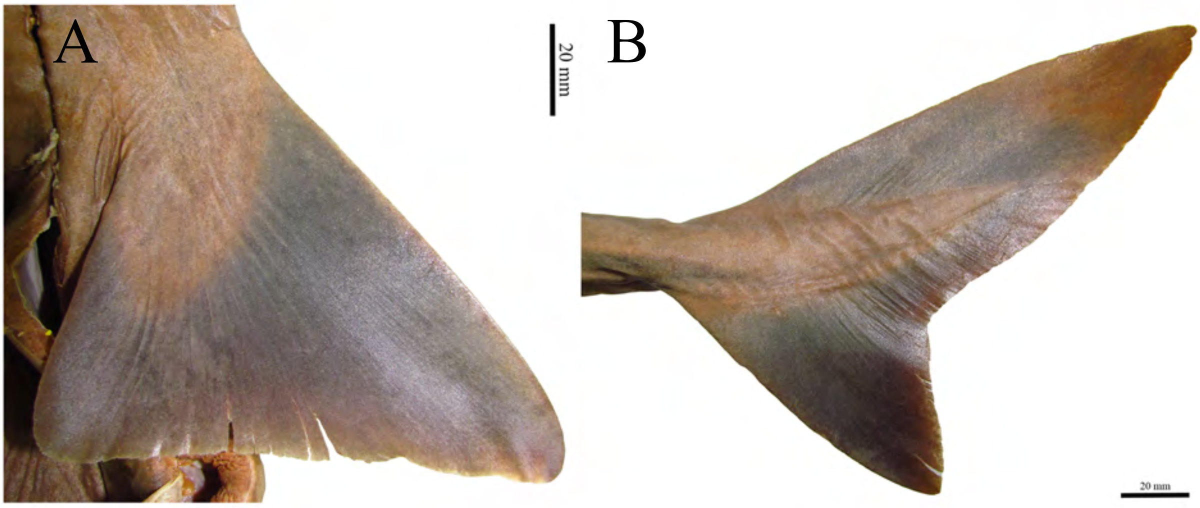

Figure 193. Pectoral (A) and caudal (B) fins of *Flakeus lalannei*, MNHN 2005-1012, adult female, 810 mm TL.

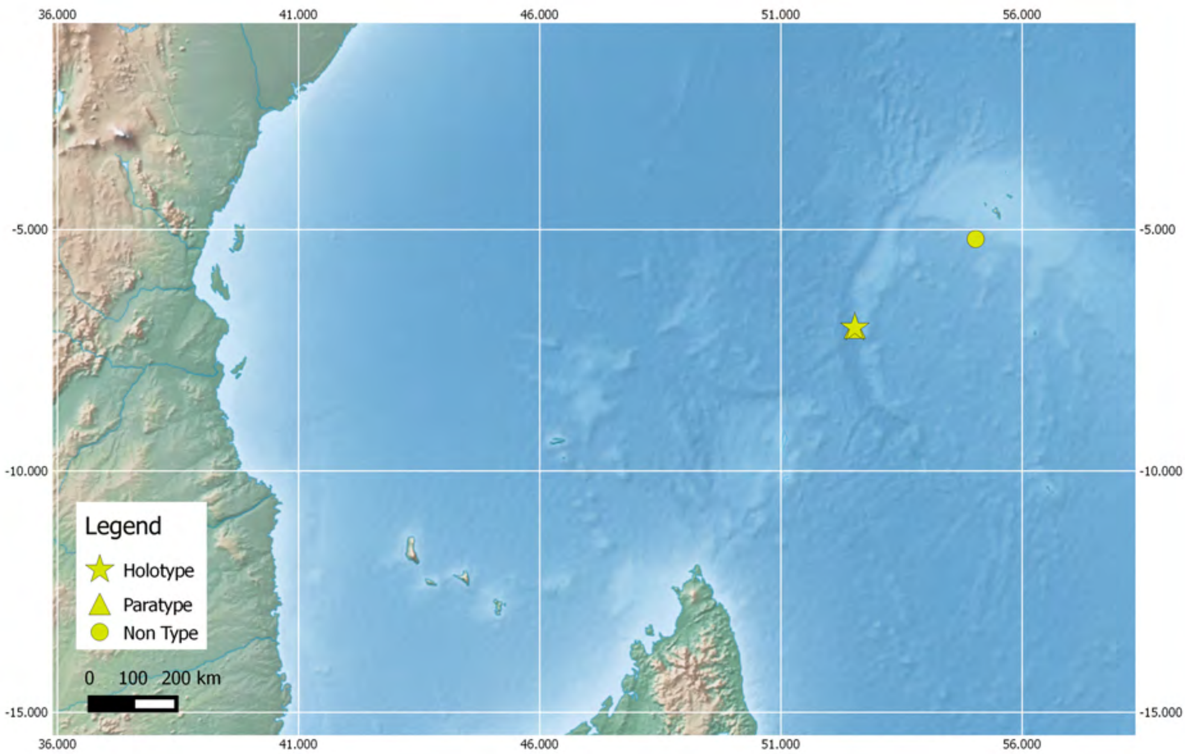

Figure 194. Map of geographical distribution of *Flakeus lalannei* in the West Indian Ocean.

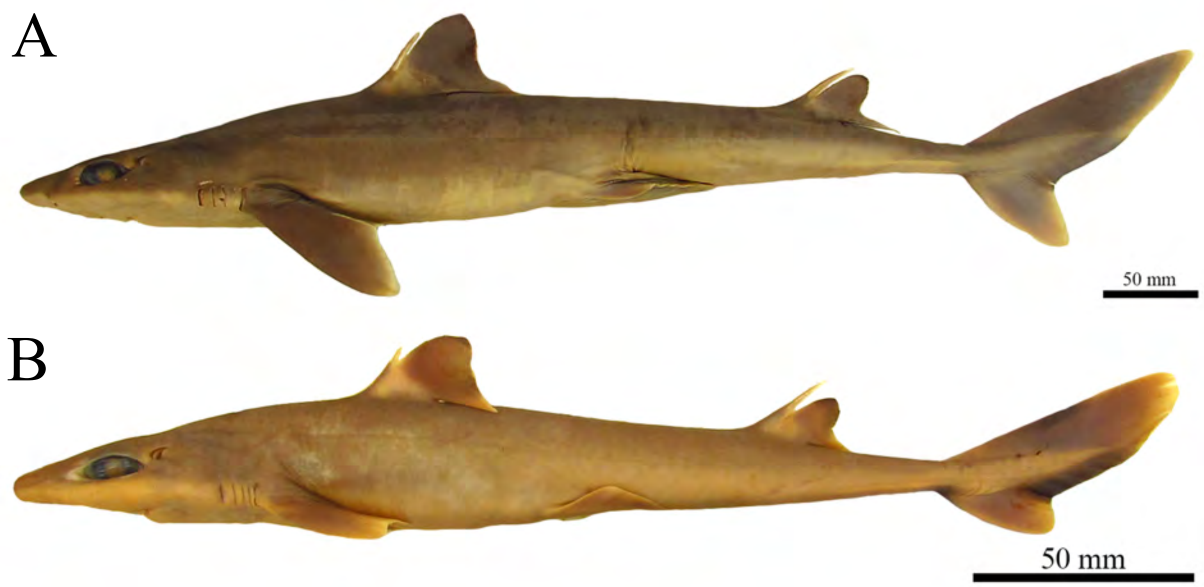

Figure 195. Types of *Flakeus grahami* in lateral view. A: holotype, CSIRO H 4476-01, adult male, 602 mm TL; B: paratype, CSIRO H 1312-9, juvenile male, 278 mm TL.

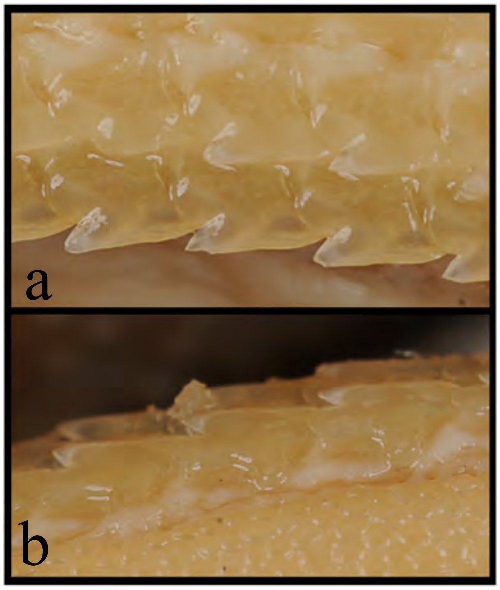

Figure 196. Upper (a) and lower (b) teeth of holotype of *Flakeus grahami*, CSIRO H 4476-01, adult male, 602 mm TL.

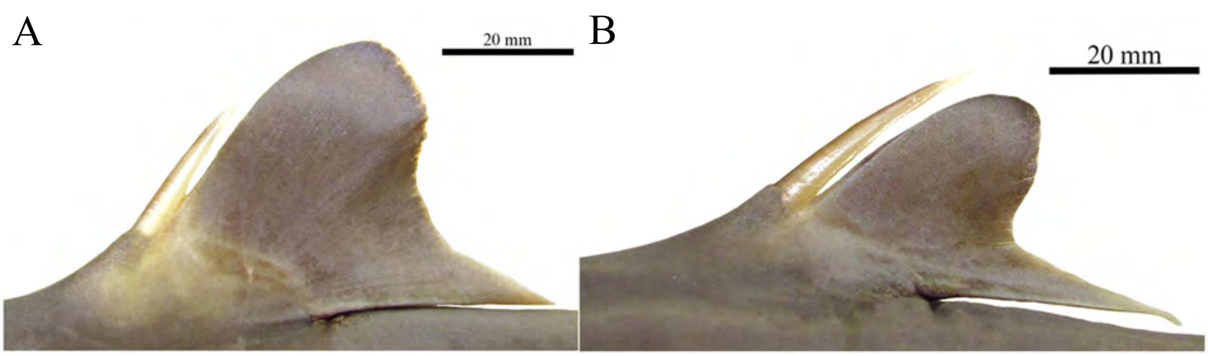

Figure 197 First (A) and second (B) dorsal fins of holotype of *Flakeus grahami*, CSIRO H 4476-01, adult male, 602 mm TL.

Figure 198. Pectoral fin of holotype of *Flakeus grahami*, CSIRO H 4476-01, adult male, 602 mm TL in ventral view.

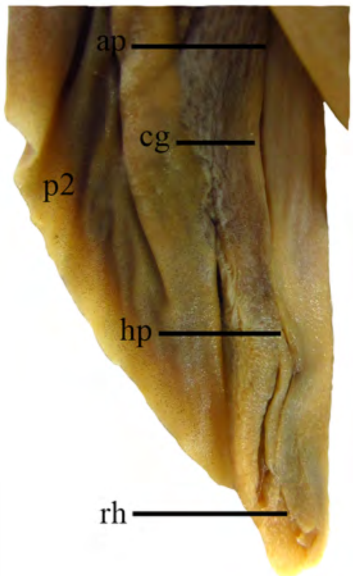

Figure 199. Clasper of holotype of *Flakeus grahami*, CSIRO H 4476-01, adult male, 602 mm TL in dorsal view. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

Figure 200. Caudal fin of *Flakeus grahami*, MZUSP not catalogued, adult male, 565 mm TL, showing black caudal bar and upper black caudal blotch.

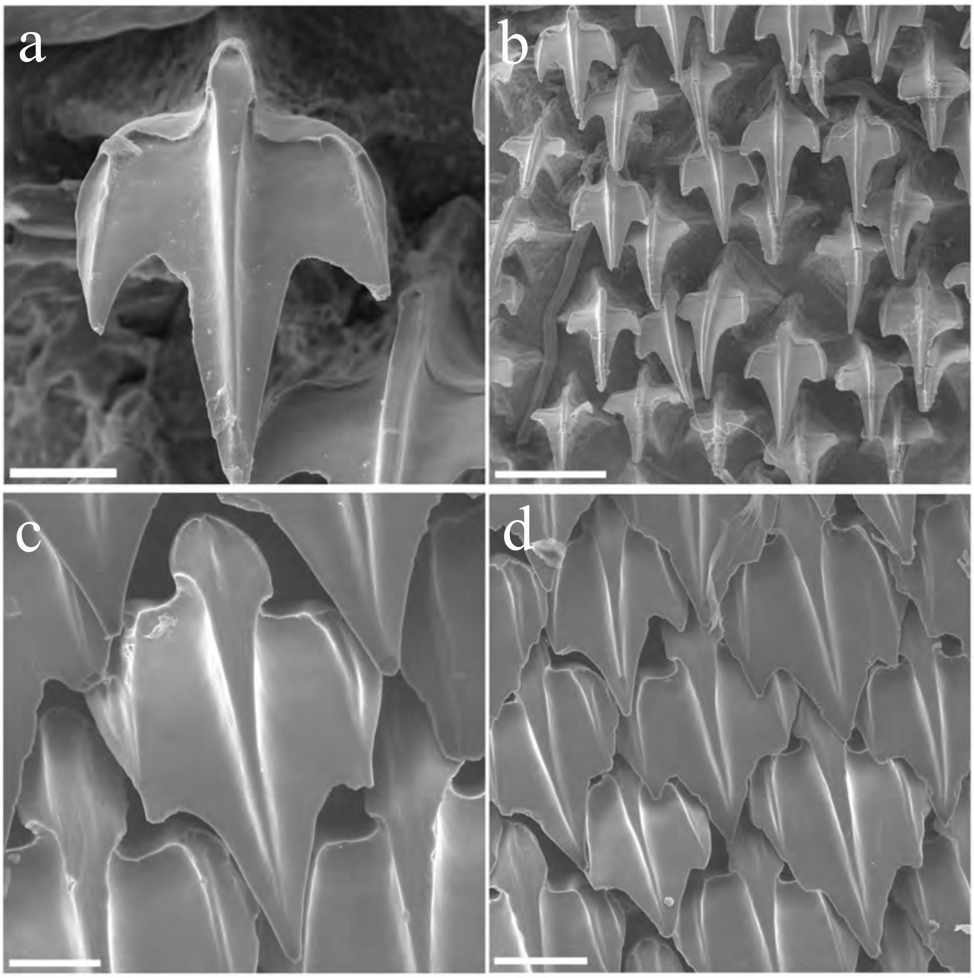

Figure 201. Scanning electron microscopy of dermal denticles of *Flakeus grahami*. a,b: AMS I 15526-002, juvenile female, 307 mm TL; c,d: MZUSP not catalogued, adult male, 565 mm TL. Scale bars: 50 µm (a,c), 100 µm (d), 200 µm (b).

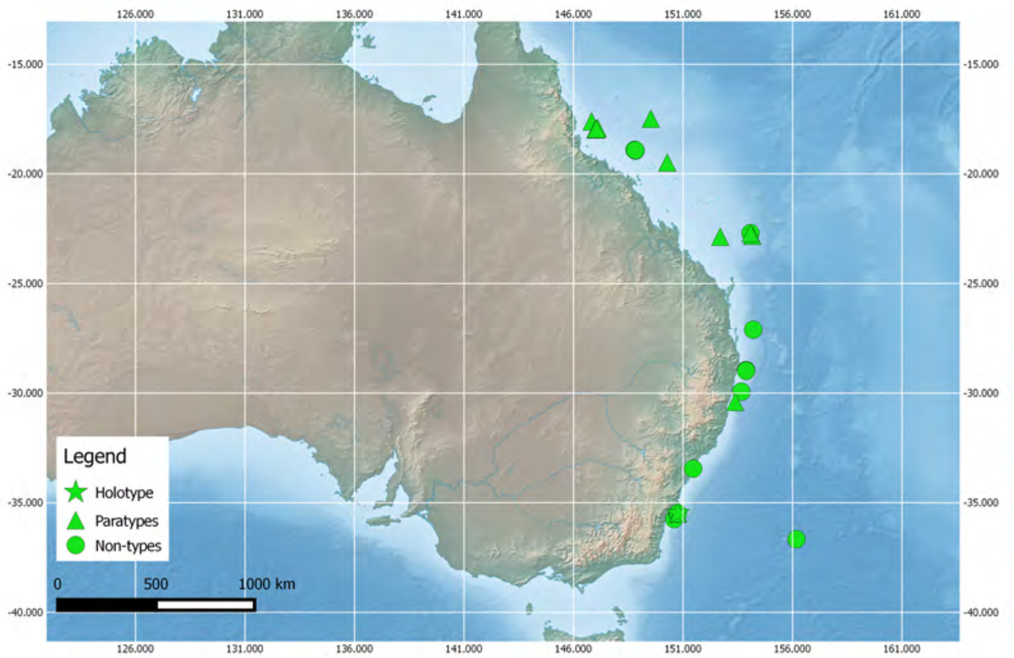

Figure 202. Map of Australia, showing the geographical distribution of *Flakeus grahami*.

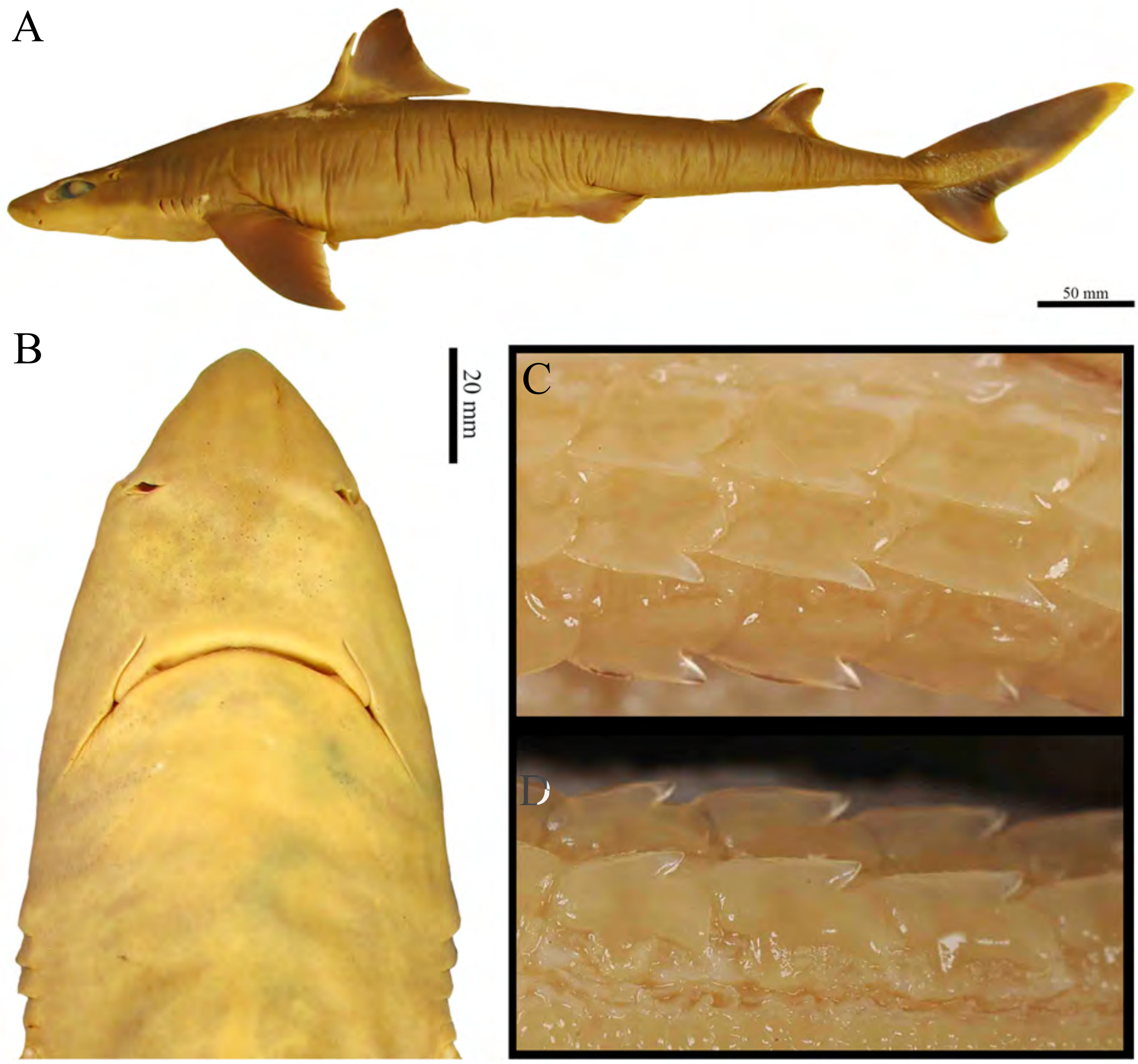

Figure 203. Holotype of *Flakeus edmundsi*, CSIRO H 2566-01, adult male, 610 mm TL in lateral (A) and ventral (B) views. Upper (C) and lower (D) teeth are also shown.

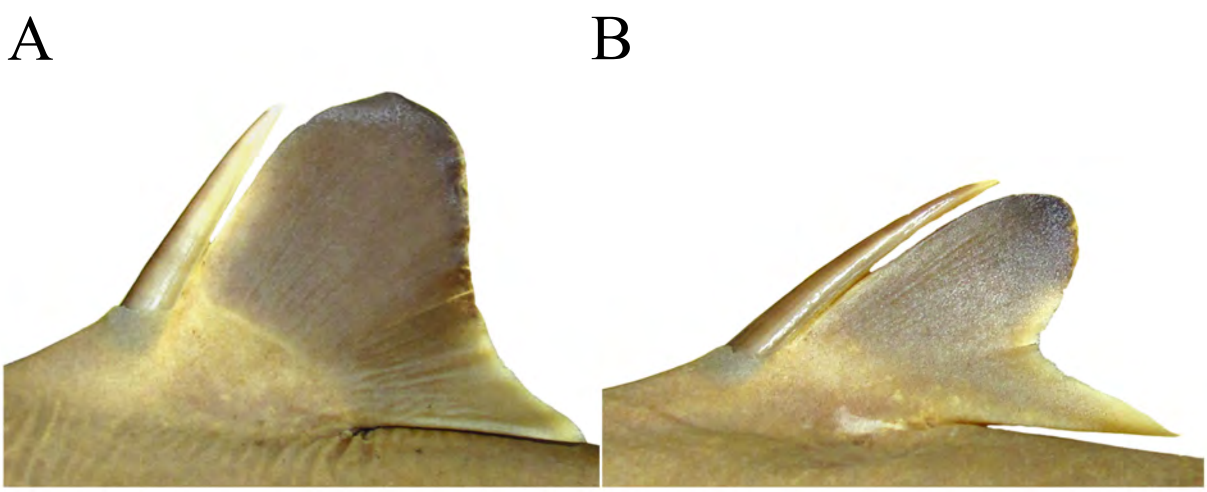

Figure 204. First (A) and second (B) dorsal fins of *Flakeus grahami*, CSIRO H 2605-07, juvenile female, 510 mm TL.

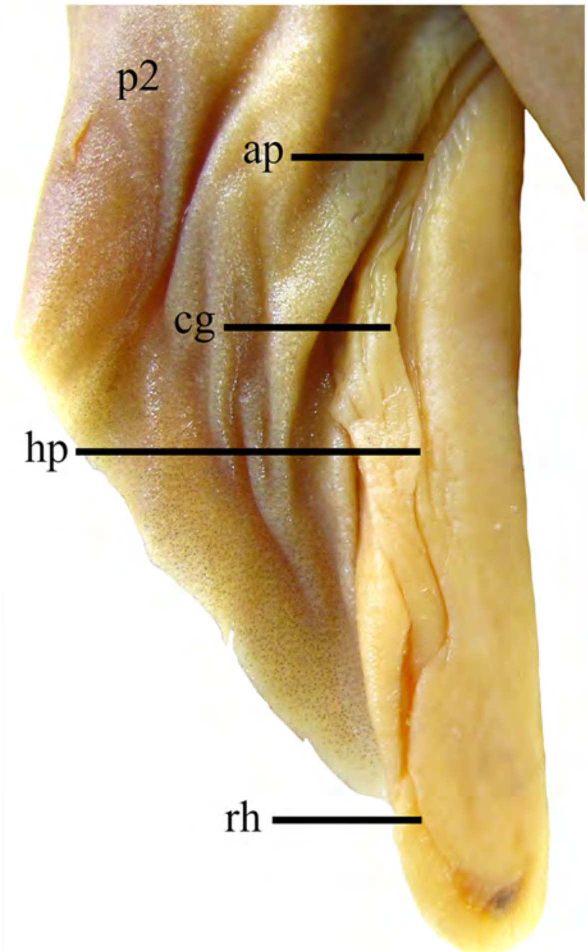

Figure 205. Clasper of holotype of *Flakeus edmundsi*, CSIRO H 2566-01, adult male, 610 mm TL in dorsal view.

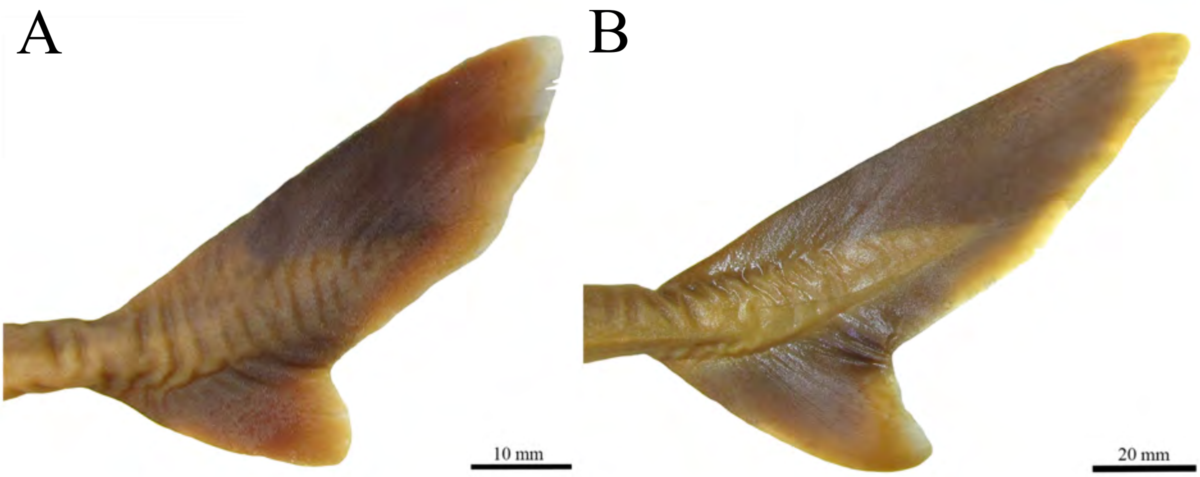

Figure 206. Caudal fin of *Flakeus edmundsi*, showing variations on dark caudal bar. A: paratype, CSIRO H 1207-06, neonate female, 299 mm TL; B: holotype, CSIRO H 2566-01, adult male, 610 mm TL.

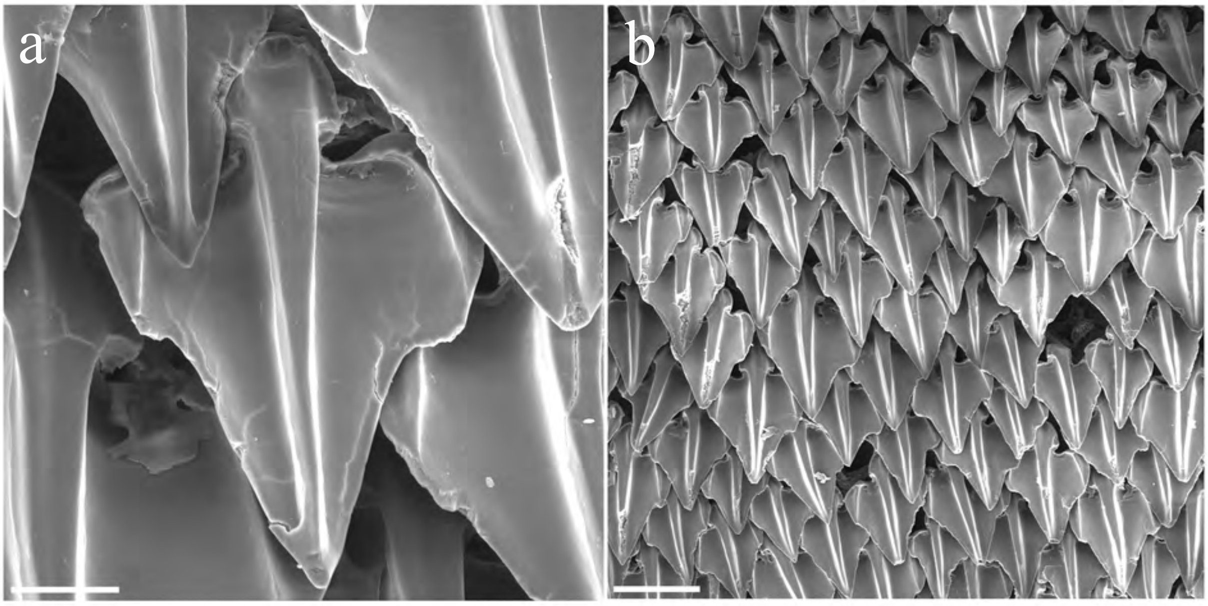

Figure 207. Dermal denticles of *Flakeus edmundsi*, CSIRO H 2619-10, adult female, 665 mm TL. Scale bars: 50 µm (a), 200 µm (b).

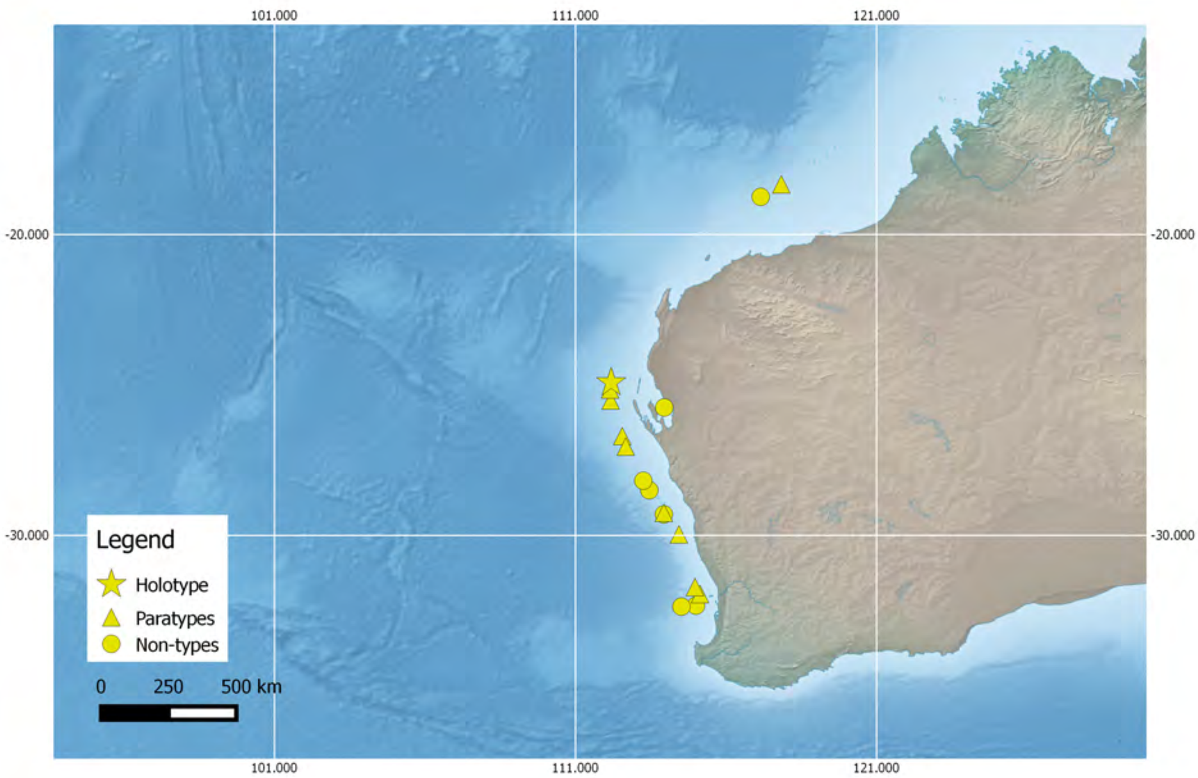

Figure 208. Map of Westerm Australia, showing the geographical distribution of *Flakeus edmundsi*.

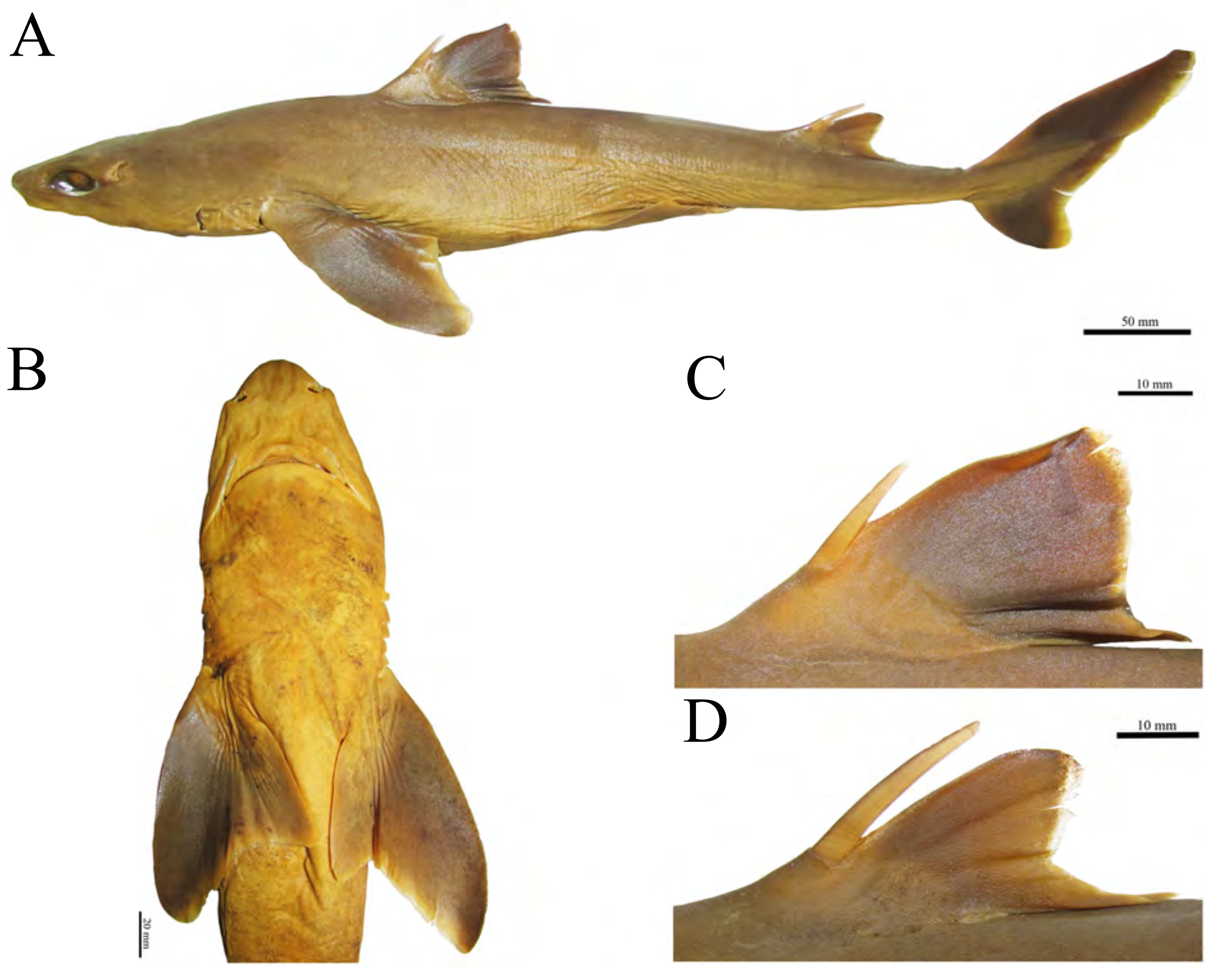

Figure 209. Holotype of *Flakeus* sp. 1, SAIAB 25389, adult male, 543 mm TL in lateral (A) and ventral (B) views, and detail of first (C) and second (D) dorsal fins.

