Flávia de Figueiredo Petean

Taxonomic review and comparative morphology of the species of the genus *Isistius* Gill, 1864 (Chondrichthyes: Squaliformes: Dalatiidae)

Revisão taxonômica e morfologia comparada das espécies do gênero *Isistius* Gill, 1864 (Chondrichthyes: Squaliformes: Dalatiidae)

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Dissertação apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção do Título de Mestre em Ciências Biológicas, na Área de Zoologia.

Orientador: Prof. Dr. Marcelo Rodrigues de Carvalho

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Prof. Dr. Marcelo Rodrigues de Carvalho
Orientador

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Resumo

O gênero *Isistius* Gill (1864) pertence à família Dalatiidae e atualmente apresenta três espécies válidas na literatura: *Isistius brasiliensis* Quoy & Gaimard (1824), *I. plutodus* Garrick & Springer (1964) e *I. labialis*, Meng, Zhu & Li (1985). A espécie mais comum, *I. brasiliensis*, tem uma ampla distribuição geográfica e pode ser encontrada em mares subtemperados e tropicais do mundo; uma análise comparativa detalhada de exemplares provenientes de diferentes localidades nunca foi feita. Neste estudo, examinou-se detalhadamente a variação morfológica desta espécie ao longo de sua distribuição, elucidando se ela representa apenas uma espécie distribuída mundialmente, e se *I. labialis* é um sinônimo júnior. A outra espécie, *I. plutodus*, é conhecida apenas por alguns exemplares, levantando dúvidas acerca de sua validade, dado que *I. brasiliensis* é amplamente distribuído. Foi feita uma análise comparativa detalhada destes indivíduos a fim de testar a validade da espécie. Estudaram-se os holótipos de todas as espécies nominais de *Isistius*. Assim, este estudo analisou detalhadamente a morfologia externa, como coloração, dentição, dentículos dérmicos, proporções corporais, e interna, como esqueleto, musculatura e canais da linha lateral, das espécies conhecidas além de examinar aspectos morfométricos e merísticos que auxiliaram na melhor definição do gênero e forneceram subsídios morfológicos relevantes que podem integrar futuras análises filogenéticas dentro da família.

Abstract

The genus *Isistius* Gill (1864) belongs to the family Dalatiidae and has currently three valid species recognized in the literature: *Isistius brasiliensis* Quoy & Gaimard (1824), *I. plutodus* Garrick & Springer (1964), and *I. labialis* Meng, Zhu & Li (1985). The most common species, *I. brasiliensis*, has a wide geographic distribution and can be found in subtemperate and tropical seas circumglobally; a comparative analysis of specimens from different localities throughout its range, however, has never been done. In the present study, the morphological variation of this species along its entire distribution has been thoroughly analyzed, elucidating that it represents a single widespread species and that *I. labialis* is a junior synonym of *I. brasiliensis*. The other species, *I. plutodus*, is known from only few specimens, raising doubts about its validity in light of the widespread distribution of *I. brasiliensis*. A detailed comparative analysis of available material of *I. plutodus* was undertaken to test its validity. Type specimens of all nominal species available in *Isistius* were also studied. Therefore, the present study analyzed in detail the external morphology (coloration, dentition, dermal denticles, and body proportions), and internal morphology (skeleton, musculature, and lateral line canals) of the known species of *Isistius*, also covering morphometric and meristic aspects, to better define the genus and provide relevant morphological data that may integrate future phylogenetic analyses of genera within the family.

I. Introdução

Elasmobranchii é um clado, como definido por Maisey (1984), formado por tubarões e raias recentes, além dos fósseis *Palaseospinax*, *Synechodus*, *Hybodus*, *Xenacanthus*, and *Ctenacanthus*. Compagno (1973) sugeriu que elasmobrânquios viventes diferem daqueles do Paleozoico. Compagno (1973, 1977) e Carvalho (1996) nomearam as formas viventes de tubarões e raias, além de dois gêneros fósseis (*Palaeospinax* e *Synechodus*) como Neoselachii, o que é diferente de Elasmobrânquios recentes. Porém, Maisey (2012) definiu que a palavra Elasmobranchii deveria ser usada em referência a tubarões e raias “modernos” (grupo-coroa neoseláquios e seus parentes fósseis imediatos), e sugeriu que as palavras Elasmobranchii e Neoselachii fossem sinônimas, como o grupo original “Elasmobranchii” é usado informalmente e não diagnosticável. Além disso, Maisey (1984) uniu todos os elasmobrânquios modernos por uma série complete de radiais calcificados pericondralmente na nadadeira dorsal anterior; enameloide disposto de forma aleatória sobre os dentes, e Carvalho (1996) definiu elasmobrânquios recentes por caracteres que podem ser revertidos a níveis menos inclusivos: presença de cartilagens extrabranquaiais na hyomandibula; presença de *adductor mandibulae superficialis*; coracoides direito e esquerdo fusionados; e dentes com “aventais”.

Elasmobranchii recentes, ou Neoselachii, tem 1221 espécies viventes válidas (Naylor *et al.*, 2012) e incluem tubarões e raias que podem ser reconhecidos por cinco, seis ou sete fendas branquiais em cada lado da cabeça. Atualmente, há 680 espécies de raias conhecidas (Naylor *et al.*, 2012), que são caracterizadas pelas nadadeiras peitorais expandidas, achatadas e fusionadas à lateral da cabeça, acima das fendas branquiais (Compagno *et al.*, 2005a). Além disso, há 541 espécies válidas de tubarões (Naylor *et al.*, 2012) que podem ser cilíndricos ou achatados, e não tem nadadeiras peitorais fusionadas à cabeça.

Uma das ordens mais diversas de elasmobrânquios é Squaliformes, com 132 espécies válidas (Naylor *et al.*, 2012) em sete famílias: Echinorhinidae, Squalidae, Centrophoridae, Etmopteridae, Somniosidae, Oxynotidae e Dalatiidae. Esses tubarões, que variam amplamente em tamanho, tem duas nadadeiras dorsais com ou sem espinhos e ausência de nadadeira anal, sulcos labiais proeminentes; ausência de barbilhões rostrais; coluna vertebral na nadadeira caudal elevada e formando um lobo caudal dorsal moderadamente longo, sendo que o ventral varia de ausente a muito pronunciado. Há cinco fendas branquiais, todas à frente da origem das nadadeiras peitorais; narinas não conectadas à boca por sulcos e espiráculos posteriores aos olhos, os quais estão posicionados na região lateral da cabeça e não apresentam membranas nictitantes (Compagno, 1973).

Tubarões da família Dalatiidae ocorrem em águas profundas, entre 200 e 1800 metros, nas zonas epi-, meso- e, provavelmente, batipelágicas, sendo caracterizados pelo focinho curto sem barbilhões; dentes com cúspides fortes e diferentes nas mandíbulas superior e inferior, sendo os dentes superiores estreitos e pontiagudos, enquanto os inferiores são largos, em formato de lâmina e maiores que os superiores (Compagno, 1984). Há duas pequenas nadadeiras dorsais, sendo a área da primeira menor ou igual à da segunda, sem espinhos. A única exceção é *Squaliolus*, que possui um espinho em frente à primeira nadadeira dorsal (Shirai, 1992a). A nadadeira anal é ausente e a caudal é fortemente assimétrica, com o lobo ventral variando de ausente a muito pronunciado. O corpo e as nadadeiras possuem coloração acinzentada e órgãos luminescentes podem estar presentes (Compagno, 1984; Claes *et al.*, 2014).

Atualmente, há sete gêneros na família, *Dalatias*, *Euprotomicroides*, *Euprotomicrus*, *Heteroscymnoides*, *Mollisquama*, *Squaliolus* e *Isistius*, todos monoespecíficos, com exceção de *Squaliolus*, com duas espécies, e *Isistius*, com três (Compagno, 2005).

1. Histórico taxonômico

Linnaeus, em 1758, descreveu o gênero *Squalus* como tubarões com cinco fendas branquiais na lateral da cabeça e ausência de nadadeira anal, corpo longo e afunilado posteriormente, além de boca terminal. Ele também descreveu, na página 233, a espécie *Squalus centrina* com espinhos dorsais e corpo subtriangular. Broussonet (1780) descreveu outra espécie, *La Liche*, ainda não utilizando a nomenclatura binomial proposta por Linnaeus. Esta espécie tinha pele com espinhos e assemelhava-se a outra espécie descrita pelo mesmo autor e no mesmo livro, *L'Aiguillat*. Mas, *La Liche* diferenciava-se da outra espécie pela ausência de espinhos nas nadadeiras dorsais e pelas nadadeiras pélvicas serem muito próximas da cauda. A segunda nadadeira dorsal era maior que a primeira e era usada para distinguir uma espécie da outra. Nenhuma desses espécies pode, atualmente, ser considerada um sinônimo de *Isistius*; porém, elas foram o alicerce para as descrições que seguiram.

Bonnaterre (1788) dividiu os peixes em grupo e citou *La Liche* descrita por Broussonet (1780). Ele a inseriu na Primeira Classe (Peixes Cartilaginosos) e no Terceiro Gênero (*Squalus*, espécimes com 4-7 fendas branquiais a partir da superfície ventral do corpo). Cuvier (1817) descreveu os gêneros *Scymnus* e *Centrina*, sendo o primeiro equivalente a *La Liche* Broussonet (1780) e o segundo a *Squalus* (*S. centrina* Linnaeus, 1758). Todos os caracteres descritos por Cuvier para *Scymnus* são os mesmos para *Centrina*, com exceção dos espinhos das nadadeiras dorsais, como mencionado previamente por Broussonnet (1780), mesmo que ele a tenha nomeado como *L'Aiguillat*. Os dentes inferiores de *Scymnus* eram afiados e distribuídos em uma ou duas fileiras, enquanto os superiores eram estreitos, pontiagudos e organizados em várias fileiras. Um indivíduo que foi coletados no Oceano Índico foi notado por sua pequena primeira nadadeira dorsal. Era possível distinguir *Scymnus* de outras espécies cuja primeira nadadeira dorsal estava acima das pélvicas e a segunda muito posteriormente.

Quoy & Gaimard (1824) descreveram um novo sub-gênero, *Leiche*, que eles aparentemente sinonimizaram ao gênero *Scymnus* Cuvier (1817). Eles também descreveram uma nova espécie a partir de um indivíduo macho, *Leiche Laborde* (=*Scymnus bispinatus* Cuvier, um nome aparentemente não disponível e que nunca foi descrito), e mencionaram outro indivíduo fêmea muito pequeno. Este exemplar tinha o formato do corpo similar a *L. Laborde*, mas a mandíbula inferior era desproporcionalmente grande, a boca era mais próxima ao focinho, nadadeiras dorsais maiores e ausência de espinho ventral (o que atualmente pode-se compreender que ele se referia ao clásper, dado que era uma fêmea). Ambos os lobos caudais eram profundamente divididos, com coloração marrom claro, e uma ampla faixa escura na região ventral da cabeça. Eles a nomearam *Leiche du Brésil* sobre o nome *Scymnus brasiliensis* Cuvier (Figure 1). Essa referência é levemente confusa, pois Cuvier nunca mencionou ambas espécies *Scymnus bispinatus* e *Scymnus brasiliensis* que são supostamente sinônimos sênior de *Leiche Laborde* e *Leiche du Brésil*, respectivamente. Assim, parece que Quoy & Gaimard deram duas opções para os nomes dessas novas espécies: uma usando "*Leiche*" e outra "*Scymnus* Cuvier". Porém, o suposto novo nome "*Leiche*" pode ser um erro de escrita do nome *La Liche* Broussonnet (1780).

Bennett (1840) encontrou dois espécimes bioluminescentes cujas descrições são muito detalhadas e similares ao que é atualmente conhecido como *Isistius*. Ele os nomeou *Squalus fulgens*, seguindo Linnaeus (1758), e não mencionou as descrições de Quoy & Gaimard (1824), que já haviam percebido a existência de um novo grupo de espécimes similares a *Squalus* e descreveram novos gêneros e espécies. Bennett indicou que era uma nova espécie de *Squalus* que pertencia ao sub-gênero *Scymnus*. Porém, como as regras para nomear espécies ainda não estavam muito claras, ele sugeriu que a nova espécie fosse *Squalus fulgens*, Além disso, ele não mencionou a coleção cientifica na qual estes exemplares foram depositados, tornando impraticável a avaliação de sua validade como *Isistius*.

Müller & Henle (1841), em sua revisão dos gêneros e espécies descritos para elasmobrânquios, inseriram três famílias na quarta divisão de Squali: Spinaces, Scymni e Squatinae. Na família Scymni, há três gêneros *Scymnus* Cuvier, *Echinorhinus* Blainville e *Pristiophorus* Müller & Henle. O primeiro deles é dividido em dois sub-gêneros: *Scymnus* e *Laemargus*. Por fim, eles consideraram essas duas espécies como pertencentes ao sub-gênero *Scymnus*: *Scymnus (Scymnus) Lichia* Bonaparte e *Scymnus (Scymnus) brasiliensis* Cuvier.

Müller & Henle descreveram a espécie *Scymnus (Scymnus) brasiliensis* com uma aba nasal no final do focinho e dentes inferiores não serrilhados. Nadadeiras peitorais pequenas e arredondadas, que eram maiores em cima do que na base; nadadeiras pélvicas quadradas, com ângulos arredondados na parte anterior e pontiagudos na posterior; primeira nadadeira dorsal anterior à origem das nadadeiras pélvicas; segunda nadadeira dorsal entre a primeira e a base da caudal; ambas nadadeiras dorsais arredondadas na região anterior e prolongadas posteriormente em um angulo agudo, com a margem superior reta; ambas muito pequenas e com a mesma altura; base da segunda nadadeira dorsal maior que a primeira; lobo inferior da nadadeira caudal relativamente grande. Escamas pequenas, sem ponta e com uma depressão no centro.

Os mesmos autores dividiram essa espécie em duas variações: *Scymnus (Scymnus) brasiliensis torquatus* (Figure 1) e *Scymnus (Scymnus) brasiliensis unicolor* (Figure 2). A primeira tinha uma coloração marrom, sendo mais clara na região ventral e com uma faixa mais escura ventral à cabeça. As margens das nadadeiras peitorais e a parte ventral da caudal eram brancas. Enquanto o segundo exemplar tinha a mesma coloração que o primeiro, as nadadeiras pélvicas eram mais escuras e ele não apresentava a faixa mais escura sob a cabeça. Ambos os tipos dessas variações estão localizados no Muséum national d’Histoire naturelle, em Paris, assim como o tipo de *Scymnus brasiliensi* Quoy & Gaimard,1824, que é o mesmo exemplar de *S. (S.) b. torquatus*.

Posteriormente, Kner (1864) descreveu um novo gênero, *Leius*, e espécie, *Leius ferox* (Figure 3), cujo holótipos está no Naturhistorisches Museum, em Viena, na Áustria. Neste espécime, o ânus estava entre as nadadeiras ventrais; o lobo superior da nadadeira caudal era amplamente truncado; e coloração marrom escuro. O autor sugeriu que este espécime pertencesse a um grupo próximo a *Scymnus* e *Laemargus*, mas muito diferente de *Scymnus bispinatus* Quoy & Gaimard, e possivelmente também um sinônimo de *Somniosus brevipinna* Les[?].

Porém, Gill (1864), em sua sinopse de tubarões americanos do leste, descreveu o novo gênero *Isistius* para a família Scymnoidea baseado na espécie *Scymnus brasiliensis* Müller & Henle, que era característico por suas pequenas nadadeiras dorsais posteriormente localizadas no comprimento do corpo. Posteriormente, Gill (1896) explicou que o motivo pelo qual ele alterou o nome *Scymnus* para *Isistius* era devido à existência prévia de um grupo de Coleoptera criado por Kugelmann (1794) (*apud* Gill, 1896).

Rochebrune (1885) descreveu outra espécie para o gênero *Isistius* Gill, *I. marmoratus*. Esta espécie tinha um corpo estreito e arredondado, focinho obtuso e boca pequena e inferior; dentes curtos; primeira nadadeira dorsal na terça parte do comprimento do corpo. Embora Rochebrune tenha escrito que o exemplar está no Museo Bouvieri e que foi coletado na “Landana e toda a Gâmbia”, ambos museu e local de coleta não foram encontrados. Eugène-Louis Bouvier (1856-1944) foi “Professor de Entomologia no Museu de Paris (MNHN) de 1895 a 1931. Em 1885 ele tinha apenas 29 anos e estava dando os primeiros passos de sua carreira. Nenhuma coleção em nome de Bouvier for registrada no Museu (MNHN). Assim, se houver tipos, eles podem ser considerados perdidos.” (Huber, 2000 *in* http://www.killi-data.org/researches-huber-pz-lacazei.php).

Garrick & Springer (1964) descreveram outra espécie para *Isistius, I. plutodus* (Figure 4), com fórmula dental 14+1+14/9+1+9; presença de um curto pedúnculo caudal e pequena nadadeira caudal, com o lobo inferior tendo a metade do comprimento do superior; segunda nadadeira dorsal notavelmente mais alta que a primeira; ausência de colar escuro bem definido e sem manchas na nadadeira caudal.

Por fim, Meng, Zhu & Li (1985) descreveram a mais recente espécie do gênero, *Isistius labialis* (Figure 5). Ela pode ser diferenciada de *I. plutodus* por ter um colar escuro e dez dentes a mais na mandíbula inferior; e diferencia-se de *I. brasiliensis* por ter dobras no lábio inferior, assim como a altura das nadadeiras pélvicas, que são iguais ou maiores que a primeira e segunda nadadeiras dorsais, enquanto em *I. brasiliensis* elas são maiores.

Com relação à nomenclatura da família Dalatiidae, Gray (1851) é o supostamente o autor a ter nomeado a família, como ele escreveu uma lista de exemplares e os dividiu em grupos inclusivos sucessivos. Porém, ele mencionou um subfamília chamada Dalatiana que contem aqueles tubarões que não tem espinhos nas nadadeiras dorsais. Dentro dessa subfamília, ele incluiu dois gêneros: *Dalatias* e *Echinorhinus*. Em *Dalatias* ele incluiu as espécies *Dalatias lichia* (=*Dalatias licha*) e *Dalatias brasiliensis*. A última pode ser identificada como um sinônimo de *Isistius brasiliensis*.

Gray (1851) foi o primeiro autor a usar o nome "Dalatias" para determinar e identificar um grupo de tubarões, já que esse nome tornou-se disponível em 1810, quando Rafinesque descreveu um novo gênero e duas espécies *Dalatias Sparophagus* e *Dalatias Nocturnus*.

Porém, o primeiro autor a usar a palavra "Dalatiidae" foi Gill (1893) quando ele inseriu a subfamília Dalatiana Gray (1851) e modificou seu nome para Dalatiina, junto com Somniosina.

2. Morfologia das espécies reconhecidas atualmente como válidas

Algumas das características distintivas do gênero descrito por Gill são focinho curto com comprimento menor que 2/5 do comprimento da cabeça; lábios expandidos e sugadores, que permitem ao tubarão prender-se à presa como uma lampreia; dentes superiores e inferiores muito diferentes entre si, sendo os superiores pequenos, com cúspides agudas e não serrilhadas, enquanto os inferiores são maiores; fileiras de dentes variam de 29-37 e de 19-31 nas mandíbulas superiores e inferiores, respectivamente. Ambas nadadeiras dorsais não apresentam espinhos; a segunda dorsal é um pouco maior que a primeira, mas ambos os comprimentos das bases são iguais; nadadeiras peitorais com margens curtas, estreitas e arredondadas; nadadeira caudal varia de assimétrica a quase simétrica, com um curto lobo dorsal e o ventral varando de curto a longo (Compagno, 1984).

A coloração é, geralmente, cinza ou marrom, e as pontas das nadadeiras são mais claras (Compagno, 1984; Garrick & Springer, 1964), com exceção da nadadeira caudal, que tem manchas mais escuras em sua porção posterior em *I. brasiliensis*. A porção dorsal é marrom escura e a ventral é mais clara. Há um colar ventral ao redor da região branquial que se diferencia do resto do corpo por ter coloração marrom mais escuro somente em *I. brasiliensis* e *I. labialis*. Toda a superfície ventral, com exceção do colar, tem uma rede de pequenos fotóforos que emitem um brilho esverdeado que pode durar até três horas após a morte (Compagno, 1984). Bennett (1840) descreveu que após a morte do exemplar, o brilho luminosos desapareceu completamente do abdômen e gradualmente do resto do corpo, permanecendo ao redor das mandíbulas e nadadeiras.

A espécie *Isistius brasiliensis* é diagnosticada por focinho curto com quase o mesmo comprimento que os olhos, que são anteriores mas distantes o suficiente entre si para não permitir que o indivíduo possua visão binocular. Os dentes estão organizados em 31-37 ou 25-31 em cada fileira de superiores e inferiores, respectivamente, e os inferiores são maiores que os superiores. O espaço entre as nadadeiras dorsais é duas vezes o comprimento da base da primeira dorsal e o espaço entre a intersecção o da segunda dorsal e a origem da caudal é maior que duas vezes o comprimento da base da segunda dorsal. A altura da segunda nadadeira dorsal é igual à da primeira e as nadadeiras pélvicas são maiores que das dorsais; a nadadeira caudal é grande e, aproximadamente, simétrica, sendo que o lobo inferior é longo e maior que 2/3 do comprimento da margem dorsal da caudal. Além disso, há um colar escuro proeminente na região branquial (Compagno, 1984).

Isistius brasiliensis tem distribuição geográfica oceânica e circumtropical e é encontrado no Oceano Atlântico das Bahamas e Sudeste do Brasil a Cabo Verde, da Guiné a Serra Leoa, e do sul da Angola à África do Sul. No Oceano Índico essa espécie ocorre das Ilhas Maurício à Nova Guiné e Austrália Ocidental. Finalmente, no Oceano Pacífico ela é encontrada do Japão ao Havaí e Galápagos (Compagno, 1984).

Espécimes de *I. brasiliensis,* cujo holótipo é uma fêmea coletada na costa do Brasil, são conhecidos por sua migração diária vertical. Strasburg (1963) descreveu exemplares coletados de 63 a 200 m de profundidade. Como o autor sugere, eles foram coletados em regiões tropicais e próximas a ilhas, onde há espécimes maiores que em mar profundo. Isto pode significar que regiões rasas possam ser áreas de reprodução para essa espécie. Widder (1998) afirmou que a migração vertical de *I. brasiliensis* pode ser uma adaptação comportamental que atrai predadores visuais, pois a contra-iluminação permite que o colar ventral fique mais evidente, já que é a única região sem fotóforos.

As espécies nominais atualmente consideradas sinônimas de *I. brasiliensis* são: *Scymnus (Scymnus) brasiliensis torquatus* Müller & Henle, 1839; *Scymnus (Scymnus) brasiliensis unicolor* Müller & Henle, 1839; *Squalus fulgens* Bennett, 1840; *Leius ferox* Kner, 1864; e *Isistius marmoratus* Rochebrune, 1885.

Em relação à maturidade sexual, Parin (1966) afirmou que machos são imaturos até 31.4 cm, enquanto Jahn & Haedrich (1987) expuseram que a maturidade é atingida até 36 cm, quando os testículos estão desenvolvidos. Em fêmeas, Bigelow & Schroeder (1948) descreveram um exemplar adulto de 39 cm; Gadig & Gomes (2002), uma fêmea grávida de 43.1 cm; Parin (1966) um adulto de 44 cm com sete ovos. Porém, Jahn & Haedrich (1987) também afirmaram que fêmeas atingem a maturidade aos 39 cm.

A espécie *Isistius plutodus* é similar a *I. brasiliensis*; porém, ela tem apenas de 17-19 dentes em cada fileira (*vs.* 25-31), os quais são maiores. O focinho é curto com, aproximadamente, o mesmo tamanho ou menos que a primeira nadadeira dorsal; o espaço entre a inserção da segunda nadadeira dorsal e a origem da caudal é, aproximadamente, do mesmo tamanho que a base da segunda dorsal, cuja altura é 1/3 maior que a primeira. As nadadeiras pélvicas são arredondadas e menores que a as dorsais. A nadadeira caudal é pequena e assimétrica, e o lobo ventral é curto e menor que metade do tamanho da margem dorsal da caudal. Não há colar escuro ao redor da região posterior ventral da cabeça, assim como manchas escuras na ponta da nadadeira caudal (Compagno, 1984). Garrick & Springer (1964) descreveram *I. plutodus* e foram os primeiros a revisar o gênero quando analisaram o exemplar coletado no Golfo do México após comparações detalhadas com exemplares de *I. brasiliensis*.

Isistius plutodus ocorre no Oceano Atlântico Nordeste, no Golfo do México e no Oceano Pacífico Noroeste, próximo ao Japão. Quando comparado a *I. brasiliensis*, *I. plutodus* tem distribuição restrita ou está presente em águas mais profundas. Como ela tem nadadeiras dorsais e caudal curtas, pode ser possível que *I. plutodus* seja menos ativa quando se trata de natação (Compagno, 1984).

A espécie *Isistius labialis* é, aparentemente, muito similar a *I. brasiliensis* e pode, inclusive ser um sinônimo. Os dentes superiores são descritos como mais numerosos (43 *vs.* 31-37); porém, foram contados 35 dentes superiores (17+1+17) no holótipo durante uma visita a Guangzhou (South China Sea Fisheries Research Institute). Os olhos são posicionados bem anteriormente na cabeça e a nadadeira caudal é menos simétrica, sendo o lobo ventral menor que em *I. brasiliensis* (Compagno, *et al.*, 2005). Esta espécie, cujo holótipo foi coletado no Mar do Sul da China, é pouco conhecida e, provavelmente, oceânica. Há apenas dois exemplares conhecidos: o holótipo (no SCSFRI, Guangzhou, China) e um que foi coletado próximo a Papua Nova Guiné (Oceano Pacífico) e está depositado no Florida Museum of Natural History (Gainesville, USA). Se esta espécie for válida, ela pode ter uma distribuição maior do que é atualmente conhecido e pode ser confundida com *I. brasiliensis,* o qual tem uma distribuição mundial em águas tropicais e subtropicais.

3. Características Ecológicas

Indivíduos de *Isistius* não são bons nadadores e são ectoparasitas de grandes peixes e cetáceos, que são provavelmente atraídos por sua bioluminescência (com base em informações relacionadas a *Isistius brasiliensis*, já que se sabe muito pouco sobre as outras espécies. Os lábios espessos, cartilagens labiais fortes e a faringe modificada são usados para se prender à presa; e os dentes inferiores, cortantes, mordem a pele e fazem um movimento circular, removendo um pedaço de carne da presa; grandes peixes, como marlins, atuns, tubarões e raias, assim como mamíferos (focas, baleias e golfinhos).

O fígado é repleto de óleo e as pequenas nadadeiras dorsais e peitorais sugerem uma flutuabilidade neutra. Ademais, os dentes inferiores são ingeridos quando substituídos pro uma nova fileira, reciclando cálcio (Compagno, *et al.*, 2005) Mas, essas características são descritas para *I. brasiliensis*, e devem haver mais estudos em relação a *I. plutodus* para analisar a musculatura mandibular e hióide para inferir se os hábitos alimentares são os mesmos. Para *I. brasiliensis* há o estudo de Shirai e Nakaya, 1992.

Gadig & Gomes (2002) analisaram alguns exemplares de *I. brasiliensis* e inferiram que o gênero *Isistius* é vivíparo lecitotrófico e que nascem de 6 a 12 indivíduos por gestação. Embora pouco se saiba à respeito do modo reprodutivo do tubarão charuto, acredita-se que ilhas oceânicas possam prover um ambiente propício para o crescimento de juvenis (Strasburg, 1963).

Assim, propõe-se que seja feito um estudo mais detalhado a cerca da variação morfológica encontrada em *I. brasiliensis,* já que esta espécie possui distribuição mundial, a fim de se verificar a validade das espécies *I. plutodus* e *I. labialis*. O principal objetivo é elucidar e descrever em detalhes as espécies existentes no gênero com base em análises morfológicas, morfométricas, merísticas e de distribuição geográfica. Além disso, será possível diferenciar as morfologias existentes e concluir se as espécies nominais disponíveis para *Isistius* representam as mesmas espécies com uma ampla distribuição, ou se são espécies diferentes. Isto se deve ao fato de que a literatura relativa ao grupo é escassa e que Garrick & Springer fizeram a única revisão do gênero em 1964, além de uma nova espécie ter sido descrita em 1985.

4. Bioluminescência

Bioluminescência é a produção de luz visível por um organismo devido a uma reação química. Há apenas duas famílias de Chondrichthyes que são capazes de produzir luminescência: Etmopteridae e Dalatiidae. Em Dalatiidae, os órgãos fotogênicos (fotóforos) são formados por pequenas taças pigmentadas que cobrem um único fotócito (célula fotogênica), que é rodedeado por uma ou várias células da lente. Observando o arranjo ventral relativamente simples de fotórofos (padrão luminoso) de Dalatiidae, sugeriu-se que ele usem sua luminescência para contra-iluminação (Claes & Mallefet, 2008).

Reif (1985) encontrou dois padrões de fotóforos em tubarões: (A) numerosos fotóforos no lado ventral e poucos no dorsal, e ao mesmo tempo em que o número de fotóforos diminui, o de células pigmentares aumenta. Essa distribuição de fotóforos é observada em *I. brasiliensis*, *I. plutodus*, *D. licha* e *E. bispinatus*. Como essas espécies predam grandes peixes e mamíferos, pode ser possível que não vivam em cardumes. Assim, sua luminescência pode estar de acordo com o modelo de contra-iluminação. (B) Ocorre majoritariamente em etmopterídeos e o padrão de distribuição dos fotóforos varia de espécie para espécie. Novos fotóforos são continuamente adicionados durante o crescimento, compensando o aumento da área.

O ancestral comum dos tubarões modernos não era demersal, nem muito rápido. Então, os vários tipos de escamas em tubarões luminescentes podem ter origem nesse ancestral. As escamas encontradas em *I. brasiliensis*, *D. licha* e *E. bispinatus* nunca são trocadas, mas aumentam em número à medida que a área da pele aumenta. Fotóforos são encontrado entre e sobre as escamas (Reif, 1985).

O mesmo autor (Reif, 1985) também distinguiu três funções para as escamas placóides: (A) proteção da pele contra ectoparasitas e epibiontes; (B) proteção contra abrasão em tubarões demersais que vivem em substratos arenosos ou rochosos; e (C) redução do atrito pela influência da camada estrutural adjacente em tubarões com rápida natação. Reif (1985) sugeriu que os fotóforos em Dalatiidae possam servir como contra-iluminadores, fazendo com que esses tubarões fiquem invisíveis enquanto atacam suas presas.

Widder (1998) e Parin (1966) estudaram a bioluminescência em *Isistius brasiliensis* e concluíram que esses exemplares tem milhares de fotóforos muito pequenos (0,03 mm a 0,05 mm de diâmetro) que formam uma rede densa ao redor das escamas e cobre toda a superfície ventral do corpo, exceto no colar escuro. Bennett (1840) foi o primeiro a descrever a bioluminescência em tubarões charutos. Widder (1998) sugeriu que o padrão luminescente encontrado é direcionado a predadores visuais com acuidade visual excepcionalmente alta ou deve funcionar a um curto alcance incomum. Ele também sugeriu que as presas sejam atraídas a grandes distâncias pelo que aparenta ser a silhueta de um pequeno peixe. Parece que, em *I. brasiliensis*, a contra-iluminação possa funcionar como uma forma de encontrar alimento.

As espécies de *Etmopterus*, como *E. spinax*, possuem estruturas fotogênicas que são controladas por dois tipos diferentes de substâncias: hormônios e neurotransmissores, contrários a todos os organismos luminosos intrínsecos (como organismos que produzem luz sem a ajuda de bactérias simbiontes), nos quais o controle fisiológico é exclusivamente nervoso (Claes & Mallefet, 2009, 2011). Também afirmam que os fotóforos de tubarões são intrínsecos e que não contem bactérias simbiontes luminosas, mas um sistema luminoso intrínseco que controla a luminescência. O espectro luminescente de *Isistius brasiliensis* tem seu pico em um comprimento de onda consideravelmente mais curto (455 nm) que o da luz solar encontrada na profundidade em que vive (470–480 nm), sugerindo que ou os fotóforos desses tubarões não estão envolvidos em camuflagem por contra-iluminação ou não bem alinhados com essa função, a não ser que essa camuflagem seja direcionada para organismos de profundidade que não apresentam visão colorida especializada (Claes, *et al.*, 2010).

Claes *et al.* (2012) estudaram a luminescência em *Squaliolus aliae* e encontraram que substâncias nervosas e hormonais a controlam, e que agem através da movimentação dos pigmentos dentro dos melanóforos que recobrem os fotócitos. Porém, eles encontraram algumas diferenças no controle hormonal comparativamente a Etmopteridae. O controle dos fotóforos em Dalatiidae aparenta ser um intermediário entre a mudança fisiológica de cor de elasmobrânquios e o controle da luminescência em etmopterídeos. Evolutivamente, a aparição única da luminescência em tubarões parece ser mais favorável, no caso em que ela tenha aparecido nos dalatiídeos e desenvolveu-se posteriormente nos etmopterídeos. Durante a evolução de Dalatiidae, eles podem ter adquirido essa característica como uma forma de camuflagem, estando adaptados ao modo de vida pelágico durante o limite C/T. Então, os Etmopteridae modificaram o controle fisiológico e a organização inicial dos fotóforos permitindo que eles realizassem outras funções.

Fotóforos encontrados na região ventral de tubarões podem estar organizados para a camuflagem por contra-iluminação. Além disso, essa capacidade de camuflagem é provavelmente a única função dos fotóforos em Dalatiidae, já que ele não formam padrões de distribuição complexos (Claes *et al.*, 2012).

O colar escuro de *Isistius* rompe o padrão de contra-iluminação e Widder (1998) hipotetizou que ele possa funcionar como uma emboscada por imitar algumas possíveis presas de grandes predadores. Porém, não há dados experimentais ou comportamentais para suportar essa hipótese, e várias presas comumente predadas por *Isistius* são filtradoras (Berra & Hutchins, 1990; e Dwyer & Visser, 2011) ou organismos megacarnívoros (Dwyer & Visser, 2011; Hoyos-Padilla *et al.*, 2013) para os quais tal mecanismo é inútil. Claes *et al.* (2014) propuseram uma explicação alternativa: o colar escuro de *I. brasiliensis* pode servir como um método de reconhecimento intraespecífico funcionalmente análogo às marcações laterais em Etmopteridae.

Davis *et al.* (2014) sugerem que o sistema de fotóforos em peixes-lanterna tem duas funções: uma para camuflagem contra predadores (fotóforos ventrais ao corpo) e uma para reconhecimento intraespecífico (fotóforos laterais ao corpo). Johnsen *et al.* (2004) afirmaram que muitos contra-iluminadores são migradores verticais e podem ser encontrados próximos à superfície à noite, e que a iluminação de fundo depende se a lua está presente. Devido à grande variabilidade da luz que descende próxima à superfície à noite, uma contra-iluminação eficaz requer um sistema mais sofisticado do que é preciso durante o dia. Espécimes devem ter um controle considerável sobre a cor da luz que produzem (Yung & Mencher, 1980).

Fotóforos de contra-iluminação, ou camuflagem ventral, funcionam durante o dia e são esperados a emitir comprimentos de onda mais estreitos com picos entre

470–480 nm, similares à luz descendente do sol nas águas profundas do oceano. (Herring, 1983). O espectro luminoso de emissão em bactérias tem pico entre 475–500 nm e amplas metades de comprimentos de ondas. Eles são usados com propósito de contra-iluminação por inúmeras espécies de peixes costeiras e por algumas poucas oceânicas.

II. Introduction

Elasmobranchii is a clade, defined by Maisey (1984), formed by recent sharks and rays, and the fossil genera *Palaseospinax*, *Synechodus*, *Hybodus*, *Xenacanthus*, and *Ctenacanthus*. Compagno (1973) suggested that living Elasmobranchs differ from Paleozoic ones. Compagno (1973, 1977), and Carvalho (1996) named the living forms of sharks and rays, plus two fossil genera (*Palaeospinax* and *Synechodus*) Neoselachii, which is different from recent Elasmobranchs. However, Maisey (2012) defined the word Elasmobranchii to be used when referring to “modern” sharks and rays (crown-group neoselachians and their immediate fossil relatives), and suggested the usage of words Elasmobranchii and Neoselachii as synonyms, as the original “Elasmobranchii” is used informally and undiagnosable. Besides, Maisey (1984) united all modern elasmobranchs by a complete series of perichondrally calcified radials in the anterior dorsal fin; and haphazardly fibered enameloid in the teeth, and Carvalho (1996) defined recent elasmobranchs by characters that can be reversed at less inclusive levels: presence on extrabranchial cartilages on hyomandibula; presence of *adductor mandibulae superficialis*; right and left coracoids fused; and teeth with “aprons”.

Recent Elasmobranchii, or Neoselachii, has 1221 living valid species (Naylor *et al.*, 2012) and include sharks, rays, and skates that can be recognized by five, six, or seven gill slits at each side of the head. Currently, there are 680 known species of rays (Naylor *et al.*, 2012), which are characterized by expanded and flattened pectoral fins fused to lateral of the head right above the gill slits (Compagno *et al.*, 2005a). Furthermore, there are 541 shark valid species (Naylor *et al.*, 2012) that can be cylindrical or flattened and do not have pectoral fins fused to the head.

One of the most diverse elasmobranch orders is Squaliformes, with 132 valid species (Naylor *et al.*, 2012) in seven families: Echinorhinidae, Squalidae, Centrophoridae, Etmopteridae, Somniosidae, Oxynotidae, and Dalatiidae. These sharks, which vary greatly in size, have two dorsal fins, with or without spines, and lack an anal fin; labial furrows are prominent; lack rostral barbels; vertebral column at the caudal fin elevated and forming a moderately long dorsal caudal lobe, and the ventral lobe varying from absent to very marked. There are five gill slits, all in front of the origin of pectoral fins; nostrils are not connected to the mouth by furrows; and spiracles are behind the eyes, which are at the lateral region of the head and do not have lower nictitating membranes (Compagno, 1973).

Sharks of the family Dalatiidae occur in deep water, between 200 and 1800 meters, at the epi-, meso-, and, probably, bathypelagic zones, being characterized by showing short snout without barbels; teeth with strong cusps and different at upper and lower jaws, being the upper ones narrow and pointy and the lower wide, blade-like and bigger than the upper (Compagno, 1984). There are two small dorsal fins, with the area of the first smaller than or equal to the second, without spines. The only exception is *Squaliolus*, which has a spine in front of the first dorsal fin (Shirai, 1992a). The anal fin is absent and the caudal is strongly asymmetric, with its lower lobe varying from absent to strongly marked. The body and fins are greyish and luminescent organs might be present (Compagno, 1984; Claes *et al.*, 2014).

Currently, there are seven genera in the family, *Dalatias*, *Euprotomicroides*, *Euprotomicrus*, *Heteroscymnoides*, *Mollisquama*, *Squaliolus* and *Isistius*, all being monospecific, with the exception of *Squaliolus*, with two species, and *Isistius*, with three (Compagno, 2005).

1. Taxonomic history

Linnaeus, in 1758, described the genus *Squalus* as sharks with five gill slits at the lateral of the head and absence of anal fin, long and tapering body, and terminal mouth. He also described, on page 233, the species *Squalus centrina* with dorsal spines and sub-triangular body. Broussonet (1780) described another species, *La Liche*, not yet using the binomial nomenclature proposed by Linnaeus. It had a very spiny skin resembling a species he called *L'Aiguillat*, another species he described in the same book. But *La Liche* differed from it by lacking dorsal spines, and by ventral fins very close to the tail. The second dorsal fin was bigger than the first one, and was used to distinguish one species from the other. None of these two species can be, nowadays, considered synonyms of any *Isistius* species; however, they were the foundations for subsequent descriptions for members of the order.

Bonnaterre (1788) divided the fishes in groups and cited *La Liche* described by Broussonet (1780). He inserted it in the First Class (Cartilaginous Fishes), and Third Genera (*Squalus*, specimens with 4-7 openings growing of the ventral surface of the body). Cuvier (1817) described the genus *Scymnus* and *Centrina*, being the first one equivalent to *La Liche* Broussonett (1780) and the second to *Squalus* (to *S.*

centrina Linnaeus 1758). All the characters he described for *Scymnus* are the same to *Centrina*, with the exception of dorsal fin spines, as previously mentioned by Broussonnet (1780), even though he had named it *L'Aiguillat*. The lower teeth of *Scymnus* were sharp and arranged in one or two rows, while the upper were narrow, pointy, and arranged in many rows. One individual that had been collected in the Indian Ocean was noticeable by its small first dorsal fin. It was possible to distinguish *Scymnus* from other species in which the first dorsal fin was over the ventral fins, and the second dorsal far posteriorly.

Quoy & Gaimard (1824) described a new subgenus, *Leiche*, which they apparently synonymyzed with the genus *Scymnus* Cuvier (1817). They also described a new species based on a male specimen, *Leiche laborde* (=*Scymnus bispinatus* Cuvier; a name apparently not available, having never been described), and mentioned another very small female specimen, which had the body shape of *L. laborde*, but its lower jaw was disproportionately big, the mouth was closer to the snout, dorsal fins were larger and there was no ventral spine. Both caudal lobes were deeply divided and its color was light brown, with a wide darker band at the ventral side of the head. They named it *Leiche du Brésil* after Cuvier's *Scymnus brasiliensis* Figure 1. This reference is slightly confusing, as Cuvier never mentioned the species *Scymnus bispinatus* and *Scymnus brasiliensis* that were supposedly senior synonyms of *Leiche Laborde* and *Leiche du Brésil*, respectively. Therefore, it seems that Quoy & Gaimard gave two options for the names of these new species: one using "*Leiche*", and other using "*Scymus* Cuvier". However, the supposedly new name "*Leiche*" might be a misspelling of *La Liche* Broussonet (1780).

Bennett (1840) found two bioluminescent specimens whose descriptions are very detailed and similar to what is currently know as *Isistius*. He named them *Squalus fulgens*, following Linnaeus (1758) and he did not mention the descriptions of Quoy & Gaimard (1824) and Cuvier (1817), who had already noticed a new group of specimens similar to *Squalus* and described new genera and species. Bennett indicated it was a new species of *Squalus* that belonged to the sub-genus *Scymnus*. However, as the rules to name species were not very clear at the time, he suggested it be called *Squalus fulgens*. Besides, he did not mention the whwerabouts of these specimens, making it not possible to evaluate their identification as species of *Isistius*.

Müller & Henle (1841), in their revision of the described genera and species of elasmobranchs, inserted three families in the fourth division of Squali: Spinaces, Scymni and Squatinae. The family Scymni contains the genera *Scymnus* Cuvier, *Echinorhinus* Blainville, and *Pristiophorus* Müller & Henle. The former is divided in two subgenera: *Scymnus* and *Laemargus*. At last, these two species were considered as belonging to the subgenus *Scymnus*: *Scymnus (Scymnus) Lichia* Bonaparte and *Scymnus (Scymnus) brasiliensis* Cuvier.

Müller & Henle described the species *Scymnus (Scymnus) brasiliensis* with a nasal flap at the end of the snout and lower teeth not serrated; rounded and small pectoral fins, which were bigger at the top than at the base; squared pelvic fins, with rounded angles at the front and pointy posterior part; first dorsal right before the origin of the pelvic fins; second dorsal in between the first dorsal fin and the base of the caudal one; both dorsal fins were rounded at the anterior part and prolonged posteriorly in an acute angle, with a straight upper margin; both were very small and had the same height; second dorsal base length was bigger than the first one; lower lobe of caudal fin relatively big. Scales were small, pointless and with a depression at their middle.

The same authors divided this species into two varieties: *Scymnus (Scymnus) brasiliensis torquatus* (Figure 1) e *Scymnus (Scymnus) brasiliensis unicolor* (Figure 2). The former had a brown color, being lighter at the ventral side, and with a wide darker band bellow the head. The pectoral fin margins and the lower part of the caudal fin were white. While the second specimen had the same coloration as the first one, the pelvic fins were darker and it lacked the darker band bellow the head. Both type specimens are located in the Muséum national d'Histoire naturelle, in Paris (the type of *Scymnus brasiliensis* Quoy & Gaimard is the same specimen that is the type of *S. (S.) b. unicolor*).

Later, Kner (1864) described a new genus, *Leius*, and species, *Leius ferox* (Figure 3), whose holotype is in the Naturhistorisches Museum, in Vienna, Austria. In this specimen, the anus was between the ventral fins; the upper lobe of the caudal fin widely truncated; dark brown coloration. The author suggested this specimen belonged to a group closer to *Scymnus* and *Laemargus*, but very different from *Scymnus bispinatus* Quoy & Gaimard and, possibly, was also a synonym of *Somniosus brevipinna* Les? [sic].

However, Gill (1864), in a synopsis of eastern American sharks, described the new genus *Isistius* in the family Scymnoidea based on the species *Scymnus brasiliensis* Müller & Henle, which was distinctive by its similar dorsal fins that were posteriorly located on the body. Later, Gill (1896) explained the reason why he altered the name *Scymnus* to *Isistius* that was due to the previous existence of *Scymnus* as a name in Coleoptera created by Kugelmann (1794) (*apud* Gill, 1896).

Rochebrunne (1885) described another species for the genus *Isistius* Gill, *I. marmoratus*. This species was described as having a narrow and rounded body, obtuse snout, small and inferior mouth; short teeth; first dorsal fin at the posterior third of the body. Although Rochebrune indicated the specimen was located in the Museo Bouvieri and was collected in "Landana and the entire Gambia", both the museum and the site of collection could not be found. Eugène-Louis Bouvier (1856-1944) was a "Professor of Entomology at the Paris Museum (MNHN) from 1895 till 1931. In 1885, he was only 29 year old in the early steps of his career. No Bouvier's collection is registered [sic] in the Paris MNHN. Therefore, types (if any) may be hypothesized as lost" (Huber, 2000 *in* http://www.killi-data.org/researchers-huber-pz-lacazei.php).

Garrick & Springer (1964) described another *Isistius* species, *I. plutodus* (Figure 4), with the dental formula 14+1+14/9+1+9; presence of a short caudal peduncle and small caudal fin, having the lower lobe half the length of the upper lobe; second dorsal fin remarkably taller than the first; no well-defined dark collar and without caudal fin markings.

At last, Meng, Zhu & Li (1985) described the most recent species of the genus, *Isistius labialis* (Figure 5). They proposed it could be differentiated from *I. plutodus* by having the dark collar and 10 more teeth in the lower jaw; and from *I. brasiliensis* by having folds at the lower lip and by the length of the pelvic fins, which are equal to the first and second dorsal fins, while in *I. brasiliensis* they are greater.

With regards to the nomenclature of the family Dalatiidae, Gray (1851) is supposed to have coined the family name, as he wrote a list of specimens and divided them in successively inclusive groups. However, he mentioned a subfamily called Dalatiana that encompassed those sharks that lack dorsal spines. Within this subfamily, he included two genera: *Dalatias* and *Echinorhinus*. In *Dalatias* he included the species *Dalatias lichia* (=*Dalatias licha*) and *Dalatias brasiliensis*. The last one can be identified as a synonym of *Isistius brasiliensis*.

Gray (1851) was the first to ever use the name "Dalatias" to determine and identify a group of sharks since this name became available in 1810, when Rafinesque described the new genus and both species *Dalatias Sparophagus* and *Dalatias Nocturnus*.

However, the first author to use "Dalatiidae" was Gill (1893) when he included in it the subfamily Dalatiana Gray (1851), modified to Dalatiina, together with Somniosina.

2. Morphology of currently recognized species

Some of the distinctive characteristics of the genus described by Gill are short snout with length smaller than 2/5 of head length; expanded, sucker lips, allowing the shark to attach to its prey as a lamprey; lower and upper teeth very different from each other, being the upper small, with acute cusps and not-serrated, while the lower are bigger; teeth rows vary from 29-37 and 19-31 in the upper and lower jaws. Both dorsal fins do not have spines; the second dorsal is a little bigger than the first one, but both base lengths are the same; pectoral fins have short, narrow and rounded edges; caudal fin varies from asymmetric to almost symmetric, with a short upper lobe and short to long lower one (Compagno, 1984).

The coloration is, usually, grey or brown, and the tips of the fins are lighter (Compagno, 1984; Garrick & Springer, 1964), with the exception of the caudal fin, which has dark ends in *I. brasiliensis*. The dorsal portion is dark brown and ventral is lighter. There is a collar around the branchial region that differentiates from the rest of the body for being dark brown, only in *I. brasiliensis* and *I. labialis*. The whole ventral surface, with the exception of the dark collar, has a net of small photophores that emit a green glow, which can last until three hours after death (Compagno, 1984). Bennett (1840) described that after the death of the specimen, the luminous glow completely disappeared from the abdomen and gradually from the rest of the body, remaining longer around the jaws and fins.

The species *Isistius brasiliensis* is diagnosed by short snout with almost the same length as the eyes, which are anterior, but far enough from each other, not allowing the individual to have binocular vision. Teeth are arranged in 31-37 or 25-31 rows, and the lower are bigger than the upper. The space between the dorsal fins is twice the base length of the first dorsal, and the space between the intersection of the second dorsal and the origin of the caudal is bigger than twice the base length of the second dorsal. The height of the second dorsal is equal to the first one, and the pelvic fins are bigger than the dorsal ones; the caudal fin is big and, approximately, symmetric, and the lower lobe is long and bigger than 2/3 of the dorsal caudal margin length. Besides, there is a prominent dark collar at the branchial region (Compagno, 1984).

Isistius brasiliensis has an oceanic and circumtropical geographic distribution and is found at the Atlantic Ocean from Bahamas and Southeast of Brazil to Cape Verde, from Guinea to Sierra Leone and from South of Angola to South Africa. At the Indian Ocean it occurs from Mauritius to New Guinea and Western Australia. Finally, at the Pacific Ocean it is found from Japan to Hawaii and Galapagos Islands (Compagno, 1984).

Specimens of *I. brasiliensis*, whose holotype is a female collected at the coast of Brazil, are know by dial vertical migration. Strasburg (1963) described specimens collected from 63 to 200 m of depth. As the author suggested, they were collected in tropical regions, and close to islands there were bigger specimen than in deep sea. It can mean that shallow regions might be nursery areas for this species. Widder (1998) affirmed that the vertical migration of *I. brasiliensis* might be a behavioral adaptation that attracts visual predators, because the counterillumination allows the ventral collar to be more evident, as it is the only region photophore-free.

The nominal species currently considered synonyms of *I. brasiliensis* are: *Scymnus (Scymnus) brasiliensis torquatus* Müller & Henle, 1839; *Scymnus (Scymnus) brasiliensis unicolor* Müller & Henle, 1839; *Squalus fulgens* Bennett, 1840, *Leius ferox* Kner, 1864, and *Isistius marmoratus* Rochebrune, 1885.

When it comes to sexual maturity, Parin (1966) affirms that males are immature until 31.4 cm, while Jahn & Haedrich (1987) state that maturity is reached at 36 cm, when testis are developed. In females, Bigelow & Schroeder (1948) described an adult of 39 cm; Gadid & Gomes (2002), a pregnant specimen of 43.1 cm; Parin (1966), an adult of 44 cm with seven eggs. However, Jahn & Haedrich (1987) also stated that females are mature at 39 cm.

The species *Isistius plutodus* is similar to *I. brasiliensis*; however, it has only 17-19 teeth rows (*vs.* 25-31), which are bigger. The snout is short, with, approximately the same size as eye length, which are far anterior at the head; the interdorsal space is the same size or smaller than the first dorsal fin; the space between the second dorsal fin insertion and the dorsal origin of the caudal is approximately the same size as the second dorsal base length, whose height is 1/3 bigger than the first one. The pelvic fins are rounded and smaller than the dorsal fins.

The caudal fin is small and asymmetric, and the ventral lobe is short and smaller than half the size of the dorsal caudal margin. There is no dark collar around the posterior region of the head, as well as dark tips at the caudal fin (Compagno, 1984). Garrick & Springer (1964) described *I. plutodus* and were the first to revise the genus when analyzed a specimen collected at the Gulf of Mexico after detailed comparisons with specimens of *I. brasiliensis*.

Isistius plutodus occurs at the Northwestern Atlantic Ocean, in the Gulf of Mexico, and at the Northwestern Pacific Ocean, near Japan. When it is compared to *I. brasiliensis*, *I. plutodus* has a restrict distribution or is present in deeper waters. As it has small dorsal and caudal fins, it might be possible that *I. plutodus* is less active when it comes to swimming (Compagno, 1984).

The species *Isistius labialis* is, apparently, very similar to *I. brasiliensis*, and may even be a synonym. The upper teeth rows are described as more numerous (43 *vs.* 31-37); however, there were counted 35 upper teeth (17+1+17) in the holotype during a visit to Guangzhou (South China Sea Fisheries Research Institute). The eyes are well anterior at the head and the caudal fin is less symmetric, being its ventral lobe smaller than in *I. brasiliensis* (Compagno, *et al.*, 2005). This species, whose holotype was collected at the South of China, is poorly known and, probably, oceanic. There are only two known specimens: the holotype (at SCSFRI, Guangzhou, China) and one that was collected close to Papua New Guinea (Pacific Ocean) and is deposited at the Florida Museum of Natural History (Gainesville, USA). If this species is valid, it might have a wider distribution than what is currently known and may be mistaken with *I. brasiliensis*, which has a worldwide distribution in tropical and subtropical waters.

3. Ecological Characteristics

Individuals of *Isistius* are not good swimmers and are ectoparasites of large fishes and cetaceans, which are probably attracted by its bioluminescence (based on information on *Isistius brasiliensis*, and as there is little known about the other two species). The thick lips, strong labial cartilages and modified pharynx are used to attach to the prey, and the sharp lower teeth are employed to bite the skin and make a circular turn, removing a piece of flesh from the prey (big fishes, such as marlins, mackerels, tunas, sharks and rays, as well as marine mammals such as seals, whales, and dolphins).

The liver full of oil and the small dorsal and pectoral fins suggest neutral buoyancy. The lower teeth are ingested when replaced by a new row, recycling calcium (Compagno, *et al.*, 2005). But, these characteristics are described only for *I. brasiliensis*, and there should be more studies regarding *I. plutodus* to analyze the mandibular and hyoid musculature to infer if the feeding habits are the same. For *I. brasiliensis* there is Shirai & Nakaya (1992).

Gadig & Gomes (2002) analyzed some specimens of *I. brasiliensis* and inferred that the genus *Isistius* is viviparous lecithotrophic and that the number of neonates varies from 6 to 12 individuals. Although little is known regarding the reproductive mode of the cookiecutter shark, it is believed that oceanic islands may provide a propitious environment for the growth of juveniles (Strasburg, 1963).

4. Bioluminescence

Bioluminescence is the production of visible light by an organism due to a chemical reaction. There are only two Chondrihcthyan families that are capable of producing luminescence: Etmopteridae and Dalatiidae. In Dalatiidae, the photogenic organs (photophores) are made of a small-pigmented cup covering a single photocyte (photogenic cell), which is surrounded by one or several lens cells. Observing the relatively simple ventral photophore arrangement (luminous pattern) of the Dalatiidae, it has been suggested that they would use their luminescence for counter-illumination (Claes & Mallefet, 2008).

Reif (1985) found two patterns of photophores in sharks: (A) numerous photophores at the ventral side and rare on dorsal side, and at the same degree that photophores numbers decrease, the number of pigment cells increase. This photophore distribution is seen in *I. brasiliensis*, *I. plutodus*, *D. licha*, and *E. bispinatus*. As these species prey on bigger fishes and mammals, it might be possible they are not schooling. So, their luminescence may be in accordance with the countershading model. (B) Occur mostly on etmopterids, and the photophores pattern of distribution varies from species to species. New photophores are continuously added during growth, compensating the increase in area.

The common ancestor of modern sharks was neither demersal nor very fast. So, the various scale types of luminescent sharks might have their origin on this ancestor. The scales found in *I. brasiliensis*, *D. licha*, and *E. bispinatus* are never replaced, but increase in number in the same way as the skin area increases.

Photophores are found in between and on the scales (Reif, 1985).

The same author (Reif, 1985) also distinguished three functions of placoid scales: (A) protection of skin against ectoparasites and epibionts; (B) protection against abrasion in demersal sharks which live on sandy and rocky substrates; and (C) reduction of drag by influence of the boundary layer structure in fast swimming sharks. Reif (1985) also suggests that the photophores in Dalatiidae may serve as countershading, making these sharks invisible when they waylay their prey.

Widder (1998) and Parin (1966) studied the bioluminescence in *Isistius brasiliensis* and concluded that these specimens have thousands of really small photophores (0.03 mm to 0.05 mm in diameter) that form a dense network around the edges of the scales and cover the entire ventral surface of the body, except for dark collar. Bennett, 1840, was the first to describe the bioluminescence in cookiecutter sharks. Widder, 1998, suggested that the luminescence pattern found is directed toward visual predators with unusually high acuity or it must function at unusually close range. He also suggested that the preys are lured into striking distances by what appears to be the silhouette of a small fish. It appears that, in *I. brasiliensis*, counterillumination may function as a way of finding food.

The *Etmopterus* species, such as *E. spinax*, possess photogenic structures that are controlled by two different types of substances: hormones and neurotransmitters, contrary to all intrinsically luminous organisms (as organisms that produce light without the help of bacterial symbionts), in which the physiological control was exclusively nervous (Claes & Mallefet, 2009, 2011). It is also stated that shark photophores are intrinsic, and they do not contain symbiotic luminous bacteria, but an intrinsic luminous system that control the luminescence switching. The luminescence spectrum of *Isistius brasiliensis* peaks at a considerably shorter wavelength (455 nm) than that of the sunlight found in the oceanic water where it leaves (470-480 nm), suggesting that either the photophores of this shark are not involved in camouflage by counterillumination or not well tuned for this purpose unless this camouflage is directed towards deep-sea organisms lacking specialized color vision (Claes *et al.*, 2010).

Claes *et al.* (2012) studied luminescence at *Squaliolus aliae* and found that nervous and hormonal substances control it, and they act through the movement of pigments inside the melanophores covering the photocytes. However, they found some differences at the hormonal control compared to Etmopteridae. The dalatiid photophore control seems to be an intermediate between the elasmobranch physiological color change and etmopterid luminescence control. Evolutionary, it might be in favor of a unique apparition of luminescence in sharks, first appearing in dalatiids, evolving later in etmopterids. During Dalatiidae evolution, they may have acquired this feature as a way of camouflage, being adapted to their pelagic lifestyle during C/T boundary. Then, Etmopteridae modified the physiological control and the organization of initial photophores allowing them to accomplish additional tasks.

Photophores found at the ventral side of sharks seem to be arranged for camouflage by counterillumination. Besides, this camouflage capacity is likely the only function of dalatiid photophores, as they do not form complex patterns (Claes *et al.*, 2012).

The *Isistius* “dark collar” breaches the counterilluminating pattern and Widder (1998) has hypothesized it acts as an ambush by mimicking some possible preys of great predators. However, no experimental or behavioral data exist to support this hypothesis and numerous common preys of the shark are either filter-feeders (Berra & Hutchins, 1990, and Dwyer & Visser, 2011), or megacarnivorous organisms (Dwyer & Visser, 2011, and Hoyos-Padilla *et al.*, 2013) for which such a mechanism is useless. Claes *et al.*, 2014, propose alternative explanation: the dark collar of *I. brasiliensis* might actually serve as a method of intraspecific recognition functionally analogous to the etmopterid lateral markings.

Davis *et al.*, 2014 suggests that the photophore system in lanternfishes has two roles: one for camouflage from predators (ventral body photophores), and one for species recognition (lateral body photophores). Johnsen *et al.*, 2004, affirmed that many counterilluminators are vertical migrators and can be found near the surface at night, and the background illumination depends on whether the moon is present. Due to a great variability in downwelling light near the surface at night, effective counterillumination requires a much more sophisticated system than is needed during the day. Specimens should have considerable control over the color of the light they produce (Young & Mencher, 1980).

Counterilluminating, or ventral camouflage, photophores function during the day and are expected to have a narrow bandwidth emission with a peak at about 470-480 nm, similar to that of downwelling daylight in deep oceanic water (Herring, 1983). The emission spectra of luminous bacteria have peaks in the 475–500 nm range and broad half bandwidths. They are used for counterillumination purposes both by numerous coastal species of fish and by a few oceanic species.

III. Objectives

To taxonomically revise the species of the genus *Isistius* through a thorough comparative morphological study, investigating in detail the external morphology (including morphometrics, dentition, and dermal denticles), internal morphology (meristic data, skeleton, musculature, and lateral line canals), and geographic distribution of specimens of Isistius. More specific objectives are to advance a more detailed definition of the genus and its valid species, and to precisely characterize the morphological variation present in the type-species *I. brasiliensis* (thereby elucidating the validity of *Isistius labialis* and other nominal species available in *Isistius*). Furthermore, relevant morphological data will be described that may be applicable in future phylogenetic studies within the family Dalatiidae.

IV. Material and Methods

Almost all individuals of *Isistius* in museum collections worldwide were studied. The number of examined specimens of *I. brasiliensis* is 243 (including the two type specimens of *I. labialis*) and eight *I. plutodus*. Besides, 101 dalatiid specimens were also analyzed: 32 specimens of *Dalatias licha*, 15 of *Squaliolus aliae*, 23 of *Squaliolus laticaudus*, 31 of *Euprotomicrus bispinatus*, one each of *Heteroscymnoides marleyi* and *Mollisquama parini*. Other specimens, including type material deposited in collections in which access was not possible, were studied through data and photographs provided by collections staff (e.g. *Euprotomicroides zantedeshia* in Hamburg). Furthermore, six specimens of Etmopteriidae were studied: three *Aculeola nigra*, one *Centroscymnus fabricii*, one *Etmopterus lucifer*, and one *Miroscyllium sheikoi*; one Oxynotidae: *Oxynotus bruniensis*; and one Rajiform: *Rioraja agassizii*. The specimens were from the Institutions on Table 1.

Among the examined specimens are included all holotypes of nominal species available in *Isistius*, with the exception of *I. marmoratus* Rochebrune (1885) and *Squalus fulgens* Bennett (1840). This is due to the fact that the whereabouts of these specimens were not mentioned by the authors, and they were not found in any collection or database.

All analyzed specimens were previously fixed in formalin and preserved in ethanol 70%, isopropyl alcohol 50%, or formalin 50%. The individuals were measured and, when possible, dissected and radiographed.

1. Morphometrics

Mophometrics is the study of shape and its relation to size. Taxonomists use it as a way of measuring the existing differences between species, making references for comparisons. Organic systems should go through modifications in their proportions between their portions to keep their functional equivalence throughout their growth. These alterations are called allometry (Peres-Neto, 1995).

The measurements point-to-point followed Compagno (1984), Compagno (2001) e Last *et al.* (2007) (Table 2). They were taken with a caliper 0.01 mm of precision, except the biggest lengths (TL, PCL, PD2, PD1, SVL, and PP2), which were measured with a tape 0.1 cm. With the measurements, it was possible to make tables with the absolute numbers and relative ones to total body length for comparison.

2. Meristic analyses

The teeth were counted using a stereomicroscope. However, most specimens had their mouth shut, making it tough to be counted. The teeth were only counted if it was possible to do it until the last one. When it was not possible to count them on both sides, just one was counted and it was inferred to be the same at the other side, being the symphyseal teeth in the middle in the lower row, or with no symphyseal teeth in the upper row.

The vertebrae were counted trough radiographs, or direct counting at cleared and stained specimens, but not all the scientific collections had an available x-ray machine to radiograph the specimens. The counts were made following the classification monospondylous and diplospondylous (Compagno, 1970). However, as the x-ray machines did not always have a high definition, it was not possible to count the diplospondylous vertebrae to the end of the caudal fin of every specimen.

The monospondylous vertebrae are those that extend posteriorly to the neurocranium and have only one center by myotome; the diplospondylous ones have two centers by myotomes and their transition is at, approximately, the vertical line of pelvic fins origin. It is possible to differentiate both vertebral types due to ther size, since the first ones are bigger and easily identified (Compagno, 1970).

3. Clearing-and-staining

Four cleared and stained (C&S) specimens of *Isistius brasiliensis* were analyzed: one of the embryos described by Gadig & Gomes (2002) (AC.UERJ 928), one of the specimens used by Shirai & Nakaya (1992) (HUMZ 86585), the specimen USNM 215948, and the mandibular, hyoid and branchial arches of the specimen MZUSP not catalogued. The methodology concerning clear and staining follows Dingerkus & Uhler, 1977. No whole specimen of *Isistius* was cleared and stained due to their big size and few available individuals in each collection.

Concerning specimens of other dalatiid genera, two *Squaliolus laticaudus* specimens (HUMZ 74972 and HUMZ 74974) were analyzed. Besides, some etmopterid specimens were also studied: *Aculeola nigra* (HUMZ 90412), *Etmopterus* *lucifer* (HUMZ 35480) and *Miroscyllium sheikoi* (HUMZ 74982), and Oxynotidae, *Oxynotus bruniensis* (HUMZ 91383).

4. Morphological descriptions

To study their anatomy, specimens were manually dissected with scalpels, blades, scisors, and forceps; however, due to the same reason why the clear and staining was tough to be done (few available specimens is each colelction), eight dissected specimens of *Isistius brasiliensis* of the following collections were studied: Australian Museum, Bernice Pauahi Bishop Museum, Coleção de Elasmobrânquios do Departamento de Biologia Animal e Vegetal da Universidade Estadual do Rio de Janeiro, Hokkaido University Museum, Museu de Zoologia da Universidade de São Paulo, Muséum national d'Histoire naturelle, National Museum of Nature and Science, Natural History Museum. Nonetheless, the specimen from NHM did not have the data concerning its collecting information.

All the analyzed specimens were photographed to ascertain possible questionings relative to them. The external morphological analysis of the specimens was the observation of the relative position of the eyes, mouth, nostrils, gill openings and spiracles, as well as their respective color and presence or lack of photophores. These, in most casesm could be seen by naked eye, if they were many; however, the certainty of their presence was assured through a stereomicroscope.

Furthermore, the dermal denticles of distinct body regions were removed from some specimens from different geographic localities to study and compare them, and try to find morphological differences in between them. Their analyses were made through a scanning electron microscope DSM Zeiss 940 at the Instituto de Biociências, Universidade de São Paulo (IB-USP). The skin samples with 1 cm of diameter removed from specimens preserved in alcohol 70% had to be put on distilled water, be left to dry, glued to a stub with araldite, left on a heater, and finally pass through a metallization process in which a layer of gold is placed over it. Then, the scanning process took place with the beam electrons interacting with the sample and producing topographic images that could be read.

Upper teeth removed with a scalp, left on a solution of methylene blue and alcohol, and photographed with a Leica Microscope MSV266. The whole lower teeth row were removed from Meckel's cartilage and also photographed with the same microscope at the Laboratório de Icitiologia (IB-USP).

The dissection the mandibular, hyoid and gill arches allowed the analysis of the internal morphology and the description of their muscles and cartilages. All the fins (pectoral, pelvic, caudal, first and second dorsal) were dissected for the description of the cartilages and their variations in each specimen.

The description of caudal skeleton followed Little & Bemis (2004); claspers Jungersen (1899), and Gilbert & Heath (1972); mandibular and hyoid arches Shirai & Nakaya (1992); teeth morphology Herman *et al.* (1989). When not mentioned otherwise, the description followed Shirai (1992a) and Compagno (1988).

5. Anatomical abbreviations

Lateral line canals

avioc – antero-ventral portion of the infraorbital canals
hyc – hyomandibular canals
ioc – infraorbital canals
ll – lateral line
mdc – medial canal
nas – nasal
poc – preorbital canals
pnl – prenasal canal
spt – supratemporal canal
soc – supraorbital canals

Mouth nomenclature

gm – gum
lf – lip fold
lpc – upper lip cover
opk – deep oral pocket
pmg – posterior mouth groove
prop – preoral pouch
slc – flesy sack for the upper labial cartilages

Skeleton, ligaments and foramens

II – optic foramen
III – oculomotor foramen
IV – trochlearis foramen
V – foramen for a branch of facialis
V-VII – prootic foramen
VI – abducens foramen
IX – glossopharyngeo foramen
X – vagus foramen
β – beta cartilage
alc – anterior upper labial cartilage
apv – anterior pelvic basal
ax – axial
b1 – intermediate segment
bad – basal cartilage of dorsal fin
bb – basibranchial
bdp – basidorsal element
bh – basihyal
bpv – pelvic basipterygium
btp – basitrabecular process
bvp – basiventral elements
cav – cranial cavity
cb – ceratobranchial
cch – large concavities on ceratohyal

ch – ceratohyal
com – lateral commissure
dic – interdorsal elements
eac – elongate accessory cartilage
eb – epibranchial
ec – ethmoidal canal
eec – ectethmoidal chamber
elf – endolymphatic fossa
ep – epiphyseal organ
exb – extrabranchial cartilage of branquial arches
exh – extrabranchial cartilage of hyoid arch
fca – foramen for the carotid artery
feld – endolymphatic duct
fpn – foramen for the pectoral fin nerves
fvn – foramen for pelvic fin nerves
g – end-style
gop – groove for the orbital process
gp – gill pickax
gr – gill rays
hb – hypobranchial
hm – hyomandibula
hmf – hyomandibular fossa
iow – interorbital wall
jhm – joint cartilage of hyomandibula
lag – lateral auditive groove
lhc – ligamentum hyomandibulo-hyoideum
ljs – ligamentous complex
llc – lower labial cartilage
lmh – ligamentum mandibulo-hyoideum
lpp – lateral prepelvic process
ma – mandibula
mad – articular fossa
mag – magnum foramen
mfl – accessory cartilage of mandibula
mk – mandibular knob
ms – mesopterygium
mta – metapterygial axis
mt – metapterygium
nas – nasal cartilage
ns – nasal capsule
occ – occipital condyle
ohc – occipital hemicentrum
op – orbital process
opp – opistotic process
otf – otic flange
pal – palatine
pap – palatine plate
pb – pharyngobranchial
pcf – precerebral fossa
pff – prefrontal fontanel
plc – posterior upper labial cartilage
plf – perilymphatic fenestra
poc – preorbital canal
potp – postotic process
pqc – quadrate concavity
pr – propterygium
psb – efferent artery of the pseudobranchial
pqd – condyle of quadrate plate
pub – puboischiadic bar
qup – quadrate plate
rc – rostral keel
rd – dorsal marginal cartilage

rds – radials
rdp – proximal radials
rdd – distal radials
rp – rostral process
rv – ventral marginal cartilage
sc – scapula
scp – scapular process
ser – subethmoidal crest
soc – supraorbital crest
spn – supraneural elements
t3 – accessory terminal cartilage
spc – spiracular
tr – transbasal canal
tv – ventral terminal cartilage
vc – vertebral centra
vmbc – ventromedial branchial cartilages

<u>Musculature</u>

am – adductor mandibulae
ams – adductor mandibulae superficialis
av – adductor pelvicus
cbs – constrictors branchiales superficialis
ccl – cucullaris
chd – constrictor hyoideus dorsalis
chv – constrictor hyoideus ventralis
coa – coraco-arcualis
cob – coraco-branchiales
cod – constrictor dorsalis
coh – coraco-hyoideus
dl – dilatator of clasper
dpe – depressor pectoralis
dv – depressor pelvicus
epx – epaxial
ex – extensor of clasper
fxc – flexor caudalis
gco – genio-coracoideus
gcoe – genio-coracoideus externus
hpx – hypaxial
id – inclinator dorsalis
im – intermandibularis
llb – levator labialis
lpe – levator pectoralis
lv – levator pelvicus
oes – constrictor oesophagi
olm – outer lip muscle
rex – rectus externus
rif – rectus inferior
rit – rectus internus
rsp – rectus superior
so – suborbitalis
sp – siphon of clasper

V. Chapter 1: Definition of *Isistius* (Gill, 1864), *Isistius brasiliensis* (Quoy & Gaimard, 1824), and *Isistius plutodus* Garrick & Springer, 1964

The morphometric characterizations of the genera *Isistius* and *Dalatias* are presented in Table 3, and of genera *Squaliolus, Euprotomicrus, Heteroscymnoides*, and *Mollisquama* in Table 4. All *I. labialis* measurements fall within the variation encountered in *I. brasiliensis*. Some measurements such as PD1, IDS, DCS, PPS, TLV are fairly different between species, with very slightly overlapping ranges whilst others, such as HDL and INW are very similar, with the ranges of values mostly overlapped.

Order Squaliformes Compagno, 1973

Family Dalatiidae Gill, 1893

1. *Isistius* Gill, 1864

Synonymy

Isistius Gill, 1864: 264 (gender masculine; type species: *Scymnus brasiliensis* Müller & Henle, 1941, by monotypy, equals *Scymnus brasiliensis* Quoy & Gaimard, 1824);

Leius Kner, 1864, 9 (gender masculine; type species: *Leius ferox* Kner, 1864, by monotypy); Günther, 1909: 490 (brief description).

Diagnosis. This genus is differentiated from the other Dalatiidae ones mainly by its dark collar at ventral side of the head, posteriorly to the mouth and between the gill openings. Both dorsal fins of *Isistius* are located well posteriorly and the origin of the first one is at the vertical line right anterior to pelvic origin (Figure 6). The distance between the dorsal fins varies from 6 to 9% of total length and the origin of the second one is, approximately, at the vertical line of the free rear tip of the pelvic fins. Besides, both fins have similar sizes while the second is less than 1% of total length higher. In *Dalatias*, the first dorsal origin is at the vertical line of the pectoral fin free rear tip, while the origin of the second is at the line of the pelvic fin insertion, and the space between them is 20% of total length, besides having similar sizes. In *Euprotomicroides*, the first dorsal origin is posterior to the free rear tip of the pectoral fins and the second dorsal originates at the vertical line of the origin of the pelvic fins, and the second is slightly bigger than the first one. In *Euprotomicrus*, the second dorsal is twice the size of the first, and it originates at the medial portion of the body, between the insertion of the pectoral fins and the origin of the pelvic, and the second originates at the vertical line of the insertion of the pelvic fins. When it comes to the genus *Heteroscymnoides*, both dorsal fins have similar sizes, and the first originates at the vertical line of the insertion of the pectoral, and the second at the insertion of pelvic fins. In *Mollisquama*, both dorsal fins are close to each other, as it is in *Isistius*, besides their similar sizes, and the first one originates right anterior to the vertical line of the origin of the pelvic fins and the second right after the free rear tip of the same fins. In *Squaliolus*, the first dorsal fin has a small spine (0.5 to 2% TL) and its length is, approximately, 0.7 times smaller than the second, besides having a wide space between them (2.5 times bigger than in *Isistius*), as the first originates immediately posterior to the vertical line of pectoral fin insertion and the second at the line of pelvic insertion. Regarding the caudal fin, the upper lobe is 5% TL longer than the lower one in *Isistius* (Figure 7). The caudal fin of *Dalatias* is very similar to *Isistius*, however, there is no distinguishable lower postventral margin and the upper one forms the whole margin. In *Euprotomicroides*, the caudal fin shape is similar to *Isistius*, but its upper postventral margin is bigger and its lower postventral margin is smaller. When it comes to *Euprotomicrus*, both caudal lobes are well developed and more symmetrical, resembling *Isistius*. However the ventral corner of the terminal marginal coincides with the posterior ending of the vertebral column and forms a very short posterior prolongation, as it is seen in *Squaliolus*, whose caudal fin is very similar to *Euprotomicrus* and *Heteroscymnoides*. In *Mollisquama*, the caudal fin shape is very similar to *Isistius*, however the upper postventral and subterminal margins are bigger, and both dorsal and ventral lobes have rounded corners. When it comes to shape and size of the head, in *Isistius* it is triangular in dorsal view, and the snout is slightly rounded and tapering anterior to the eyes. In *Dalatias*, the head is also triangular, but its snout is more rounded than *Isistius*. In Euprotomicroides, *Heteroscymnoides*, and *Mollisquama* the head is rectangular and the anterior portion is narrower. However, in the last one it is more rounded and shorter. In *Euprotomicrus* and in *Squaliolus*, the head is also rectangular, however, the anterior region is slightly triangular and there is a subtle medial prominence at the most anterior portion, between the nostrils.

Regarding the dentition, the lower teeth of *Isistius* are proportionately much bigger than the upper (3.2 to 6.2x), and they are rectangular at their base and triangular at their apex, not serrated. The upper teeth are triangular, not-serrated and pointed, arranged in three rows. The lower and upper dentition of the genus *Dalatias* are very similar to *Isistius*; however, the proportions are different (2.4x), as well as the lower teeth, which are serrated in *Dalatias*. *Euprotomicroides*, *Euprotomicrus* (2.8x), *Heteroscymnoides*, and *Squaliolus* (1.5x) lower teeth, although having similar shape as *Isistius*, are narrower and have one straight side of the triangular shape, while the upper teeth are triangular and pointed. In *Mollisquama*, the lower teeth, although being rectangular at the base and triangular at the apices, are narrower, pointed and directed to the sides, not to the center of the mouth, as in *Isistius*, while the upper teeth are also similar to what has been previously described. The spiracle length is more than 10% of head length, being proportionately the biggest within the family Dalatiidae.

Etymology

The generic epithet *Isistius* comes from the Greek words *isos* (equal) and *istios* (sail), which a reference for the almost symmetrical caudal fin.

Family Dalatiidae Gill, 1893

Genus *Isistius* Gill, 1865

1.1 *Isistius brasiliensis* (Quoy & Gaimard, 1824)

(Figure 8)

Synonymy

Scymnus brasiliensis Quoy & Gaimard, 1824 (p. 198, original description, not figured.; type locality: Rio de Janeiro bay, Brazil); Garman, 1899: 40 (history of the species); Rochebrune, 1883: 48 (C. Verde); Ribeiro, 1907: 205 (references);

Squalus (Scymnus) fulgens Bennett, 1840: 255 (description, size, eggs, luminescence, trop. Pacif. near Christmas I.); Bennett, 1860: 66 (luminescence, a second trop. Pacif. spec); Waite, 1897: 196 (reference);

Scymnus (Scymnus) brasiliensis (var. *torquatus* and var. *unicolor*) Müller and Henle, 1841: 92 (description, Mauritius, C. Verde at St. Jago, Rio de Janeiro); Duméril, 1865: 453 (references, description, Mauritius);

Dalatias brasiliensis Gray, 1851: 76 (description, Isle of France, St. Jago, Rio de Janeiro).

Scymnus torquatus: Duméril, 1861: 261 (name only, St. Jago, C. Verde); Waite, 1897: 196 (reference);

Leius ferox Kner, 1865: 10, pl. 4, fig. 2 (description, illustration, Australia); Schmeltz, 1866: 13 (South Seas); Waite, 1897: 196 (reference); Johann, 1899: 152 (luminescence); Whitley, 1940: 149 (description, illustration, luminosity, Aust.);

Isistius brasiliensis: Günther, 1870: 429 (references, description, S. Pacif. and Gulf of Guinea specimens); Bleeker, 1874: 68 (species at Madagascar); Peters, 1876: 853 (Indian Oc, Lat. 14° 23' S, Long. 118° 16' E); Rochebrune, 1883: 48 (C. Verde); Dean, 1891: 513 (specimen remained aglow for three hours in an aquarium); Sauvage, 1891: 5, 511 (spec. in Paris Mus.); Waite, 1897: 194, 195 (Lord Howe Is., description); Garman, 1899: 34, pl.1, fig. 1, pi. 2-3, pl. 69, fig. 2 (description, size, number of teeth, anat. Near Galapagos); Johann, 1899: 152 (luminescence); Burckhardt, 1900a: 559, 566, 568 (luminescence), fig 5 (distribution of luminous organs); Burckhardt, 1900b: 488 (body shape); Waite, 1900: 195, fig. I, 2 (number of teeth, largest recorded spec, Lord Howe I.); Fatio & Spiess, 1902: 534 (Burkhardt's description of brain); Hebb, 1903: 289 (Burkhardt's description of brain); Waite, 1904: 188 (references, Lord Howe Island); Leriche, 1905: 95 (teeth comparison with *I. trituratus*); Mangold, 1907: 583 (luminescence); Ribeiro, 1907: 169, 205 (description, references, Brazil);Brauer, 1908: 133, pl. 2 (luminescence); Regan, 1908: 55 (classiffication, size); Burckhardt, 1911: 26 (description of brain), figs 16-23 (drawings of brain); Giglioli, 1912: 72, 109 (luminescence); Lydekker *et al.*, 1912: 421 (light emission); Garman, 1913: 238, 239 (references, description); Jordan *et al.*, 1913: 23 (old localization records, Fiji, Japan); Lampe, 1914: 214, fig. 2 (no. of lower teeth, sizes, 3 spec, off Sierra Leone, W. Afr.); Metzelaar, 1919: 191 (references); Ribeiro, 1923: 26 (same as Ribeiro, 1907); Fowler and Ball, 1926: 5 (footnote that *Echinorhinus brucus* Fowler, 1923, from Hawaii, was actually *I. brasiliensis*); Whitley, 1927: 3 (Fiji); Fowler, 1928: 23 (descr., refs., Honolulu); Duncker and Mohr, 1929: 84 (size, depth of capture. Ecuatorial Pacif. near New Guinea, Lat. 00° N, Long. 146° 5' E); Fowler, 1930: 497 (distribution); Mem. Bishop Mus., 1931: 314 (references); Bull. Amer. Mus. Nat. Hist., 1936: 87 (references, description); Parr, 1937: 1 (north of Bahamas); Beebe and Tee-Van, 1941: 121 (references); Fowler, 1941: 270 (references, description, distribution, luminescence); Arqu. Zool. Estado Sao Paulo, 1942: 129 (Brazil); Tinker, 1944: 28 (description, habitat, size); Bigelow and Schroeder, 1945: 146, fig. 55 (description, illustration, habits, range); Fishery Leaflet, 1945: 25 (key to species), 146 (description, distribution), 147 (drawings); Bigelow & Schroeder, 1948: 509-513 (description, references, range, drawings); Grey, 1956: 94 (recorded depth); King & Ikehara, 1956: 18 (morphometry), fig 2 (lateral view); Bigelow & Schroeder, 1957: 11 (pré-oral furrow), 109 (caudal fin drawing), 124 (bioluminescence); Backus, 1960: 245 (records); McCormick *et al.*, 1963: 357 (luminescence); Strasburg, 1963: 33 (22 collected specimens), 34 (collection data, nursery, map), 35 (anatomy, feeding habit), 36 (teeth photograph), 37 (graphic of teeth length and width), 38 (teeth arrangements); Garrick & Springer, 1964: 681 (morphometry); Gill, 1964: 264 (footnote - name); Hulley & Penrith, 1966: 228 (differences with *Euprotomicroides*); Hubbs *et al.*, 1967: 9 (comparison with *Euprotomicrus bispinatus*), 14, 15 (bioluminescence), 20 (differences with *Eupromicrus bispinatus*); Lewis, 1969: 721 (stomach oils); Isouchi, 1970 (Eastern Pacific); Jones, 1971: 791 (bites on pelagic fishes and cetaceans); Beardsley Jr. *et al.*, 1975: 107 (crates wounds in istiophorids); Compagno, 1977: 308 (jaw movement), 309 (drawings of neurocranium and jaws); Figueiredo, 1977: 8 (key to Squalidae species from Brazil), 9 (short description), fig. 8 (drawing); Thomson & Simanek, 1977: 248 (drawing caudal region); Bass, 1978: 576 (Mozambique channel); Hodgson & Mathewson, 1978: 576 (Mozambique channel); Seigel, 1978: 602 (comparison with *Squaliolus laticaudus*), 603 (three specimens), 605 (Atlantic, Indian, North and South Pacific), 606 (distribution, cold Pacific waters, equatorial waters from Atlantic), 607 (lower teeth different from *Squaliolus laticaudus*; neural and hemal arches well calcified), 608 (clasper), 609 comparisons with *Squaliolus* and *Euprotomicrus), 610* (internal organs), 612 (feeding habit, reproductive mode); Norris & Dohl, 1980: 846 (bites); Cadenat & Blache, 1981: 105 (key, description), 106 (morphometric measurements), fig 80 (image of specimen and jaws), fig 81 (drawings of specimen and dermal denticles), 109 (dermal denticles); Moss, 1981/2: 28 (biting mechanism);Perrin *et al*, 1981: 594 (bites); Taylor *et al.*, 1983: 110 (report of biting *Megachasma pelagios*); Compagno, 1984: 93, 94, 96 (diagnose, range and biology), 108, 109 (feed on big squids), 109 (semiparasite), 228 (bites *Megachasma pelagios*); Kullander & Fernholm, 1985: 66 (phylogenetic distribution of the hypothalamic ventricular channals); Reif, 1985: 112 (five specimens), 113 (ventral photophores, drawing of photophores), 115 (big scales, concave), 116 (drawing of photophore distribution); Le Beouf & McCosker, 1987 Lessa *et al.*, 1999: 28 (collected elasmobranchs), 55 (oceanic species), 57 (visual records); Sadowsky *et al*, 1987: 660 (first occurrence), 661 (bites); Reddy & Griffith, 1988: 11 (table of injuries), 12 (bites), fig 2 (image of bite); Sadowsky *et al.*, 1988: 919 (25 to 31 lower teeth); Fulton, 1990: 124 (bites in a seal); Nakano & Tabuchi, 1990: 60 (small, bathy-, and epipelagic, tropical and subtropical, from 1980-85), 61 (map, frequency of distribution of males and females), 62 (total length and ovary weight); Wetherbee *et al.*, 1990 (feeds on marine mammals): 30 Wetherbee *et al.*, 2012: 241 (unusual tooth and jaw morphology); Würsig & Jefferson, 1990: 46 (bites); Choy, & Hiruki, 1992: 3 (bites); Raschi, & Tabit, 1992: 129 (photophores), 135 (lack of denticles around mouth); Shirai, 1992a: anatomical description; Shirai, 1992b: 516 (examined material); Alcorn & Westlake, 1993: 3 (three bites); Anderson & Ahmed, 1993: 54 (bites); Bres, 1993: 135 (common and scientific names); Hiruki, *et al.*, 1993 (a): fig 4 (frequency of bites), fig 8 (bites), 464 (injuries); Hiruki, *et al.*, 1993 (b): 470 (bites); Gadig, 1994: 33 (bites at Fernando de Noronha), 43 (bites), 44 (Southeast/South/Northeast/North of Brazil), 45 (key, description); Ito, *et al.*, 1994: 483 (bite posteriorly above the opercle), fig 2 (picture of the bite at a specimen of *Gasterochisma melampus*); Jefferson & Leatherwood, 1994: 2 (bites); Mullin *et al.*, 1994: 467 (bites); Stacey *et al.*, 1994: 455 (bites); Ellis & Shackley, 1995: 162 (teeth size); Zanelatto *et al.*, 1995: 142 (bites); Gasparini & Sazima, 1996: (bites); Mikhalev, 1997: 18 (bites); Amorim *et al.*, 1998: 623, 629 (abundance in Santos); Delgado-Estrella, *et al.*, 1998: 133 (bites); Gadig, 1998: 50 (cartilaginous fishes from Sao Paulo coast); MacLeod, 1998: 72 (bites); McKinnell & Seki, 1998: 131 (50 specimens caught); Stehmann & Krefft, 1998: 24 (luminescence), 25 (clasper structure); Stehmann *et al*, 1999: 613 (common species and wide range); Widder, 1998: 267 (feeding habits), 268 (calcified cartilages), 269, 270 (bioluminescence), 271 (oral vacuum), 272 (calcified jaws); Mazzoleni & Schwingel, 1999: 114 (Itajaí harbor), 115 (surface longline); Visser, 1999: 518 (bites); Bozzano & Collin, 2000: 192 (eight species), 194 (topographic distribution), 197 (drawing og topographic distribution of cells), 199 (area histograms *vs.* frequency of cells), 204 (unique retinal topography); Walker & Hanson, 1999: 1324 (bites); Fish & Shannahan, 2000: 1069 (neutrally buoyant); Gonzalez & Magenta-da-Cunha, 2000 (differences in biting with *Squaliolus laticaudus*); Addink & Smeenk, 2001: 47 (bites); Kiraly *et al.*, 2000: 2 (deep sea sharks from ZEE, USA), 8 (photographs), 8,9 (habitat, biology and distribution at ZEE); Lucas & Hooker, 2000: 49 (bites on beaked whales); Baird, *et al.*, 2001: 989 (bites); Gadig, 2001: 30 (Brazil), 84-86 (key, image, description, range, biology), 224 (pelagic), 232 (oceanic-pelagic), 233 (mesopelagic), 239 (Northeast, Central, Southeast, South), 243 (only representative of Squaliformes due to bites), 244 (Central), 265 (all coast, except Rio Grande do Norte); Heithaus, 2001: 58 (cetacean ectoparasite), 59 (cetacean remains found in stomach), 64 (found in pelagic, deep ocean, temperate and tropical waters); Gadig, 2001: 30 (fauna diversity of Brazilian sharks), 84 (key to species, short description), 224, 232 (oceanic pelagic shark), 239, 243, 244, 259, 265 (Northeast, Central, Southeast, and South of Brazil); Micarone *et al.*, 2001: 124 (species that cause wounds); Motta & Wilga, 2001: 136 (unique biting behavior); Soto, 2001(a): 66 (systematic checklist), 93 (distribution, records, material in Brazil, synonyms); Gadig & Gomes, 2002: 1323 (morphometric data), fig 1 (female and nine embryos); Soto & Mincarone, 2001: 23 (female caught by longline); Belcher & Lee Jr., 2002: 3 (bite); Motta *et al.*, 2002: 24 (bite); Pérez-Zayas *et al.*, 2002: 309 (bites), 310 (drawing of mouth and teeth); Shimada, 2002: 70 (jaws); Azevedo, *et al.*, 2003: 412 (bites); Cavanagh *et al.*, 2003: 35, 36 (distribution), 168 (least concern species); Hutchins *et al.*, 2003: 139 (bite on *Megachasma pelagios*), 152 (vertical migration), 154 (drawing), 155 (description, distribution, habitat and behavior); Matott, 2003: 6 (unique feeding mechanism); Moore *et al.*, 2003: 388 (distribution and biogeography may be inferred by bites in swordfishes); Silva-Jr & Sazima, 2003: 1 (bites); Zidowitz, 2003: (biology and comparison with *I. plutodus*); Benz & Bullard, 2004: 395 (drawing); Haney, *et al.*, 2004: 410 (bites); Johnsen *et al.*, 2004: 1, 2 (presence of photophores); Makino, *et al.*, 2004: 169 (suspects for biting), 170 (a fish was caught with a specimen of *I. brasiliensis* biting it); Peach & Rouse, 2004: 236 (pit organ); Sielfeld & Kawaguchi, 2004: 80 (more occidentally), 83 (species list); Smith *et al.*, 2004: fig 24.134 (drawing); Soto & Mincarone, 2004: 7 (taxonomic list), 70 (ten lots); Abercrombie *et al.*, 2005: 779 (tested with primers of *Sphyrna*); Bacilieri, 2005: 11 (occasionally caught by midwater trawl); Coello, 2005: 34 (known from Ecuador); Compagno & Kyne, 2005: 23 (not reported for the region yet); Compagno *et al.*, 2005a: plate 14 (distribution, description, drawings), 127 (drawings of specimen and teeth, description, distribution, biology); Compagno *et al.*, 2005b: 55 (Philippines); Dean *et al.*, 2005: 357 (exception to megacarnivores); den Haring *et al.*, 2005: appendix 5 (not identified by shark fishermen); Gonzalez, 2005: anexo II (Southeast of Brazil); Lamilla & Bustamante, 2005: 9 (Chile), 24 (identification), 60 (common names); Musick & Ellis, 2005: 59 (6-12 eggs/year); Van Den Hoff *et al.*, 2005: fig 2 (image of a bite); Bertilsson-Friedman, 2006: 362 (bites); Cunha & Gonzalez, 2006: 466 (viviparous lecithotrophic reproduction); DINARA/FAO, 2006: 34 (Atlantic: Brazil, Mexico; Pacific: Chile, Ecuador), 45 (common names in each country); George & Zidowitz, 2006: 76 (AT (südl. Teil), deep sea); Kyne *et al.*, 2006: 15 (not threatened); Nelson, 2006: 59 (bite on a *Megachasma pelagios*); Priede *et al.*, 2006: 1437 (from surface to 3500 m); Sigler *et al.*, 2006: 402 (bites); White *et al.*, 2006: 62 (key features, distribution, habitat, biology, fisheries); Yearsley *et al.*, 2006: 16 (small toothed cookicutter shark); Bossart, *et al.*, 2007: 235, 236 (10-21 bites in each whale); Brownell Jr. *et al.*, 2007: 3 (bites); Burdin *et al.*, 2007: 8 (bites); Kyne & Simpfendorfer, 2007: 30 (circumglobal distribution, tropical and temperate, epi-, meso-, and e bathypelagic), 79 (female and nine embryos); Lisney & Collin, 2007: 268 (Body mass, axial eye diameter, habit and habitat); Mejía-Falla *et al.*, 2007: 127 (literature, Pacific Ocean, oceanic), 135 (not confirmed in Colombian waters); Nunan & Senna, 2007: 163 (1907, continental slope), 164 (deeper than 200 m); Ohishi *et al.*, 2007: 628 (bites); Ramsay & Wilga, 2007: 679 (preys bigger then mouth size), 680 (drawing of jaw articulation); Silva-Jr *et al.*, 2007: 507, 508, 509 (bites); Souto *et al.*, 2007: 22 (few bites); Anderson & LaBarbera, 2008: (teeth serie); Babcock & Nakano, 2008: 473 (reported to ICCAT); Bermúdez Villapol, *et al.*, 2008: 158 (bite); fig 6 (wound at a whale); Bunkley-Williams, *et al.*, 2008: 264 (turtle leeches at bite wounds); Compagno, 2008: 19 (pelagic diversity); Fergusson *et al.*, 2008: 221 (the only predator on adult *Odontaspis ferox*); Greenber, 2008: 7 (45 cm and bites); Hazin *et al.*, 2008: 214 (caught in subsurface longline), 215 (not caught by Japanese fleet); Jucá-Queiroz *et al.*, 2008: 78 (Ceara State, Brazil); Mandelman *et al.*, 2008: 435 (bites); Mannering & Hiller, 2008: 1351 (tooth comparision to *Centroselachus crepidater*); Meneses, 2008: 38 (unique biting behavior), fig 5 (photograph of a specimen); Petersen *et al.*, 2008: 63, 64 (bycatch composition); Renner & Bell, 2008: 102 (possible bite); Van Waerebeek *et al.*, 2008: 6 (bites); Weir *et al.*, 2008: 1227 (30-40 bins caught); Bornatowski *et al.*, 2009: 2 (sharks of Paraná-coast), south-western Atlantic); Camhi *et al.*, 2009: 9, 43, 75 (pelagic); Claes & Mallefet, 2009: 3684 (failure to induce luminescence using acetylcholine and adrenaline); Goto, *et al.*, 2009: 1 (distribution and depth); Lowry *et al.*, 2009: 2484 (bite); Santos & Gadig, 2009: 4 (highest number of identified cetacean preys together with *Carcharodon carcharias*); Souto *et al.*, 2009: 1 (interactions with seals); Velozo *et al.*, 2009: 3 (bites); Aguiar & Valentin, 2010: 568 (ectoparasite); Claes *et al.*, 2010: 28 (spectrum of luminescence); Deakos *et al.*, 2010: 122 (bite); Gomes *et al.*, 2010: 41 (short description), 59 (wounds on Megachasma pelagios); Largacha *et al.*, 2010: 1 (description), 2 (17 specimens), 3 (biometric data), 4 (males length and weight); Mendonça *et al.*, 2010: 32 (sample characterization); Menezes, 2010: table 1 (marine fishes from Brazil); Papastamatiou *et al.*, 2010: 362 (small, pelagic, tropical and subtropical); Sáez & Pequeño, 2010: 479 (key), 480 (tooth description); Sáez *et al.*, 2010: 622 (key), 626 (coloration), 633 (Squalomorphii from Chille); Straube *et al.*, 2010: 909 (not sister-clade of Etmopteridae based on RAG2 dataset), fig 3 (maximum likelihood based phylogram of RAG1 data), 914 (monophyletic group alongside with bioluminescent species *Dalatias licha* and *Squaliolus aliae* based on RAG1 dataset); White & Dharmadi 2010: 1365 (bites); Castro, 2011: 95 (luminous organs that resemble those of *Centroscyllium fabricii*), 140 (weel-known species within the genus), 141 (key to species), 145-150 (identification, range, biology, relation to humans, drawings of specimen and teeth, picture of dermal denticles); Claes *et al.*, 2011: 4 (non-luminous pigmented zone); Dwyer & Visser, 2011: 111 (temperatures from 18 to 26^{o} Celsius, eight records in New Zealand), 112 (bite), 113 (distribution in New Zealand), 130 (size of bite is compatible with shark size), 132 (wider distribution than what is known); Claes *et al.*, 2012: 1691 (predatory use of camouflage); Gardiner *et al.*, 2012: 358 (ambush predator in open water, with retinal areae); Heithaus & Vaudo, 2012: 519 (prey manipulation); Hoyos-Padilla *et al.*, 2012: 2 (small predator), 4 (Eastern Pacific, 3500 m depth, daily vertical migration, ventral photophores, dark collar); Iglésias, 2012: 26 (key), 81 (species from ICCANAM); Kyne *et al.*, 2012: 40 (least concern), 142 (North and Central America, and Caribbean sharks, rays, and chimaeras at Red List); Motta & Huber, 2012: 155 (bioluminescence to lure pelagic predators), 160, 169 (unique biting behavior), fig 6.14 (drawing of jaws), 191 (replacement of complete row of teeth); Musick *et al.*, 2012: 58 (circumtropical, mesopelagic, vertical migration), 65 (oceanic, pelagic, caught in 10 FAO regions); Naylor *et al.*, 2012(a): 65 (molecular analysis for 3 individuals), 128 (distance-p and K2P to NADH2), 147 (representative specimens); Naylor *et al.*, 2012(b): 42 (phylogenetic relationships hypothesis); Wenzel & Suárez, 2012 (Cape Verde); Ebert *et al.*, 2013a: 166, 167, 170 (destribuion, description, behavior, drawings); Ebert *et al.*, 2013b: 298 (Taiwan, least concern); Ebert *et al.*, 2013 (c): 10 (first reported to Taiwanese waters in 1993); Trape, 2013: 4 (Senegal); Ebert

& Stehmann, 2013: 132 (comparison to *I. plutodus*, collected more frequently), 133 (Eastern and Central-Estern Atlantic), 135 (different behavior from *Squaliolus laticaudus*);White & Last, 2013: 236, 237 (senior synonym of *I. labialis*), 243 (comparative material); Claes *et al.*, 2014: 1 (ventral photophore-free area), fig 4 (predation risk modeling); Helfman & Burgess, 2014: 27 (teeth shape); Munroe *et al.*, 2014: 319 (ectoparasitic feeding strategy); Rosa & Gadig, 2014: 90 (described from Brazil), 93 (Brazilian marine chondrichthyans), 97 (previously mentioned by Figueiredo (1977) by occurring at the South of Brazil);

Iristius ferox: Schmeltz, 1866: 10 (South Seas);

Isistius braziliensis: Macleay, 1881: 368 (ref., Aust.); Science News Letter, 1941: 328 (bioluminescence); Morris *et al.*, 1983: 296 (sterol composition of liver); Williams, 2001: 214 (teeth size increase with growth in body size); Sielfeld & Kawaguchi, 2004: 85 (number of individuals x species x space and frequency);

Isistius marmoratus Rochebrune, 1885: 98 (description, Senegambia);

Leius brasiliensis: Günther, 1909: 490-1 (references, description);

Scymnus fulgens: Giglioli, 1912: 72, 109 (luminescence);

Isistius sp. (species not identified, probably *I. brasiliensis*): Daniel, 1934: 266 (eye comparison to *Squatina*); White, 1937: 70 (teeth with once cusp); Moss, 1977: 359 (big lower cutting teeth); Maisey, 1983: 50 (teeth substitution regulated); Johnson & Wolman, 1984: 35 (bites); Bonde & O'Shea, 1989: 448 (bites); Clark & Kristof, 1990: 278 (feeding habit similar to Dalatias); Compagno, 1990: 45 (top predatorso), 63 (drawings of microceanic sharks); Foster & Hare, 1990: 50 (bites); Shirai & Nakaya, 1990: 351 (no process to support the eye, muscle geniocoracoideus); Miyake et al., 1992: 286 (rostral cartilage as a rod); Carvalho, 1996: 41 (rostrum not trough-shaped); Laurito, 1996: 87 (High Guayacán) 88 (Upper Paleocone, lower and upper teeth different from each other), 91 (pelagic, tropical, subtropical, and temperate, Eocene); Shirai, 1996: 16 (visceral skeleton, hypobranchial bar in Dalatiidae, except Isistius), 24 (politomy of Dalatiidae, Somniosidae and Oxynotus), 33 (Dalatiidae); Jefferson & Barros, 1997: 3 (bites); Zerbini & Santos, 1997: 105 (bites); Peach & Marshall, 2000: 1133 (pit organs have not yet been located); Wardle et al., 2000: 640 (bites); Adnet & Cappetta, 2001: 242 (second diversification at the boundary Turonian-Coniacian), 247 (teeth characters matrix), 248 (list of authors); Best, 2001: 281 (bites), 288 (percentage of bites in each Ocean); Pitman et al, 2001: 498 (bites); Soto, 2001b: 32 (similar feeding habit as Centroscymnus coelolepis); Dalebout, et al., 2002: 599, 604 (bites and distribution); Jefferson & Curry, 2003: 2 (bites); Kriwet, 2003: 588 (teeth morphology similar to Folipistrix digitulus sp. nov.); Dalebout, et al., 2004: 350 (bites); Kriwet, & Benton, 2004: 188 (deep water group no affected from Cretaceous to Tertiary); Wilga & Lauder, 2004: 142 (deep-sea shark, high pectoral fin insertion); Borsa & Robineau, 2005: 467 (bites); Meneses et al., 2005: 80 (Sergipe), 82 (bites); Souza et al., 2005: 132, 134 (bites); Claridge, 2006: 6 (bites); 26 (bites at an adult female and an unknown immature); Fitzpatrick et al., 2006: 397 (wounds on a specimen of Rhincodon typus); Kocsis, 2007: 30 (Upper Paleocene, France, South and North America); McSweeney, et al., 2007: 688 (bites); Baird, et al., 2008: 11 (bites and diel vertical migrations); Steiner et al., 2008: 3 (bites); Neto et al., 2009: fig 3 (image of a bite), 4 (bites); Araújo et al., 2010: 4 (bite); Klug & Kriwet, 2010: 335 (supertree, sister-group with Dalatias), 337 (Dalatiidae: Euprotomicroides + [Euprotomicrus + Squaliolus] + [Dalatias + Isistius]), 338 (phylogenetic tree: supertree + stratigraphy); Lane, 2010: 25 (lack of optical peduncle); Vialle et al., 2011: 243 (Mazan, France); Iserbyt & De Schutter, 2012: 150 (tropical oceanic); Dolce & Wilga, 2013: 86 (gill slit characters), 97 (small body micropelagic), 98 (micropelagic ecomorphotype), appendix 1 (standardized mean of gill slit length), appendix 2 (standardized mean of inter-gill slit distance and number of slits over the pectoral fin), appendix 3 (analysis of variance among gill slit length), appendix 4 (analysis of variance among inter-gill distances); Maisey et al., 2014: 590 (simultaneous replacement of teeth);

Isistius labialis Meng, Zhu & Li, 1985: 442 (description of new species); Compagno *et al.*, 2005a: plate 14 (distribution, description, drawing), 128 (drawings of specimen and teeth, description, distribution); Kyne & Simpfendorfer, 2007: 30 (South China Sea; mesopelagic), 79 (known by only one specimen); Compagno, 2008: 19 (pelagic diversity); Camhi *et al.*, 2009: 19, 44, 75 (pelagic, data deficient); Klug & Kriwet, 2010: 332 (drawings); Dwyer & Visser, 2011: 111 (South China Sea), 112 (only one known specimen); Claes *et al.*, 2012: 1691 (known by one specimen); Ebert & Stehmann, 2013: 133 (only one known specimen from Central-Western Pacific); Ebert *et al.*, 2013 (a): 166, 167, 171 (distribuion, description, behavior, drawings); White & Last, 2013: 236, 237 (synonymy, remarks), fig 10 (photograph – lateral view), fig 11 (photograph – ventral view, and teeth). **[NEW SYNONYM]**.

Holotype: MNHN A-7787, female 172 mm TL, Western Atlantic, Brazil, Expédition D. de Freycinet 1817-1820. (Figure 1)

Diagnosis. A species of *Isistius* differentiated from its only congener, *I. plutodus*, by the following characters: a more rounded and longer snout (*vs*. shorter and less rounded snout in *I. plutodus*), with preorbital, prenasal and preoral snout lengths proportionately greater at 15.56%, 6.29% and 32.47% *vs.* 10.62%, 4.40% and 22.22% of head length in *I. plutodus*, respectively); interorbital distance is 25,53% of head length (*vs.*17.33% in *I. plutodus*); interdorsal space is almost twice head length (9.13% *vs.* 5.64%); second dorsal fin almost same height as first (*vs.* second dorsal fin higher than the first one in *I. plutodus*); lower symphyseal tooth height is approximately 1.5 times smaller (1.41% *vs.* 2.08%), as well as tooth base length (0.62% *vs.* 1.08%); lower symphyseal tooth 5% shorter than adjacent teeth in *I. brasiliensis*, whereas they are the same height in *I. plutodus*; tooth formula for upper/lower teeth 15+15/12+1+13 (*vs.*12+12/9+1+9); lower teeth proportionally smaller, only 3 times greater than upper teeth (*vs.* 6 in *I. plutodus*). Gum at the mouth wavy and lateraly short in *I. brasiliensis* (straight and lateraly long in *I. plutodus*); upper postventral margin of caudal fin smaller than lower postventral margin (*vs.* upper margin greater than lower in *I. plutodus*). General body color in *I. brasiliensis* is a lighter brown than *I. plutodus*; ventral dark collar proportionately smaller in *I. brasiliensis* (posterior end at the level of pectoral fin origin) than in *I. plutodus* (posterior end at the level of pectoral fin insertion). Morphology and proportions of neurocranium also differs between both species (Table 5): neurocranium in *I. brasiliensis* has a greater nasobasal length (56.08% *vs.* 54.17%), a longer otic capsule, and greater width across postorbital processes. Relative to nasobasal length, *I. brasiliensis* has the same proportionally larger measurements cited above, as well as a greater basal plate width at orbital notches, and greater width across postorbital processes, even though the postorbital process itself is smaller in *I. brasiliensis* than in *I. plutodus* (8.58% *vs.* 11.31%).

Description

Complete morphometric characterization of this species is in Table 6, tooth count in **Table 7**, and vertebrae counts in Table 8 (specimens from Atlantic and

Indian Oceans), and Table 9 (specimens from Pacific Ocean and those with no information regarding locality). Measurements of specimens from Atlantic, Pacific, and Indian Oceans were compared with each other (Table 10). No discrepancy between the measurements was found whatsoever. There were ten analyzed specimens that did not have locality data; as no difference was found between the specimens from different oceans, it is not possible to infer from where these specimens came from.

The specimens were divided in males and females for comparison, but the only measurement that is clearly different between both sexes is pelvic length (9.56% *vs.* 7.97% in males and females, respectively). Immature and mature females (limit: 39 cm) and males (limit: 36 cm) were compared in Table 11 (females), and Table 12 (males). In females, the measurements that have the most allometric differences between immature and mature specimens are PP1, HDL, PG1, PSP, POB, PRN, EYL, DCS, PPS, PCA, and CFL. In males, these measurements are PP2, PG1, POR, EYL, EYH, CLO, and CLI.

1.1.1 External morphology

Trunk cylindrical and slender, tapering toward pelvic and caudal fins origins. Caudal fin length about 5.5 times predorsal length. Caudal peduncle without lateral ridges and almost symmetrical with both height and width with same sizes (approximately 1.9% of TL). Lateral outline of head rectangular, being conical anteriorly to mouth. Its dorsal profile is parallel to the ventral one, slopping a little toward the bulbous, rounded tip of snout. Preorbital length short, 6.4 times in head length; interorbital space 1.5 times eye length. Eyes large (18% of head length), anteriorly rounded and with a posterior angle. Spiracle large (2 % of TL), dorsal, behind the eye, a little oblique (inner portion directed a little posteriorly), with a flap in its anterior portion; prespiracular length 4.15 times the spiracle length. Its shape is oval, with the largest width being transverse to the body axis. Gill slits very small (1-0.8% of TL), the first bigger than the fifth, well behind the eye and right in front of pectoral fin origin.

Nostrils in front of head, anteroventrally positioned; anterior portion of nostrils rounded, with a short process and an elongated posterior portion, which is inclined to the central axis of the body, not forming barbels. Internarial length almost equal to prenarial length. Mouth wide, transverse (7.2% of TL), with lateral skin folds and deep grooves (25% of head length); thick and striated lower lip. The *upper lip* *cover* (lpc) is a continuum with the lower ventral surface of the head anterior to mouth, and from its lateral and internal portion arises a thick and naked *lip fold* (lf). This fold is a short tissue at the corner of the mouth directed to the caudal region and is slightly turned toward the medial region of the lower jaw; its distal portion is located right posterior to the anterior portion of the lower lip, it is rounded and can be seen when the mouth is shut and the upper lip cover coats almost its whole length. Immediately dorsal to the upper lip cover there is a thick and wavy *gum* (gm), and a *flesy sack for the upper labial cartilages* (slc). Dorsal to this lip fold there is a deep groove that extends from anteriorly to the labial cartilages until almost the posterior ending of the lower jaw. From the corner of the mouth to the posterior region, it is called *posterior mouth groove* (pmg) and is so long that it almost reach the ventral collar. At the corner of the mouth it is named *deep oral pocket* (opk), and this portion is immediately dorsal to the lip fold. Anterior to the corner of the mouth, there is a *preoral pouch* (prop) that is dorsal to the labial cartilages joint and the upper labial cartilage (Figure 9) (Shirai & Nakaya, 1992).

Pectoral fins originating immediately posterior to fifth gill slits. Pectoral fins terminate abruptly. with straight posterior margins, their length 7.5 times in predorsal body length, or 2.6 times in head length. Anterior margins straight and almost parallel to body axis, and posterior margins almost perpendicular to body axis, with corners slightly curved. Inner margins slightly oblique directing toward the ventral side at their most posterior portion. Pectoral base 3.4 times height of the first gill slit. Dorsal fins without spines. First dorsal very small and obliquely inclined rearward. Its origin a little in front of pelvic fins (about equal to internarial space) but very posterior to tip of pectorals. Origin of first dorsal about two thirds of precaudal body length. First dorsal base length 1.7 times its height and about 15% of head length. Posterior edge straight and the free lower tip forms an acute angle. Second dorsal fin slightly higher and longer than the first. Both its base length and height 1.15 times those of first dorsal fin. Origin somewhat above pelvic fin free rear tip. Base of second dorsal 1.7 times its height and about 17% of head length. Posterior margin of second dorsal similar to first dorsal, although its free rear tip has a prolongued filament.

Interspace between second dorsal and caudal fins slightly greater, about 1.13 times space between second dorsal and caudal fins. Caudal fin asymmetrical with the end of vertebral column slightly upturned. Dorsal margin 1.4 times preventral margin, the latter originating slightly anterior to the upper. Terminal margin of dorsal caudal lobe almost straight and perpendicular to body axis, but with a slight inclination; end of dorsal margin posterior to end of subterminal margin. Subterminal notch at posterior end of vertebral column, and subterminal margin parallel to body axis. The upper postventral margin almost half the size of lower postventral margin. Pelvic fin origins posterior to insertion of first dorsal fin, but anterior to its free rear tip. The base is almost three times first dorsal base length. Female pelvic fins with a smooth lateral angle and almost straight rear tip; in males, lateral angle smaller, and pelvic fin shorter, with claspers in adults slightly longer than the end of the fin. In ventral view, the most distal portion of the clasper is white, and forms a triangle: along the internal portion it is straight, the outer portion is oblique is directed toward the inner side and the base in very oblique, forming a continuing line with the fin’s margin until the inner portion of the clasper tip. In dorsal view, the clasper groove originates from its most anterior portion, almost at the dorsal insertion of the fin on the body. The groove is somewhat straight and dorsal along the clasper axis and ends at the gland. The claspers of juveniles do not reach the rear tip of the pelvic fin.

1.1.2 Teeth

Teeth unicuspid and heterogeneous, smooth-edged; in average, 31 (16+15) upper teeth in a row with no symphyseal teeth; narrow, sharp-ended, a little oblique to the sides (left and right sides, respectively) and, usually, in three rows, being multiserial in function. Upper teeth roots are pseudolobated and there is a sulcus dividing each lobe of the root in an almost quadrate shape (Figure 10). In average, 26 (12+1+13) lower teeth in a row, with a symphyseal tooth at the middle, which is slightly shorter than the parasymphyseal ones and is at the longitudinal line between booth upper parasymphyseal teeth directed to opposite sides. Lower teeth are have straight up triangular cusp and flat base in only one active row (the others are upside down, inside lower jaw) (Figure 11). Lower teeth much bigger than upper ones (symphyseal lower – 5.42 mm – and parasymphyseal upper – 1.70 mm – in an adult specimen), and those toward angles of jaw are shorter and wider than those at symphysis, with only a trace of the triangular tip (commissural lower – 3.72 mm – and upper – 0.88 mm – in an adult specimen). The proportion between upper and lower teeth is, in average, 3. Bases of lower teeth are interlocked and form a single functional series, with each root completely exposed on the outer face and the inner side adheres closely to the lower jaw.