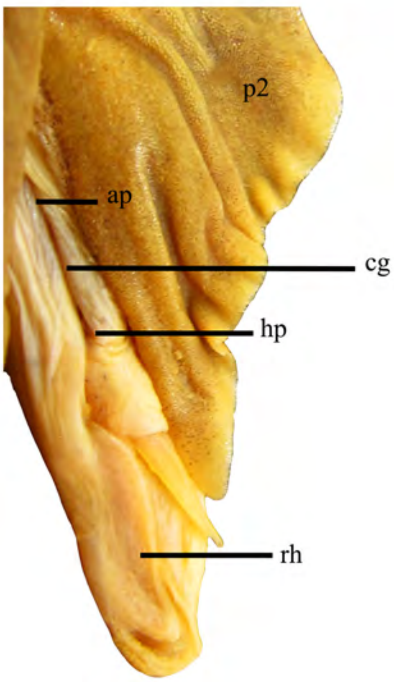

Figure 210. Clasper of paratype of *Flakeus* sp. 1, SAIAB 21858, adult male, 455 mm TL in dorsal view. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

Figure 211. Caudal fin of holotype of *Flakeus* sp. 1, SAIAB 25389, adult male, 543 mm TL.

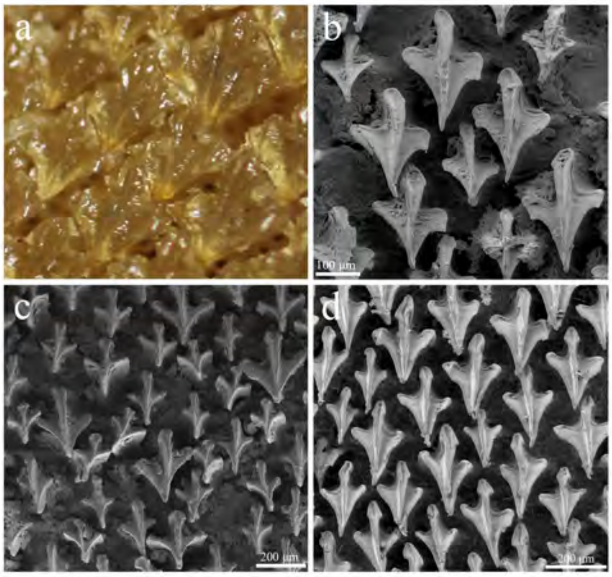

Figure 212. Dermal denticles of *Flakeus* sp. 1: a: BMNH 1900.11.6.14, female, 565 mm TL, paralectotype of *Flakeus acutipinnis*; and scanning electron microscopy: b: paratype of *Flakeus* sp. 1, SAIAB 21858, male, 455 mm TL; c: BMNH 1912.12.10.45-46, female, 441 mm TL; d: SAM 12992, male, 535 mm TL.

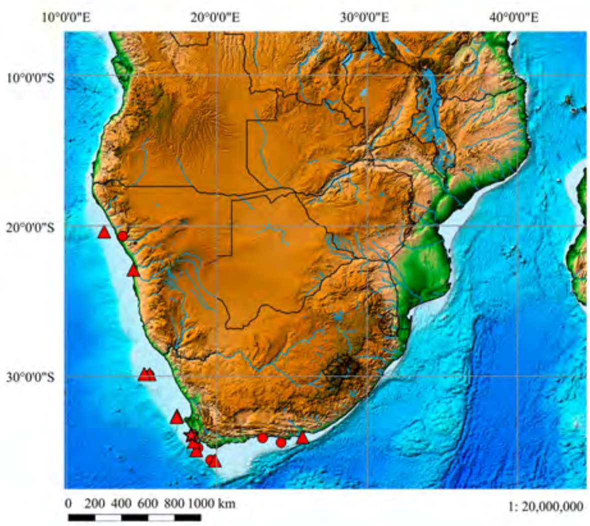

Figure 213. Map of geographical distribution of *Flakeus* sp. 1, showing the location of its holotype (red star), paratypes (red triangle) and non-type specimens (red dots) in the Eastern Atlantic and West Indian Oceans.

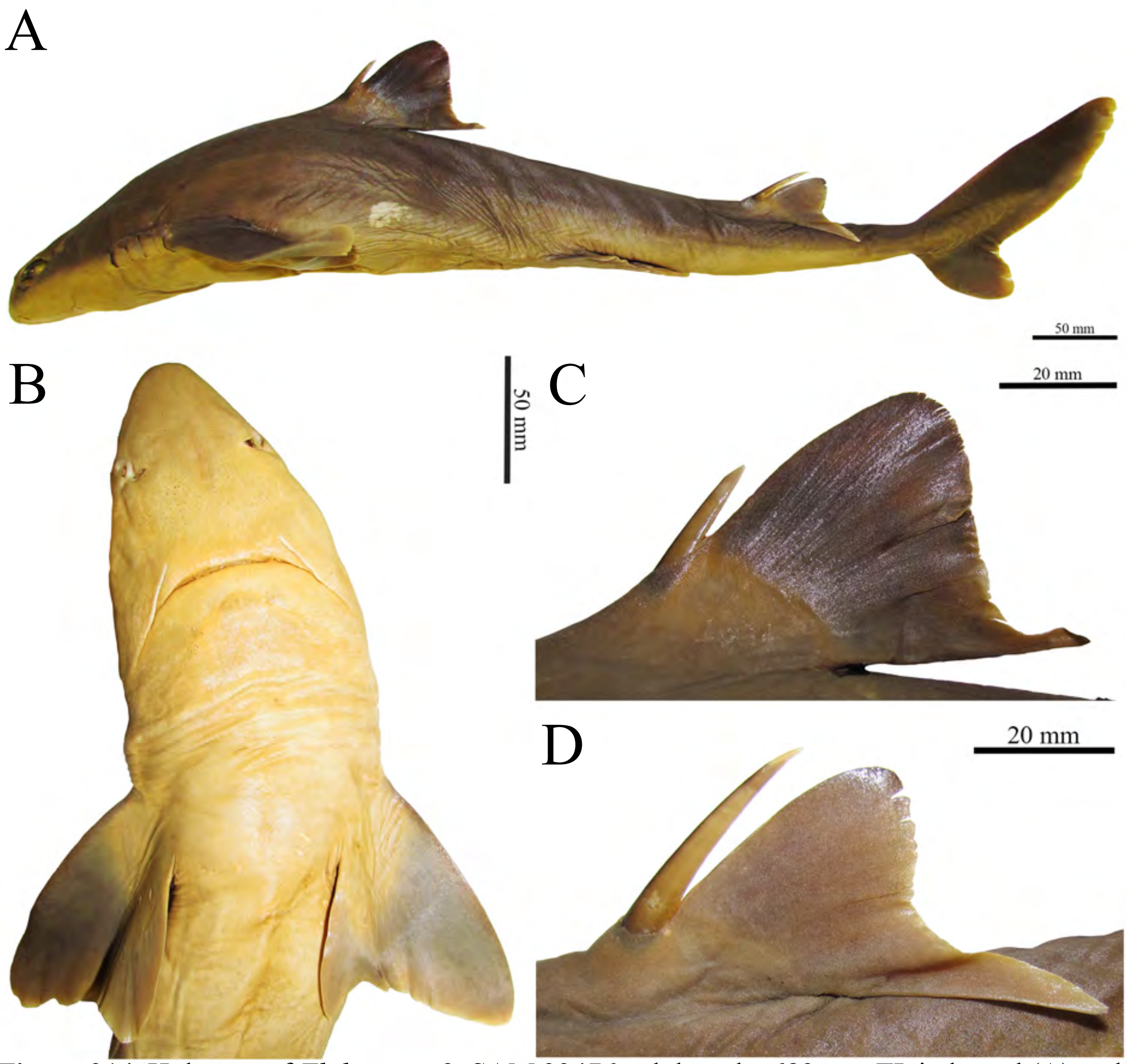

Figure 214. Holotype of *Flakeus* sp. 2, SAM 33476, adult male, 683 mm TL in lateral (A) and ventral (B) views, and detail of first (C) and second (D) dorsal fins.

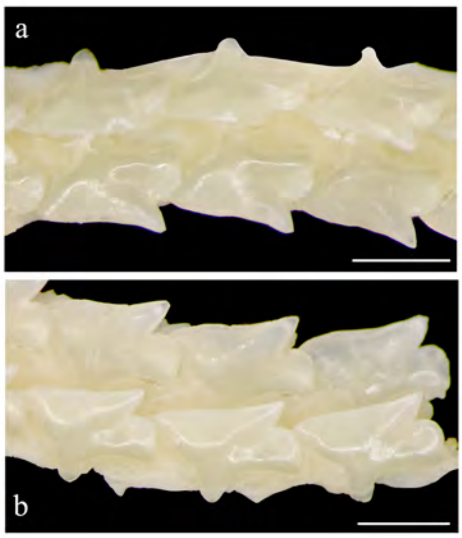

Figure 215. Upper (a) and lower (b) teeth of *Flakeus* sp. 2, SAM 34004, adult female, 740 mm TL. Scale bar: 2 mm.

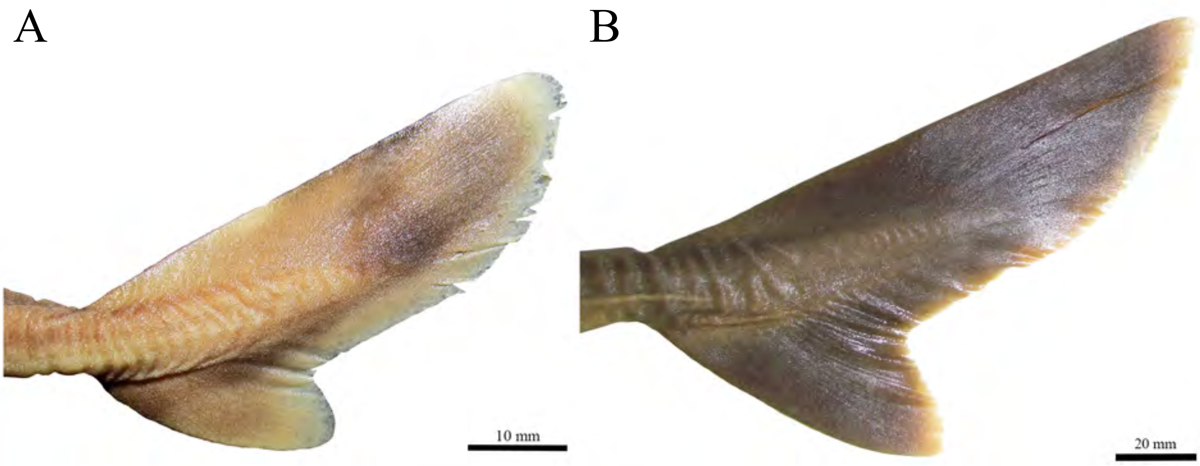

Figure 216. Caudal fin of *Flakeus* sp. 2, showing variations with growth in coloration. A: SAM 38334, juvenile male, 282 mm TL; B: paratype, SAM 34004, adult male, 700 mm TL.

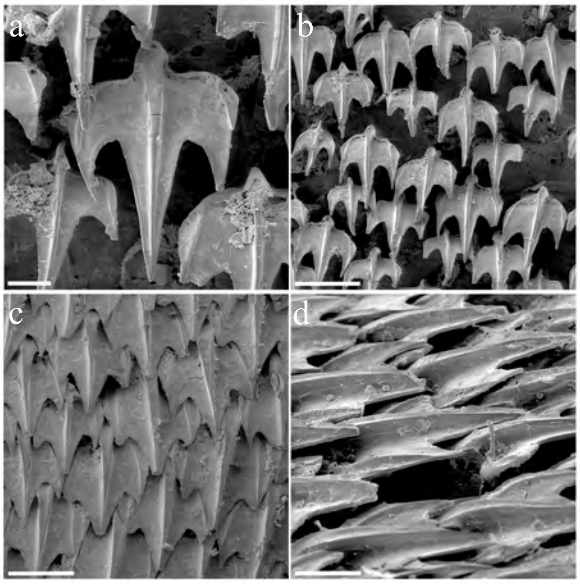

Figure 217. Scanning electron microscopy of dermal denticles of *Flakeus* sp. 2. a,b: SAIAB 26419, juvenile female, 450 mm TL; c,d: SAM SAM 32611, adult male, 695 mm TL. Scale

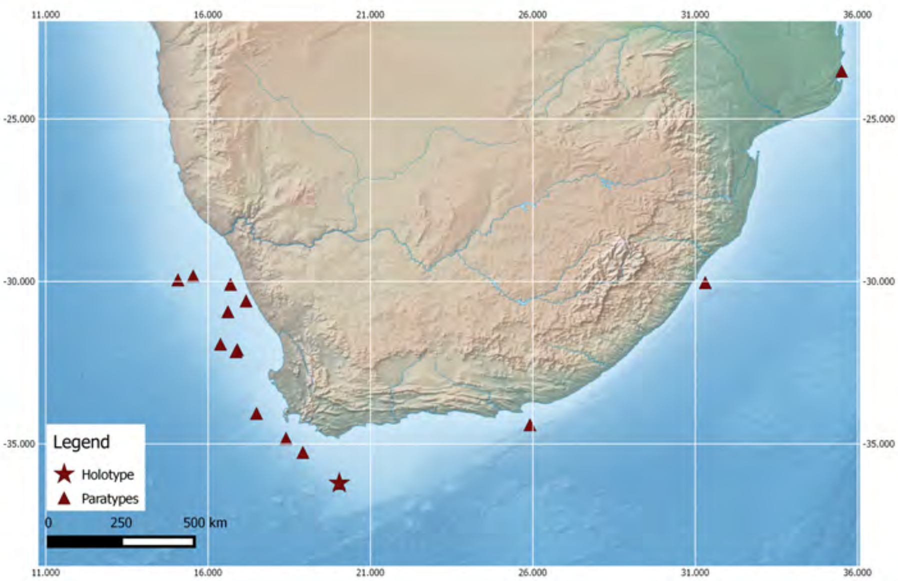

Figure 218. Geographical distribution of *Flakeus* sp. 2 in Southern Africa.

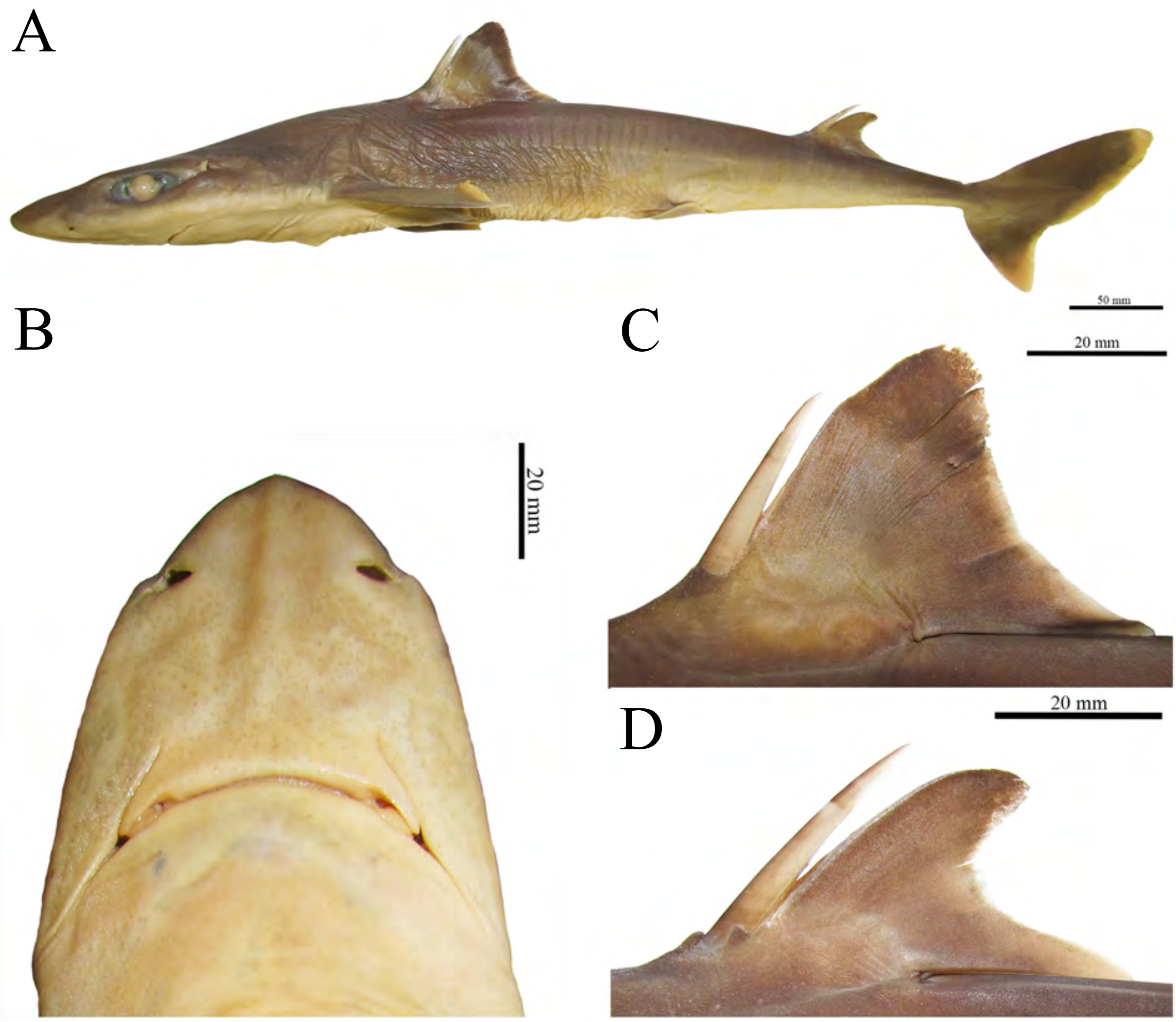

Figure 219. Holotype of *Flakeus* sp. 3, SAIAB 189449, adult female, 590 mm TL in lateral (A) and head ventral (B) views, and detail of first (C) and second (D) dorsal fins.

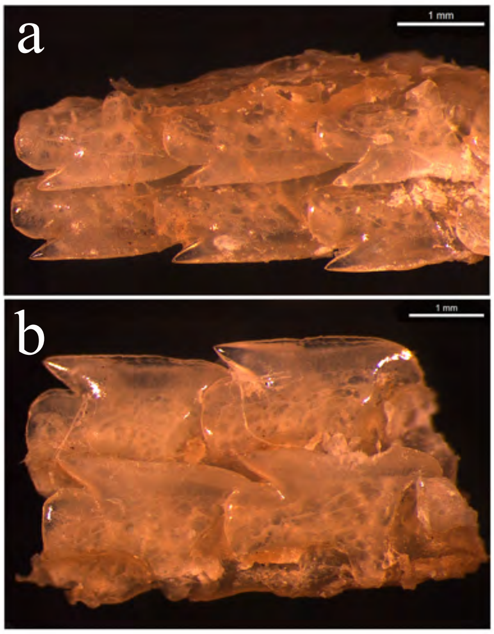

Figure 220. Upper (a) and lower (b) teeth of paratype of *Flakeus* sp. 3, SAIAB 189449, juvenile female, 513 mm TL. Scale bar: 1 mm.

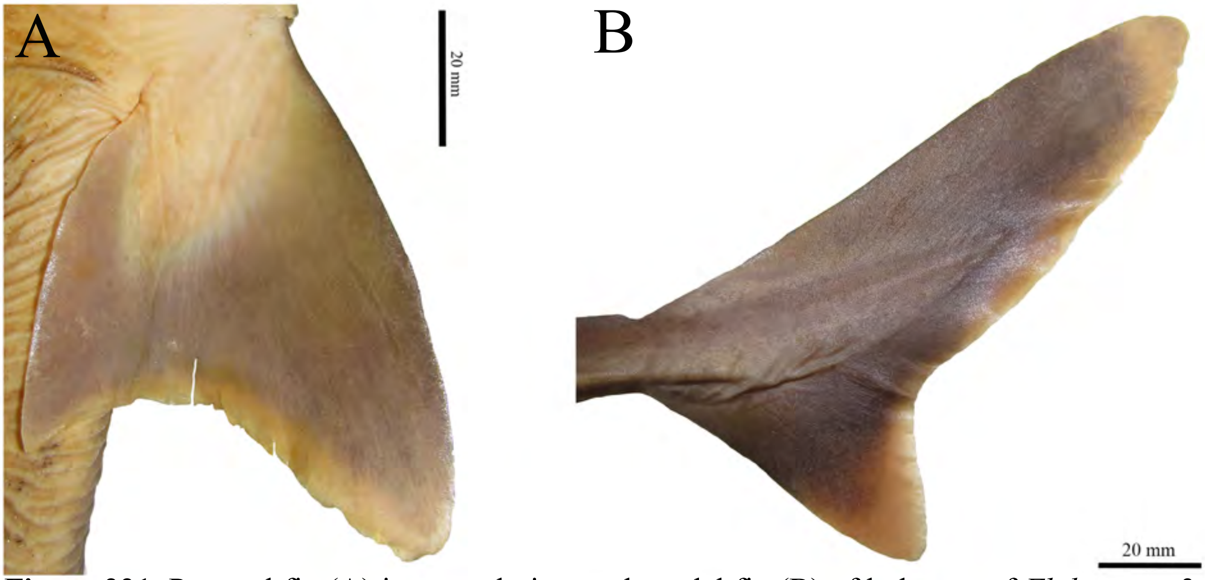

Figure 221. Pectoral fin (A) in ventral view and caudal fin (B) of holotype of *Flakeus* sp. 3, SAIAB 189449, adult female, 590 mm TL.

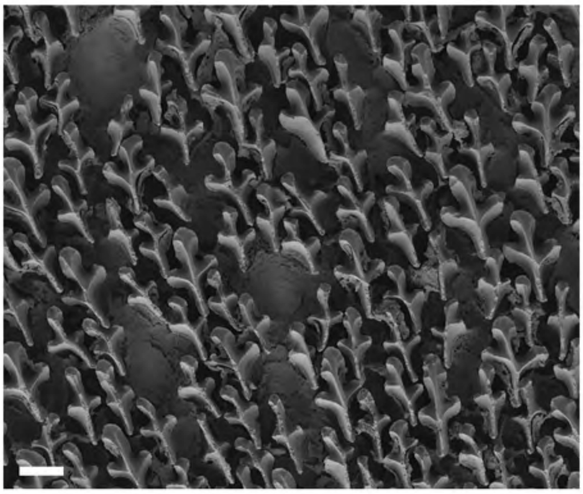

Figure 222. Scanning electron microscopy of paratype of *Flakeus* sp. 2, SAIAB 189449, juvenile female, 513 mm TL, showing shape of dermal denticles. Scale bar: 100 µm.

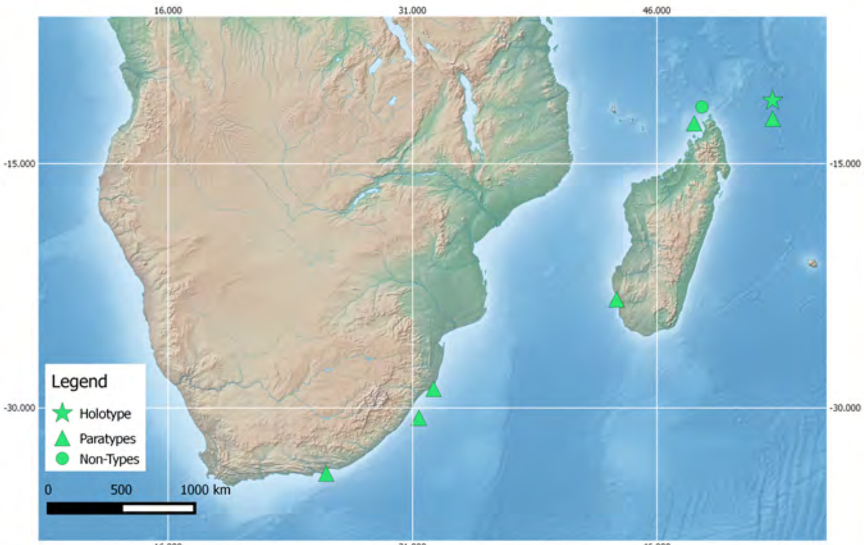

Figure 223. Geographical distribution of *Flakeus* sp. 3 in Southern Africa.

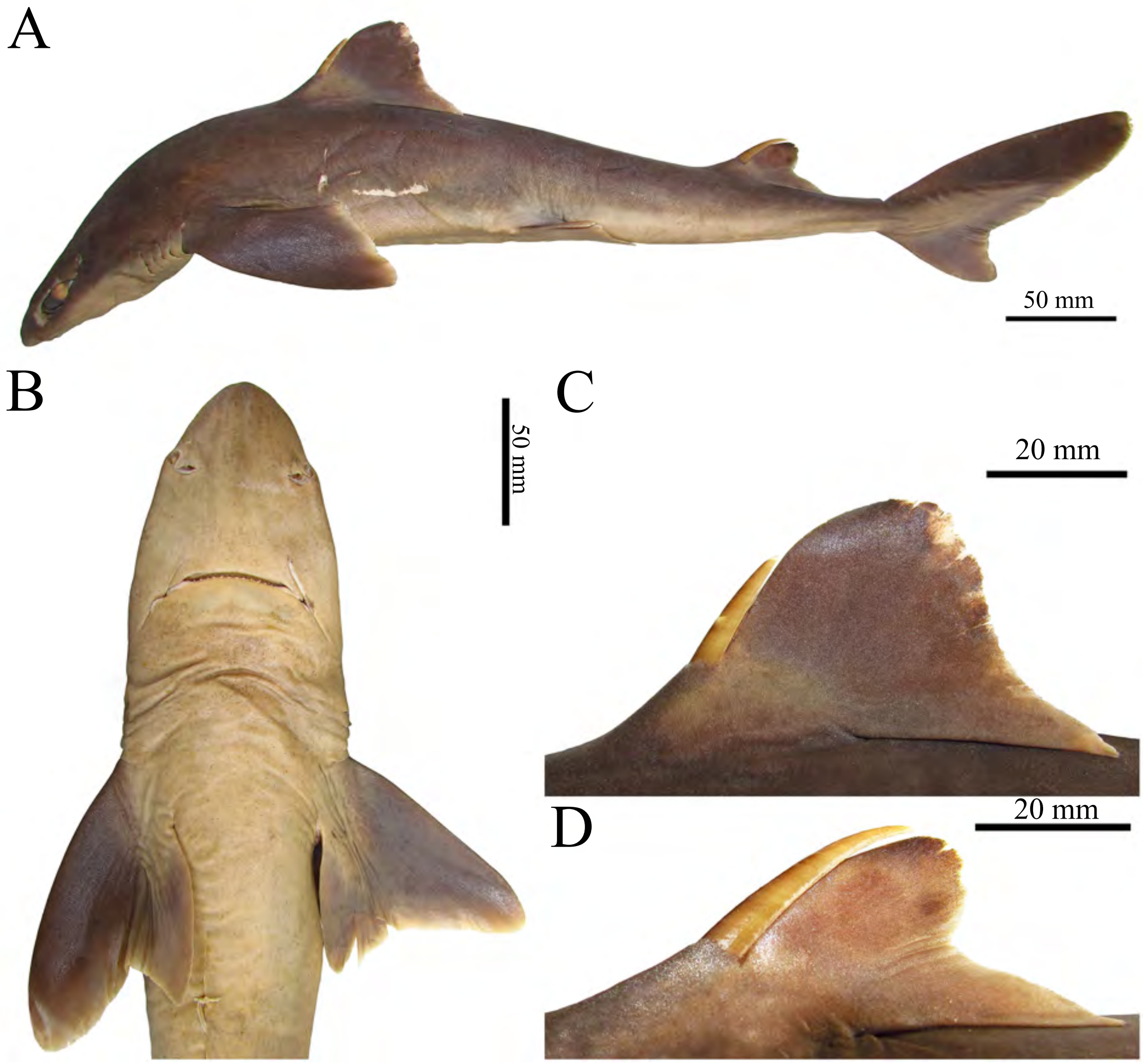

Figure 224. Holotype of *Flakeus* sp. 4, HUMZ 91806, juvenile female, 557 mm TL. A: lateral view; B: ventral view; C: first dorsal fin; D: second dorsal fin.

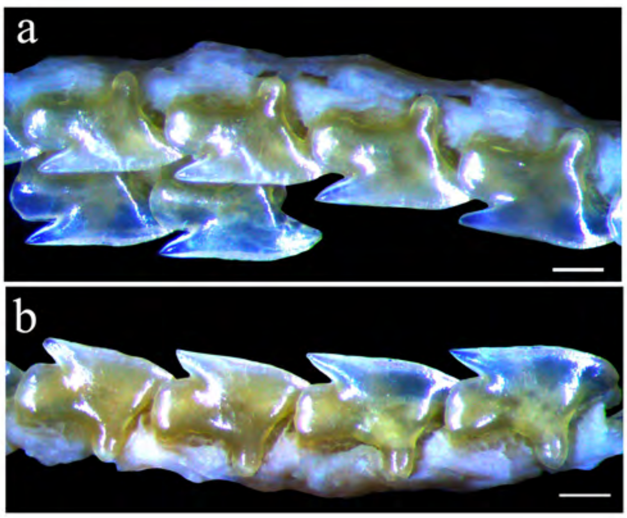

Figure 225. Upper (a) and lower (b) teeth of holotype of *Flakeus* sp. 4, HUMZ 91806, juvenile female. Scale bar: 1 mm.

Figure 226. Detail of caudal fin of holotype of *Flakeus* sp. 4, HUMZ 91806, juvenile female.

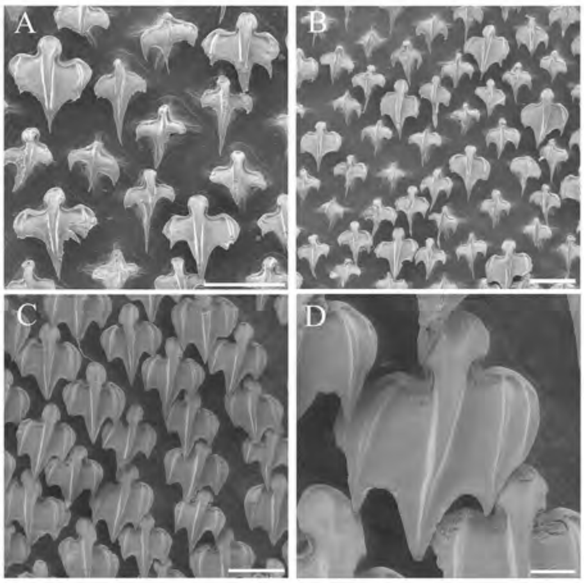

Figure 227. Dermal denticles of *Flakeus* sp. 4: a,b: holotype, HUMZ 91806, juvenile female; c,d: paratype, UERJ 1661, adult male. Scale bars: 200 µm (a-c); 50 µm (d).

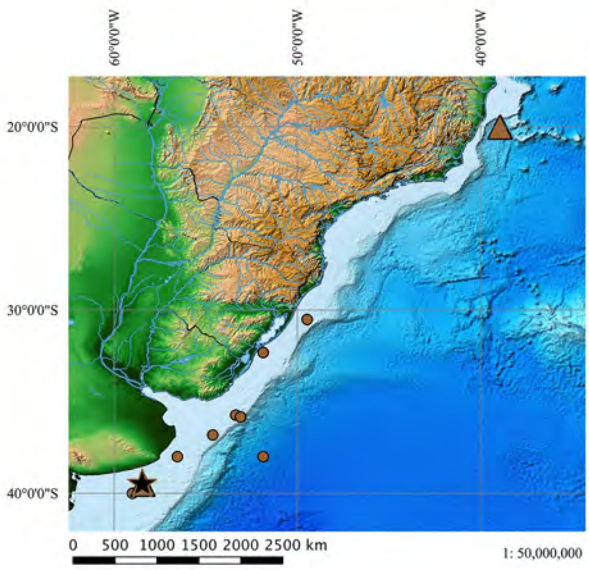

Figure 228. Map of geographical distribution *Flakeus* sp. 4 in the Southwestern Atlantic Ocean. Black star: location of holotype; brown triangle: location of paratypes; brown circle: location of non-type specimens.

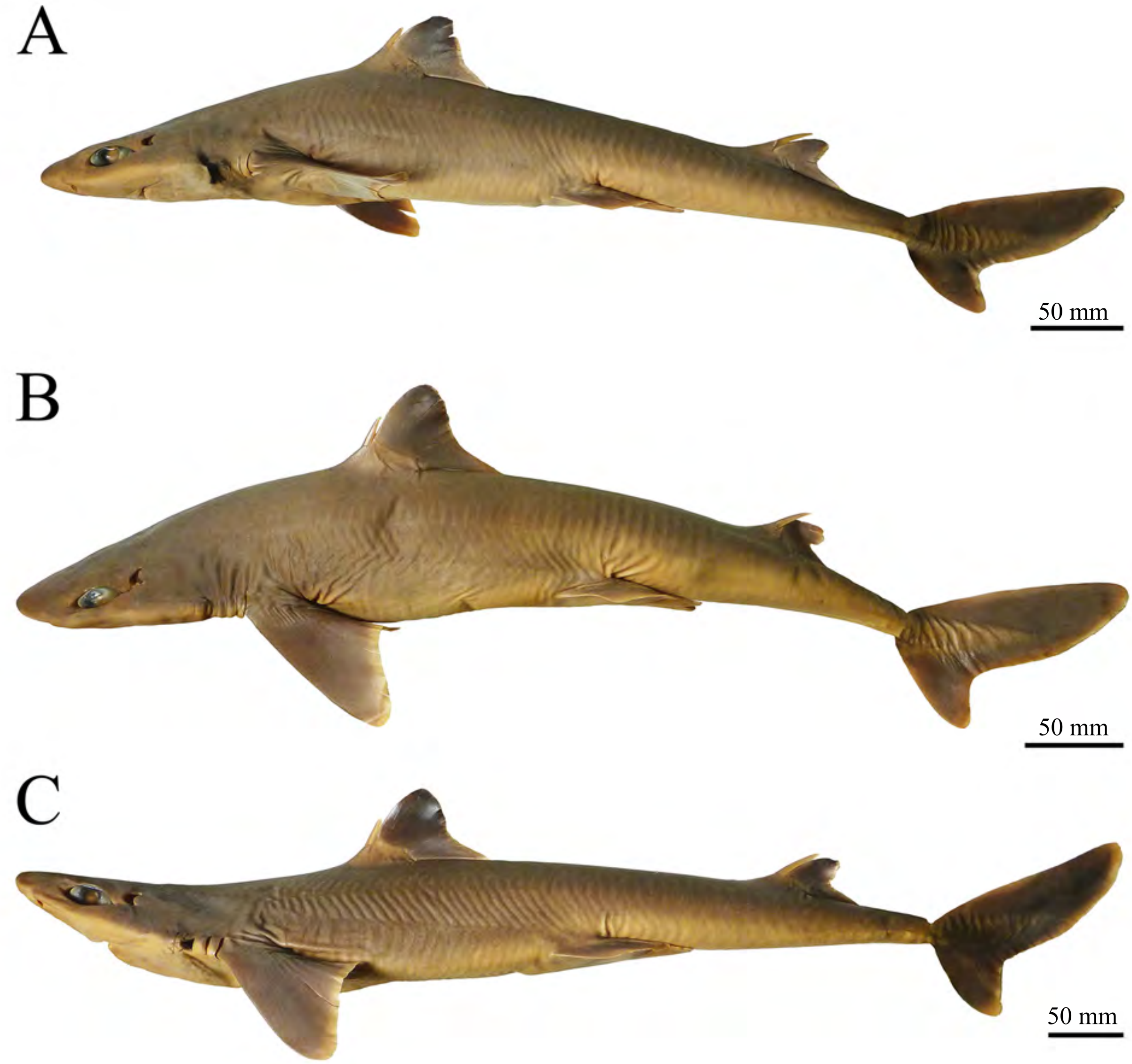

Figure 229. *Flakeus* sp. 5 in lateral view. A) holotype, MNRJ 30180, adult male, 590 mm TL; B) paratype, MNRJ 30178, adult male, 615 mm TL; C) paratype, MNRJ 30179, adult male, 690 mm TL.