1.1.3 Coloration

Light or dark brown body with dorsal side slightly darker than the lower. Darker brown ventral collar around the branchial region, which begins posteriorly to mouth and ends at the origin of pectoral fins. The color of collar is the same as the dorsal side, and it is easily distinguished from the body. All fins brown with white borders at the posterior end of ceratotrichia, forming a uniform white line. Both dorsal and ventral endings of caudal fin have a darker brown area, even though the margins are white, with the exception of subterminal margin. Some specimens might have a variation in coloration, such as absence of dark collar, white fin tips and darker brown area on caudal fin.

1.1.4 Dermal denticles

Dermal denticles have no regular alignment, are closely spaced, and there is exposed skin between them; small, very low, with no distinction between pedicel and blade. There is no acute medial cusp and medial ridges at the crown (Figure 12, Figure 13). They have a squared shape at the base and a trapezoidal one at height; almost symmetrical. Four inclined bases and one side (“crown”) on top, all concave and forming a quadrate depression. Bellow and between the four bases, there are four smaller ones, also concave. Bellow the denticles structure, at the base, many small concave indentations. Transversely truncate apically, quadrilateral in outline, but occasionally polygonal, with concave margins and rounded corners.

1.1.5 Luminescent markings

Photophores are black, small, annular elements that that measure approximately 200 µm (Figure 14). They are usually present on the ventral side of the body, from the tip of snout to the posterior end of vertebral column, including lips, ventro-lateral wall of eyes, ventral fins, and claspers in males (except their white tip). However, there is no photophore on the ventral dark collar. On the dorso-lateral side there might be photophores on the head, lateral of pectoral fins, dorsal and caudal fins. There is a wide variation of presence and position of photophores, ranging from complete absence of these structures to presence on both ventral and dorsal sides, and fins. The only conspicuous feature is its absence on ventral collar in every specimen.

1.1.6 Geographic distribution

Distributed worldwide in tropical and subtemperate waters. Known from the Western (from south of Brazil to Gulf of Mexico) to Eastern Atlantic (South Africa to Mauritania and Cape Verde), Western (Tasmania to Japan, including Indonesia and Taiwan) to Eastern Pacific (Easter Is., Galapagos Is. to Baja California) including French Polynesia and Hawaii, and Indian Oceans (Indonesia and Mauritius). Tropical oceanic, epi- to mesopelagic; from 20-3,700 m of depth, and water temperature ranging, approximately, from 8 to 29°C (Parin, 1966) (

Figure 15).

1.1.7 Etymology

The specific epitet *brasiliensis* is due to the fact that the first specimen was collected from the Brazilian coast, in Rio de Janeiro.

1.1.8 Common names

English: cookiecutter shark; Portuguese: tubarão charuto; Spanish: tollo cigarro; French: squalelet féroce; German: Zigarrenhai.

1.1.9 Remarks

All of the existing holotypes of nominal species considered junior synonyms of *Isistius brasiliensis* were examined: *Scymnus brasiliensis* Quoy & Gaimard (1824), *Scymnus brasiliensis torquatus* Müller & Henle (1841), *Scymnus brasiliensis unicolor* Müller & Henle (1841), *Leius ferox* Kner (1864), and *Isistius labialis* Meng, Zhu & Li (1985). The holotypes of *Squalus fulgens* (Bennett, 1840) and *Isistius marmoratus* Rochebrune (1885) were not found in any collection, as the authors who described them did not mention the collection in which they could have deposited the specimens.

The holotypes of the nominal species *Scymnus brasiliensis* and *Scymnus brasiliensis torquatus* are the same specimen, the former described by Quoy & Gaimard (1824) and the latter was described as a subspecies of *I. brasiliensis* by Müller & Henle (1841). This specimen was collected before 1824 and is in poor condition, besides being a juvenile. Therefore, its measurements are not very accurate due to some damage on the fins and body shrinkage.

Another holotype, also described by Müller & Henle (1841), *Scymnus brasiliensis unicolor* is not in a good condition either, although this specimen is a big adult (470 mm). The name given, *unicolor,* is a reference to the absence of the ventral dark collar in between the gills. However, this specimen's color is a very dark brown and the difficulty in observing the collar might be a result of its dark color. Many other analyzed specimens also lacked the collar.

On the description of *Isistius labialis*, Meng, Zhu & Li (1985) mentioned, besides other features, the presence of a rounded projection on lower lip of specimen. But since this characterist was not observed in any other specimen, it may be considered another variation among *Isistius brasiliensis*.

Although the holotypes have some morphological differences between them, as well as many examined specimens, it is not enough to identify distinct morphotypes and populations by regions. Therefore, *Isistius brasiliensis* is a very diverse species and there are specimens with variable colours, sizes and porportions (Figure 16).

1.1.10 Analyzed material

(243 analyzed specimens)

<u>Southwestern Atlantic</u>
C.DBAV.UERJ 1635, 1 ex., female 431 mm TL, Southwestern Atlantic, 23-24° S, 130 nautical miles off São Paulo, Brazil, 20 Mar 1995; C.DBAV.UERJ 1636, 8 ex., embryos 112-120 mm TL, Southwestern Atlantic, 23-24° S, 130 nautical miles off São Paulo, Brazil, 20 Mar 1995; C.DBAV.UERJ 1660.1, 1 ex., female 420 mm TL, Southwestern Atlantic, Brazil; C.DBAV.UERJ 1671, 1 ex., male, Southwestern Atlantic, Brazil; MNHN 0000-4891, 1 ex., female 209 mm TL, Southwestern Atlantic, South of Brazil, 23°00'00" S, 43°16'59" W, depth 250 m, 1863; MNHN A-7787 (Holotype of *Scymnus brasiliensis*, *Scymnus torquatus* and *Isistius brasiliensis*), 1 ex., female 172 mm TL, Southwestern Atlantic, Brazil, Expédition D. de Freycinet 1817-1820; MZUSP 16360, 1 ex., male 470 mm TL, Southwestern Atlantic, South of Brazil, 29°38'33,33' S, 46°20'00,01" W, 24 May 1976; ZMH 103780, 1 ex., male 321 mm TL, Southwestern Atlantic, 23°02'00" S, 33°19'00" W, 1966;

<u>Southeastern Atlantic</u>
CAS 222996,1 ex., male 377 mm TL, Southeastern Atlantic, Angola, 7°58'60" S, 12°35'60" E, depth 630 m, 16 Apr 2005; MCZ 57370, 1 ex., male 282 mm TL, Southeastern Atlantic, Angola, 11°23' S, 10°55' E, depth 190-200 m, 4 Jun 1971; MNHN 1991-6827, 1 ex., male 382 mm TL, Southeastern Atlantic, Angola, 10°30'00" S, 11°55'01" E, depth 1756-1756 m, Campagne Walda 23cy15; NHM

1982.9.22.1, 2 ex., female 385 e 461 mm TL, Southeastern Atlantic, 21° 34,4' S, 8° 9,8' E and 32°108' S, 36°21,7' E, 182>? m, 1604 e 1000>0 m, 1764; SAIAB 64998, 1 ex., female 405 mm TL, Southeastern Atlantic, Angola, 5 Mar 2001; SAIAB 65007, 1 ex., female 395 mm TL, Southeastern Atlantic, Angola, 12 Mar 2001; SAIAB 65972, 1 ex., female 288 mm TL, Southeastern Atlantic, Angola; ZMH 108396, 1 ex., male 286 mm TL, Southeastern Atlantic, 30°09'00” S, 5°26'00” E, 1971; ZMH 108492, 2 ex., male 395 mm TL and female 466 mm TL, Southeastern Atlantic, 33°00'00” S, 7°50'00”E, 1971; ZMH 108493, 1 ex., male 371 mm TL, Southeastern Atlantic, 33°00'00” S, 7°50'00” E, 1971; ZMH 109991, 1 ex., male 262 mm TL, Southeastern Atlantic, 15°45'00” S, 6°06'00” W, 1971.

Northwestern Atlantic

MCZ 55447, 1 ex., male 392 mm TL, Northwestern Atlantic, Gulf of Mexico, 29°32’ N, 93°16’ W, depth 405-460 m, 20:11-23:32h, 19 Jun 1966; MCZ 55498, 1 ex., male 375 mm TL, Northwestern Atlantic, Caribbean Sea, 13°51’ N, 70°15’ W, 27 May 1966; MCZ 58094, 1 ex., female 153 mm TL, Northwestern Atlantic, Amazon, 1°41’ N, 40°37’ W, depth 0-80 m, Mar 1977; MCZ 58096, 2 ex., male 158 mm TL, female 224 mm TL, Northwestern Atlantic, Amazon, 0° 1’ N, 37°40’ W; MCZ 36039, 1 ex., male 382 mm TL, Northwestern Atlantic, Bahamas, 25°11’ N, 77°19’ W, depth 800-1000 m, 30 Jan 1938; NMW 78801, 1 ex., female 163 mm TL, Northwestern Atlantic, 25° N, 70° W; TCWC 3985.01, 1 ex., male 397 mm TL, Northwestern Atlantic, Gulf of Mexico, 23° 12’36” N, 90° 44’5.94” W, depth 3700 m; TCWC 5130.01, 1 ex., female 257 mm TL, Northwestern Atlantic, Caribbean Sea, 20°48’ N, 92°55’60” W, depth 2270 m; TCWC 5131.01, 1 ex., female 178 mm TL, Northwestern Atlantic, Gulf of Mexico, 19°7’48” N, 94°5’30” W, depth 935-950 m; TCWC 8770-09, 1 ex., female 446 mm TL, Northwestern Atlantic, Caribbean Sea, 19°46’0” N, 82°9’ W; UF 207807, 1 ex., female, Northwestern Atlantic, Bahamas, 23°42’ N, 76°38’ W; UF 232917, 1 ex., male 406 mm TL, Northwestern Atlantic, Bahamas, 23°38’ N, 77°6’ W; UF 35686, 2 ex., males 358 e 395 mm TL, Northwestern Atlantic, Gulf of Mexico, 29°4’ N, 87°37’ W; YPM ICH 3727, 1 ex., female 428 mm TL, Northwestern Atlantic, Bahamas, Ocean tongue, 7000 ftm SE of Booby Rocks;

Northeastern Atlantic

MCZ 55495, 1 ex., male 386 mm TL, Northeastern Atlantic, Cape Verde, 16°14’ N, 20°44’ W, 14 Nov 1970; MCZ 55496, 1 ex., male 375 mm TL, Northeastern Atlantic, Cape Verde, 16°28’ N, 19°45’ W, 14 Nov 1970; MCZ 55497, 1 ex., male ?, Northeastern Atlantic, Cape Verde, 16°32’ N, 19°35’ W, 13 Nov 1970; MNHN 0000-1179, 1 ex., female, 210 mm TL, Northeastern Atlantic, Cape Verde, 15°07’01” N, 23°34’59” W, Expédition Dumont d'Urville 1826-1829; NHM 1994.9.28.4, 1 ex., female 356 mm TL, Atlantic; NHM 1995.8.22.11, 1 ex., male 365 mm TL, Northeastern Atlantic, Cape Verde, 17° 43' N, 25° 23' W, depth 510-0 m; NHM 1996.7.10.29, 1 ex., female 427 mm TL, Northeastern Atlantic, Gambia, 10° 54,7' N, 20° 30’ W, depth 510-405 m; NHM 1996.9.11.10, 1 ex., male 393 mm TL, Northeastern Atlantic, Cape Verde, 17° 41' N, 25° 23' W; UF 165691, 1 ex., female 173 mm TL, Northeastern Atlantic, Liberia, 12° N, 28°57’ W; UF 224595, 1 ex., Northeastern Atlantic, Nigeria, 3°30’ N, 4°51’ E; UF 224657, 1 ex., female, Northeastern Atlantic, Nigeria, 5°57’ N, 2°49’ E; ZMH 103882, 1 ex., male 384 mm TL, Northeastern Atlantic, 19°11'00” N, 21°58'00” W, 1966; ZMH 109456, 1 ex., male 386 mm TL, Northeastern Atlantic, 17°24'00” N, 22°57'00” W, 1971; ZMH

109828, 1 ex., male 391 mm TL, Northeastern Atlantic, 17°27'00” N, 22°55'00” W, 1971;

Central Atlantic
MCZ 41350, 1 ex., male 271 mm TL, Central Atlantic, 3°02’ N, 21°19’ W, 27 Apr 1961; MCZ 41351, 1 ex., male 331 mm TL, Central Atlantic, 0°15’ S, 18°40’ W, 26 Apr 1961; MCZ 41352, 1 ex., male 274 mm TL, Central Atlantic, 11°16’60” N, 30° W, depth 0-230 m; MCZ 41353, 1 ex., male 349 mm TL, Central Atlantic, 02°10’ S, 17°23’ W, depth 250-350 m, 21 Apr 1961; MCZ 55499, 1 ex., male 274 mm TL, Central Atlantic, 11°17’ N, 30°00’ W, depth 0-230 m, May 1961; MCZ 57371, 1 ex., male 158 mm TL, Central Atlantic, 1°20’ S, 27°37’ W, 22h, 25 Feb 1963; MCZ 58095, 1 ex., female 170 mm TL, Central Atlantic, 5°32’00” N, 34°40’ W, depth 0-75 m, Mar 1977; NRM 9026, 1 ex., Central Atlantic, 03° 25' S, 24° 30' W, 17 Mar 1890; ZMH 106154, 1 ex., male 185 mm TL, Central Atlantic, 3°00'00” S, 26°16'00” W, 1968;

Pacific
HUMZ 126958, 1 ex., female 421 mm TL, Pacific, 14 Feb 1983; MNHN 1997-3575, 1 ex., male 385 mm TL, Pacific, Campagne Caride 6; NHM 1868.6.22.41, 1 ex., female 226 mm TL, Pacific;

Southwestern Pacific
AMS I.9280, 1 ex., female 424 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 31° 31' S, 159° 05' E, 1908; AMS IA.1427, 1 ex., female 449 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 31° 31' S, 159° 5' E, 1923; AMS I.5427, 1 ex., female 345 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 31° 31' S, 159° 5' E, 1903; AMS IA.128, 1 ex., female 393 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 31° 31' S, 159° 5' E, 1920; AMS I.14058, 1 ex., male 370 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 31° 31' S, 159° 5' E, 1917; AMS I.29996-001, 1 ex., female 191 mm TL, Southwestern Pacific, Coral Sea, Osprey Reef, 1,5 miles west of entrance, Australia, 13° 54' S, 146° 33' 30" E, 1988; AMS I.16150-001, 1 ex., female 506 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 31° 32' S, 159° 4' E, 1971; AMS I.32445-001, 1 ex., female 160 mm TL, Southwestern Pacific, Queensland, Coral Sea, east of Orford Ness, Australia, 11° 30' 3" S, 145° 14' 36" E, 1988; AMS I.4308, 1 ex., male 385 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 31° 31' S, 159° 5' E, 1900; AMS IA.8061, 1 ex., ?, Southwestern Pacific, New South Wales, off Sydney, Australia, 33° 50' S, 151° 18' E, 1939; AMS I.7883, 1 ex., female 340 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 1907; AMS IB.2523, 1 ex., female 491 mm TL, Southwestern Pacific, New South Wales, 120 miles SE Sydney, Australia, 34° 50' S, 153° E , 1950; AMS I.43092-001, 1 ex., male 395 mm TL, Southwestern Pacific, Coral Sea, Australia, 10° 51' 43" S, 149° 44' 6" E, 1995; AMS I.43094-001, 1 ex., male 362 mm TL, Southwestern Pacific, Coral Sea, Australia, 10° 51' 43" S, 149° 44' 6" E, 1995; AMS I.42095-006, 1 ex., male 169 mm TL, Southwestern Pacific, Coral Sea, Australia, 12° 59' 52" S, 151° 19' 37" E, 1997; AMS I.27639-002, 1 ex., male 393 mm TL, Southwestern Pacific, New South Wales, east of Kiama, Australia, 34° 39' S, 151° 18' E, 1988; AMS I.43073-001, 1 ex., male 205 mm TL, Southwestern Pacific, Coral Sea, Australia, 12° 33' 39" S, 153° 50' 38" E, 1995; AMS I.42066-002, 1 ex., female 244 mm TL, Southwestern Pacific, Coral

Sea, Australia, 14° 36' 7" S, 151° 21' 18" E, 1997; AMS I.43100-001, 2 ex., female 330 e 364 mm TL, Southwestern Pacific, Coral Sea, Australia, 11° 1' 22" S, 149° 43' 8" E, 1995; AMS I.42172-002, 1 ex., female 189 mm TL, Southwestern Pacific, Coral Sea, Australia, 10° 53' 56" S, 150° 9' 21" E, 1997; AMS I.42003-004, 1 ex., male 238 mm TL, Pacific, Coral Sea, Australia, 13° 55' 58" S, 148° 12' 50" E, 1997; AMS I.42058-001, 1 ex., male 255 mm TL, Southwestern Pacific, Coral Sea, Australia, 14° 41' 20" S, 151° 19' 26" E, 1997; AMS I.42038-001, 1 ex., male 370 mm TL, Southwestern Pacific, Coral Sea, Australia, 15° 12' 14" S, 149° 34' 51" E, 1997; AMS I.42030-001, 1 ex., male 188 mm TL, Southwestern Pacific, Coral Sea, Australia, 15° 3' 57" S, 149° 20' 56" E, 1997; AMS IA.3792, 1 ex., female 360 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 31° 31' S, 159° 5' E, 1929; AMS I.24161-002, 1 ex., female 358 mm TL, Southwestern Pacific, New South Wales, Lord Howe Is., Australia, 31° 28' S, 159° 9' E, 1983; AMS I.28069-001, 1 ex., Southwestern Pacific, New South Wales, off Shoalhaven Heads, Australia, 34° 53' S, 151° 14' E, 1988; AMS I.28748-004, 1 ex., Southwestern Pacific, New South Wales, Tasman Sea, off Sydney, Australia, 33° 49' 30" S, 152° 33' 48" E, 1989; CSIRO CA 190, 1 ex., male 455 mm TL, Southwestern Pacific, New South Wales, east of Bermagui, Australia, 36°27'15.75" S, 150°14'27.59" E, depth 494 m, 1978; CSIRO CA 191, 1 ex., male 375 mm TL, Southwestern Pacific, New South Wales, east of Bermagui, Australia, 36°30'0.56" S, 150°14'27.91" E, depth 74 m, 1978; CSIRO CA 3137, 1 ex., male 402 mm TL, Southwestern Pacific, Australia, New South Wales, off Macquarie harbor, 31°26'28.22" S, 153° 4'4.76" E; CSIRO CA 3302, 1 ex., male 342 mm TL, Southwestern Pacific, Australia, New South Wales, Bougainville Reef, 16°50' S, 147°02’ E, 1979; CSIRO H 4714, 1 ex., female 443 mm TL, Southwestern Pacific, Australia, Tasman Sea, Lord Howe Ridge, 28°59' S, 160°22' E, 1997; CSIRO H 5150-01, 1 ex., male 485 mm TL, Southwestern Pacific, Australia, New South Wales, 300 miles east of Coffs Harb, 30°17'47.61" S, 153°10'33.91" E, 1999; CSIRO H 6008-01, 1 ex., male 376 mm TL, Southwestern Pacific, Australia, Tasman Sea, Norfolk Ridge, 29°29' S, 167°33' E, depth 200 m, 2003; CSIRO T 544, 1 ex., male 404 mm TL, Southwestern Pacific, Australia, Tasmania, 33 miles east of Flinders, 40°5'59.06" S, 148°28'47.89" E, 1981; CSIRO T 718, 1 ex., male 438 mm TL, Southwestern Pacific, Australia, Tasmania, 33 miles east of Flinders, 40°5'59.06" S, 148°28'47.89" E, 1981; CSIRO H 3722-01, 1 ex., male 305 mm TL, Southwestern Pacific, Australia, Queensland, Coral Sea, 16°38' S, 152°10' E, 1994; HUMZ 141845, 1 ex., female 445 mm TL, Southwestern Pacific, 30° S, 165° E, Hokuyo-maru vessel, 30 Aug 1995; HUMZ 141846, 1 ex., male 420 mm TL, Southwestern Pacific, 12°59’60 S, 159° E, Hokuyo-maru vessel, 09 Apr 1995; MCZ 60364, 1 ex., female 156 mm TL, Southwestern Pacific, New Britain trench, 6°40’60” S, 150°43’ E; MCZ 60365, 1 ex., female 373 mm TL, Southwestern Pacific, Queensland, Coral Sea, 17°33’ S, 148°47’ E, depth 400 m, 22 Jun 1981; MCZ 60366, 1 ex., male 178 mm TL, Southwestern Pacific, Queensland, Coral Sea, 17°13’ S, 148°20’ E, 19:07-00:10h, 23, 24 May 1981; MCZ 60367, 2 ex., female 478 e 462 mm TL, Southwestern Pacific, Queensland, Coral Sea, 17°7’ S, 148°E, depth 500 m, 00:30-05:50h, 24 Jun 1981; MNHN 1996-0464, 1 ex., male 413 mm TL, Southwestern Pacific, Coral Sea, New Caledonia, 17,5° S, 167,5° E, depth 1010 m, cc327; MNHN 1996-0465, 1 ex., male 409 mm TL, Southwestern Pacific, Coral Sea, New Caledonia, 17,5° S, 167,5° E, depth 1010 m, p27472; MNHN 1997-3574, 1 ex., female 480 mm TL, Southwestern Pacific, Coral Sea, New Caledonia, 24°48’00” S, 170°07’01” E, Campagne Halipro 2, bt21, 1996; MNHN 1997-3576, 1 ex., male 388 mm TL, Southwestern Pacific, Coral Sea, New Caledonia, 17,5° S, 167,5° E, Campagne Mola 3; MNHN 1997-3578, 1 ex., male 178 mm TL, Southwestern Pacific, Coral Sea, New Caledonia, 17,5° S, 167,5° E, Campagne Mola 3; MNHN 1997-3579, 1 ex., male 172 mm TL, Southwestern Pacific, Coral Sea, New Caledonia, 17,5° S, 167,5° E, Campagne Mola 2; MNHN 1997-3580, 1 ex., female 275 mm TL, Southwestern Pacific, Coral Sea, New Caledonia, 22,16° S, 165,83° E, depth 530-540 m, Campagne Diaphus 7, TL12; MNHN 1997-3581, 1 ex., male 382 mm TL, Southwestern Pacific, Coral Sea, New Caledonia, 17,5° S, 167,5° E, Campagne Mola 3, fab25; NHM 1997.5.21.56, 1 ex., male 419 mm TL, Southwestern Pacific, 24° 21,02' S, 170° 1,02' W, depth 1140-1188 m;

Eastern Pacific
MCZ 1005, 1 ex., female 475 mm TL, Eastern Pacific, Galapagos Is., 2°34’ N, 92°6’ W, 2992 m, 05 Apr 1891; SIO 52-413, 1 ex., male 396 mm TL, Eastern Pacific, Galapagos Is., surface, 0° N, 100° W;

Southeastern Pacific
MNHN 1987-1306, 1 ex., male 385 mm TL, Southeastern Pacific, Polynesia, 22° S, 140° W; 1971; NMW 76230 (Holotype of *Leius ferox* Kner, 1864), 1 ex., female, 162 mm TL, Southeastern Pacific, Australia, Polynesian triangle, 1866; SIO 02-136, 1 ex., male 397 mm TL, Southeastern Pacific, 15°19.2’ S, 115°47.4’ W; SIO 69-345, 1 ex., female 467 mm TL, Southeastern Pacific, North of Easter Is., 25°48’ S, 108°47.5’ W, depth 0-2000 m; SIO 73-162, female 332 mm TL, Southeastern Pacific, French Polynesia, 24°56.6’ S, 155°14.7’ W, depth 1000 mwo; USNM 190035, 1 ex., male 365 mm TL, Southeastern Pacific, 2°54’ S, 113°8’ W; USNM 190036, 1 ex., male 163.71 mm TL, Southeastern Pacific, Polynesia, 9°32’30” S, 139°51’ W; USNM 190037, 1 ex., female 190.27 mm TL, Southeastern Pacific, Polynesia, 6°26’ S, 139°52’ W; USNM 190038, 1 ex., female 250 mm TL, Southeastern Pacific, Polynesia, 4°32’ S, 142°49’ W; USNM 190040, 1 ex., female 170 mm TL, Southeastern Pacific, Polynesia, 9°33’ S, 139°49’30” W; USNM 190041, 1 ex., male 226 mm TL, 9°34’ S, 139°52’ W, Southeastern Pacific, Marquesas Is., 9°34’ S, 139°52’ W; USNM 190042, 1 ex., male 178 mm TL, 9°34’ S, 139°52’ W Southeastern Pacific, Polynesia, 11°22’ S, 139°27’ W; USNM 190043, 1 ex., female 179.84 mm TL, 9°34’ S, 139°52’ W, Southeastern Pacific, Polynesia, 9°17’ S, 139°16’ W;

Northwestern Pacific
ASIZP 0059802, 1 ex., male 411 mm TL, Northwestern Pacific, Taiwan, 13 Oct 1998; FRIP 00573, 1 ex., female 299 mm TL, Northwestern Pacific, Taiwan; FRIP00573 (F33), 1 ex., male 421 mm TL, Northwestern Pacific, Taiwan; HUMZ 69173, 1 ex., female 372 mm TL, Northwestern Pacific, Japan, Chichijima, Ogasawara, 12.5° N, 158° E, Mar 1975; HUMZ 87120, 1 ex., female 447 mm TL, Northwestern Pacific, 12.5° N, 158° E, Hokusei-maru vessel, 24 Jan 1980; HUMZ 89900, 1 ex., female 520 mm TL, Northwestern Pacific, 12.5° N, 158° E, Hokusei-maru vessel; HUMZ 124775, 1 ex., male 405 mm TL, Northwestern Pacific, 10.6° N, 175° E; HUMZ 203771, 1 ex., male 450 mm TL, Northwestern Pacific, Japan, Ogasawara Is., 27° 8'59.32" N, 142°15'56.73" E; HUMZ 208882, 1 ex., male 224 mm TL, Northwestern Pacific, 12° N, 142° E, 14 Jun 2010; MCZ 1368S, 1 ex., female 463 mm TL, Northwestern Pacific, Japan, Sagami Bay, 35°7’ N, 139°22’6” E, Dec 1906; NMW 50132, 1 ex., male 361, Northwestern Pacific, Singapore, 1877; SCSFRI S07257 (Holotype of *Isistius labialis*), 1 ex., female 442 mm TL, Northwestern

Pacific, South China Sea, 18°41’-19°32’ N, 112°31’-113°57’ E, depth 520 m, Oct 1980; SIO 80-176,1 ex., male 382 mm TL, Northwestern Pacific, Taiwan, 28°07.5’ N, 146°11’ E, depth 3000 mwo; UF 79884, 1 ex., male, Northwestern Pacific, Papua-New-Guinea; UW 021822, 1 ex., female 394 mm TL, Northwestern Pacific, 42°1’0.12” N, 158°1’ W, 9 Oct 1989; UW 047600, 1 ex., male 490 mm TL, Northwestern Pacific, Japan, 39°46’60” N, 160°55’ E, 1 Aug 1991;

Northeastern Pacific

ANSP 111459, 1 ex., female 322 mm TL, Northeastern Pacific, Hawaii, Honolulu, Jul 1919; BPBM 5559, 1 ex., ? 280 mm TL, Northeastern Pacific, Hawaii, Oahu, Waikiki, 19 Oct 1966; BPBM 24959, 1 ex., female 255 mm TL, Northeastern Pacific, Hawaii, off Kailua Kona, 0-308 m, 19 Ago 1964; LACM 46046-1, 1 ex., male 325 mm TL, Northeastern Pacific, Hawaii, 10 Sep 1785; SIO 73-157, 1 ex., male 412 mm TL, Northeastern Pacific, Hawaii, 28°20.3’ N, 155°07.2’ W, depth 3000 mwo; SIO 73-413, 2 ex., males 403 e 423 mm TL, Northeastern Pacific, Hawaii, 23°14’ N, 152°44’ W; SIO 78-183, 1 ex., male 393 mm TL, Northeastern Pacific, 29°26.5’ N, 119°44’ W; USNM 190033, 1 ex., 228 mm TL, Northeastern Pacific, Hawaii, 17°29.30’ N, 157°05’ W; USNM 215947, 1 ex., male 364 mm TL, Northeastern Pacific, Hawaii, 21°24’54” N, 158°24’54” W; USNM 215948, C&S, Northeastern Pacific, Hawaii, 21°15’ N 158°15’ W; USNM 418822, 1 ex., female 192 mm TL, Northeastern Pacific, Hawaii, 20°58’48” N, 158°28’54” W; USNM 418823, 1 ex., male 195 mm TL, Northeastern Pacific, Hawaii, 21° 22'24" N, 158° 14'36" W; USNM 418838, 1 ex., female 250 mm TL, Northeastern Pacific, Hawaii, 21°59’36” N, 158°27’18” W; UW 021809, 1 ex., male 403 mm TL, Northeastern Pacific, 40°7’0.12” N, 157°15’ W, 8 Oct 1989; UW 021895, 1 ex., female 466 mm TL, Northeastern Pacific, 37°22’0.12” N, 170°31’0.1” W, 28 Aug 1989;

Central Pacific

BPBM 3504, 1 ex., male 400 mm TL; BPBM 24471, 1 ex., female 363 mm TL, Central Pacific, 3°32’ N, 144°59’ W, depth 50 m, 22 May 1969; BPBM 24490, 2 ex., male 220 e 260 mm TL, Central Pacific, 1° N, 144°50’ W, depth 50 m, 25 May 1969; BPBM 24500, 1 ex., female 266 mm TL, Central Pacific, 0° N, 145° W, depth 50 m, 25 Jul 1969; BPBM 24501, 1 ex., female 332 mm TL, Central Pacific, 0° N, 145° W, depth 50 m, 26 Jul 1969; BPBM 24502, 2 ex., female 364 e 402 mm TL, Central Pacific, 0° N, 145° W, depth 20-100 m, 29 Jul 1969; BPBM 24506, 1 ex., male 350 mm TL, Central Pacific, 3°30’ S, 145° W, depth 75 m, 3 Aug 1969; BPBM 24538, 2 ex., male 165 e 230 mm TL, Central Pacific, 3°29’ N, 144°54’ W, depth 50 m, 30 Oct 1969; BPBM 24543,1 ex., female 211 mm TL, Central Pacific, 03°30’ S, 145° W, depth 20 m, 4 Nov 1969; BPBM 24544, 1 ex., female 227 mm TL, , Central Pacific, 3°11’ S, 145°1’ W, depth 80 m, 6 Nov 1969; BPBM 24545, 4 ex., male and female 211-360 mm TL, Central Pacific, 0°10’ N, 144°36’ W, depth 50 m, 9 Nov 1963; BPBM 24548, 1 ex., ? 240 mm TL, Central Pacific, 0°03’ N, 144°31’W, depth 50 m, 11 Nov 1969; BPBM 24549, 2 ex., male 272 e 217 mm TL, Central Pacific, 0° N, 144°44’ W, depth 50 m, 13 Nov 1969; BPBM 25284, 1 ex., female 204 mm TL, Central Pacific, 04°05’ S, 167°51’ W, depth 120-135 m, 14 Feb 1966; BPBM 26281, 1 ex., female 240 mm TL, Central Pacific, 7°52’ S, 135°03’ W, depth 0-200 m, 21 Aug 1956; BPBM 26909, 1 ex., ? 249 mm TL, Central Pacific, 0°44’ S, 149°46’ W, depth 320 feet, 2 Nov 1958; LACM 46044-1, 1 ex., male 215 mm TL, Central Pacific, 5° N, 145° W; LACM 46047-1, 1 ex., male 191 mm TL, Central Pacific, 0° N 145° W, 9 Nov 1969; LACM 46048-1, male 161 mm TL, Central Pacific, Polynesia, 4°25’

S, 142°44’ W, 1 Dec 1960; LACM 55936-1, 1 ex., female 220 mm TL, Central Pacific, 0°30’ N, 25° W, 23 Feb 1963; MNHN 1996-0725, 1 ex., male 425 mm TL, Central Pacific, 0°1'59" N, 139°55'59" W, depth 700 m, Campagne Caride 5, 177, 1824; MNHN 1996-0726, 1 ex., male 377 mm TL, Central Pacific, 0° N, 139°52’59” W, depth 750 m, Campagne Caride 5, 166, 1969; MNHN 1996-0727, 1 ex., male 411 mm TL, Central Pacific, 0°01’59” S, 140°04’01” W, depth 510 m, Campagne Caride 5, 263, 1969; MNHN 1996-0728, 1 ex., male 405 mm TL, Central Pacific, 0°01’59” S, 140°04’01” W, depth 510 m, Campagne Caride 5, 263, 1969; MNHN 1996-0892, 1 ex., male 206 mm TL, Central Pacific, 9,9° S, 141,88° W, Campagne Caride 5; MNHN 1997-3577, 1 ex., female 266 mm TL, Central Pacific, 0° N, 140°52' W, depth 1180 m, Campagne Caride 3, 1969; MNHN 1997-3739, 1 ex., male ?, Central Pacific, 10° S, 140° W, Campagne Caride 3; USNM 164174, 1 ex., female 187 mm TL, Central Pacific, Line Is., 2°09’ N, 158°14’ W; USNM 190034, 1 ex., female 374 mm TL, Central Pacific, 0°5’ N, 159°51’ W; USNM 190039, 1 ex., male 344 mm TL, Central Pacific, Line Is., 3°56’ N, 150° W; USNM 221045, 1 ex., female 448 mm TL, Central Pacific, Line Is., 0°01’ S, 149°44’ W; ZMH 10215, 1 ex., female 209 mm TL, Central Pacific, 0° N, 146°05‘00” W, 1908;

Indian

MNHN 0000-1178 (Holotype of *Isistius brasiliensis* Quoy & Gaimard, 1824 (Séret, 1987) and *Scymnus unicolor* Valenciennes, 1839 (Valenciennes 1839)), 1 ex., female 471 mm TL, Indian Ocean, Reunion Is., 20° S, 55° E; NMW 60844, 1 ex., female 318 mm TL, Indian, Mauritius, 1887;

No Data

HUMZ 126957, 1 ex., female ? mm TL; HUMZ 126959, 1 ex., female ? mm TL, Hokuyo-maru vessel; HUMZ 126960, 1 ex., male 385 mm TL, Hokuyo-maru vessel; HUMZ 126961, 1 ex., female ? mm TL, Hokuyo-maru vessel; HUMZ 126962, 1 ex., female 475 mm TL, Hokuyo-maru vessel; HUMZ 177913, 1 ex., male 410 mm TL; NHM 1996.2.14.33, 1 ex., female 427 mm TL; NHM 1998.8.9.12113, 1 ex., male 372 mm TL; NHM 2000.2.24.13, 1 ex., female 376 mm TL; USNM 164173, 1 ex., male 167 mm TL; USNM 221043, female 463 mm TL; USNM 221044, 2 ex., female 380 mm TL e male 389 mm TL.

Família Dalatiidae Gill, 1893

Gênero *Isistius* Gill, 1864

1.2 *Isistius plutodus* Garrick & Springer, 1964

(Figure 17**)**

Synonymy

Isistius plutodus Garrick & Springer, 1964 (p. 679, original description, fig. 1A, and 2A and C.; type locality: off the coast of Alabama, Gulf of Mexico): Jones, 1971: 791 (feeding habit poorly known, might be similar to *Isistius brasiliensis*); Cadenat & Parin, 1975 (first Pacific Ocean record); Figueiredo, 1977: 9 (short mention); Blache, 1981: 105 (key), 109 (description); Compagno, 1981/2: 9, 10 (proportionately, the biggest teeth within living sharks); Compagno, 1984: 96 (diagnose, range and biology); Reif, 1985: 113 (pattern of photophores similar to *Dalatias licha* and *Isistius brasiliensis*); Gadig, 1994: 33 (bites at Fernando de Noronha), 43 (bites), 44 (South of Brazil), 45 (key), 47 (description); Jahn & Haedrich, 1987: 298

(comparative notes, distribution), 299 (morphometry), fig 47 (plug of flesh in stomach); Sadowsky *et al.*, 1988; Howe & Springer, 1993: 16 (list of types at NMH), 11 (taxa); Mullin *et al.*, 1994: 467 (bites); Amorim *et al.*, 1998: 623, 629 (abundance in Santos); Lessa *et al.*, 1999: 28 (collected species), 55 (oceanic species), 57 (epipelagic at South/Southeastern Brazil); Kiraly *et al.*, 2000: 2 (deep sea sharks from ZEE, USA), 9 (habitat, biology and distribution at ZEE, USA; Gadig, 2001: 30 (Brazil), 84 (key), 86-87 (image, description, range, biology), 224 (pelagic), 232 (oceanic-pelagic), 233 (mesopelagic), 239 (Southeast, South); Soto, 2001a: 66 (systematic checklist), 93, 94 (records, material in Brazil); Soto & Mincarone, 2001: 23 (same feeding strategy as the other Dalatiidae); Pérez-Zayas *et al.*, 2002: 308 (no record of bites in marine mammals), 309 (shape of bite); Moore *et al.*, 2003: 388 (distribution and biogeography may be inferred by bites in swordfishes); Zidowitz, 2003: (biology and comparison with *I. brasiliensis*); Makino, *et al.*, 2004: 169 (suspects for biting); Soto & Mincarone, 2004: 7 (taxonomic list), 70 (one lot); Zidowitz *et al.*, 2004 (primeiro registro da espécie no Atlântico Nordeste); Compagno *et al.*, 2005a: plate 14 (distribution, description, drawing), 128, 129 (drawings of specimen and teeth, description, distribution, biology); Kyne *et al.*, 2005: 321 (new reports); DINARA/FAO, 2006: 34 (Atlantic: Brazil, Mexico), 45 (common names in each country); George & Zidowitz, 2006: 76 (AT (südl. Teil), deepsea); Kyne *et al.*, 2006: 15 (no significant threat); Yearsley *et al.*, 2006: 16 (bigtooth cookiecutter shark); Kyne & Simpfendorfer, 2007: 9 (vertical migration); Silva-Jr *et al.*, 2007: 509 (bites of *I. brasiliensis*); Souto *et al.*, 2007: 22 (bites); Compagno, 2008: 19 (pelagic diversity); Renner & Bell, 2008: 102 (possible bite); Bornatowski *et al.*, 2009: 2 (sharks of Paraná-coast), south-western Atlantic); Camhi *et al.*, 2009: 9, 44, 75 (pelagic); Souto *et al.*, 2009: 2 (bites); Largacha *et al.*, 2010: 1 (19 dentes inferiores e maiores que em *Isistius brasiliensis* e 29 dentes superiores); Castro, 2011: 140 (porrly-known species within the genus), 141 (key to species), 151-152 (identification, range, drawings of specimen and teeth, picture of dermal denticles); Dwyer & Visser, 2011: 111 (wide range), 112, 113 (bite); Claes *et al.*, 2012: 1691 (known by ten specimens); Kyne *et al.*, 2012: 40 (least concern), 142 (red list of sharks, rays, and chimaeras from North and Central America, and Caribbean); Musick *et al.*, 2012: 58 (widely distributed, deeper than *I. brasiliensis*), 65 (oceanic, pelagic, caught in 3 FAO regions); Wenzel & Suárez, 2012 (Cape Verde); Ebert & Stehmann, 2013: 126 (description), 131 (drawing); Ebert *et al.*, 2013a: 166, 167, 171 (destribuion, description, drawings); White & Last, 2013: 236 (different from *I. brasiliensis* and *I. labialis*); Dulvy *et al.*, 2014: 8 (species of least concern); Rosa & Gadig, 2014: 93 (Brazilian marine chondrichthyans);

Isistius plotudus: Falcón-Matos, *et al.*, 2003: 164 (bites);

Isistius plutodon: Wetherbee *et al.*, 2012: 241 (unusual tooth and jaw morphology).

Holotype. USNM 188386 (holotype), female 416 mm TL, Western Atlantic, Gulf of Mexico, Mississippi delta, 28°58’ N, 88°18’ W, 545-445 fms, Oct 27, 1960. (Figure 4)

Diagnosis. A species of *Isistius* differentiated from its only congener, *I. brasiliensis*, by the following characters: a shorter and less rounded snout (*vs.* longer and more rounded snout in *I. brasiliensis*); preorbital, prenasal and pré-oral lengths proportionately smaller than in *I. brasiliensis* (10.62%, 4.40% and 22.22% *vs.* 15.56%, 6.29% and 32.47% of head length); interorbital distance 17.33% of head length (*vs.* 25.53% in *I. brasiliensis*); interdorsal space almost half the size than in *I brasiliensis* (5.64% *vs.* 9.13%); second dorsal fin higher than the first one (*vs.* second dorsal fin almost the same height as the first one in *I. brasiliensis*); lower symphyseal teeth height is approximately 1.5 bigger (2.08% *vs.* 1.41%), as well as base length

(1.08% *vs.* 0.62% in *I. brasiliensis*); lower symphyseal tooth the same height as adjacent teeth in *I. plutodus*, whereas it is, approximately, 5% lower than the adjacent teeth in *I. brasiliensis*; approximate teeth formula for upper/lower teeth is 12+12/9+1+9 (*vs.* 15+15/13+1+13), lower teeth proportionally greater, 6 times greater than upper teeth (*vs.* 3 in *I. brasiliensis*). Gum at the mouth straight and lateraly long (*vs.* wavy and lateraly short in *I. brasiliensis*); upper postventral margin of caudal fin greater than lower postventral margin (*vs.* upper margin smaller than lower in *I. brasiliensis*). General body color in *I. plutodus* is a darker brown than *I. brasiliensis*; ventral dark collar proportionately bigger in *I. plutodus* (posterior end at the level of pectoral fin insertion) than in *I. brasiliensis* (posterior end at the level of pectoral fin origin). Morphology and proportions of neurocranium also differs between both species (Table 5): neurocranium of *I. plutodus* has a wider nasal capsule than *I. brasiliensis* (11.74% *vs.* 10.25%), as well as greater distance between nasal apertures, and length of postorbital process (6.13% *vs.* 4.81%). Relative to nasobasal length, *I. plutodus* has the same proportionately larger measurements cited above, as well as greater length of nasal capsule, width of nasal aperture, and distance from dorsal edge of anterior fontanel to base of medial rostral cartilage (15.42% *vs.* 14.08% in *I. brasiliensis*).

Description

Morphometric characterization of this species at

Table 13, and meristic data, such as tooth and vertebrae counts at **Table 7** and Table 14, respectively.

1.2.1 External morphology

Trunk cylindrical and slender tapering toward pelvic and caudal fins origins. Predorsal length about 4.5 times caudal fin length. Caudal peduncle without lateral ridges and width is 0.8 times the height. Lateral outline of head rectangular, being conical anteriorly to mouth. Its dorsal profile is parallel to the ventral one, slopping a little toward the bulbous, rounded tip of snout. Eyes large (20.6% of head length), rounded, and with a posterior angle. Preorbital length short, 11.4% of head length; interorbital space 0.82 times eye length Spiracle large (10.3% of HDL), dorsal, behind the eye, a little oblique (inner portion directed a little posteriorly), with a flap in its anterior portion; prespiracular length 3.74 times the spiracle length. Their shape is oval, with the largest width being transverse to the body axis. Gill slits very small (0.86-0.66% of TL), the first bigger than the fifth, well behind the eye and right in front of pectoral fin origin.

Nostrils anterior at head, slightly ventral; anterior portion rounded, with a short process, and an elongated posterior portion, inclined to the central axis of the body, and lack of barbels. Internarial length 1.42 times prenarial length. Mouth wide, transverse (7.4% of TL), with lateral skin folds and deep grooves (21.6% of head length); thick lower wrinkly lip. The *upper lip cover* (lpc) is a continuum with the lower ventral surface of the head anterior to mouth, and from its lateral and internal portion arises a thick and naked *lip fold* (lf). This fold is a short tissue at the corner of the mouth directed to the caudal region and is slightly turned toward the medial region of the lower jaw; its distal portion is located right posterior to the anterior portion of the lower lip, it is rounded and can be seen when the mouth is shut and the upper lip cover coats almost its whole length. Immediately dorsal to the upper lip cover there is a thick and straight *gum* (gm), and a *flesy sack for the upper labial cartilages* (slc) Dorsal to this lip fold there is a deep groove that extends from anteriorly to the labial cartilages until almost the posterior ending of the lower jaw. From the corner of the mouth to the posterior region, it is called *posterior mouth groove* (pmg) and is so long that it almost reach the ventral collar. At the corner of the mouth it is named *deep oral pocket* (opk), and this portion is immediately dorsal to the lip fold. Anterior to the corner of the mouth, there is a *preoral pouch* (prop) that is dorsal to the labial cartilages joint and the upper labial cartilage (Figure 18) (Shirai & Nakaya, 1992).

Pectoral fins originating immediately posterior to fifth gill slits. The fins terminate abruptly; their lengths 10.4% of predorsal body length. Anterior margins straight and almost parallel to body axis, and posterior margins almost perpendicular to body axis, with corners a little curved. Inner margins slightly oblique directing toward the ventral side at their most posterior portion. Pectoral base 2.9 times the first gill slit. Dorsal fins without spines. First dorsal very small and obliquely inclined rearward. The middle of its base at the origin of pelvic fins, but very posterior to tip of pectorals. Origin of first dorsal at about 3/4 of precaudal body length. Base length 1.93 times the fin’s height and about 21.6% of head length. Posterior edge straight, forming a triangle with the anterior margin, and the free lower tip forms an acute angle. Second dorsal fin slightly higher and longer than the first. Second dorsal base length 1.48 times its height, and the relations of the second dorsal with the first dorsal are: second dorsal base 1.11 times the first, and second dorsal height 1.45 times the first. Second dorsal fin origin above the end of pelvic fin free rear tip. Its posterior margin similar to first dorsal, although its free rear tip has a prolonged filament. Interspace between first and second dorsals slightly bigger (about 1.23 times) than the space between second dorsal and caudal fins.

Caudal fin is asymmetrical, and the posterior end of the vertebral column is slightly directed upwards. Dorsal margin 2.14 times the preventral one, the latter originating a little in advance of the upper. Terminal margin of dorsal caudal lobe is oblique: The dorsal margin posterior end is posterior to the subterminal margin end. The upper postventral margin is more than twice the lower postventral margin. Pelvic fins origins posterior to insertion of first dorsal fin, but anterior to its free rear tip. The pelvic fin length is 0.92 times the first dorsal length. Female pelvic fins with a smooth lateral angle and almost straight rear tip; in males, the lateral angle is even smaller and the fin is shorter, with claspers that, in adults, are a little longer than the end of the fin. In ventral view, the most distal portion of the clasper is white, and forms a triangle: along the internal portion it is straight, the outer portion is oblique is directed toward the inner side and the base in very oblique, forming a continuing line with the fin’s margin until the inner portion of the clasper tip. In dorsal view, the clasper groove originates from its most anterior portion, almost at the dorsal insertion of the fin on the body. The groove is somewhat straight and dorsal along the clasper axis and ends at the gland. The claspers of juveniles do not reach the rear tip of the pelvic fin.

1.2.2 Teeth

Teeth unicuspid and heterogeneous, smooth-edged; in average, 25 (13+12) upper teeth in a row, narrow, sharp-ended, a little oblique to the sides (left and right sides, respectively) and, usually, in three rows, being multiserial in function. The root of upper teeth is bilobated with a small sulcus dividing both lobes with rounded edges. (Figure 19). In average, 19 (9+1+9) lower teeth in a row, straight up triangular cusp and flat base in only one active row (the others are upside down, inside lower jaw) (Figure 20). Lower teeth much bigger than upper ones, and those toward angles of jaw are shorter and wider than those at symphysis, with only a trace of the triangular tip. Bases of lower teeth interlocked and form a single functional series, with each root completely exposed on the outer face and the inner side adheres closely to the lower jaw.

1.2.3 Coloration

Light or dark brown body with dorsal side slightly darker than the lower. Darker brown ventral collar around the branchial region that is the same color as the dorsal side, and is easily distinguished from the body. The anterior portion of darker collar is at the level of the first gill slit, and its posterior portion is posterior to the level of pectoral fin insertion. All fins brown, with white tips. Both dorsal and ventral endings of caudal fin have a dark brown area, even though the margins are white. Some specimens have variations on the coloration, like the absence of the dark collar, white fin tips and caudal fin darker brown area.

1.2.4 Luminescent markings

Photophores are black, small, annular elements that measure approximately 200µm (Figure 21). They are usually present on the ventral side of the body, from the tip of snout to the posterior end of vertebral column, including lips, ventro-lateral wall of eyes, ventral fins, and claspers in males (except their white tip). However, there is no photophore on the ventral dark collar. On the dorso-lateral side there might be photophores on the head, lateral of pectoral fins, dorsal and caudal fins. There is a wide variation of presence and position of photophores, ranging from complete absence of these structures to presence on both ventral and dorsal sides, and fins. The only conspicuous feature is its absence on ventral collar in every specimen.

1.2.5 Dermal denticles

Dermal denticles have no regular alignment, and are closely spaced, with exposed skin between them; small, very low, with no distinction between pedicel and blade. There is no acute medial cusp and medial ridges at the crown (Figure 22). Square shape at base and trapezium at height; almost symmetrical. Four inclined bases and one side (“crown”) on top, all concave and forming a quadrate depression. Bellow and between the four bases, there are four smaller ones, also concave. Bellow the denticles structure, at the base, many small concave indentations. Transversely truncate apically, quadrilateral in outline, but occasionally polygonal, with concave margins and rounded corners.

1.2.6 Geographic distribution

Known from the Southwestern (Southeast coast of Brazil), Southeastern (South Africa) (Matthias Stehmann, pers. comm.), Northwestern (Gulf of Mexico and Florida) (Mark Grace, pers. comm.), and Northeastern Atlantic; and Southwestern (Australia) and Northwestern Pacific (Japan) (Parin, 1975). Possibly circumglobal. Epi- to mesopelagic, 40-1,300 m of depth (**Figure 23**).

1.2.7 Etymology

The specific epithet *plutodus* comes from the Greek words *ploutos* (wealth, abundance) and *odous* (tooth), in reference to its very big lower teeth compared to body size.

1.2.8 Common names

English: largetooth cookiecutter shark; Portuguese: tubarão charuto dentuço; Spanish: tollo cigarro dentón; French: squalelet dentu; German: Großzahn-Zigarrenhai.

1.2.9 Remarks

Only eight specimens were observed, measured and photographed. However, this species is easily recognizable but its very large lower teeth and small interorbital distance when compared to *Isistius brasiliensis*. The holotype used by Garrick & Springer to describe the species has probably lost its coloration, as it has a caramel color and lacks the darker collar, as well another analyzed specimen from the Gulf of Mexico (Figure 24). However, from the original photograph used by those authors at the original description of *Isistius plutodus* (Figure 25), the dark collar is distinguishable. Therefore, the supposedly lack of collar is a misinterpretation of the coloration, since the body color of *I. plutodus* is darker than *I. brasiliensis*.

1.2.10 Analyzed material

(eight analyzed specimens)

<u>Southwestern Atlantic</u>

ZUEC-PIS 8332, female, 329 mm TL, Rio Grande do Sul coast, Brazil, 30°30'S, 50°06'W, longline, 1300m depth, 17 Sep 1987;
ZUEC-PIS 8333, male, 333 mm TL, Eastern coast of Brazil, from Bahia to Rio Grande do Sul, 17°-35°S, 27°-52°W, longline.

<u>Northwestern Atlantic</u>
UF 232954, female ?? mm TL, Northwestern Atlantic, Biscayne Bay, 1976; USNM 188386 (Holotype), female 416 mm TL, Northwestern Atlantic, Gulf of Mexico, Mississippi Delta, 28°58’ N, 88°18’ W, depth 545-445 fms, 27 Oct 1960;

<u>Northeastern Atlantic</u>
ZMH 9368, 1 ex., female 426 mm TL, Northeastern Atlantic, 44°00,82' N, 28°31,37' W, 03 Aug 2000;

<u>Southwestern Pacific</u>
AM I.43044-001, 1 ex., male 334 mm TL, Southwestern Pacific, Australia, Coral Sea, 14°17'31" S, 151°21'10" E, 1995; AM I.28924-001, 1 ex., female ?? mm TL, Southwestern Pacific, Australia, New South Wales, off Newcastle, 33° S, 152° E, 1988;

<u>Northwestern Pacific</u>
HUMZ, 1 ex., male 330 mm TL, Northwestern Pacific, off Ogasawara, 29° N, 141°55’ E, depth 40-780 m, 19 Dez 2010.

VI. Chapter 2: Other Dalatiidae genera

1. *Dalatias* Rafinesque, 1810

1.1. *Dalatias licha* (Bonnaterre, 1788)

1.1.1 Definition

Body fusiform, moderately elongate, snout short, subconical end obtusely rounded. Head 21.4% of total length, thick and fleshy lips, spiracles almost 2% of TL, eyes moderate, about twice (48% TL) as long as snout. Spiracle on dorsal side of head little above level of eye, semilunate, slightly shorter than horizontal diameter of eye. Interdorsal space 20% TL, two spineless dorsal fins with similar shapes and sizes: the origin of the first immediately posterior to the vertical line of pectoral fin free rear end, and the origin of the second dorsal at the line of pelvic fin. Caudal fin very asymmetric with ventral caudal lobe almost absent (Figure 26). Vertebral counts on Table 14: monospondylous vertebra varying from 33 to 40 and diplospondylous from 28 to 36 (Figure 27).

1.1.2 Teeth

Teeth unicuspid and heterogeneous, smooth-edged; upper teeth in a row, narrow, sharp-ended, a little oblique to the sides (left and right sides, respectively) and, usually, in three rows, being multiserial in function (Figure 28). Lower teeth in, usually, two rows, a little inclined to the lateral triangular cusp and flat base. Lower teeth much bigger than upper ones and cusp serrated. Bases of lower teeth interlocked and form a single functional series, with each root completely exposed on the outer face and the inner side adheres closely to the lower jaw.

1.1.3 Coloration

Uniform grey color or dark brown at the body; fins a little darker with white tips. Lips paler than body (Figure 29).

1.1.4 Dermal denticles

Dermal denticles aligned toward to posterior end of the body, with no differences between dorsal, ventral, caudal areas. Relatively wide interspace between each denticle, which are divided into two regions not clearly differentiated: denticles crown

(DCR) and base (BAS) (Figure 30). Large base, and crown with a pointy distal portion, almost parallel to the base. The base has four corners, in a star-like shape. From it arises the crown with four oblique and concave sides. The upper portion, seen from above, is rhomboidal, with one corner much longer than the others. Along the axis that runs from one to corner to the longest one, there is an elevated line. The four sides are elevated on their borders and, between them and the middle line there are two concave areas.

1.1.5 Geographic distribution of analyzed specimens

Analyzed specimens of the species *Dalatias licha* occur on Gulf of Mexico and Mediterranean Sea; Southwestern Indian Ocean (South of Madagascar); Western Pacific Ocean (Taiwan, South and Southeastern Australia), being the holotype and paratype the ones collected on South Australia (Figure 31).

1.1.6 Analyzed material

(32 analyzed specimens)

Northwestern Atlantic

USNM 157844, 1 ex., female 370 mm TL, Northwestern Atlantic, Gulf of Mexico, 29°11’ N, 88°03’ W;

Northeastern Atlantic

AMNH 1217, 1 ex., ? embryo 143 mm TL, Northeastern Atlantic, Mediterranean Sea, Italy; MCZ 910, 1 ex., female 370 mm TL, Northeastern Atlantic, Mediterranean Sea, France, Jul 1885; MCZ 949, 1 ex., female 422 mm TL, Northeastern Atlantic, Mediterranean Sea, France, Jul 1886; MCZ 966, 1 ex., female embryo 234 mm TL, Northeastern Atlantic, Mediterranean Sea, Sicily, 37°59’ N, 12°25’ E, Jun 1890; UF 42106, 1 ex., male 358 mm TL, Northeastern Atlantic, Mediterranean Sea, Dec 1984;

Southwestern Pacific

AMS E.3702 (Holotype), 1 ex., male 1160 mm TL, Southwestern Pacific, Australia, South Australia, Great Australian Bight, 127°-129° E; AMS E.12876 (Paratype), 1 ex., male 496 mm TL, Great Australian Bight, Southwestern Pacific, Australia, 32° S, 127° E, Jun 1913; AMS I.15975-018, 1 ex., female 560 mm TL, Southwestern Pacific, Australia, New South Wales, 35 miles SE of Newcastle, 33°10'58.80" S, 152°22'58.80" E, 29 Apr 1971; AMS I.15990-009, 1 ex., female 560 mm TL, Southwestern Pacific, Australia, New South Wales, 30 miles NE of Batemans, 35°32'60.00" S, 150°42'57.60" E, 08 Jul 1971; AMS I.16596-007, 1 ex., male 455 mm TL, Southwestern Pacific, Australia, New South Wales, off Sydney, 33°27' S, 152° 6'57.60" E, 10 Oct 1972; AMS I.18125-001, 8 ex., male 391 mm TL, female 393 e 400 mm TL, Southwestern Pacific, Australia, New South Wales, east of Broken Bay, 33°34'58.80" S, 151°30' E, 11 Dec 1974; AMS I.18764-007, 1 ex., male 470 mm TL, Southwestern Pacific, Australia, New South Wales, east of Kembla harbour, 34°32'60.00" S, 151°18' E, 29 May 1975; AMS I.19082-005, 1 ex., female 408 mm TL, Southwestern Pacific, Australia, New South Wales, NE of Crowdy Head, 9 Nov 1975; AMS I.19198-004, 1 ex., female 396 mm TL, Southwestern Pacific, Australia, New South Wales, east of Broken Bay, 33°51' S, 151°40'58.80" E, 04 May 1976; AMS I.43469-001, 1 ex., male 414 mm TL, Southwestern Pacific, Australia, Ulladulla, 35°21' S, 150°28'58.80" E, 12 Aug 1993;

Northwestern Pacific

UF 159698, 1 ex., female 373 mm TL, Northwestern Pacific, Taiwan, Tashi fish market, 25 May 2005; NMMBA not-catalogued, 1 ex., female 468 mm TL, Northwestern Pacific, Taiwan, Chang-b.h., 19 Mar 2012;

Southwestern Indian

CSIRO H5823-01, 1 ex., male 415 mm TL, Southwestern Indian, 33°13’ S, 44°34’ E, depth 970 m, 2000; HUMZ 74173, 1 ex., male 450 m TL, Southwestern Indian, 33°21.5’ S, 44°16.1’ E, depth 782 m, 20 Jun 1977; HUMZ 74586, 1 ex., male 445 mm TL, Southwestern Indian, 33°19’ S, 44°13’ E, depth 770 m, 04 Ago 1977; HUMZ 74605, 1 ex., female 472 cm TL, Southwestern Indian, 33°19’ S, 44°13’ E, depth 770 m, 04 Aug 1977; SAIAB 189435, 1 ex., male 575 mm TL, Southwestern Indian, Off Northern Madagascar, 12°28’ S, 48°10’ E, 27 Sep 2009;

No Data

AMNH 19446, 4 ex., female embryo 311 mm TL, 19 Out 2009; HUMZ M392, 1 ex., male 408 mm TL; NSMT P68123, 1 ex., male 484 mm TL.

2 *Squaliolus* Smith & Radcliffe in Smith, 1912

2.1 *Squaliolus laticaudus* Smith & Radcliffe in Smith, 1912

2.1.1 Definition

A very small cigar-shaped shark, with no more than 25 cm in total length, a long and pointed snout. First dorsal fin with a minute spine, which may be covered by skin in some specimens, at the level of the rear ending of pectoral fin. Second dorsal fin spineless, 50% bigger than the first one, and originating at the level of insertion of pelvic fin. Caudal fin nearly symmetrical (**Figure 32**). Vertebral counts on Table 14: monospondylous vertebra varying from 28 to 32 and diplospondylous from 25 to 33 (Figure 33)

2.1.2 Coloration

Body light to dark brown; darker spot at the dorsal part of the ceratotrichia of the pectoral fin; pelvic and dorsal fins are white and the caudal fin also has a white spot at its middle posterior end. Dense net of photophores covering the whole ventral region of the body and decreasing progressively to the dorsal side, where the photophores are sparser (

Figure 34).

2.1.3 Geographic distribution of analyzed specimens

Analyzed specimens of *Squaliolus laticaudus* were provinient from Western and Eastern North Atlantic Ocean (Gulf of Mexico, North of Amazon river mouth, and Northwestern of Africa); Eastern Indian Ocean (Northwestern of Australia); Western Pacific (Japan, Taiwan, and Phulippines), being the holotype and paratype from Philippines (Figure 35).

2.1.4 Analyzed material

(23 analyzed specimens)

<u>Northwestern Atlantic</u>
UF 176528, 1 ex., female 106,84 mm TL, Northwestern Atlantic, Gulf of Mexico, 27°53’23.4” N, 91°9’58.2” W, depth 274 m; USNM 187941, 1 ex., female 137,51 mm TL, Northwestern Atlantic, Gulf of Mexico, 28°59’ N, 88°37’ W; USNM 365693, 4 ex., Northwestern Atlantic, Gulf of Mexico, 29°11’ N, 87°55’ W, 21 Nov 1961;

<u>Northeastern Atlantic</u>
ANSP 106248, 1 ex., male 219 mm TL, Northeastern Atlantic, Madeira Is., Funchal, 1947;

<u>Southweastern Atlantic</u>
MNRJ 30199, 1 ex., male 216 mm TL, Southwestern Atlantic, Branzilian continental slope, REVIZEE D-463, 22 Jun 1999;

<u>Northwestern Pacific</u>
AMNH 239379, 1 ex., female 116,24 mm TL, Northwestern Pacific, Taiwan, Tungkan harbour, 22.27°58.3’ N, 120.26°38.6’ E; AMNH 242686, 1 ex., female 224,7 mm TL, Northwestern Pacific, Taiwan, Suao, Nan Fassao fish market, 23 Mar 2007; HUMZ 74973, 1 ex., female 254 mm TL, Northwestern Pacific, Kyushu-Palau ridge, 29 Jan 1978; HUMZ 74975, 1 ex., female 232 mm TL, Northwestern Pacific, Kyushu-Palau ridge, 11 Feb 1978; LACM 36021-1, 1 ex., female 125,56 mm TL, Northwestern Pacific, Philippines, Sulu Sea, 8°18.7’ N, 121°12’ E, 4 Jun 1975; LACM 36022-1, 1 ex., female 94,96 mm TL, Northwestern Pacific, Philippines, Sulu Sea, 3 Jun 1975; LACM 36279-2, 1 ex., female 106,31 mm TL, Northwestern Pacific, Japan, Suruga Bay, Mar Jun 1976; LACM 36279-7, 1 ex., female 127,24 mm TL, Northwestern Pacific, Japan, Suruga Bay, Mar Jun 1977; SIO 00-155, 1 ex., female 172,25 mm TL, Northwestern Pacific, Taiwan, 22°13’ N, 120°32’ E, depth 200-300 m; SIO 00-178, 1 ex., female 91,71 mm TL, Northwestern Pacific, Taiwan, 22°16’ N, 120°19’ E, depth 200 m; SIO 83-127, 3 exs., male 101,91 mm TL, male 120,67 mm TL, Northwestern Pacific, Japan, 35°15’ N, 139°10’ E; USNM 70259 (Holotype), 1 ex., male 142,98 mm TL, Northwestern Pacific, Philippines, Batangas Bay; USNM 76679 (Paratype), 1 ex., female 108,33 mm TL, Northwestern Pacific, Philippines; USNM 398487, 1 ex., Northwestern Pacific, Taiwan, Dong-gang fish market, 12 Nov 2009;

Southeastern Indian
CSIRO CA3355, 1 ex., female 144,54 mm TL, Southeastern Indian, Western Australia, SW of Rowley Shoals, 18°40’ S, 117°11’ E, depth 398 m, 1982; CSIRO H1215, 1 ex., male 158,57 mm TL, Southeastern Indian, Western Australia, 1988; CSIRO H1624-01, 1 ex., female 170,08 mm TL, Southeastern Indian, Western Australia, close to Rowley Shoals, 17°46’ S, 118°42’ E, depth 375 m, 1988;

No Data
HUMZ 95249, 1 ex., female 245 mm TL, ?, 05 Nov 1981.

2.2 *Squaliolus aliae* Teng, 1959

2.2.1 Definition

A very small cigar-shaped shark similar to *S. laticaudus,* not reaching more than 21 cm in total length, with a long and pointed snout. First dorsal fin with a minute spine, which may be covered by skin in some specimens, at the level of the rear ending of pectoral fin. Second dorsal fin spineless, 50% bigger than the first one, and originating at the level of insertion of pelvic fin. Caudal fin nearly symmetrical (Figure 36). Vertebral counts on Table 14: 29 monospondylous and 28 diplospondylous vertebra on the only radiographed specimen with no identification regarding site of collection (Figure 37)

2.2.2 Coloration

Body light to dark brown; darker spot at the dorsal part of the ceratotrichia of the pectoral fin; pelvic and dorsal fins are white and the caudal fin also has a white spot at its middle posterior end.

2.2.3 Dermal denticles

Dermal denticles with no regular alignment, sparse, with skin exposed between them; small, very low, with no distinction between pedicel and blade (Figure 38). No acute medial cusp and medial ridges at the crown. Not a perfect square shape at base and trapezium at height; a little asymmetrical, as each side is not exactly parallel to the opposite one. Four inclined bases and one side (“crown”) on top, all concave and forming a quadrate depression. Transversely truncate apically, quadrilateral in outline, but occasionally polygonal, with concave margins and acute corners.

2.2.4 Geographic distribution of analyzed specimens

Few specimens of *Squaliolus aliae* are known, but all from Western Pacific Ocean (Japan, Taiwan, and Northwestern Australia (Figure 35).

2.2.45 Remarks

Many specimens of *Squaliolus laticaudus* and *S. aliae* were analyzed, including the holotype and paratype of the former. However, no character concerning external morphology, morphometrics, and meristics were found to identify two different morphotypes. Many specimens of *Squaliolus laticaudus* and *S. aliae* were analyzed, including the holotype and paratype of the former. However, no characters from external morphology, morphometrics, and meristics were found to identify two different morphotypes. The validity of *S. aliae* is therefore questionable (*Squaliolus* is presently under revision; Petean & Carvalho, in prep.).

2.2.6 Analyzed material

(15 analyzed specimens)

Northwestern Pacific
BPBM 32767, 1 ex., female 100.93 mm TL, Northwestern Pacific, Japan, Honshu, Suruga Bay, 29 May 1979; BPBM 32768, 1 ex., male 110.01 mm TL, Northwestern Pacific, Japan, Honshu, Suruga Bay, 03 Jun 1979; CSIRO H6296-05, 1 ex., female 108.95 mm TL, Northwestern Pacific Taiwan, Tashi fish market; CSIRO H6297-04, 1 ex., female 124.81 mm TL, Northwestern Pacific Taiwan, Tashi fish market; CSIRO H7403-03, 1 ex., female 201.16 mm TL, Northwestern Pacific Taiwan, Kaohsiung; HUMZ 119285, 1 ex., female 179 mm TL , Northwestern Pacific, Japan; NMMBA 11102, 1 ex., female 84.59 mm TL, Northwestern Pacific, TongKang Fishmaket, 12 Jan 2011; NMMBA 15220, 1 ex., female 199.4 mm TL, Northwestern Pacific, Changbin, Taitung, 17 Nov 2011; USNM 399935, 1 ex., female 128.1 mm TL, Northwestern Pacific, Taiwan; USNM 402441, 2 ex., female 196 mm TL, and male 146 mm TL, Northwestern Pacific, Taiwan.

Southwestern Pacific
AMS I.20515-001, 1 ex., female 97 mm TL, Southwestern Pacific, Australia, East of Sydney; AMS I.30411-001, 1 ex., female 215 mm TL, Southwestern Pacific, Australia, East of Kiama; AMS I.42175-004, 1 ex., male 85 mm TL, Southwestern Pacific, Coral Sea; AMS I.43064-001, 1 ex., male 134 mm TL, Southwestern Pacific, Coral Sea;

Eastern Indian
CSIRO H6416-02, 1 ex., female 189.46 mm TL, Eastern Indian, Northwestern Australia, Ashmore Terrace

3. *Euprotomicrus* Gill, 1864

3.1 *Euprotomicrus bispinatus* (Quoy & Gaimard, 1824)

3.1.1 Definition

A cylindrical small shark, reaching maximum 26 cm, with a bulbous snout, small gill slits. First dorsal fin spineless, small and a little anterior to pelvic fin origin. Second dorsal fin also spineless, but 42% longer than the first. It originates at the level pelvic fin middle base length and extend until almost the caudal fin origin. Caudal fin nearly symmetrical (Figure 39). Vertebral counts on Table 14: monospondylous vertebra varying from 31 to 33 and diplospondylous from 24 to 32 (Figure 40)

3.1.2 Coloration

Body light to dark brown. Great amount of photophores, making the specimen darker (Figure 42). Bases of pectoral fins the same color as the body, but the skin over the ceratotrichia has a darker spot at the most dorsal part, which becomes bigger towards the tip of the fins, while the rest of the fin is white. This pattern is not seen at the other fins, which are white, except at the base. The other exception is the caudal fin that has a white spot at the middle of its posterior end.

3.1.3 Dermal denticles

Dermal denticles with no regular alignment, closely spaced, with skin exposed between them; small, very low, with no distinction between pedicel and blade. No acute medial cusp and medial ridges at the crown (Figure 41). Square shape at base and trapezium at height; almost symmetrical. Four inclined bases and one side (“crown”) on top, all concave and forming a quadrate depression. Bellow and between the four bases, there are four smaller ones, also concave. Bellow the denticles structure, at the base, many small concave indentations. Transversely truncate apically, quadrilateral in outline, but occasionally polygonal, with concave margins and rounded corners.

3.1.4 Geographic distribution of analyzed specimens

Analyzed specimens of *Euprotomicrus bispinatus* were from wide range of sites: South Atlantic, Indian (western, north and eastern), and Pacific (north, south, and eastern), being the holotype from Mauritius, Indian (Figure 43).

3.1.5 Analyzed material

(31 analyzed specimens)

South Atlantic
LACM 55938-1, male 207 mm TL, South Atlantic, 35°18’ S, 18°39’ W, 16 Apr 1971;

Southeastern Atlantic
LACM 55939-1, female, Southeastern Atlantic, 15°59’ S, 2°2’ E, 31 May 1971;

Southwestern Pacific
MCZ 41717, male 97 mm TL, Southwestern Pacific, Fiji, 18°21’ S, 178°21’ E, 20 Nov 1928; SIO 76-237, male 223 mm TL, Southwestern Pacific, New Zealand, 37°48.2’ S, 175°46.7’ W, surface;

Southeastern Pacific
MCZ 45900, male 204.4 mm TL, Southeastern Pacific, 33°48’ S, 90°17’ W, surface, 19 Jan 1966; SIO 58-309, male 159.44 mm TL, Southeastern Pacific, 14°17’ S, 108°52’ W, surface; SIO 72-4, male 130.15 mm TL, Southeastern Pacific, 13°08’ S, 122°19’ W, surface; SIO 76-119, male 205.02 mm TL, Southeastern Pacific, French Polynesia, 27°59.6’ S, 155°02’ W, surface; SIO 76-235, male 208.82 mm TL, Southeastern Pacific, French Polynesia, 24°25.8’ S, 154°57.5’ W, surface; SIO 76-236, male 189.11 mm TL, Southeastern Pacific, French Polynesia, 25°15’ S, 154°59.8’ W, surface; USNM 190032, male 111 mm TL, Southeastern Pacific, 13°38’ S, 110°34’ W.;

Northeastern Pacific
BPBM 33481, male 154.97 mm TL, Northeastern Pacific, Hawaii, 28 Aug 1987; BPBM 40404, female 257 mm TL, Northeastern Pacific, off California, 85 miles SW of Long Beach; BPBM 40983 (2 specimens), male 150.82 mm TL, female 256 mm TL, Northeastern Pacific, Hawaii, surface, 27 Apr 2009; BPBM 25281, Northeastern Pacific, Hawaii; CAS 20431, female 225 mm TL, Northeastern Pacific, off California, 19 Nov 1948; LACM 55941-1, male 223 mm TL, Northeastern Pacific, Mexico, 30°15’ N, 116°27’ W; LACM 6988-1, female 204 mm TL, Northeastern Pacific, 35°08’ N, 137°28’ W, 20 May 1961; LACM 6989-1, female 224 mm TL, Northeastern Pacific, 35°13’ N, 130°36’ W, 02 Jun 1961; LACM 6990-1, female 266 mm TL, Northeastern Pacific, 33°11’ N, 131°24’ W, 05 Jun 1965; SIO 66-111, male 206.1 mm TL, Northeastern Pacific, 29°51’ N, 175° W, surface; SIO 68-432, male 169.28 mm TL, Northeastern Pacific, Hawaii, 22° N, 155°50’ W, surface; SIO 98-173 (2 specimens), male 196.2 mm TL, female 235 mm TL, Northeastern Pacific, 29°15’ N, 144°43’ W, surface; USNM 164176, female 161 mm TL, Northeastern Pacific, 18°24’ N, 175°12’ W; UNSM 190031, female 240 mm TL, Northeastern Pacific, Midway Island, 32°46’ N, 176°42’ W; UW 110386, male 133.56 mm TL, Northeastern Pacific, Hawaii, 23°46’60” N, 163°41’60” W, 11 Nov 2002;

Indian
MNHN 0000-1216 (Holotype), female 196 mm TL, Indian, Mauritius, 20° S, 55° E; SIO 66-110, male 205 mm TL, Indian, Maldives, 1° S, 74° E, surface;

No Data

LACM 46049-1, female 205 mm TL, 01 Jul 1979.

4. *Heteroscymnoides* Fowler, 1934

4.1 *Heteroscymnoides marleyi* Fowler, 1934

4.1.1 Definition

A small, short shark, that can reach up to 36 cm. Bulbous snout, long head (31% TL), and small gill slits. First dorsal fin originates at the level of pectoral fin insertion and second dorsal at the pelvic fin insertion; both fins with almost same length. Caudal fin near asymmetrical, with a subterminal notch (Figure 44). Vertebral counts on Table 14: 33 monospondylous and 33 diplospondylous vertebra on the holotype and only radiographed specimen (Figure 45).

4.1.2 Coloration

Light to dark brown color at the body and lighter fin tips.

4.1.3 Geographic distribution of known specimens

There are only three known specimens of *Heteroscymnoides marleyi*. The holotype is from Southwestern Indian Ocean (South Africa), and the other two individuals from South Eastern Atlantic and South Eastern Pacific Ocean (Figure 46).

4.1.4 Analyzed material

<u>Southwestern Indian</u>

ANSP 53046 (holotype), female 122.56 mm TL, Indian Ocean, South Africa, Natal, 01 Apr 1923.

5. *Mollisquama* Dolganov, 1984

5.1 *Mollisquama parini* Dolganov, 1984

5.1.1 Definition

Small, dark shark, with a blunt snout, and presence of a post-pectoral fin base luminous pocket. Interorbital distance 9% TL, and spiracle 6% of head length. First dorsal fin slightly anterior to pelvic fin origin, and second dosal posterior to the level of free rear margin of pelvic fin. Caudal fin asymmetrical, with the subterminal notch the same size as the upper margin of ventral lobe (**Figure 47**).

5.1.2 Coloration

Body dark grey; pectoral, pelvic and caudal fins with white tips; gray dorsal fins, as the rest of the body. White color at the region of gill slits.

5.1.3 Geographic distribution of known specimens

There are only two known specimens of *Mollisquama parini*. The holotype was collected at the Nazca Ridge, on Southeastern Pacific, and the other individual on the Gulf of Mexico (Figure 48).

5.1.4 Analyzed material

<u>Northwestern Atlantic</u>
TU 203676, male 145 mm TL, Northwestern Atlantic, Gulf of Mexico, 04 Feb 2010.

5. *Euprotomicroides* Hulley & Penrith, 1966

5.1 *Euprotomicroides zantedeschia* Hulley & Penrith, 1966

5.1.1 Definition

A small cigar-shaped shark with a short, blunt snout. Bigger gill slits, when compared to other Dalatiidae genera, which get bigger posteriorly, with the 5th gill slit more than twice the size of the 1st one. First dorsal fin insertion slightly posterior ot pectoral fin free rear margin, and second dorsal a little anterior to pelvic fin origin; second dorsal fin bigger than the first on, and the inner margin forms an extension. Asymmetrical caudal fin, with a subterminal notch (**Figure 49**).

5.1.2 Coloration

Body dark grey; pectoral, pelvic and caudal fins with white tips; gray dorsal fins, as the rest of the body.

5.1.3 Geographic distribution of known specimens

There are only two know specimens of *Euprotomicroides zantedeschia*, and its holotype is from Southeastern Atlantic Ocean (South Africa), while the other specimen was collected at Southwestern Atlantic, near Brazilian coast (Figure 50).

VII. Chapter 3: Morphology of *Isistius*

1. *Isistius brasiliensis*

Specimens of *Isistius brasiliensis* have 37-44 monospondylous, 18-24 precaudal diplospondylous and 9-23 postcaudal diplospondylous vertebrae. On radiographs the transition is observed between both kinds of vertebrae between the both dorsal fins (Figure 51).

<u>Skeleton</u>

<u>Neurocranium.</u> (Figure 52)

The neurocranium is chondrified and encloses the brain, olphactory bulbs, eyes, and auditory organs, besides forming the palate. In squalean sharks, the auditive region is large, wide, well chondrified and rounded. It is externally divided on four regions, from the most anterior to posterior: ethmoidal (rostrum and nasal capsules), orbital (orbits, basal plate, and cranial roof between them), otic (otic capsules, cranial roof and basal plate between them), and occipital (posterior end of neurocranium) (Compagno, 1988; Shirai, 1992a).

The ethmoidal region is the most anterior and it is where the *nasal capsule* (ns) and *rostral process* (rp) are. The rostral process is reduced as it is only a longitudinal cartilaginous elevation that is weakly prolonged forward the neurocranium; however it is a long a slender cartilage which posterior portion starts immediately anterior to the epiphyseal organ, and its height is slightly taller than the nasal capsule dorsal wall. The rostral process is a cartilage that is only connected to the neurocranium at its most anterior part, in between the nasal cavities, while its length is supported by connective tissue and Lorenzini ampullae.

The *prefrontal fontanel* (pff) is an anterior aperture to the *cranial cavity* (cav) and a tough and fibrous membrane covers it. It is located at the posterior extremity of the ethmoidal region and has a rhomboidal shape, with the posterior region being slightly more acute than the anterior one. The foramen of the *epiphyseal organ* (ep) is a perforation at the cranial roof, it is located posterior to the prefrontal fontanel, and it also has an oval shape, but it is slender and shorter than the pff. The *precerebral fossa* (pcf) opens immediately anterior to the prefrontal fontanel and it is occupied by a gelatinous mass. The nasal capsules laterally restrict this shallow concavity in shape of wedge, and the anterior edge (rostral process) expands anteriorly and supports the rostrum.

The nasal capsule protects dorsally the olfactory organs and from every side the nasal cavity. Each capsule is ventrally opened, with an anterolateral nasal aperture, where are the openings for inflow and outflow of water for the cavities in each olfactory organ. The olfactory cavity anterior wall is dorsally curved, forms the roof and joins to the preorbital wall, enclosing the posterior wall of the nasal capsule, and joins to the preorbital process and to the supraorbital crest, forming the orbit internal wall. The posterior wall of the nasal capsule has a ventro-lateral process that forms an acute curved tip.

Each nasal capsule has an irregular pore at its anteroventral region, at which is the *nasal cartilage* (nas). This is an anelar element that supports the nostril and the nasal lobes and it is not closed, as its most posterior portions afunilate and form pointed endings that do not meet. The right and left nasal capsules compose the ventral surface of the ethmoidal region with a space between them. This space, the internasal septum, develops and forms the *ectethmoidal chamber* (eec). The *subethmoidal crest* (ser) is a mid-ventrally elevated cartilage which posterior end is at the anterior one of the ventral edge of the interorbital wall. This crest reaches the rostrum and forms the *rostral keel* (rc). From the posterior portion of the nasal capsule's ventral side, arise two cartilaginous pieces from the subethmoidal crest that are directed latero-anteriorly, and closer to the nasal cartilages they change their path and direct towards the mid-length of subethmoidal crest. They meet their opposite unit at the subethmoidal crest and divide the ectethmoidal chamber into an anterior and a posterior portion.

The orbital region occupies more than one third of the neurocranium and encloses the eye and a structure for jaw suspesion. The *supraorbital crest* (soc) is a dorsal elevation of the neurocranium at its lateral edges above the eyes. At the medial side of these crests there are longitudinal grooves and their anterior region there are foramens, *preorbital canal* (poc), for the ramifications of the nerves *ophthalmicus superficialis* and *ophthalmicus profundus*. The *ethmoidal canal* (ec), through which pass the ramus *ophthalmicus superficialis* (of the *ethmoidal* nerve), is located anteriorly at the nasal capsule and laterally to the preorbital canal. Both are in the longitudinal grooves that border the supraorbital crest.

The *interorbital wall* (iow) supports many foramens for cranial nerves and blood vessels. The *optic foramen* (II) is located at the medial portion of this wall. The *prootic foramen* (V-VII: for the nerves *trigeminus* and *facialis*, except the ramus *hyomandibularis* of the *facialis*, which is located posteriorly to the lateral comissure) is located at the posterior border of the interorbital wall. The nerves *oculomotor* (III) and *trochlearis* (IV) have their own foramens that are behind and above the optic foramen at the interorbital wall, respectively. The foramen of the nerve *abducens* (VI) is right in front of the prootic one.

One efferent artery of the *pseudo-branchial* (psb) has a foramen together with the ramus *hyomandibularis* of the *facialis* right behind the lateral comissure. The optic peduncle is absent in *Isistius*. The medial portion of the interorbital wall is not chondrified and a resistant membrane encloses it. This is a fenestra of the cranial cavity and the optic nerve goes through.

The *lateral comissure* (com), at the posterior border of the orbital region externaly encloses one way of the jugular vein. The articular facet, a *groove for the orbital process* (gop) is located below and anteriorly to the prootic foramen. The *basal angle* (ba) is a transverse crest of the basicranium that supports the jaw medially and it is immediately behind the groove for the orbital process. Posteriorly to it, there is the *basitrabecular process* (btp) that is a lateral expansion of the suborbital área and supports an ascending process of the palatoquadrate and it is strongly expanded laterally and forms a wide palatine surface.

The otic and occipital regions are the whole posterior portion to the orbit. These two areas form a cranial capsule without a division line. At the posterior end of the supraotic region, between the otic capsules, there is the *endolymphatic fossa* (elf), which is an ovoid deep concavity. There are two paired perfurations at this concavity: a foramen for the *endolymphatic duct* (feld) and the *perilymphatic fenestra* (plf), but as the *endolymphatic fossa floor* is wide open both the duct and the fenestra go through it (feld + plf). The *opistotic process* (opp) is well developed and expanded dorso-laterally.

Immeditely posterior to the endolymphatic fossa, the neurocranium posterior wall is widely expanded and posteroventrally inclined. The *magnum foramen* (mag) is located at the medial portion of this wall. There is an articular facet below the magnum foramen, the basioccipital fovea, which is filled by the *occipital hemicentrum* (ohc). This hemicentrum is articulated to the first vertebral centrum;

axial articulation. Beside this articular facet, the *occipital condyle* (occ) is articulated to the basiventral process of the first vertebra (co-lateral articulation). The foramens of the nerves *glossopharyngeo* (IX) and *vagus* (X) open at the posterior wall of the neurocranium, being the first more lateral than the other; dorsally to the *vagus* there is a foramen one-third its size for a blood vessel.

There is a longitudinal groove, the *lateral auditive groove* (lag), at the otic lateral wall for the jugular vein and the *hyomandibularis* of the *facilais*. The *hyomandibular fossa* (hmf), at which the proximal end of the hyomandibula attaches to, is located at the posterior end od the otic lateral wall. The dorsi-posterior crest of the fossa is laterally expanded and ventrally forms the *postotic process* (potp).

The ventral side of the otic region is a wide and flat surface that forms the *palatine* (pal). At the anterior portion of the palatine there is a foramen for the *carotid artery* (fca).

Mandibular arch. (Figure 53)

It is composed by the palatoquadrate and mandibular. The first forms the upper jaw and is divided into two pieces of cartilage, the *palatine plate (*pap) and the *quadrate plate (qup).* Near the junction with the palatine plate, the quadrate plate supports the *orbital process* (op) dorsally for the orbital articulation. Its most external portion ventrally there is the ending of the upper teeth rows, and dorsally there is an *otic flange* (otf), which is an elevation at the cartilage. The external surface of the quadrate plate is depressed and forms a concavity for the *adductor mandibulae*. The articular facet for the jaw-joint at the posterior end of the ventral edge has a large *condyle* (pqd) and a small quadrate *concavity* (pqc). The palatine plate of the palatoquadrate supports the most upper teeth rows.

The *mandibular* (ma), Meckel’s cartilage, is much larger than both the palatine and quadrate cartilages together and supports the lower jaw. It is divided into right and left portions and each has a flap-like *accessory cartilage* (mfl) made of weakly calcified tissue, flexible and probably related to *Isistius* peculiar feeding habit (Shirai & Nakaya, 1992). Lower teeth rows occupy almost the whole mandible forming a semicircular teeth row, and the only free portions are the most lateral where it articulates with the quadrate plate. At the dorsi-posterior corner, a large *articular fossa* (mad) receives the large *quadrate condyle* (pqd). Immediately dorsal to it, a pronounced *mandibular knob* (mk) stands out, fitting into the small *quadrate (*pqc)

(Figure 54). A developed *ligamentous complex* (ljs) supports the mandibular knob and the hyoid arch. The mandibule bears a process at its ventroposterior edge, where there is an insertion for a thick ligament, the *ligamentum mandibulo-hyoideum* (lmh).

The labial cartilages support the upper lip and its corner with lower lip. They are composed of two *upper cartilages*, the *posterior* (plc) and the *anterior* (alc) (Figure 55), and a *lower* one (llc), which are connected to each other at the mouth corner.

Dorsal to the quadrate cartilage and lateral to the neurocranium, immediately posterior to the post-orbital process, there is a minute cartilage, the *spiracular* (spc) that supports the filaments of the spiracle. It is a flat cartilage with the shape similar to a rectangle positioned vertically on the head, and its dorsal portion is concave.

Hyoid arch. (Figure 53)

It supports the mandible posterointernally and is composed by the paired cartilages hyomandibula and ceratohyal, and the single basihyal cartilage. The *hyomandibula* (hm) is the dorsal element of the arch and joins with the neurocranium at the *hyomandibular fossa* (hmf) on the auditory capsule. It has a general rectangular box shape with depressions and protuberances; its longest length is transversal to body length, the second longest length is the one along the body axis and its thinner portion is its height, which is parallel to body height. In dorsal view, the upper portion of the hyomandibula has a depression at its mid-postero-medial region, and its medial and posterior corner is elevated. At this corner there is a minute cartilage, the *joint cartilage of hyomandibula* (jhm), which is a very small, flat and oval cartilage. The lateral elevation of the corner continues latero-intenally and reaches the medial and anterior corner. This wall at the middle of the hyomandibula is the one that is articulated with the neurocranium at the *hyomandibular fossa* (hmf) together with the joint cartilage of hyomandibula at the posterior corner. The latero-anterior region of the hyomandible articulates with the mandibular knob

The *ceratohyal* (ch) extends anteromedially and it is a very robust cartilage. Its dorsal portion is slightly rounded, and it articulates to the latero-posterior corner of the hyomandible (Figure 54) by the *ligamentum hyomandibulo-hyoideum* (lhc). Ventro-anteriorly to the ligament the ceratohyal is a cylinder for one fifth of its length and enlarges in a rectangle shape for two fifths of its length. At the rest of the ceratohyal length it is cylindrical and thinner than its previous shapes. Its distal ending is in a triangular form, and this is where it articulates with the basihyal, and its ventroposterior margin is expanded for the interhyoideus muscle. Immediately posterior to the ligamentum hyomandibulo-hyoideum there is another ligament that unites the lateral corner of mandibule together with the ceratohyal: *ligamentum mandibulo-hyoideum* (lmh). As these two tissues are sided it is tough to tear them apart and it resembles a unique ligament joining the latero-posterior corner of the hyomandible, the dorsi-posterior region of the ceratohyal and the lateral corner of the mandibule.

The *basihyal* (bh) is an unpaired element supporting the anterior portion of the tongue at a floor of the oral cavity. It is band-like shaped, very wide, and positioned transversally to body axis. It has two *large concavities* (cch), one at each posteroventral surface, for the joint with the ceratohyals.

The *gill rays* (gr), elongated radially and branching off, are supported by the ceratohyal. There are two origins for the gill rays at the postero-internal side of each ceratohyal, and they subdivide themselves in more than ten rays each. The *extrabranchial cartilage* (exh) on the hyoid arch is a ray-like element with a somewhat broad proximal end, supporting the dorsal and ventral margins of the hyoidean hemibranch (Figure 56).

<u>Branchial arches.</u> (Figure 57)

The branchial basket has five sets of branchial arches. From dorsal to ventral aach branchial arch is composed of the pharyngobranchial, epibranchial, ceratobranchial, hypobranchial, and basibranchial cartilages, these last ones are the only branchial cartilages which are not paired and are positioned in the mid-ventral portion of the branchial basket. The *pharyngobranchials* (pb) extend posterointernally with a tapering proximal ending lying over the pharynx. Their distal ends are attached to the ventral surface of vertebrae by ligamentous tissue. The pharyngobranchial of arch 5 is united with epibranchial 5, and this cartilage is also fused with pharyngobranchial 4 forming a *gill pickax* (gp) (Shirai, 1992a). The *epibranchial cartilages* (eb) are distally articulated with proximal ends of pharyngobranchials, and proximally articulated with the distal portion of the respective ceratobranchial.

The *ceratobranchials* (cb) are long, thick, and flat cartilages. They form the ventro-lateral wall of pharynx and carry gill filaments with epibranchials. The lateral first third of the *ceratobranchial 5* (cb5) is equal to the other four ceratobranchials:

straight, with both sides parallel to each other. However, the other two-thirds of the cb5 expands laterally and becomes wider until its distal portion, which has an acute angle. The antero-lateral side is slightly longer and forms the angle, while the medial-anterior side is shorter; the line connecting these two corners is parallel to body axis.

The *hypobranchials* (hb) form the basibranchial copula with basibranchials at the floor of the pharynx. However, there is just only one pair of cartilages at this postion and it cannot be named due to the unavailability of comparative material and literature. This pair of cartilages forms a “V”, which opening is directed toward the anterior portion of the body. They do not articulate with each other, as there are another single cartilages in between them. They are almost cylindrical, elongated, and their proximal end (at the middle of the branchial basket) is rounded and a little bigger than the rest of the cartilage, which sides are almost parallel to each other, but tapering a little towards the distal portion. They are supposed to be hypobranchial (?) cartilages.

The *basibranchials* (bb) are unpaired elements positioned over the heart region. There are two distiguinshable single cartilages posterior to what were called hypobranchials (?). The most anterior of these cartilages is shorter than the other. Its anterior portion is rounded and each corner articulates with the hypobranchials (?). It tapers towards its posterior part and it is truncated at its end. The second cartilage seems like a continuum with the previous one, as its anterior part has the same width as the previous posterior ending. It is longer than the first, tapers to the posterior portion of the branchial basket, and its ending is very thin and almost forms a pointy ending. Anterior to these two cartilages that were called basibranchials, and between both rounded portions of the hypobranchial (?) cartilages, there are two very small and poorly calcified cartilages. Both of them have a triangular shape, but the most anterior one is bigger than the other and it is pointed to the anterior portion of the body. The base of the other triangle is parallel to base of the first and it points toward the posterior portion of the body. Therefore, the second triangle points to the rounded part of the anterior portion of the truncated basibranchial. These two triangles, although being barely calcified and very small compared to the other branchial cartilages, are also called basibranchials, as they are single cartilages and positioned in the mid-ventral region of the branchial-basket.

Gill rays (gr) are slender cartilages supported by the epibranchial and ceratobranchial, and are present in all arches, except 5. *Gill rakers* are absent in all arches. The *extrabranchial cartilage* (exb) is present in all arches.

There are paired cartilages, called here *ventromedial branchial cartilages* (vmbc) that are ventral to the branchial basket and contact dorsally the ceratobranchials. These cartilages are very flattened, poorly calcified, and are in number of two. The most anterior one is a single cartilage, and the other three are fused to each other at their dorsal part, and then form three distinct pieces that run ventrally along the internal portion of the branchial arches. These cartilages separate the internal region of the branchial arches from the hypobranchial and jaw musculature. Therefore, it seems like they provide a support for this musculature, which is very robust in *Isistius*.

Dorsal fins. (Figure 59)

Composed by two separate unities, the anterior and posterior (first and second dorsal fins). Supported by *basal cartilage* (bad) and many *radials* (rds), which do not reach the margin of the fins (aplesodic style). No fin spine is present. The basal cartilage is separated from dorsal column, triangular shaped in both dorsal fins with the most acute portion anterior to the broad one, and deeply inserted in the body. The acute portion may have an upturn at its end. At its posterior-dorsal portion there is an elevation at the cartilage, which is usually at its the border. First dorsal with five to nine radials, second dorsal with nine to 12: all with different sizes and shapes. Usually, in the first dorsal, there are two to four small radials and one medium sized in between them; above this last one there is a radial with the shape of a slender half-moon, and a small radial at its anterior end. There might be a cartilage perpendicular to the fin axis and, when it is present, it is at the side of the first radial, and may be connected to it or not. The second dorsal fin also has one or two lateral cartilages, which are perpendicular to the fin's axis. There are one to four small radials next to the basal cartilages with one or two medium sized ones. Above these there is another medium sized radial, which supports the slender half-moon shaped radial at the most posterior portion of the fin. At the anterior end of this radial, there are one to three small cartilages along the fin's curvature. As it is seen in the first fin, the basal cartilage of the second fin also has an elevation at its posterior-dorsal end, as well as an upturn at its anterior end.

<u>Pectoral girdle and fins.</u> (Figure 60)

The pectoral girdle (scapulocoracoid) is an elongate cartilage that surrounds the body ventrally. At its middle portion there is an irregular process posteriorly directed, supporting the fins. The upper portion is the *scapula* (sc) that has the *scapular process* (scp) at its distal part.

A unique cartilage, scapulocoracoid, forms the pectoral girdle that is divided into an upper (scapula) and lower (coracoid) portions, the last one meets its opposite part at the most ventral region, and it is not possible to see their junction, as it is only one long cartilage. In ventral view, coracoid almost flat, and oblique: anterior portion more dorsal than posterior one. After the meeting of both sides of coracoid, which is very narrow, each part goes almost parallel to the other for a short length, then the angle between them increases and they direct to opposite sides at the most posterior portion, where they make a curve and form the scapula. This portion has a *foramen for the pectoral fin nerves* (fpn) and some indentations, where the pectoral fin and pectoral associated musculature attach to it. At the most distal part of the pectoral girdle there is the scapular process that is a portion of the cartilage that afunilates toward its end, directs posteriorly, and is seen at dorsal wall of the body, below the skin and sided by the epaxial musculature.

The pectoral fin skeleton is composed of the basal cartilages and many radials. In *Isistius*, there is only one basal, and it may be the fusion of the *propterygium* (pr), *mesopterygium* (ms), and *metapterygium* (mtx). This basal cartilage connects the distal cartilages of the fin, and the radials to the pectoral girdle. The basal supports, approximately, seven proximal radials, each with a distal radial. The *metapterygial axis* (mta) is a dorsi-posterior cartilaginous piece that is larger and shorter than the proximal radial immediately ventral to it. This cartilage supports, from its most ventral to dorsal side, three proximal radials with three distal ones, four single distal radials, and a proximal and a distal radials. Each radial is slender; from the most ventral to dorsal they get longer, and there might be intermediate radials in some specimens. In those, the distal radials are a disc on top of the intermediate ones. The number of proximal, intermediate and distal radials vary among different specimens.

<u>Pelvic girdle and fins.</u> (Figure 61)

The only cartilage that forms the pelvic girdle is the *puboischiadic bar* (pub) that is transverse to the body length. Each lateral posterior ending of this bar forms an articular facet for the pelvic fin. The *lateral prepelvic process* (lpp) is directed lateraly at the puboischiadic bar and forms a somewhat pointed projection just before the pelvic fin. At ventral view, on the latero-ventro-posterior region of the puboischiatic bar there is a depression in which sits the *foramen for pelvic fin nerves* (fvn).

The pelvic fin comprises the *pelvic basipterygium* (bpv), which is elongated anteroposteriorly, and many radials. Specimens usually have from eleven to thirteen *radials* (rds). The anteriormost element is the *anterior pelvic basal* (apv) and has almost a triangular shape. Its most apical portion is larger than the proximal and it is directed latero-posteriorly from both the basipterygium and the puboischiatic bar. It supports two or three distal radial pieces. The posteriormost radial, which is also enlarged, has a wide base and may be divided into two radial pieces that, in turn, might have a distal radial each. The basal radials are longer and have smaller ones at their distal end. Each pelvic radial is composed of an elongate proximal piece and one or two distal pieces, and these numbers vary in each specimen.

In males, the basipterygium supports clasper cartilages at its distal end. Males also have a differentiated medial radial, which is curved toward the clasper

Claspers. (**Figure 62**)

Nine cartilages form the clasper. In ventral view, from the most anterior region to the tip of the clasper, there is the only *intermediate segment* (b1) followed by the *axial* (ax), which extends at almost the end of the clasper, where it is less calcified, thinner and pointed, and is called *end-style* (g). At approximately the medium length of the axial cartilage it starts tapering toward the end-style, and its lateral part (external to the clasper) is oblique, while its medial part continues straight to the end. This is where the *ventral marginal cartilage* (rv) is, with its most anterior portion pointed, getting larger at its posterior end. It is a flattened cartilage and is very attached to the axial. Posterior to the ventral marginal cartilage there is the *ventral terminal cartilage* (tv), which is almost rectangular and its medial portion is sided with the end-style, and both end at the same line. At the postero-lateral region of the ventral marginal cartilage and between it and the ventral terminal cartilage there is the *accessory terminal cartilage* (t3), which is some sort of spine, being stout and short. Dorsal to the tv, t3 and half of the lengths of ax and rv there is the *dorsal marginal cartilage* (rd), which is seen in ventral view also forming the most posterior tip of the gland.

At the dorsal view, above the intermediate segment and connecting it to the axial cartilage, there is the *beta cartilage* (β), which reinforces the joint of clasper shaft to pelvic basipterygium (Compagno, 1979). It is a rectangular cartilage and a little curved at its intermediate portion toward the medial side of the clasper. At the first-fifth of the axial cartilage length there is the anterior part of the *dorsal marginal cartilage* (rd), which has a rhomboidal shape, as both its anterior and posterior endings are pointed and it is enlarged horizontally and vertically at its middle portion. This cartilage sits over the axial and its posterior ending is at the anterior one of the end-style. In *Isistius* there is an unknown (?) cartilaginous piece lateral to the dorsal marginal. This cartilage is rectangular in its anterior portion and both sides are parallel on its length until the posterior part of the end-style, where it tapers and forms a triangle at the clasper gland. Its medial side sits dorsal to the axial and end-style cartilages and, together with the dorsal marginal they form both sides of the sperm duct, which is os the dorsal side of the axial and end-style cartilages. This cartilage

<u>Caudal fin.</u> (Figure 63)

It is formed by the vertebral centra in the middle line and above each centrum there is a *basidorsal element* (bdp), whereas in between them there is an *interdorsal elements* (dic). While the vertebral centra are cylindrical lateraly, the basidorsals are rhomboidal and inclined posteriorly, and the intercalars are triangular with their base at the dorsal portion and the most acute angle reaching the vertebral centra. The intercalars appear until the middle of the caudal fin, and are absent toward its end. Above the basidorsals and intercalars there are *supraneural elements* (spn), which are elongate cartilages oblique to the vertebral column length and directed posteriorly. There are, approximately, 30 supraneural spines, which are not correlated one by one to basidorsals and intercalars. The initial supraneural spines are differentiated from the posterior ones; they are in number of five or six, approximately, and they do not have the shape of a spine, as they are minute cartilaginous pieces that resemble rectangles. Ventral to the vertebral centra there are *basiventral elements* (bvp), which might be the fusion of haemal arches and haemal spines, and they are in, approximately, 20 unities. At the most posterior end of the caudal fin the last dorsal and ventral cartilages are somewhat fused together with the vertebral centrum and form a structure named hypural, which is usually divided into two pieces. The most anterior one still has the vertebral centrum and resembles a rectangle, while the last piece of cartilage resembles a trapezium, as there is a straight base and the apix has one side longer than the other. From the most anterior basiventral until the middle of the caudal fin, these cartilages have a protuberance at their ventral portion, which is a lateral projection. Anterior to the basiventrals there are some irregular cartilaginous pieces ventral to the vertebral centra. These pieces may vary from two to six and their shape is not uniform, as there are cylindrical, square, rectangular, triangular cartilages.

Musculature

Head.

The external oculomotor muscles comprise four rectus and two oblique muscles. The rectus muscles originate from the posterior portion of the eye capsule, at the eyestalk, and insert on the eyeball, although they cannot be seen from the outside, as they attatch to the portion of the eye that is directed toward the neurocranium. These muscles are *rectus superior* (rsp), *rectus internus* (rit), *rectus inferior* (rif), and *rectus externus* (rex). The *rectus superior* inserts at the upper portion of the eyeball. The *rectus internus* and *rectus externus* are complementary; although they originate at opposite sides at the neurocranium, but both at the preorbital wall, they insert at the posterior portion of the eyeball: the *internus* on the upper portion and the *externus* on the lower one. The *rectus inferior* is opposite to the *superior* at its origin and insertion, as it inserts on the most ventral portion of the eyeball. The oblique muscles are *obliquus superior* (obs) and *obliquus inferior* (obi). These muscles originate on the opposite side of the rectus muscles, at the postorbital wall. Their origin is close to each other, but the *obliquus superior* inserts on the upper side of the eyeball, while the *obliquus inferior* inserts on the lower side.

Mandibular arch. (Figure 64)

These muscles are associated with the jaws (mandibular and palatoquadrate cartilages). When the skin is removed, the *adductor mandibulae superficialis* (ams) is the first muscle to be seen. It is considered to be the lower portion of another muscule, the *adductor mandibulae* (am). But, in *Isistius*, these two muscles are completely separated from each other and the *ams* is postioned over the *am*. The *adductor mandibulae superficialis* originates at the Meckel's cartilage and inserts through a tendon on a tissue at the postorbital process of the neurocranium. It is a slender muscle and is positioned parallel to the head axis. Its complementary muscle, the *adductor mandibulae*, is located beneath the *ams*, at the upper portion of the jaw, and its origin is on the posterior portion of the postorbital process. The *adductor mandibulae* has a dorsal and a ventral portion that can be seen by an intersected septum; however, these two portions are not totally apart from each other and are not considered two distinct muscles. The *am* passes in between the neurocranium and the quadrate cartilages, right behind and a little underneath the eye, and inserts with a tendon on the Meckel's cartilage. The *adductor mandibulae* is a thick muscle that connects with another one, the *suborbitalis* (so). It is difficult to tear these two muscles apart, as the last one originates on the subethmoidal crest (*ser*), runs along it and under the eyeball, and inserts on the on a soft tissue at the upper lip. However, it forms a muscular continuum with de *adductor mandibulae* that goes from the most anterior portion of the subethmoidal crest until the upper lateral wall of the neurocranium.

Below the *adductor mandibulae superficialis* and above the *adductor mandibule* there is another muscle, the *levator labialis* (llb). Its origin is on the upper portion of the quadrate cartilage and its insertion is on the connective tissue on the outer side of the lower labial cartilage. It origins large (almost the same size as the outer side of the palate artilage) and tapers toward its end, that forms a diagonal strip on the side of the head. Behind the *adductor mandibulae* there is the muscle *constrictor dorsalis* (cod), which is located between the orbit and the spiracle, at the most internal region. The origin of this muscle is on the upper lateral wall of the neurocranium.

Hyoid arch. (Figure 64)

These muscles are the dorsal and ventral sheets of the constrictor hyoideus and are associated to the hyomandibula and ceratohyal directly, and generally continue to the constrictor branchiales superficialis posteriorly. The *constrictor hyoideus dorsalis* (chd) is a short muscle and its fibers are perpedicular to body axis; but it is wide and goes from the posterior region of the spiracle to a little further than the end of Meckel's cartilage. Its origin is on the dorso-lateral wall of the epaxial musculature and it has three points of insertion: at the posterior wall of the spiracle (forming the wall of this structure); in between the articulation of the dorsal margin of mandibular, quadrate and hyomandibular cartilages forming a triangle; and at the dorso-latero-posterior corner of hyomandibula. The *constrictor hyoideus ventralis* (chv) is a ventral muscle that is separated from the *intermandibularis* (im), which is ventral to it, by a thin fascia. Almost its whole length is ventrally covered by ampullae of Lorenzini and connective tissue. This muscle originates from a seam of connective tissue at midventral line and inserts on the ventroposterios edge of the ceratohyal.

Branchial constrictors. (Figure 64)

The branchial muscles comprise the constrictors and three other that were not examined: *interbranchialis, adductor arcuum branchialium* and *arcualis dorsalis*. The *constrictors branchiales superficialis* (cbs) are five unities, each covering externally a different branchial arch, beginning with the hyoid arch. As there are too much ampullae of Lorenzini and connective tissues, it is challenging to tear each bundle apart from the others. The anterior portion of these muscles originates at the dorso-lateral wall of the epaxial musculature and the posterior at the *cucullaris* (ccl). They are located posteriorly to the *constrictor hyoideus dorsalis,* in almost a continuum, and they are inserted on connective tissues at the latero-ventral side of the body that do not reach the middle line. It is from these connective tissues that *constrictor hyoideus ventralis* originates.

Hypobranchial spinal muscles. (Figure 64)

These muscles are located beneath the basibranchials. The *genio-coracoideus* (gco) is a thick and narrow muscle that strongly inserts on the mandibular cartilage symphysis and becomes a thin and wide muscular sheet towards the posterior portion that, together with a fascia, originates at a posterior portion of the *rectus cervicis*. It is after the level of the coracoid that this muscle is clearly just one sheet and becomes thinner and wider; besides, it is before this level that both sides of the muscular sheet become apart and connected by a connective tissue. This origin is at the level of the pectoral fins and its most lateral portion is connected to the muscles at fin base. The fascia that covers the *constrictor hyoideus ventralis* (chv) comes from between both sides of the *genio-coracoideus,* which has left and right portions at its most anterior portion, close to the mandibule. There is a muscle slip, the *genio-coracoideus externus* (gcoe), which is a paired structure that arises from the antero-lateral surface of coracoid. Both right and left slips meet at the anteriormost portion of coracoid and go ventrally, converging to the *genio-coracoideus*. (Figure 64, F)

The *rectus cervicis* is muscle with two sheets and it is dorsal to the *genio-coracoideus*. Both portions are divided by a transverse septum that divides the muscle in an anterior, the *coraco-hyoideus* (coh), and a posterior *coraco-arcualis* (coa) part. The *coraco-hyoideus* is a wide and thick muscle that inserts on the ventro-posterior surface of the basihyal cartilage. A little in front of the coracoid level there is the spetum that divides it and determines the *coraco-arcualis,* which originates at the ventro-anterior side of coracoid. In the midlle of the longitudinal axis of the *coraco-arcualis,* approximately over the coracoid, comes down from a dorsal region a fascia that passes through both sides of this muscle and joins to the dorsal portion of the *genio-coracoideus*, which is ventral to it. There is a thick sheet of connective tissue that covers the *coraco-hyoideus* ventrally, anterior to its opening.

The *coraco-branchiales* (cob) are slips of muscles immediately below the floor of the pharynx. The most anterior one is the *coraco-branchialis 1* (cob1) that originates from a dorsal posterior portion of the *coraco-hyoideus* and inserts on the postero-lateral part of the basihyal cartilage, dorsal to *coraco-hyoideus* insertion on the same cartilage. These two muscular bundles surround the articulation of the ceratohyal and the basihyal is ventrally and dorsally.

There are two muscular bundles dorsal and thinner to the *rectus cervicis,* one at each side. They originate at the most dorsal portions of coracoid and are separated from the branchial arches only by a fascia. There is another dorsal and medial single muscular bundle dividing the base origin of the *rectus cervicis* that originates from the most anterior portion of coracoid and pericardium. It seems like a thin medial wall muscule right below the basibranchials.

Other visceral muscles.

The *cucullaris* (ccl) is a trapezoidal muscle sheet located above the branchial region. It originates on the dorso-lateral fascia of the epaxial musculature, immediately posterior to *constrictor hyoideus dorsalis*, and ends on the anterior surface of scapula. It inserts on the dorsal end of extrabranchial cartilages. The *constrictor oesophagi* (oes) is a circular and thick muscle that surrounds the oesophagus. On its most anterior portion it attaches to the ceratobranchial 5, and both posterior basibranchials. It is related to the dorsal region of the gill pickax.

Pectoral fin and girdle. (Figure 65)

There are two associated muscles with the pectoral fin: the *levator pectoralis* (lpe) and the *depressor pectoralis* (dpe). The *levator pectoralis* covers half of the anterior, the dorsal and half of the posterior sides of the pectoral fin. It is a bigger muscle than the *depressor pectoralis*; it originates on the posterior portion of scapula, covers the dorsal half of the anterior and posterior pectoral radials, and it inserts on the ending of those radials. The *depressor pectoralis* covers the ventral portion of the anterior and posterior sides of the radials. Both muscles are connected to the *rectus cervicis*.

The hypaxial musculature completely coats the coracoid, as it is a continuum with *rectus cervicis*, and it originates on the posterior portion of the girdle, very close to the fin. There are muscular bundles inserted on the anterior and on the posterior sides of the coracoid, as well as ventrally, and the girdle it totally nested within the musculature.

Pelvic fin. (Figure 66)

There are three muscles composing the pelvic fins: levator, adductor and depressor. The *levator pelvicus* (lv) is a muscle that originates on the ventro-lateral surface of the hipaxial body musculature and inserts on the dorsal side of the pelvic fin, reaching the radials. It starts at the beginning of the pelvic girdle, and supports the fin until the ceratotrichia. It does not cover the whole dorsal surface of the fin and it ends at a diagonal line from the end of the base of the fin until almost the external lateral corner of the fin. The ventral muscle, the *adductor pelvicus* (av), supports the rest of the dorsal side of the fin. This muscle originates from the most central part of the puboischiatic bar and from some connective tissue found in between both fins; it inserts on the ventral posterior portion of the basipterygium and ends at its distal portion. As it covers the internal region of the ventral side of the pelvic fin, the *adductor pelvicus* (av) makes a turn, surrounding the basipterygium and it is also found on the dorsal side of the fin, at its most internal portion. The other pelvic muscle is the *depressor pelvicus* (dv), which is also ventral and originates from the pubuischiadic bar. However, it originates from the ventral side of this cartilage and covers almost all of its length and width. The only portion of theis cartilage that is left exposed is the medial portion, which can be seen in a rhomboidal shape. The *depressor pelvicus* covers the part of the ventral side of the pelvic fin that is not covered by the *adductor pelvicus*. So, it also extends further than the previous muscle and reaches and inserts on the ventral side of the radials. There are approximately one muscular bundle per radial.

Clasper. (Figure 67)

Four muscles compose the clasper musculature, and their nomenclature follows Jungersen (1899). There are two bundles of the *extensor* both running at the same direction, but one is more dorsal and internal to the other. These are dorsal muscles that originate from the posterior portion of the pubuischiatic bar. They are dorsal to the *adductor pelvicus* and cover it almost completely. Posterior to them, at the dorsal distal part of the clasper, there is the *dilatator,* which is the most internal muscle and inserts on the gland through a long and thick tendon. The *dilatator* makes a turn on the inner portion of the clasper and is also found on its ventral side. Its tendon is apparent on the ventral side too, and inserts on the ventral portion of the gland. Therefore, there are no muscles inserting on the gland, just the tendon of the *dilatator*. The other clasper muscle is the outer lip, which is dorsal and external to e clasper. It is a bundle that originates at the line of the distal part of the *extensor*, runs at the side of the unknown (?) cartilaginous piece lateral to dorsal marginal and ends right before the spur. The last clasper muscle is the *compressor,* which is a wide and flat muscle laying ventrally to the *adductor pelvicus* and *depressor pelvicus*.

Dorsal fins. (Figure 68)

Each dorsal fin skeleton base is covered by the *inclinator dorsalis* (id), which is a wide and flat muscle slip. It originates at the ventral margin of basal elements and at the body musculature, and it inserts on radials and ceratotrichia; and it does not reach the vertebral column. This muscle is present on each side of the dorsal fin and on both fins.

Caudal fin. (Figure 69)

Epaxial (epx) and hypaxial (hpx) muscles cover the caudal fin skeleton. The *flexor caudalis* (fxc) is at the base of the lower caudal lobe, originates from the ventral surface of the hypaxial musculature and inserts on the distal ends of basiventral processes and ceratotrichia of the lower caudal lobe. The epicordal radials are exposed and not covered by any musculature.

Lateral line canals

The lateral line canals are seen at each lateral wall of the specimens and reach nearly the end of the caudal fin. These canals start being parallel to each other from above the gill openings. At the head there are many distinct canals, and they are named following Chu & Wen (1979).