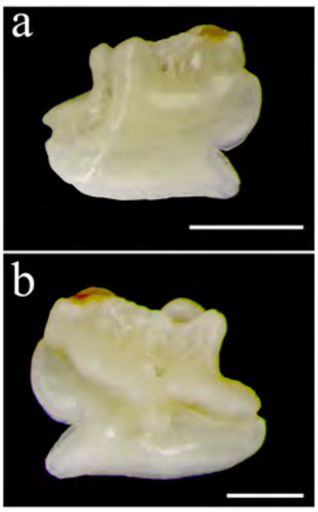

Figure 230. Upper tooth of paratype of *Flakeus* sp. 5 in labial (a) and lingual (b) views, MNRJ 30179, adult male, 690 mm TL. Scale bar: 2 mm.

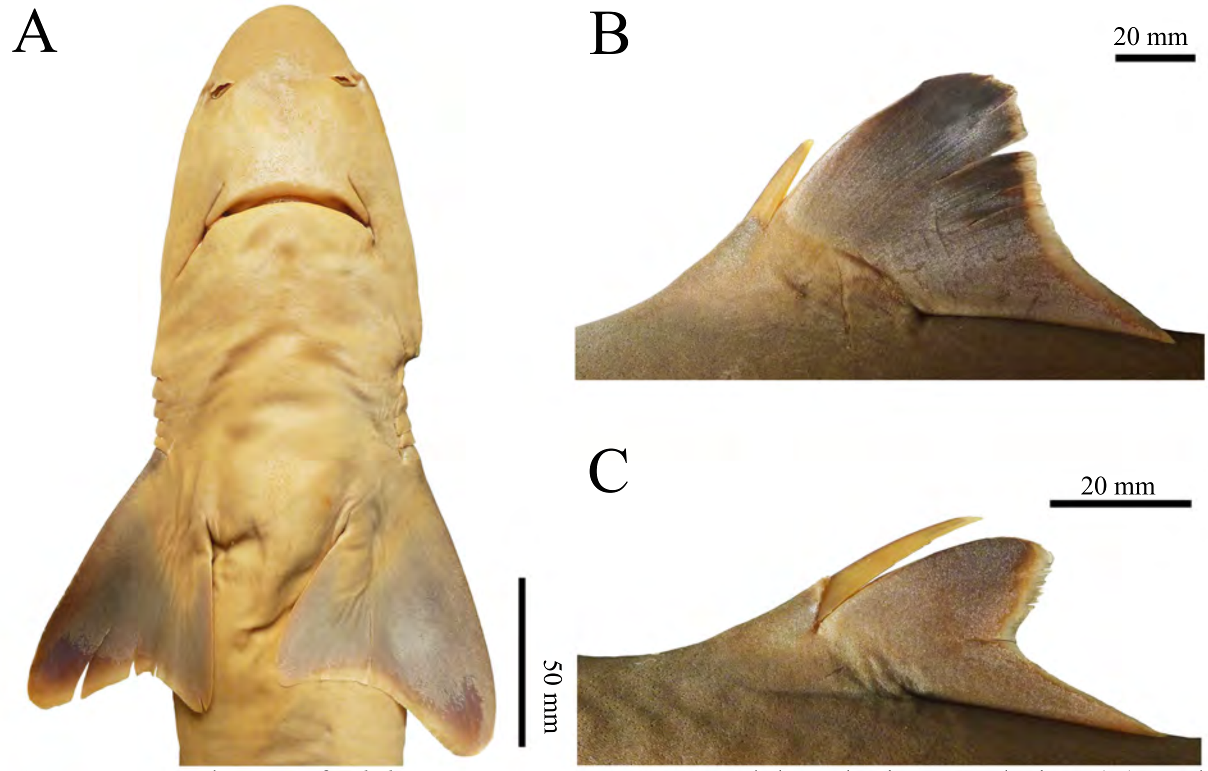

Figure 231. Holotype of *Flakeus* sp. 5, MNRJ 30180, adult male, in ventral view (A), and detail of first (B) and second (C) dorsal fins.

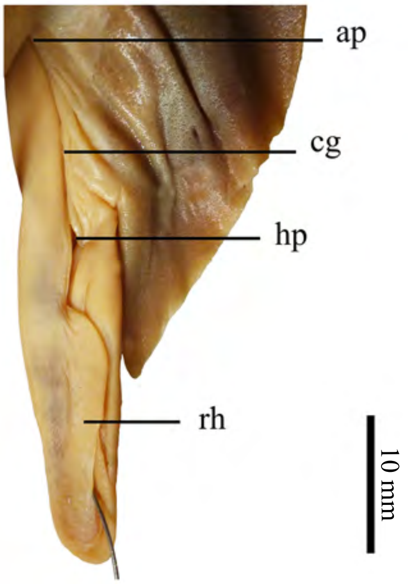

Figure 232. Clasper of holotype of *Flakeus* sp. 5, MNRJ 30180, adult male, 590 mm TL in dorsal view, showing its external morphology. Abbreviations: apopyle (ap); clasper groove (cg); hypopyle (hp); pelvic fin (p2); rhipidion (rh).

Figure 233. Caudal fin of holotype of *Flakeus* sp. 5, MNRJ 30180, adult male, 590 mm TL.

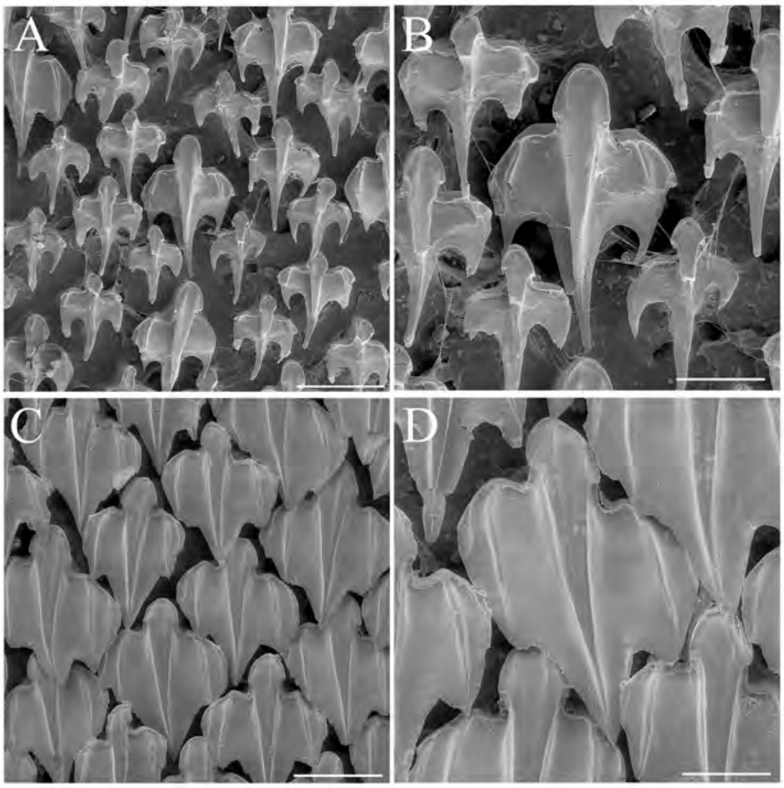

Figure 234. Dermal denticles of *Flakeus* sp. 5. a,b: holotype, MNRJ 30180; c,d: paratype, MNRJ 30178. Scale bars: 200 µm (a,c); 100 µm (b,d).

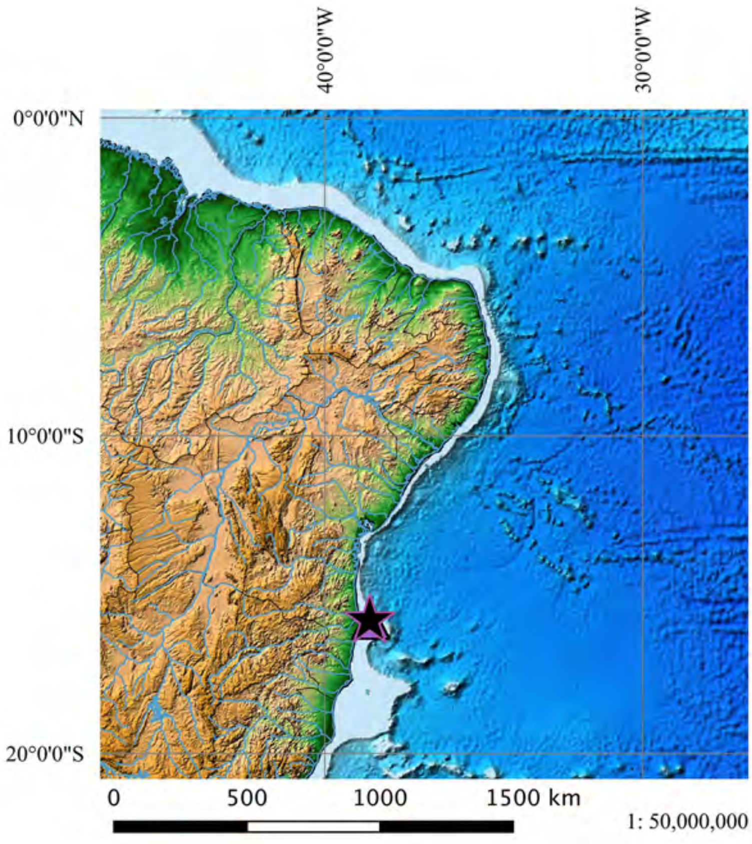

Figure 235. Map of the Southwestern Atlantic Ocean, showing the geographical distribution of *Flakeus* sp. 5. Black star: location of holotype; purple triangle: location of paratypes.

Figure 236. Holotype of *Flakeus* sp. 6, UERJ 1111, adult female, 700 mm TL in lateral view.

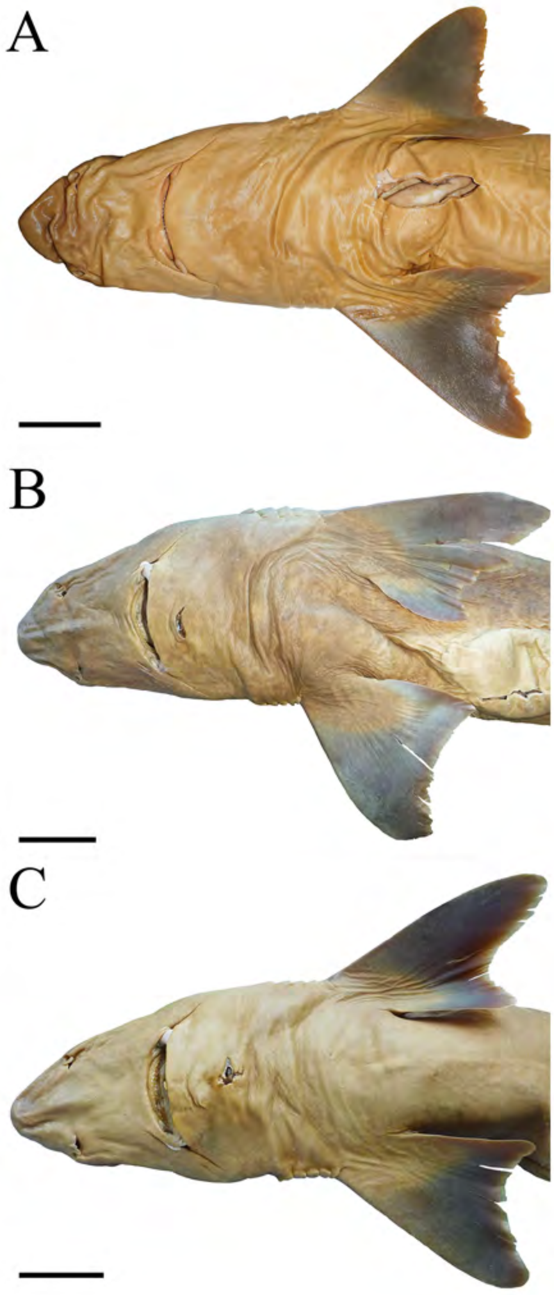

Figure 237. *Flakeus* sp. 6 in ventral view. A: holotype, UERJ 1111, adult female, 700 mm TL; B: paratype, UERJ 1741, adult female, 850 mm TL; C: paratype, UERJ 1819, adult female, 740 mm TL. Scale bar: 50 mm.

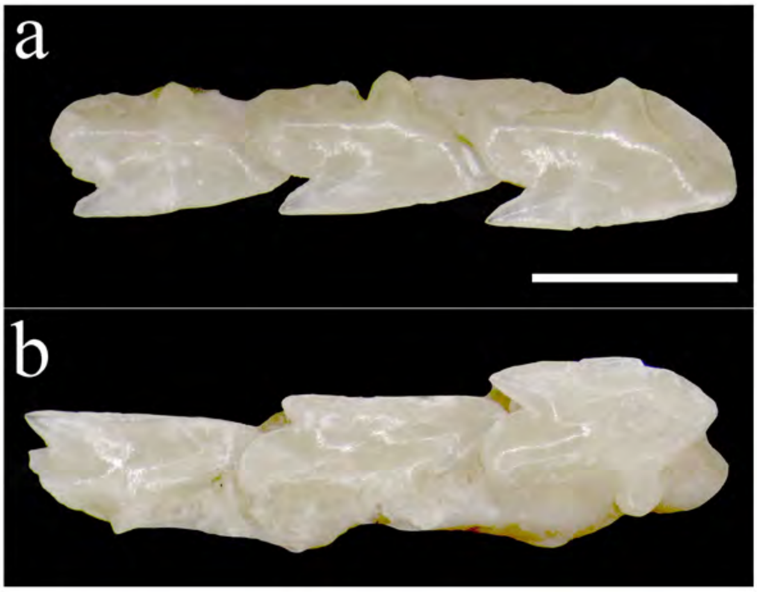

Figure 238. Upper (a) and lower (b) teeth of holotype of *Flakeus* sp. 6. Scale bar: 2 mm.

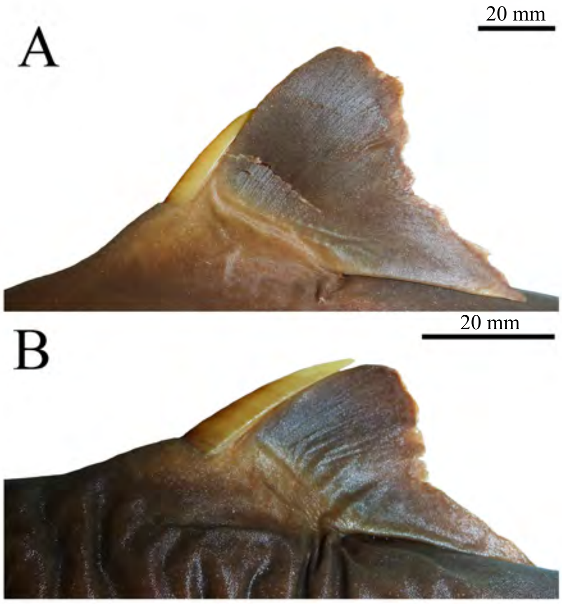

Figure 239. First dorsal fin (A) and second dorsal fin (B) of holotype of *Flakeus* sp. 6, UERJ 1111, adult female.

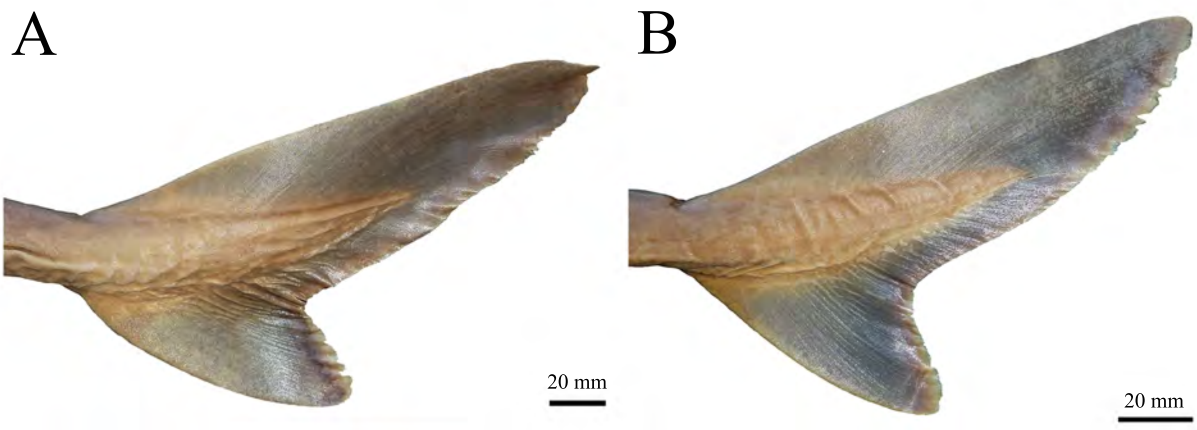

Figure 240. Caudal fin of *Flakeus* sp. 6. A: paratype, UERJ 1741, adult female; B: paratype, UERJ 1819, adult female.

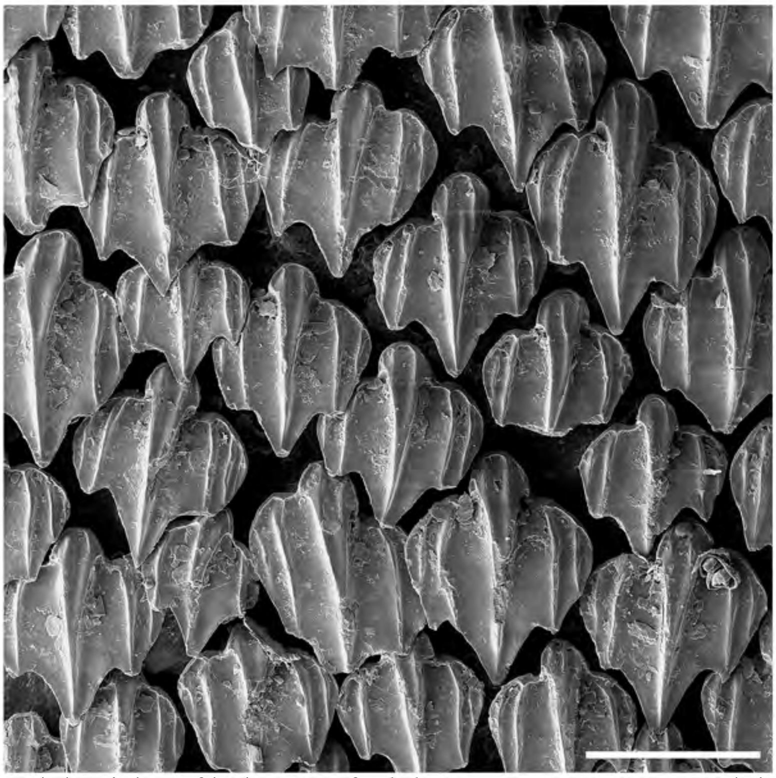

Figure 241. Dermal denticles of holotype of *Flakeus* sp. 6, UERJ 1111, adult female, 700 mm TL. Scale bar: 200 µm.

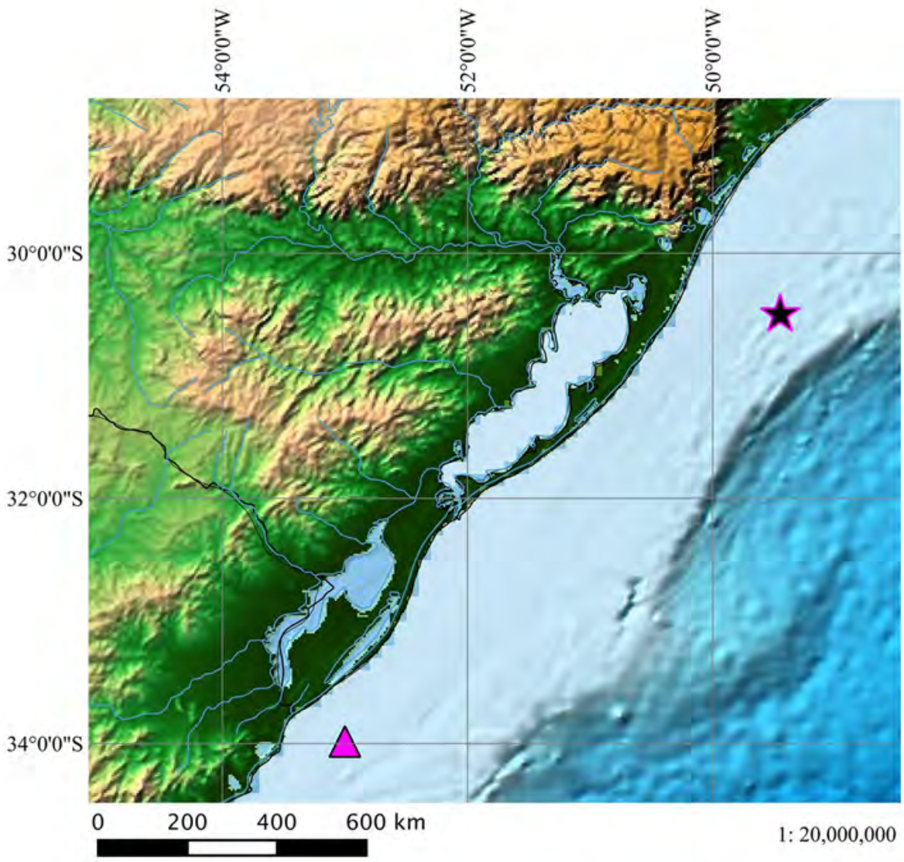

Figure 242. Map of the Southwestern Atlantic Ocean, showing the type locality of *Flakeus* sp. 6. Black star: location of holotype; magenta triangle: location of its paratypes.

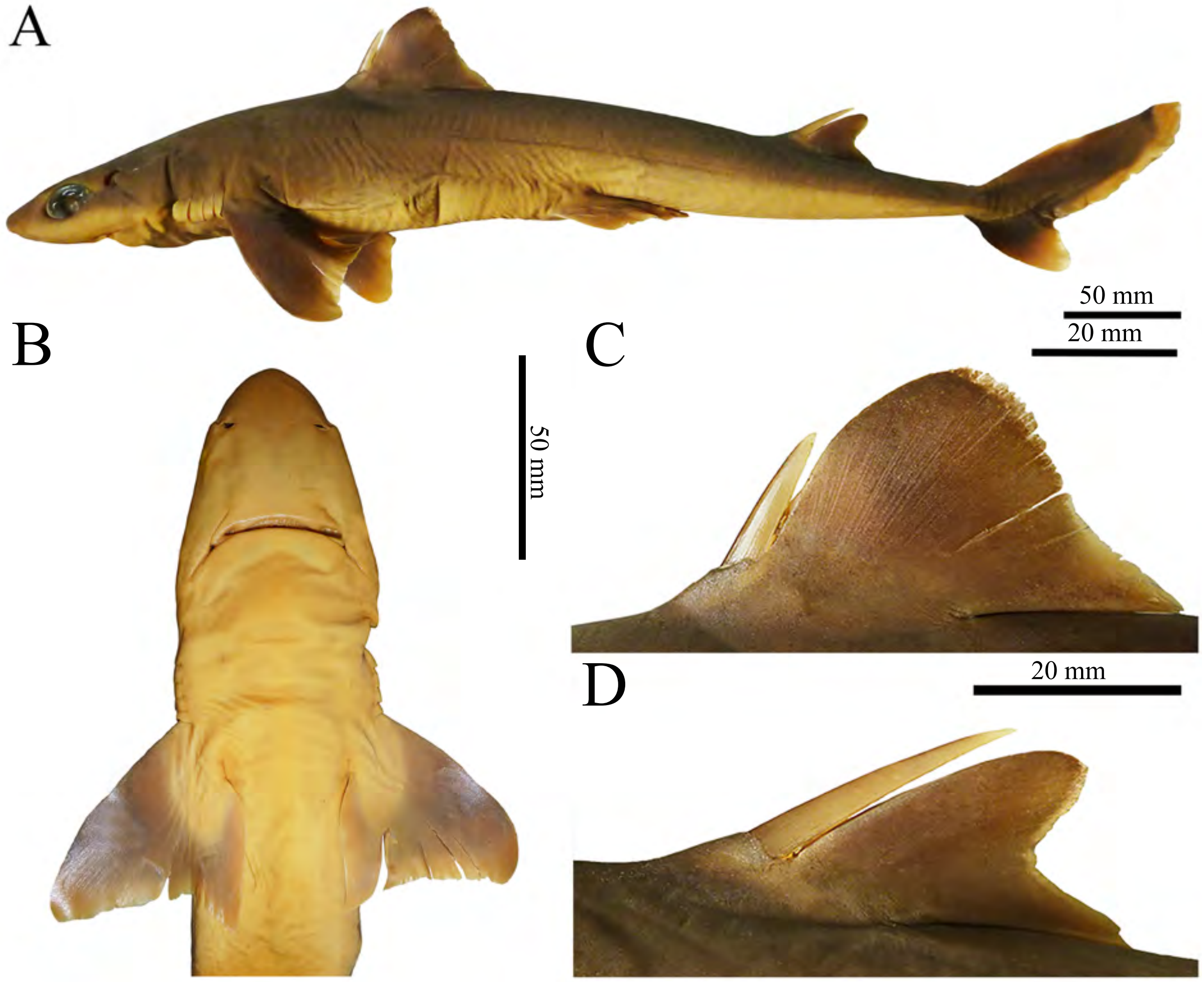

Figure 243. Holotype of *Flakeus* sp. 7, MNRJ 30188, adult male, 525 mm TL in lateral (A) and ventral (B) views, and first (C) and second dorsal fins (D).

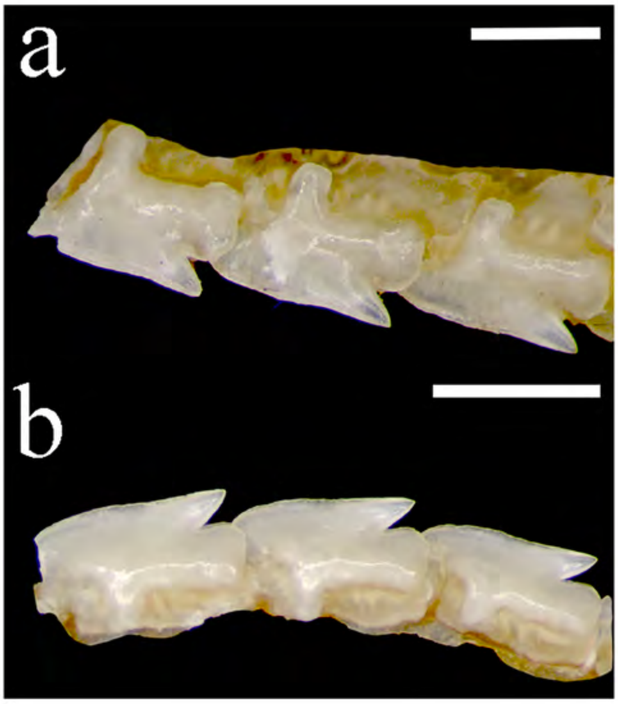

Figure 244. Upper (a) and lower (b) teeth of paratype of *Flakeus* sp. 7, MNRJ 30184, adult male, 480 mm TL. Scale bar: 2 mm.

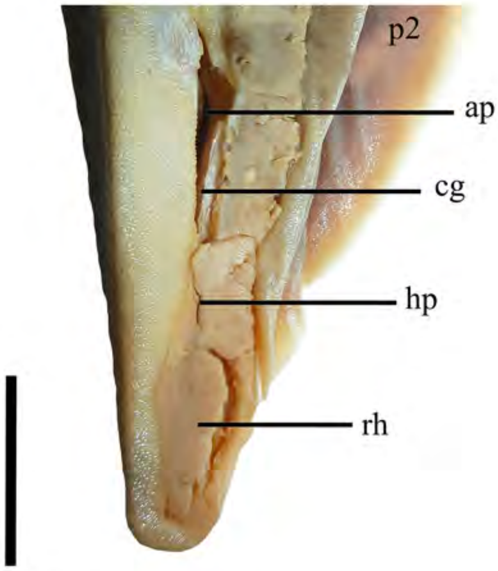

Figure 245. External view of clasper of paratype of *Flakeus* sp. 7, MNRJ 30184, adult male in dorsal view. Scale bar: 10 mm. Abbreviations: apopyle (ap); clasper groove (cg); hypopyle (hp); pelvic fin (p2); rhipidion (rh).

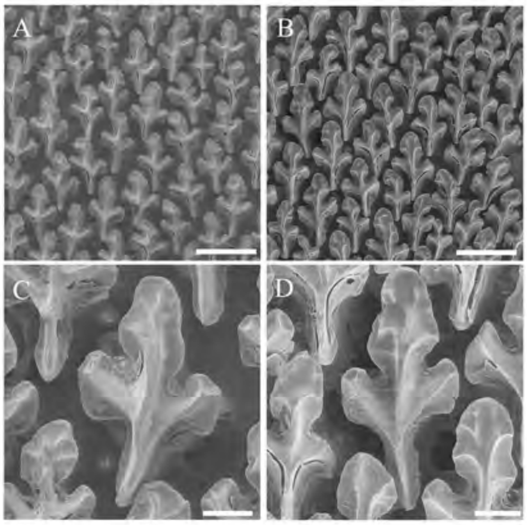

Figure 246. Dermal denticles of holotype (MNRJ 30188) and paratype (MNRJ 30186) of *Flakeus* sp. 7. Scale bars: 200 µm (a, b); 50 µm (c, d).

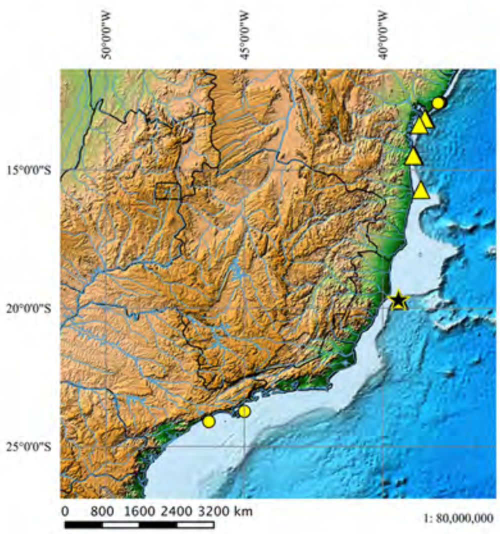

Figure 247. Map of geographical distribution of *Flakeus* sp. 7 in the Southwestern Atlantic Ocean. Black star: location of holotype; yellow triangle: location of paratypes; yellow circle: location of non-type specimens.

Chapter 3

Taxonomic and morphological revision of the genus *Cirrhigaleus* Tanaka, 1912 highlights new interpretations regarding its systematic position within Squaliformes

Abstract

Cirrhigaleus comprise a genus of barbel-bearing dogfish sharks whose morphological characteristics and similarities with the genus *Squalus* are upon incessant discussions on literature. Generic reallocation of the nominal species "*asper*" is often suggested to *Squalus* due to lacking of elongate nasal barbels and presence of upper precaudal pit. Separation between *C. barbifer* and *C. australis* are based on overlapped characteristics, indicating the difficulty on providing efficient diagnostic characters. Geographical distribution and morphological limits between these two species are still uncertain in some regions of the Pacific Ocean. Recent investigations on specimens of *C. australis* from Indonesia and North Australia noticed great intraspecific variations that further contributed to the taxonomic confusion onto the genus. A taxonomic and morphological revision of *Cirrhigaleus* was conducted in order to better define morphologically the genus, to elucidate the correct generic allocation of *C. asper*, and to provide efficient characters for species identification. Diagnosis and redescription of each valid species recognized in the present study are provided based on new material and comparisons with congeners. *Cirrhigaleus* is supported as valid, although its taxonomic classification within Squalidae is questioned. A new family of the order Squaliformes is proposed to integrate the genus, according to new phylogenetic evidences and recent comparative analysis on skeletal compounds between its congeners and members of the family Squalidae.

Resumo

Cirrhigaleus compreende um gênero de tubarões com barbilhões nasais cujas características morfológicas e similaridades com o gênero *Squalus* estão sob incessantes discussões na literatura. A realocação genérica da espécie nominal "*asper*" para *Squalus* é frequentemente sugerida devido a ausência de barbilhão nasal e presença de sulco pré-caudal superior. A separação morfológica entre *C. barbifer* e *C. australis* são baseados em caracteres sobrepostos, indicando a dificuldade em fornecer caracteres diagnósticos eficientes. A distribuição geográfica e os limites morfológicos entre essas duas espécies ainda são incertas em áreas do Oceano Pacífico. Investigações recentes em espécimes de *C. australis* da Indonésia e Norte da Austrália notaram variações intraespecíficas que também contribuem para a confusão taxonômica dentro do gênero. Uma revisão taxonômica de *Cirrhigaleus* foi conduzida a fim de melhor definir morfologicamente o gênero, esclarecer a correta alocação genérica de *C. asper,* e fornecer caracteres eficientes para a identificação das espécies válidas. Diagnose e descrição para cada espécie válida reconhecida no presente estudo são fornecidas baseada em novo material analisado e comparações entre congêneres. A validade de *Cirrhigaleus* é suportada, porém sua classificação taxonômica dentro de Squalidae é questionada. Uma nova família dentro de Squaliformes é proposta para abrigar este gênero de acordo com novas evidências filogenéticas, incluindo análises comparativas recentes de componentes do esqueleto entre espécies de *Cirrhigaleus* e membros da família Squalidae.

Introduction

Cirrhigaleus is a genus comprised by three nominal species: *Cirrhigaleus barbifer* Tanaka, 1912; *Cirrhigaleus asper* (Merrett, 1973); *Cirrhigaleus australis* White, Last & Stevens, 2007. *Cirrhigaleus barbifer* is recognized in waters of Japan, New Zealand, Indonesia and New Caledonia, and Western Australia (Tanaka, 1912; Garrick & Paul, 1971; Fourmanoir & Rivaton, 1979; Compagno *et al*., 2005; White *et al*., 2007; Kempster *et al*., 2013) while *C. australis* occurs exclusively in Australia and possibly in New Zealand (White *et al*., 2007; Ebert *et al*., 2013). *Cirrhigaleus asper* is recorded in the Western Indian Ocean, Southwestern Atlantic Ocean, Hawaiian Islands and Gulf of Mexico (Merrett, 1973; Bass *et al*., 1976; Gomes *et al*., 1997; Compagno *et al*., 2005; Ebert *et al*., 2013).

The genus was originally described as monotypic based on the Japanese species as the unique group within Squaliformes that bears elongate nasal barbels (Tanaka, 1912). The distinctive nasal barbel (short or elongate) is an extension of the second lobe of anterior nasal flap of nostrils and it is considered the only efficient diagnostic character for differentiating this genus from *Squalus* till recently (e.g. Garman, 1913; Fowler, 1941; Garrick & Paul, 1971; White *et al*., 2007). Discussions about its validity as a separate genus in the family Squalidae rose up after morphological similarities on dorsal spines, spiracles, dermal denticles, dentition and shape of dorsal and caudal fins were reported between these two genera by Garman (1913), followed by Fowler (1941), that considered *Cirrhigaleus* as a subgenus within *Squalus*.