From above the gill openings, where the canals are more distant from each other, they begin getting closer other, they begin getting closer and then become parallel again in between the spiracles. At this point, they spiracles. At this point, they make a curved turn toward each other and meet at the middle forming a middle forming a corner that is pointed towards the posterior portion of the body. This line, which is curved line, which is curved anteriorly and joins at the middle, is the *supratemporal canal* (spt). Anteriorly to it, the (spt). Anteriorly to it, the lateral canals, which are named *supraorbital canals* (suc), are close to each other are close to each other and begin getting apart in curved lines that are above the eyes. At the very beginning At the very beginning of the supraorbital canals, before the divergence of another canal laterally, these canal laterally, these canals are called *preorbital canals* (poc). At the junction of the supraorbital and supraorbital and preorbital canals there is the origin of the *infraorbital canals* (ioc) at both sides (Figure both sides (Figure 70). They run perpendicular to the body axis, between the spiracle and eye, pass by the lateral side of the head and go to the ventral side (Figure 71. Lateral view of lateral line canals of the head of *Isistius brasiliensis*.

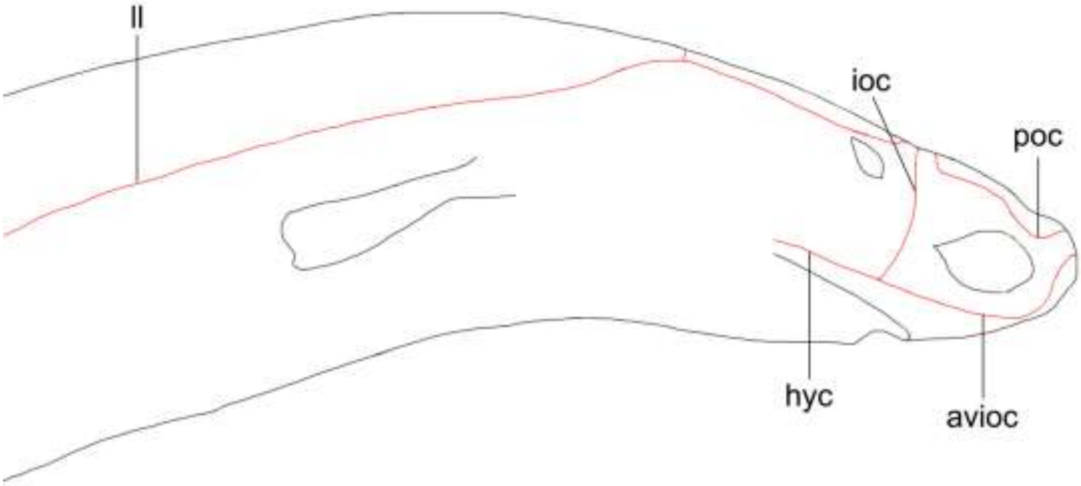

Figure 72). Dorsally, the supraorbital canals make another opening curve more anterior to the eyes, and then they return to a parallel position. This point is dorsi-posterior to the nostrils and the supraorbital canals go almost straight to the ventral side of the head, and it is called *prenasal canal* (pnl). Ventro-posterior to the nostrils, the prenasal canals do a short turn toward each other and join, forming only one line.

This line, the *medial canal* (mdc), does a short run in the middle of the ventral head, between the snout and the mouth. The medial canal then separates into two lines, which are a little inclined anteriorly, forming an obtuse angle between them that is opened anteriorly. These two canals are called *nasal* (nas) and, after directing toward the snout, the do a turn and direct to the posterior portion. These turns on both sides form an acute angle, which openings are directed toward the caudal portion. Then, the nasal canal does a subtle turn toward the eye and meet another canal that run below the eyes, the *antero-ventral portion of the infraorbital canals* (avioc) (Figure 71).

On the dorsal portion of the snout there are two canals that encircle the nostrils. They are external to the most anterior portion of the supraorbital canals, and make a curve around the nostrils running to ventral side of the head, even though they are not ramifications of the supraorbital. However, right after the end of the nostrils, these canals make a turn and direct toward the eyes, where they run along below the eyes. At the midpoint of these antero-ventral portion of the infraorbital canals that is where there is the junction with the nasal canals. Right after the eyes, the avioc join with the infraorbital canals themselves that come from the dorsal side, and after this point, they are called *hyomandibular canals* (hyc). They continue along the ventro-lateral portion of the head, and end posteriorly to the mouth, together with the end of the skin of the labial furrow. No mandibular canal was observed.

2. ***Isistius plutodus***

Since *Isistius plutodus* resembles *I. brasiliensis* in almost every morphological character, the following descriptions are very similar to those for *I. brasiliensis*. Specimens of *Isistius plutodus* have 43-45 monospondylous, 23-26 precaudal diplospondylous and 22-27 postcaudal diplospondylous vertebrae (Table 14). On the radiograph of the holotype it is possible to identify the transition between both kinds of vertebra (Figure 73).

Skeleton

Neurocranium. (Figure 74)

The neurocranium is a chondrified skeleton that encloses the encephalon, olphactory bulbs, eyes, and auditive organs, besides forming the palate. It is externally divided on four regions, from the most anterior to posterior: ethmoidal (rostrum and nasal capsules), orbital (orbits, basal plate, and cranial roof between them), otic (otic capsules, cranial roof and basal plate between them), and occipital (posterior end of neurocranium) (Compagno, 1988; Shirai, 1992a).

The ethmoidal region is the most anterior one and it is where the *nasal capsule* (ns) and *rostral process* (rp) are. The rostral process is very reduced as it is only a longitudinal cartilaginous elevation that is weakly prolonged forward the neurocranium and shorter than the nasal capsule height.

The nasal capsule protects dorsally the olfactory organs and from every side the nasal cavity. Each capsule is ventrally opened, with a ventrolateral nasal aperture, where are the openings for inflow and outflow of water for the cavities in each olfactory organ. The olfactory cavity anterior wall is dorsally curved, forms the roof and joins to the preorbital wall, forming the posterior wall of the nasal capsule, and joins to the preorbital process and to the supraorbital crest, forming the orbit internal wall (Compagno, 1988).

The nasal capsule has an irregular pore at its anteroventral end, at which are the *nasal cartilages* (nas). These are anelar elements that support the nostrils and the nasal lobes, although they are not circular, as the nasal cartilage is not closed. Each element, at its posterior portion afunilates and forms a pointy ending, not reach its complementary side. The right and left nasal capsules compose the ventral surface of the ethmoidal region with a space between them. This space, the internasal septum, develops and forms the *ectethmoidal chambre* (eec), which is separated into two by the *subethmoidal crest* (ser) that is a ventral elongate cartilage which posterior ending is at the anterior one of the ventral interorbital wall and reaches the rostrum forming the *rostral keel* (rc). From the posterior portion of the nasal capsule’s ventral side, arise two cartilaginous pieces from the subethmoidal crest that are directed latero-anteriorly, and closer to the nasal cartilages they change their path and direct towards the mid-length of subethmoidal crest But, they do not meet and there is a wide space at this region.

The *prefrontal fontanel* (pff) is an anterior aperture to the *cranial cavity* (cav). It is located at the posterior extremity of the ethmoidal region and has a semi-circular shape, with the anterior region being almost straight and posterior curved. This fontanel is located immediately anterior to a short elevation at the middle end of the cranial roof.

The foramen of the *epiphyseal organ* (ep) is a small perforation of the cranial roof and it is located right posterior to the prefrontal fontanel, with its most anterior portion at the elevation post-prefrontal fontanel. It has an oval shape and its largest length is parallel to body axis. The *precerebral fossa* (pcf) opens immediately in front of the prefrontal fontanel and it is occupied by a gelatinous mass. The nasal capsules laterally restrict this shallow concavity in shape of wedge, and the anterior edge (rostral process) expands anteriorly and supports the rostrum. The *cartilaginous plate* (ra) forms the rostrum and it is developed at the anterior end of the rostral process helping the conexion with the nasal capsule.

The orbital region occupies more than one third of the neurocranium and encloses the eye and a structure for jaw suspesion. The *supraorbital crest* (soc) is a dorsal elevation of the neurocranium at its lateral edges that are above the eyes from the region immediately posterior to the nasal capsule until the post-orbital process. The main ramifications of the nerves *ophthalmicus superficialis* and *ophthalmicus profundus* go through a foramen, the *preorbital canal* (poc), which is an opening half the size of the prefrontal foramen located at the anterior region of the of a longitudinal groove at the medial sie of the supraorbital crest. The *ethmoidal canal* (ec), through which goes the ramus *ophthalmicus superficialis* (of the *ethmoidal* nerve), is located anterior and lateral to the preorbital canal, not reaching the mid-length of the nasal capsule. Both are in the longitudinal grooves that border the supraorbital crest, and there is a deeper groove connecting these two openings.

The *interorbital wall* (iow) supports many foramens for cranial nerves and blood vessels. The *optic foramen* (II) is located at the medial portion of this wall, in a foramen in between both sides of the wall, at the posterior portion of the interorbital wall tissue. The medial portion of the interorbital wall is not chondrified and a resistant membrane encloses it. This is a fenestra of the cranial cavity and the optic nerve goes through it. The *prootic foramen* (V-VII: for the nerves *trigeminus* and *facialis*, except the ramus *hyomandibularis* of the *facialis*, which is located posteriorly to the lateral comissure) is located at the posterior border of the interorbital wall. The nerves *oculomotor* (III) and *trochlearis* (IV) have their own foramens that are posterior and dorsal to the optic foramen at the interorbital wall, respectively. The foramen of the nerve *abducens* (VI) is at the postero-dorsal region of the interorbital wall, ventral to the postorbital process.

One efferent artery of the *pseudo-branchial* (psb) has a foramen together with the ramus *hyomandibularis* of the *facialis* right behind the lateral comissure. The *lateral comissure* (com), at the posterior border of the orbital region externaly encloses one way of the jugular vein. The articular facet, a *groove for the orbital process*, gop, is located below and anteriorly to the prootic foramen. The *basal angle* (ba) is a transverse crest of the basicranium that supports the jaw medially and it is immediately behind the groove for the orbital process. Posteriorly to it, there is the *basitrabecular process* (btp) that is a lateral expansion of the suborbital area and supports an ascending process of the palatoquadrate and it is strongly expanded laterally and forms a wide palatine surface.

The otic and occipital regions are the whole posterior portion of the neurocranium from the orbit. These two areas form a cranial capsule without a division line. At the posterior end of the supraotic region, between the otic capsules, there are two paired perfurations: a foramen for the *endolymphatic duct* (feld) and the *perilymphatic fenestra* (plf). However, in *Isistius* and *Zameus* the *endolymphatic fossa floor* is wide open and the *endolymphatic duct* goes through it (feld + plf). The *opistotic process* (opp) is well developed and slitghtly inclined dorso-posteriorly at its distal region (Shirai, 1992a).

Immeditely behind the endolymphatic fossa, the neurocranium dorsi-posterior wall is expanded and posteroventrally inclined. The *magnum foramen* (mag) is located at the medial portion of the posterior and vertical to body axis wall. There is an articular facet ventral to the magnum foramen, and beside to this articular facet, the *occipital condyle* (occ) is articulated to the basiventral process of the first vertebra (co-lateral articulation). The foramens of the nerves *glossopharyngeo* (IX) and *vagus* (X) open at the posterior wall of the neurocranium, being the first more external than the other. Immediately dorsal to the n. vagus foramen there is a foramen one-third its size for a blood vessel.

There is a shallow longitudinal groove, the *lateral auditive groove* (lag), at the otic lateral wall for the jugular vein and the *hyomandibularis* of the *facilais*. The *hyomandibular fossa* (hmf), at which the proximal end of the hyomandibula attaches to, is located at the posterior end od the otic lateral wall. The dorso-posterior crest of the fossa is laterally expanded and its ventral portion forms the *postotic process* (potp) that is a latero-anterior expansion somewhat rounded.

The ventral side of the otic region is a wide and flat surface that forms the *palatine* (pal) and it is oblique to the body axis, as its distal portion is more anterior and ventral to its proximal region. Logitudinally, at the anterior portion of the palatine, there is a foramen for the *carotid artery* (fca). There is no *foramen for the orbital artery* (foa).

Mandibular arch.

It is composed by the palatoquadrate and mandibular. The first forms the upper jaw and is divided into two pieces of cartilage, the *palatine plate (*pap) and the *quadrate plate (*qup*)*. Near the junction with the palatine plate, the quadrate plate supports the *orbital process* (op) dorsally for the orbital articulation. On the ventro-lateral portion of the quadrate plate there are the first teeth of the upper teeth rows, and dorsally there is an *otic flange* (otf), which is a process at the cartilage directed anteriorly and with an acute corner that is curved laterally. The ventral surface of the quadrate plate is depressed and forms a concavity for the *adductor mandibulae*, which sits over this surface, partially supported by the otic flange and its lateral straight side. There is another smaller process at the mid-dorsal region of the quadrate, which is an elevation one-third the size of the otic flange. The articular facet for the jaw-joint at the posterior end of the ventral edge has a large *condyle* (pqd) and a small quadrate *concavity* (pqc). The palatine plate has a triangular shape and supports most upper teeth rows. The connection between both plates of the palaquadrate is not linear, as the lateral portion of the palatine is slightly ventral to the quadrate.

The *mandibule* (ma), Meckel's cartilage, is much larger than both the palatine and quadrate cartilages together and supports the lower jaw. It is divided into right and left portions and each has a flap-like *accessory cartilage* (mfl) made of weakly calcified tissue, and flexible. Lower teeth rows occupy the whole anterior portion of the mandible forming a semicircular teeth row, and the only free portions are the most lateral where it articulates with the quadrate plate. At the dorsi-anterior corner, a large *articular fossa* (mad) receives the large *quadrate condyle* (pqd). Dorsal to it, a pronounced *mandibular knob* (mk) stands out posteriorly, fitting into the small *quadrate plate (*pqc) (Figure 75). The hyoid arch with developed *ligamentous complex* (ljs) supports this mandibular knob. The mandibule bears a process at its ventro-latero-posterior edge, where there is an insertion for a thick ligament, the *ligamentum mandibulo-hyoideum* (lmh).

The labial cartilages support the upper lip and its corner with lower lip. They are composed of two *upper cartilages*, the *posterior* (plc) and the *anterior* (alc), and a *lower* one (llc), which are connected to each other at the mouth corner.

Dorsal to the quadrate cartilage and lateral to the neurocranium, immediately posterior to the post-orbital process, there is a minute cartilage, the *spiracular* (spc) that supports the filaments of the spiracle. It is a flat cartilage with the shape similar to a rectangle positioned vertically on the head, and its dorsal portion is concave.

Hyoid arch.

It supports the mandible posterointernally and is composed by the paired cartilages hyomandibula and ceratohyal, and the single basihyal cartilage. The *hyomandibula* (hm) is the dorsal element of the arch and joins with the neurocranium at the *hyomandibular fossa* (hmf) on the auditory capsule. It has a general rectangular box shape with depressions and protuberances; its longest length is transversal to body length, the second longest length is the one along the body axis and its thinner portion is its height, which is parallel to body height. In dorsal view, the upper portion of the hyomandibula has a depression at its mid-postero-medial region, and its medial and posterior corner is elevated. At this corner there is a minute cartilage, the *joint cartilage of hyomandibula* (jhm), which is a very small, flat and rhomboidal cartilage. The lateral elevation of the corner continues latero-intenally and reaches the medial and anterior corner. This wall at the middle of the hyomandibula is the one that is articulated with the neurocranium at the *hyomandibular fossa* (hmf) together with the joint cartilage of hyomandibula at the posterior corner. The latero-anterior region of the hyomandible articulates with the mandibular knob

The *ceratohyal* (ch) extends anteromedially and it is a very robust cartilage that has a slight curvature at the posterior fifth of its length. Its posterior portion is slightly rounded, and it articulates to the latero-posterior corner of the hyomandible by the *ligamentum hyomandibulo-hyoideum* (lhc). The distal ending of ceratohyal is in a triangular form, and this is where it articulates with the basihyal, and its ventroposterior margin is expanded for the interhyoideus muscle. Immediately posterior to the ligamentum hyomandibulo-hyoideum there is another ligament that unites the lateral corner of mandibule together with the ceratohyal: *ligamentum mandibulo-hyoideum* (lmh). As these two tissues are sided it is tough to tear them apart and it resembles a unique ligament joining the latero-posterior corner of the hyomandible, the dorsi-posterior region of the ceratohyal and the lateral corner of the mandibule. The ceratohyal also supports, internally, the *gill rays* (gr). There are two main branches, which are ramified into many smaller branches.

The *basihyal* (bh) is an unpaired element supporting the anterior portion of the tongue at a floor of the oral cavity. It is band-like shaped, very wide, and positioned transversally to body axis. It has two *large concavities* (cch), one at each posteroventral surface, for the joint with the ceratohyals.

Branchial arches.

The branchial basket has five sets of branchial arches. From dorsal to ventral sides, each branchial arch is composed of the pharyngobranchial, epibranchial, ceratobranchial, hypobranchial, and basibranchial cartilages. The last ones are the only branchial cartilages which are not paired and are positioned in the mid-ventral portion of the branchial basket. The *pharyngobranchials* (pb) extend posterointernally with a tapering proximal ending lying over the pharynx. Their distal ends are attached to the ventral surface of vertebrae by ligamentous tissue. The pharyngobranchial of arch 5 is united with epibranchial 5, and this cartilage is also fused with pharyngobranchial 4 forming a *gill pickax* (gp) (Shirai, 1992a). The *epibranchial cartilages* (eb) are distally articulated with proximal ends of pharyngobranchials, and proximally articulated with the distal portion of the respective ceratobranchial.

The *ceratobranchials* (cb) are long, thick, and flat cartilages. They form the ventro-lateral wall of pharynx and carry gill filaments with epibranchials. The proximal third of the *ceratobranchial 5* (cb5) is equal to the other four ceratobranchials: straight, with both sides parallel to each other. However, its distal portion expands laterally and becomes wider until it reaches the hypobranchial.

The *hypobranchials* (hb) form the basibranchial copula with basibranchials at the floor of the pharynx. However, there is just only one pair of cartilages at this postion and it cannot be correctly named due to the unavailability of comparative material and literature. This pair of cartilages forms a “V”, whose opening is directed toward the anterior portion of the body. They do not articulate with each other, as there are another single cartilages in between them. They are flat, elongated, and their proximal end (at the middle of the branchial basket) is rounded and a little bigger than the rest of the cartilage, whose sides are almost parallel to each other, but tapering a little towards the distal portion. They are supposed to be hypobranchial 5 (?) cartilages as the only ceratobranchials that articulate with them are the fifth ones. The cartilaginous piece at the left is wider than the other at its most posterior region. This asymmetrical arrangement might be exclusive to the analyzed specimen, or it might be a condition for all specimens of *I. plutodus*.

The *basibranchials* (bb) are unpaired elements positioned over the heart region. There are two distiguinshable single and slender cartilages posterior to what were called hypobranchials 5 (?). The most anterior of these cartilages is longer than the other. Its anterior portion is pointy and each antero-lateral side articulates with the hypobranchials 5 (?). It tapers towards its posterior part and it is truncated at its end. The second cartilage seems like a continuum with the previous one, as its anterior part has the same width as the previous posterior ending. It is shorter than the first, tapers to the posterior portion of the branchial basket, and its ending is very thin and almost forms a pointy ending.

Anterior to these two basibranchials, and between both posterior portions of the hypobranchial 5 (?) cartilages, there are two other elements. The most posterior one has a ventral protuberance at the middle of the branchial basket, which is not the center of this cartilage as it is not symmetrical. At its left side, this element is flat and parallel to the left hypobranchial 5 (?) for one-fourth of its length. At the right side, this cartilage ends after the protuberance, at the medial side of the right hypobranchial 5 (?). The other element is anterior to the previous one and it is positioned at the middle axis of the branchial basket. It is a rhomboid cartilage and both pointy edges are along the body axis. These two cartilages might also be basibranchials, but there is no support in literature to help their identification. This asymmetry might be an anomaly exclusive to this species or it may be present on the species. However, to verify this condition, more specimens should be dissected.

Gill rays (gr) are slender cartilages on the gill itself, which supported by the epibranchial and ceratobranchial except arch 5. *Gill rakers* (rk) are absent in *Isistius plutodus*. The *extrabranchial cartilages* (exb) are present in every arch with dorsal and ventral elements. At dorsal edges these cartilages are enlarged and flattened distaly and transversely.

There are some cartilages that are ventral to the branchial basket, but articulate dorsally with the ceratobranchials. These cartilages are very flattened, poorly calcified, and appear to be in number of two. The anteriormost one is a single cartilage, the other is a unique cartilaginous piece that form three distinct pieces running ventrally along the internal portion of the branchial arches, and the dorsal part resembles a fusion of the three ventral ones. These cartilages separate the internal region of the branchial arches from the hypobranchial and jaw musculature. Therefore, it seems like they provide a support for this musculature as it very thick in *Isistius*. Due to their relative position to branchial basket, these cartilages might be named *ventromedial branchial cartilages* (vmbc).

Dorsal fins. (Figure 76)

Composed by two separate unities, the anterior and posterior (first and second dorsal fins). Both are supported by a *basal cartilage* (bad) and many *radials* (rds) that do not reach the margin of the fins (aplesodic style). No fin spine is present. Basal cartilages are apart from dorsal column, triangular shaped in both dorsal fins with the most acute portion anterior to the broad one, and deeply inserted in the body. The acute portion may have an upturn at its dorsal distal part. At its posterior-dorsal portion there is a protuberance at the cartilage, which is usually at its the border. First dorsal with six radials, second dorsal twelve: all with different sizes and shapes. In the first dorsal, there are three small radials dorsi-posterior to a medium sized; vento-posteriorly to these there is a quadrate radial that is bigger than the previous ones and, posterior to it there is the sixth radial in the of a slender half-moon.

The second dorsal fin has a lateral cartilage, which is transverse to body axis. There are five small radials dorsi-posterior to the basal one, and ventral to those there is a medium radial cartilage with a small one posteriorly to it. Ventral to them, there is a trapezoidal medium cartilage and a small one ventro-anterior to it, and ventral to these there is another trapezoidal medium cartilage which most ventral portion is curved forming a portion perpendicular to the other radials. Posterior to both trapezoidal medium radials there is a big radial, which is followed by a slender half-moon shaped radial as large as it.

Pectoral girdle and fins.

The pectoral girdle (scapulocoracoid) is composed of elongate cartilages that surrounds the body ventro-laterally. The lower and anterior portion is the *coracoid* (co) and the upper portion is the *scapula* (sc) that has the *scapular process* (scp) at its distal part.

The scapulocoracoid is a structure formed by two paired cartilages: the left and right sides. In ventral view the coracoid is almost straight, and the line of junction of both sides is along the medial side of each piece of cartilage. Posterior to this junction both sides of coracoid are thinner and they form an acute angle directed toward the caudal region. At the pectoral fin level the cartilages turn dorsally and form the scapula. This portion has a *foramen for pectoral fin nerves* (fpn), and has some indentations, where the pectoral fin attaches to it. At the most distal part of the pectoral girdle there is the scapular process that is a portion of the cartilage that afunilates toward its end, directs dorsi-posteriorly, and is seen at dorsal wall of the body, below the skin and sided by the epaxial musculature.

The pectoral fin skeleton is composed of the basal cartilages and many radials. In *Isistius*, there is only one basal, and it may be the fusion of the *propterygium* (pr), *mesopterygium* (ms), and *metapterygium* (mtx). This basal cartilage connects the radials to the pectoral girdle. The basal supports, approximately, seven proximal radials, each with a distal radial, and the five dorsal ones also have intermediate radials. The *metapterygial axis* (mta) is a cartilaginous piece dorsi-posterior to the basal one that is larger and shorter than the proximal radial immediately ventral to it. This cartilage supports, four proximal radials with a distal radial each and no intermediate one. Each radial is slender, and from the most ventral to dorsal they get longer.

Pelvic girdle and fins.

The only cartilage that forms the pelvic girdle is the *pubuischiadic bar* (pub) that is transverse to the body length. Each lateral posterior ending of this bar forms an articular facet for the pelvic fin. The *lateral prepelvic process* (lpp) is directed lateraly at the antero-lateral region of the puboischiadic bar and forms a subtle projection.

The pelvic fin comprises the *pelvic basipterygium* (bpv), which is elongated anteroposteriorly, and many radials. The dissected specimen has eight *radials* (rds), being the seven lateral radials slender and cylindrical, while the medial one is curved medially towards the clasper. The lateral element is the *anterior pelvic basal* (apv) and has almost a triangular shape. Its proximal portion is larger than the distal and it is directed latero-posteriorly from the basipterygium, while supporting one distal radial. Each pelvic radial is composed of an elongate proximal piece and one distal piece.

In the male analyzed specimen, the basipterygium supports clasper cartilages at its distal end, and the medial pelvic radial is differentiated into a curved cartilage toward the axial cartilage of the clasper and its anterior origin is at the intermediate segment of the clasper.

Claspers.

Nine cartilages form the clasper. In ventral view, from the most anterior region to the tip of the clasper, there is the only *intermediate segment* (b1) followed by the *axial* (ax), which extends at almost the end of the clasper, where it is less calcified, thinner and pointed, and is called *end-style* (g). At approximately the medium length of the axial cartilage it starts tapering toward the end-style, and its lateral part (external to the clasper) is oblique, while its medial part continues straight to the end. This is where the *ventral marginal cartilage* (rv) is, with its most anterior portion pointed, getting larger at its posterior end. It is a flattened cartilage and is very attached to the axial. Posterior to the ventral marginal cartilage there is the *ventral terminal cartilage* (tv), which is almost rectangular and its medial portion is sided with the end-style, and both end at the same line. At the postero-lateral region of the ventral marginal cartilage and between it and the ventral terminal cartilage there is the *accessory terminal cartilage* (t3), which is some sort of spine, being stout, short, with a wider and slightly ventraly curved distal portion. Dorsal to the tv, t3 and half of the lengths of ax and rv there is the *dorsal marginal cartilage* (rd), which is seen in ventral view also forming the most posterior tip of the gland.

At the dorsal view, above the intermediate segment and connecting it to the axial cartilage, there is the *beta cartilage* (β), which reinforces the joint of clasper shaft to pelvic basipterygium (Compagno, 1979). It is a rectangular cartilage and a little curved at its intermediate portion toward the medial side of the clasper. At the first-fifth of the axial cartilage length there is the anterior part of the *dorsal marginal cartilage* (rd), which has a rhomboidal shape, as both its anterior and posterior endings are pointed and it is enlarged horizontally and vertically at its middle portion. This cartilage sits over the axial and its posterior ending is at the anterior one of the end-style. In *Isistius* there is an unknown (?) cartilaginous piece lateral to the dorsal marginal. This cartilage is rectangular in its anterior portion and both sides are parallel on its length until the posterior part of the end-style, where it tapers and forms a triangle at the clasper gland. Its medial side sits dorsal to the axial and end-style cartilages and, together with the dorsal marginal they form both sides of the sperm duct, which is os the dorsal side of the axial and end-style cartilages.

Caudal fin. (Figure 77).

It is formed by the vertebral centra in the middle line and above each centrum there is a *basidorsal element* (bde), whereas in between those there is an *interdorsal element* (ide). While the vertebral centra are cylindrical lateraly, the basidorsals are trapezoidal with the base at the dorsal portion of the ventebral centrum, and the intercalars are inverted trapezia with their base at the dorsal portion and the most acute angle reaching the vertebral centra. The intercalars appear until the middle of the caudal fin, and are absent toward its end, while the basidorsals are seen almost until the posterior end of the caudal fin. Dorsal to the basidorsals and interdorsals there are *supraneural elements* (spe), which are elongate cartilages oblique to the vertebral column length and directed dorsi-posteriorly. There are 30 supraneural spines, and they are elevated from the first third of their length until their distal region. The proximal, ventral, part of the supraneurals is at the level of the basidorsals and dorsal intercalars, while the other two-thirds of their length forms a right angle and are in higher level. At the anterior part of the caudal fin there are five cartilaginous elements that are different from the others as they are not elongate and inclined, and are shorter. These anteriormost *epichordal radials* (epc) are squared and small cartilages.

Below the vertebral centra there are *haemal spines* (hms) probably fused to *heamal arches* (hma) forming a unique basiventral element, and they are in 18. From the anterior part of the caudal fin until its middle the basiventrals are curved ventro-laterally and enlarged at their most ventral portion. Anterior to the basiventrals there are four small cartilage pieces, the *prehypochordal cartilages* (phc) that are ventral to the haemal arches and at the beginning of the caudal fin. These cartilages are short in height and the anteriormost one is longer and its anterior region tapers toward the head. Towards the posteriormost end of the caudal fin the ventral cartilages get smaller until they no longer exist. The vertebral centra, posterior to the region where there is no ventral element, is elongate and tapers towards its end.

Musculature

Head.

The external oculomotor muscles comprise four rectus and two oblique muscles. The rectus muscles originate from the posterior portion of the eye capsule, at the eyestalk, and insert on the eyeball, although they cannot be seen from the outside, as they attatch to the portion of the eye that is directed toward the neurocranium. These muscles are *rectus superior* (rsp), *rectus internus* (rit), *rectus inferior* (rif), and *rectus externus* (rex). The *rectus superior* inserts at the upper portion of the eyeball, right above the eyestalk. The *rectus internus* and *rectus externus* are complementary; although they originate at opposite sides at the neurocranium, but both at the preorbital wall, they insert at the posterior portion of the eyeball: the *internus* on the upper portion and the *externus* on the lower one. The *rectus inferior* is opposite to the *superior* at its origin and insertion, as it inserts on the most ventral portion of the eyeball. The oblique muscles are *obliquus superior* (obs) and *obliquus inferior* (obi). These muscles originate on the opposite side of the rectus muscles, at the postorbital wall. Their origin is close to each other, but the *obliquus superior* inserts on the upper side of the eyeball, while the *obliquus inferior* inserts on the lower side.

<u>Mandibule arch.</u>

These muscles are associated with the jaws (mandibular and palatoquadrate cartilages). When the skin is removed, the *adductor mandibulae superficialis* (ams) is the first muscle to be seen. It is considered to be the lower portion of another muscule, the *adductor mandibulae* (am). But, in *Isistius*, these two muscles are completely separated from each other and the *ams* is postioned over the *am*. The *adductor mandibulae superficialis* originates at the Meckel’s cartilage and inserts through a tendon on a tissue at the postorbital process of the neurocranium. It is a slender muscle and is positioned parallel to the head axis. Its complementary muscle, the *adductor mandibulae*, is located beneath the *ams*, at the upper portion of the jaw, and its origin is on the posterior portion of the postorbital process. The *adductor mandibulae* has a dorsal and a ventral portion that can be seen by an intersected septum; however, these two portions are not totally apart from each other and are not considered two distinct muscles. The *am* passes in between the neurocranium and the quadrate cartilages, right behind and a little underneath the eye, and inserts with a tendon on the Meckel’s cartilage. The *adductor mandibulae* is a thick muscle that connects with another one, the *suborbitalis* (so). It is difficult to tear these two muscles apart, as the last one originates on the subethmoidal crest (*ser*), runs along it and under the eyeball, and inserts on the on a soft tissue at the upper lip. However, it forms a muscular continuum with de *adductor mandibulae* that goes from the most anterior portion of the subethmoidal crest until the upper lateral wall of the neurocranium.

Absence of the muscle *levator labialis* (Figure 78). Behind the *adductor mandibulae* there is the muscle *constrictor dorsalis* (cod), which is located between the orbit and the spiracle, at the most internal region. The origin of this muscle is on the upper lateral wall of the neurocranium.

Hyoid arch.

These muscles are the dorsal and ventral sheets of the constrictor hyoideus and are associated to the hyomandibula and ceratohyal directly, and generally continue to the constrictor branchiales superficialis posteriorly. The *constrictor hyoideus dorsalis* (chd) is a short muscle and its fibers are perpedicular to body axis; but it is wide and goes from the posterior region of the spiracle to a little further than the end of Meckel's cartilage. Its origin is on the dorso-lateral wall of the epaxial musculature and it has three points of insertion: at the posterior wall of the spiracle (forming the wall of this structure); in between the articulation of the dorsal margin of mandibular, quadrate and hyomandibular cartilages forming a triangle; and at the dorso-latero-posterior corner of hyomandibula. The *constrictor hyoideus ventralis* (chv) is a ventral muscle that is separated from the *intermandibularis* (im), which is ventral to it, by a thin fascia. Almost its whole length is ventrally covered by ampullae of Lorenzini and connective tissue. This muscle originates from a seam of connective tissue at midventral line and inserts on the ventroposterios edge of the ceratohyal.

Branchial constrictors.

The branchial muscles comprise the constrictors and three other that were not examined: *interbranchialis*, *adductor arcuum branchialium* and *arcualis dorsalis*. The *constrictors branchiales superficialis* (cbs) are five unities, each covering externally a different branchial arch, beginning with the hyoid arch. As there are too much ampullae of Lorenzini and connective tissues, it is challenging to tear each bundle apart from the others. The anterior portion of these muscles originates at the dorso-lateral wall of the epaxial musculature and the posterior at the *cucullaris* (ccl). They are located posteriorly to the *constrictor hyoideus dorsalis*, in almost a continuum, and they are inserted on connective tissues at the latero-ventral side of the body that do not reach the middle line. It is from these connective tissues that *constrictor hyoideus ventralis* originates.

Hypobranchial spinal muscles.

These muscles are located beneath the basibranchials. The *genio-coracoideus* (gco) is a thick and narrow muscle that strongly inserts on the mandibular cartilage symphysis and becomes a thin and wide muscular sheet towards the posterior portion that, together with a fascia, originates at a posterior portion of the *rectus cervicis*. It is after the level of the coracoid that this muscle is clearly just one sheet and becomes thinner and wider; besides, it is before this level that both sides of the muscular sheet become apart and connected by a connective tissue. This origin is at the level of the pectoral fins and its most lateral portion is connected to the fins' muscles base. The fascia that covers the *constrictor hyoideus ventralis* (chv) comes from between both sides of the *genio-coracoideus*, which has left and right portions at its most anterior portion, close to the mandibule. There is a muscle slip, the *genio-coracoideus externus* (gcoe), which is a paired structure that arises from the antero-lateral surface of coracoid. Both right and left slips meet at the anteriormost portion of coracoid e go ventrally, converging to the *genio-coracoideus*.

The *rectus cervicis* is muscle with two sheets and it is dorsal to the *genio-coracoideus*. Both portions are divided by a transverse septum that divides the muscle in an anterior, the *coraco-hyoideus* (coh), and a posterior *coraco-arcualis* (coa) part. The *coraco-hyoideus* is a wide and thick muscle that inserts on the ventro-posterior surface of the basihyal cartilage. A little in front of the coracoid level there is the spetum that divides it and determines the *coraco-arcualis*, which originates at the ventro-anterior side of coracoid. In the midlle of the longitudinal axis of the *coraco-arcualis*, approximately over the coracoid, comes down from a dorsal region a fascia that passes through both sides of this muscle and joins to the dorsal portion of the *genio-coracoideus*, which is ventral to it. There is a thick sheet of connective tissue that covers the *coraco-hyoideus* ventrally, anterior to its opening.

The *coraco-branchiales* (cob) are slips of muscles immediately below the floor of the pharynx. The most anterior one is the *coraco-branchialis 1* (cob1) that originates from a dorsal posterior portion of the *coraco-hyoideus* and inserts on the postero-lateral part of the basihyal cartilage, dorsal to *coraco-hyoideus* insertion on the same cartilage. These two muscular bundles surround the articulation of the ceratohyal and the basihyal is ventrally and dorsally.

There are two muscular bundles dorsal and thinner to the *rectus cervicis*, one at each side. They originate at the most dorsal portions of coracoid and are separated from the branchial arches only by a fascia. There is another dorsal and medial single muscular bundle dividing the base origin of the *rectus cervicis* that originates from the most anterior portion of coracoid and pericardium. It seems like a thin medial wall muscule right below the basibranchials.

Other visceral muscles.

The *cucullaris* (ccl) is a trapezoidal muscle sheet located above the branchial region. It originates on the dorso-lateral fascia of the epaxial musculature, immediately posterior to *constrictor hyoideus dorsalis*, and ends on the anterior surface of scapula. It inserts on the dorsal end of extrabranchial cartilages. The *constrictor oesophagi* (oes) is a circular and thick muscle that surrounds the oesophagus. On its most anterior portion it attaches to the ceratobranchial 5, and both posterior basibranchials. It is related to the dorsal region of the gill pickax.

Pectoral fin and girdle.

There are two associated muscles with the pectoral fin: the *levator pectoralis* (lpe) and the *depressor pectoralis* (dpe). The *levator pectoralis* covers half of the anterior, the dorsal and half of the posterior sides of the pectoral fin. It is a bigger muscle than the *depressor pectoralis*; it originates on the posterior portion of scapula, covers the dorsal half of the anterior and posterior pectoral radials, and it inserts on the ending of those radials. The *depressor pectoralis* covers the ventral portion of the anterior and posterior sides of the radials. Both muscles are connected to the *rectus cervicis*.

The hypaxial musculature completely coats the coracoid, as it is a continuum with *rectus cervicis*, and it originates on the posterior portion of the girdle, very close to the fin. There are muscular bundles inserted on the anterior and on the posterior sides of the coracoid, as well as ventrally, and the girdle it totally nested within the musculature.

Pelvic fin.

There are three muscles composing the pelvic fins: levator, adductor and depressor. The *levator pelvicus* (lv) is a muscle that originates on the ventro-lateral surface of the hipaxial body musculature and inserts on the dorsal side of the pelvic fin, reaching the radials. It starts at the beginning of the pelvic girdle, and supports the fin until the ceratotrichia. It does not cover the whole dorsal surface of the fin and it ends at a diagonal line from the end of the base of the fin until almost the external lateral corner of the fin. The ventral muscle, the *adductor pelvicus* (av), supports the rest of the dorsal side of the fin. This muscle originates from the most central part of the puboischiatic bar and from some connective tissue found in between both fins; it inserts on the ventral posterior portion of the basipterygium and ends at its distal portion. As it covers the internal region of the ventral side of the pelvic fin, the *adductor pelvicus* (av) makes a turn, surrounding the basipterygium and it is also found on the dorsal side of the fin, at its most internal portion. The other pelvic muscle is the *depressor pelvicus*, which is also ventral and originates from the pubuischiadic bar. However, it originates from the ventral side of this cartilage and covers almost all of its length and width. The only portion of theis cartilage that is left exposed is the medial portion, which can be seen in a rhomboidal shape. The *depressor pelvicus* covers the part of the ventral side of the pelvic fin that is not covered by the *adductor pelvicus*. So, it also extends further than the previous muscle and reaches and inserts on the ventral side of the radials. There is approximately one muscular bundle per radial.

Clasper.

Four muscles compose the clasper musculature, and their nomenclature follows Jungersen, 1899. There are two bundles of the *extensor* both running at the same direction, but one is more dorsal and internal to the other. These are dorsal muscles that originate from the posterior portion of the pubuischiatic bar. They are dorsal to the *adductor pelvicus* and cover it almost completely. Posterior to them, at the dorsal distal part of the clasper, there is the *dilatator*, which is the most internal muscle and inserts on the gland through a long and thick tendon. The *dilatator* makes a turn on the inner portion of the clasper and is also found on its ventral side. Its tendon is apparent on the ventral side too, and inserts on the ventral portion of the gland. Therefore, there are no muscles inserting on the gland, just the tendon of the *dilatator*. The other clasper muscle is the outer lip, which is dorsal and external to e clasper. It is a bundle that originates at the line of the distal part of the *extensor*, runs at the side of the unknown (?) cartilaginous piece and ends right before the spur. The last clasper muscle is the *compressor*, which is a wide and flat muscle laying ventrally to the *adductor pelvicus* and *depressor pelvicus*.

Dorsal fins.

Each dorsal fin skeleton base is covered by the *inclinator dorsalis* (id), which is a wide and flat muscle slip. It originates at the ventral margin of basal elements and at the body musculature, and it inserts on radials and ceratotrichia; and it does not reach the vertebral column. This muscle is present on each side of the dorsal fin and on both fins.

Caudal fin.

Epaxial (epx) and hypaxial (hpx) muscles cover the caudal fin skeleton. The *flexor caudalis* (fxc) is at the base of the lower caudal lobe, originates from the ventral surface of the hypaxial musculature and inserts on the distal ends of basiventral processes ans ceratotrichia of the lower caudal lobe. The epicordal radials are exposed and not covered by any musculature.

Lateral line canals

The lateral line canals are seen at each lateral wall of the specimens and reach nearly the end of the caudal fin. These canals start being parallel to each other posteriorly to scapula. At the head there are many distinct canals, and they are named following Chu & Wen (1979).

From above the gill openings, where the canals are more distant from each other, they begin getting closer and then become parallel again right before the spiracles, however, the distance between them is less than half of the distance throught the body length. Between the spiracles, they make a curved turn toward each other and meet at the middle forming a semicircle, whose convex side is directed towards the posterior portion of the body. This semicircle is the *supratemporal canal* (spt). Anteriorly to it the lateral canals are almost parallel and close to each other, and are called *preorbital canals* (poc). Immediatelly anterior to them there is the origin of the *infraorbital canals* (ioc), which run perpendicular to the previous canal, to the ventral side of the head, passing between the spiracle and eye. In a continue line with the preorbital canals, they begin getting apart in curved lines anteriorly above the eyes, and are called *supraorbital canals* (soc). These canals make another opening curve more anterior to the eyes, then they return to the previous position, but further anteriorly. This position is right between the nostrils and they go almost straight to the ventral side of the head (Figure 79).

At this ventral side, the dorsal supraorbital canals are called *prenasal canals* (pnl). After running mid-ventrally and between the nostrils, the prenasal canals do a short turn toward each other and join, forming only one very short line. This line, the *medial canal* (mdc), does a brief run in the middle of the ventral head, between the snout and the mouth. The medial canal then separates into two lines, which are perpendicular to the body axis and form a 180-degrees angle between them. These two canals are called *nasal* (nas) and, after running double the length of the medial canal, the do a 90-degrees turn and direct posteriorly. Then, the nasal canal does a subtle turn towards the eye and meets another canal that run below the eyes, the *antero-ventral portion of the infraorbital canals* (avioc) (**Figure 80**).

On the dorsal portion of the snout there are two canals that encircle the nostrils. They are external to the most anterior portion of the supraorbital canals, and make a curve around the nostrils running to ventral side of the head. However, right after the end of the nostrils, these canals make a turn and direct toward the eyes, where they run along below the eyes (Figure 81). At the midpoint of these antero-ventral portions of the infraorbital canals that is where there is the junction with the nasal canals. Right after the eyes, the avioc join with the infraorbital canals that come from the dorsal side, and after this point, they are called *hyomandibular canals* (hyc). They continue along the ventro-lateral portion of the head, and end posteriorly to the mouth, together with the end of the skin of the labial furrow. No mandibular canal was observed.

3. Remarks: lateral line canals in *Dalatias licha*

The lateral line canals are seen at each lateral wall of the specimens and reach half the length of the caudal fin. These canals start being parallels to each other posteriorly to scapula. At the head there are many distinct canals, and they are named following Chu & Wen (1979).

From above the gill openings, where the canals are a little more distant from each other, they begin getting close8r and then become parallel again immediately behind the spiracles. Between the spiracles, they make a curved turn toward each other and meet at the middle, forming a line that is not completely transverse to body axis, but with both concave sides directed towards the anterior region. This line with is the *supratemporal canal* (spt).

Right anterior to supratemporal canals, as a continuum with the lateral line, there is a very short canal named *preorbital* (poc) that is slightly inclined to the middle of the head. After this short length, there is a lateral ramification at each side forming the *infraorbital canals* (ioc) that run between the spiracle and eye. Anteriorly to this ramification, the preorbital canals are called *supraorbital canals* (soc), which start getting closer to each other in a curved line right above the level of eyes (Figure 82).

Then, these canals get apart in front of the eyes, forming a great curve at each side, and finally turn toward the point in between the nostrils, where they get close and parallel again. These canals run to ventral side of the head and, posterior to the end of the nostrils, they start to run in direction to each other and are named *prenasal canals* (pnl). They meet each other at the middle of the ventral side of the head and form a very short line, with a length of only one pore, called *medial canal* (mdc).

The medial canal then separates into two lines forming an angle a little bigger than 180 degrees between them, which is directed to the caudal region. These two canals are called *nasal* (nas) and, after running three times the length of the medial canal, the do a turn a little bigger than 90 degrees directed to the posterior portion. Then, the nasal canals run for the same length as previously mentioned and do another turn a little bigger than 90 degrees, but the angle is pointed toward the snout.

The nasal canals run almost the whole length of the eyes, below them. Just anterior to the mouth’s corner the nasal canal makes a short elevation in direction to dorsal side, and returns to the original alignment at the mouth’s corner. At the beginning of this elevation there is a ramification with the *antero-ventral interorbital canal* (avioc), forming a small acute angle with the nasal canal and running toward the lower portion of the eye. Its length is, approximately, the same as the first and second turns of the nasal canal. Below the eye, this avioc makes a turn toward the caudal region in an acute angle. It runs along the postero-ventral region of the eye and meets the infraorbital canal that comes from the dorsal side, almost perpendicular to the body axis, in between the eye and spiracle.

Posterior to the ramification from which emerged this canal, the nasal canal is called *hyomandibular* (hyc). It continues along the ventro-lateral portion of the head, besides the mouth, and ends posteriorly to it, together with the end of the skin of the labial furrow. There is a pair of canals at each side of the posterior region of the mouth. Each *mandibular* (mc) canal is oblique and runs from the posterior corner of the mouth to a postero-medial region. These canals are a little bigger than the supratemporal canal, they end anteriorly to the hyomandibular ending, and they have many short ramifications on both sides (Figure 83).

On the dorsal portion of the snout there are two canals (avioc) that encircle the nostrils. They are external to the most anterior portion of the supraorbital canals, and make a curve around the nostrils running to ventral side of the head. However, right after the end of the nostrils, these canals make a turn and direct toward the eyes, where they run along below the eyes. At the midpoint of these antero-ventral portions of the infraorbital canals that is where there is the junction with the nasal canals.

VIII. Discussion

1. Taxonomic Revision

Concerning the nomenclature of the family Dalatiidae, it is currently regarded as being named by Gray (1851). This author was the first one to create a group using the name "*Dalatias*", a genus that was described in 1810 by Rafinesque. Gray defined a subfamily named "Dalatiana" under the family Squalidae referring to species which lacked dorsal spines, and included two genera: *Dalatias* and *Echinorhinus*. Within the genus *Dalatias* he added two species among others: *Dalatias lichia* and *Dalatias brasiliensis.*

However, the first author to use the name "Dalatiidae" was Gill, 1893, when he synonymized it to the family "Scymnidae" Müller & Henle, 1815. As there is no work of Müller & Henle from 1815, it is inferred that it is a reference to the family "Scymni" Müller & Henle, 1841, that included species whose dorsal fins lacked spines. As Gill, 1864, changed the name "*Scymnus*" to "*Isistius*", the change in family name was a consequence. Gill (1893) included 2 subfamilies within the new family Dalatiidae: Somniosna and Dalatiina. Therefore, the author of the name "Dalatiidae" is Gill, 1893, instead of Gray, 1851.

Another issue regarding nomenclature is observed in both genus *Isistius* and *Euprotomicrus*, which is a mistake concerning the year of publication of Gill's paper describing both. It is currently known that both were described in 1865; however, this work by Gill was published on 1864 instead. On an article entitled "Synopsis of the Eastern American Sharks" he writes a synonymy of those sharks and, on page 264, at the synonymy of the species *Somniosus microcephalus,* he mentions the family Scymnoidae and puts an asterisk besides it to write on a footnote the genera that belong to it. Among these genera he includes *Isistius* and *Euprotomicrus,* two names that have never been used before. He writes a short description of *Isistius*: "it is distinguished by its similar posterior dorsals and caudal fin", and he synonymizes it with *Scymnus brasiliensis* Müller & Henle. Gill does the same with *Euprotomicrus*: "teeth like *Somniosus*, but in moderate number and very small first dorsal", and also synonymizes it with *Scymnus labordii* Müller & Henle. Therefore, when referring to the genera *Isistius* and *Euprotomicrus,* the responsible author for those names is Gill (1864).

There are, currently, three valid species within the genus *Isistius*: *I. brasiliensis*, *I. plutodus* and *I. labialis*. After an extensive research over the existing literature and examinations of almost all specimens of *Isistius* ever collected, the taxonomic revision was developed. The most important observation regards the variation among the species *Isistius brasiliensis*, and the suggestion that *I. labialis* is not a valid species, but one more specimen that is within *I. brasiliensis*'s variation. Therefore, there should be only two valid species on the genus *Isistius*: *I. brasiliensis* and *I. plutodus* (Table 15).

There are differences in coloration, such as the absence of the darker collar, as first mentioned by Müller & Henle (1841), at the description of *Scymnus brasiliensis unicolor*. This specimen comes from the Western Indian Ocean, as well as another specimen deposited at the Natural History Museum of Vienna, Austria. While the type does not show the darker collar, the other specimen does. A recently caught specimen from Eastern Indian Ocean, which was not examined in person, but through photographs of the fresh specimen shared by Dr. William White (CSIRO), has the most common coloration observed in *Isistius brasiliensis*. It has a dark brown color on the dorsal side and on the ventral collar, while the ventral side of the body has a lighter brown color. These are the only known specimens from the Indian Ocean, and although the type seems to lack the darker collar, it may be inferred that it is a result of some combined factors, such as its very dark color on the dorsal and ventral side of the body, and its poor conservation conditions.

There are also some variations in colorations in *Isistius plutodus*, as the holotype used by Garrick & Springer (1964), to first describe the species. The authors affirmed there was no ventral dark collar on the specimen, and described the specimen with a dark brown color on dorsal and ventral sides, with the exception of a paler ventral region between the mouth and gill openings. However, Dr. Geroge Burgess (FLMNH) made it available the original photographs used by Stewart Springer to describe the new species and, after carefully examining the images, it is possible to notice a distinct coloration on the ventral region (Figure 25). The extension of this difference in shade coincides to what is observed in other specimens of *I. plutodus.* The ventral light brown color posterior to mouth mentioned by Garrick & Springer, usually precedes the darker collar in many analyzed specimens. Furthermore, when analyzing the holotype itself, which is currently not dark brown as mentioned by them, but a light caramel color, it is possible to see a subtle difference in coloration at the posterior end of the supposed collar. Besides, Mark Grace (Research Fish Biologist at NOAA) shared a photograph of a fresh specimen of *Isistius plutodus* recently collected at the Gulf of Mexico. This specimen has a dark brown color on its dorsal side and ventral collar, and a light brown color on its ventral side. This specimen's coloration resembles other analyzed specimens of *I. plutodus*. Therefore, since the holotype currently does not show the same coloration used by Garrick & Springer to describe the species in 1964, it is probably a consequence of the preservation in alcohol. And the lack of ventral collar mentioned by them might be a misinterpretation of the specimen's coloration.

Besides the differences observed on the ventral dark collar in both species, there are also a variety of combinations of shades on specimens. The white tips on all fins, the darker region on the distal portion of the caudal fin (with the exception of the tips, which are usually white) and on the center of all fins are shades that might change depending on the specimen. Furthermore, while some recently collected and better preserved specimens show a vivid brown color, older and poorly preserved ones may vary from dark brown to a very pale yellow. However, in those where it is possible to observe the ventral dark collar, if the specimen is lighter than expected, the collar is also lighter, even though it is darker then the rest of ventral side.

Another feature that is variable among *Isistius* specimens is the presence of photophores. Generally, it is possible to observe their existence without a stereomicroscope, as they seem to be small black dots mainly on the ventral surface. The photophores also contribute to giving a darker coloration to specimen depending on their frequency and spacing between each other. As there is no photophore on the ventral collar, if the specimen has many photophores, the ventral collar might not be so easily differentiated, as the individual will have a darker ventral side. There might also be some photophores on the dorsal side of the head, lateral region of pectoral fins, dorsal, caudal and pelvic fins, and claspers, with the exception of their white tip. However, many specimens lack photophores on their whole body; or they might have some only ventral side and none on dorsal side; and they may not show any photophores on fins. The shared feature among all specimens is the absence of photophores on the ventral collar region. Even though a specimen may not have a distinguishable collar, there is no photophore on this region. As a result, both *Isistius brasiliensis* and *I. plutodus* show variations in colorations, ventral collar and photophore distribution which may be due to poor conservation conditions, or the effect of alcohol on the specimens.

An additional trait that can facilitate the identification of *Isistius* species is the gum: while it wavy and short on *I. brasiliensis*, it is straight and longer on *I. plutodus*. Likewise the differences in hardiness of mandibular and hyoid arches, as well as the absence of the upper posterior labial cartilage and the muscle *levator labialis*, these traits altogether may have some consequences on the feeding mechanism of *I. plutodus*. This is due to the fact that the combination of these features on *I. brasiliensis* is responsible for its feeding ability; as some of them are absent or subtler in *I. plutodus*, there might be some ecological and functional implications yet unknown.

Besides the gum, the relative size of symphyseal lower teeth in relation to the parasymphyseal one is also a characteristic that differentiates both species. In *I. brasiliensis*, the lower symphyseal tooth is, approximately, 5% shorter than those adjacent to it, while in *I. plutodus* they are the same height.

2. Comparative Morphology

The anatomy of both *Isistius* species is very similar in terms of cartilage size, shape and number, as well as musculature, apart from some subtle differences, which are mentioned as follows. Whenever possible, there are comparisons with other Dalatiidae, Etmopteridae or Oxynotidae genera, whose data were taken from analyzed specimens or from literature.

2.1. Skeleton

Since the skeleton of *I. brasiliensis* and *I. plutodus* resemble a lot each other, the hyoid arches, pelvic girdles and fins, and caudal fins are not mentioned bellow, as there is no significant difference among them, besides no outstanding morphological structure.

2.1.1. Neurocranium (Figure 52, Figure 74)

The neurocranium in *Isistius* is externally divided on four regions, as in other squaleans, from the most anterior to posterior: ethmoidal (rostrum and nasal capsules), orbital (orbits, basal plate, and cranial roof between them), otic (otic capsules, cranial roof and basal plate between them), and occipital (posterior end of neurocranium) (Compagno, 1988; Shirai, 1992a).

The rostrum is slender, longitudinal cartilage at the dorsal anteriormost region of ethmoidal portion. In *I. brasiliensis* it is only connected to the neurocranium at its most anterior part, in between the nasal cavities, while its length is supported by connective tissue and Lorenzini ampullae. While in *I. plutodus* the rostral process is very reduced as it is only a longitudinal cartilaginous elevation that is weakly prolonged forward the neurocranium and shorter than the nasal capsule height.

The nasal capsules are positioned below the rostrum and they restrict the olfactory organ dorsal, ventral, and anteriorly. However, there are some anterior and ventral openings, which differ between both species of *Isistius*. The nasal apertures are similar in their shape, in which there is a rounded dorso-lateral opening connected ventro-laterally to another opening that has a cylindrical shape. The sizes of these openings are 7.67% and 7.91% of HDL in *I. brasiliensis,* and *I. plutodus*, respectively. The right and left nasal capsules compose the ventral surface of the ethmoidal region with a space between them. This space, the internasal septum, develops and forms the *ectethmoidal chamber* (eec), which is separated in right and left sides by the *subethmoidal crest* (ser) that is a mid-ventrally elevated cartilage which posterior end is at the anterior one of the ventral edge of the interorbital wall, reaching the rostrum forming the *rostral keel* (rc). From the posterior portion of the nasal capsule's ventral side, arise two cartilaginous pieces from the subethmoidal crest that are directed latero-anteriorly, and closer to the nasal cartilages they change their path and direct towards the mid-length of subethmoidal crest. While in *I. plutodus* these cartilages do not meet, in *I. brasiliensis* they meet their opposite at the subethmoidal mid-length and divide the ectethmoidal chamber into an anterior and a posterior region.

The anterior wall of the orbit region, which is the same as the posterior wall of the nasal cavity, has a ventro-lateral process: the ectethmoidal process. Whereas this process is more flattened dorsi-ventrally and the angle from which it arised of the wall is bigger in *I. brasiliensis,* in the other species it has a pointy ventro-lateral ending, and this orbital anterior wall is almost perpendicular to body axis.

Both species have a membranous interorbital wall covering the wide-open gap in this wall, which, accordingly to Shirai, 1992a, is a unique feature of *Isistius*. This opening is proportionately bigger in *I. plutodus*, as it almost reaches the neurocranium roof, the anterior orbital wall, and the ventral portion of the interorbital wall. As the gap is wide, the ventral wall is thinner than in *I. brasiliensis*.

In *I. brasiliensis* the epiphyseal pit is posterior to the level of preorbital canals, and in *I. plutodus* it is slightly anterior to them. Besides, on the last species, the distance between the epiphyseal pit and the prefrontal fontanel is much smaller and there is a dorsal elevation between these two foramens, which are both reduced in size. However, in *I. brasiliensis*, the prefrontal fontanel is triangular foramen at the level of the ethmoidal canal and it is not only bigger than the epiphyseal pit in the species, but also of these two foramens in *I. plutodus*. The endolymphatic fossa is very similar in both species; however, in *I. brasiliensis* it is deeper in the neurocranium roof.

When it comes to neurocranium morphometry, although *I. brasiliensis* has a wider distance across postorbital processes in terms of nasobasal length (49.46% *vs.* 41.50%), the length of only one process in bigger in *I. plutodus* (4.15 mm *vs.* 3.99 mm), even when this species representative has a smaller total length (Table 5). The basitrabecular process is much bigger and pronounced in *I. brasiliensis* than in the other species, since it is larger (width from left to right edges in terms of head length: 22.89% *vs.* 21.88%), and the angle from which it arises of the palatine is much wider. The basal angle is also a difference in these two neurocraniums, since in *I. plutodus* its anterior portion is concave and, at the level of the foramen for the carotid artery it makes an abrupt turn towards the postero-medial portion of neurocranium. In *I. brasiliensis*, the basal angle, instead of curved, has an antero-lateral rectangular shape. The length of otic capsule is bigger in *I. brasiliensis* in terms of nasobasal length (32.19% *vs.* 29.29%), and the hyomandibular fossa in *I. plutodus* is closer to the foramens for pseudobranchial artery and the hyomandibular branch of facialis, as the otic capsule is reduced.

2.1.2. Mandibular arch (Figure 53)

Despite the cartilages shapes, joints, and positions being a lot alike between *I. brasiliensis* and *I. plutodus*, on the first species the cartilages are tougher and more robust.

The labial cartilages, which support the upper lip and its corner with the lower lip, are composed of two *upper cartilages*, the *posterior* (plc) and the *anterior* (alc), and a *lower* one (llc) that are connected to each other at the mouth corner. However, in *I. plutodus*, only two labial cartilages were observed: the lower and one upper labial cartilage (Figure 75).

2.1.3. Branchial arches (Figure 57)

In *Isistius* there are five pairs of branchial arches supporting the gills. Each gill is composed of dorsal and ventral elements. The dorsal ones are the pharygobranchials (on the roof of the pharynx), and the epibranchials. These two elements can be compared to the hyomandible of the hyoid arch. The ventral elements are the ceratobranchials, which are comparable to the ceratohyal of hyoid arch, and the hypo-, and basibranchials. In this genus, there is only one visible pair of hypobranchials and, as they are connected to the fifth ceratobranchials, they could be considered to be the fifth hypobranchials. As no other paired element was observed on the analyzed specimens of *Isistius*, it could be hypothesized this species lost the four anteriormost hypobranchials, or they are fused to the remaining fifth. However, an ontogenetic study should be done in order to clear understand what has happed to these cartilages.

A similar structure is found in *Trigonognathus* as described by Shirai and Okamura (1992) even though there are two pairs of cartilages anterior to what might be considered hypobranchials 5. Another shared similarity between these two genera is the presence of only one basibranchial. As this cartilaginous piece is directly connected to the hypothesized hypobranchials 5, it could possibly be the fifth basibranchial. Posterior to the basibranchial 5, there is another cartilage with a similar shape as the previous one, but tapering posteriorly. As it lies dorsal to the heart, it may be considered the basibranchial copula (Compagno, 1999). Shirai (1992a) defines a basibranchial copula as comprising basibranchials 4 and 5, and hypobranchial 5, which is not the case, since these cartilages seem to be distinct from each other in *Isistius*. Therefore, this posteriormost basibranquial cartilage could be the elongate accessory cartilage of Gegenbaur (1898) (*apud* Shirai (1992a)).

This unique arrangement of hypo-, and basibranchials observed in *Isistius*, with only one pair of hypobranchials and one cartilaginous piece of the other, is not observed in other Dalatiidae genera. The analyzed specimen of *Dalatias licha* (HUMZ 74585), which was studied by Shirai (1992a) has a pair of basibranchials connected antero-laterally to ceratohyal 3 and posteriorly to a wide and single cartilage (which is anterior to the basibranchial copula). Anterior to these basibranchials 3 there are two single cartilages positioned in the mid-ventral region of the branchial basket. The posterior one has a posterior extension that does not connect to any other cartilage, and lateral extensions that connect to ceratobranchials 2. Therefore, this cartilage might be called hypobranchial bar 2, as suggested by Shirai, (1992a) since it can possibly be a fusion of the hypobranchials and the basibranchial 2. Anterior to it there is the other single and similar cartilage that Shirai (1992a) named hypobranchial bar 1, as it connects laterally to ceratobranchials 1. These two single cartilages may be considered a fusion of a basibranchial to two hypobranchials as they are single cartilages positioned in the mid-ventral line of the basibranchial region, and they connect laterally to ceratobranchials.

A cleared and stained analyzed specimen of *Squaliolus laticaudus* (HUMZ 74974) was also described by Shirai (1992a). Similar to what was observed in *Dalatias,* the anteriormost cartilage at the basibranchial region is a single cartilaginous piece that is connected to ceratobranchial 2. However, posterior to it, there is a minute single cartilage that is connected to it. So, the anteriormost might be the fused hypobranchials 2, while the posterior one could be the basibranchial 2. Connected to ceratobranchials 3 are the hypobranchials 3, which in turn are posteriorly connected to a single cartilage that may be called basibranchial 3. This basibranchial is in between two paired cartilages, which are connected to ceratobranchials 4. So, this pair might represent the hypobranchials 4. These three cartilaginous pieces, hypobranchials 4 and basibranchial 3 are posteriorly connected to a wide cartilage. This last one is then antero-laterally connected to ceratobranchials 5, and posteriorly to the basibranchial copula.

In *Isistius*, the ceratobranchial 1 is far from the basihyal, which is a wide cartilage positioned dorsal to Meckel and somewhat inside its concavity. This condition is also observed in *Dalatias*, in which the ceratobranchials 1 are connected to the hypobranchial bar 1. However, in *Isistius*, the ceratobranchials 1 to 4 do not connect to any other cartilages, while in *Dalatias* they connect to bars, hypobranchials and basibranchials. But this lack of connection between ceratobranchials 1 and basihyal is not observed in *Squaliolus laticaudus*. So, other Dalatiidae genera should be studied in order to better understand this arrangement.

The absence of a connection between ceratobranchial 1 and basihyal, as well as the possible absence (or fusion) of hypo-, and basibranquials 1 to 4 leaves a wide empty space at the ventral region of the pharynx. Besides, as the basihyal is not connected to the ceratobranchial 1 its movements can be broad. So, as suggested by

Shirai & Nakaya (1992a) this particular structure observed in *Isistius* may be related to the retraction of the basihyal due to its unusual feeding behavior.

Shirai (1992a), on the description of the branchial arches of *Isistius*, mentioned that in this genus the gill pickax is slightly different from other genera, as in *Isistius* it is the fusion of not only pharyngobranchials 4 and 5, and epibranchial 5, but also the epibranchial 4 is included in this cartilaginous piece. However, this fusion of epibranchial 4 to the gill pickax was not observed in any analyzed specimen of *Isistius*. So, it should not be an apomorphic characteristic of this genus.

Ventrally to the branchial basket there are some poorly calcified cartilages that cover the ventromedial portion of the arches. They are dorsally connected to ceratobranchials (almost at their articulation with the epibranchials) and they extend until the ventral end of the muscle *constrictor branchialis superficialis*, surrounding laterally the muscle *coraco-arcualis*. Although only specimens of the genus *Isistius* were dissected in order to understand these cartilages, they were also superficially seen in a specimen of *Dalatias licha* (NMMBA N/C). However, in radiographs of other Dalatiidae genera, it was possible to observe four darker slits at the branchial region, which could be these cartilaginous pieces described above (Figure 45, Figure 84, Figure 85).

Fürbringer (1903), at the description of four species of rays, *Torpedo marmorata*, *Raja clavata*, *Trygon pastinaca* (=*Dasyatis marmorata*), and *Myliobatis aquila*, mentions the presence of a minute cartilaginous piece at the ventro-lateral region of each branchial arch, which he called “extra-septa cartilage”. Although these cartilages might seem to be the extrabranchials, they are positioned over the muscle *constrictor superficialis ventralis*, and over each arch, not lateral to it. Another author, Allis (1918), at the description of branchial arches’ muscles of *Raia clavata*, also mentions the presence of the extra-septa cartilage. As previously described, this cartilage is present at the muscle *constrictor*, and it is small, elongate and positioned transversely to the musculature over each branchial arch. Marion (1905) also shows these small ventro-lateral cartilages on a specimen of *Raia erinacea* (=*Raja erinaceus*); however, even though the author draws them, he does not describe these cartilages and states that they might not always be present. But when they do, these minute cartilages are over the lateral portion of the muscle *constrictor ventralis*, as Fürbringer and Allis also elucidated it.

A specimen of *Rioraja agassizii* was dissected with the intention of studying these "extra-septa cartilages", since they are barely mentioned on literature and they do not resemble the known extrabranchial cartilages even in their position or shape. In the specimen, it was found a flattened, small cartilage ventro-laterally to each branchial arch, and over the muscle *constrictor superficialis ventralis*.

Taking into account the resulting cladograms of Shirai (1992a) and Carvalho (1996), in which rays are more derived and have an origin within sharks, it could be inferred that the lateral gills in sharks changed their position into being ventral in rays. This external displacement results from an internal one, in which the internal angle between epi-, cerato-, and basibranchials has enlarged and, consequently, the gill openings have moved. The cartilages observed in *Isistius* and other related genera, which are ventromedial to branchial arches, may have also gone under a displacement together with the branchial arches themselves. However, their direction of movement could have been the opposite: instead of going from the ventral region to a medial one, following the route of the arches, they went from a ventromedial position to a ventrolateral one. Besides, these cartilages are considerably great in *Isistius*, as they occupy half the length of the *constrictor brachialis superficialis*. However, on the analyzed specimen of *Rioraja* and according to Fürbringer (1903) and Allis (1918) the "extra-septa cartilages" are small. So, there might have happened a decrease in size, besides the position rotation.

If this hypothesis is taken into account, the ventromedial branchial cartilages observed in Dalatiidae might be a similar structure to what was described by Fürbringer (1903), Allis (1918), seen on *Rioraja*, and may improve the answers regarding the Elasmobranch evolution. However, there is not enough data to support this hypothesis, and many more specimens of Dalatiidae, as well as other orders of elasmobranchs should be dissected to understand if these cartilages are similar and if they could be comparable.

2.1.4. Dorsal fins (Figure 59, Figure 76)

Both dorsal fins are very variable among the analyzed specimens of *Isistius*, even though they share the cartilaginous arrangement. These fins are composed by two separate unities, the anterior and posterior (first and second dorsal fins), and are supported by a *basal cartilage* (bad), and many *radials* (rds) that do not reach the margin of the fins (aplesodic style). No fin spine is present in any Dalatiidae species, except on the first dorsal fin of *Squaliolus*, whose spine might be hidden underneath the skin.

Basal cartilages are apart from dorsal column, triangular shaped in both dorsal fins with the most acute portion anterior to the broad one, and deeply inserted in the body. The acute portion may have an upturn at its dorsal distal part that varies in angle. At its postero-dorsal portion there is a protuberance at the cartilage, which is at its the border. Both dorsal fins with six to twelve radials: all with different sizes and shapes, and ventro-posteriorly to the radials there is always a half-moon shaped cartilage, that may vary in size and angle of curvature.

In the first dorsal, there are small, medium and big radials dorsi-posterior to the basal cartilage. In *I. brasiliensis*, it is common to observe a separate cartilage ventro-posteriorly to the previous ones, which quite often in perpendicular to body axis. The analyzed specimen of *I. plutodus* did not show this cartilage; however it does not mean this species lacks it. As the dorsal fins are variable, it may have been one specimen that does not show it, and it might be present in others.

The second dorsal fin has a ventro-posterior radial that is curved laterally and forms a 90-degrees angle with the fin’s axis. This lateral radial was also observed on the first dorsal fin of a specimen of *Squaliolus laticaudus* (HUMZ 74974), on the second dorsal fin of *Etmopterus lucifer* (HUMZ 35480), *Myroscyllium sheikoi* (HUMZ 74982), *Oxynotus bruniensis* (HUMZ 91383). However, in both analyzed specimens of *Dalatias licha* (HUMZ 74585, HUMZ 74603, and NMMBA N/C), no lateral expansion of a radial was observed in any dorsal fin. Besides, there is a dorsi-posterior invagination of the basal cartilage that Shirai, 1992a, called a spine rod, since a similar structure supports the fin spine in other species.

Holmgren (1941) on the description of the dorsal fins of *Dalatias licha*, mentioned the presence of a spine on the first dorsal with dentin and enamel, whereas it is always absent on the second fin. As there are some ventro-anterior cartilages on both dorsal fins of *Dalatias* that are not supported by the basal cartilage, Holmgren (1941) named them also as basals. However, Fürbring (1904) named those cartilages “radials”, and there is only one basal cartilage. This same author previously described the dorsal fins of *Dalatias* with the presence of a spine; a rudimentary one on the first and a more pronounced spine on the second. Even though these authors mentioned the presence of a spine on both or only on the second dorsal fin of *Dalatias*, no structure was observed on specimens. Although there is the rod, used by Shrai (1992a) to describe the indentation on the dorsi-anterior portion of the basal cartilage, no evidence of a spine was found.

2.1.5. Pectoral girdle and fins (Figure 60)

The pectoral girdle, or scapulocoracoid, surrounds the body ventro-laterally and it is inserted in the musculature posterior to the gills. In *Isistius*, it has an “U” shape on its most anterior portion, which is ventral to the heart and, and its posterior parts are directed postero-laterally until the pectoral fins, where the girdle turns to the dorsal side. The scapulocoracoid consists of a ventral coracoid bar and a dorso-lateral scapular process on each side, which are directed posteromediodorsally (Compagno, 1999).

In *I. plutodus* the scapulocoracoid is a structure formed by two paired cartilages: the left and right sides. In ventral view the coracoid is almost straight, and the line of junction of both sides is along the medial side of each piece of cartilage. Posterior to this junction both sides of coracoid are thinner and they form an acute angle directed toward the caudal region. At the pectoral fin level the cartilages turn dorsally and form the scapula. However, in *I. brasiliensis*, the scapulocoracoid is a unique cartilage divided into an upper (scapula) and lower (coracoid) portions, the last one meets its opposite part at the most ventral region, and it is not possible to see their junction, as it is only one long cartilage.

At the pectoral fin level there is a *foramen for pectoral fin nerves* (fpn), and some indentations, where the pectoral fin attaches to it. At the most distal part of the pectoral girdle there is the scapular process that is a portion of the cartilage that afunilates toward its end, directs dorsi-posteriorly, and is seen at dorsal wall of the body, below the skin and sided by the epaxial musculature.

The pectoral fin skeleton is composed of the basal cartilages and many radials. In *Isistius*, there is only one basal, and it may be the fusion of the *propterygium* (pr), *mesopterygium* (ms), and *metapterygium* (mtx). This basal cartilage connects the distal cartilages of the fin, and the radials to the pectoral girdle. The basal supports, approximately, seven proximal radials, each with a distal radial. The *metapterygial axis* (mta) is a dorsi-posterior cartilaginous piece that is larger and shorter than the proximal radial immediately ventral to it. This cartilage supports proximal and distal radials. Each radial is slender; from the most ventral to dorsal they get longer, and there might be intermediate radials in some specimens. In those, the distal radials are a disc on top of the intermediate ones. The number of proximal, intermediate and distal radials varies among different specimens.

As observed on a specimen of *Dalatias licha* (NMMBA N/C) and of *Euprotomicrus bispinatus* (BPBM 40404), as well as described by Shirai (1992a) all Dalatiidae show only one basal cartilage at the pectoral fin.

2.1.6. Claspers (Figure 62)

As observed for other cartilages, the species *I. brasiliensis* and *I. plutodus* are very similar. And the clasper's structure is also a lot alike between them. In both examined specimens of *Isistius brasiliensis* (MNHN 1996-0465 and UFPB 2669), the claspers are different from those described so far. Jungersen, 1899, described claspers of *Somniosus microcephalus* and compared it to those of *Squalus acanthias*, *Etmopterus pusillus*, and *Dalatias licha*; Gilbert & Heath (1972), *Squalus acanthias* and *Mustelus canis*; Compagno (1988) many Carcharhiniformes. These descriptions and definitions were used to describe the clasper of *I. brasiliensis*.

Jungersen (1899) described the dorsal marginal cartilage for *Somniosus* as an "elevated, hard calcified ridge anteriorly beginning as quite low, posteriorly becoming higher and higher, as well as thicker, and bearing in the posterior half an edge, folded to the dorsal side, irregularly indented, and collarlike". Gilbert & Heath (1972) said that both ventral and dorsal marginal cartilages are fused to the stem, which is the axial, and posterior to them there are four terminal cartilages. Compagno, 1988, said that in most sharks the clasper shaft, or sperm duct, has a pair of marginal cartilages fused to the axial cartilage. In carcharhinoids, the dorsal marginal forms a curved dorsomedial wall, and the ventral marginal a comparable dorsolateral wall. Despite these definitions, the dorsal marginal cartilage found in *I. brasiliensis* is fused to the axial and forms an elevation that begins anterior to the end-style and end at its middle. This cartilage supports the medial side of the sperm duct and, as defined by Compagno (1988) the ventral marginal should support the other side. However, in *I. brasiliensis*, the ventral marginal is completely ventral and does not form any part of the sperm duct. So, on the other side of the sperm duct, there is another flat and long cartilage, that extends until the most distal part of the clasper, and whose tip has almost no skin covering it and is poorly calcified, which can be seen from the difference in color and flexibility.

This cartilage that forms the outer wall of the sperm duct can also be seen ventrally, behind the ventral terminal cartilage and spur. As it is a poorly calcified distal part of a dorsal cartilage, it might be the dorsal terminal that has fused to another cartilage. However, by the definition of Jungersen (1899) a dorsal terminal cartilage is connected proximally to the dorsal marginal and it is supported by the end-style. It is a continuation of the dorsal marginal. As it is not the case in *I. brasiliensis,* since this tip is not connected to the dorsal marginal, it cannot be named as a dorsal terminal cartilage.

The proximal portion of this cartilage resembles the description of the higher and lateral part of the dorsal marginal by Jungersen (1899). However, as the sperm duct in *I. brasiliensis* runs between the actual dorsal marginal cartilage and this unknown one, there might have been an evolutionary change. The unknown cartilage may be the higher portion of the dorsal marginal cartilage observed in *Somniosus* that, in *Isistius,* is separated from it by the sperm duct.

On the other hand, it could also be an accessory dorsal marginal cartilage. However, this cartilage was identified by Jungersen (1899) and named by Compagno, 1988, as a movable structure that articulates with the dorsal marginal. Therefore, since this unknown cartilage does not articulate with the dorsal marginal, it cannot be called an accessory dorsal cartilage.

So, this cartilage will remain unnamed until the claspers of more species and genera are studied. There should be made a detailed description of the claspers of *Dalatias*, *Euprotomicrus*, and *Squaliolus* to better understand the cartilages the form the clasper in Dalatiidae. Then, species of other families, like Etmopteridae, Oxynotidae, and Somniosidade should also be analyzed as a mean of comparison to understand how these structures may have evolved in different groups and try to name them. If possible, an ontogenetic study would help the understanding of clasper's cartilages formation.

2.2 Musculature

As previously mentioned, both species *Isistius brasiliensis* and *Isistius plutodus* are morphologicaly very similar; therefore, as the musculature is greatly preserved among close taxa, the only distinctive difference between these species is on the mandible musculature. The majority of musculature complexes are not mentioned bellow: neurocranium, hyoid and branchial arches, hypobranchial, pectoral and pelvic girdles and fins, clasper, dorsal and caudal fins. It is due to the fact that there is no exceptional structure on the musculature of *Isistius*.

Mandible arch (Figure 64)

The overall structure of the mandibular muscles is a lot alike between *I. brasiliensis* and *I. plutodus*. Not only the muscles have approximately the same proportionate size to the head's size, but they also occupy the same relative positions. However, a peculiar muscle, the *levator labialis* (llb), which is a layer below the *adductor mandibulae superficialis* (ams) and a layer above the *adductor mandibulae* (am), and makes the connection of the dorso-lateral portion of the quadrate plate with the lower labial cartilage is not present on the species *Isistius plutodus*.

To ascertain if this feature was exclusive to the only dissected specimen of *I. plutodus* (ZUEC 8333) or if it might be a characteristic of the species, another mandibular region was dissected. The specimen ZUEC 8332 was used for this purpose and no *levator labialis* was found. As both specimens are from the coast of Brazil, it still cannot be conclusive, as specimens from other regions should be studied in order to understand the variability of this species.

So far, the muscle *levator labialis*, which was supposed to be an apomorphy of the genus *Isistius* (Shirai, 1992a), is exclusive of the species *I. brasiliensis*. However, it is intriguing that *I. plutodus* lacks this muscle, since it plays an important role on cookiecutter sharks feeding mechanism.

2.3. Lateral Line

(Figure 70, Figure 71, Figure 72, Figure 79, **Figure 80**, Figure 81, Figure 82, Figure 84)

The lateral line canals pattern in the genus *Isistius* is extremely similar, apart from slight curvatures of the *supraorbital canal* (soc), which has more indentions of *I. plutodus*; and the position of the *supratemporal canal* (spt) that is exactly in between the spiracles in *I. brasiliensis*, and just a little posterior to them in *I. plutodus*.

Ventrally, the differences are at the *nasal canal* (nas), whose curvature immediately posterior to the *medial canal* (mdc) is steeper in *I. brasiliensis*. Besides the angle in which this canal meets the *antero-ventral infraorbital canal* (avioc) that is almost right, while the *nasal canal* is slightly turned anterior at the point where it meets the avioc.

The canal *antero-ventral infraorbital* (avioc) was named as it has no connection anteriorly with the *supraorbital* canal (soc). It is a somewhat anterior and ventral portion of the *infraorbital* that runs anteriorly below the eyes and makes a lateral curve around the nostrils, where it does not connect to any other canal. As the nomenclature of the lateral line canals followed Chu & Wen (1979), and the only Squaliform described by them was *Squalus*, this canal was not mentioned, since there is no similar canal in the genus.

The *mandibular canal* was not observed in any specimen of *Isistius*; however, it should not be conclusive that this canal is not present on the genus, since the skin posterior to mouth is thin and there are much connective tissue, which may be easily cut during dissection and, consequently, damaging the possible canal.

Dorsally, the lateral line canals of *Dalatias* resemble those of *Isistius*, except for the position of the *supratemporal canal* (spt) that is slightly anterior to the spiracles. Ventrally, *Dalatias* shows mandibular canals at the posterior corner of the mouth, one at each side, with many ramifications. Besides, in *Dalatias* there is a peculiar insertion of the *interorbital canal* (ioc) on the *nasal canal* (nas) to form the *hyomandibular canal* (hyc) posteriorly. Below the eye and lateral to the mouth, the *nasal* has a small curvature directed dorsally before changing to a more ventral position. The *interorbital* inserts on the anterior portion of this elevation. However, differently from *Isistius*, the *interorbital* does not insert perpendicularly, as it goes ventrally and anteriorly, reaching the mid-length of the eye. At this point, this canal does a brusque curve posteriorly, towards the *nasal canal*. This canal distribution is no frequently observed in sharks.

3. Geographic distribution

(**Figure 15**, **Figure** 23)

Specimens of the genus *Isistius* have a worldwide distribution, as both species do. *Isistius brasiliensis* is found in the Atlantic, Pacific and Indian Oceans, with the highest latitudes: 42°N, 41°SW, and 25°SE in Pacific, 29°NW, 18°NE, 29°SW, and 32°SE in Atlantic, and 19°SW and 31°SE in Indian. A similar distribution is found for *Isistius plutodus*, even though there is no known specimen from Indian Ocean and Eastern Pacific: 29°NW, and 32°SW in Pacific, and 29°NW, 44°NE, 25°SW, and 32°SE in Atlantic. As the Temperate Zones occur from the Tropics of Cancer and Capricorn until the Arctic and Antarctic Circles, which encompasses the latitudes from 30° to 60° degrees North and South, the genus *Isistius* is present on the North and South Temperate Zones of the planet. However, most specimens occur on the Torrid Zone, in between the Tropics.

The majority of specimens are known from sites closer to the coast than open sea. It may be due to a slow swimming condition, or to the fact that they might breed close to shallow waters (Strasburg, 1963). However, as it was concluded that *Isistius brasiliensis* and *I. plutodus* are unique species with worldwide distributions, and no distinct populations among each species, it is questionable how the same species may occur on Atlantic and Pacific Oceans even if there is no known specimen in between them, for example, in the south of South America. There are two possible explanations for this wide distribution, considering that the specimens are good swimmers and able to travel long distances. The first one is that, unfortunately, no specimen of *Isistius* was ever collected at the south of South America due to lack of collection expeditions or because it is not common to capture these individuals, as they are mostly caught through bycatch. Another possible explanation is that this genus does not occur on this south, as the specimens would need to go below 55°S to pass from Atlantic to Pacific Oceans. Since no specimen of *Isistius* was ever caught in latitudes higher than 44°N and 41°S, it is not very probable that they could go from one Ocean to another below South America.

However, the south of Africa is at 34°S, which is a latitude that these specimens are known. So, specimens swimming below Africa and going to Indian Ocean could explain their distribution. From Indian to Pacific, they could go below (38°S) or above (10°S) Australia. So, it might describe how specimens of *I. brasiliensis* are found all over the world in between the temperate zones. Even though no specimen of *I. plutodus* is known from the Indian Ocean, this hypothesis should not be disregarded, as the absence of specimens in this Ocean might be a misrepresentation due to poor collection expeditions and difficulties in capturing this species.

4. Biology of *Isistius*

4.1. Bioluminescence

Bioluminescence is the production of visible light by an organism due to a chemical reaction (Claes & Mallefet, 2008). Among sharks, bioluminescence occurs in only two families: Etmopteridae and Dalatiidae. Even though these families comprise, approximately, 12% of sharks' diversity, their bioluminescence has not been deeply studied until recently. It might be due to their habitat, which is in the deep sea, or their rarity. The most studied genus is *Etmopterus* with regards to morphology of photophores, as well as light control; however, there have been some studies in a Dalatiidae genus, *Squaliolus*. It was not possible to study photophore morphology in *Isistius*; therefore, we assume it is similar to *Squaliolus*.

In Dalatiidae, there are photophores at the whole ventral surface of the specimens. In *Isistius*, there is a dark collar at the ventral surface, which is more pigmented than the ventral side of the body, but has the same amount of melanin as found at the dorsal side (Figure 86). This collar reaches the branchial openings and that is where it joins the dorsal coloration. Its length is from a little in front of the first branchial opening line until the line of pectoral fin origin. When observed with a stereomicroscope, the photophores look like a black ring located in between, and sometimes above, the dermal denticles. Claes & Mallefet (2010) observed the same structure in *Etmopterus spinax*. They also described that the black rings are composed by the chromatophores of the iris when it is fully opened, which allowed the observation of the bluish photocytes inside. However, it was not possible to analyze the morphology of photophores in *Isistius*, but it can be implied it is similar to what has been described for etmopterids. Although the black ring seen in etmopterids are described as being the pigments in chromatophores of the iris, dalatiids also show these black rings despite not having the iris. Therefore, this structure should be better studied in dalatiid specimens.

In most bioluminescent animals, simbiont bacteria produce the light; and this is not case for sharks, as they have an intrinsic method of emitting light. The main function of the luminescence might be counter-illumination, which is a camouflage that cloaks the emitter's silhouette by matching the physical characteristics of residual down-welling light (Claes *et al*., 2014).

The photophore in etmopterids is composed by many photocytes comprised in a pigmented sheath that has some blood sinuses. At the side of the photophore that is directed to the outer side of the body there is a pigmented iris-like structure, which is located in between the photocytes and lens cells. Therefore, the light is produced by the photocytes, passes through the iris depending on whether it is open or not, and then through the lens cells that will spread the light (Claes & Mallefet, 2009).

In dalatiids, more specifically in *Squaliolus*, the photophore morphology is a little different from *Etmopterus*. Instead of many photocytes inside a pigmented sheath with blood sinuses, there is only one photocyte and no blood vessel. Besides, there is no iris that could control the light emission, but some numerous pigmented cells present in the epidermis that help to control the light emission by obliterating the photocytes. The same lens cells seen in *Squaliolus* are found in etmopterids (Claes *et al.*, 2012).

Some authors have published hypotheses regarding the origin of bioluminescence in sharks and if it is an evolutionary convergence or a characteristic that appeared only once and evolved differentially in the families. To try to understand the evolution of bioluminescence and the sharks in which it occurs, we need to understand their morphology and control in each family.

Both *Etmopterus* species studied, *E. splendidus* (Claes *et al.*, 2011) and *E. spinax* (Claes & Mallefet, 2009), show similarities when it comes to photophore morphology, in addition to control mechanisms of luminescence in cartilaginous fishes. Claes & Mallefet (2009) provided the first evidence for a hormonal control of luminosity in sharks. When they tried to induce the photophores by classical neutransmitters, like adrenaline, noradrenaline, carbachol, 5-HT, and GABA, they observed no reaction, as well as absence of reaction to KCL. These results show that the control of bioluminescence in these sharks is not under neural influence.

Nevertheless, the hormones melatonin (MT) and prolactin (PRL) showed different responses, but both being stimulatory. While MT may induce a slow increase in light intensity that can last for hours, PRL induces a quicker response, which lasts for one hour. On the other hand, the hormone α- melatonin-stimulating (α-MSH) had an inhibitory effect on photophore luminescence. Since hormones circulate through blood vessels, there are some blood sinuses that go through the pigmented sheath of the photophore and act on a specific target.

In etmopterids, the hormones melatonin and prolactin act on the photocytes and stimulate the light production. They also act at the iris and the layer gets thinner and allows the light to passes through it. The inhibitory hormone is α-MSH acts directly at the iris, but has an opposite action as the previous hormones, as it stimulates the dispersion of the pigments at the chromatophores.

These hormones are the same used for elasmobranch’s pigmentation in those that are cryptic. Besides, the slowly increasing luminescence provided by hormones’ induction is an advantage for these sharks that are daily vertical migrators and are in a constant change of external luminosity, which is gradual. Sharks have a pineal window, and it helps them detect external light; therefore, the pineal gland controls the secretion of the hormone MT. When the shark is in shallow water, where the light is more intense, the pineal gland should secrete more MT, which stimulates the light production at the photophores and, as a consequence, the animal will glow brighter. Thus, it is camouflaged and shines accordingly to the light that is coming from above. The opposite situation is also true: when the shark goes deeper, the pineal window detects the light outside is decreasing. So, the pineal gland secrets less MT hormone and, therefore, the animal will shine less and will not glow brighter than the depth in which it is.

In cryptic elasmobranchs, there is a control of color change, which is made by the same hormones that control bioluminescence in etmopterids and dalatiids. Both prolactin and α-MSH stimulate the dispersion of the pigments on the melanophores that are punctate in shape in *Potamotrygon reticulatus* (Visconti *et al.*, 1999). Gelsleichter & Evans (2012) studied the pigmentation in elasmobranchs and found the most common chromatophores in this group is the melanophore, a cell with melanin. When there is a stimulus, α-MSH is produced at the pituitary gland and binds to hormone receptors in melanophores and promotes skin darkening by the dispersion of the pigment.

Hence, there should be more studies regarding photophores' morphology and control in Dalatiidae in order to better compare it with previous studies already done for Etmopteridae and try to understand the evolution of such a significative trait, which is the light emission in sharks.

4.2. Feeding Habits

Many specimens of *Isistius brasiliensis*, when cut open, had pieces of flesh inside their stomach (Figure 87, Figure 88). Jones (1971), and Shirai & Nakaya (1992), tried to explain how this species attacks its preys by biting, turning its body around and removing a piece of flesh, also known as a "cookie", and leaving the prey with a rounded wound. Many authors published papers reporting wounds in marine animals and acknowledging cookiecutter sharks made them. There is a list of authors and the species in which they noticed the wounds on Table 16.

The reported species of cetaceans are *Arctocephalus townsendi, Arctocephalus tropicalis, Balaenoptera borealis, Balaenoptera brydei, Balaenoptera musculus, Balaenoptera musculus brevicauda, Balaenoptera physalus, Balaenoptera* sp., *Delphinus* sp., *Feresa attenuate, Globicephala macrorhynchus, Globicephala melas, Grampus griseus, Kogia breviceps, Kogia sima, Lagenodelphis hosei, Megaptera novaeangliae, Mesoplodon densirostris, Mesoplodon grayi, Mesoplodon layardii, Mesoplodon mirus, Mesoplodon perrini, Mesoplodon stejnegeri, Mesoplodon* spp., *Mirounga angustirostris, Mirounga leonine, Monachus schauinslandi, Orcinus orca, Peponocephala electra, Phocoena phocoena, Physeter macrocephalus, Pseudorca crassidens, Sotalia guianensis, Stenella attenuata, Stenella clymene, Stenella coeruleoalba, Stenella longirostrus, Steno bredanensis, Tursiops truncates, Ziphius cavirostris*. The reported species of fishes are *Acanthocybium solandri* (Wahoo, scombrid fish), *Coryphaena hippurus* (dolphinfish), *Gasterochisma melampus* (butterfly kingfish), *Katsuwonus pelamis* (skipjack tuna), *Lampris guttatus* (opah), *Makaira mazara, Makaira nigricans* (blue marlin), *Remora australis* (whalesucker), *Ruvettus pretiosus* (oilfish), *Taractichthys steindachneri* (sickle pomfret), *Tetrapturus angustirostris* (shortbill spearfish), *Tetrapturus audax* (Striped marlin), *Thunnus alalunga, Thunnus albacares, Thunnus atlanticus, Thunnus obesus* (tuna), *Trachipterus jacksonensis* (blackflash ribbonfish), and *Xiphias gladius* (swordfish). Wounds on the sharks *Carcharodon carcharias* (great white shark), *Megachasma pelagios* (megamouth), *Prionace glauca* (blue shark), and *Rhincodon typus* (whale shark). There were also reported wounds on a human corpse (*Homo sapiens*) in Okinawa, Japan, and on a hawksbill sea turtle, *Eretmochelys imbricata*.

There has not been any published report of wounds of cookiecutter sharks on the giant oarfish, *Regalescus glesne*, so far. However, the specimen found dead on Oceanside, California, on October 21st, 2013, and deposited at SCRIPPS has wounds on its body. So, this is the first report of wounds of cookiecutter shark bites on a giant oarfish (Figure 89).

As mentioned by Strasburg (1963), there were found many pieces of squids inside cookiecutter sharks' stomachs, like beaks and tentacles. This author also compared the volume of ingested squids with the shark's size: a shark of 480 ml and a squid of 500 ml, and states that it is possible to happen, as *Isistius* usually prey on bigger specimens due to big and unusual jaw structure.

A common scenario when examining the stomach contents of *Isistius* is to find lower teeth (Figure 90). Strasburg (1963) suggests these are replacement teeth and he states that a specimen between 140 mm and 501 mm may have 15 teeth replacements, which represents a loss from 435 to 465 teeth. These teeth might be from cannibalism on other *Isistius*, or may be some teeth that are swallowed when they fall due to a tough bite. However, Strasburg found a whole row on the stomach of a specimen, also suggesting that the teeth fall together, all in a row. Therefore, these teeth may be found in stomach before they can be digested.

IX. Conclusions

- The genus *Isistius* and *Euprotomicrus*, which are currently regarded as being described by Gill (1865), are actually from Gill (1864). Besides, the family Dalatiidae, which is know to be described by Gray (1851), was indeed first mentioned by Gill (1893);
- There are two valid species for the genus *Isistius*: *I. brasiliensis* (Quoy & Gaimard, 1824) and *I. plutodus* Garrick & Springer, 1964, both with a worldwide distribution. Nominal species for which type specimens fall within the observed variation encountered in *I. brasiliensis* are: *Scymnus brasiliensis* Quoy & Gaimard (1824), *Scymnus brasiliensis torquatus* Müller & Henle (1841), *Scymnus brasiliensis unicolor* Müller & Henle (1841), *Leius ferox* Kner, 1864, *Isistius marmoratus* Rochebrune (1885), *Squalus fulgens* Bennett (1840), and the newest synonym *Isistius labialis* Meng, Zhu & Li (1985);
- Both valid species are highly similar, but morphometrics can help differetiate them, as well as tooth count and size, and caudal fin morphology;
- The muscle *levator labialis*, which plays an important role in the feeding mechanism of *Isistius brasiliensis* was not observed in *I. plutodus*, as well as the upper posterior labial cartilage. These absecences, in addition to having less robust mandibular and hyoid arches in *I. plutodus*, may have some implications for this species feeding habit;
- A group of cartilages observed on the ventromedial position of the branchial basket was observed in both *Isistius* species, as well as on radiographs of other Dalatiidae genera. There is no mention to these cartilages on recent literature, apart from some descriptions of similar structures in Rajiformes. There should be done a detailed study regarding these cartilages to verify if they are present in other taxa to, maybe, infer wether they might be the same as those in Rajiformes;
- In the clasper skeleton, a different cartilage was observed in *Isistius*, on the dorsolateral portion. It might be the dorsal marginal cartilage that separated into two pieces due to the change in the sperm duct path. However, it is not conclusive since claspers of related species should also be studied in order to understand this change in the sperm duct, as well as the appearance of this cartilaginous piece;

X. Conclusões

- Os gêneros *Isistius* e *Euprotomicrus*, que são atualmente considerados descritos por Gill (1865), são, na verdade, de 1864. Além disso, a família Dalatiidae, que é conhecida por ter sido descrita por Gray (1851), foi de fato mencionada pela primeira vez por Gill (1893);
- Há duas espécies válidas para o gênero *Isistius*: *I. brasiliensis* (Quoy & Gaimard, 1824) e *I. plutodus* Garrick & Springer, 1964, ambas com distribuição mundial. Espécies nominais para cada exemplar tipo encontram-se dentro da variação observada para *I. brasiliensis* são: *Scymnus brasiliensis* Quoy & Gaimard (1824), *Scymnus brasiliensis torquatus* Müller & Henle (1841), *Scymnus brasiliensis unicolor* Müller & Henle (1841), *Leius ferox* Kner, 1864, *Isistius marmoratus* Rochebrune (1885), *Squalus fulgens* Bennett (1840) e o novo sinônimo *Isistius labialis* Meng, Zhu & Li (1985);
- Ambas as espécis válidas são extremamente similares, mas a morfometria auxilia em sua diferenciação, assim como a contagem e o tamanho dos dentes, além da morfologia da nadadeira caudal;
- O músculo *levator labialis*, que tem um papel importante no mecanimo de alimentação em *Isistius brasiliensis* não foi observado em *I. plutodus*, além da cartilagem labial superior posterior. Essas ausências somadas aos arcos mandibular e hioide menos robustos em *I. plutodus* podem ter algumas implicações no hábito alimentar desta espécie;
- Observou-se um grupo de cartilagens na região ventro-medial da cesta branquial em *Isistius*, assim como em radiografias de outros gêneros de Dalatiidae. Não há referências a essas cartilagens na literatura recente, além de algumas descrições de estruturas similares em Rajiformes. Deve haver um estudo detalhado dessas cartilagens para verificar se elas estão presentes em outros táxons para, talvez, inferir se elas possam ser as mesmas que as encontradas em Rajiformes;
- Na porção dorso-lateral do esqueleto do clásper de *Isistius* observou-se uma cartilagem diferente. Ela pode ser a cartilagem marginal dorsal que se separou em duas porcoes devido à alteração no caminho do ducto espermático. Porém, não é conclusivo já que devem ser estudados clásperes de espécies

relacionadas para se entender essa mudança no ducto espermático, assim como o surgimento dessa peça cartilaginosa;

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Tables

Table 1. List of Institutions where the analyzed specimens came from.

Institution	**Abbreviation**
Academia Sinica, Taiwan	ASIZP
Academy of Natural Sciences	ANSP
American Museum of Natural History	AMNH
Australian Museum	AM
Bernice Pauahi Bishop Museum	BPBM
Burke Museum of Natural History and Culture	UW
California Academy of Sciences	CAS
Coleção de Elasmobrânquios do Departamento de Biologia Animal e Vegetal da Universidade do Estado do Rio de Janeiro	C.DBAV.UERJ
Coleção de Peixes do Museu de Zoologia da Unicamp	ZUEC-PIS
Commonwealth Scientific and Industrial Research Organisation	CSIRO
Fisheries Research Institute	FRI
Florida Museum of Natural History	FLMNH
Los Angeles County Museum of Natural History	LACM
Museu de Zoologia da Universidade de São Paulo	MZUSP

Museu Nacional da Universidade Federal do Rio de Janeiro	MNRJ
Muséum national d'Histoire naturelle	MNHN
Museum of Comparative Zoology	MCZ
Museum of Natural History - Vienna	NMW
National Museum of Marine Biology and Aquarium	NMMBA
National Museum of Natural History	USNM
National Museum of Nature and Science	NSMT
Natural History Museum	NHM
Natural History Museum and Institute Chiba	CBM
Scripps Institute of Oceanography	SCRIPPS
South China Sea Fisheries Research Institute	SCSFRI
Swedish Museum of Natural History	NRM
Texas Cooperative Wildlife Collection	TCWC
The Hokkaido University Museum	HUMZ
The South African Institute for Aquatic Biodiversity	SAIAB
Tulane University	TU
Universidade Federal da Paraíba	UFPB
Yale Peabody Museum	YPM

Zoological Museum Hamburg Fish Collection	ZMH

Table 2. Morphometric measurements used in this study, with the corresponding abbreviations, following Compagno (1984), Compagno (2001) e Last *et al.* (2007). All measurements were taken with a precision of 0.01 mm except for measurements marked with an asterisk (*), that were taken with 1 mm precision.

Morphometric character		**Methodology**
Total length	**TL**	Greatest direct distance between snout tip and caudal-fin apex
Precaudal length	**PCL**	Direct distance from snout tip to origin of upper caudal lobe
Pre-second dorsal length	**PD2**	Direct distance from snout tip to second dorsal-fin origin
Pre-first dorsal length	**PD1**	Direct distance from snout tip to first dorsal-fin origin
Pre-vent length	**SVL**	Direct distance from snout tip to anteror end of cloaca
Prepelvic length	**PP2**	Direct distance from snout tip to pelvic-fin origin
Prepectoral length	**PP1**	Direct distance from snout tip to exposed base of pectoral fin
Head length	**HDL**	Direct distance from snout tip to upper edge of the fifth gill slit
Prebranchial length	**PG1**	Direct distance from snout tip to upper edge of the first gill slit
Prespiracular length	**PSP**	Direct distance from snout tip to anteror margin of spiracle
Preorbital length	**POB**	Direct distance from snout tip to fleshy, anterior margin of orbit
Prenarial length	**PRN**	Direct distance from snout tip to anteror edge of outer nostril
Preoral length	**POR**	Direct distance from snout tip to upper jaw
Pre-inner nostril length	**PINL**	Direct distance from snout tip to inner edge of nostril
Inner nostril-labial furrow space	**INFL**	Shortest distance between nostrils and upper labial furrow
Mouth width	**MOW**	Distance between apices of labial pleats (junction of labbial furrows and postoral grooves)
Labial furrow length	**ULA**	Distance from apex of labial pleat to anteror edge of furrow

Internarial space	**INW**	Shortest distance between the two nostrils
Interorbital space	**INO**	Distance between softinterorbit in natural state (taken at mid-length of eye)
Eye length	**EYL**	Length of eye, not including eye socket
Eye height	**EYH**	Height of eye
Spiracle length	**SPL**	Maximum width of opening
First gill-slit height	**GS1**	Vertical height of first gill slit (not following profile of gill)
Fifth gill-slit height	**GS5**	Vertical height of fifth gill slit (not following profile of gill)
Interdorsal space	**IDS**	Shortest distance between first dorsal-fin insertion and second dorsal-fin origin
Dorsal-caudal space	**DCS**	Shortest distance between second dorsal-fin insertion and origin of upper caudal lobe
Pectoral-pelvic space	**PPS**	Direct distance from pectoral-fin insertion to pelvic-fin origin (taken on ventral side)
Pelvic-caudal space	**PCA**	Direct distance from pelvic-fin insertion to origin of lower caudal lobe (taken on ventral side)
First dorsal length	**D1L**	Distance from first dorsal-fin origin to apex of free rear tip
First dorsal anterior margin	**D1A**	Distance from first dorsal-fin origin to point of greatest curvature of apex of fin
First dorsal base length	**D1B**	Distance from first dorsal-fin origin to first dorsal-fin inserton
First dorsal height	**D1H**	Greatest vertical height from fin base to apex of fin
First dorsal inner margin	**D1I**	Distance from first dorsal-fin insertion to apex of free rear tip
First dorsal posterior margin	**D1P**	Distance from points of greates curvature of the first dorsal-fin apex and apex of free rear tip
Second dorsal length	**D2L**	Distance from second dorsal-fin origin to apex of free rear tip
Second dorsal anterior margin	**D2A**	Distance from second dorsal-fin origin to point of greatest curvature of apex of fin
Second dorsal base length	**D2B**	Distance from second dorsal-fin origin to first dorsal-fin insertion

Second dorsal height	**D2H**	Greatest vertical height from fin base to apex of fin
Second dorsal inner margin	**D2I**	Distance from second dorsal-fin insertion to apex of free rear tip
Second dorsal posterior margin	**D2P**	Distance from points of greates curvature of the second dorsal-fin apex and apex of free rear tip
Pectoral anterior margin	**P1A**	Distance from pectoral-fin origin to apex of fin (measured from ventral surface)
Pectoral inner margin	**P1I**	Distance from pectoral-fin insertion to apex of free rear tip (measured from ventral surface)
Pectoral base length	**P1B**	Distance from pectoral-fin origin to pectoral-fin insertion (measured from ventral surface)
Pectoral posterior margin	**P1P**	Distance between points of greatest curvature of pectoral-fin apex and free rear tip (measured from ventral surface)
Pelvic length	**P2L**	Distance from pelvic-fin origin (use finger to find origin) to point of greatest curvature of apex (measured from ventral surface)
Pelvic heigth	**P2H**	Greatest width of pelvic fin (measured from ventral surface)
Pelvic inner margin	**P2I**	Distance from pelvic-fin insertion to apex of free rear tip (measured on ventral surface)
Dorsal caudal margin	**CDM**	Distance from origin of upper caudal lobe to point of greatest curvature of apex of dorsal caudal lobe
Preventral caudal margin	**TLV**	Distance from origin of lower caudal lobe to point of greatest curvature of apex of ventral caudal lobe
Upper postventral caudal margin	**TLU**	Distance from greatest angle of caudal fork to point of greatest curvature of apex of dorsal caudal lobe
Lower postventral caudal margin	**TLL**	Distance from greatest angle of caudal fork to point of greatest curvature of apex of ventral caudal lobe
Caudal fork width	**CFW**	Perpendicular distance from greatest angle of caudal fork to dorsal caudal margin
Caudal fork length	**CFL**	Distance from greatest angle of caudal fork to origin of lower caudal lobe

Head width at nostrils	**HANW**	Width of head at anterior margin of nostrils
Head width at mouth	**HAMW**	Width of head at level of anterior margin of mouth
Head width	**HDW**	Width of head at fifth gill slit
Trunk width	**TRW**	Width of body at pectoral-fin insertions
Abdomen width	**ABW**	Width of body at first dorsal-fin insertion
Tail width	**TAW**	Width of body at pelvic-fin insertions
Caudal peduncle width	**TLW**	Width of caudal peduncle in front of caudal groove
Head heigth	**HDH**	Vertical height of head at fifth gill slit
Trunk heigth	**TRH**	Vertical height of body at pectoral-fin insertions
Abdomen heigth	**ABH**	Vertical height of body at first dorsal-fin insertion
Tail heigth	**TAH**	Vertical height of body at pelvic-fin insertions
Caudal peduncle heigth	**TLH**	Vertical height of caudal peduncle in front of caudal groove
Clasper outer length	**CLO**	Distance between lateral junction of pelvic-fin inner margin to apex of clasper
Clasper inner length	**CLI**	Distance between connecton of the clasper base dorsally with the tail to apex of clasper
Clasper base width	**CLB**	Width of clasper at pelvic-fin insertion

Table 3. Morphometric characterization of the genera *Isistius* (n = 226) and *Dalatias* (n = 32).

	Isistius						***Dalatias***					
	Range				**Mean**	**SD**	**Range**				**Mean**	**SD**
	mm		**%TL**		**%TL**	**%TL**	**mm**		**%TL**		**%TL**	**%TL**
TL	112.14	520	-	-	348.44	-	143	1260	-	-	463.91	212.69
PCL	97.83	445	77.06	138.76	86.16	2.90	109	1007	62.71	79.92	76.05	2.85
PD2	31	378	7.19	101.56	72.67	2.95	92	795	50.75	64.34	60.80	2.39
PD1	69.04	317	52.35	66.67	62.09	1.55	58	450	29.80	40.56	35.75	1.87
SVL	74.23	340	54.07	70.61	66.43	2.19	89	780	51.03	65.52	60.61	2.55
PP2	69.29	326	52.91	80.56	63.77	1.98	78	725	21.62	60.34	53.82	6.50
PP1	24.16	100.36	16.96	25.81	20.18	1.01	39	250	17.29	27.27	21.23	1.69
HDL	24.89	102.11	17.40	25.11	20.34	0.88	38	232	16.19	26.57	21.41	1.77
PG1	19.93	83.51	13.91	20.82	16.40	0.86	30	191	9.31	20.98	16.95	1.88
PSP	10.5	41.94	6.91	11.16	8.32	0.71	12.65	100	3.42	11.19	9.56	1.39
POB	3.08	17.01	1.63	4.15	2.82	0.45	4.86	54	1.31	4.78	4.07	0.61
PRN	0.83	7.9	0.49	3.44	1.13	0.28	2.34	37	0.86	2.94	1.89	0.34
POR	6.5	35.08	3.74	11.75	5.75	0.85	10.75	67	4.57	7.52	6.28	0.58
PINL	0.99	10.2	0.39	2.45	1.46	0.35	6.64	17	1.47	2.70	2.15	0.26
INFL	6.43	31.61	2.50	11.16	5.78	1.05	15.44	50	4.31	6.97	5.85	0.51
MOW	8.58	41.8	5.86	11.57	7.30	0.91	15.44	80	5.52	7.19	6.59	0.47
ULA	5.69	29.13	2.29	9.29	4.74	0.87	4.28	17	0.86	2.81	2.14	0.42
INW	1.44	7.6	0.75	2.09	1.35	0.17	1.97	40	0.50	3.60	2.80	0.55
INO	6.21	28.63	2.91	6.56	4.31	0.42	10.16	75	4.57	7.14	6.18	0.56
EYL	4.57	17.76	2.92	5.46	3.98	0.46	7.89	45.72	1.98	8.16	3.88	1.00
EYH	2.87	13.46	1.70	3.86	2.69	0.31	4	17	0.34	3.66	2.03	0.58
SPL	1.81	10.68	1.50	2.96	2.07	0.21	4.55	20	0.78	3.18	1.81	0.36

GS1	1.13	6.53	0.52	1.46	0.93	0.15	4.46	25	1.03	2.30	1.82	0.29
GS5	0.6	5.11	0.35	1.81	0.73	0.10	5.91	30	1.38	2.59	2.07	0.30
IDS	8.93	51.03	3.56	11.01	7.51	1.06	30.5	296	16.78	23.49	20.67	1.27
DCS	9.19	54.25	6.23	13.23	8.95	0.89	15.5	124	8.38	21.08	10.29	2.11
PPS	40.04	214	28.90	45.02	40.71	1.33	64.52	410	24.89	33.02	28.84	1.69
PCA	20.08	93.61	14.40	20.83	17.00	1.25	28.2	160	8.84	13.97	11.71	0.99
D1L	4.86	34.36	4.20	8.54	7.31	0.42	17.97	144	7.68	11.43	9.61	0.77
D1A	3.16	27.15	2.82	6.76	5.24	0.56	16.41	136	7.01	10.79	9.31	0.87
D1B	3.51	17.35	2.16	4.94	3.66	0.42	7.6	73	3.25	5.79	4.55	0.50
D1H	1.99	14.9	1.19	3.51	1.97	0.25	9.68	60	2.70	4.76	3.39	0.49
D1I	0.57	19.7	0.15	4.40	3.53	0.39	9.86	71	3.97	5.70	4.93	0.47
D1P	2.06	19.41	1.26	4.24	3.11	0.36	9.54	141	2.91	11.19	4.37	1.36
D2L	6.11	37.91	3.73	8.99	7.46	0.44	21.7	122	8.14	11.00	9.86	0.62
D2A	3.5	25.4	3.02	6.79	5.30	0.47	21.7	79	6.27	10.96	9.74	0.86
D2B	4.14	20.48	2.69	5.17	4.13	0.36	13.47	70	4.76	6.69	5.50	0.48
D2H	1.47	15.4	1.27	3.80	2.61	0.33	10.52	63	3.43	5.00	4.14	0.39
D2I	1.61	20.64	1.17	4.60	3.43	0.34	9.51	84	3.88	6.67	4.53	0.54
D2P	2.19	21.36	1.92	4.94	3.69	0.40	11.97	150	4.24	11.90	5.23	1.40
P1A	6.19	41.72	5.41	10.53	7.48	0.95	23.37	120	5.32	14.01	11.62	1.65
P1I	1.68	101	0.74	6.53	4.10	0.69	4.27	62	0.76	6.76	4.05	2.31
P1B	3.2	21.44	2.31	4.70	3.07	0.34	9.49	91	3.71	7.22	4.75	0.61
P1P	4.03	30.12	2.41	6.63	4.25	0.58	15.48	181	4.18	14.37	6.99	1.93
P2L	3.37	47.98	2.89	11.84	8.08	0.95	22.97	145	5.95	12.50	11.12	1.14
P2H	2.35	23.65	1.14	5.02	2.20	0.60	14.58	70	4.09	6.23	5.10	0.52
P2I	1.91	26.51	0.50	10.11	2.83	1.53	7	258	0.60	20.48	4.59	3.24
CDM	7.15	81.19	6.01	17.86	14.62	0.81	57.15	230	18.10	26.37	23.15	1.58
CPV	7.62	59.8	5.95	13.69	8.73	0.82	25.92	102	8.79	21.39	12.70	3.67

CPU	4.9	53.19	2.81	11.41	9.28	1.12	12.58	69	5.26	8.43	6.24	0.61
CPL	2.58	33.26	1.75	9.51	3.88	0.61	21.15	78.15	5.26	16.15	8.02	3.30
CFW	5.24	34.05	4.40	7.43	5.50	0.54	15.19	65	4.63	6.49	5.82	0.52
CFL	7.89	41.84	5.46	15.35	7.54	0.74	48.08	215	17.81	22.22	20.56	0.98
HANW	2.16	18.6	1.90	4.59	2.48	0.33	9.81	50	2.33	10.98	4.16	1.33
HAMW	10.76	44.98	6.95	15.78	8.60	0.84	23.33	92	6.21	10.77	9.36	0.99
HDW	7.75	57.45	6.81	13.74	8.72	0.63	25.86	145	8.50	11.84	10.70	0.96
TRW	6.87	57.17	4.13	11.34	8.06	1.28	27.88	53.06	7.16	11.08	8.78	1.12
ABW	3.59	31.77	2.48	6.89	3.89	0.54	14.36	97	4.37	8.34	5.93	0.96
TAW	3.41	30.63	2.08	6.64	3.59	0.54	6.89	27	2.23	4.18	3.54	0.50
CPW	1.13	13.41	0.91	2.82	1.50	0.26	4.81	29	1.34	3.65	2.21	0.39
HDH	8.2	47.86	4.71	11.83	7.97	1.07	21.41	66	5.69	9.92	8.28	0.90
TRH	8.59	53.32	4.38	12.06	8.02	1.30	25.27	66	5.69	10.40	8.24	1.34
ABH	5.23	41.47	3.72	9.00	5.27	0.77	21.33	41.53	6.31	9.95	7.93	1.25
TAH	4.59	31.81	2.86	6.90	3.97	0.53	13.54	31.75	3.16	6.76	5.22	0.88
CPH	2.32	11.61	1.28	2.50	1.65	0.14	7.14	42	2.07	5.38	3.07	0.52
CLO	1.36	12.91	0.74	3.23	1.96	0.42	0.9	32.65	0.22	7.26	0.95	1.70
CLI	2.3	32.58	0.84	8.20	5.10	1.01	5.56	86	1.55	7.41	3.04	1.56
CLB	0.47	7.24	0.26	1.88	0.85	0.21	0.46	13.23	0.11	2.94	0.47	0.68

Table 4. Morphometric characterization of the genera *Squaliolus* (n = 36), *Euprotomicrus* (n = 34), *Heteroscymnoides* (n = 1), and *Mollisquama* (n = 1).