Bigelow & Schroeder (1948, 1957), however, stated that the nasal barbels together with lack of upper and lower precaudal pits, and of caudal keels in *Cirrhigaleus barbifer* are sufficient characteristics for considering it as a valid genus. Garrick & Paul (1971) agreed with these authors but noticed that lateral caudal keels in the caudal peduncle are present in this species. Additional differences with *Squalus* regarding length of snout and head (shorter in *Cirrhigaleus*), length and height of dorsal fins (shorter and taller in *Cirrhigaleus*), size of dermal denticles (about twice in *Cirrhigaleus*), and counts of teeth and vertebrae were reported by Garrick & Paul (1971). Despite of it, these studies still emphasized morphological similarities between *Cirrhigaleus* and *Squalus.*

Merrett (1973) described *Squalus asper* for the Western Indian Ocean without making comparative analysis with *Cirrhigaleus*. Similarities on teeth, terminal cartilages of claspers, vertebral counts and morphometric with *S. acanthias* and *S. blainvillei* from this region were sufficient for placing it into the genus *Squalus*, according to this author. Merrett (1973) further concluded that *S. asper* has intermediate characteristics between these two nominal species (except for size of dermal denticles) when considering the definition of groups of species within *Squalus* proposed by Garrick (1960), which was the start up for later and incessant debates in the literature regarding its taxonomic status (e.g. Bass *et al.*, 1976; Compagno, 1984; Compagno *et al.*, 2005; Figueirêdo, 2011).

Bass *et al*. (1976) first attempted to morphological similarities between *S. asper* and *Cirrhigaleus barbifer* regarding the nasal barbels and tall dorsal fins but these authors addressed them for a new group of species within *Squalus*: the group *S.asper*. According to

Bass *et al*. (1976), the group is also characterized by absence (or weakly evident) of upper precaudal pit, large dermal denticles, and head and snout small and blunt.

Later, Shirai (1992) supported *Cirrhigaleus* as monophyletic and sister-group of *Squalus* based on phylogenetic analysis of morphological characters. Three sinapomorphies are currently provided for *Cirrhigaleus* (Shirai, 1992): absence of supraethmoidal processes in the neurocranium; absence of upper precaudal tip; nasal barbels innervated by a branch buccopharyngeal of facial nerve (VII). Recent studies on molecular analysis of CO1 and NADH2 genes on the genus have also supported *Cirrhigaleus* as monophyletic as well (e.g. Naylor *et al*., 2012a,b). However, Naylor *et al*. (2012b) recognized it as sister-group of the species *S. acanthias* and *S. suckleyi*, and that this group together are separated from the remaining species of the family Squalidae. Naylor *et al*. (2012b) then suggested that all species of *Cirrhigaleus* should be reallocated within *Squalus* in order to support the monophyly of the latter genus. These findings are the first attempt to reinvestigate the phylogenetic relationships of *Cirrhigaleus* within Squalidae.

More recently, White *et al*. (2007) noticed difficulties on providing efficient diagnostic characters for separating *C. barbifer*, *C. australis* and *C. asper*, indicating the necessity on reinvestigating the morphology of its species. Ramos (2009) and Figueirêdo (2011) again brought up new doubts regarding the correct generic allocation of *C. asper* based on material from Southwestern Atlantic Ocean and attempted that morphological characters that support the genus should be revised.

In the present study, the genus *Cirrhigaleus* is revised taxonomic and morphologically based on material from different geographical regions and analysis of type material. New diagnostic characters for differentiating its species are provided and the allocation of *C. asper* into the family Squalidae is discussed.

Material and methods

Methodology is summarized in the section “Materiais e Métodos” of this thesis.

Family Cirrhigaleidae new family

Type genus: *Cirrhigaleus* Tanaka, 1912.

Etymology: Family-group name is formed, according to the provisions under the Article 16.2 of ICNZ, based on the entire name of its type genus *Cirrhigaleus*.

Definition. Cirrhigaleidae differs from members of Squaliformes, including Squalidae, by bearing nasal barbel in the anterior margin of nostrils that it is innervated by a branch buccopharyngeal of the facial nerve (VII). It is also characterized by having dorsal spines markedly elongate, usually transcending greatly the apex of its dorsal fin. *Cirrhigaleus* has body trihedral in cross-section, conspicuously arched dorsally and humped at belly, with tail fusiform and short. Cirrhigaleidae shares with Squalidae and *Centrophorus* teeth unicuspid and cusp oblique. It shares with Squalidae dorsal spine ungrooved in front of each dorsal fin, caudal fin without subterminal notch and presence of lateral keel in the caudal peduncle. *Cirrhigaleus* has pectoral articulation comprised by procondyle and meso-metacondyle, clasper with accessory ventral marginal 2 cartilage, and pelvic articulation formed by a dorsal condyle + facet and ventral condyle.

The new family Cirrhigaleidae is established herein to comprise a monogeneric group of three barbel-bearing species of dogfish sharks: *Cirrhigaleus barbifer*, *Cirrhigaleus asper* and *Cirrhigaleus australis*.

Comparisons within Squaliformes. Cirrhigaleidae shares with members of Squaliformes absence of anal fin, dorsal spine in front of at least one of dorsal fin, and dignatic heterodonty. As it is observed for Squalidae, Cirrhigaleidae has lateral keels in the caudal peduncle, caudal fin without subterminal notch, and dorsal spines ungrooved, which is in contrast to Centrophoridae, Dalatiidae, Etmopteridae, Somniosidae, and Oxynotidae. Cirrhigaleidae and Squalidae also share weak dignatic heterodonty in which upper and lower teeth are similar in morphology but differ in size, length and width of apron and cusp while dignatic heterodonty is conspicuous in other families within Squaliformes with lower teeth usually turning narrower labial-lingually. Other feature of the barbel-bearing sharks is dorsal fins upright, equally tall and large, and body trihedral, a condition similar to Oxynotidae. Species of *Cirrhigaleus* also have conspicuous rough skin that it is similar to those of Somniosidae and Oxynotidae. Caudal fin of *Cirrhigaleus* exhibits transition continuous between upper and lower lobes, a condition distinct from Squalidae and Centrophoridae. Upper labial furrow bears fold and lower labial furrow lacks the fold in species of Cirrhigaleus , which it is a condition similar to *Centrophorus* and *Squalus*.

Cirrhigaleidae is distinct from Squalidae on lacking precaudal pits, spiracles above the eyes dorsally, eyes with anterior and posterior margins notched, upper labial furrow very short with thick fold, second dorsal fin with origin over or just prior pelvic free rear tips, and dermal denticles with cusplets at posterior margin of the crown. *Cirrhigaleus* further differentiates from *Squalus* and *Flakeus* by absence of supraethmoidal processes and vestigial antorbital cartilage in the neurocranium, absence of hook-like rostral cartilages, and five terminal cartilages.

Cirrhigaleus Tanaka, 1912

Cirrhigaleus Tanaka, 1912: (original description, illustrated; Sagami Sea, Japan; type by monotypy); Bigelow & Schroeder, 1948: 451 (cited; Northwest Pacific Ocean). Bigelow & Schroeder, 1957: 18, 19, 24, 37-38 (cited, revision, description; Northwest Pacific Ocean); Garrick & Paul, 1971: 1-13 (revision, description, illustrated; Northwest and Southwest Pacific Oceans); Bass *et al*., 1976: 9, 10 (cited; Northwest Pacific Ocean); Compagno, 1984: 61-62 (description, revision; North to South Pacific Oceans); Compagno, 1999: 472 (listed; West Indian Ocean, Central Pacific Ocean, North Atlantic Ocean); Yuanding & Qingwen, 2001: 292-293 (listed; Northwest Pacific Ocean); Nakabo, 2002: 155 (listed; Southern Japan, Ryukyu Islands, New Zealand); Compagno *et al*., 2005: 71-73 (revision; Pacific, Atlantic and Indian Oceans); Last *et al*., 2007: (cited); Ebert *et al*., 2013: 74, 80-82 (cited, description; Pacific, Atlantic and Indian Oceans); Nakabo, 2013: 194 (listed; Southern Japan, Ryukyu Islands, New Zealand).

Squalus (subgenus *Cirrhigaleus*) Garman, 1913: 457 (description; Northwest Pacific Ocean); Fowler, 1941: 262 (description; Northwest Pacific Ocean).

Phaenopogon Herre, 1935: 121-124 (original description, illustrated; type species *Phaenopogon barbulifer*; type by monotypy; unnecessary replacement name for *Cirrhigaleus*).

Squalus: Fowler, 1936: 69 (cited; Northwest Pacific Ocean); Bass *et al*., 1976: 8-20 (revision, description; Western Indian Ocean, Northwest and Southwest Pacific Oceans).

Type species: *Cirrhigaleus barbifer* Tanaka, 1912 by monotypy.

Definition: See definition of family above.

Identification key to species of *Cirrhigaleus*.

1. - Anterior margin of nostrils with nasal barbel conspicuously elongate and thin, often reaching anterior margin of mouth; dermal denticles with conspicuous cusplets at posterior margin of the crown; upper labial furrow short, its length between 0.9%–1.1% of TL; pectoral fins with anterior margin elongate, its length 14.8%–16.9% of TL…………..……..**2**

- Anterior margin of nostrils with nasal barbel short and thick, slightly transcending posterior margin of nostrils; dermal denticles with cusplets inconspicuous and weak at posterior margin of crown; upper labial furrow large, its length between 1.4%%–1.6% of TL; pectoral fins with anterior margin small, its length 12.5%–14.4% of TL)……………....…………………………...…………………………***Cirrhigaleus asper***

2. - Body dark brown; narrow internarial space, its width 3.0%–3.4% of TL; small pre-branchial distance, corresponding to 14.8%–16.8% of TL; caudal fin short, its dorsal caudal margin length 20.5%–20.6% of TL; dermal denticles with single cusplet on each side posteriorly……………………………...…………………….………***Cirrhigaleus barbifer***

- Body light grey; internarial space broad, its width 3.6%–3.9% of TL; elongate pre-branchial distance, corresponding to 16.4%–18.4% of TL; caudal fin elongate, its dorsal caudal margin length 19.2%–21.8% of TL; dermal denticles with two cusplets on each side posteriorly……………..…………………..……………………...….***Cirrhigaleus australis***

Cirrhigaleus barbifer **Tanaka, 1912**

(**Northern Mandarin dogfish; Barbel-bearing squaloid shark; Hige-zune** in Japanese)

Figures 248–256; Tables 59, 62

Cirrhigaleus barbifer Tanaka, 1912: 151-154; pl. XLI, figs. 156-162 (original description, illustrated; type by monotypy; Sagami Sea, Japan); Bigelow & Schroeder, 1948: 451 (cited; Northwest Pacific Ocean). Bigelow & Schroeder, 1957: 18, 19, 24, 37-38 (cited, revision, description; Northwest Pacific Ocean); Garrick & Paul, 1971: 1-13 (revision, description, illustrated; Northwest and Southwest Pacific Oceans); Compagno, 1984: 61-62 (description, revision; Western Pacific Ocean); Last & Stevens, 1994 (in part): 48, 68 (cited, description; Northwest and Central Pacific Ocean, New Zealand); Compagno & Niem, 1998 (in part): 1203-1224 (listed, cited; Western Pacific Ocean, New Zealand); Compagno, 1999: 472 (listed); Yuanding & Qingwen, 2001: 292-293 (listed; Northwest Pacific Ocean); Nakabo, 2002: 155 (listed; Southern Japan, Ryukyu Islands, New Zealand); Compagno *et al*., 2005: 73 (description; Western Pacific Ocean); Ebert *et al*., 2013: 74-82 (cited, description; Western Pacific Ocean); Nakabo, 2013: 194 (listed; Southern Japan, Ryukyu Islands, New Zealand).
Squalus barbifer Garman, 1913: 457 (description; Northwest Pacific Ocean); Fowler, 1941: 262 (description; Northwest Pacific Ocean); Bass *et al*., 1976: 9, 10 (cited; Northwest Pacific Ocean); Fourmanoir & Rivaton, 1979: 436 (listed; Southwest Pacific Ocean).
Phaenopogon barbulifer Herre, 1935: 121-124 (original description, illustrated; type by original designation).

Holotype. ZUMT 3397 (lost), adult male, 855 mm TL, collected at Tokyo Fish Market, Japan.

Paratypes: Unknown.

Type locality: Sagami Sea, Japan

Non-type material (34 specimens): CSIRO H 5875-09, adult female, 978 mm TL, Tanjung Luar, Indonesia, 08°45’S,116°35’E; HUMZ 95177, juvenile female, 584 mm TL, East China Sea, 28°54.2’N,128°29.3’E; HUMZ 101533, juvenile male, 650 mm TL, Okinawa, Japan, 27°16.2’N, 127°27’E; HUMZ 197852, adult female, 870 mm TL, off Kanaya, Gulf of Tokyo, Japan; MNHN 1997-3568, adult female, 800 mm TL, New Caledonia; NMNZ P 5105, juvenile female, 930 mm TL, between Mayor and White Islands, North Island, New Zealand, 37°25’S,176°40’E; NMNZ P 5163, adult female, 1045 mm TL, 10 miles off White Island, North Island, New Zealand, 45°56’S,170°30’E; NMNZ P 5204, adult female, 1195 mm TL, off Mayor Island, North Island, New Zealand, 37°35’S,176°40’E; NMNZ P 5205, five neonate females, 80-87 mm TL; four neonate males, 83-85 mm TL, off Mayor Island, North Island, New Zealand, 37°35’S,176°40’E; NMNZ P 7366, adult female, 1272 mm TL, Mayor Island, North Island, New Zealand, 37°20’S,176°20’E; NMNZ P 7367, adult female, 1230 mm TL, Mayor Island, North Island, New Zealand, 37°19’S,176°15’E; NMNZ P 7681, adult male, 1040 mm TL, Tauranga, North Island, New Zealand, 37°41’S,176°10’E; NMNZ P 8030, adult male, 980 mm TL, South Auckland, North Island, New Zealand, 37°39’S,176°13.5’E; NMNZ P 17635, adult female, 866 mm TL, Hikurangi Trough, Hawke’s Bay, North Island, New Zealand, 39°58.65’S,178°8.20’E; NMNZ P 28732, two adult females, 1128-1189 mm TL, New Zealand; NMNZ P 34452, adult male, 990 mm TL, Kermadec Islands, New Zealand, 28°50.80’S,177°50.400’W; NMNZ P 34817, juvenile male, 790 mm TL, Kermadec Islands, New Zealand, 33°4.900’S,179°34.300’W; NMNZ P 34821, adult male, 971 mm TL, Kermadec Islands, New Zealand, 32°23.40’S,179°13.60’W; NMNZ P 38074, adult male, 1020 mm TL, Southern Norfolk Ridge, New Zealand, 32°40’S,167°37’W; NMNZ P 42489, juvenile male, 710 mm TL, Tony B Seamount, West of Norfolk Ridge, New Zealand, 34°31.850’S,168°47.500’E; NMNZ P 42734, adult female, 1110 mm TL, off “The Faces”, Kaikoura, New Zealand, 42°28’S,173°46’E; NMNZ P 43052, neonate female, 77 mm TL, off Mayor Island, New Zealand, 37°35’S,176°40’E; NMNZ P 46806, juvenile female, 760 mm TL, Three King Islands, Southwest Norfolk Ridge, New

Zealand, 34°36.700'S,168°56.300'E; NMW 98257, adult female, 960 mm TL, precise locality unknown, Asia.

Diagnosis. *Cirrhigaleus barbifer* is distinguished from its congeners by having body dark brown dorsally (vs. light grey for *C. australis* and *C. asper*), teeth with apron conspicuously broad (vs. narrower), and dermal denticles with a single cusplet on each side (vs. one or two tiny cusplets in *C. asper* vs. two cusplets in *C. australis*). It is easily distinct from *C. asper* by having nasal barbels moustache-like and well elongate, often reaching the mouth (vs. nasal barbel markedly short, slightly transcending the posterior margin of nostrils), and from *C. australis* by having more elongate upper labial furrow (1.1% of TL for *C. barbifer* vs. 0.9% for holotype, 0.9%–1.0% of TL for paratypes of *C. australis*), narrower internarial space (3.0%–3.4% vs. 3.6%, 3.6%–3.9% of TL for *C. australis*), and more slender second dorsal spine (its base length 0.8%-0.9% vs. 1.1%, 1.0%–1.1% of TL for *C. australis*).

Description. Single value is for holotype of *Phaenopogon barbulifer*. Ranges values are for other non-type material from Japan.

External morphology (Figs. 248–255; Tabs. 59, 62). Body conspicuously robust and trihedral, markedly humped dorsal and ventrally throughout all its extension, turning slender caudally from pelvic fin insertion to caudal fin origin; body with greatest depth at first dorsal fin insertion (its height 17.1%, 8.6%-14.1% of TL); head height 0.8, 0.9-1.1 times trunk height and 0.8, 0.8-0.9 times abdomen height; pre-second dorsal length much greater than dorsal-caudal distance (61.0%, 60.8%-63.6% of TL vs. 8.9%, 7.5%-7.9% of TL). Head small (its length 19.5%, 18.8%-20.7% of TL), depressed and very narrow anteriorly (its width at nostrils 7.6%, 6.4%-7.5% of TL), broader posteriorly near the gill slits (26.7%, 13.7%-15.7%

of TL); head width 1.0, 1.0-1.2 times trunk width and 1.3, 1.1-1.5 times wider than abdomen width.

Snout rounded and conspicuously short (preorbital length 5.5%, 5.6%-6.4% of TL) with anterior margin of the nostril bilobed; distance from nostrils to the snout tip about equal to its distance to upper labial furrow; first lobe of nostril broad and large, although much smaller than second lobe; second lobe of nostril conspicuously elongate as nasal barbells, usually reaching anterior margin of mouth (it extends posterior margin of mouth in juveniles), its length 5.4%-6.1% of TL or fitting 3.1-3.8 times in head length. Eyes oval and elongate, its length 5.2, 2.0-4.3 times greater than its height and 0.6, 0.8-1.1 times prenarial length; its anterior margin concave, slightly notched posteriorly, well prominent dorsally. Spiracles crescent and broad, its length 2.3, 0.9-1.2 times eye length, located lateral-posteriorly and above the eyes. Gill slits vertical, somewhat concave, and very tall with fifth gill slit height 3.1%, 2.0%-2.4% of TL, corresponding to 1.5, 1.1-1.2 times first gill slit height.

Preoral length equal to mouth width. Upper labial furrow markedly small, its length 1.1%, 1.1% of TL with fold very short and broad; lower labial furrow elongate, lacking fold. Mouth strongly arched and wide, its width 2.2, 2.3-2.4 times broader than internarial space and 1.9, 1.9-2.0 times prenarial length. Teeth similar in both jaws, unicuspid, flattened labial-lingually and alternate; teeth markedly broad and low with upper teeth smaller than lower teeth; cusp short and somewhat cylindrical, oblique and directed laterally; mesial cutting edge slightly concave on upper jaw and straight on lower jaw; mesial heel conspicuously tapered and pointed; distal heel rounded; apron short and markedly broad; apron narrower on upper jaw than lower jaw. Median tooth evident on both jaws, usually narrower than the following teeth; media tooth with cusp vertical, mesial cutting edge convex, both mesial and labial heels rather pointed. Three series of functional teeth on both jaws; upper jaw with 14-1-13 teeth rows; lower jaw with 11-1-11 teeth rows.

Dorsal fins conspicuously upright and vertical, both equally tall and large with length of first dorsal fin 1.1, 0.9-1.0 times second dorsal fin length; first dorsal fin height 1.0, 1.0-1.1 times second dorsal fin height. First dorsal fin markedly slender and rounded at the apex, broad at its base (base length 8.9%, 8.3%-8.7% of TL); anterior margin concave, and posterior margin straight but concave near free rear tip; inner margin short, its length 5.6%, 5.4%-6.3% of TL; first dorsal fin height 1.8, 1.6-1.7 times greater than its inner margin length. First dorsal spine origin posterior to the free rear tip of the pectoral fin in adults; first dorsal spine concave, narrow, and markedly large (its length 5.2%, 6.0% of TL); first dorsal spine not reaching the fin apex, its length one-half of first dorsal fin height. Origin of second dorsal fin just anterior to the free rear tip of the pelvic fins.

Interdorsal space 1.1, 1.1-1.2 times prepectoral length. Second dorsal fin slender, rounded and lobulate at apex, broad at its base (base length 8.5%, 8.9%-9.7% of TL); second dorsal anterior margin concave; posterior margin straight, although concave near the free rear tip (slightly falcate in juveniles); second dorsal height 1.7, 1.7-1.9 times its inner margin length; inner margin short (its length, 5.7%, 4.8%-5.9% of TL) with free rear tips almost over origin of caudal fin. Second dorsal spine narrow and well elongate (its length 7.5%, 7.1%-7.6% of TL), corresponding to three-fourth the second dorsal fin height; second dorsal spine length 1.4, 1.3 times length of first dorsal spine almost reaching fin apex in adults (it exceeds fin apex in juveniles).

Pectoral fin markedly broad, although narrow anteriorly at base (its base length 5.4%, 4.3%-4.9% of TL) and broad posteriorly (posterior margin length 13.1%, 11.3%-11.4% of TL); anterior margin and inner margin evidently convex, and posterior margin slightly concave; apex and free rear tips markedly rounded, never lobulate; apex not transcending the horizontal line traced at free rear tip; pectoral anterior margin length 2.0, 1.7-2.0 times greater than inner margin length, and 1.3, 1.4-1.5 times posterior margin length; pectoral posterior margin 0.8, 0.8-1.5 times trunk height. Pectoral-pelvic space 1.3, 1.3-1.5 times pelvic-caudal distance.

Pelvic-caudal distance 1.0, 0.8-0.9 times interdorsal space. Pelvic fins nearest second dorsal fin than first dorsal fin; pelvic fin large, its length 1.7-1.8 times in interdorsal space. Pelvic fins conspicuously broad, pentagonal in pair with both anterior and inner margins convex; rounded apex; free rear tips triangular, although rounded and lobulated on males; pelvic length 1.5, 1.1-1.2 times length of preventral caudal margin. Clasper well elongate and thick, its outer length 1.7% of TL in juveniles and 3.7%-10.0% of TL in adults from New Zealand; clasper groove markedly large and vertical, placed lateral-dorsally; apopyle and hypopyle very narrow, located at the opposite extremities of clasper groove; rhipidion flap-like, conspicuously tapered and elongate, placed laterally.

Caudal peduncle broad in cross-section and conspicuously short; its dorsal-caudal distance 2.5, 2.8-3.0 times smaller than the interdorsal space; lateral keel prominent laterally almost as a fold, since insertion of second dorsal fin to behind origin of caudal fin; upper and lower precaudal pits absent. Caudal fin with rectangular dorsal caudal lobe with posterior tip rounded; dorsal-caudal margin well elongate, its length 1.2, 1.0-1.1 times head length, and 2.6, 1.8-1.9 times larger than preventral caudal margin; dorsal caudal margin straight; upper postventral caudal margin markedly concave, although straight proximally; lower postventral caudal margin convex and very short; preventral caudal margin straight and conspicuously small, its length 1.5, 1.8-2.1 times inner margin length of pelvic fin; ventral caudal tip rounded; caudal fork inconspicuous with transition between upper and lower caudal lobes clearly continuous; caudal fork wide, its width 8.2%, 7.0%-8.4% of TL.

Dermal denticles (Fig. 255). Dermal denticles tricuspid and bat-like, somewhat imbricate, large and markedly broad at the crown; denticles with its width as large as its length; cusps pointed with median cusp much more elongate than lateral ones; median ridge conspicuous, elongate, thin and tall, transcending anteriorly the crown base; lateral ridges slender, short and low, markedly convex anteriorly; median furrow large and profound, placed anteriorly over median ridge; lateral furrow short and profound, present anteriorly over each lateral ridge; one or two secondary cusps (or cusplets) sometimes present on each side of posterior crown base; secondary cusps much smaller than lateral cusps.

Coloration. Body brownish grey dorsal and laterally, white ventrally. Nasal barbells white, slightly grey at its lateral and ventrally in the distal end. Dorsal fins also grey, somewhat light grey posteriorly in the submarginal bar; white posterior margin from the apex to its middle line; free rear tips discreetly white. Dorsal spines dark brown, white at its tips. Pectoral fins dark grey dorsally with uniformly white posterior margin, somewhat white ventrally with large light grey blotches. Pelvic fins also grey dorsally with white posterior margin, white ventrally with large light grey blotches. Caudal fin dark grey throughout all its extension; postventral margins narrowly white; black caudal stripe evident anteriorly.

Vertebral counts (Tab. 63). 115 total vertebra; 88 precaudal vertebra; 27 caudal vertebra; 50 monospondylous vertebra.

Geographical distribution (Fig. 256). It occurs in the Japanese waters, Indonesia, New Caledonia and possibly New Zealand.

Etymology. The epithet "*barbifer*" refers to the conspicuously elongated second lobe of the nostril that forms a well prominent barbell.

Remarks.

Type specimens of *Cirrhigaleus barbifer.* Tanaka (1912) described both genus and species based in a single mature male collected at Tokyo Fish Market in Japan, and deposited under the catalogue number ZUMT 3397. According to Dr. Sakamoto, the holotype is lost. Many authors (e.g. Fowler, 1941; Bigelow & Schroeder, 1957) made references to the holotype based on the illustration provided by Tanaka (1912) rather than to the specimen itself, which indicates that the holotype had never left the museum for analysis by other authors and probably was lost during I and II World War. No other specimen from *C. barbifer* exits at fish collection from ZUMT as it was verified during the present study, suggesting that a neotype should be designated for this species.

The Sagami Sea is the type locality of *C. barbifer* by original indication even though its holotype was not expressly collected in this region. Interestingly, there is no specimen collected from this region in the fish collections from Japan and it seems that new specimens are rarely catched in Japanese waters. The nearest locality of one single specimen is Gulf of Tokyo, which it is a good candidate for neotype of this species.

Morphological comparisons with *Cirrhigaleus australis*. *Cirrhigaleus barbifer* is frequently reported from North to South Pacific waters between Japan, Taiwan and Indonesia (White *et al*., 2007), New Caledonia and Vanuatu (Fourmanoir & Rivaton, 1979) as well as New Zealand (Garrick & Paul, 1971). Recently, a new species of the genus, *C. australis*, was described as restricted to Southern Australia and possibly to New Zealand (White *et al*., 2007) but few studies still recognize *C. barbifer* in Western Australia (e.g. Kempster *et al*., 2013). These two nominal species have similar characteristics of external morphology, making it difficult to separate them. Dermal denticles are tricuspid and conspicuously broad with one and two secondary cusps on each side for both species, respectively, which it is in disagreement with White *et al*. (2007) who only noticed this character for *C. australis*. Dental formula of *C. barbifer* is also congruent with *C. australis*. Vertebral counts overlap between them and it is consistent with observations of Garrick & Paul (1971), White *et al*. (2007) and Kempster *et al*. (2013).

Cirrhigaleus barbifer is easily distinct from *C. australis* on body color as it was noticed previously by White *et al*. (2007), and Kempster *et al*. (2013). These authors observed differentiation on morphometrics that are also supported herein: more elongate second dorsal spine for *C. barbifer* (7.1%–7.6% of TL vs. 6.4% for holotype of *C. australis*); shorter preventral caudal margin (10.8%–11.6% of TL vs. 11.7% of TL); larger eye (its diameter 3.6%–4.3% vs. 3.3% of TL); more elongate upper labial furrow (1.1% vs. 0.9% of TL). The current results additionally noticed that specimens of *C. barbifer* is distinct from holotype of *C. australis* by: larger pre-caudal length (79.1%–79.9% vs. 78.4% of TL); shorter pre-branchial length (14.8%–16.8% vs. 17.1% of TL); anterior margin of first dorsal fin more elongate (13.5%–14.3% vs. 12.2% of TL); larger anterior margin of pectoral fin (its length 15.3%–16.9% vs. 15.2% of TL); dorsal-caudal margin of caudal fin smaller (20.5%–20.6% vs. 21.6% of TL); length of anterior nasal flap larger in *C. barbifer* (5.4%–6.1% vs. 5.0% of TL). Length of first dorsal spine, base length and height of the second dorsal fin, prenarial length, interdorsal space, and length of pectoral posterior margin varied among them, according to White *et al*. (2007) but these differences are not observed in the present study.

Morphological variations in *Cirrhigaleus barbifer*. Ontogenetic variations are markedly noticed among specimens of *C. barbifer* and it is more apparent than in species of the family

Squalidae. Origin of first dorsal fin is anterior or over pectoral free rear tips in juveniles of *C. barbifer* while it is conspicuously posterior to it in adults. No other species within Squalidae exhibit similar variations with growth, except *S. acanthias*. Length of both dorsal spines also varies with growth in which juveniles of *C. barbifer* have first dorsal spine much smaller than in adults, reaching half of first dorsal height. Second dorsal spine in adults transcends half of second dorsal height, almost reaching its apex. Exceptions, however, are observed for specimens from Indonesia that show first dorsal spine larger than second dorsal spines in adults (in juveniles it is not yet known because of lacking of specimens for analysis).

Nasal barbels exceed posterior margin of mouth in juveniles while in adults it reaches anterior margin of mouth or just before it, which it is in agreement with observations of Garrick & Paul (1971). These authors also noticed decreasing with growth of preoral length, eye length, heights of first and second dorsal fins, and length of dorsal-caudal margin of caudal fin among specimens from New Zealand and Japan. Our results, however, do not show uniform variation from juvenile to adult related to preoral length (7.5% for juvenile vs. 7.8%, 7.1% of TL from small to larger adults) and eye length for *C. barbifer* (4.0% vs. 3.6%, 4.3% of TL). Length of dorsal caudal margin is constant with growth in specimens from Japan (20.6% vs. 20.5%, of TL). Height of first and second dorsal fins increase with growth in these specimens (first dorsal height 8.9% vs. 10.0%, 10.8% of TL; second dorsal height 8.8%, 9.3%, 10.3% of TL). Garrick & Paul (1971) also observed that anterior margin of pectoral fin reduces in length with growth, in contrast to the current results. Specimens from New Zealand did not exhibit uniform variation with growth in any of these characters, which it is in disagreement with findings of Garrick & Paul (1971).

Cirrhigaleus barbifer from Japan, New Zealand, Indonesia and New Caledonia overlaps in many characteristics of external morphology that include shape of dermal denticles, dentition, and body color. Vertebral counts are also similar between these specimens (not yet observed for specimens from New Zealand and New Caledonia). Great morphometric variations, however, are observed between specimens of *C. barbifer* from Japan and Indonesia: shorter interdorsal space for Japanese specimens (21.9%–22.4% of TL vs. 24.5% of TL); shorter dorsal-caudal space (7.5%–7.9% of TL vs. 9.1% of TL); shorter pelvic-caudal space (18.4%–20.5% of TL vs. 21.0% of TL); smaller pectoral fin (posterior margin length 11.3%–11.4% of TL vs. 11.8% of TL; its inner margin length 8.3%–8.9% of TL vs. 9.5% of TL); narrower and smaller head (width of head at nostrils 6.4%–7.5% of TL vs. 7.8% of TL; head length 18.8%–20.7% of TL vs. 23.0% of TL); shorter second dorsal spine for Japanese specimens (7.1%–7.6% of TL vs. 7.9% of TL). The Indonesian specimen has larger first dorsal spine than *C. barbifer* from Japan (its length 8.3% of TL vs. 6.0% of TL), according to the present study and White *et al*. (2007). It also has larger pre-branchial length (18.9% of TL vs. 14.8%–16.8% of TL for Japanese specimens), preoral length (8.1% of TL vs. 7.1%–7.8% of TL), and greater distance between nostrils (3.6% of TL vs. 3.0%–3.4% of TL),

These results agree with White *et al*. (2007) that the Indonesian specimen may represent a different species. However, the lack of representatives from this region for better comparisons impedes its taxonomic support and thus it is considered as a variation of *C. barbifer*. White *et al*. (2007) supported this hypothesis based on comparisons with *C. australis* and recent molecular investigations between specimens from these two regions, although the latter assumption was provided as a personal communication from Dr. B. Ward and no other study has been published yet till now. The current analysis of a specimen from New Caledonia shows similar variations with specimens of *C. barbifer* from Japan and Indonesia, including preoral length, distance from nostrils to labial furrow, length of upper labial furrow, and length of anterior nasal flap, which it is much greater in the specimens from New Caledonia.

Specimens from New Zealand exhibit evident intraspecific variations, including in body color, dentition and shape of dermal denticles. It also has greater range of external measurements (e.g. precaudal length; pre-first and pre-second dorsal length; interdorsal space; dorsal-caudal distance; pectoral-pelvic distance; pelvic-caudal distance; size of first and second dorsal fins; length of dorsal spines). These results suggest that more than one morphological group of *Cirrhigaleus* occurs in New Zealand waters. Vertebral counts for these specimens are extremely needed for comparisons with its congeners in order to verify its identification.

Additional material from Indonesia and New Caledonia is still challenging for morphological and/or molecular-based analysis. Future investigations on the genus *Cirrhigaleus* from these regions and New Zealand will elucidate its conspecificity and verify if *C. barbifer* has in fact geographical distribution broader than its congeners.

Comparative material. SU 13901 (holotype of *Phaenopogon barbulifer* Herre, 1935), adult female, 730 mm TL, Misaki Bay, Japan. Specimens of *C. australis* and *C. asper* listed in this Chapter.

Cirrhigaleus asper (Merrett, 1973)

(Roughskin spurdog)

Figures 257–263; Tables 60, 62–63

Squalus asper Merrett, 1973: 93-110, figs. 1-6, pl. Ib (original description, illustrated; type by original designation; Seychelles Islands); Bass *et al.*, 1976: 2, 9-11, 18-20, 65, 59, figs. 8, 12 (description; Western Indian Ocean); Compagno, 1984: 110, 114 (description; Western Indian Ocean, Central Pacific Ocean, Western North and Central Atlantic Ocean); Bass *et al.*, 1976: 9, 10 (cited, described, revised; Western Indian Ocean); Bass *et al*., 1986: 60-61 (cited; Southeast Atlantic Ocean).

Cirrhigaleus asper Shirai, 1992: 35, 106 (systematics; Indian Ocean); Compagno, 1999: 472 (listed); Compagno, 2002: 381-382 (listed, cited; North and Central Atlantic, West Indian Ocean); Gadig & Gomes, 2003: 27 (listed; West Indian and Western Atlantic Oceans); Heemstra & Heemstra, 2004: 54 (cited; Western Indian Ocean); Compagno *et al*., 2005: 72, pl. 2 (description; Pacific, Atlantic and Indian Oceans);

White *et al*., 2007: 19, 27 (cited; Western Indian Ocean); Ebert *et al*., 2013: 53-55, 243 (description, cited; Indian Ocean); Ebert *et al*., 2013: 74, 81 (cited, description; Indian and Western Atlantic Oceans).

Holotype. BMNH 1972.10.10.1, adult male, 880 mm TL, off Aldabra Island, Seychelles, Western Indian Ocean, 09°27'S,46°23.5'E, 219 meters depth; Collector: Royal Society Indian Ocean Deep Slope Fishing Expedition, 1969; Collected on 10 February, 1969.

Paratypes (3 specimens): BMNH 1972.10.10.2, adult male, 847 mm TL, off Astove Island, Seychelles, Western Indian Ocean, 10°04'S,47°43'E, 329 meters depth, collected on 19 January, 1969; BMNH 1972.10.10.3, adult female, 865 mm TL, off Farquhar Island, Seychelles, Western Indian Ocean, 10°10'S,51°12'E, 274 meters depth, collected on 24 January, 1969; BMNH 1972.10.10.4, adult female, 1002 mm TL, off Assumption Island, Seychelles, Western Indian Ocean, 09°43'S,46°29'E, 600 meters depth, collected on 9 January, 1969. Paratypes with collector same as holotype.

Type locality: Aldabra Island, Seychelles, Western Indian Ocean.