	Squaliolus						***Euprotomicrus***						***Heteroscymnoides***		***Mollisquama***	
	Range				**Mean**	**SD**	**Range**				**Mean**	**SD**				
	mm		**%TL**		**%TL**	**%TL**	**mm**		**%TL**		**%TL**	**%TL**	**mm**	**%TL**	**mm**	**%TL**
TL	84.59	254	-	-	100.71	49.64	97	266	-	-	191.54	41.36	122.56	122.56	145	145
PCL	73	218	82.47	89.60	85.44	1.83	79	229	81.44	92.20	85.44	2.11	100.05	81.63	111	76.55
PD2	58	175	64.38	72.92	67.96	2.00	63	251	63.07	114.09	69.15	8.12	80.08	65.34	87	60.00
PD1	32	110.2	34.69	49.04	38.43	2.62	51	138	34.63	56.36	52.29	3.41	44.66	36.44	69	47.59
SVL	55	179	61.94	72.47	66.72	2.45	59	172	51.68	66.67	62.49	2.67	77.12	62.92	79.7	54.97
PP2	52	167	60.28	70.36	64.04	2.16	56	161	51.02	62.86	59.22	2.24	71.48	58.32	74.2	51.17
PP1	26.28	69.73	25.22	35.50	29.55	2.30	24.88	58.88	20.69	27.10	24.15	1.80	36.53	29.81	33.07	22.81
HDL	26.49	69.33	25.52	35.91	29.87	2.16	23.78	59.76	20.54	27.17	24.11	1.66	38.06	31.05	33.78	23.30
PG1	22.23	59.63	21.00	27.76	24.15	1.69	20.27	45.49	15.32	21.21	18.82	1.56	32.58	26.58	27.19	18.75
PSP	15.58	42.46	13.81	20.83	17.59	1.55	14.6	29.13	9.99	15.05	12.60	1.19	23.46	19.14	16.02	11.05
POB	8.05	19.84	6.32	11.99	9.48	1.18	7.37	14.63	4.50	7.90	6.14	0.75	15.62	12.74	10.78	7.43
PRN	2.76	8.56	2.16	5.54	3.73	0.73	2.73	6.72	1.42	3.31	2.48	0.44	4.94	4.03	3.57	2.46
POR	10.88	34.32	8.38	17.33	14.23	1.74	11.03	22.89	7.28	11.46	9.85	1.08	17.37	14.17	13.82	9.53
PINL	3.15	10.12	2.69	5.12	3.97	0.59	2.9	7.54	1.87	3.47	2.70	0.44	4.71	3.84	6.33	4.37
INFL	9.09	30.03	10.28	13.63	11.71	0.85	9.94	21.67	7.45	10.25	8.99	0.77	15.11	12.33	10.34	7.13
MOW	6.11	16.92	5.72	8.12	6.71	0.51	7.76	17.12	5.93	8.01	6.91	0.55	9.43	7.69	8.89	6.13
ULA	1.91	12.44	1.80	6.22	4.53	0.70	2.94	9.97	2.65	4.72	3.95	0.44	4.22	3.44	3.27	2.26
INW	2.15	5.44	1.95	3.40	2.29	0.30	2.53	5.43	1.54	3.17	2.21	0.35	3.81	3.11	6.35	4.38
INO	7.49	17.26	5.99	9.47	8.02	0.74	8.06	19.7	5.75	9.87	8.04	0.87	11.83	9.65	13	8.97
EYL	4.72	13.85	3.87	6.25	5.12	0.65	5.2	10.9	3.72	6.16	4.59	0.54	4.71	3.84	5.59	3.86
EYH	3.33	10.57	2.95	4.72	3.90	0.49	4.03	7.62	2.48	4.15	3.33	0.40	3.29	2.68	1.82	1.26

SPL	2.23	6.01	1.95	3.22	2.53	0.30	2.87	6.13	1.90	3.07	2.39	0.30	1.66	1.35	2.21	1.52
GS1	1	3.25	0.75	1.80	1.20	0.26	1.07	3.86	0.60	1.84	1.27	0.28	1.61	1.31	0.99	0.68
GS5	0.57	3.05	0.57	1.32	0.96	0.24	0.97	3.16	0.55	2.76	1.11	0.37	1.12	0.91	1.37	0.94
IDS	17.45	71.29	19.03	30.92	24.69	2.45	12.05	37.18	10.81	25.18	13.92	2.49	26.31	21.47	11.93	8.23
DCS	6.51	21.3	6.60	9.62	7.84	0.80	7.52	24.32	7.48	11.92	8.83	0.81	12.51	10.21	-	-
PPS	24.52	94.54	27.20	38.33	31.64	2.96	28.95	98.6	23.37	37.10	32.70	2.70	27	22.03	32.27	22.26
PCA	13.68	37.46	12.49	18.42	15.70	1.36	19.74	48.21	15.59	24.43	19.00	1.73	20.87	17.03	22.01	15.18
D1L	10.08	25.93	9.32	12.84	11.04	0.77	5.9	15.24	3.69	6.51	5.52	0.67	16.49	13.45	12.46	8.59
D1A	6.5	15.6	4.78	9.81	7.31	1.31	4.2	11.98	3.24	4.99	4.02	0.63	10.71	8.74	9.79	6.75
D1B	4.96	14.62	4.74	8.06	6.07	0.80	1.73	6.75	1.62	3.11	2.34	0.37	8.22	6.71	7.04	4.86
D1H	1.24	6.15	1.28	3.07	2.21	0.44	1.16	4.11	1.02	1.83	1.41	0.23	3.86	3.15	3.76	2.59
D1I	4.07	12.31	3.66	5.88	4.96	0.52	3.41	9.08	1.52	4.13	3.19	0.54	7.86	6.41	5.89	4.06
D1P	5.59	13.42	4.17	5.78	4.96	0.59	2.89	6.41	1.56	2.98	2.29	0.58	6.19	5.05	5.36	3.70
D2L	11.8	41.37	13.29	17.20	15.19	0.93	13.6	37.09	11.06	14.89	13.14	1.03	14.75	12.03	-	-
D2A	0	7.71	2.55	3.15	2.85	0.42	2.46	6.38	1.52	4.58	3.00	1.53	-	-	-	-
D2B	8.89	29.63	9.16	13.35	11.00	0.93	9.49	27.1	7.42	10.98	9.06	0.79	7.9	6.45	-	-
D2H	0.69	4.31	0.69	1.89	1.28	0.31	1.86	4.74	1.07	2.16	1.63	0.29	2.29	1.87	-	-
D2I	3.68	12.46	2.60	5.29	4.24	0.58	4.3	12.28	1.92	4.85	4.10	0.59	5.11	4.17	-	-
D2P	-	-	-	-	-	-	10.31	25.68	10.12	11.67	10.81	0.79	-	-	-	-
P1A	8.02	25.02	7.88	11.68	9.78	0.75	10.33	28.73	8.57	11.78	10.19	0.76	12.67	10.34	15.15	10.45
P1I	4.41	14.9	4.65	7.81	6.16	0.73	6.38	17.15	5.12	8.21	6.48	0.72	6.03	4.92	4.23	2.92
P1B	2.67	10.5	2.51	4.83	3.63	0.49	3.1	649	3.13	334.54	13.77	57.58	4.84	3.95	9.01	6.21
P1P	3.99	20.51	2.79	9.37	5.78	1.43	6.37	21.41	4.22	9.59	7.53	1.10	4.28	3.49	8.4	5.79
P2L	7.3	25.64	7.42	11.65	9.54	1.02	8.19	28.12	7.49	10.94	9.73	0.77	10.33	8.43	12.23	8.43
P2H	1.75	6.93	1.33	3.87	2.53	0.66	2.39	8.24	1.30	3.63	2.40	0.73	2.17	1.77	-	-
P2I	1.89	11.67	1.54	6.27	4.09	1.05	1.93	13.36	0.96	6.00	2.76	1.50	4.06	3.31	2.05	1.41
CDM	11.36	35.68	11.71	16.09	14.14	1.05	16.22	41.37	12.79	16.72	14.79	1.05	21.32	17.40	33.74	23.27

CPV	10.77	28.62	9.84	14.95	11.90	1.23	12.72	31.01	10.08	16.05	11.89	1.18	17.53	14.30	19.98	13.78
CPU	7.7	24	6.40	10.56	8.57	1.06	8.59	25.51	7.47	10.27	9.11	0.76	-	-	19.3	13.31
CPL	2.89	14.89	2.98	6.02	4.54	0.67	5.23	15.64	3.43	7.35	5.01	0.88	-	-	6.65	4.59
CFW	7.22	17.62	6.03	8.18	7.12	0.58	9.59	20.4	6.23	9.89	7.65	0.80	-	-	11.46	7.90
CFL	8.85	23.3	6.60	11.66	9.47	1.33	14.07	26.64	8.53	14.61	10.44	1.14	-	-	16.5	11.38
HANW	4.34	11.74	4.01	6.76	5.49	0.65	5.3	20.2	3.28	9.67	4.91	1.03	9.25	7.55	8.94	6.17
HAMW	8.31	22.1	8.13	10.89	9.38	0.63	8.86	21.96	5.02	10.83	9.22	1.03	13.71	11.19	15.98	11.02
HDW	6.82	23.72	6.42	10.79	9.17	0.86	7.75	25.83	7.76	11.74	9.82	0.98	11.66	9.51	13.82	9.53
TRW	6.11	22.71	6.00	10.70	9.06	1.09	6.29	21.53	5.67	10.48	8.68	1.07	-	-	7.61	5.25
ABW	4.96	24.54	5.22	11.10	7.54	1.40	3.68	13.84	3.32	6.62	4.93	0.86	7.62	6.22	4.97	3.43
TAW	2.58	11.61	2.72	4.79	3.82	0.57	3.14	11.18	2.83	5.08	3.80	0.59	3.85	3.14	5.16	3.56
CPW	1.44	4.36	1.28	2.41	1.66	0.27	1.57	4.73	1.05	2.15	1.53	0.25	1.82	1.48	3.13	2.16
HDH	6.43	33.96	7.56	13.37	10.06	1.12	9.14	24.58	6.62	11.43	9.49	0.86	10.28	8.39	14.73	10.16
TRH	6.79	38.86	7.86	15.30	10.56	1.45	8.53	26.36	7.68	11.98	9.86	0.96	-	-	12.02	8.29
ABH	5.47	45.08	6.44	17.75	10.24	2.51	4.56	22.16	4.70	10.07	7.14	1.30	8.77	7.16	9.61	6.63
TAH	4.91	17.22	4.73	6.78	5.66	0.67	3.77	12.18	3.48	5.23	4.35	0.50	7,03	-	6.72	4.63
CPH	1.65	4.42	1.40	2.12	1.78	0.18	1.94	4.23	1.26	2.00	1.64	0.17	2.73	2.23	3.61	2.49
CLO	1.41	10.41	1.28	4.70	2.69	0.87	0.9	9.41	0.93	5.16	3.12	1.10	-	-	0.57	0.39
CLI	3.23	16.48	2.94	7.53	5.05	1.15	3.17	16.64	3.27	8.29	6.20	1.62	-	-	1.76	1.21
CLB	0.65	3.41	0.58	1.54	0.94	0.27	0.4	3.63	0.41	1.63	1.13	0.41	-	-	0.84	0.58

Table 5. Neurocranium measurements, following Compagno, 1988. Specimens of *Isistius brasiliensis* (MNHN 1996-0465, TL = 409 mm, HDL = 82.92 mm) and *Isistius plutodus* (ZUEC 8333, TL = 333 mm, HDL = 67.73 mm). (NB: nasobasal length)

Measurements	***I. brasiliensis* (MNHN 1996-0565)**				***I. plutodus* (ZUEC 8333)**			
	mm	%TL	%HDL	%NB	mm	%TL	%HDL	%NB
Nasobasal length	46.5	11.37	56.08	46.5	36.69	11.02	54.17	36.69
Width across nasal capsules	18.09	4.42	21.82	38.90	13.82	4.15	20.40	37.67
Width of nasal capsule	8.5	2.08	10.25	18.28	7.95	2.39	11.74	21.67
Length of nasal capsule	10.32	2.52	12.45	22.19	8.48	2.55	12.52	23.11
Width of nasal aperture	6.36	1.56	7.67	13.68	5.36	1.61	7.91	14.61
Distance between nasal apertures	4.82	1.18	5.81	10.37	4.69	1.41	6.92	12.78
Distance from dorsal edge of anterior fontanelle to base of medial rostral casrtilage	6.55	1.60	7.90	14.09	5.66	1.70	8.36	15.43
Width of anterior fontanelle	2.12	0.52	2.56	4.56	1.67	0.50	2.47	4.55
Width of basal plate at orbital notches	2.52	0.62	3.04	5.42	1.59	0.48	2.35	4.33
Length of orbit	22.1	5.40	26.65	47.53	17.31	5.20	25.56	47.18
Length of postorbital process	3.99	0.98	4.81	8.58	4.15	1.25	6.13	11.31
Length of otic capsule	14.97	3.66	18.05	32.19	10.75	3.23	15.87	29.30
Width across suborbital shelves	18.98	4.64	22.89	40.82	14.82	4.45	21.88	40.39
Width across otic capsules	13.23	3.23	15.96	28.45	9.12	2.74	13.47	24.86
Width across postorbital processes	23	5.62	27.74	49.46	15.23	4.57	22.49	41.51

Table 6. Morphometric characterization of the species *Isistius brasiliensis*, including holotype of the junior synonyms *Scymnus brasiliensis* (MNHN A-7787), *Scymnus brasiliensis unicolor* (MNHN 0000-1178), *Leius ferox* (NMW 76230), and *I. labialis* (SCSFRI S07257). All values are presented as percentage of total length (TL), except TL that is given in mm

	MNHN A-7787		**MNHN 0000-1178**		**NMW 76230**		**SCSFRI S07257**		**n**	**Range**				**Mean**	**SD**
	mm	**%TL**	**mm**	**%TL**	**mm**	**%TL**	**mm**	**%TL**		**mm**		**%TL**		**%TL**	**%TL**
TL	172.00	-	471	-	162	-	442	-	226	112.14	520.00	-	-	335.54	-
PCL	133.35	77.53	404	85.77	131.95	81.45	381	86.20	225	97.83	445	77.06	138.76	85.14	4.48
PD2	109.76	63.81	343	72.82	109.91	67.85	317	71.72	226	31	378	7.19	101.56	70.83	5.04
PD1	90.05	52.35	285	60.51	91.68	56.59	262	59.28	226	69.04	317	52.35	66.15	59.41	1.77
SVL	97.89	56.91	304	64.54	102.28	63.14	294	66.52	220	74.23	340	54.07	70.21	63.92	2.48
PP2	95.41	55.47	288	61.15	95.15	58.73	280	63.35	226	69.29	326	52.91	80.56	60.74	2.79
PP1	34.46	20.03	94.62	20.09	36.9	22.78	89.31	20.21	226	24.16	100.36	16.96	25.81	20.61	1.31
HDL	35.11	20.41	96.38	20.46	35.85	22.13	88.98	20.13	224	24.89	102.11	17.40	25.11	20.84	1.25
PG1	28.71	16.69	77.52	16.46	30.13	18.60	72.6	16.43	223	19.93	83.51	13.91	20.82	16.95	1.08
PSP	15.1	8.78	37.23	7.90	16.33	10.08	38.16	8.63	222	10.5	41.94	7.16	11.16	8.95	0.74
POB	4.87	2.83	13.63	2.89	6.39	3.94	13.13	2.97	222	3.08	17.01	1.82	4.15	3.24	0.37
PRN	2.29	1.33	6.75	1.43	2.72	1.68	5.57	1.26	215	0.83	7.9	0.49	3.44	1.31	0.27
POR	11.08	6.44	24.07	5.11	12.02	7.42	26.64	6.03	207	6.5	35.08	5.11	11.75	6.77	0.77
PINL	2.46	1.43	8.31	1.76	3.71	2.29	7.23	1.64	199	0.99	10.2	0.39	2.45	1.56	0.32
INFL	19.19	11.16	27.07	5.75	11.55	7.13	25.69	5.81	212	6.43	31.61	2.50	11.16	6.44	0.93
MOW	17.08	9.93	41.8	8.87	10.79	6.66	32.33	7.31	206	8.58	41.8	5.86	11.57	7.41	0.89
ULA	8.04	4.67	29.13	6.18	8.98	5.54	23.82	5.39	213	5.69	29.13	2.29	9.29	5.22	0.80
INW	2.79	1.62	6.57	1.39	3.39	2.09	5.11	1.16	214	1.44	7.6	0.75	2.09	1.39	0.18
INO	8.36	4.86	21.11	4.48	9.61	5.93	22.49	5.09	223	6.21	28.63	3.91	6.56	5.31	0.49
EYL	7.69	4.47	16.89	3.59	7.71	4.76	13.79	3.12	213	4.57	17.76	2.92	5.46	3.86	0.53
EYH	4.44	2.58	10.48	2.23	4.51	2.78	8.88	2.01	213	2.87	13.46	1.70	3.86	2.64	0.39

SPL	4.01	2.33	10.66	2.26	3.69	2.28	8.61	1.95	223	1.81	10.68	1.50	2.96	2.14	0.27
GS1	1.51	0.88	3.3	0.70	1.2	0.74	4.2	0.95	217	1.13	6.53	0.52	1.46	1.02	0.16
GS5	1.25	0.73	3.26	0.69	1.13	0.70	2.87	0.65	218	0.6	5.11	0.35	1.81	0.80	0.16
IDS	15.19	8.83	44.88	9.53	13.85	8.55	40.19	9.09	225	8.93	51.03	6.95	11.01	9.10	0.81
DCS	21.48	12.49	45.03	9.56	17.99	11.10	48.24	10.91	225	9.19	54.25	7.61	13.23	10.48	0.98
PPS	53.24	30.95	178	37.79	57.48	35.48	168.94	38.22	225	40.04	214	28.90	44.62	36.80	2.34
PCA	28.73	16.70	72.63	15.42	27.29	16.85	78.37	17.73	225	20.08	93.61	14.46	20.83	17.74	1.22
D1L	9.98	5.80	30.23	6.42	12.4	7.65	30.9	6.99	221	4.86	34.36	4.20	8.16	6.39	0.61
D1A	7.16	4.16	18.51	3.93	9.86	6.09	21.7	4.91	221	3.16	27.15	2.82	6.09	4.76	0.51
D1B	5.33	3.10	13.56	2.88	5.64	3.48	14.28	3.23	225	3.51	17.35	2.16	4.54	3.04	0.40
D1H	2.55	1.48	8.97	1.90	2.43	1.50	8.31	1.88	220	1.99	14.9	1.19	3.51	1.77	0.29
D1I	3.84	2.23	17.63	3.74	7.12	4.40	17.43	3.94	222	0.57	19.7	0.15	4.40	3.36	0.47
D1P	4.15	2.41	15.69	3.33	3.45	2.13	13.94	3.15	218	2.06	19.41	1.26	4.24	2.82	0.42
D2L	9.07	5.27	32.13	6.82	13.33	8.23	31.82	7.20	224	6.11	37.91	3.73	8.99	6.96	0.66
D2A	8.24	4.79	15.26	3.24	9	5.56	20.16	4.56	226	3.5	24.48	3.02	5.92	4.53	0.51
D2B	5.99	3.48	15.07	3.20	6.78	4.19	15.47	3.50	226	4.14	19.23	2.69	4.98	3.50	0.42
D2H	2.49	1.45	8.92	1.89	3.5	2.16	9.29	2.10	225	1.47	15.4	1.27	3.80	2.01	0.30
D2I	2.7	1.57	17.23	3.66	7.46	4.60	16.44	3.72	224	1.61	20.64	1.17	4.60	3.54	0.51
D2P	3.99	2.32	21.01	4.46	5.63	3.48	16.55	3.74	222	2.19	21.36	1.92	4.94	3.48	0.48
P1A	10.04	5.84	27.04	5.74	14.67	9.06	30.49	6.90	226	6.19	41.72	5.41	10.53	7.99	0.97
P1I	7.28	4.23	21.14	4.49	9.95	6.14	15.52	3.51	226	1.68	101	0.74	6.53	4.46	0.75
P1B	7.66	4.45	18.9	4.01	5.72	3.53	16.13	3.65	226	3.2	21.44	2.65	4.70	3.58	0.37
P1P	4.14	2.41	18.69	3.97	10.64	6.57	19.8	4.48	226	4.03	30.12	2.41	6.63	4.79	0.76
P2L	9.27	5.39	37.74	8.01	15.51	9.57	37.06	8.38	226	3.37	47.98	2.89	11.84	8.74	1.40
P2H	3.63	2.11	15.27	3.24	5.37	3.31	16.04	3.63	218	2.35	23.65	1.32	5.02	2.71	0.73
P2I	2.17	1.26	12.68	2.69	5.91	3.65	13.75	3.11	223	1.91	26.51	0.50	10.11	2.83	1.40
CDM	26.42	15.36	66.81	14.18	27.02	16.68	59.69	13.50	224	7.15	81.19	6.01	17.86	15.01	1.28

CPV	20.22	11.76	48.49	10.30	19	11.73	46.77	10.58	221	7.62	59.8	6.66	13.69	10.74	0.99
CPU	13.6	7.91	42.63	9.05	15.66	9.67	34.98	7.91	216	4.9	53.19	2.81	11.41	9.56	1.11
CPL	6.55	3.81	27.48	5.83	8.46	5.22	21.95	4.97	216	2.58	33.26	2.27	9.51	5.55	0.70
CFW	11.44	6.65	28.11	5.97	9.86	6.09	25.04	5.67	219	5.24	34.05	4.44	7.43	6.07	0.49
CFL	15.69	9.12	38.54	8.18	16.7	10.31	35.21	7.97	215	7.89	41.84	6.69	15.35	8.57	0.88
HANW	3.65	2.12	12.15	2.58	4.41	2.72	11.37	2.57	213	2.16	18.6	1.90	4.59	2.64	0.36
HAMW	17.21	10.01	44.98	9.55	14.6	9.01	39.9	9.03	213	10.76	44.98	6.95	15.78	9.05	0.90
HDW	13.54	7.87	46.68	9.91	11.92	7.36	48.28	10.92	217	7.75	57.45	6.81	13.74	9.46	0.88
TRW	11.44	6.65	43.27	9.19	11.89	7.34	45.05	10.19	203	6.87	57.17	4.13	11.34	8.51	1.12
ABW	7.9	4.59	21.92	4.65	7.02	4.33	27.15	6.14	209	3.59	31.77	2.48	6.89	4.69	0.70
TAW	7.06	4.10	21.02	4.46	5.68	3.51	21.65	4.90	220	3.41	30.63	2.08	6.64	4.33	0.65
CPW	3.02	1.76	7.81	1.66	3.22	1.99	7.7	1.74	220	1.13	13.41	0.91	2.82	1.88	0.32
HDH	10.79	6.27	38.82	8.24	14.26	8.80	36.31	8.21	210	8.2	47.86	4.71	11.83	8.10	1.08
TRH	11.52	6.70	39.97	8.49	13.48	8.32	35.89	8.12	200	8.59	53.32	4.38	12.06	8.27	1.32
ABH	7.19	4.18	30.66	6.51	7.44	4.59	30.53	6.91	209	5.23	41.47	3.74	9.00	5.97	0.95
TAH	6.33	3.68	20.46	4.34	7.83	4.83	25.81	5.84	220	4.59	31.81	2.93	6.90	4.56	0.63
CPH	3.15	1.83	9.74	2.07	3.14	1.94	8.8	1.99	220	2.32	11.61	1.35	2.50	1.91	0.20
CLO	-	-	-	-	-	-	-	-	107	1.36	12.91	0.74	3.23	1.98	0.73
CLI	-	-	-	-	-	-	-	-	107	2.3	32.58	0.84	8.20	5.16	1.78
CLB	-	-	-	-	-	-	-	-	107	0.47	7.24	0.26	1.88	0.95	0.40

Table 7. Upper and lower teeth count, and hypothetical teeth formula of specimens of *Isistius brasiliensis* and *I. plutodus*.

		Min	Max	Mean	SD	n	Formula
I. brasiliensis	upper	17	39	31.27	4.23	56	16+15
	lower	15	31	26.39	3.67	83	12+1+13
I. plutodus	upper	19	28	24.4	3.58	5	13+12
	lower	17	19	18.5	1	4	9+1+9

Table 8. Vertebral counts of specimens of *Isistius brasiliensis* from Atlantic and Indian Oceans.

	SW Atl	SE Atl	NW Atl	NE Atl	Central Atl	Indian
Monospondylous	37, 40, 41, 42, 43	37, 41, 42	39, 40, 41, 44	40, 42	40, 41, 42, 43	41
Precaudal Diplospondylous	18, 20, 21	18, 21, 22	20, 21, 22, 24	21, 23, 24	21, 22, 23	40
Postcaudal Diplospondylous	13, 20, 22	18	11, 14, 18, 21, 22	15, 20, 22	17, 18, 21	22

Table 9. Vertebral counts of specimens of *Isistius brasiliensis* from Pacific Ocean and two specimens with no information regarding the locality.

	SW Pac	SE Pac	NW Pac	NE Pac	Central Pac	E Pac	No info
Monospondylous	40, 41, 42	39, 41, 42	40, 42	41, 42	39, 40, 41, 42, 43, 44	40, 41	40, 41
Precaudal Diplospondylous	20, 22	20, 22	18, 19, 20, 21, 23	19, 20, 21, 22	19, 20, 21, 22, 23, 24	20, 21	20, 22
Postcaudal Diplospondylous	15, 19, 21	16, 20, 23	19, 20, 21	14, 15, 16, 18, 19, 22	9, 13, 14, 16, 20, 21, 22	21, 23	18, 21

Table 10. Morphometric characterization of the specimens of *Isistius brasiliensis* from the three distinct Oceans. Only the means and the number of examined specimens.

	ATLANTIC	**n**	**PACIFIC**	**n**	**INDIAN**	**n**
TL	296.25	62	348.88	152	394.50	2
PCL	85.48%	61	85.04%	152	85.03%	2
PD2	70.65%	62	70.90%	152	70.85%	2
PD1	59.44%	62	59.42%	152	58.71%	2
SVL	64.06%	59	63.87%	149	64.03%	2
PP2	60.75%	62	60.74%	152	61.23%	2
PP1	20.95%	62	20.48%	152	20.35%	2
HDL	21.02%	60	20.79%	152	20.46%	2
PG1	17.13%	59	16.89%	152	16.51%	2
PSP	9.17%	59	8.88%	151	8.46%	2
POB	3.31%	59	3.21%	151	2.95%	2
PRN	1.39%	56	1.27%	147	1.37%	2
POR	6.90%	50	6.77%	145	5.16%	2
PINL	1.62%	44	1.54%	143	1.57%	2
INFL	6.64%	56	6.38%	147	5.78%	2
MOW	7.56%	53	7.36%	146	7.82%	2
ULA	5.03%	57	5.28%	147	6.04%	2
INW	1.41%	55	1.37%	147	1.62%	2
INO	5.47%	60	5.25%	151	5.00%	2
EYL	4.04%	59	3.80%	142	3.73%	2
EYH	2.66%	59	2.65%	142	2.08%	2
SPL	2.13%	59	2.14%	152	2.03%	2
GS1	0.98%	58	1.03%	147	0.94%	2
GS5	0.81%	59	0.80%	147	0.85%	2

IDS	9.06%	61	9.10%	152	9.64%	2
DCS	10.54%	61	10.44%	152	10.59%	2
PPS	36.78%	62	36.78%	151	37.06%	2
PCA	17.96%	61	17.64%	152	16.95%	2
D1L	6.32%	61	6.43%	148	5.76%	2
D1A	4.68%	60	4.79%	149	4.28%	2
D1B	3.16%	61	3.00%	152	2.72%	2
D1H	1.86%	59	1.73%	149	2.15%	2
D1I	3.22%	61	3.41%	149	3.39%	2
D1P	2.78%	59	2.86%	147	2.56%	2
D2L	6.84%	62	7.01%	150	6.48%	2
D2A	4.54%	62	4.53%	152	3.64%	2
D2B	3.65%	62	3.45%	152	3.20%	2
D2H	2.03%	62	2.01%	151	2.13%	2
D2I	3.38%	62	3.61%	150	3.26%	2
D2P	3.35%	61	3.54%	149	3.81%	2
P1A	7.72%	62	8.11%	152	6.02%	2
P1I	4.56%	62	4.40%	152	4.73%	2
P1B	3.56%	62	3.59%	152	3.43%	2
P1P	4.80%	62	4.78%	152	3.38%	2
P2L	8.55%	62	8.79%	152	7.46%	2
P2H	2.49%	59	2.78%	147	3.07%	2
P2I	2.41%	61	3.00%	151	2.35%	2
CDM	14.70%	60	15.11%	152	14.28%	2
CPV	10.44%	59	10.84%	151	10.64%	2
CPU	9.19%	55	9.68%	151	9.47%	2
CPL	5.34%	55	5.62%	151	5.71%	2

CFW	6.13%	58	6.03%	151	5.72%	2
CFL	8.78%	54	8.47%	150	7.96%	2
HANW	2.78%	55	2.58%	147	2.85%	2
HAMW	9.11%	57	9.05%	147	9.29%	2
HDW	9.27%	59	9.54%	147	9.65%	2
TRW	8.21%	57	8.62%	138	9.12%	2
ABW	4.63%	58	4.70%	143	5.09%	2
TAW	4.23%	58	4.34%	150	4.61%	2
CPW	1.80%	58	1.91%	150	1.75%	2
HDH	8.16%	57	8.05%	143	9.60%	2
TRH	8.32%	56	8.25%	136	9.27%	2
ABH	5.96%	58	5.97%	143	6.52%	2
TAH	4.52%	58	4.56%	150	4.68%	2
CPH	1.95%	58	1.90%	150	1.99%	2
CLO	2.01%	30	1.95%	72	-	0
CLI	5.32%	30	5.07%	72	-	0
CLB	1.03%	30	0.93%	72	-	0

Table 11. Morphometric data of immature and mature female specimens of *Isistius brasiliensis*. All values are presented as percentage of total length (TL), except TL that is given in mm.

	IMMATURE FEMALES							**MATURE FEMALES**						
	RANGE				**Mean**	**SD**	**n**	**RANGE**				**Mean**	**SD**	**n**
	mm		**%TL**		**%TL**	**%TL**		**mm**		**%TL**		**%TL**	**%TL**	
TL	112.14	385	-	-	238.8	84.9	66	393	520	-	-	460.8	31.0	53
PCL	97.83	329	77.1%	90.1%	84.7%	2.2%	66	331	445	81.6%	87.2%	84.8%	1.2%	53
PD2	82.53	275	63.8%	78.0%	70.7%	2.2%	66	31	378	7.2%	74.5%	70.6%	9.0%	53
PD1	69.04	229	52.4%	64.6%	59.4%	2.2%	66	230	317	55.5%	62.5%	60.1%	1.4%	53
SVL	74.23	264	54.1%	70.2%	63.8%	2.8%	64	249	340	59.0%	69.0%	65.1%	2.2%	51
PP2	69.29	290	52.9%	80.6%	60.9%	3.6%	66	237	326	54.4%	65.0%	62.1%	2.1%	53
PP1	24.16	90.5	19.2%	25.8%	21.3%	1.3%	66	77.8	100.36	17.0%	20.8%	19.3%	0.9%	53
HDL	24.89	82.64	19.4%	25.1%	21.5%	1.2%	64	76.52	102.11	17.4%	21.2%	19.6%	0.8%	53
PG1	19.93	66.07	15.7%	20.8%	17.6%	1.1%	63	63.5	83.51	13.9%	17.2%	15.9%	0.6%	53
PSP	10.5	35.9	8.1%	11.2%	9.4%	0.7%	63	31.5	41.94	7.2%	8.8%	8.2%	0.4%	53
POB	3.08	12.88	2.7%	4.2%	3.3%	0.3%	63	8.63	16.38	1.8%	3.7%	3.0%	0.3%	53
PRN	0.83	7.18	0.7%	3.4%	1.3%	0.4%	62	4.26	7.9	0.9%	2.0%	1.2%	0.2%	50
POR	6.5	28.15	5.2%	8.7%	7.0%	0.8%	63	22.71	35.08	5.1%	7.8%	6.3%	0.6%	48
PINL	1.16	6.85	0.7%	2.3%	1.5%	0.3%	59	3.9	10.2	0.8%	2.2%	1.4%	0.3%	45
INFL	6.43	26.14	2.5%	11.2%	6.9%	1.2%	62	20.8	31.61	4.6%	6.8%	5.8%	0.5%	49
MOW	8.58	30.92	6.4%	11.6%	7.9%	1.0%	62	25.2	41.8	6.1%	8.9%	6.9%	0.5%	49
ULA	5.69	20.67	2.3%	7.5%	5.2%	0.8%	62	12.2	29.13	3.0%	6.6%	4.9%	0.7%	49
INW	1.44	7.42	1.1%	2.1%	1.4%	0.2%	61	4.87	7.14	1.1%	1.6%	1.3%	0.1%	51
INO	6.21	22.13	4.0%	6.6%	5.4%	0.5%	64	19.8	28.63	4.2%	6.1%	5.1%	0.4%	52
EYL	4.57	15.59	3.3%	5.5%	4.3%	0.5%	60	13.07	17.76	2.9%	3.9%	3.4%	0.2%	50
EYH	2.87	10.26	1.7%	3.9%	2.9%	0.4%	60	8.4	13.46	2.0%	2.9%	2.4%	0.2%	50

SPL	1.81	9.52	1.6%	2.9%	2.2%	0.3%	63	6.8	10.68	1.6%	2.4%	2.0%	0.2%	53
GS1	1.13	4.75	0.6%	1.4%	1.0%	0.2%	63	2.8	6.53	0.7%	1.5%	1.0%	0.1%	51
GS5	0.6	3.68	0.4%	1.8%	0.8%	0.2%	63	2.62	5.11	0.6%	1.1%	0.8%	0.1%	51
IDS	8.93	38.66	7.0%	10.6%	8.9%	0.9%	66	32.2	51.03	7.5%	10.6%	9.0%	0.7%	52
DCS	9.19	43.79	7.6%	13.2%	11.0%	1.0%	66	37.4	53.29	8.1%	11.5%	9.8%	0.8%	53
PPS	40.04	146.23	28.9%	40.5%	36.9%	2.0%	66	142	214	35.9%	44.6%	39.0%	1.6%	52
PCA	20.08	74.32	15.9%	20.8%	17.9%	1.1%	66	62.53	93.61	14.5%	19.4%	16.6%	1.0%	53
D1L	4.86	28.5	4.3%	7.7%	6.3%	0.8%	64	25.11	34.36	5.6%	7.4%	6.3%	0.4%	52
D1A	3.16	19.91	2.8%	6.1%	4.6%	0.6%	64	18.11	27.15	3.9%	5.6%	4.7%	0.4%	52
D1B	3.51	14.11	2.4%	4.5%	3.1%	0.4%	66	10	17.35	2.2%	4.0%	3.0%	0.4%	52
D1H	1.99	9.2	1.3%	3.2%	1.8%	0.3%	64	6.28	14.9	1.3%	3.5%	1.9%	0.4%	51
D1I	2.03	15.05	1.3%	4.4%	3.2%	0.6%	64	10.93	19.7	2.3%	4.1%	3.4%	0.3%	52
D1P	2.06	14.28	1.3%	3.9%	2.8%	0.5%	62	7.97	19.41	1.7%	4.2%	2.9%	0.4%	51
D2L	6.11	30.85	3.7%	8.5%	6.9%	0.9%	65	23.19	37.91	5.5%	7.9%	6.8%	0.5%	53
D2A	3.5	20.66	3.0%	5.7%	4.5%	0.6%	66	15.26	24.48	3.2%	5.2%	4.4%	0.4%	53
D2B	4.14	16.46	2.9%	4.5%	3.6%	0.5%	66	12.12	19.23	2.7%	4.8%	3.4%	0.4%	53
D2H	1.47	10.6	1.3%	3.7%	1.9%	0.3%	66	7.17	15.4	1.7%	3.8%	2.1%	0.4%	52
D2I	1.61	16.12	1.2%	4.6%	3.4%	0.7%	65	11.71	20.64	2.5%	4.4%	3.5%	0.4%	53
D2P	2.19	15.86	1.9%	4.9%	3.3%	0.6%	65	10.47	21.36	2.5%	4.7%	3.6%	0.5%	52
P1A	6.19	33.74	5.4%	10.5%	8.2%	1.1%	66	25.05	41.72	5.6%	9.1%	7.5%	0.8%	53
P1I	3.43	18.77	2.5%	6.5%	4.8%	0.8%	66	11.86	22.68	2.8%	5.6%	4.2%	0.6%	53
P1B	3.2	15.38	2.6%	4.5%	3.6%	0.4%	66	11.8	21.44	3.0%	4.2%	3.5%	0.3%	53
P1P	4.03	21.93	2.4%	6.6%	4.8%	1.0%	66	14.66	30.12	3.3%	6.3%	4.7%	0.6%	53
P2L	3.37	35.63	2.9%	9.6%	7.6%	1.3%	66	30.81	46.95	7.5%	10.7%	8.5%	0.7%	53
P2H	2.4	15.95	1.8%	4.2%	2.9%	0.6%	63	13.19	23.65	3.0%	4.5%	3.6%	0.4%	50
P2I	1.94	14.78	1.3%	10.1%	3.1%	1.1%	64	9.52	23.9	2.3%	6.1%	3.4%	0.6%	53
CDM	7.15	62.97	6.0%	17.7%	14.9%	2.0%	65	55.1	81.19	12.6%	16.7%	14.8%	0.8%	53

CPV	7.62	48.57	6.7%	13.7%	10.9%	1.4%	63	40.6	59.8	8.9%	12.5%	10.4%	0.6%	52
CPU	4.9	42.03	4.3%	11.3%	9.4%	1.4%	60	17.87	53.19	3.8%	11.4%	9.7%	1.1%	50
CPL	2.58	22.8	2.3%	9.5%	5.3%	1.0%	60	18.32	33.26	4.4%	7.0%	5.7%	0.5%	50
CFW	5.24	24.96	4.4%	7.1%	6.0%	0.5%	61	21.38	34.05	5.1%	7.4%	6.0%	0.5%	52
CFL	7.89	40.07	6.7%	15.3%	9.0%	1.2%	59	31.32	41.84	6.7%	9.1%	8.0%	0.5%	50
HANW	2.16	12.3	1.9%	4.3%	2.6%	0.4%	61	8.92	18.6	2.0%	4.6%	2.5%	0.5%	50
HAMW	10.76	36.81	7.9%	11.9%	9.5%	0.7%	63	32.6	44.98	7.5%	9.5%	8.4%	0.4%	49
HDW	7.75	41.71	6.8%	13.7%	9.4%	1.0%	62	36.04	57.45	7.9%	11.4%	9.8%	0.8%	51
TRW	6.87	35.88	5.6%	11.1%	8.2%	1.1%	59	32.7	57.17	7.3%	11.3%	9.2%	1.1%	49
ABW	3.59	19.96	3.1%	5.5%	4.2%	0.6%	60	16.88	31.77	4.3%	6.9%	5.3%	0.6%	48
TAW	3.41	19.84	2.8%	5.2%	4.0%	0.5%	65	16.27	30.63	4.0%	6.6%	5.0%	0.5%	50
CPW	1.13	10.4	1.0%	2.8%	1.8%	0.3%	64	6.56	13.41	1.4%	2.8%	2.1%	0.3%	50
HDH	8.2	36.14	5.6%	11.8%	8.3%	1.2%	59	28.45	47.86	6.7%	9.9%	8.3%	0.9%	49
TRH	8.59	38.55	4.4%	12.0%	8.4%	1.4%	59	25.83	53.32	5.8%	11.3%	8.6%	1.2%	48
ABH	5.23	27.41	4.0%	7.4%	5.4%	0.7%	60	21.8	41.47	5.1%	9.0%	6.8%	1.0%	48
TAH	4.59	22.66	3.1%	6.1%	4.4%	0.5%	65	18.56	31.81	3.9%	6.9%	5.2%	0.7%	50
CPH	2.36	8.02	1.3%	2.4%	1.9%	0.2%	64	7.66	11.61	1.8%	2.5%	2.0%	0.1%	50

Table 12. Morphometric data of immature and mature male specimens of *Isistius brasiliensis*. All values are presented as percentage of total length (TL), except TL that is given in mm.

	IMMATURE MALES							**MATURE MALES**						
	RANGE				**Mean**	**SD**	**n**	**RANGE**				**Mean**	**SD**	**n**
	mm		**%TL**		**%TL**	**%TL**		**mm**		**%TL**		**%TL**	**%TL**	
TL	158	358	-	-	239.7	64.6	45	361	425	361	425	390.8	17.2	32
PCL	129	374	79.2%	138.8%	85.9%	9.5%	45	304	362	82.6%	89.9%	85.2%	1.5%	31
PD2	106	326	64.0%	101.6%	70.5%	5.1%	45	254	305	68.8%	73.2%	71.2%	1.3%	32
PD1	91	211	55.6%	66.2%	58.4%	1.8%	45	211	256	57.3%	61.5%	59.4%	1.3%	32
SVL	99	231	57.6%	67.9%	62.5%	2.1%	43	225	280	58.6%	67.9%	64.0%	2.1%	32
PP2	94	220	54.5%	63.2%	59.2%	2.2%	45	213	260	55.3%	64.7%	60.4%	1.9%	32
PP1	33.91	81	19.3%	23.4%	21.2%	1.0%	45	73.87	88.26	18.2%	24.0%	20.5%	1.0%	32
HDL	35.75	82.74	19.6%	23.7%	21.6%	1.1%	45	72.95	88.64	19.5%	23.2%	20.7%	0.7%	32
PG1	29	66.56	16.1%	20.1%	17.7%	0.9%	45	57.91	73.15	14.3%	18.3%	16.7%	0.7%	32
PSP	15.54	34.02	7.8%	11.1%	9.4%	0.6%	45	30.97	38.42	7.9%	10.1%	8.9%	0.4%	32
POB	4.83	13.25	2.7%	4.1%	3.3%	0.4%	45	10.34	17.01	2.7%	4.1%	3.4%	0.4%	32
PRN	1.24	4.76	0.5%	1.9%	1.3%	0.3%	45	3.07	7.12	0.8%	1.8%	1.4%	0.2%	31
POR	10.16	26.32	6.1%	11.8%	7.1%	0.9%	42	20.5	28.31	5.4%	7.4%	6.5%	0.5%	29
PINL	0.99	6.4	0.4%	2.2%	1.5%	0.3%	42	3.82	9.23	1.0%	2.4%	1.7%	0.4%	28
INFL	9.74	23.94	5.3%	8.1%	6.9%	0.7%	42	20.12	29.12	4.9%	7.6%	6.3%	0.6%	31
MOW	11.71	26.04	5.9%	9.5%	7.7%	0.8%	40	22.61	35.74	5.9%	9.5%	7.1%	0.8%	31
ULA	6.77	20.75	4.1%	9.3%	5.7%	1.1%	43	15.58	26.37	4.3%	6.2%	5.2%	0.5%	31
INW	1.92	4.86	0.8%	1.6%	1.4%	0.2%	43	4.52	7.6	1.2%	2.1%	1.5%	0.2%	31
INO	8	20.89	4.5%	6.2%	5.4%	0.4%	45	17.22	24.1	4.5%	6.2%	5.6%	0.3%	32
EYL	6.68	14.25	3.3%	5.1%	4.2%	0.4%	44	12.5	15.52	3.2%	4.0%	3.6%	0.2%	32
EYH	4.69	10.03	2.2%	3.5%	2.9%	0.3%	44	7.45	13.12	1.9%	3.4%	2.5%	0.3%	32

SPL	3.1	8.42	1.5%	3.0%	2.3%	0.3%	45	6.86	9.95	1.8%	2.6%	2.2%	0.2%	32
GS1	1.32	4.24	0.7%	1.4%	1.0%	0.2%	43	2.14	5.56	0.5%	1.4%	1.0%	0.2%	32
GS5	0.88	3.03	0.3%	1.0%	0.8%	0.1%	43	1.78	4.18	0.4%	1.1%	0.7%	0.1%	32
IDS	11.51	37.66	7.3%	11.0%	9.2%	0.9%	45	29.45	41.96	7.9%	10.6%	9.1%	0.8%	32
DCS	16.51	41.92	8.3%	12.9%	10.8%	0.9%	45	33.17	43.84	8.9%	11.8%	10.0%	0.7%	31
PPS	50.65	136.66	30.5%	39.0%	35.1%	2.1%	45	120.9	167.82	32.4%	40.7%	35.6%	1.9%	32
PCA	29.38	71.31	17.3%	20.4%	18.7%	0.8%	45	62.63	74.21	15.3%	18.9%	17.5%	0.9%	31
D1L	9.98	24.92	5.0%	7.5%	6.5%	0.5%	44	16.06	29.46	4.2%	8.2%	6.5%	0.7%	32
D1A	7.24	19.09	3.5%	5.9%	4.8%	0.5%	45	14.31	22.2	3.7%	5.8%	4.8%	0.5%	32
D1B	4.2	11.55	2.2%	3.9%	3.0%	0.4%	45	9.96	15.36	2.6%	4.0%	3.2%	0.4%	32
D1H	2.32	7.02	1.3%	2.0%	1.7%	0.2%	44	4.83	8.56	1.2%	2.1%	1.7%	0.2%	32
D1I	4.84	13.7	2.8%	3.9%	3.4%	0.3%	45	0.57	16.44	0.1%	4.3%	3.4%	0.7%	32
D1P	3.84	12.49	2.3%	3.6%	2.8%	0.4%	45	6.22	13.48	1.6%	3.5%	2.8%	0.4%	32
D2L	10.14	27.23	5.9%	8.3%	7.0%	0.5%	45	22.417	32.45	5.8%	9.0%	7.2%	0.7%	32
D2A	7.01	18.59	3.7%	5.6%	4.6%	0.5%	45	15.19	23.28	3.9%	5.9%	4.8%	0.6%	32
D2B	5.2	14.89	3.0%	4.5%	3.6%	0.4%	45	10.48	17.99	2.7%	5.0%	3.6%	0.5%	32
D2H	2.7	8.42	1.3%	2.6%	2.0%	0.3%	45	6.62	10.69	1.7%	2.6%	2.1%	0.2%	32
D2I	4.39	14.81	2.6%	4.4%	3.6%	0.4%	45	11.09	16.58	2.9%	4.3%	3.6%	0.4%	32
D2P	3.83	14.96	2.3%	4.3%	3.5%	0.4%	45	10.22	17.6	2.7%	4.7%	3.6%	0.5%	32
P1A	14.53	32.55	6.8%	10.4%	8.8%	0.8%	45	22.95	35.53	6.2%	8.9%	7.5%	0.7%	32
P1I	1.68	17.32	0.7%	6.5%	4.9%	0.9%	45	12.13	19.28	3.2%	5.0%	4.2%	0.4%	32
P1B	5.33	14.87	2.8%	4.7%	3.7%	0.4%	45	12.06	18.04	3.0%	4.7%	3.6%	0.3%	32
P1P	6.77	20.43	3.6%	6.6%	4.8%	0.7%	45	15.62	24.92	4.1%	6.5%	5.0%	0.5%	32
P2L	12.87	38.61	6.8%	11.1%	8.8%	0.8%	45	20.74	47.92	5.1%	11.4%	10.1%	1.2%	32
P2H	2.35	9.49	1.3%	2.8%	2.1%	0.3%	43	5.3	11.62	1.5%	3.0%	2.2%	0.4%	32
P2I	2	9.34	0.6%	4.1%	2.2%	0.9%	45	1.91	26.51	0.5%	6.5%	3.5%	2.2%	32
CDM	24.25	53.58	13.7%	17.9%	15.4%	0.9%	45	51.34	67.03	12.6%	16.7%	15.1%	0.9%	31

CPV	16.58	38.93	10.2%	13.3%	11.3%	0.7%	45	35.79	48.01	8.7%	12.5%	10.6%	0.8%	31
CPU	14.28	37.66	8.0%	10.8%	9.4%	0.6%	45	10.74	43.24	2.8%	10.7%	9.5%	1.4%	31
CPL	6.35	21.73	3.4%	6.6%	5.4%	0.6%	45	19.54	27.02	4.9%	7.0%	5.8%	0.4%	31
CFW	8.7	24.52	5.0%	7.1%	6.1%	0.5%	45	19.73	26.42	5.0%	6.7%	6.1%	0.5%	31
CFL	14.49	30.86	7.6%	10.8%	8.9%	0.7%	45	28.9	36.63	7.5%	9.5%	8.5%	0.5%	31
HANW	3.69	9.64	2.0%	2.9%	2.6%	0.2%	43	8.82	12.93	2.3%	3.3%	2.9%	0.3%	31
HAMW	13.97	32.21	7.9%	15.8%	9.6%	1.2%	43	30.67	37.12	7.8%	9.9%	8.7%	0.5%	31
HDW	14.03	32.1	6.9%	11.2%	9.2%	0.7%	42	30.04	42.51	7.8%	11.3%	9.5%	0.7%	32
TRW	10.45	29.53	4.1%	9.6%	8.1%	1.1%	37	26.92	39.39	7.2%	10.4%	8.6%	0.9%	31
ABW	5.33	22.56	2.5%	6.5%	4.3%	0.6%	43	15.59	22.88	4.0%	5.8%	5.0%	0.5%	31
TAW	4.47	16.22	2.1%	5.2%	3.9%	0.5%	45	13.07	20.38	3.4%	5.6%	4.5%	0.5%	32
CPW	1.9	7.29	0.9%	2.5%	1.7%	0.3%	45	5.6	11.03	1.5%	2.6%	2.0%	0.3%	31
HDH	10.61	31.04	4.7%	11.3%	7.9%	1.1%	42	24.85	41.96	6.1%	10.9%	8.2%	1.1%	32
TRH	10.88	30.34	5.8%	10.7%	8.1%	1.1%	35	21.14	46.42	5.6%	12.1%	8.2%	1.5%	31
ABH	7.26	24.06	3.7%	6.9%	5.3%	0.6%	43	20.49	30.53	5.0%	8.4%	6.4%	0.6%	31
TAH	5.66	16.27	2.9%	5.3%	4.2%	0.4%	45	14.11	20.31	3.5%	5.6%	4.4%	0.5%	32
CPH	2.32	7.05	1.4%	2.1%	1.8%	0.2%	45	6.74	8.81	1.7%	2.3%	1.9%	0.1%	31
CLO	1.36	8.52	0.7%	2.4%	1.2%	0.3%	45	5	12.91	1.4%	3.1%	2.5%	0.4%	32
CLI	3.33	24.92	1.9%	7.1%	3.3%	0.9%	45	15.03	29.68	4.2%	7.4%	6.4%	0.7%	32
CLB	0.47	3.63	0.3%	1.0%	0.5%	0.2%	45	2.8	7.24	0.8%	1.9%	1.3%	0.2%	32

Table 13. Morphometric characterization of the species *Isistius plutodus*.

	USNM 188386 (holotype)		**n**	**Range**				**Mean**	**SD**
	mm	**%TL**		**mm**		**%TL**		**%TL**	**%TL**
TL	416	416	6	329	426	-	-	-	-
PCL	356	85.6%	6	284	378	85.6%	88.7%	87.2%	1.3%
PD2	308	74.0%	6	245	323	73.4%	75.8%	74.5%	0.9%
PD1	269	64.7%	6	210	284	63.2%	66.7%	64.8%	1.3%
SVL	292	70.2%	6	215	295	65.3%	70.6%	68.9%	1.9%
PP2	281	67.5%	6	213	286	64.7%	67.9%	66.8%	1.2%
PP1	76.18	18.3%	6	65.5	86.04	18.3%	20.2%	19.7%	0.7%
HDL	78.69	18.9%	6	65.68	83.76	18.9%	20.3%	19.8%	0.5%
PG1	62.77	15.1%	6	52.21	65.2	15.1%	16.8%	15.8%	0.6%
PSP	28.74	6.9%	6	24.06	31.19	6.9%	8.8%	7.7%	0.7%
POB	6.78	1.6%	6	6.78	10.37	1.6%	3.1%	2.4%	0.5%
PRN	3.13	0.8%	6	2.14	4.76	0.7%	1.4%	1.0%	0.3%
POR	16.42	3.9%	6	13.33	20.68	3.7%	6.2%	4.7%	0.9%
PINL	3.55	0.9%	6	3.32	5.91	0.9%	1.8%	1.4%	0.4%
INFL	19.82	4.8%	5	13.32	22.87	3.1%	6.2%	5.1%	1.2%
MOW	34.49	8.3%	5	22.18	34.49	5.9%	8.3%	7.2%	0.9%
ULA	16.43	3.9%	6	11.5	24.5	3.5%	5.8%	4.3%	0.9%
INW	5.59	1.3%	6	3.67	6.59	1.1%	1.5%	1.3%	0.2%
INO	13.7	3.3%	6	9.57	13.7	2.9%	3.9%	3.3%	0.3%

EYL	15.63	3.8%	6	13.5	16.22	3.6%	4.7%	4.1%	0.4%
EYH	10.8	2.6%	6	8.34	11.22	2.5%	3.1%	2.7%	0.2%
SPL	9.01	2.2%	6	5.82	9.01	1.8%	2.2%	2.0%	0.1%
GS1	3.14	0.8%	6	2.46	3.73	0.7%	1.1%	0.8%	0.1%
GS5	2.97	0.7%	6	2.05	2.97	0.6%	0.7%	0.7%	0.0%
IDS	27.82	6.7%	6	11.75	27.82	3.6%	7.3%	5.9%	1.3%
DCS	33.71	8.1%	6	22.84	33.71	6.2%	8.4%	7.4%	0.8%
PPS	185.12	44.5%	6	146.62	191	44.1%	45.0%	44.6%	0.3%
PCA	68.01	16.3%	6	52.57	68.01	14.4%	18.4%	16.3%	1.3%
D1L	33.36	8.0%	6	26.49	34.04	8.0%	8.5%	8.2%	0.2%
D1A	22.37	5.4%	6	17.73	25.45	5.2%	6.8%	5.7%	0.6%
D1B	16.24	3.9%	6	13.47	16.66	3.9%	4.9%	4.3%	0.4%
D1H	10.34	2.5%	6	6.38	10.34	1.9%	2.5%	2.2%	0.2%
D1I	15.38	3.7%	6	10.94	17.02	3.3%	4.1%	3.7%	0.3%
D1P	15.33	3.7%	6	9.79	15.88	2.9%	3.7%	3.4%	0.3%
D2L	32.33	7.8%	6	25.23	34.4	7.7%	8.3%	8.0%	0.2%
D2A	25.2	6.1%	6	18.27	25.4	5.5%	6.8%	6.1%	0.4%
D2B	19.17	4.6%	6	14.77	20.48	4.4%	5.2%	4.8%	0.3%
D2H	14.17	3.4%	6	8.68	14.93	2.6%	3.5%	3.2%	0.4%
D2I	12.68	3.0%	6	9.13	13.93	3.0%	3.5%	3.3%	0.2%
D2P	16.64	4.0%	6	11.34	18.42	3.4%	4.3%	3.9%	0.3%
P1A	32.04	7.7%	6	20.69	32.04	5.7%	8.2%	7.0%	0.9%
P1I	19.2	4.6%	6	8.99	19.2	2.7%	4.6%	3.7%	0.6%
P1B	9.59	2.3%	6	7.78	10.33	2.3%	3.1%	2.6%	0.3%
P1P	14.33	3.4%	6	10.73	17.33	3.3%	4.2%	3.7%	0.4%
P2L	27.99	6.7%	6	24.91	29.18	6.7%	7.9%	7.4%	0.5%
P2H	9.45	2.3%	6	3.82	9.45	1.1%	2.3%	1.7%	0.5%

P2I	14.67	3.5%	6	2.15	16.03	0.7%	4.6%	2.8%	1.7%
CDM	57.58	13.8%	6	46.13	60.27	13.8%	14.8%	14.2%	0.3%
CPV	24.77	6.0%	6	21.67	25.89	6.0%	7.5%	6.7%	0.6%
CPU	40.84	9.8%	6	23.64	40.84	7.2%	10.2%	9.0%	1.1%
CPL	10.05	2.4%	6	5.83	10.31	1.8%	3.1%	2.2%	0.5%
CFW	19.8	4.8%	6	14.52	19.8	4.4%	5.9%	4.9%	0.6%
CFL	26.21	6.3%	6	21.69	26.21	5.5%	7.2%	6.5%	0.6%
HANW	8.61	2.1%	6	6.63	9.29	2.0%	2.8%	2.3%	0.3%
HAMW	38.19	9.2%	6	26.05	38.19	7.0%	9.2%	8.1%	0.8%
HDW	35.02	8.4%	6	25.12	35.02	7.6%	8.4%	8.0%	0.4%
TRW	26.96	6.5%	6	19.68	38.98	5.9%	9.3%	7.6%	1.4%
ABW	13.16	3.2%	6	8.34	14.98	2.5%	3.5%	3.1%	0.4%
TAW	11.58	2.8%	6	7.92	13.6	2.4%	3.5%	2.8%	0.4%
CPW	4.42	1.1%	6	3.17	4.75	1.0%	1.4%	1.1%	0.2%
HDH	33.58	8.1%	6	22.99	41.75	6.9%	9.8%	7.8%	1.0%
TRH	30.86	7.4%	6	22.79	44.04	6.8%	10.3%	7.8%	1.3%
ABH	17.51	4.2%	6	12.44	22.9	3.7%	5.4%	4.6%	0.6%
TAH	13.43	3.2%	6	9.54	16.88	2.9%	4.0%	3.4%	0.4%
CPH	5.6	1.3%	3	4.2	6.07	1.3%	1.5%	1.4%	0.1%
CLO	-	-	3	6.18	6.83	1.9%	2.1%	1.9%	0.1%
CLI	-	-	3	15.93	17.27	4.8%	5.2%	5.0%	0.2%
CLB	-	-		2.46	2.58	0.7%	0.8%	0.8%	0.0%

Table 14. Vertebral counts of female and male specimens of *Isistius brasiliensis*, *I. plutodus*, *Dalatias licha*, *Squaliolus laticaudus, S. aliae*, *Euprotomicrus bispinatus* and *Heteroscymnoides marleyi*. Counts separated by monospondylous, precaudal and postcaudal diplospondylous vertebrae.