Non-type material (40 specimens): MNHN 1884-0149, two neonate males, 138-144 mm TL, St. Paul Island, 38°40'1"S,77°30'0"E; MNHN 1884-0151, embryos, less than 90 mm TL, same locality as MNHN 1884-0149; MNHN 1959-0067, embryo male, 107 mm TL, same locality as MNHN 1884-0149; MNHN 1964-0001, neonate male, 207 mm TL, Amsterdan Island, 37°55'1"S,77°40'1"E; MNHN 1964-0003, neonate male, 253 mm TL, same locality as MNHN 1964-0001; MNHN 1986-0722, adult female, 760 mm TL, Comores, 12°0'0"S,43°25'1"E; MNRJ 30227, adult male, 970 mm TL, off Bahia coast, Brazil, 13°40'45"S,38°71'36"W; MNRJ 30228, adult male, 970 mm TL, same locality as MNRJ 30227; NUPEC uncatalogued, two adult females, 1270-1300 mm TL, unknown locality, Brazil; SAIAB 6036, juvenile male, 390 mm TL, unknown locality; SAIAB 6037, juvenile female, 380 mm TL, off Kwazulu-Natal, South Africa; SAIAB 6038, juvenile female, 320 mm TL, off Kwazulu-Natal, South Africa; SAIAB 6040, adult female, 1120 mm TL, Amatikulu, South Africa, 29.04°S,31.53°E; SAIAB 6092, neonate female, 275 mm TL; neonate male, 270 mm TL, unknown locality; SAIAB 25423, adult female, 1110 mm TL, off Coffee Bay, South Africa, 31.98°S,29.14°E; SAIAB 27027, adult female, 1090 mm TL, Kowie River mouth, Port Alfred, South Africa; SAIAB 31890, adult female, 1090 mm TL, off Gonubie, South Africa; SAM 38268, nine neonate females, 132-145 mm TL, seven neonate males, 130-137 mm TL, off Coffee Bay, Transkei, South Africa; SAM 39879, adult female, 1023 mm TL, Gulf of Mexico; UERJ 1641, adult male, 990 mm TL, off Rio de Janeiro, Brazil; USNM 220585, neonate male, 245 mm TL, unknown locality, The United States of America; USNM 217364, adult female, 1000 mm TL, Texas, The United States of America.

Diagnosis. *Cirrhigaleus asper* is distinguished from its congeners by having anterior margin of nostrils with second lobe conspicuously short as nasal barbels, and dermal denticles with median ridge broad with weak cusplets at posterior margin of crown (vs. median ridge very narrow and prominent cusplets). It also differs from *C. barbifer* and *C. australis* by larger length of upper labial furrow (1.6% of TL for holotype, 1.4%–1.6% of TL for paratypes vs. 1.1% of TL for *C. barbifer* vs. 0.9%, 0.9%–1.0% of TL for *C. australis*), and shorter length of pectoral anterior margin (14.4%, 12.5%–13.9% of TL vs. 15.3%–16.9% for *C. barbifer* vs. 15.2%, 14.8%–16.1% of TL for *C. australis*).

Cirrhigaleus asper is further distinguished from *C. barbifer* by having larger precaudal length (81.3%, 80.6%–81.7% of TL vs. 79.1%–79.9% of TL for *C. barbifer*), pre-branchial length (18.4%, 17.0%–18.8% of TL vs. 14.8%–16.8%) and internarial distance (3.6%, 3.7%–3.8% of TL vs. 3.0%–3.4% of TL).

Description. Single values are for holotype. Ranges between brackets are for paratypes and non-type specimens from Indian Ocean, respectively.

External morphology (Figs. 257–262; Tabs. 60, 62). Body trihedral, stout and robust, conspicuously arched dorsally from anterior margin of spiracle to pelvic fin insertion, turning more slender to the tail; body with greatest width at head than at trunk and abdomen; head width 1.5 (1.1–1.4, 0.9–1.4) times greater than trunk width and 1.8 (1.3–1.7, 0.9–1.7) times wider than abdomen width; body equally deep from head to abdomen with head height 0.9 (0.9–1.1, 0.8–1.1) times trunk height and 0.9 (1.0–1.1, 0.7–1.3) times abdomen height. Head flattened anteriorly and elongate, its length 22.4% (21.1%–22.6%, 20.3%–24.3%) of TL; head narrower at nostrils than at mouth (its width at nostrils 7.7%, 6.9%–7.3%, 7.8%–10.2% of TL; width at mouth 12.5%, 12.6%–13.4%, 11.6%–13.3% of TL). Eyes markedly elliptical with anterior and posterior margins notched; eyes conspicuously large, its length 4.5% (4.2%–4.5%, 3.6%–6.0%) of TL, corresponding to 5.8 (3.6–5.0, 2.1–5.0) times greater than its height. Prespiracular length 0.5 (0.5, 0.5–07) times prepectoral length and 1.7 (1.7–1.8, 1.5–1.8) times preorbital length. Spiracles crescent, located posteriorly and above the eyes; spiracles conspicuously large, its length 0.3 (0.3, 0.2–0.4) times eye length. Gill slit somewhat concave, vertical and markedly tall with fifth gill slit 1.1 (1.2–1.4, 1.0–1.4) times higher than first gill slit.

Snout rounded and short with preorbital length 6.5% (6.0%–6.5%, 6.5%–8.4%) of TL; nostrils equally distant to snout tip and mouth with prenarial length 0.9 (1.0–1.2, 1.0–1.2) times distance from nostrils to upper labial furrow and 0.5 (0.5–0.6, 0.5–0.6) times preoral length; nostrils with anterior margin bilobate and markedly broad; second lobe of anterior nostrils larger than first one, although not elongated as nasal barbells; anterior nasal flap with its length 1.5% (1.2%–1.3%, 1.0%–2.4%) of TL, corresponding to 14.7 (15.9–19.0, 9.6–22.5) times smaller than head length. Mouth arched and broad (its width 8.1%, 8.2%–8.3%, 7.4%–

8.8% of TL); upper labial furrow markedly small, its length 1.6% (1.4%–1.6%, 1.5%–2.8%) of TL with a small and thick fold; lower labial furrow also small, without fold. Teeth similar in both jaws, labial-lingually flattened, very broad but low at the crown; lower teeth larger than upper teeth; teeth unicuspid with cusp thick and large, somewhat upright and lateral; mesial cutting edge straight and diagonal; distal heel rounded; mesial heel pointed; apron very short and markedly wide. Three series of functional teeth on both jaws; upper jaw with 14–14 (14–13, 13–13) teeth rows; lower jaw with 12–12 (12–11, 12–12) teeth rows.

Dorsal fins conspicuously upright and vertical, both equally tall with first dorsal fin height 1.0 (1.0–2.1, 1.0–1.2) times height of second dorsal fin; first dorsal fin as large as second dorsal fin, its length 1.0 (0.9–1.5, 1.0–1.2) times length of second dorsal fin. Origin of the first dorsal fin located posteriorly to apex of pectoral fin, although near to it in most specimens. First dorsal fin with anterior margin convex and large, its length 13.7% (11.8%–12.4%, 11.2%–13.4%) of TL; posterior margin straight and large, its length 10.1% (8.0%–9.4%, 6.9%–10.2%) of TL; first dorsal apex narrow; free rear tip pointed; first dorsal fin conspicuously tall, its height 1.3 (1.3–1.5, 1.0–1.4) times greater than preorbital length and 1.6 (1.4–1.6, 1.5–2.1) times greater than inner margin length of first dorsal fin. First dorsal spine thick (its base width 1.1%, 1.1%–1.3%, 0.6%–1.2%) of TL) and markedly elongate, its length 5.7% (3.4%–6.1%, 1.9%–6.3%) of TL; first dorsal spine not reaching the fin apex, its length 0.7 (0.4–0.7, 0.2–0.7) times height of first dorsal.

Interdorsal space almost equal to prepectoral length, corresponding to 1.1 (1.0, 0.8–1.2) times the latter and 2.4 (2.3–2.6, 2.0–3.0) times larger than dorsal-caudal space. Origin of second dorsal fin over free rear tips of pelvic fins. Second dorsal fin with anterior margin convex and large, its length 13.9% (7.8%–13.5%, 11.5%–13.8%) of TL; posterior margin markedly falcate and elongate, its length 6.9% (3.9%–7.9%, 5.8%–8.0%) of TL; apex of second dorsal fin conspicuously slender and lobulated; free rear tip pointed. Second dorsal spine thick (its base width 1.0%, 0.9%–1.0%, 0.9%–1.2% of TL), and elongate, its length 7.3% (3.4%–5.3%, 4.3%–7.2%) of TL and not reaching the fin apex with its length 0.9 (0.4–1.4, 0.6-0.9) times height of second dorsal fin; second dorsal spine slightly larger than first one (its length 1.3, 0.6–1.4, 0.9–2.2 times length of first dorsal spine).

Pectoral fin conspicuously wide distally and square-like; pectoral anterior margin convex and elongate, its length 1.7 (1.5–1.7, 1.4–1.9) times larger than inner margin length, and corresponding at least to one-half the distance between pectoral and pelvic fins; inner margin markedly convex; posterior margin straight and large, its length 10.5% (8.7%–12.0%, 9.7%–12.9%) of TL; apex and free rear tip of pectoral fins conspicuously rounded and broad, not lobulated and almost reaching the same length. Pectoral-pelvic distance 1.1 (1.0–1.3, 0.7–1.5) times pelvic-caudal space; the latter 1.0 (1.0, 0.9–1.3) times interdorsal space. Pelvic fins in the midline between first and second dorsal fin, although nearest to second dorsal fin in some paratypes and non-type specimens. Pelvic fins markedly broad with anterior margin somewhat convex, posterior margin straight; pelvic apex rounded and conspicuously wide; free rear tips rounded and lobulated, although more slender in males. Claspers in adults slender and flattened ventrally; claspers very short its inner length 1.1, (1.2, 0.4–0.6) times pelvic inner margin length, transcending pelvic free rear tips; clasper groove very large, vertical, placed dorsally; apopyle and hypopyle with narrow apertures, located proximal and distally in the clasper groove, respectively; rhipidion flap-like, markedly narrow and short (not reaches distal end of clasper), attached medial-distally to clasper.

Caudal peduncle very short, its length 9.5% (8.2%–9.3%, 7.4%–10.1%) of TL with lateral keel prominent and thick since insertion of second dorsal fin to behind origin of caudal fin; upper and lower precaudal pits absent. Caudal fin rather rectangular with dorsal caudal margin convex anteriorly and turning straight until the dorsal tip; dorsal caudal margin 0.9 (0.8–0.9, 0.8–1.0) times head length and 1.7 (1.7–1.8, 1.7–3.2) times larger than length of preventral caudal margin; dorsal caudal tip pointed; upper post-ventral caudal margin concave, although straight near the dorsal tip; lower post-ventral caudal margin straight; preventral caudal margin convex and short, its length 1.8 (1.9–3.1, 1.4–2.6) times larger than inner length of pelvic fin; caudal fin slightly continuous between lobes and markedly broad at fork, its width 7.8% (7.1%–7.6%, 6.8%–13.0%) of TL.

Dermal denticles (Fig. 262). Dermal denticles tricuspid and heart-shaped, conspicuously broad at the crown and imbricated; denticles with its width as large as its length; median cusp prominent, pointed and elongate; lateral cusps very short to inconspicuous; one or two secondary cusplets on each side of posterior edge of crown, tiny and weak; median ridge strong, high and markedly wide with conspicuous anterior furrow and often two small ridges on each side; median ridge projecting anteriorly beyond the crown base; one or two lateral ridges on each side, almost straight, tall and well elongate, reaching posterior edge of crown; lateral furrow very profound and wide, placed aside each lateral ridge.

Coloration. Body brownish-grey dorsally and white ventrally; pectoral, pelvic, dorsal and caudal fins darker than the rest of the body. Pectoral fins with inner and posterior margins homogenously white. Pelvic fins pale ventrally with inner and posterior margins broadly white. First and second dorsal fins broadly white from the apex and posterior margin to the free rear tip, lighter at the fin base near the dorsal spine. Dorsal fin spines brown, white at its base and at the tip. Caudal fin also brown with white postventral margins, except at the dorsal tip; ventral caudal tip broadly white; dorsal caudal margin white, although not near the dorsal tip; ventral lobe with white basal marking; caudal stripe light brown.

Vertebral counts (Tab. 63). Monospondylous vertebrae 52 (50–51; 49–51); precaudal vertebrae 87 (87–90; 85–89); caudal vertebrae 29 (29–32; 27–30); total vertebrae 116 (119; 115–117).

Geographical distribution (Fig. 263). It occurs in the Indian and West Atlantic Oceans from Seychelles to South Africa, and Texas in U.S.A to Rio de Janeiro in Brazil.

Etymology. The name of this species refers to the rough texture of the skin due to large and thick dermal denticles.

Comparative material. All specimens listed in this Chapter.

Remarks.

Preserved condition of type specimens. Type specimens of *Cirrhigaleus asper* are well preserved at the NHM in London, providing efficient assessments for the morphological characterization of this nominal species. Some inner organs were taken out from the stomach for all these material probably during the collecting process. Skin samples from the head, left side of the body below first dorsal fin, at the mouth, and dorsally in the caudal penduncle were taken for analysis of the dermal denticles by Merrett. This author also made large incisions from posterior corner of the mouth to fifth gill slit for counting teeth and for analysis of gill rakers of holotype and paratypes.

Left pectoral fin of the holotype lacks its free rear tip and it comprises the only main damage for this specimen that it seems to be due to natural incidents before capture. One of the paratypes (BMNH 1972.10.10. 2) has similar damage but in the apex of right pectoral fin. Another paratype (BMNH 1972.10.10.4) lost its second dorsal fin partially, although its second dorsal spine is still present. Dorsal spines are also well preserved although some of them worned down with the time for BMNH 1972.10.10.2 in the first dorsal spine and both BMNH 1972.10.10.3 and BMNH 1972.10.10.4 in the second dorsal spine.

Morphological variations in *Cirrhigaleus asper*. Specimens of *C. asper* exhibit few morphological variations with growth and it is noticed for the first time in the present study. However, these variations are not comparable to those noticed for *C. barbifer* that make difficult to properly identify the species in earlier stages of maturity. Secondary lobe of anterior margin of nostrils decreases in length with growth for *C. asper* (1.4%–2.4% of TL in juveniles vs. 1.0%–1.4% of TL in adults), a condition similar to *C. barbifer*. Preoral length (8.8%–11.1% of TL in juveniles vs. 7.3%–8.4% of TL in adults), eye length (4.8%–6.0% of TL in juveniles vs. 3.6%–4.3% of TL in adults) and length of dorsal-caudal margin (20.7%–23.2% of TL in juveniles vs. 18.8%–19.7% of TL in adults) decrease as well in specimens of *C. asper*, which it differs from specimens of *C. barbifer* that show heterogeneous decreasing with growth.

Other ontogenetic variations are noticed for *C. asper*, for instance: interdorsal space (19.2%–22.8% of TL in juveniles vs. 22.5%–24.1% of TL in adults); distance from pectoral fin to pelvic fin (17.6%–25.6% of TL in juveniles vs. 25.2%–33.0% of TL in adults); precaudal length (76.4%–79.6% of TL in juveniles vs. 83.5%–84.8% of TL in adults); and pre-second dorsal length (60.0%–62.5% of TL in juveniles vs. 67.0%–68.3% of TL in adults). *Cirrhigaleus barbifer* exhibits similar variations with exception to interdorsal space that it is constant with growth.

In contrast to the Japanese species, length of dorsal spines in *C. asper* and origin of first dorsal fin do not varies with growth. Heights of first and second dorsal fins in specimens of *C. asper* also do not change with maturity, which it differs from *C. barbifer* that increase in size. Distance between pelvic fins and caudal fin, and dorsal-caudal space are constant with growth in *C. asper*, differing from *C. barbifer* that decrease in adults. Pelvic fins are always nearest to the second dorsal fin from juveniles to adults of *C. asper* like it is observed for its congeners.

Specimens of *C. asper* from the West Atlantic Ocean show differences in external morphometric with specimens from the Indian Ocean. Preorbital length is greater in specimens from the Indian Ocean (6.5%–8.4% of TL) than in specimens from West Central Atlantic (5.9%–6.0% of TL) and Southwest Atlantic Oceans (6.0%–6.3% of TL). Prenarial length is greater in specimens from Indian Ocean (4.2%–5.7% of TL vs. 2.9%–3.1% of TL for West Central Atlantic vs. 3.6%–4.2% of TL in Southwest Atlantic). Preoral length is also larger in specimens from the Indian Ocean (7.3%–11.1% of TL vs. 5.3%–6.9% of TL vs. 6.1%–7.3% of TL). Great differences are observed with specimens from Western Central Atlantic but preserved conditions of this material may interfere in these interpretations and needs to be analyzed through additional material in the future.

Specimens from the Southwestern Atlantic Ocean also show smaller prepectoral length, length of head, pre-first branchial length and pre-spiracular distance than type material of *C. asper*. External morphology, including dentition and dermal denticles, overlaps between these specimens. Analysis of vertebral counts on specimens from the South Atlantic Ocean was not yet observed for comparisons.

Cirrhigaleus australis **White, Last & Stevens, 2007**

(**Southern Mandarin dogfish**)

Figures 264–270; Tables 61–63

Cirrhigaleus barbifer: Last & Stevens, 1994 (in part): 48, 68 (cited, description; Southwest Pacific Ocean); Compagno & Niem, 1998 (in part): 1203–1224 (listed, cited; Southwest Pacific Ocean).

Cirrhigaleus australis White, Last & Stevens, 2007: 19–30 (original description, illustrated; type by original designation; Australia); Ebert *et al*., 2013: 74, 81 (cited, description; Southwest Pacific Ocean).

Holotype. CSIRO H 5789-01, adult female, 970 mm TL, East of Bicheno, Tasmania, Australia, 41°55'S, 148°37'E, 360–414 meters depth. Collected on 18 May 2002.

Paratypes (3 specimens): AMS I 19154-001, juvenile female, 705 mm TL, off Brush Island, New South Wales, Australia, 35°34'S, 150°45'E, 493 meters depth, collected on 6 July 1976; AMS I 27022-001, adult female, 1205 mm TL, Northeast of Sydney, New South Wales, Australia, 33°00'S, 152°00'E, 640 meters depth, collected on March 1986; AMS I 42891-001, adult female, 1085 mm TL, Southeast of Green Cape, New South Wales, Australia, 37°30'S, 150°30'E, 400 meters depth, collected on 3 November 2003.

Type locality: Bicheno, Tasmania, Australia.

Non-type material (7 specimens): AMS I 45670-001, juvenile male, 630 mm TL, Britannia Seamount, New South Wales, Australia; CSIRO H 7042-01, juvenile male, 510 mm TL, Browns Mount, New South Wales, Australia, 34°02'S,151°39'E; CSIRO H 7042-02, juvenile female, 639 mm TL, locality same as CSIRO 7042-01; CSIRO H 7042-03, juvenile female, 634 mm TL, locality same as CSIRO 7042-01; CSIRO H 7042-04, juvenile female, 605 mm TL, locality same as CSIRO 7042-01; CSIRO H 7048-01, adult male, 993 mm TL, east of Tweed Heads, New South Wales, Australia, 28°17'S,153°53'E; CSIRO H 7064-01, juvenile female, 705 mm TL, Northeast of Yamba, New South Wales, Australia, 29°11'S,153°52'E.

Diagnosis. *Cirrhigaleus australis* is distinguished from its congeners on having body light grey dorsally (vs. dark brown), and dermal denticles with two or more cusplets lateral-posteriorly (vs. single cusplets on each side for *C. barbifer* vs. one or two weak cusplets in *C. asper*). *Cirrhigaleus australis* is clearly distinct from *C. asper* by having nasal barbel moustache-like and well elongate, usually reaching the mouth (vs. nasal barbel very short, transcending posterior margin of nostrils). It can be separated from *C. barbifer* by smaller upper labial furrow, its length 0.9% for holotype, 0.9%–1.0% of TL for paratypes (vs. 1.1% of TL for *C. barbifer*), and wider internarial space, comprising 3.6%, 3.6%–3.9% of TL (vs. 3.0%–3.4% of TL for *C. barbifer*).

Adult specimens of *C. australis* is also different from those of *C. barbifer* on having: shorter pre-first dorsal length in *C. australis* (30.7% vs. 31.8%–33.3% of TL); dorsal-caudal space more elongate (9.0% vs. 7.5%–7.6% of TL); larger distance from pelvic fin to caudal fin (21.9% vs. 18.4%–20.5% of TL); more elongate head (its length 22.0% vs. 18.8%–20.7% of TL for *C. barbifer*); narrower pectoral fins (its anterior margin length 14.6% vs. 15.5%–16.9% of TL for *C. barbifer*; its inner margin length 8.1% vs. 8.3%–8.9% of TL for *C. barbifer*; its posterior margin length 10.8% vs. 11.4% of TL for *C. barbifer*); lower dorsal fins with first dorsal height 9.8% (vs. 10.0%–10.8% of TL for *C. barbifer*), and second dorsal height 8.7% (vs. 9.3%–10.3% of TL for *C. barbifer*); smaller caudal fin, its dorsal-caudal margin length 20.1% (vs. 20.5% of TL for *C. barbifer*), and length of pre-ventral caudal margin 10.0% (vs. 11.0%–11.6% of TL for *C. barbifer*).

Description.

External morphology (Figs. 264–269; Tabs. 61, 62). Body trihedral, strongly robust and humped in all its extension, conspicuously arched from posterior margin of the eye to pelvic fin insertion with belly noticeable ventrally (more slender when juveniles than in adults); body equally wide from head to abdomen with head width 1.0 (0.9–1.1, 1.0–1.2) times trunk width, and 1.0 (1.3–1.6, 1.1–1.8) times abdomen width; body deepest at trunk and abdomen with head height 0.7 (0.9–1.5, 0.9–1.0) times trunk height, and 0.7 (0.8–1.5, 0.8–1.0) times abdomen height. Head very small, its length 20.0% (20.2%–22.6%, 18.2%–22.0%) of TL, flattened and narrow anteriorly, humped and broader posteriorly near the mouth; head width at nostrils 7.1% (6.5%–7.5%, 6.5%–7.7%) of TL, and at mouth 11.8% (10.4%–12.6%, 11.5%–13.6%) of TL. Eyes oval and elongate, its length 3.3% (3.1%–3.9%, 3.7%–4.4%) of TL and corresponding to 2.1 (2.2–3.1, 2.4–3.6) times its height; anterior margin of eye convex, posterior margin slightly notched, prominent dorsally. Spiracles crescent and wide, its length 0.8 (0.9–1.5, 0.8–1.3) times eyes height, placed lateral-posteriorly and above the eyes. Gill slits vertical and slightly concave, tall with height of fifth gill slit 2.3% (2.2%–2.4%, 2.0%–2.6%) of TL, corresponding to 1.3 (1.1–1.4, 0.9–1.1) times first gill slit height.

Snout very short (preorbital length 6.5%, 5.8%–7.2%, 5.9%–7.2% of TL) and conspicuously rounded at the tip; nostrils equally nearest snout tip and upper labial furrow, its prenarial length 0.9 (0.9–1.0, 0.9–1.1) times distance from nostrils to upper labial furrow; anterior nasal flap bilobate with second lobe markedly elongate as barbells, almost reaching anterior margin of mouth in adults (young specimens have barbels markedly beyond the posterior margin of the mouth); anterior nasal flap length 5.0% (4.4%–5.9%, 5.3%–7.1%) of TL, corresponding to 4.0 (3.6–5.1, 2.6–4.2) times in head length.

Short distance from mouth to snout tip (preoral length 7.3%, 6.9%–8.0%, 7.7%–8.6% of TL). Mouth strongly arched and wide, its width 1.9 (1.7–1.8, 1.6–1.9) times prenarial length, and 2.2 (1.8–2.2, 2.0–2.3) times broader than internarial space. Upper labial furrow markedly short, its length 0.9% (0.9%–1.0%, 1.2%–1.6%) of TL, with fat fold; lower labial furrow elongate, lacking a fold. Teeth similar in both jaws, compressed labial-lingually, conspicuously broad and low; teeth of upper jaw much smaller than those of lower jaw; teeth unicuspid with cusp pointed, thin, cylindrical and short, directed laterally; mesial cutting edge somewhat convex, although diagonally; mesial and distal heels rounded; apron slender and short, larger on lower teeth than upper teeth. Three series of functional teeth on both jaws; upper jaw with 12–12 (13–12, 14–14) teeth rows; lower jaw with 10–10 (10–10, 11–11) teeth rows.

Dorsal fins conspicuously upright and vertical, both equally tall with first dorsal fin height 1.0 (0.9–1.1, 1.0–1.2) times height of second dorsal fin; first dorsal fin as large as second dorsal fin, its length 1.0 (1.0–1.2, 0.9–1.0) times length of second dorsal fin. Origin of first dorsal fin beyond the free rear tips of pectoral fins in adults. First dorsal fin markedly slender with apex rounded, and broad on its base (base length 8.4%, 8.2%–8.8%, 7.7%–9.2% of TL); anterior margin convex and large, its length 12.2% (13.6%–13.9%, 11.7%–14.6%) of TL; posterior margin concave and elongate, its length 10.6% (9.6%–11.4%, 9.4%–11.3%) of TL; inner margin short, its length 6.3% (4.9%–6.8%, 5.3%–6.5%) of TL with pointed free rear tip; first dorsal fin height 1.6 (1.4–2.0, 1.6–1.8) times greater than its inner margin length, and 1.5 (1.4–1.9, 1.3–1.7) times preorbital length. First dorsal spine straight, markedly elongate, although never reaching the fin apex, its length 5.7% (2.5%–5.2%, 3.1%–6.4%) of TL, corresponding to two-fourth the height of first dorsal fin. Interdorsal distance 1.2 (1.1–1.2, 1.0–1.2) times pre-pectoral length, and 3.0 (2.5–2.9, 2.3–2.7) times greater than dorsal-caudal space.

Origin of second dorsal fin posterior to free rear tips of pelvic fins. Second dorsal fin slender at the tip, apex rounded and lobulate, broad at its base (base length 9.6%, 9.2%–10.0%, 9.0%–10.1% of TL); anterior margin convex and large, its length 14.2% (13.5%–14.8%, 13.6%–14.8%) of TL; posterior margin strongly concave, not falcate (half-moon shaped in juveniles); second dorsal fin height 1.7 (1.5–2.1, 1.5–1.9) times greater than its inner margin length; inner margin also short, its length 5.5% (4.5%–6.3%, 4.8%–5.8%) of TL. Second dorsal spine convex and broad (its base width 1.1%, 1.0%–1.1%, 0.8%–1.2% of TL), conspicuously elongate, its length 6.4% (5.9%–7.6%, 5.5%–8.1%) of TL; second dorsal spine corresponding to 1.1 (1.4–2.3, 1.3–2.1) times length of first dorsal spine and three-forth the height of second dorsal fin, exceeding the fin apex in juveniles only.

Pectoral fin narrow, although broader posteriorly than anteriorly (its base length 5.0%, 4.5%–5.1%, 4.4%–4.9% of TL); anterior and inner margins markedly convex; posterior margin slightly concave, never greater than the trunk height when adpressed laterally (posterior margin length 0.6, 0.9–1.1, 0.9–1.1 times trunk height); apex and free rear tips of pectoral fin rounded and wide (sometimes lobulate in paratypes) with apex transcending horizontal line traced at free rear tip; pectoral anterior margin length 1.5 (1.3–1.4, 1.2–1.5) times posterior margin length, and 1.8 (1.7–1.8, 1.6–1.9) times inner margin length.

Pelvic fin nearest to second dorsal fin than to first dorsal fin; length pelvic fin 1.7 (1.6–1.9, 1.6–2.1) times in interdorsal space. Pelvic fins conspicuously broad, pentagonal with anterior margin slightly convex, inner margin straight, and posterior margin somewhat concave; markedly rounded at apex; free rear tips triangular and lobulate; pelvic length 1.1 (1.0–1.3, 1.0–1.3) times length of preventral caudal margin. Claspers in adults flattened ventrally and markedly wide but narrower distally; claspers very short its inner length 0.5–1.2 times pelvic inner margin length, exceeding pelvic free rear tips; clasper groove elongate, vertical, placed dorsally; apopyle with narrow aperture, located anterior in the clasper groove; hypopyle with broad aperture, placed in the distal end of clasper groove, anteriorly the rhipidion; rhipidion flap-like, slender and large, attached medial-distally to clasper.

Pelvic-caudal space 0.9 (0.9–1.0, 0.9–1.0) times interdorsal space. Caudal peduncle thick in cross-section and conspicuously short with dorsal-caudal distance 7.5% (8.0%–8.6%, 7.8%–9.1%) of TL, corresponding to 3.0 (2.5–2.9, 2.3–2.7) times smaller than interdorsal space; lateral keel prominent almost as a fold, since second dorsal fin insertion to backwards origin of caudal fin; upper and lower precaudal pits absent. Caudal fin conspicuously rectangular; dorsal caudal margin straight and elongate, its length 1.1 (0.9–1.0, 0.9–1.2) times head length and 1.8 (1.7–1.9, 1.8–2.0) times greater than length of preventral caudal margin; posterior caudal tip rounded; upper post-ventral margin convex, evidently straight proximally; lower post-ventral margin convex; preventral caudal margin somewhat straight and small, its length 2.0 (1.6–2.2, 1.7–2.3) times greater than length of pelvic inner margin; ventral caudal tip rounded; transition between upper and lower caudal lobes continuous; caudal fork markedly broad, its width 7.6% (7.5%–8.0%, 7.2%–8.6%) of TL.

Dermal denticles (Fig. 269). Dermal denticles tricuspid and bat-like, imbricate, large and markedly broad at the crown; denticles with its width as large as its length; cusps pointed with median cusp much larger than lateral ones; median ridge prominent and elongate, thin and tall, transcending slightly the anterior base of the crown; lateral ridges thin, short and low, convex laterally; median furrow elongate and profound, placed over median ridge; lateral furrow short and deep over each lateral ridge; one secondary cusp (or cusplet) sometimes present on each side of posterior base of the crown; secondary cusp as large as lateral cusp.

Coloration. Body light grey dorsal and laterally, white ventrally. Nasal barbels white, and slightly grey lateral-proximally. First dorsal fin dark grey with white posterior margin from its apex to the free rear tip, submarginal bar light grey, white spots in the anterior margin near its apex. Second dorsal fin also dark grey with whitish posterior margin until its midline, and submarginal bar light grey. Dorsal spines white, greyish proximal and distally, although whitish at the tips. Pectoral fins grey dorsally and light grey ventrally, with inner and posterior margins discreetly whitish at its edge. Pelvic fins also grey, lighter ventrally, with posterior margin sparsely whitish. Caudal fin dark grey, whitish medially; post-ventral margins white but not uniform, broadly white in the dorsal and ventral tips; black caudal stripe absent. In recent collected specimens, large dark grey blotches are observed ventrally in both pectoral and pelvic fins.

Vertebral counts (Tab. 63). Monospondylous vertebrae 50 for holotype (50 for paratypes, 49–52 for non-type material); diplospondylous vertebrae 66 (64, 62–67); precaudal vertebrae 85 (86, 85–89); total vertebrae 117 (114, 114–116).

Geographical distribution (Fig. 270). It is endemic to Southern Australia from Tweed Heads to Tasmania.

Etymology. The epithet "*australis*" refers to the temperate Waters of Southern Hemisphere region from where the species is originally described.

Remarks.

Ontogenetic variations in *Cirrhigaleus australis.* Ontogenetic variations are conspicuously present among specimens of *C. australis*, which it is in agreement with findings of White *et al*. (2007). These conditions are similar to those shown for *C. barbifer* that were described earlier in this Chapter. White *et al*. (2007) noticed increasing of prepelvic length, distance from pectoral to pelvic fins, interorbital space, and length of second dorsal spine with growth. These ontogenetic variations are also supported in the current analysis. Pre-branchial length, space between pelvic and caudal fins, and eye length do not change with maturity, according to the current analysis, which it is in contrast to White *et al*. (2007).

New ontogenetic variations are founded in the present study and it was not reported previously in the literature. The position of origin of first dorsal fin varies from over or just anterior to pectoral free rear tips in juveniles while it is behind it in adults. Length of dorsal spines is larger in adults than juveniles (first dorsal spine length 6.4% of TL vs. 3.1%–4.6% of TL), and length of nasal barbels (its length 5.3% of TL vs. 6.2%–7.1% of TL). Increasing of pre-pectoral length and head length are also observed with growth for *C. australis*. Prenarial length, length of pectoral inner and posterior margins, and length of caudal fin decrease in adults of *C. australis*. In contrast, *C. barbifer* does not change with maturity of head length, prenarial length, and size of pectoral fin while its dorsal-caudal margin increase in length with growth.

Morphological comparisons with *Cirrhigaleus barbifer*. According to White *et al*. (2007), *C. australis* is distinct from *C. barbifer* by having smaller eye, shorter second dorsal spine, and shorter upper labial furrow, and these differences are also supported in the present study. The holotype of *C. australis* is further distinct from specimens of *C. barbifer* in the current analysis by precaudal length, pre-branchial distance, length of first dorsal anterior margin, length of pectoral anterior margin, and length of dorsal-caudal margin of caudal fin as it was discussed previously in this Chapter. Some paratypes also exhibit these differences but it depends on its maturity. Length of upper labial furrow and distance between nostrils definitely are efficient characters for separation between these two species because it does not vary with growth.

Many morphological differences (including morphometrics) can be hidden if specimens from different stages of maturity are compared between *C. australis* and *C. barbifer*. Comparative analysis between adult specimens of these two nominal species further reveal greater differences in external measurements, for instance: shorter pre-second dorsal length in *C. australis* (61.8% vs. 62.0%–63.8% of TL for *C. barbifer*); shorter pre-first dorsal length in *C. australis* (30.7% vs. 31.8%–33.3% of TL); larger pre-vent distance (56.6% vs. 54.4%–56.3% of TL); larger pre-branchial length (17.5% vs. 14.8%–16.8% of TL); larger interdorsal space (22.5% vs. 21.9%–22.4% of TL); dorsal-caudal space more elongated (9.0% vs. 7.5%–

7.6% of TL); larger distance between pectoral and pelvic fins (32.0% vs. 28.2%–31.8% of TL); more elongated distance from pelvic fin to caudal fin (21.9% vs. 18.4%–20.5% of TL).

Adults of *C. australis* also exhibit more elongated head (its length 22.0% vs. 18.8%–20.7% of TL for *C. barbifer*), narrower pectoral fin (its anterior margin length 14.6% vs. 15.5%–16.9% of TL; its inner margin length 8.1% vs. 8.3%–8.9% of TL; its posterior margin length 10.8% vs. 11.4% of TL), lower dorsal fins (first dorsal height 9.8% vs. 10.0%–10.8% of TL; second dorsal height 8.7% vs. 9.3%–10.3% of TL), smaller caudal fin (its dorsal-caudal margin length 20.1% vs. 20.5% of TL; pre-ventral caudal margin 10.0% vs. 11.0%–11.6% of TL) than specimens of *C. barbifer*.

Specimens of *C. barbifer* from New Zealand exhibit intermediary characteristics with *C. australis* concerning its external morphology. Most specimens from New Zealand, however, are distinct from *C. australis* by: head longer and flattened (vs. shorter and arched in *C. australis*); snout elongate and more obtuse (vs. short and rounded snout); broader dorsal fins at the fin web with straight posterior margin (vs. thinner dorsal fins at fin web with strongly concave posterior margins); caudal fin wider at the caudal fork (vs. thinner at the caudal fork); second dorsal spine transcending the fin apex (vs. not transcending the fin apex). These differences indicate that *C. australis* does not occur in New Zealand as proposed by White *et al*. (2007). However, the overlapping of external measurements between New Zealand specimens and specimens of *C. australis* as well as *C. barbifer* also suggest that these findings still need to be better investigated.

White *et al*. (2007) reported distinction on size of dermal denticles between *C. barbifer* from Indonesia and *C. australis*, which is much smaller in the latter species. Our results also show that *C. barbifer* (CSIRO H 5875-09) from Indonesia differs from *C. australis* by other aspects, such as: body much more humped dorsally; barbels do not reach anterior margin of the mouth; dorsal fins with posterior margin not well concave; dorsal spines transcending greatly the fin apex; body dark grey.

Comparative material. Specimens of *Cirrhigaleus* listed previously in this Chapter.

Discussion.

Generic allocation of *Cirrhigaleus asper*. Merrett (1973) noticed great morphological differences between the nominal species "*asper*" and species of *Squalus*, such as: size of dermal denticles (three times larger in *C. asper* than in species of Squalidae); position of origin of first dorsal fin (behind free rear tips of pectoral fins vs. prior or over free rear tips of pectoral fins in Squalidae, except for *S. acanthias*); origin of pelvic fins (just prior origin of second dorsal fin in *C. asper* vs. well anterior to second dorsal fin); length of caudal peduncle (shorter in *C. asper*), and precaudal pit (absent vs. present in Squalidae). These differences are also observed in the present study. Despite of it, Merrett (1973) replaced this nominal species into the genus *Squalus* due to similarities regarding dentition, dorsal spines, shape of dermal denticles, and absence of barbels.

Cirrhigaleus asper shares with species of Squalidae nostrils not markedly elongate as moustache, which it is in agreement with Merrett (1973), Compagno (1984), Bass *et al*. (1976), and White *et al*. (2007). Lateral nasal lobe is often slightly larger than medial lobe in species of this family as stated previously by Garrick & Paul (1971), which differs from those of *Cirrhigaleus* whose lateral nasal lobe is shorter than medial one, including *C. asper*. Medial nasal lobe of *C. asper*, *C. barbifer* and *C. australis* bears fleshy core and it is innervated by buccopharyngeal branch of facial nerve (VII), which define precisely the nasal barbel in the genus (Fig. 271). These findings are congruent with Shirai (1992) that supported *Cirrhigaleus* as a monophyletic and separate genus from *Squalus* based on this characteristic.

The nerve buccopharyngeal branch of facial nerve (VII) arise from the foramen prooticum (V-VII) at the interorbital wall and runs aside the suborbital shelf and over *suborbitalis* muscle in the palatoquadrate till it reaches the antorbital cartilage. Then, the branch buccopharyngeal runs ventrally in the subethmoidal region and reaches the nasal capsule where it splits into two different small branches. The left branch is thicker than right branch and it runs to the origin of the nasal barbel at the fleshy core. The second branch runs straight to the rostral tip and aside the rostral keel (Fig. 271).

In contrast, species of Squalidae do not bear innervation in the anterior nasal flap. In this case, medial nasal lobe is internally supported by a thin nasal cartilage, lacking fleshy core (Fig. 272). The buccopharyngeal nerve runs exclusively to the tip of the rostrum in *Squalus* and *Flakeus*, indicating that the anterior nasal flap in Squalidae does not comprise a real nasal barbel like it is noticed for species of *Cirrhigaleus*. Small innervations of the buccopharyngeal branch of facialis nerve runs to the nasal capsule, although it does not reach the anterior nasal flap in Squalidae. These results strongly support that *C. asper* is correctly allocated in *Cirrhigaleus* as it was proposed by Shirai (1992) and followed by Compagno *et al*. (2005), White *et al*. (2007), and Naylor *et al*. (2012a,b).

External morphology of *C. asper* is much more similar to its congeners than previously thought, according to the current results. It shares with *C. barbifer* and *C. australis* many characteristics, such as: body trihedral and markedly robust; dermal denticles tricuspid and conspicuously wide with some cusplets; teeth unicuspid with apron markedly broad and cusp somewhat upright; first and second dorsal fins vertical and upright, equally tall; first and second dorsal spines almost equal in length (second spine often worn down but not broken); second dorsal fin placed over pelvic free rear tips; upper labial furrow markedly short with thick fold. Analysis of the skeletal anatomy of *C. asper* gives additional support to the current hypothesis. Shirai (1992) stated that this species and *C. barbifer* lack supraethmoidal processes in the neurocranium and it is also supported in the present study. New characteristics of the neurocranium, claspers, pectoral and pelvic apparatus of *C. asper* shows to be much more similar to those of *C. barbifer* and *C. australis*[1] than to species of Squalidae.

Morphological similarities pointed out previously (e.g. Merrett, 1973; Bass *et al*., 1976) for *C. asper* and species of Squalidae regarding vertebral counts, dentition, and morphology of terminal cartilages of the claspers are also observed when *C. barbifer* and *C. australis* are included. It is important to notice that these characteristics are also present in some species of *Centrophorus*, indicating not to be efficient for characterization at genus level. The current results clearly indicate that the lacking of comparative investigations between *C. asper* and its congeners together with species of Squalidae contributed to the misunderstanding about its taxonomic status.

Validity and taxonomic classification of *Cirrhigaleus*. The current analysis proposes a new hypothesis for integrating the genus *Cirrhigaleus* into a separate and distinct group within the order Squaliformes. These findings are in disagreement with recent Systematic analysis in which *Cirrhigaleus* is considered sister-group of *Squalus*, comprising the family Squalidae (e.g. Shirai, 1992; Naylor *et al*., 2012a,b). Squalidae is defined as a group of sharks that bear teeth similar in both jaws with oblique cusp, ungrooved dorsal spines, caudal fin lacking subterminal notch, and presence of lateral caudal keel in the caudal peduncle and upper and lower precaudal pits (Müller & Henle, 1841; Garman, 1913; Fowler, 1941; Merrett, 1973; Bass *et al*., 1976; Bigelow & Schroeder, 1957; Compagno, 1984; Compagno *et al*., 2005). The latter two characteristics, however, are not observed in the genus *Cirrhigaleus*, according to the current results. Caudal keel is as a dermal fold in the genus and almost inconspicuous in young specimens of *C. australis*. Similar dermal fold is noticed for *Oxynotus* ventrally

[1] Analysis of the skeletal anatomy on species of *Cirrhigaleus* is provided on Chapter 1.

between pectoral and pelvic fins, according to the current analysis and Garman (1913), Bigelow & Schroeder (1948, 1957), and Compagno *et al.* (2005). *Centrophorus*, *Centroselachus* and *Isistius* exhibit small caudal keel laterally in the caudal peduncle as well. Teeth similar in both jaws are observed in some species of *Centrophorus*, indicating that the characteristics that define Squalidae may also be applied to other families of Squaliformes (e.g. Garman, 1913; Fowler, 1941; Bass *et al*., 1976; Compagno, 1984; Compagno *et al*., 2005).

External morphological characteristics often used to distinguish families of Squaliformes are also noticed in *Cirrhigaleus*. Species of the genus are characterized by body robust and trihedral in cross-section, and dorsal fins upright, equally tall and large, bearing dorsal spines conspicuously elongate that often exceeds apex of dorsal fins. These features are applied to species of *Oxynotus*. Absence of precaudal pits, transition between upper and lower caudal lobes conspicuously continuous, rough skin due to robust dermal denticles tricuspid with cusplets at posterior margin of the crown are additional characteristics that *Cirrhigaleus* share with other members of Squaliformes, such as, *Centrophorus*, *Somniosus*, *Dalatias*, *Centroscymnus* rather than members of Squalidae. The same problematic for providing efficient characteristics to define Squalidae are observed for other families of Squaliformes. Teeth unlike on both jaws and absence of dorsal spines are examples that overlap in more than one group, including Etmopteridae, Somniosidae, and Dalatiidae. These results suggest that the characters that define these families require further morphological revisions.

In the current study, new distinct characteristics are noticed between *Cirrhigaleus* and members of Squalidae, for instance, upper labial furrow small with thick fold (vs. upper labial furrow large and thin in *Squalus*), spiracles above the eyes dorsally (vs. eyes placed laterally behind the eyes in *Squalus*), dermal denticles with cusplets at posterior margin of the crown, and second dorsal fin with its origin over pelvic free rear tips (vs. origin of second dorsal fin far behind pelvic free rear tips in *Squalus*). Anterior margin of nostrils innervated by buccopharyngeal branch of the facial nerve in *Cirrhigaleus* also clearly separates it from members of Squalidae and supports the validity of *Cirrhigaleus* as stated previously by Shirai (1992). Exclusive morphological characteristics define higher taxonomic groups in Squaliformes such as Etmopteridae that it is characterized by having photomarks and photophores throughout the body.

Pectoral articulation comprised by procondyle and meso-metacondyle, clasper with accessory ventral marginal 2 cartilage, and pelvic articulation formed by a dorsal condyle + facet and ventral condyle observed in the present study[2] and works of Yano (1986), Shirai (1992), Silva & Carvalho (2015) and Silva (2014) are skeletal characteristics of *Cirrhigaleus* whose evolutionary condition is similar to other families in Squaliformes rather than those of *Squalus*. Lacking of rostral appendages and supraethmoidal processes in the neurocranium as well as narrow antorbital cartilage are also examples of characteristics that are similar to the conditions observed, for instance, in *Etmopterus* (e.g. Yano, 1986; Shirai, 1992; Silva & Carvalho, 2015), *Somniosus* (e.g. Jungersen, 1899) and *Centrophorus* (e.g. Yano, 1986; Shirai, 1992). These evidences provide additional support to do not include *Cirrhigaleus* within Squalidae. To be corroborated, the current hypothesis still need to be tested through investigations on the Systematics between *Cirrhigaleus* and species of Squalidae based on new and revised morphological characters[3].

Shirai (1992) and Carvalho (1996) supported that *Squalus* and *Cirrhigaleus* together are sister-group of Hypnosqualea that includes Squatiniformes, Pristiophoriformes, and Rajiformes. Despite of not supporting the monophyly of Squaliformes, Shirai (1992)

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[2] Descriptions and comparisons of skeletal components of *Cirrhigaleus* are provided in Chapter 1.

[3] See list of morphological characters provided in Chapter 1.

provided homoplastic characters for its major groups. The current study together with recent investigations on the morphological characters among members of Squaliformes (e.g. Petean, 2015; Silva & Carvalho, 2015; Vaz, 2015) indicate these characteristics vary greatly between members of different families and highlight new hypothesis on its phylogenetic relationships, like it is observed for *Cirrhigaleus*. The relationships between Squalidae and other families of Squaliformes were still uncertain till recently. Naylor *et al*. (2012b) recognized Dalatiidae as sister-group of Squalidae, including the genus *Cirrhigaleus*, based on analysis of NADH2 gene. However, morphological characters are not yet provided to support his assumptions. Investigations on the phylogeny of members of Squaliformes through molecular and/or morphological characters are required in order to clarify these findings and elucidate the evolutionary relationships of *Cirrhigaleus*.

Literature cited

Bass, A.J., D'Aubrey, J.D. & Kistnasamy, N. (1976) Sharks of the east coast of southearn Africa. VI The families Oxynotidae, Squalidae, Dalatiidae and Echinorhinidae. *Investigational Report*, 45, Oceanographic Research Institute, Durban, 1–103.

Bigelow, H.B. & Schroeder, W.C. (1948) Sharks. *In*: J.Tee-Van *et al*. (Eds.), *Fishes of the Western North Atlantic. Part 1*. Memoir Sears Foundation for Marine Research, Yale University, New Haven, pp. 1–576.

Bigelow, H.B. & Schroeder, W.C. (1957) A study of the sharks of the suborder Squaloidea. *Bulletin of the Museum of Comparative Zoology at Harvard College in Cambridge*, 117 (1), 1–150.

Carvalho, M.R. de (1996) High-level Elasmobranch Phylogeny, Basal Squaleans, and Paraphyly. *In*: Stiassny, M.L. J.; Parenti, L.R. & Johnson, G.D. (Eds.), *Interrelationships of fishes*. Academic Press Inc., San Diego, pp. 35–62.

Compagno, L.J.V. (1984) *FAO Species Catalogue. Vo. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes*. FAO Fisheries Synopsis, Rome, 4 (125), 249 pp.

Compagno, L.J.V., Dando, M. & Fowler, S. (2005) *Sharks of the World – Princeton Field Guides*. Harper Collins Publishers Ltd., London, 368 pp.

Ebert, D.A., Fowler, S. & Compagno, L.J.V. (2013) *Sharks of the World: A Fully Illustrated Guide*. Wild Nature Press, London, 528 pp.

Figueirêdo, S.T.V. (2011) Revisão taxonômica e morfológica do gênero *Squalus* Linnaeus, 1758 do oceano Atlântico Sul Ocidental (Chondrichthyes: Squaliformes: Squalidae). Unpublished MSc Thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo, 348 pp.

Fourmanoir, P. & Rivaton, I. (1979) Poissons de la pente récifale externe de Nouvelle-Calédonie et des Nouvelles-Hébrides. *Cahiers de l'Indo–Pacifique*, 1(4), 405–443.

Fowler, H.W. (1941) Contributions to the biology of the Philippine archipelago and adjacent regions. The fishes of the groups Elasmocephalii, Holocephali, Isospondyli, and Ostariophysi obtained by the United States Fisheries Steamer "Albatross" in 1907 to 1910, chiefly in the Philippine islands and adjacent seas. *Bulletin of the United States National Museum,* 100, 1–879.

Garman, S. (1913) *The Plagiostoma (sharks, skates and rays).* Memoirs of the Museum of Comparative Zoology at Harvard College, 36, Cambridge, 515 pp.

Garrick, J.A.F. (1960) Studies on New Zealand Elasmobranchii. Part XII. The species of *Squalus* from New Zealand and Australia; and a general account and key to the New Zealand Squaloidea. *Transactions of the Royal Society of the New Zealand*, 88 (3), 519–557.

Garrick, J.A.F. & Paul, L.J. (1971) *Cirrhigaleus barbifer* (Fam. Squalidae), a little known Japanese shark from New Zealand waters. *Zoology Publications, Victoria University, Wellington*, 154, 1–13.Gomes, U.L., Signori, C.N., Gadig, O.B.F. & Santos, H.R.S. (2010) *Guia para Identificação de Tubarões e Raias do Rio de Janeiro*. Technical Books, Rio de Janeiro, 234 pp.

Gomes, U.L., Lima, M.C., Paragó, C. & Quitans, A.P. (1997) *Catálogo das coleções ictiológicas do Departamento de Biologia Animal e Vegetal*. Instituto de Biologia da Universidade Estadual do Rio de Janeiro, Rio de Janeiro, Gráfica UERJ, 185 pp.

Jungersen, H. F. E. (1899) *On the appendices genitales in the greenland shark Somniosus microcephalus (Bl. Schn.) and other selachians*. The Danish Ingolf-Expedition, 2, Bianco Luno, Copenhagen: Bianco Luno, 88 pp.

Kempster, R.M., Hunt, D.M., & Human, B.A., Egeberg, C.A. & Collin, S.P. (2013) First record of the mandarin dogfish *Cirrhigaleus barbifer* (Chondrichthyes: Squalidae) from Western Australia. *Marine Biodiversity Records*, 6, e25.

Merrett, N.F. (1973) A new shark of the genus *Squalus* (Squalidae, Squaloidea) from the equatorial western Indian Ocean, with notes on the *Squalus blainvillei*. *Journal of Zoological Society of London*, 171, 93–110.

Müller, J. & Henle, J. (1841) *Systematische Beschreibung der Plagiostomen*. Berlim, 300 pp.

Naylor, G.J.P., Caira, J.N., Jensen, K., Rosana, A.M., White, W. T. & Last, P.R. (2012a) A DNA sequence-based approach to the identification of shark and rays species and its implication of global elasmobranch diversity and parasitology. *Bulletin of the American Museum of Natural History*, 367, 262 pp.

Naylor, G. J. P., Caira, J.N., Jensen, K., Rosana, A.M., Straube, N. & Lakner, C. (2012b) Elasmobranch Phylogeny: A mitochondrial estimate based on 595 species. *In*: Carrier, J.C., Musick, J.A., & Heithaus, M.E. (Eds.). *Biology of Sharks and their relatives.* 2nd ed., CRC Press., pp. 31–56.

Pettean, F.F. (2015) Revisão taxonômica e morfologia comparada das espécies do gênero *Isistius* Gill, 1864 (Chondrichthyes: Squaliformes: Dalatiidae). Unpublished MSc. Thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo, 350 pp.

Ramos, S.G.A.C. (2009) Descrição e comparação do condrocrânio de *Cirrhigaleus* Tanaka, 1912 e *Squalus* Linnaeus, 1758 (Squaliformes, Squalidae). Unpublished Monograph. Instituto de Ciências Biológicas e Ambientais, Universidade Santa Úrsula, Rio de Janeiro. 40 pp.

Shirai, S. (1992) *Squalean phylogeny: a new framework of "squaloid" sharks and related taxa*. Hokkaido University Press. Sapporo, 151 pp.

Silva, J.P.C.B. (2014) Filogenia dos principais grupos de Chondrichthyes baseada na anatomia comparada do esqueleto das nadadeiras pares e suas cinturas. Unpublished PhD Thesis. Instituto de Biociências, Universidade de São Paulo, São Paulo, 703 pp.

Silva, J.P.C.B. & Carvalho, M.R. (2015) Morphology and phylogenetic significance of the pectoral articular region in elasmobranchs (Chondrichthyes). *Zoological Journal of the Linnean Society*, 175 (3), 525–568.

Tanaka, S. (1912) Figures and descriptions of the fishes of Japan including the Riukiu Islands, Bonin Islands, Formosa, Kurile Islands, Korea, and southern Sakhalin. Figures and descriptions of the fishes of Japan, 9, 145–164.

Vaz, D.F. B. (2015) Revisão taxonômica e morfológica do gênero *Centroscymnus* Barboza du Bocage & Britto-Capello, 1864, com comentários no arranjo genérico da família Somniosidae (Chondrichthyes: Squaliformes). Unpublished Msc. Thesis, Universidade de São Paulo, São Paulo.

White, W.T., Last, P.R. & Stevens, J.D. (2007b) *Cirrhigaleus australis* n. sp., a new Mandarin Dogfish (Squaliformes: Squalidae) from the south-west Pacific. *Zootaxa*, 1560, 19–30.

Yano, K. (1986) Studies on morphology, phylogeny, taxonomy and biology of Japanese Squaloid sharks, Order Squaliformes. Unpublished PhD Thesis. Tokai University, Shimizu, 335 pp.

Table 59. External measurements for specimens of *Cirrhigaleus barbifer* expressed as percentage of the total length (% TL). Total length is expressed in milimeters. Values for holotype of *Phaenopogon barbulifer* (SU 13901) are also provided. N: number of specimens; *x*: mean; SD: standard deviation.

	Cirrhigaleus barbifer												
Measurements	Asia					New Zealand				Indonesia		New Caledonia	
	SU 13901	N	Range	*x*	SD	N	Range	*x*	SD	N	*x*	N	*x*
TL (mm)	730.0	3	650.0 - 960.0	826.7	159.5	17	710.0 - 1272.0	1013.3	165.9	1	978.0	1	800.0
PCL	76.7	3	79.1 - 79.9	79.4	0.4	17	78.5 - 86.2	81.2	2.2	1	78.9	1	84.4
PD2	61.0	3	60.8 - 63.6	62.1	1.4	17	61.0 - 68.4	63.9	2.1	1	63.4	1	66.5
PD1	32.9	3	31.8 - 33.3	32.5	0.8	17	30.3 - 43.3	32.9	2.8	1	31.9	1	35.3
SVL	54.8	3	52.5 - 56.3	54.4	1.9	17	53.2 - 59.5	55.9	1.8	1	55.7	1	54.8
PP2	50.7	3	49.2 - 53.6	51.2	2.3	17	49.7 - 55.0	52.0	1.5	1	52.4	1	50.6
PP1	21.0	3	18.1 - 20.5	18.9	1.3	17	18.2 - 22.4	20.0	1.1	1	20.4	1	20.9
HDL	19.5	3	18.8 - 20.7	19.5	1.0	17	18.9 - 23.1	20.6	1.2	1	23.0	1	23.0
PG1	16.2	3	14.8 - 16.8	15.9	1.0	17	15.9 - 18.7	17.0	0.8	1	18.9	1	19.6
PSP	9.8	3	9.5 - 10.5	9.9	0.6	17	9.9 - 11.4	10.4	0.5	1	10.3	1	11.3
POB	5.5	3	5.6 - 6.4	6.0	0.4	17	6.0 - 7.3	6.4	0.4	1	6.3	1	6.8
PRN	4.3	3	3.8 - 4.3	4.0	0.3	17	4.0 - 5.0	4.5	0.3	1	4.2	1	4.2
POR	8.7	3	7.1 - 7.8	7.5	0.3	17	7.0 - 8.3	7.6	0.4	1	8.1	1	8.2
INLF	4.3	3	3.7 - 4.9	4.3	0.6	17	4.0 - 4.9	4.4	0.3	1	4.7	1	5.3
MOW	8.1	3	7.2 - 8.0	7.7	0.5	17	7.2 - 8.8	7.8	0.4	1	7.9	1	9.0
ULA	1.1	3	1.1 - 1.1	1.1	0.0	17	1.0 - 1.4	1.2	0.1	1	1.1	1	1.5
INW	3.8	3	3.0 - 3.4	3.3	0.2	17	3.4 - 4.0	3.7	0.1	1	3.6	1	3.8
INO	8.1	3	7.6 - 8.1	7.9	0.3	17	7.2 - 8.5	7.7	0.3	1	8.1	1	8.7
EYL	2.6	3	3.6 - 4.3	4.0	0.3	17	3.3 - 4.6	3.9	0.3	1	3.6	1	4.3
EYH	0.5	3	1.0 - 1.9	1.5	0.5	17	0.7 - 1.6	1.2	0.2	1	1.1	1	0.9
SPL	1.2	3	1.2 - 1.7	1.5	0.3	17	1.1 - 1.6	1.4	0.2	1	1.6	1	1.3
GS1	2.1	3	1.8 - 2.2	2.0	0.2	17	1.6 - 2.3	2.0	0.2	1	2.2	1	2.2
GS5	3.1	3	2.0 - 2.4	2.2	0.2	17	1.9 - 2.7	2.2	0.3	1	2.7	1	2.6
IDS	22.6	3	21.9 - 22.4	22.1	0.3	17	21.2 - 26.5	23.2	1.2	1	24.5	1	23.1
DCS	8.9	3	7.5 - 7.9	7.6	0.2	17	6.9 - 9.1	7.7	0.5	1	9.1	1	7.7
PPS	27.4	3	26.2 - 31.8	28.7	2.8	17	26.8 - 35.0	30.6	2.2	1	26.9	1	30.0
PCA	21.9	3	18.4 - 20.5	19.6	1.1	17	17.6 - 22.9	20.4	1.1	1	21.0	1	21.3
D1L	14.8	3	13.9 - 14.8	14.3	0.5	17	13.6 - 15.5	14.5	0.5	1	14.6	1	15.1
D1A	13.7	3	13.5 - 14.3	13.7	0.4	17	11.9 - 14.4	13.3	0.6	1	12.7	1	12.9
D1B	8.9	3	8.3 - 8.7	8.4	0.2	17	8.4 - 9.8	8.9	0.4	1	8.3	1	9.7
D1H	10.0	3	8.9 - 10.8	9.9	0.9	17	5.7 - 10.7	9.7	1.1	1	10.1	1	10.1
D1I	5.6	3	5.4 - 6.3	5.8	0.5	17	5.2 - 6.6	5.7	0.4	1	6.3	1	5.7
D1P	10.9	3	9.0 - 10.6	9.6	0.9	17	9.0 - 11.9	10.1	0.9	1	12.2	1	12.1
D1ES	5.2	1	-	6.0	-	11	3.7 - 6.8	5.2	0.9	1	8.3	1	5.3
D1BS	1.0	3	0.8 - 0.9	0.8	0.1	17	0.5 - 1.1	0.9	0.1	1	0.9	1	0.8
D2L	14.0	3	13.9 - 15.0	14.5	0.5	17	13.3 - 15.8	14.6	0.7	1	14.5	1	14.7
D2A	13.7	3	13.3 - 14.9	14.2	0.8	17	13.1 - 14.9	14.2	0.4	1	13.3	1	13.5
D2B	8.5	3	8.9 - 9.7	9.4	0.4	17	8.8 - 10.5	9.6	0.5	1	8.8	1	9.9
D2H	9.6	3	8.8 - 10.3	9.5	0.7	17	8.3 - 10.8	9.1	0.6	1	10.0	1	10.5
D2I	5.7	3	4.8 - 5.9	5.2	0.6	17	4.4 - 5.6	4.9	0.3	1	5.6	1	4.9
D2P	8.7	3	7.3 - 10.5	8.5	1.8	17	7.2 - 9.1	8.2	0.6	1	10.5	1	8.7
D2ES	7.5	2	7.1 - 7.6	7.4	0.3	14	4.4 - 9.3	6.7	1.4	1	7.9	1	8.0
D2BS	1.2	2	0.8 - 0.9	0.8	0.0	17	0.8 - 1.3	1.0	0.1	1	0.9	1	1.2
P1A	17.1	3	15.3 - 16.9	15.9	0.9	17	14.1 - 16.7	15.4	0.9	1	15.8	1	16.6
P1I	8.5	3	8.3 - 8.9	8.5	0.3	17	7.5 - 8.8	8.3	0.4	1	9.5	1	9.4
P1B	5.4	3	4.3 - 4.9	4.6	0.3	17	4.2 - 5.8	4.9	0.4	1	4.5	1	5.0
P1P	13.1	3	11.3 - 11.4	11.3	0.1	17	8.3 - 12.1	10.5	1.0	1	11.8	1	12.7
P2L	13.3	3	12.2 - 13.2	12.9	0.6	17	11.9 - 14.8	13.1	0.7	1	13.5	1	14.4
P2I	6.0	3	5.4 - 6.2	5.8	0.4	17	5.0 - 8.3	6.1	0.9	1	6.9	1	6.5
CDM	23.3	3	20.5 - 20.6	20.5	0.0	16	18.0 - 21.3	19.7	0.9	1	20.7	1	15.0
CPV	9.0	3	10.8 - 11.6	11.1	0.4	17	9.4 - 11.2	10.4	0.5	1	11.7	1	10.3
CFW	8.2	3	7.0 - 8.4	7.7	0.7	17	7.4 - 8.4	7.8	0.3	1	8.2	1	5.5
HANW	7.6	3	6.4 - 7.5	6.9	0.6	17	6.4 - 7.4	6.8	0.3	1	7.8	1	7.9
HAMW	11.4	3	11.0 - 12.7	12.1	1.0	17	11.2 - 13.2	11.9	0.5	1	13.2	1	12.5
HDW	26.7	3	13.7 - 15.7	14.6	1.0	17	13.1 - 16.8	14.9	1.0	1	16.9	1	16.5
TRW	27.4	3	11.2 - 14.9	13.1	1.9	17	11.5 - 16.4	13.7	1.5	1	13.9	1	17.2
ABW	20.5	3	9.3 - 12.8	10.8	1.8	17	7.3 - 12.6	9.8	1.6	1	14.0	1	14.1
HDH	13.0	3	7.2 - 12.5	10.1	2.7	17	8.2 - 12.0	10.3	1.1	1	12.9	1	13.1
TRH	16.4	3	7.6 - 13.3	10.3	2.9	17	6.3 - 17.7	11.4	2.8	1	13.8	1	14.9
ABH	17.1	3	8.6 - 14.1	11.5	2.8	17	7.8 - 17.0	12.5	3.0	1	15.6	1	15.7
CLO	-	1	-	1.7	-	7	1.2 - 10.0	4.1	2.9	-	-	-	-
CLI	-	1	-	3.5	-	7	3.2 - 8.8	6.0	2.3	-	-	-	-
ANLF	-	3	5.4 - 6.1	5.6	0.4	17	4.5 - 6.2	5.4	0.4	1	5.9	1	6.4

Table 60. External measurements for *Cirrhigaleus asper* expressed as percentage of the total length (% TL).TL is expressed in milimeters. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	Holotype	Paratypes			*Cirrhigaleus asper* Western Indian Ocean				Western Central Atlantic Ocean				Southwestern Atlantic Ocean			
	BMNH 1972.10.10.1	BMNH 1972.10.10.2	BMNH 1972.10.10.3	BMNH 1972.10.10.4	N	Range	*x*	SD	N	Range	*x*	SD	N	Range	*x*	SD
TL (mm)	880.0	847.0	865.0	1002.0	11	253.0 - 1120.0	641.6	390.3	2	1000.0 - 1023.0	1011.5	16.3	5	960.0 - 1300.0	1098.0	171.4
PCL	81.3	81.7	80.7	80.6	11	76.4 - 84.8	80.4	3.3	2	79.7 - 81.5	80.6	1.3	5	76.9 - 94.5	82.6	6.9
PD2	63.3	64.9	64.0	63.5	11	60.0 - 68.3	63.6	3.3	2	63.0 - 64.0	63.5	0.7	5	62.5 - 70.9	64.7	3.5
PD1	32.5	32.5	34.9	34.5	11	30.4 - 35.2	33.6	1.5	2	31.8 - 36.0	33.9	3.0	5	31.3 - 33.1	32.4	0.7
SVL	52.3	56.6	51.7	53.4	11	45.1 - 61.6	54.1	4.6	2	50.8 - 52.0	51.4	0.8	5	51.0 - 57.5	54.2	2.4
PP2	48.1	51.0	49.2	50.2	11	42.8 - 58.3	51.6	4.3	2	47.9 - 50.0	48.9	1.5	5	47.4 - 54.7	51.2	3.3
PP1	21.8	21.3	21.7	20.8	11	19.8 - 23.4	22.1	1.0	2	15.0 - 20.3	17.7	3.8	5	18.6 - 20.8	19.9	1.1
HDL	22.4	21.9	22.6	21.1	11	20.3 - 24.3	22.9	1.1	2	22.0 - 23.0	22.5	0.7	5	19.8 - 21.3	20.6	0.6
PG1	18.4	17.0	18.8	17.6	11	17.4 - 20.4	18.9	0.9	2	17.6 - 19.0	18.3	1.0	5	16.5 - 17.7	17.3	0.5
PSP	11.3	11.0	11.2	10.9	11	10.0 - 14.3	12.0	1.2	2	9.6 - 11.1	10.3	1.0	5	9.4 - 10.5	10.1	0.4
POB	6.5	6.5	6.3	6.0	11	6.5 - 8.4	7.2	0.6	2	5.9 - 6.0	6.0	0.1	5	6.0 - 6.3	6.1	0.1
PRN	4.3	4.9	4.8	4.6	11	4.2 - 5.7	5.0	0.4	2	2.9 - 3.1	3.0	0.2	5	3.6 - 4.2	4.0	0.2
POR	8.1	7.9	8.8	8.2	11	7.3 - 11.1	9.1	1.2	2	5.3 - 6.9	6.1	1.1	5	6.1 - 7.3	6.9	0.5
INLF	4.5	4.0	4.3	4.4	11	3.8 - 4.9	4.5	0.4	2	2.8 - 4.1	3.5	0.9	5	3.5 - 4.1	3.7	0.3
MOW	8.1	8.2	8.3	8.2	11	7.4 - 8.8	8.3	0.4	2	8.3 - 9.0	8.7	0.5	5	7.7 - 9.2	8.2	0.6
ULA	1.6	1.6	1.6	1.4	11	1.5 - 2.8	1.8	0.4	2	2.1 - 2.1	2.1	0.1	5	1.5 - 1.9	1.7	0.2
INW	3.6	3.7	3.8	3.7	11	3.5 - 4.8	4.0	0.4	2	3.2 - 3.4	3.3	0.2	5	3.3 - 3.9	3.7	0.2
INO	8.2	8.3	8.5	8.1	11	8.1 - 10.1	8.9	0.6	2	8.2 - 8.7	8.4	0.4	5	7.3 - 8.3	7.7	0.4
EYL	4.5	4.5	4.2	4.3	11	3.6 - 6.0	5.0	0.8	2	2.3 - 4.1	3.2	1.2	5	2.0 - 4.9	2.8	1.2
EYH	0.8	1.3	0.9	0.9	11	1.1 - 2.5	1.7	0.4	2	0.9 - 1.0	1.0	0.1	5	0.8 - 1.3	1.1	0.2
SPL	1.2	1.4	1.2	1.3	11	1.3 - 1.7	1.4	0.2	2	1.3 - 1.4	1.3	0.0	5	1.1 - 1.4	1.2	0.1
GS1	2.1	2.3	1.9	2.2	11	1.7 - 2.7	2.2	0.3	2	1.8 - 2.6	2.2	0.6	5	1.6 - 2.5	2.0	0.3
GS5	2.4	2.7	2.6	2.9	11	2.1 - 3.2	2.7	0.3	2	2.3 - 3.0	2.7	0.5	5	1.9 - 2.6	2.2	0.3
IDS	23.1	21.8	21.9	21.3	11	19.2 - 24.1	21.4	1.9	2	22.5 - 24.0	23.2	1.1	5	23.2 - 24.6	24.0	0.6
DCS	9.5	9.3	8.3	8.2	11	7.4 - 10.1	8.9	1.0	2	7.5 - 10.0	8.8	1.7	5	9.5 - 10.8	10.3	0.5
PPS	26.1	28.2	21.1	22.6	11	17.6 - 33.0	25.7	4.8	2	22.5 - 29.0	25.7	4.6	5	24.5 - 31.5	28.7	2.8
PCA	23.5	22.3	21.0	20.9	11	20.7 - 24.6	22.2	1.4	2	22.0 - 25.0	23.5	2.1	5	20.5 - 24.0	22.5	1.3
D1L	14.8	14.8	13.8	14.2	11	12.3 - 15.8	13.9	1.2	2	15.5 - 16.7	16.1	0.9	5	13.9 - 15.4	14.4	0.6
D1A	13.7	12.4	11.8	12.3	11	11.2 - 13.4	12.2	0.7	2	13.7 - 14.5	14.1	0.6	5	10.8 - 12.8	11.8	0.7
D1B	9.4	8.9	8.6	8.7	11	7.0 - 10.0	8.4	1.1	2	9.5 - 9.6	9.6	0.1	5	8.4 - 10.0	9.3	0.7
D1H	8.6	8.5	9.5	8.2	11	7.7 - 9.6	8.6	0.6	2	9.1 - 9.9	9.5	0.6	5	7.7 - 9.1	8.2	0.6
D1I	5.3	6.0	5.8	5.6	11	4.2 - 6.4	5.4	0.6	2	6.2 - 6.3	6.3	0.1	5	4.7 - 6.2	5.7	0.6
D1P	10.1	8.0	9.2	9.4	11	6.9 - 10.2	8.5	1.2	2	10.9 - 11.8	11.3	0.6	5	9.2 - 10.2	9.5	0.4
D1ES	5.7	3.4	6.1	5.8	9	1.9 - 6.3	3.8	1.6	1	-	7.6	-	3	4.3 - 6.1	5.3	0.9
D1BS	1.1	1.3	1.2	1.1	11	0.6 - 1.2	0.9	0.2	2	1.3 - 1.4	1.3	0.1	5	1.1 - 1.5	1.2	0.2
D2L	14.6	13.4	14.6	9.3	11	12.1 - 14.8	13.4	0.8	2	13.6 - 15.2	14.4	1.1	5	11.4 - 14.8	12.9	1.4
D2A	13.9	12.8	13.5	7.8	11	11.5 - 13.8	12.6	0.8	2	13.9 - 14.2	14.0	0.2	5	10.8 - 14.5	12.4	1.5
D2B	9.5	9.3	9.4	8.3	11	7.2 - 9.7	8.4	0.9	2	8.6 - 9.1	8.9	0.4	5	7.5 - 10.1	8.7	1.1
D2H	8.5	8.2	8.6	3.9	11	7.0 - 9.0	7.8	0.6	2	9.3 - 9.3	9.3	0.1	5	7.5 - 8.6	8.0	0.5
D2I	5.1	4.4	5.3	1.5	11	4.4 - 6.1	5.1	0.5	2	4.8 - 5.4	5.1	0.5	5	3.9 - 4.9	4.6	0.4
D2P	6.9	6.5	7.9	3.9	11	5.8 - 8.0	6.7	0.7	2	7.8 - 8.0	7.9	0.1	5	6.8 - 7.7	7.4	0.4
D2ES	7.3	4.7	3.4	5.3	10	4.3 - 7.2	5.4	1.0	2	6.3 - 7.6	6.9	0.9	4	5.2 - 6.6	6.0	0.7
D2BS	1.0	1.0	0.9	1.0	11	0.9 - 1.2	1.0	0.1	2	1.1 - 1.2	1.1	0.0	5	0.9 - 1.2	1.0	0.1
P1A	14.4	12.5	13.9	13.2	11	12.2 - 16.1	13.7	1.2	2	15.6 - 16.0	15.8	0.3	5	12.2 - 14.4	13.7	0.8
P1I	8.4	7.4	8.8	8.6	11	8.1 - 9.4	8.7	0.4	2	8.6 - 9.0	8.8	0.2	5	7.9 - 11.7	8.9	1.6
P1B	4.3	4.6	4.3	4.6	11	3.5 - 5.7	4.8	0.6	2	5.4 - 5.9	5.7	0.3	5	4.2 - 5.5	4.9	0.5
P1P	10.5	8.7	12.0	9.3	11	9.7 - 12.9	10.8	1.0	2	10.8 - 12.0	11.4	0.8	5	8.8 - 10.4	9.6	0.8
P2L	12.2	11.2	12.0	10.8	11	10.2 - 12.4	11.0	0.7	2	11.5 - 12.0	11.7	0.3	5	10.9 - 12.7	11.8	0.8
P2I	6.3	5.6	5.9	3.7	11	4.1 - 6.4	5.4	0.7	2	5.6 - 7.6	6.6	1.5	5	4.7 - 6.5	5.7	0.7
CDM	19.8	18.4	20.1	20.1	11	18.8 - 23.2	20.8	1.5	2	22.5 - 23.0	22.7	0.4	5	17.7 - 21.7	19.8	1.8
CPV	11.6	10.9	11.4	11.2	11	7.2 - 12.4	10.7	1.5	2	11.8 - 13.0	12.4	0.8	5	9.4 - 13.0	10.9	1.4
CFW	7.8	7.1	7.5	7.6	11	6.8 - 13.0	7.9	1.7	2	8.0 - 8.2	8.1	0.1	5	6.9 - 7.4	7.2	0.2
HANW	7.7	6.9	7.0	7.3	11	7.8 - 10.2	8.9	1.0	2	7.2 - 7.9	7.5	0.5	5	6.1 - 9.2	7.5	1.1
HAMW	12.5	13.4	12.8	12.6	11	11.6 - 13.3	12.6	0.5	2	12.1 - 12.5	12.3	0.3	5	10.8 - 12.2	11.5	0.6
HDW	14.0	13.8	14.4	15.5	11	2.2 - 19.3	13.4	4.3	2	14.3 - 26.0	20.2	8.2	5	11.1 - 23.4	20.7	5.3
TRW	9.4	10.1	12.8	13.8	11	2.5 - 18.8	12.1	4.2	2	20.5 - 30.5	25.5	7.1	5	19.7 - 24.6	22.1	2.1
ABW	8.0	9.0	8.7	11.6	11	2.3 - 20.6	10.4	4.7	2	14.7 - 21.0	17.8	4.5	5	15.2 - 21.4	18.8	2.3
HDH	11.5	9.8	12.1	12.1	11	1.4 - 15.8	9.7	3.5	2	11.7 - 15.0	13.4	2.3	5	9.4 - 13.1	11.3	1.5
TRH	12.1	8.9	12.2	13.7	11	1.7 - 16.1	10.7	3.9	2	12.7 - 21.0	16.9	5.9	5	9.1 - 15.1	12.0	2.3
ABH	12.9	9.6	12.5	10.7	11	1.6 - 14.7	10.5	3.7	2	11.2 - 20.0	15.6	6.2	5	10.0 - 14.6	12.5	1.9
CLO	4.2	4.0	-	-	3	1.2 - 1.7	1.4	0.3	-	-	-	-	3	3.5 - 4.3	3.9	0.4
CLI	6.9	6.8	-	-	3	2.2 - 4.1	2.9	1.0	-	-	-	-	3	6.7 - 7.2	6.9	0.2
ANFL	1.5	1.3	1.2	1.3	8	1.0 - 2.4	1.5	0.5	-	-	-	-	-	-	-	-

Table 61. External measurements for *Cirrhigaleus australis* expressed as percentage of the total length (% TL).TL is expressed in milimeters. N: number of specimens; *x*: mean; SD: standard deviation.

Measurements	*Cirrhigaleus australis*							
	Holotype	**Paratypes**			Australia			
	CSIRO H 5789-01	AMS I 19154-001	AMS I 27022-001	AMS I 42891-001	N	Range	*x*	SD
TL (mm)	970.0	705.0	1205.0	1085.0	7	505.0 - 993.0	673.0	153.2
PCL	98.8	78.9	81.9	81.7	7	77.7 - 80.0	78.9	0.9
PD2	61.3	61.8	64.1	63.1	7	59.4 - 61.8	61.0	0.8
PD1	32.0	31.5	33.2	30.9	7	29.7 - 32.5	31.2	1.0
SVL	54.1	51.1	59.3	56.2	7	51.5 - 56.6	53.8	1.7
PP2	50.5	49.1	54.8	53.0	7	47.9 - 53.1	50.5	1.8
PP1	19.1	19.3	19.9	20.1	7	17.3 - 20.5	19.4	1.1
HDL	20.0	21.3	20.2	22.6	7	18.2 - 22.0	20.4	1.2
PG1	17.1	18.4	16.4	17.7	7	15.8 - 17.7	17.3	0.7
PSP	10.1	11.1	9.5	9.9	7	10.1 - 11.5	11.0	0.5
POB	6.5	7.2	6.0	5.8	7	5.9 - 7.2	6.7	0.5
PRN	4.0	4.6	3.9	4.1	7	4.2 - 4.9	4.6	0.2
POR	7.3	8.0	6.9	7.8	7	7.7 - 8.6	8.2	0.3
INLF	4.3	4.5	4.0	4.5	7	4.1 - 4.9	4.5	0.3
MOW	7.6	7.9	6.6	7.4	7	7.5 - 8.5	8.0	0.4
ULA	0.9	1.0	0.9	0.9	7	1.2 - 1.6	1.3	0.1
INW	3.6	3.6	3.8	3.9	7	3.5 - 4.1	3.8	0.2
INO	7.8	8.5	7.5	8.0	7	7.8 - 8.4	8.2	0.2
EYL	3.3	3.9	3.3	3.1	7	3.7 - 4.4	4.2	0.3
EYH	1.5	1.8	1.1	1.0	7	1.1 - 1.6	1.4	0.2
SPL	1.3	1.7	1.3	1.6	7	1.3 - 1.8	1.4	0.2
GS1	1.8	2.3	1.7	1.8	7	2.0 - 2.3	2.2	0.1
GS5	2.3	2.4	2.3	2.2	7	2.0 - 2.6	2.2	0.2
IDS	22.3	22.7	23.2	21.8	7	21.0 - 23.0	22.1	0.8
DCS	7.5	8.0	8.0	8.6	7	7.8 - 9.1	8.6	0.5
PPS	29.4	28.4	30.3	28.1	7	26.8 - 32.0	28.6	1.8
PCA	19.8	20.0	21.1	21.2	7	20.7 - 23.8	21.5	1.1
D1L	14.4	13.6	14.6	15.3	7	13.5 - 15.0	14.1	0.6
D1A	12.2	13.9	13.6	13.7	7	11.7 - 14.6	13.2	0.9
D1B	8.4	8.6	8.2	8.8	7	7.7 - 9.2	8.3	0.6
D1H	9.8	9.7	8.9	10.9	7	9.5 - 10.2	9.8	0.2
D1I	6.3	4.9	6.2	6.8	7	5.3 - 6.5	5.8	0.4
D1P	10.6	9.6	9.8	11.4	7	9.4 - 11.3	10.2	0.6
D1ES	5.7	5.2	-	4.7	6	3.1 - 6.4	4.1	1.3
D1BS	0.9	1.0	1.1	0.9	6	0.6 - 0.9	0.7	0.1
D2L	14.9	13.9	12.4	15.5	7	13.8 - 15.8	14.7	0.7
D2A	14.2	14.5	13.5	14.8	7	13.6 - 14.8	14.2	0.5
D2B	9.6	9.2	10.0	9.3	7	9.0 - 10.1	9.5	0.4
D2H	9.5	8.8	9.4	9.7	7	8.7 - 9.5	9.0	0.3
D2I	5.5	4.7	4.5	6.3	7	4.8 - 5.8	5.3	0.3
D2P	9.1	8.8	7.2	8.5	7	8.4 - 10.6	9.1	0.7
D2ES	6.4	7.6	5.9	6.7	7	5.5 - 8.1	6.4	1.0
D2BS	1.1	1.1	1.0	1.1	7	0.8 - 1.2	1.0	0.1
P1A	15.2	14.8	16.1	15.5	7	14.3 - 16.9	15.6	0.9
P1I	8.5	8.1	8.9	8.9	7	8.1 - 9.5	8.8	0.5
P1B	5.0	4.7	4.5	5.1	7	4.4 - 4.9	4.7	0.2
P1P	10.2	11.7	11.2	11.8	7	10.8 - 12.4	11.7	0.6
P2L	12.9	11.7	13.6	13.3	7	11.1 - 13.1	12.5	0.7
P2I	6.0	5.3	6.7	5.7	7	5.3 - 6.8	5.9	0.6
CDM	21.6	21.8	10.9	21.2	7	20.1 - 21.8	21.0	0.8
CPV	11.7	11.4	10.5	12.2	7	10.0 - 12.4	11.1	0.8
CFW	7.6	8.0	7.5	7.9	7	7.2 - 8.6	7.8	0.4
HANW	7.1	7.5	6.5	7.2	7	6.5 - 7.7	7.2	0.5
HAMW	11.8	12.6	10.4	11.6	7	11.5 - 13.6	12.6	0.8
HDW	15.9	15.1	22.8	21.4	7	14.0 - 15.5	14.8	0.5
TRW	16.5	12.9	21.0	23.3	7	12.3 - 14.8	13.4	1.0
ABW	15.5	9.6	15.8	16.1	7	8.0 - 14.5	11.5	2.3
HDH	12.8	11.3	12.0	16.1	7	9.6 - 11.8	10.8	0.9
TRH	17.5	12.2	12.9	10.9	7	10.6 - 12.8	11.7	0.8
ABH	17.4	14.0	15.4	10.9	7	9.3 - 13.8	11.9	1.8
CLO	-	-	-	-	3	1.2 - 4.4	2.3	1.8
CLI	-	-	-	-	3	3.5 - 7.2	4.9	2.0
ANFL	5.0	5.9	5.2	4.4	6	5.3 - 7.1	6.4	0.7

Table 62. Tooth counts for *Cirrhigaleus barbifer, Cirrhigaleus australis* and *Cirrhigaleus asper.*

	C. barbifer			***C. australis***			***C. asper***			
	Japan N= 3	New Zealand N= 10	Indonesia N= 1	Holotype	Paratypes N= 3	N= 7	Holotype	Paratypes	Indian Ocean N= 10	West Atlantic Ocean N= 3
upper teeth (right)	14	13	15	12	13	14	14	13–15	11–14	13–14
upper teeth (left)	14	13	15	12	12	14	14	13–13	12–14	13–14
upper intermediate tooth	1	-	-	-	-	-	-	-	-	-
lower teeth (right)	11	12	11	10	10	11	12	11–12	10–13	11–12
lower teeth (left)	11	12	11	10	10	11	12	11–11	11–14	11–12
lower intermediate tooth	1	-	-	-	-	-	-	-	-	-
upper teeth series	3	2	2	3	3	3	3	3–4	1–3	2–3
lower teeth series	3	3	3	3	2	2	3	3–4	1–3	3–3

Table 63. Monospondylous, diplospondylous, precaudal, caudal and total vertebrae for species of *Cirrhigaleus*.

	Monospondylous vertebrae															
	45	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**	**60**
C. barbifer Japan						1										
C. barbifer Indonesia					1											
C. australis Holotype						1										
C. australis Paratypes						1										
C. australis					2	1	2	1								
C. asper Holotype								1								
C. asper Paratypes						1	2									
C. asper					1	2	1									

	Diplospondylous vertebrae															
	57	**58**	**59**	**60**	**61**	**62**	**63**	**64**	**65**	**66**	**67**	**68**	**69**	**70**	**71**	**72**
C. barbifer Japan									1							
C. barbifer Indonesia											1					
C. australis Holotype										1						
C. australis Paratypes								1								
C. australis						1	2	1	1		2					
C. asper Holotype								1								
C. asper Paratypes												2	1			
C. asper								1	1	1		1				

	Precaudal vertebrae															
	75	**76**	**77**	**78**	**79**	**80**	**81**	**82**	**83**	**84**	**85**	**86**	**87**	**88**	**89**	**90**
C. barbifer Japan														1		
C. barbifer Indonesia														1		
C. australis Holotype											1					
C. australis Paratypes												1				
C. australis											1			3	2	
C. asper Holotype													1			
C. asper Paratypes													1		1	1
C. asper											1	1	1		1	

	Caudal vertebrae															
	25	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**
C. barbifer Japan			1													
C. barbifer Indonesia			1													
C. australis Holotype								1								
C. australis Paratypes				1												
C. australis		2	3	1	1											
C. asper Holotype					1											
C. asper Paratypes					1	1		1								
C. asper			1		1	2										

	Total vertebrae															
	105	**106**	**107**	**108**	**109**	**110**	**111**	**112**	**113**	**114**	**115**	**116**	**117**	**118**	**119**	**120**
C. barbifer Japan											1					
C. barbifer Indonesia												1				
C. australis Holotype													1			
C. australis Paratypes										1						
C. australis										1	3	2				
C. asper Holotype												1				
C. asper Paratypes															3	
C. asper											2	1	1			

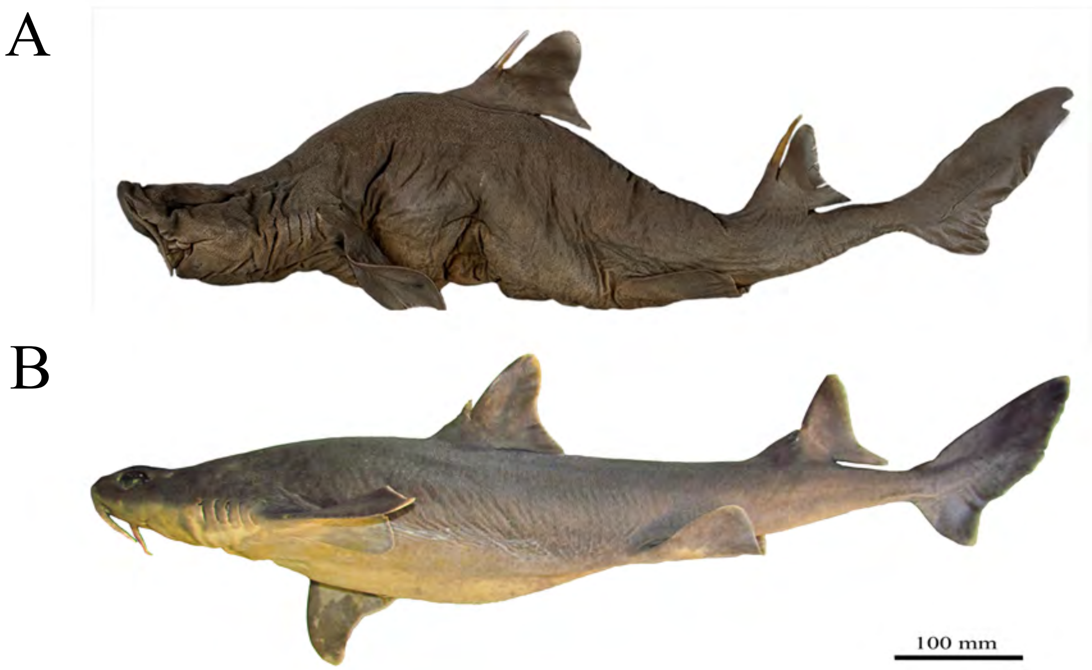

Figure 248. Specimens of *Cirrhigaleus barbifer* in lateral view. A: SU 13901, adult female, 730 mm TL, holotype of *Phaenopogon barbulifer*; B: HUMZ 197852, adult female, 870 mm

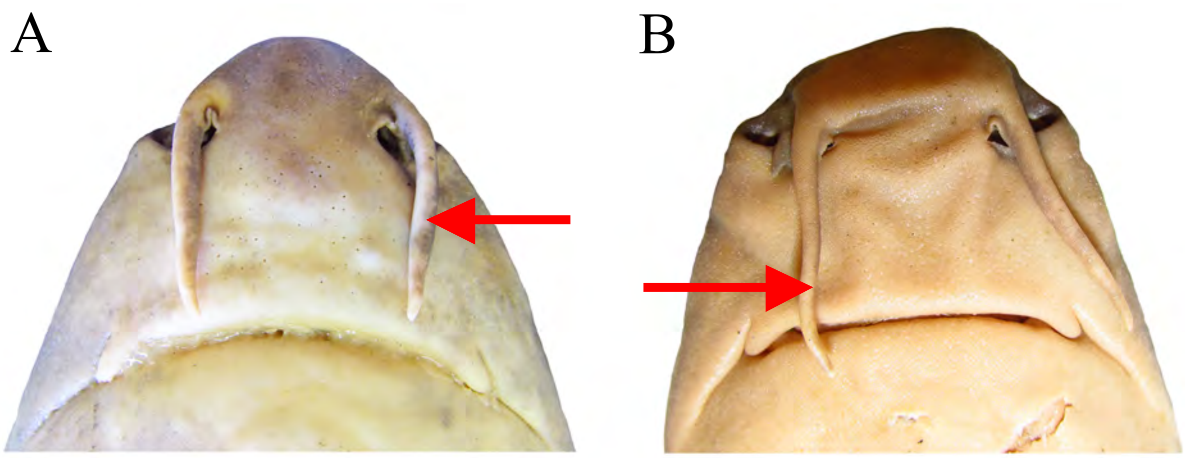

Figure 249. Anterior ventral view of head (A-B), showing nasal barbels on each side. A: HUMZ 197852, adult female, 870 mm TL; B: HUMZ 101533, juvenile male, 650 mm TL.

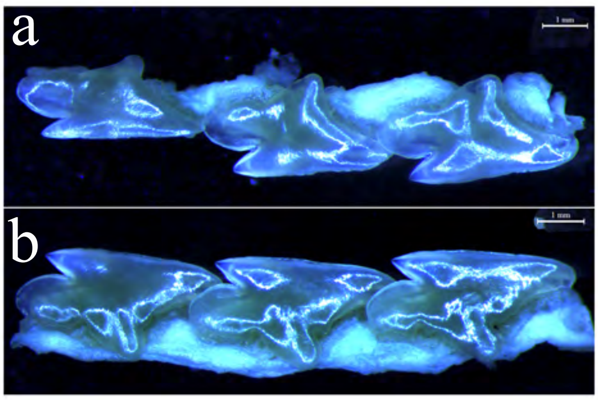

Figure 250. Upper (a) and lower (b) teeth of *Cirrhigaleus barbifer*, NMW 98257, adult female, 960 mm TL. Scale bar: 1mm.

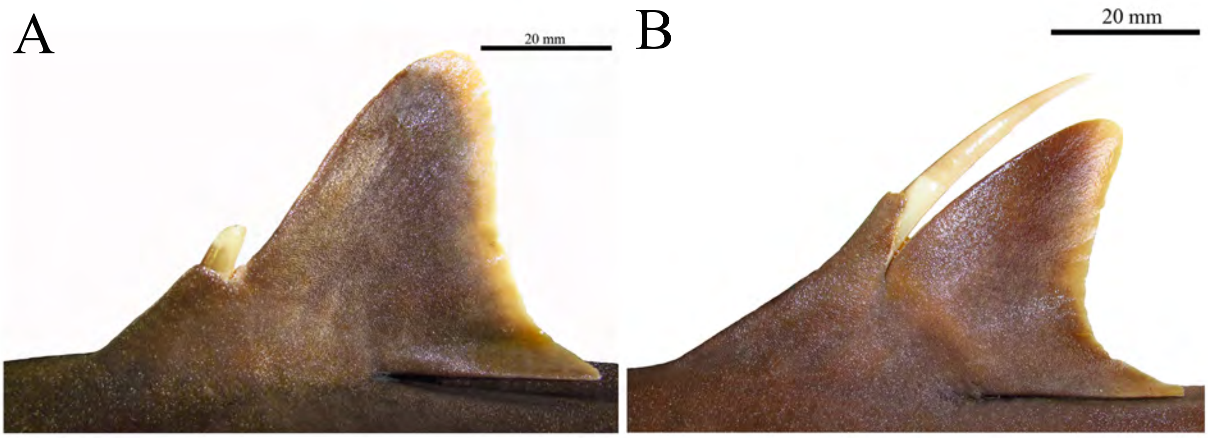

Figure 251. First (A) and second (B) dorsal fins of *Cirrhigaleus barbifer*, HUMZ 101533, juvenile male, 650 mm TL.

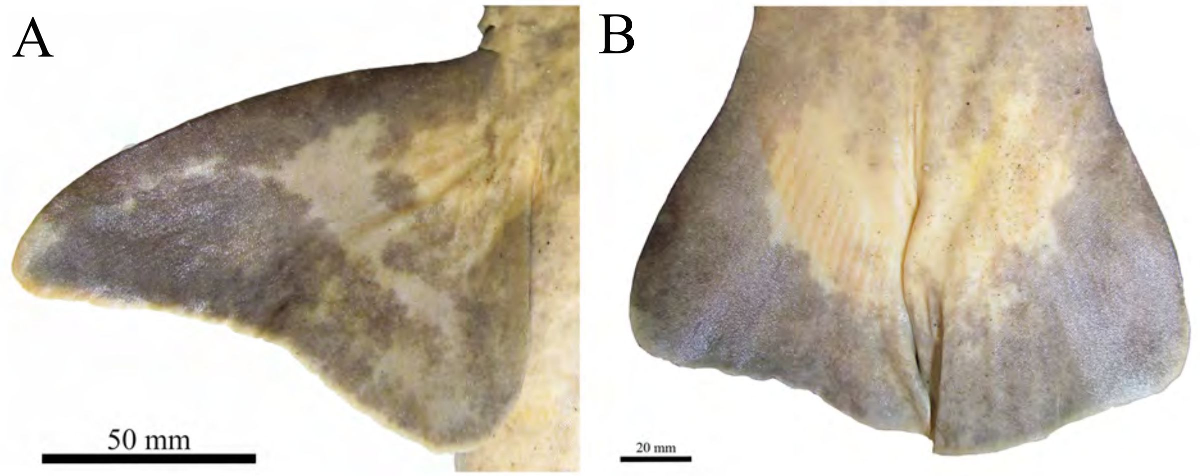

Figure 252. Pectoral (A) and pelvic (B) fins of *Cirrhigaleus barbifer*, HUMZ 197852, adult female, 870 mm TL.

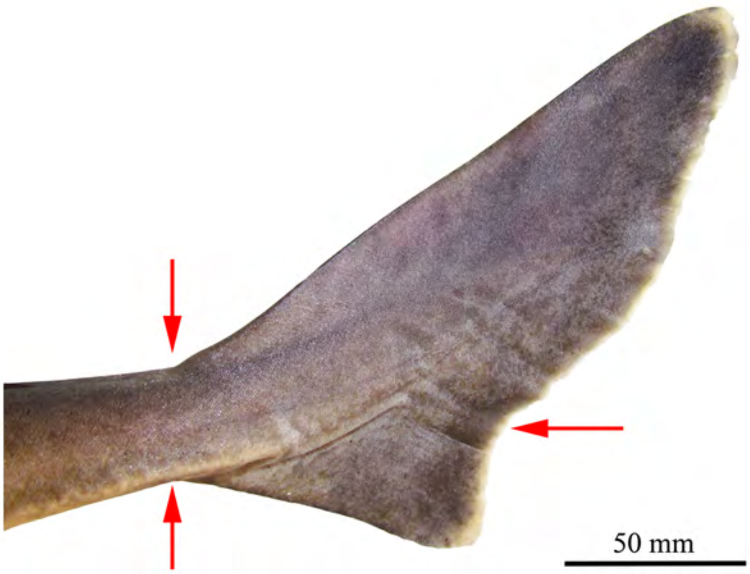

Fig. 253. Detail of caudal fin, showing lateral caudal keel, absence of precaudal pit and continuous transition between caudal lobes.

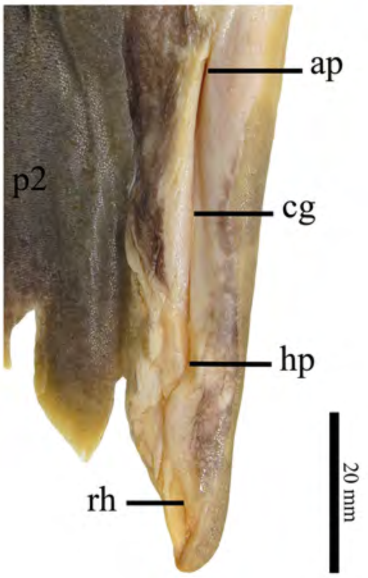

Figure 254. Clasper of *Cirrhigaleus barbifer*, NMNZ P 38074, adult male, 1020 mm TL in dorsal view. Abbreviations: ap: apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

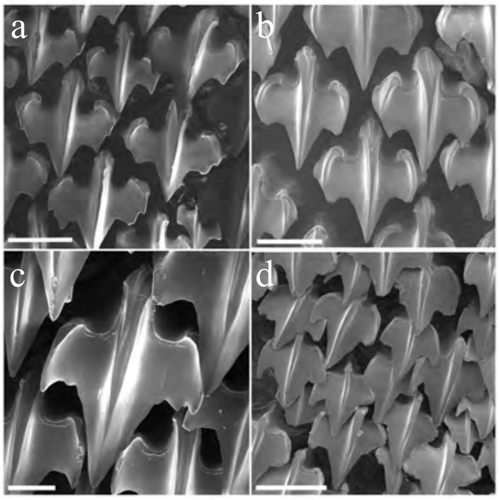

Figure 255. Scanning electron microscopy of dermal denticles of *Cirrhigaleus barbifer*. a: NMW 98257, adult female, 960 mm TL; b: CSIRO H 5875-09, adult female, 978 mm TL; c: NMNZ P 38074, adult male, 1020 mm TL; d: NMNZ P 42489, juvenile male, 710 mm TL. Scale bars: 200 µm (c); 500 µm (a,b,d).

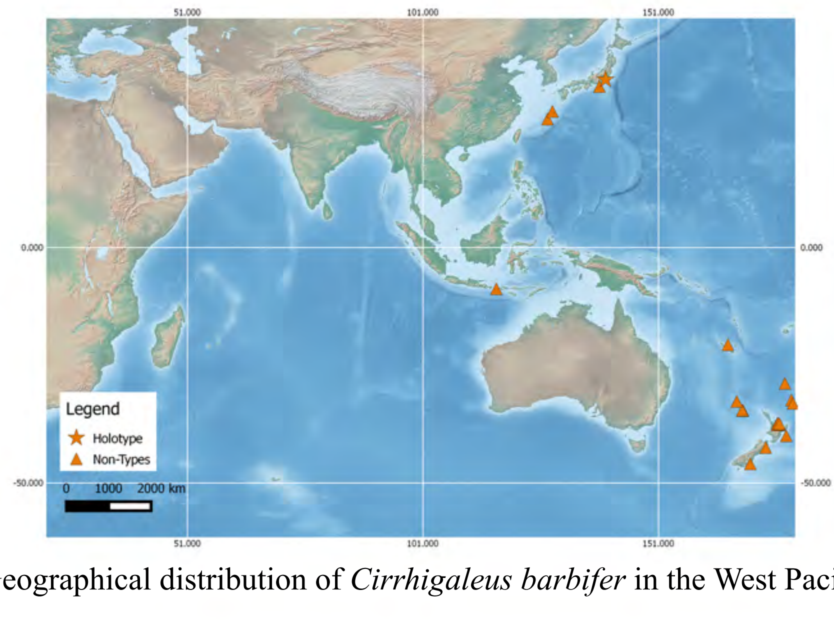

Figure 256. Geographical distribution of *Cirrhigaleus barbifer* in the West Pacific Ocean.

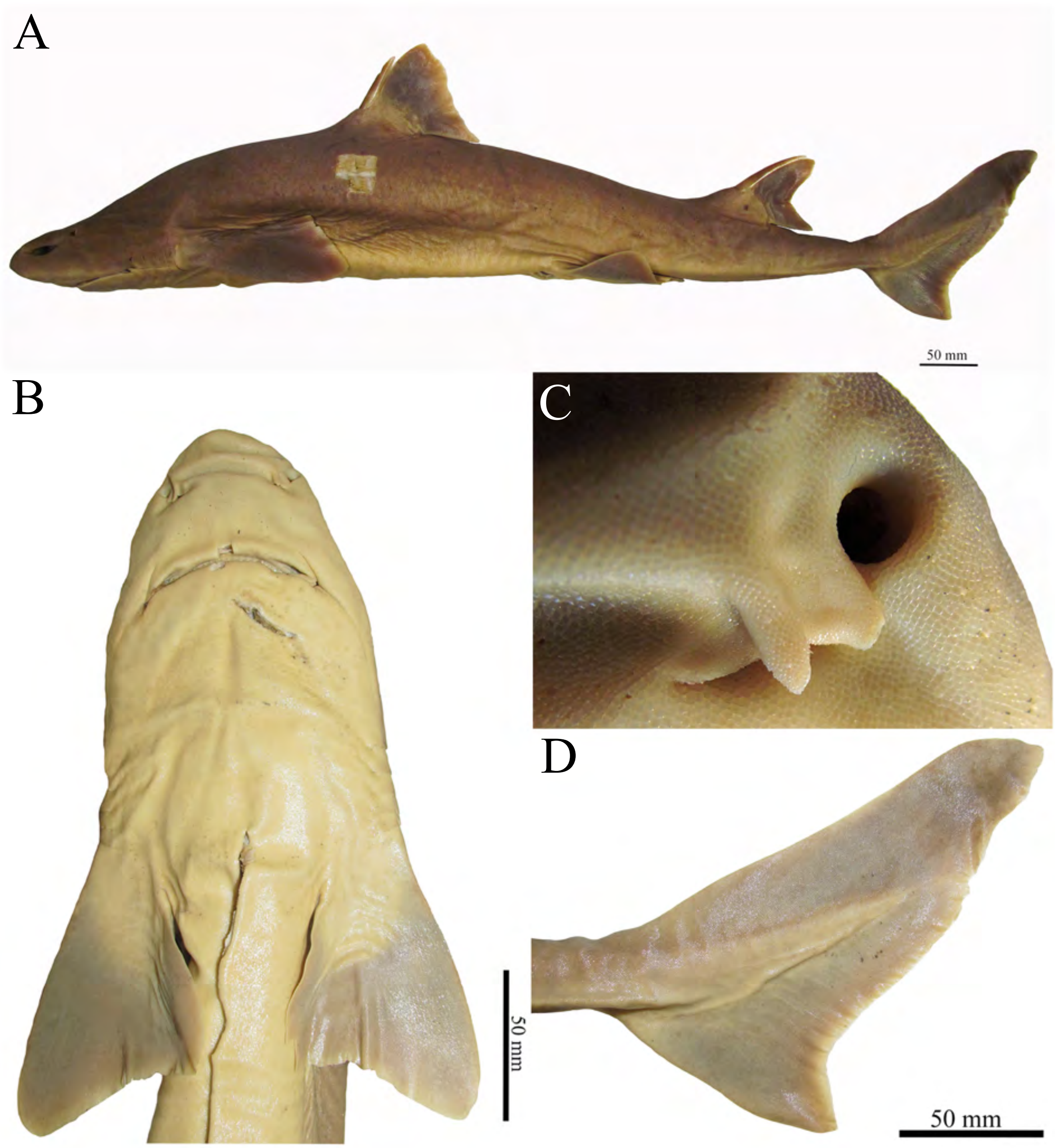

Figure 257. Holotype of *Cirrhigaleus asper*, BMNH 1972.10.10.1, adult male, 880 mm TL in lateral (A), and ventral (B) views, and detail of nasal barbel (C) and caudal fin (D).

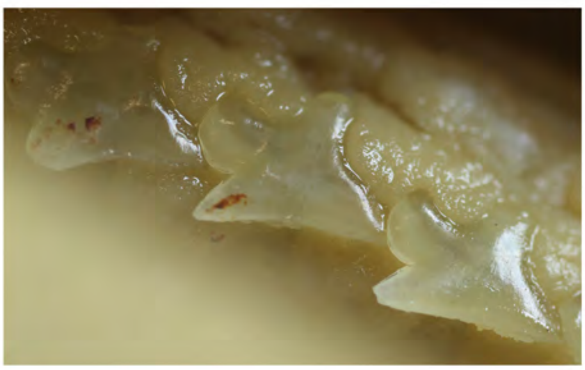

Figure 258. Upper teeth of paratype of *Cirrhigaleus asper*, BMNH 1972.10.10.2, adult male, 847 mm TL.

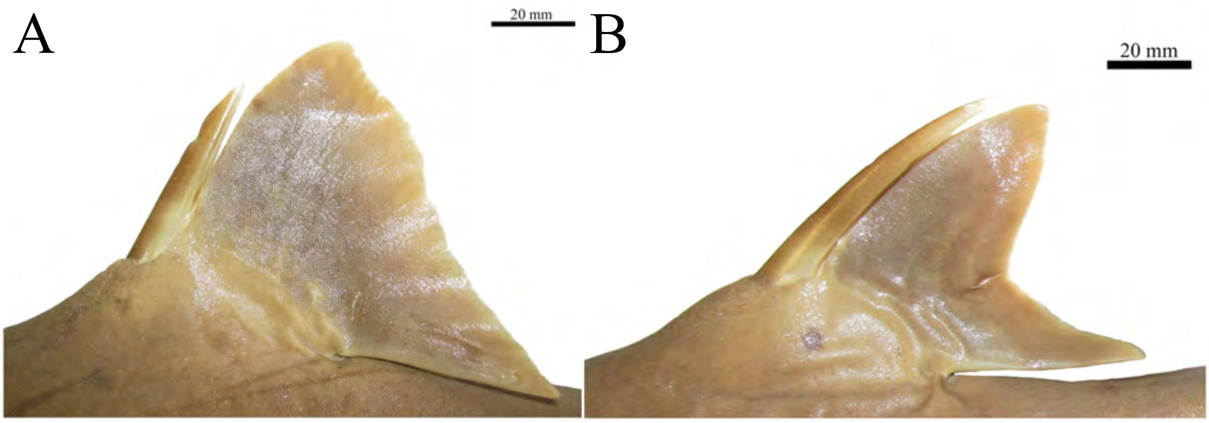

Figure 259. First (A) and second (B) dorsal fins holotype of *Cirrhigaleus asper*, BMNH 1972.10.10.1, adult male, 880 mm TL.

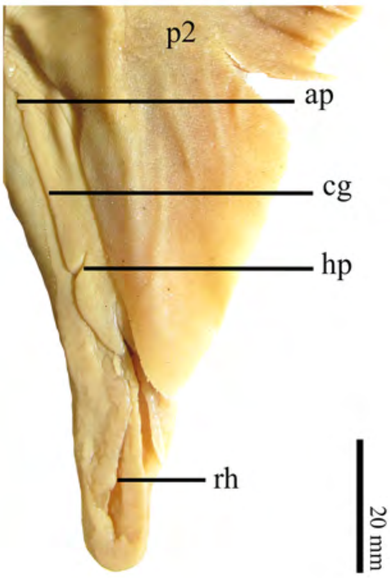

Figure 260. Clasper of paratype of *Cirrhigaleus asper*, BMNH 1972.10.10.2, adult male, 847 mm TL in dorsal view. Abbreviations: ap:apopyle; cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

Figure 261. Dermal denticles of holotype of *Cirrhigaleus asper*, BMNH 1972.10.10.1, adult male, 880 mm TL.

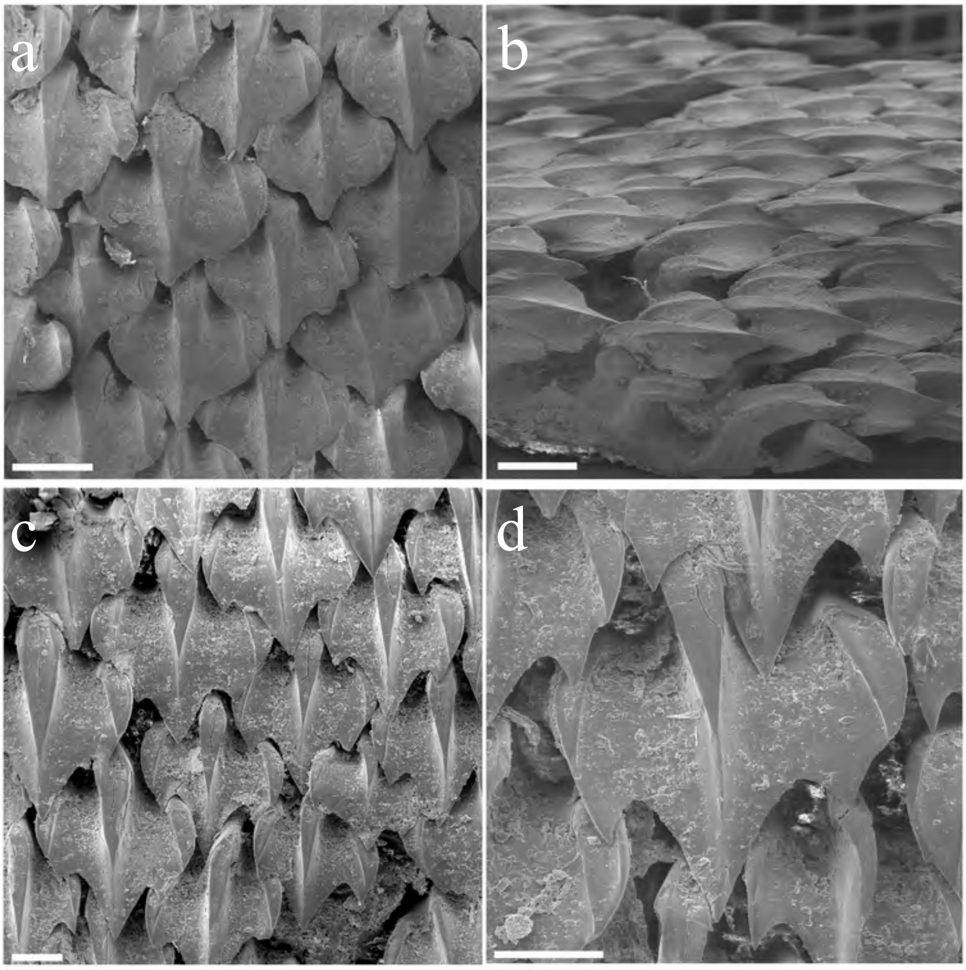

Figure 262. Scanning electron microscopy of *Cirrhigaleus asper*, showing dermal denticles. a,b: SAIAB 31890, adult female, 1090 mm TL; c,d: SAM 39879, adult female, 1023 mm TL. Scale bars: 200 µm (c,d); 500 µm (a,b).

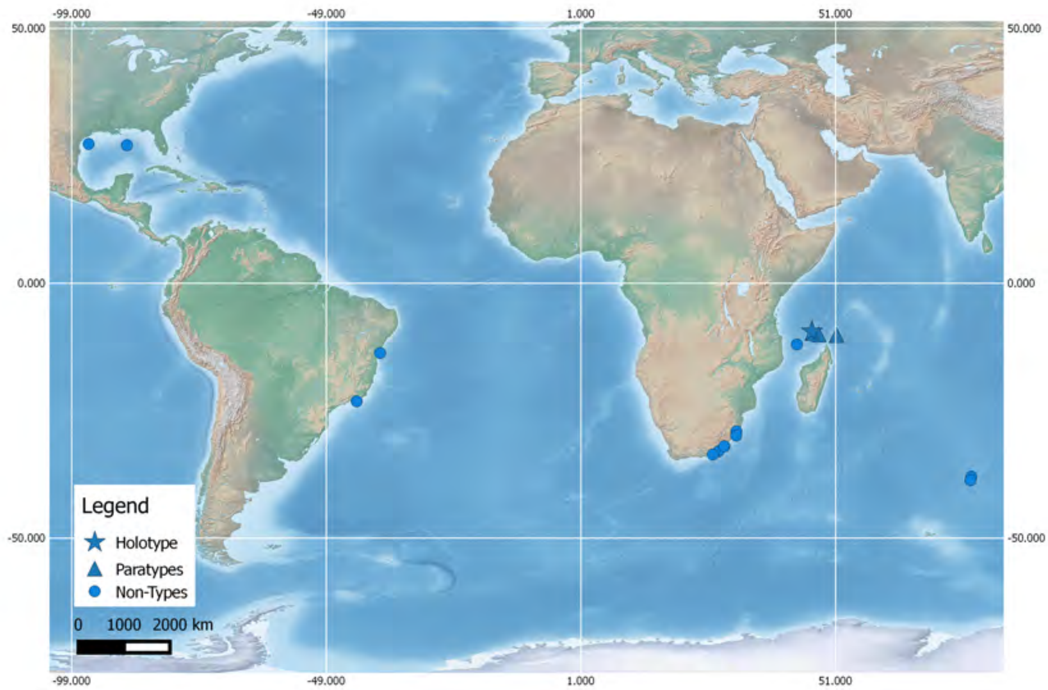

Figure 263. Map of geographical distribution of *Cirrhigaleus asper* in the Indian and Atlantic Oceans.

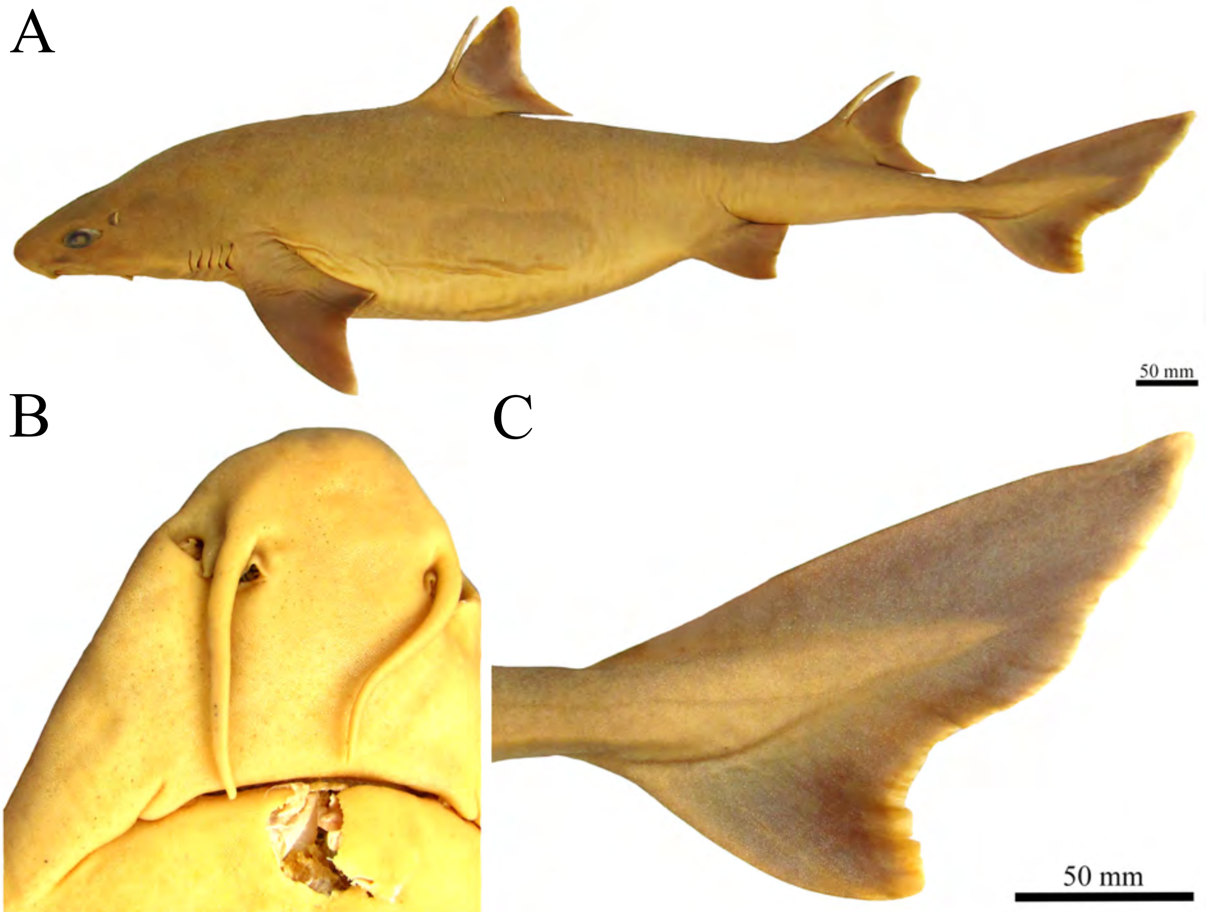

Figure 264. Holotype of *Cirrhigaleus australis*, CSIRO H 5789-01, adult female, 970 mm TL in lateral (A) and anterior ventral view (B), and detail of caudal fin (C).

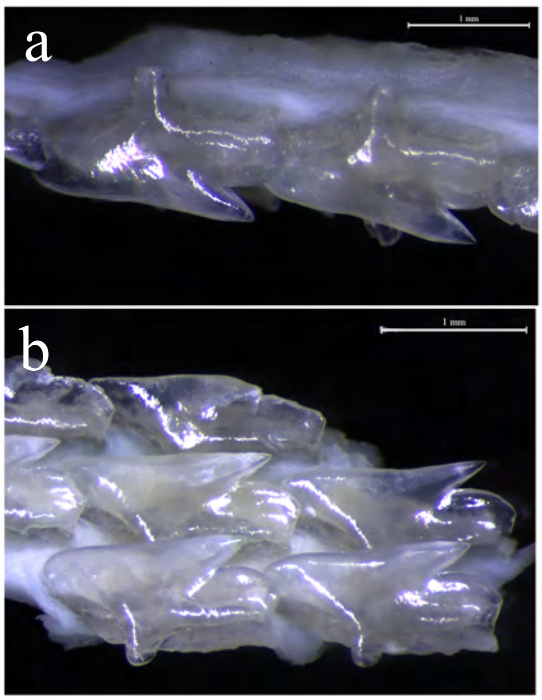

Figure 265. Upper (a) and lower (b) teeth of *Cirrhigaleus australis*, AMS I 45670-001, juvenile male, 630 mm TL. Scale bar: 1mm.

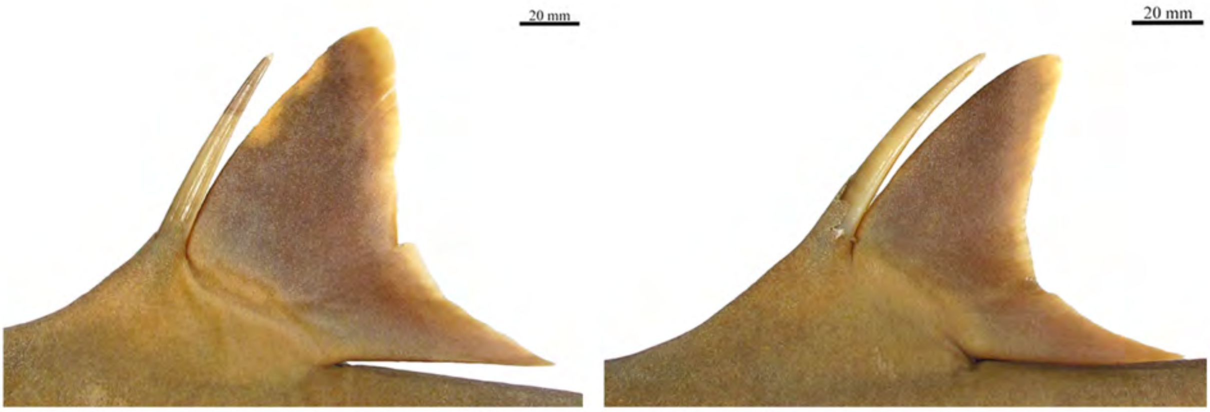

Figure 266. First (A) and second (B) dorsal fins of holotype of *Cirrhigaleus australis*, CSIRO H 5789-01, adult female, 970 mm TL.

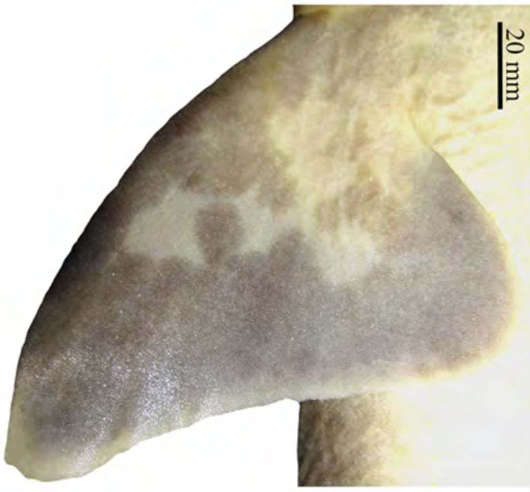

Figure 267. Pectoral fin of *Cirrhigaleus australis*, CSIRO H 7042-04, juvenile female, 605 mm TL in ventral view.

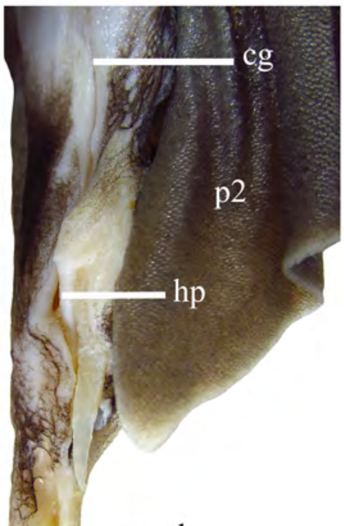

Figure 268. Clasper of *Cirrhigaleus australis*, CSIRO H 7048-01, adult male, 993 mm TL in dorsal view. Abbreviations: cg: clasper groove; hp: hypopyle; p2: pelvic fin; rh: rhipidion.

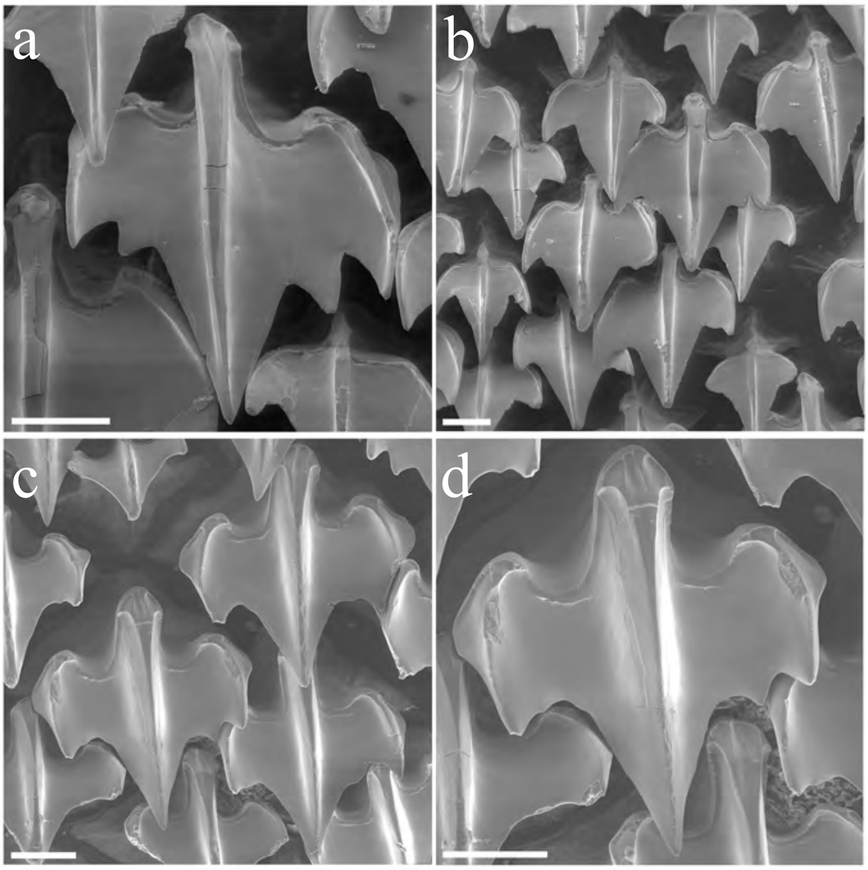

Figure 269. Scanning electron microscopy of dermal denticles of *Cirrhigaleus australis*: a,b: AMS I 45670-001, juvenile male, 630 mm TL; c,d: CSIRO H 7048-01, adult male, 993 mm TL. Scale bar: 200 µm.

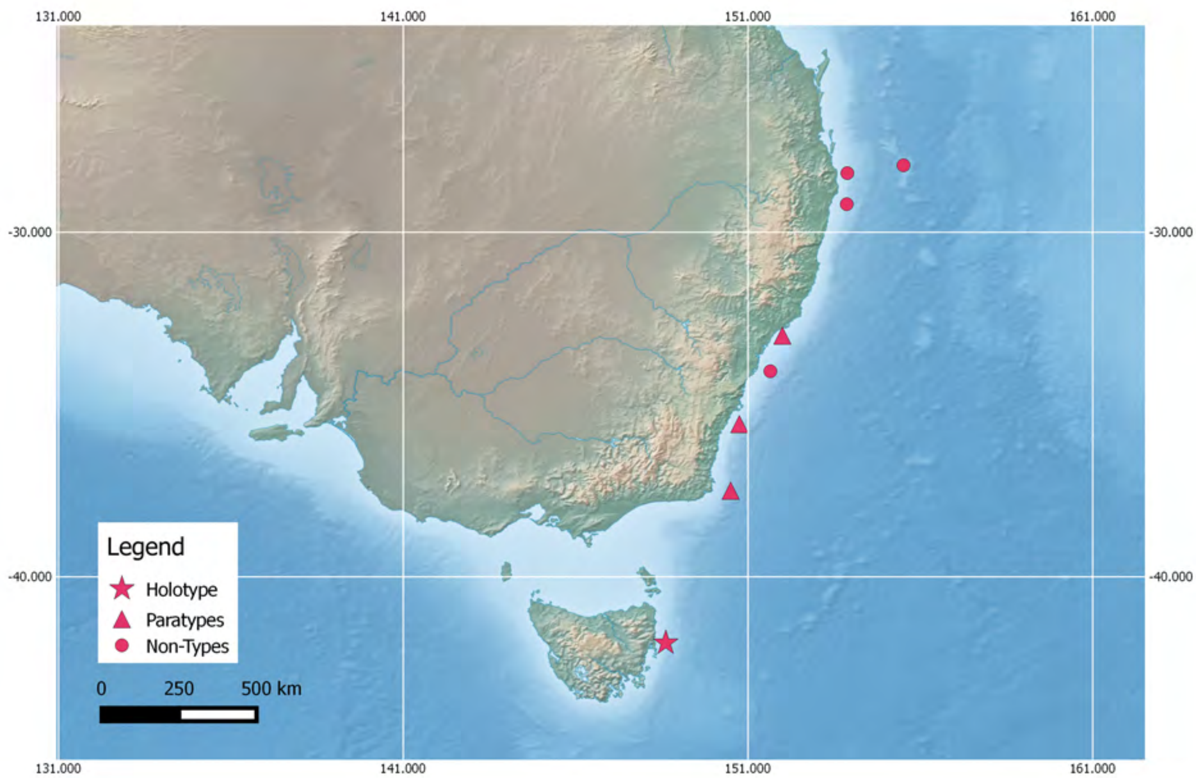

Figure 270. Map of Australia, showing the geographical distribution of *Cirrhigaleus australis*.

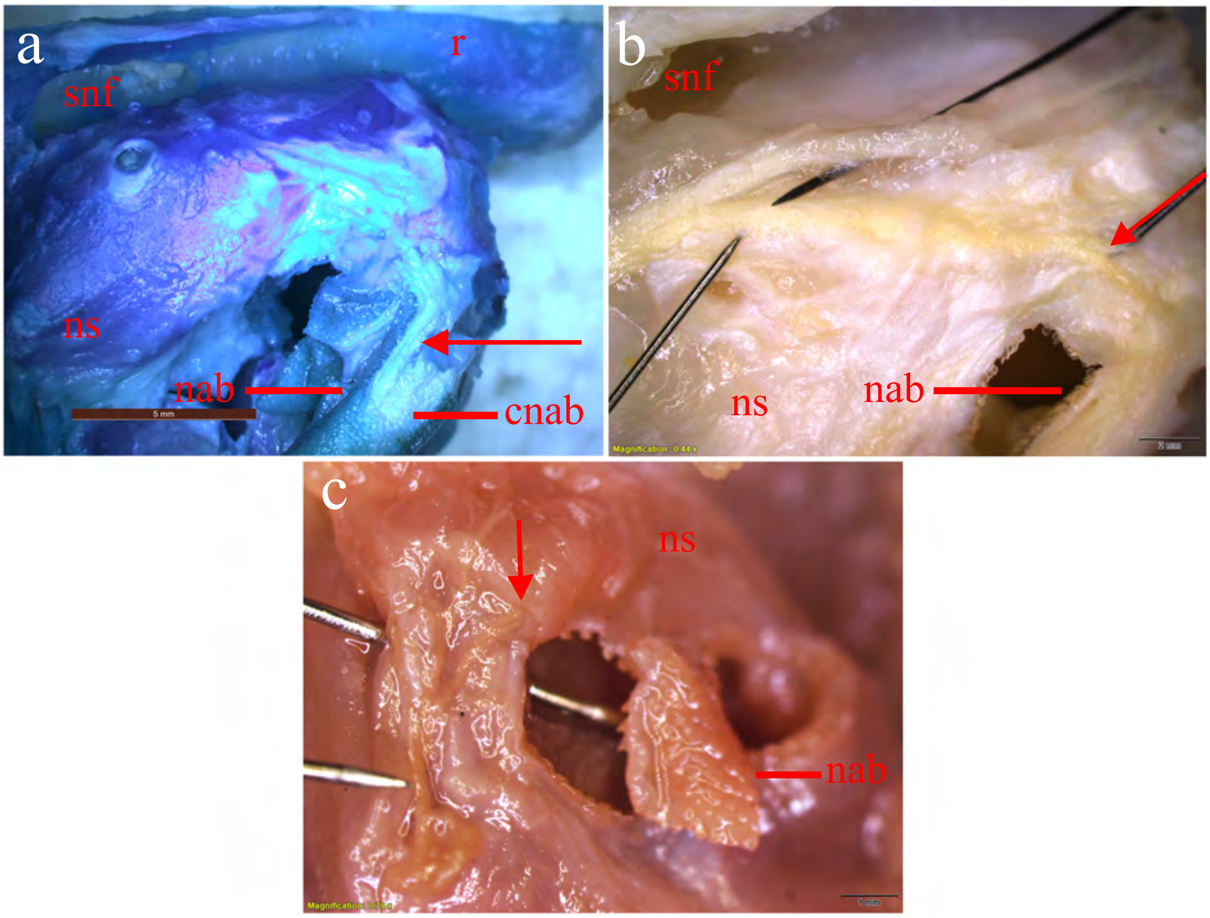

Figure 271. Nasal barbel of *Cirrhigaleus*, innervated by the buccopharyngeal branch of facial nerve (VII). a: HUMZ 95177, juvenile female, 584 mm TL; b: SAIAB 6092, neonate female, 275 mm TL; c: CSIRO H 7042-04, juvenile female, 605 mm TL. Scale bars: 5 mm (a); 1 mm (b); 2 mm (c). Abbreviations: cnab: fleshy core; nab: nasal barbel; ns: nasal capsule; r: rostrum; snf: subnasal fossa. Red arrow shows branch of buccopharyngeal nerve running to nasal capsule.

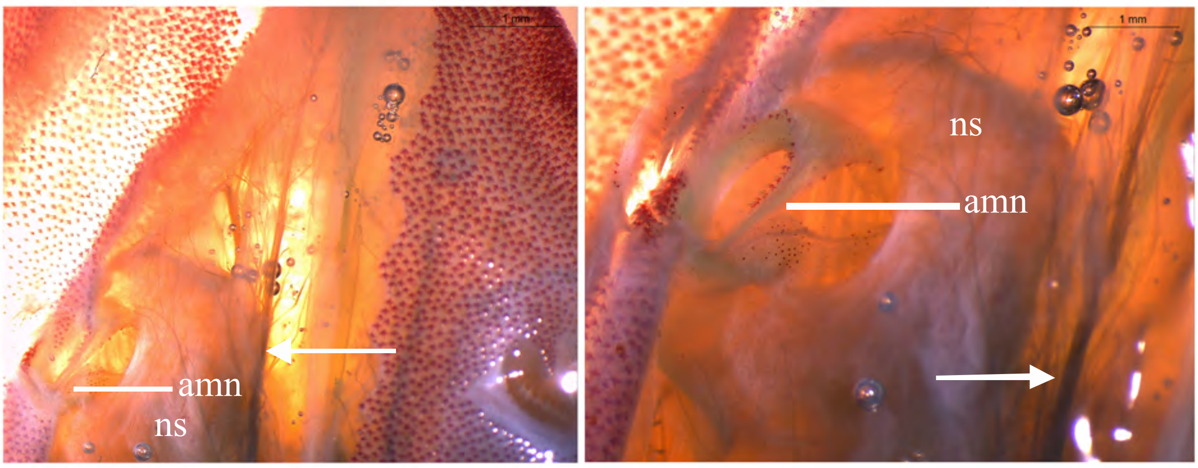

Figure 272. Anterior margin of nostril in *Squalus suckleyi*, CAS 21971, neonate female, 290 mm TL, not innervated by facial nerve (VII). Scale bar: 1mm. Abbreviations: amn: anterior margin of nostril; ns: nasal capsule. White arrow indicates the facial nerve running straight to the tip of rostrum.

Conclusões gerais

(**1**) Squalidae é composta pelos gêneros, *Squalus* e *Flakeus*, cujas espécies habitam águas dos Oceanos Atlântico, Índico e Pacífico. Os membros da família são caracterizados por: espinho dorsal sem sulco à frente de cada nadadeira dorsal; nadadeira caudal sem entalhe subterminal; sulcos pré-caudais superior e inferior presentes; um par de processos supraethmoidais no neurocrânio; margem anterior da narina curta, suportada internamente apenas por cartilagem.

(**2**) A subdivisão de *Squalus* em grupos/complexos de espécies é desnecessária, pois características morfológicas fornecidas para cada grupo são sobrepostas. Algumas espécies (*e.g. F. albifrons, F. raoulensis, F. hemipinnis, F. brevirostris*) frequentemente apresentam características adereçadas a mais de um grupo de espécie, indicando que o agrupamento de espécies semelhantes morfologicamente é ineficiente. Outras espécies com características morfológicas exclusivas (*e.g. S. acanthias, F. crassispinus, F. bucephalus, F. blainvillei, F. melanurus*) não necessitam da prévia identificação a nível de grupos de espécies.

(**3**) *Squalus* compreende três espécies de tubarões com manchas brancas dorsais: *Squalus acanthias* (espécie-tipo) presente nos Oceanos Atlântico e Pacífico Sul; *Squalus suckleyi* do Oceano Pacífico Norte Oriental; *Squalus wakiyae* do Oceano Pacífico Norte Ocidental. Esta última espécie é ressuscitada como válida e diferenciada dos congêneres com base em número de manchas brancas no corpo, formato dos dentículos dérmicos, contagem de vértebras e algumas medidas externas. As espécies de *Squalus* também apresentam: margem anterior da narina unilobada; dentículos dérmicos unicuspidados com apenas uma crista; primeiro espinho curto e nunca atingindo metade da altura da primeira nadadeira dorsal.

(**4**) A autapomorfia de *Squalus acanthias* é suportada por apresentar uma crista escapular segmentada exclusiva na cintura peitoral. O lectótipo da espécie é designado a partir de espécimes das coleções Linneanas. Variações morfológicas intraespecíficas ainda são observadas para dentição e contagem de vértebras.

(**5**) *Flakeus* é ressuscitado com 27 espécies válidas, incluindo sete espécies novas para os Oceanos Atlântico Sul e Índico Ocidental. O gênero é caracterizado por: margem anterior da narina bilobada; dentículos dérmicos unicuspidados ou tricuspidados com três cristas; primeiro espinho dorsal alongado com comprimento acima da metade da altura da primeira nadadeira dorsal.

(**6**) *Flakeus megalops* é endêmica de águas Australianas, exceto na região de Northern Territory. Variações morfológicas intraespecíficas para formato da nadadeira peitoral e dentículos dérmicos são notadas. A espécie não ocorre nos Oceanos Atlântico e Índico, e outras espécies são reconhecidas: *Flakeus* sp. 1, *Flakeus* sp. 3, *Flakeus* sp. 7.

(**7**) *Flakeus acutipinnis* é válida e endêmica do Oceano Índico Ocidental. A confusão sobre seu *status* taxonômico é devido a heterogeneidade de formas na série-tipo. *Flakeus* sp. 1 de águas africanas é reconhecida como resultado desta análise.

(**8**) *Flakeus blainvillei* é endêmica do Mar Mediterrâneo, portanto a ocorrência da mesma em outras regiões é descartada. É a única espécie dentro de Squalidae que possui dois processos cartilaginosos em cada lado da placa basal do neurocrânio.

(**9**) *Flakeus probatovi* é ressuscitada como válida e distinta de *F. blainvillei* para costa da África nos Oceanos Atlântico e Índico.

(**10**) *Squalus altipinnis* e *S. formosus* são consideradas novos sinônimos júnior de *Flakeus albifrons*. Esta última espécie ocorre entre Taiwan e Austrália e variações de coloração são observadas entre os espécimes.

(**11**) *Flakeus mitsukurii* é presente apenas no Oceano Pacífico Norte e Central. A ocorrência em regiões do Atlântico, Índico e Pacífico Sul é rejeitada. *Flakeus* sp. 2, *Flakeus* sp. 4, *Flakeus* sp. 5, e *Flakeus* sp. 6 são espécies novas reconhecidas para estas regiões.

(**12**) A análise de mais representantes de *Flakeus montalbani* provenientes da localidade-tipo ainda é necessária para a melhor caracterização da espécie. *Squalus chloroculus* é considerada sinônimo júnior desta, pois nenhuma diferença morfológica é observada.

(**13**) *Flakeus japonicus* ocorre entre Japão, Filipinas, Taiwan, Indonésia e Norte da Austrália. Sobreposição de medidas externas e contagem de vértebras os espécimes suportam *Squalus nasutus* como novo sinônimo júnior de *F. japonicus*.

(**14**) *Flakeus rancureli*, descrita de Vanuatu, é considerada sinônimo júnior de *F. melanurus*. Todos os espécimes analisados desta região também apresentam mancha preta no lobo ventral da nadadeira caudal, uma característica exclusiva de *F. melanurus*.

(**15**) *Cirrhigaleus* é um gênero válido com três espécies que apresentam barbilhão nasal: *Cirrhigaleus barbifer* do Oceano Pacífico Norte e Sul; *C. asper* dos Oceanos Atlântico e Índico; *C. australis* do Oceano Pacífico Sul Ocidental. Estas espécies têm variação ontogenética conspícua. A inserção do gênero dentro de Squalidae, contudo, é questionada já que características externas e do esqueleto das espécies refletem maior semelhança com outros grupos de Squaliformes.

(**16**) *Cirrhigaleus asper* é válida e corretamente inserida neste gênero. Diferenças de características do esqueleto entre esta espécie e representantes de *Squalus* e *Flakeus* também dão suporte para esta hipótese.

Resumo

Squalidae compreende dois gêneros de tubarões, *Squalus* e *Cirrhigaleus* cujas espécies apresentam taxonomia complexa devido à dificuldade de distinção morfológica entre elas, associado a uma incerteza à aplicação de várias espécies nominais. A revisão taxonômica e morfológica dos representantes da família foi conduzida para delimitar globalmente as espécies válidas e fornecer caracteres diagnósticos eficientes através de análises detalhada da morfologia externa e esquelética. Foram reconhecidas 30 espécies válidas para a família, classificadas em dois gêneros. *Squalus* compreende um gênero menor com três espécies de tubarões com manchas brancas no corpo. Um segundo gênero, separado de *Squalus*, é reconhecido para abrigar 27 espécies de tubarões sem manchas. Assim, a hipótese de subdivisão do gênero *Squalus* em "grupos/complexos de espécies" (grupos *S. acanthias*, *S. mitsukurii* e *S. megalops*) foi refutada. Sete espécies novas são descritas para os Oceanos Atlântico Sul e Índico Ocidental, e duas espécies nominais são ressuscitadas como válidas. Cinco espécies são propostas como novos sinônimos de outras espécies dentro deste contexto. *Cirrhigaleus* é um gênero válido e menos diverso, incluindo três espécies com barbilhão nasal. A alocação genérica da espécie nominal "*asper*", antes em constante discussões na literatura, é finalmente esclarecida para *Cirrhigaleus*. A classificação taxonômica de *Cirrhigaleus* dentro de Squalidae, contudo, é questionada e uma nova família para Squaliformes é proposta para abrigar este gênero. Características do esqueleto em Squalidae exibem complexidade e variação maior do que antes descrito. Caracteres esqueléticos são também apresentados para serem integrados em análise filogenética futura.

Palavras-chave: tubarões, Taxonomia, Morfologia, *Squalus, Cirrhigaleus,* Squalidae

Abstract

Squalidae comprises two genera of sharks, *Cirrhigaleus Squalus*, whose species have complex taxonomy due to difficulty of morphological distinction between them, associated to an uncertainty to the application of its available nominal species. A taxonomic and morphological revision of the family was conducted in order to globally delimitate the valid species and provide efficient diagnostic characters through detailed analyses of external and skeletal morphology. *Squalus* is herein recognized as a smaller group, which comprises three species of spotted-dogfish. A second genus is raised as separated from *Squalus* with 27 species of non-spotted dogsharks. Thus, the hypothesis of subdivision of *Squalus* into three groups/complexes of species (*S. acanthias*, *S. mitsukurii* and *S. megalops* groups) is refuted. Seven new species are described for the South Atlantic and West Indian Oceans, and two nominal species are resurrected as valid for the family. Five species are proposed as new synonyms from other species within this context. *Cirrhigaleus* is a valid and less diverse genus, comprising three species of barbel-bearing dogfish. Generic allocation of the nominal species "*asper*", beforehand under constant discussions on literature, is elucidated for *Cirrhigaleus*. However, taxonomic classification of *Cirrhigaleus* within Squalidae is questioned and a new family for Squaliformes is proposed to incorporate the genus. Characteristics of the skeleton in Squalidae reveal to be more complex than previously thought. Morphological characters are also provided for integrating future phylogenetic analysis.

Keywords: Sharks, Taxonomy, Morphology, *Squalus, Cirrhigaleus,* Squalidae

Appendix A

Cranial measurements in Squalidae, modified from Muñoz-Chápuli & Ramos (1989) and Compagno (1988).