FEMALES	***I. brasiliensis***	***I. plutodus***	***D. licha***	***S. laticaudus***	***S. aliae***	***E. bispinatus***	***H. marleyi***
Monospondylous	37, 39, 40, 41, 42, 43, 44	43, 44, 45	36, 37, 41	28, 29, 30, 31, 32	29	31, 32, 33	33
Precaudal Diplospondylous	18, 19, 20, 21, 22, 23, 24	23, 24, 26	10, 11, 12	15, 16, 18	17	16, 17, 18, 19, 21	18
Postcaudal Diplospondylous	17, 18, 19, 20, 21, 22, 23	22, 26, 27	27, 28	12, 13, 14, 15	13	14	15

MALES	***I. brasiliensis***	***I. plutodus***	***D. licha***	***S. laticaudus***	***S. aliae***	***E. bispinatus***	***H. marleyi***
Monospondylous	39, 40, 41, 42	43	38	32	-	-	-
Precaudal Diplospondylous	18, 20, 21, 22, 23, 24	23	11	17	-	-	-
Postcaudal Diplospondylous	19, 20, 21, 22	26	28	13	-	-	-

Table 15. Summary of some relevant morphological characters, which may distinguish *I. brasiliensis* from *I. plutodus*.

Character	***I. brasiliensis***	***I. plutodus***
Ventral dark collar	Posterior end at the level of pectoral fin origin	Posterior end at the level of pectoral fin insertion
Gum	Wavy and short	Straight and long
Symphyseal lower teeth	Approximately, 5% shorter than adjacent teeth	Same height as adjacent teeth
Proportion of lower teeth height over upper teeth height	3	6
Interdorsal space	Approximately 9.1% TL	Approximately 5.9% TL
2nd Dorsal fin height	Approximately the same as the 1st dorsal height	Bigger than the 1st dorsal height
Caudal fin	Upper postventral margin smaller then lower one	Upper postventral margin greater than the lower one

Table 16. List of reported of wounds of cookiecutter shark bites on cetaceans, fishes, turtle and a human corpse.

Authors, Year	**Species**	**Wounds on body**	**Place**
Addink & Smeenk, 2001	*Steno bredanensis*	-	Off Mauritania
Alcorn & Westlake, 1993	*Monachus schauinslandi*	-	Northeastern Hawaiian Islands
Azevedo *et al.*, 2003	*Lagenodelphis hosei*	-	Southwestern Atlantic
Baird *et al.*, 2001	*Stenella attenuata*	-	Hawaii
Baird *et al.*, 2008	*Mesoplodon*	-	Hawaii

	densirostris, Ziphius cavirostris		
Belcher & Lee, 2002	*Arctocephalus townsendi*	-	Northeastern Pacific
Bermúdez Villapol *et al.*, 2008	*Kogia sima*	-	Venezuela
Bertilsson-Friedman, 2006	*Monachus schauinslandi*	-	Hawaii
Best, 2001	*Balaenoptera edeni*	Posterior half of the body	West coast of southern Africa
Bonde & O'Shea, 1989	*Mesoplodon bidens*	Both flanks	Gulf of Mexico
Borsa & Robineau, 2005	*Mesoplodon densirostris*	On the back	New Caledonia
Bossart *et al.*, 2007	*Peponocephala electra*	-	Florida
Brownell, Jr. *et al.*, 2007	*Balaenoptera musculus*	-	North of Chile
Bunkley-Williams *et al.*, 2008	*Eretmochelys imbricata*	-	Northeastern Australia
Burdin *et al.*, 2007	*Orcinus orca*	-	Russian far east
Choy & Hiruki, 1992	*Monachus schauinslandi*	-	Pearl and Hermes Reef, Hawaii
Claridge, 2006	*Mesoplodon densirostris*	-	Intertropical, Worldwide
Dalbout *et al.*, 2002	*Mesoplodon perrini*	On the flanks	Monterey, Northeastern Pacific
Dalebout *et al.*, 2004	*Mesoplodon grayi*	Below right flank	New Zealand
Deakos *et al.*, 2010	*Tursiops truncatus*	On the right side of the body	Hawaii

Delgado-Estrella *et al.*, 1998	*Kogia breviceps*	Left pectoral fin	Gulf of Mexico
Dwyer & Visser, 2011	*Balaenoptera brydei, Balaenoptera musculus, Megaptera novaeangliae, Delphinus* sp., *Globicephala melas, Pseudorca crassi-dens, Orcinus orca*	-	New Zealand
Falcón-Matos, *et al.*, 2003	*Ziphius cavirostris*	-	Gulf of Mexico
Fitzpatrick *et al.*, 2006	*Rhincodon typus*	Left flank	Ningaloo Reef in Western Australia
Foster & Hare, 1990	*Ziphius cavirostris*	Abdominal region	Northeastern Pacific
Gasparini & Sazima, 1996	*Peponocephala electra*	Whole body	Southeastern coast of Brazil
Goto *et al.*, 2009	*Balaenoptera* sp.	-	Noerthwestern Pacific
Haney *et al.*, 2004	*Globicephala macrorhynchus*	-	Northeastern coast of Brazil
Heithaus, 2001	*Stenella longirostrus*	Whole body, except the appendages	Hawaii
Hiruki *et al.*, 1993	*Monachus schauinslandi*	-	Hawaii
Honeybrink *et al.*, 2011	*Homo sapiens, Ruvettus*	Lower chest, left calf	Hawaii

	pretiosus		
Hoyos-Padilla *et al.*, 2013	*Carcharodon carcharias*	Lateral to the corner of the mouth	Guadalupe Island, Northwestern Pacific
Ito *et al.*, 1994	*Gasterochisma melampus*	Posteriorly above the opercle	Hawaii
Jefferson & Barros, 1997	*Peponocephala electra*	-	Tropical and subtropical zones throughout the world
Johnson & Wolman, 1984	*Megaptera novaeangliae*	-	Artic to Antarctic
Le Boeuf & McCosker, 1987	*Mirounga angustirostris*	The side posterior to the flippers, on the ventrum or the back and to either side or on the midline, on the chest and neck, and just behind the ear	Northeastern Pacific
MacLeod, 1998	*Kogia breviceps*	-	Tropical and temperate waters of the Atlantic, Pacific and Indian Oceans
Makino *et al.*, 2004	*Homo sapiens*, *Lampris guttatus*	Temporal region of the head, the upper region of the back, and right	Okinawa, Japan

		elbow	
McSweeney *et al.*, 2007	*Mesoplodon densirostris, Ziphius cavirostris*	-	Hawaii
Mikhalev, 1997	*Balaenoptera borealis, B. musculus* and *B. musculus brevicauda*	-	Arabian Sea
Mincarone *et al.*, 2001	*Trachipterus jacksonensis*	-	Southeastern coast of Brazil
Moore *et al.*, 2003	*Balaenoptera physalus, Megaptera novaeangliae*	-	Cape Verde Islands
Mullin *et al.*, 1994	*Stenella clymene*	-	Gulf of Mexico
Neto *et al.*, 2008	*Megaptera novaeangliae*	Ventral region	Northeastern coast of Brazil
Norris & Dohl, 1980	*Stenella longirostris*	-	Hawaii
Ohishi *et al.*, 2007	*Kogia breviceps*	-	Pacific coast of Japan
Papastamatiou *et al.*, 2010	*Xiphias gladius, Thunnus obesus, Thunnus albacares, Katsuwonus pelamis, Taractichthys steindachneri, Lampris guttatus,*	-	Hawaii

	Acanthocybium solandri, Makaira mazara, Tetrapturus audax, Tetrapturus angustirostris		
Pérez-Zayas *et al*., 2002	*Makaira nigricans, Coryphaena hippurus, Thunnus albacares, Thunnus alalunga, Thunnus Atlanticus, Arctocephalus townsendi, Mirounga angustirostris, Balaenoptera musculus, Balaenoptera physalus, Lagenodelphis hosei, Peponocephala electra, Phocoena phocoena, Mesoplodon* spp., *Ziphius*	-	Puerto Rico and Virgin Islands

	cavirostris		
Perrin *et al.*, 1981	*Stenella clymene*	Dorsal region	Caribbean
Pitman *et al.*, 2001	*Orcinus orca*	Behind dorsal fin	Northeastern Pacific, California
Reddy & Griffith, 1988	*Monachus schauinslandi*	Dorsal, chest, and ventral (abover right front flipper) regions, and shoulder	Kure Atoll, Hawaii
Renner & Bell, 2008	*Orcinus orca*	Behind the blow hole	Adak Island, Alaska
Sadowsky *et al.*, 1988	*Prionace glauca*	Lateral region, close to 5th gill opening	South coast of Brazil
Silva-Jr & Sazima, 2003	*Remora australis*	Right flank	Fernando de Noronha, Northeastern Brazil
Silva-Jr *et al.*, 2007	*Stenella longirostris*	Posterior half of the body	Fernando de Noronha, Northeastern Brazil
Souto *et al.*, 2007	*Peponocephala electra, Grampus griseus, Stenella attenuata, Stenella coeruleoalba, Ziphius cavirostris, Physeter macrocephalus,*	-	Bahia, Northeastern Brazil

	Sotalia guianensis, Mesoplodon layardii, Kogia breviceps, Stenella clymene, Megaptera novaeangliae, Kogia sima, Pseudorca crassidens, Megaptera novaeangliae		
Souto *et al.*, 2009	*Arctocephalus tropicalis*	Distal part of the dorsal region of the left pectoral paddle, posterior portion of the back	Bahia, Northeastern Brazil
Souza *et al.*, 2005	*Mesoplodon mirus*	Dorsal region	Coast of Brazil
Stacey *et al.*, 1994	*Pseudorca crassidens*	-	Tropical, subtropical, and warm temperate seas
Steiner *et al.*, 2008	*Balaenoptera edeni*	Around the dorsal fin	Azores
Taylor *et al.*, 1983	*Megachasma pelagios*	On the throat and behind the right pectoral fin	Hawaii

Van Den Hoff *et al.*, 2005	*Mirounga leonina*	Above fore flipper	Heard and Macquarie Islands, and Prydz Bay, Southwestern Pacific
Van Waerebeek *et al.*, 2008	*Peponocephala electra*	-	Cape Verde Islands
Velozo *et al.*, 2009	*Arctocephalus tropicalis*	-	Northeastern coast of Brazil
Visser, 1999	*Orcinus orca*	-	New Zealand
Walker & Hanson, 1999	*Mesoplodon stejnegeri*	-	Adak Island, Alaska
Wardle *et al.*, 2000	*Peponocephala electra*	Dorsal surface near the base of the dorsal fin	Corpus Christi, Texas, Gulf of Mexico
Würsig & Jefferson, 1990	*Stenella atenuata*, *Stenella longirostris*	All over the body	All over the world
Zerbini & Santos, 1997	*Feresa attenuata*	Ventral surface	Coast of Brazil

Figures

Figure 1. Specimen of *Isistius brasiliensis* MNHN A-7787 (holotype of *Isistius brasiliensis* and of the junior synonym *Scymnus brasiliensis*) from Southeastern coast of Brazil, Atlantic Ocean. TL=172 mm

Figure 2. Specimen of *Isistius brasiliensis* MNHN 0000-1178 (holotype of the junior synonym *Scymnus brasilensis unicolor*) from Mauritius Island, Indian Ocean. TL=471 mm.

Figure 3. Specimen of *Isistius brasiliensis* NMW 76230 (holotype of the junior synonym *Leius ferox*) from Polynesian Triangle, Pacific Ocean. TL=162 mm

Figure 4. Specimen of *Isistius plutodus* USNM 188386 (holotype), from Gulf of Mexico. TL=416 mm

Figure 5. Specimen of *Isistius brasiliensis* SCSFRI S07257 (holotype of the junior synonym *Isistius labialis*), from South China Sea, Pacific Ocean. TL=442 mm

Figure 6. Dorsal fins of Dalatiidae species. From left to right, and from top to bottom: *Isistius brasiliensis* (CSIRO H 4714-01), *I. labialis* (SCSFRI S07257), *I. plutodus* (AMS 43044-001), *Dalatias licha* (AMS 43469-001), *Squaliolus laticaudus* (CSIRO H1215-01), *S. aliae* (NSMT-P 35505), *Euprotomicrus bispinatus* (NSMT-P 71062), *Euprotomicroides zantedeschia* (ZMH 114732), *Heteroscymnoides marleyi* (ZMH 123459), and *Mollisquama parini* (TU 203676).

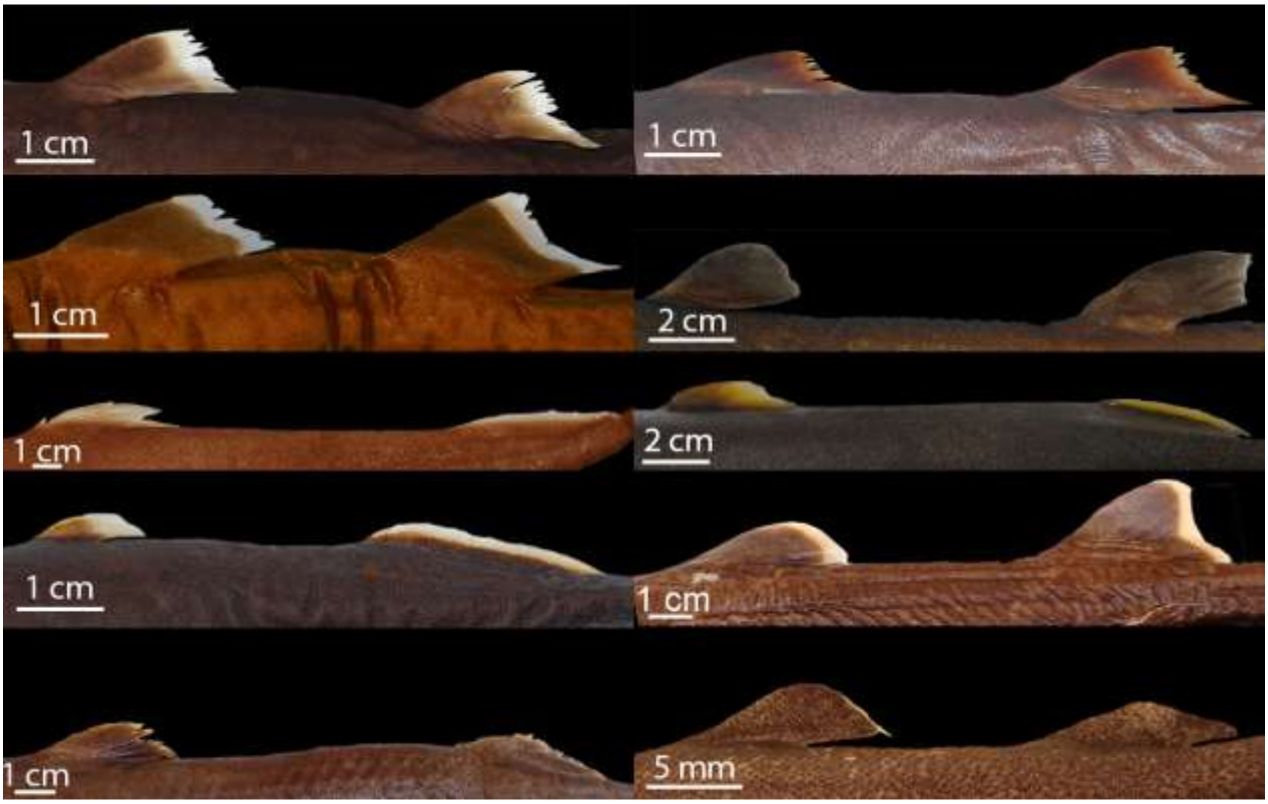

Figure 7. Caudal fins of Dalatiidae species. From left to right, and from top to bottom: *Isistius brasiliensis* (HUMZ 211104), *I. labialis* (SCSFRI S07257), *I. plutodus* (HUMZ 210817), *Dalatias licha* (AMS 12876), *Squaliolus laticaudus* (MNRJ 30199), *S. aliae* (NSMT-P 35505), *Euprotomicrus bispinatus* (NSMT-P 71062), *Euprotomicroides zantedeschia* (ZMH 114732), *Heteroscymnoides marleyi* (ZMH 108438), and *Mollisquama parini* (TU 203676).

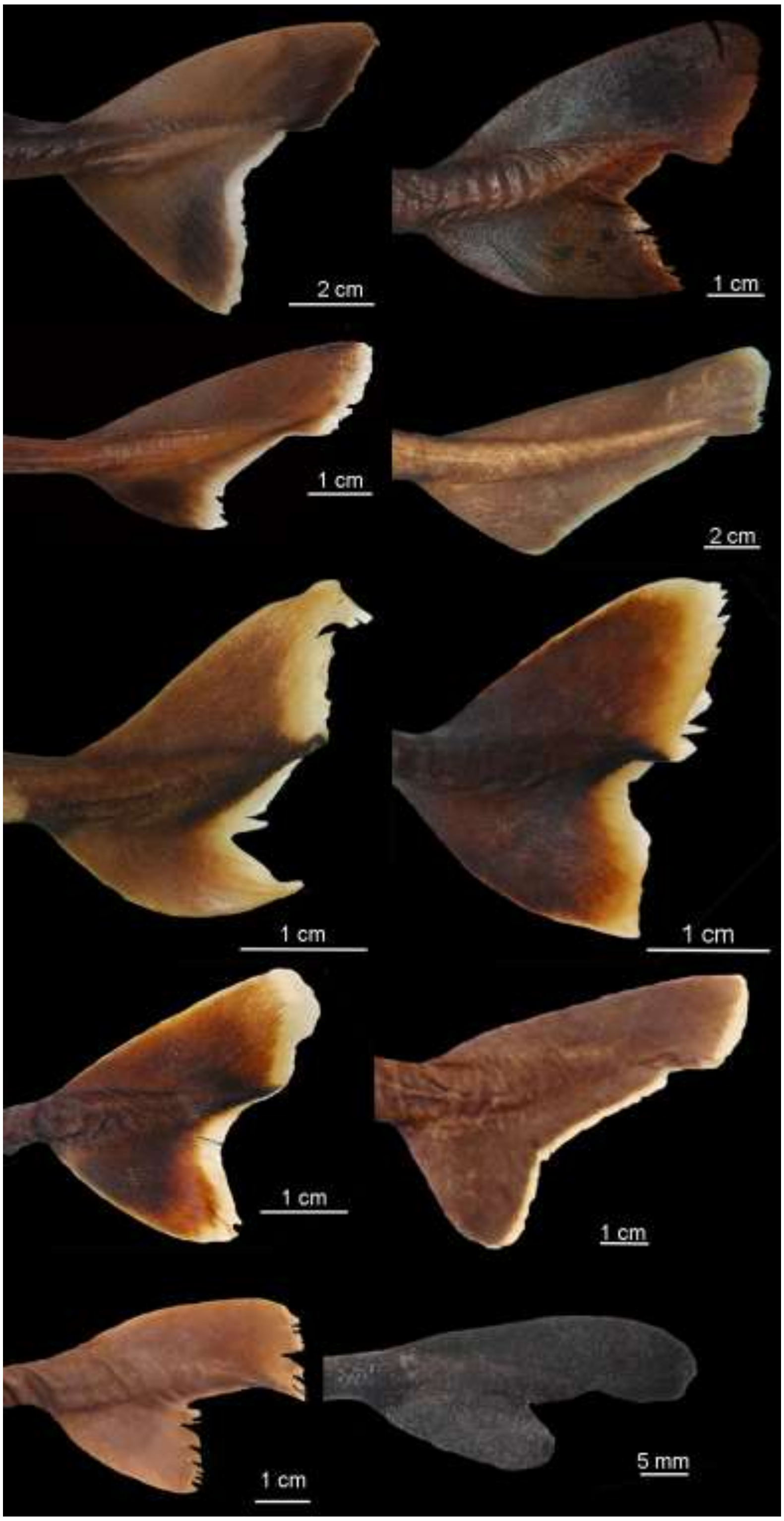

Figure 8. Lateral, dorsal, and ventral views of a specimen of *Isistius brasiliensis* (HUMZ 124775) from Northwestern Pacific Ocean.

Figure 9. Ventral view of the mouth region showing its structure in *Isistius brasiliensis* (MCZ 41352).

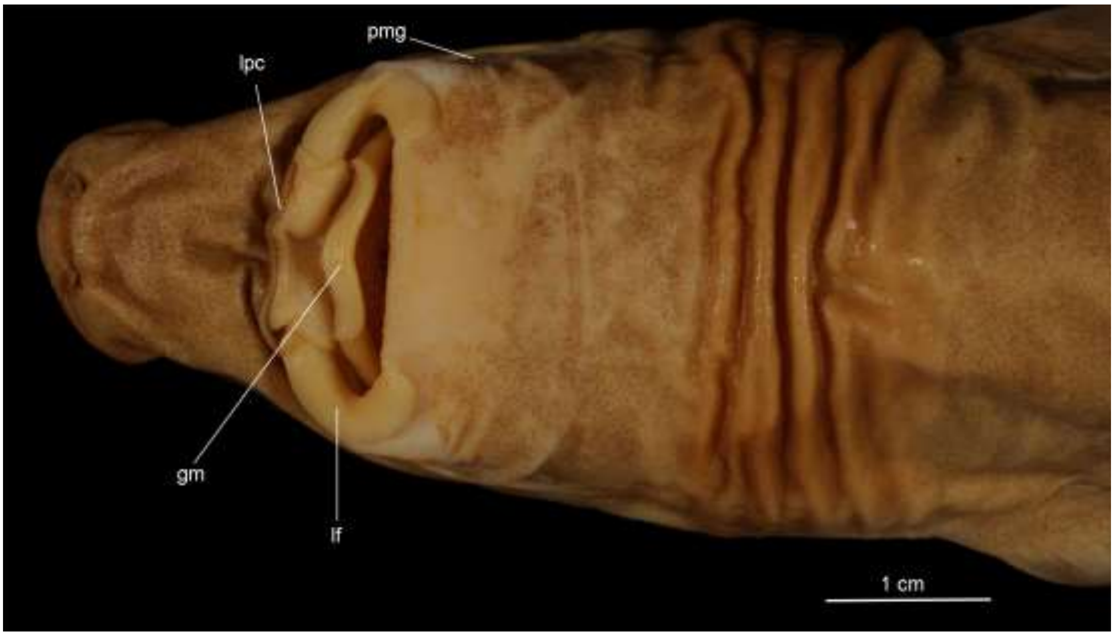

Figure 10. Upper symphyseal tooth of *Isistius brasiliensis* (MNHN 1996-0564). Top left: labial view, top right: lingual view, bottom: lateral view.

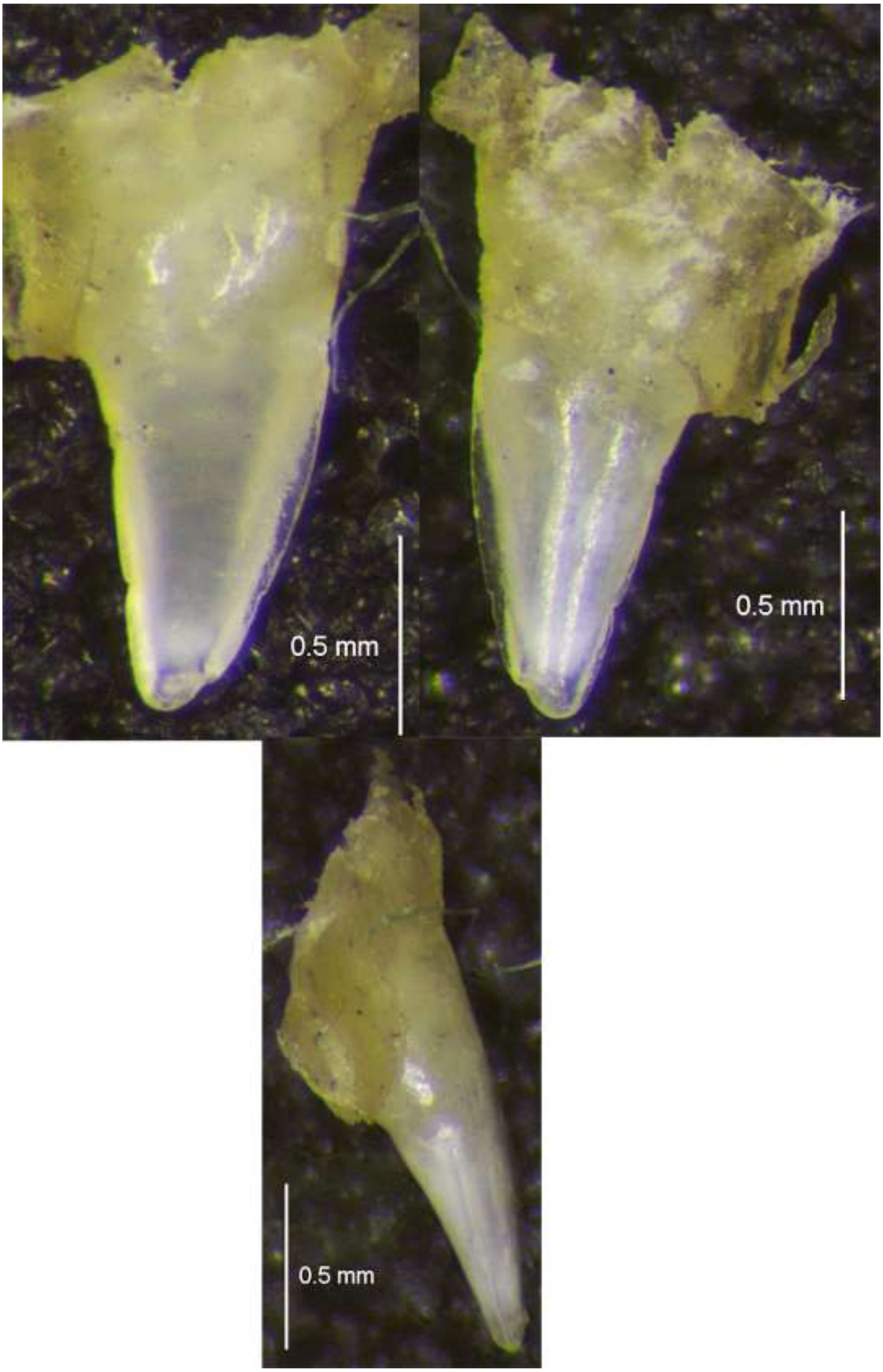

Figure 11. Lower teeth of *Isistius brasiliensis* (MZUSP N/C). Top: upper and lower teeth of *Isistius brasiliensis* MNHN 1996-0465 showing the smaller symphyseal lower tooth, and both symphyseal upper teeth in opposite directions; middle: labial view, and right parasymphyseal tooth on the right; bottom: lingual view, and right parasymphyseal tooth on the left.

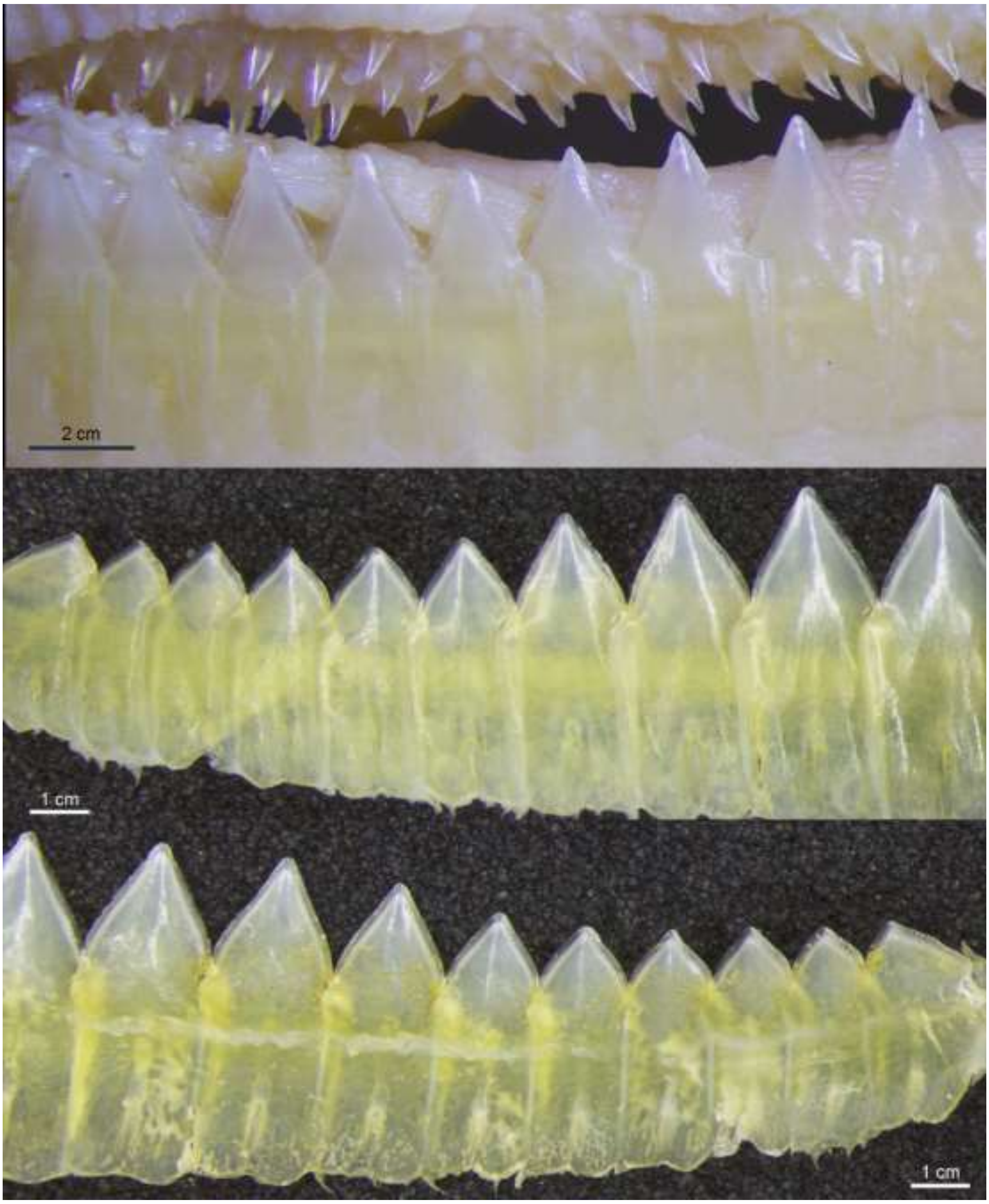

Figure 12. Dermal denticles of *Isistius brasiliensis* from Pacific Ocean (BPBM 24471 on the left and HUMZ 211104 on right).

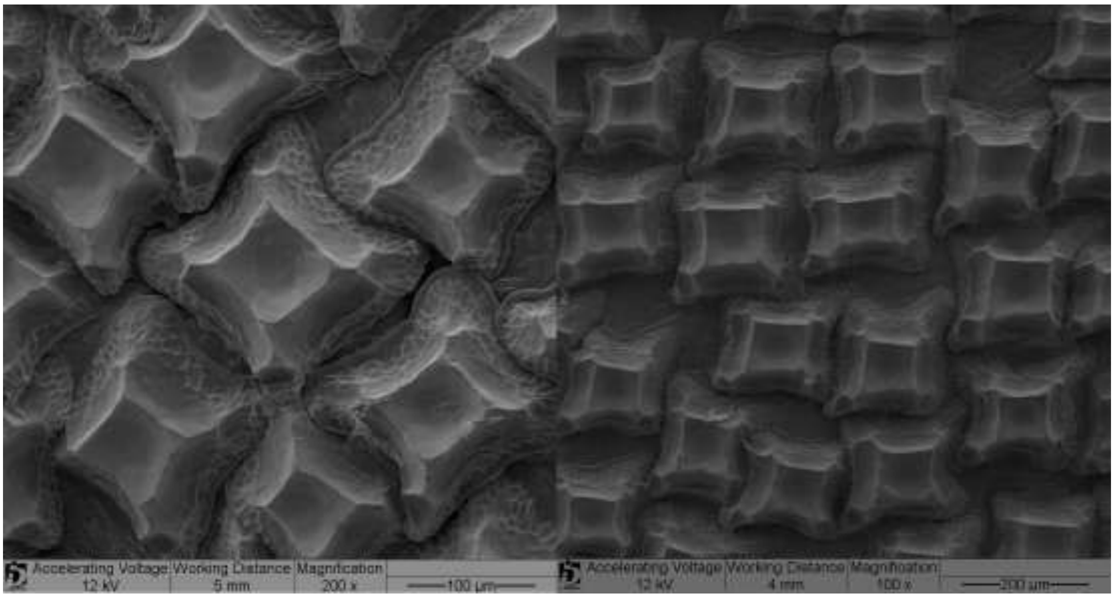

Figure 13. Dermal denticles of *Isistius brasiliensis* from Pacific Ocean (BPBM 24471), ventral region pre-collar on the left and ventral region post-collar on the right).

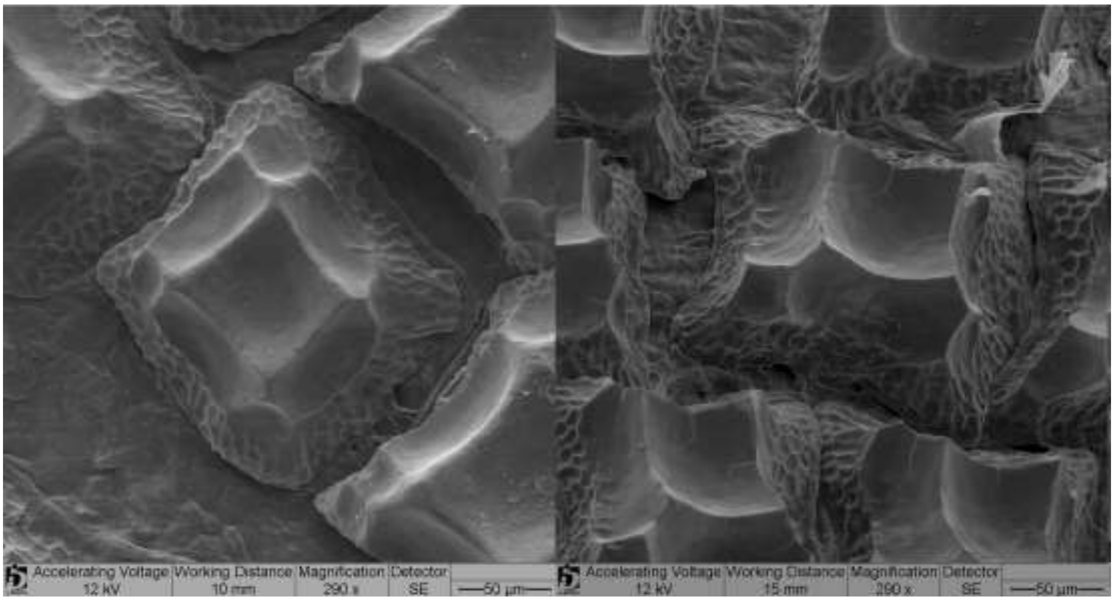

Figure 14. Image of the ventral side of *Isistius brasiliensis* (BPBM 24471). Photophores are on top of and lateral to dermal denticles in an irregular distribution.

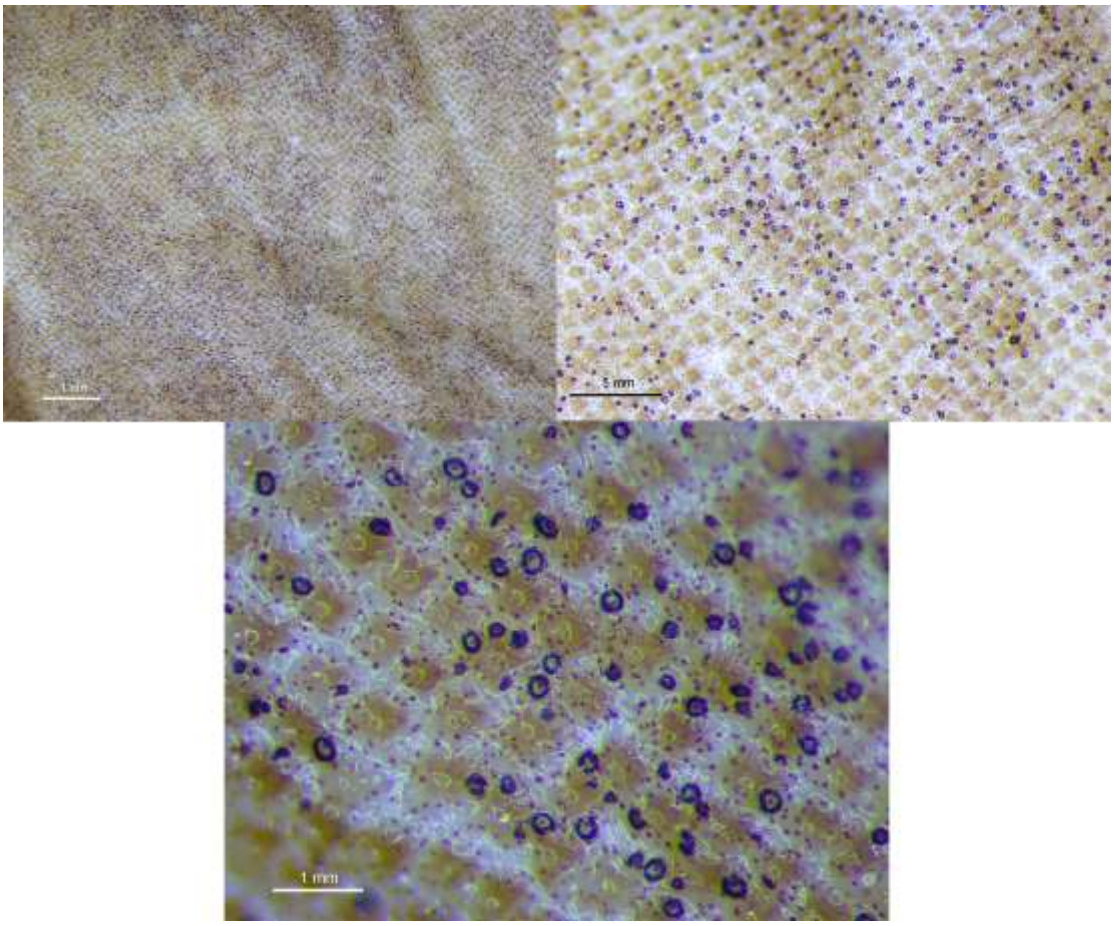

Figure 15. Distribution of *Isistius brasiliensis* (yellow circles: analyzed specimens; red stars: holotypes).

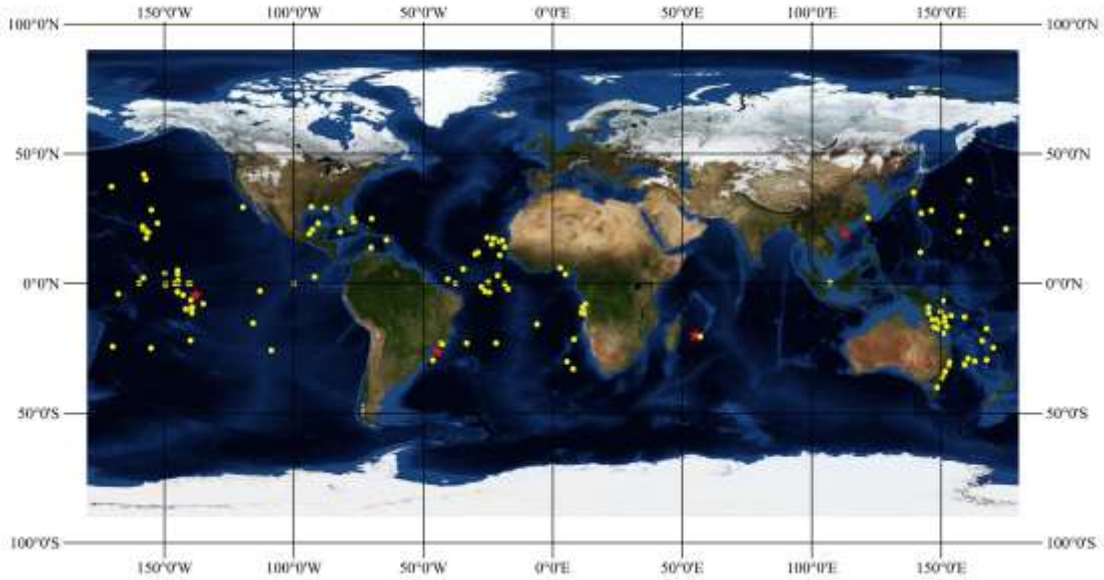

Figure 16. Specimens of *Isistius brasiliensis* showing the diversity of colors, shapes, and sizes. From left to right, and from top to bottom: CSIRO 3722 (Southwestern Pacific), MCZ 58095 (Northwestern Atlantic), HUMZ 124775 (Northwestern Pacific), UF 165691 (Northeastern Atlantic), NMW 60844 (Southwestern Indian), and ZMH 10836 (Southeastern Atlantic).

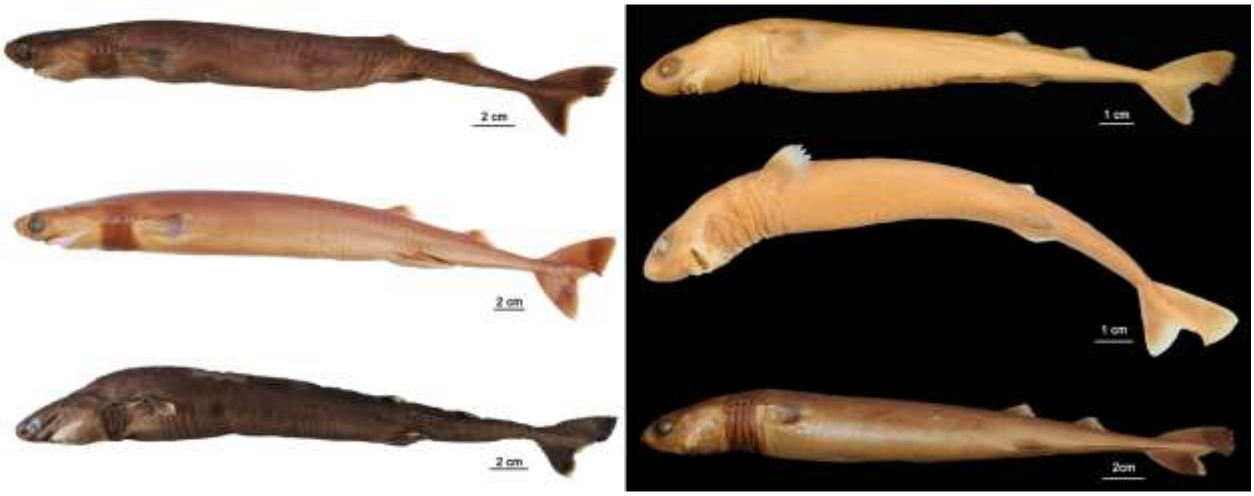

Figure 17. Lateral, dorsal, and ventral views of a specimen of *Isistius plutodus* (HUMZ 210817) from Northwestern Pacific Ocean.

Figure 18. Ventral view of the mouth region in *Isistius plutodus* (HUMZ 210817).

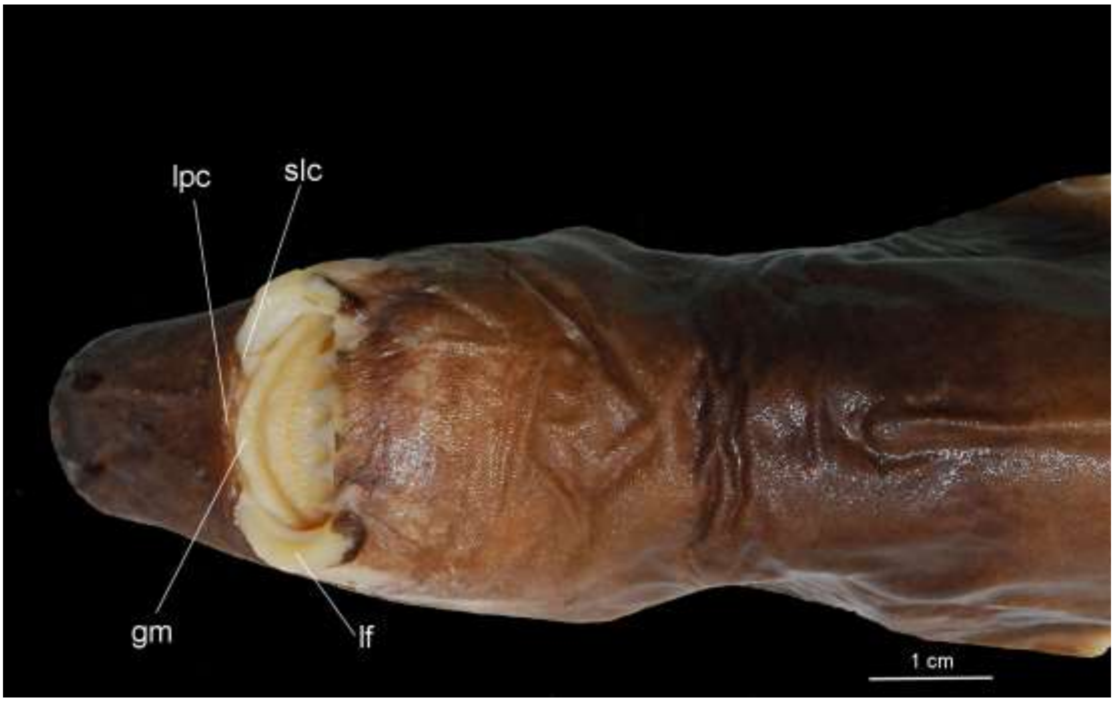

Figure 19. Upper symphyseal tooth of *Isistius plutodus* (ZUEC 8333). At top left: labial view, at top right: lingual view, on the bottom: lateral view.

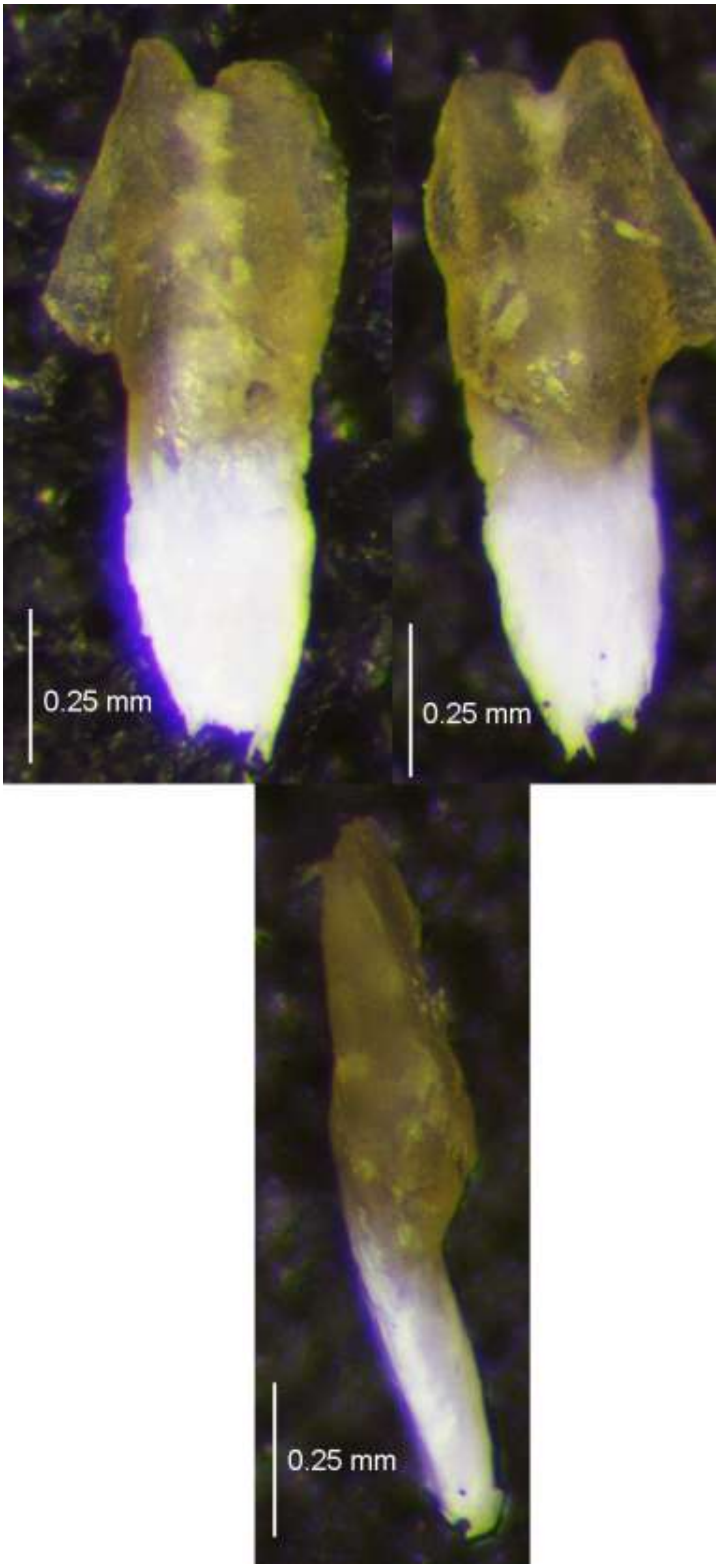

Figure 20. Lower teeth of *Isistius plutodus* (ZUEC 8333). Labial view on the left, and lingual view on the right. In each image, the symphyseal tooth is in the middle and both parasymphyseal teeth are laterally connected to it.

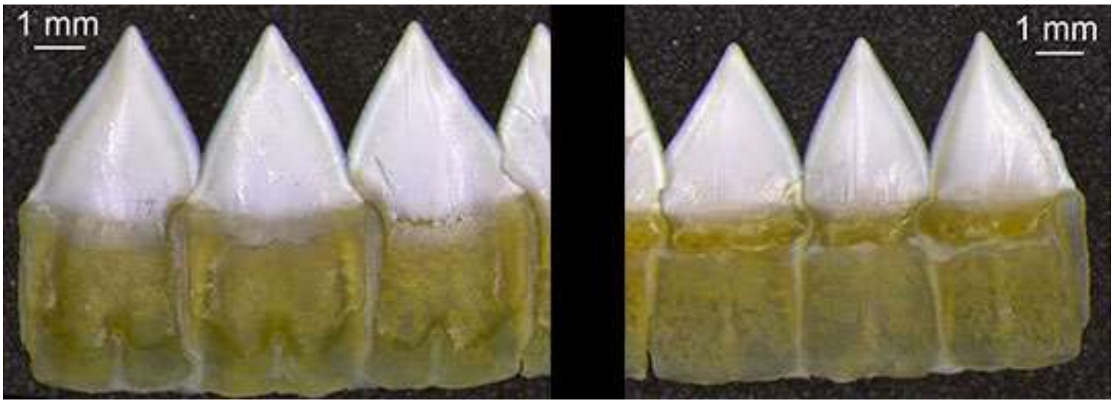

Figure 21. Image of the ventral side of *Isistius plutodus* (ZUEC 8332). Photophores on top of and lateral to dermal denticles in an irregular pattern of distribution..

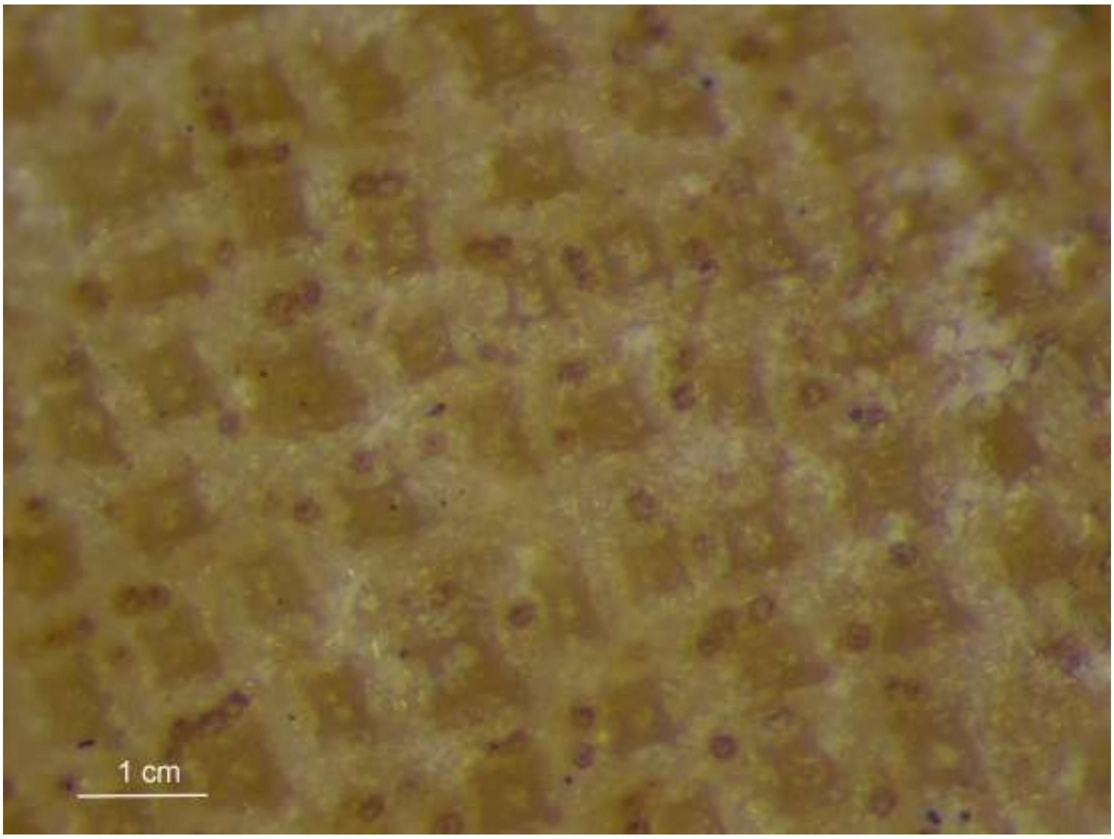

Figure 22. Dermal denticles of *Isistius plutodus* from Atlantic Ocean (ZUEC 8333).

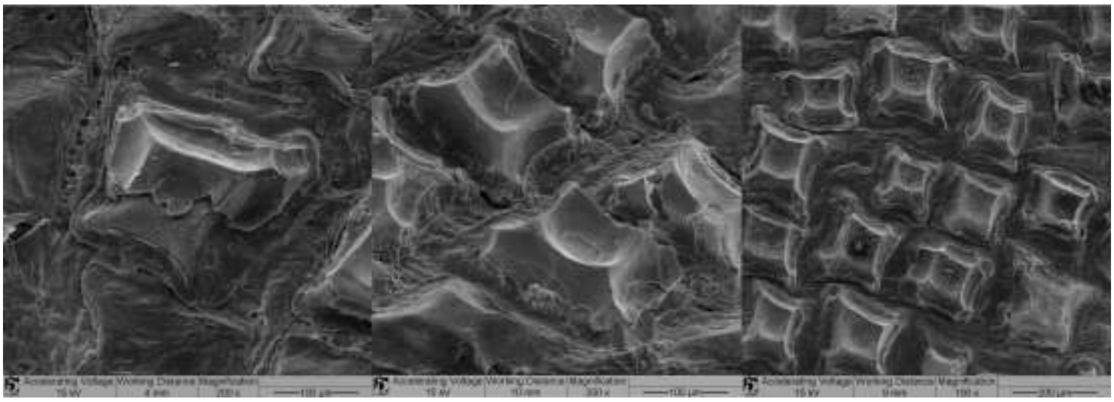

Figure 23. Distribution of *I. plutodus* (yellow circles: analyzed specimens; pink circles: specimens not examined; red star: holotype).

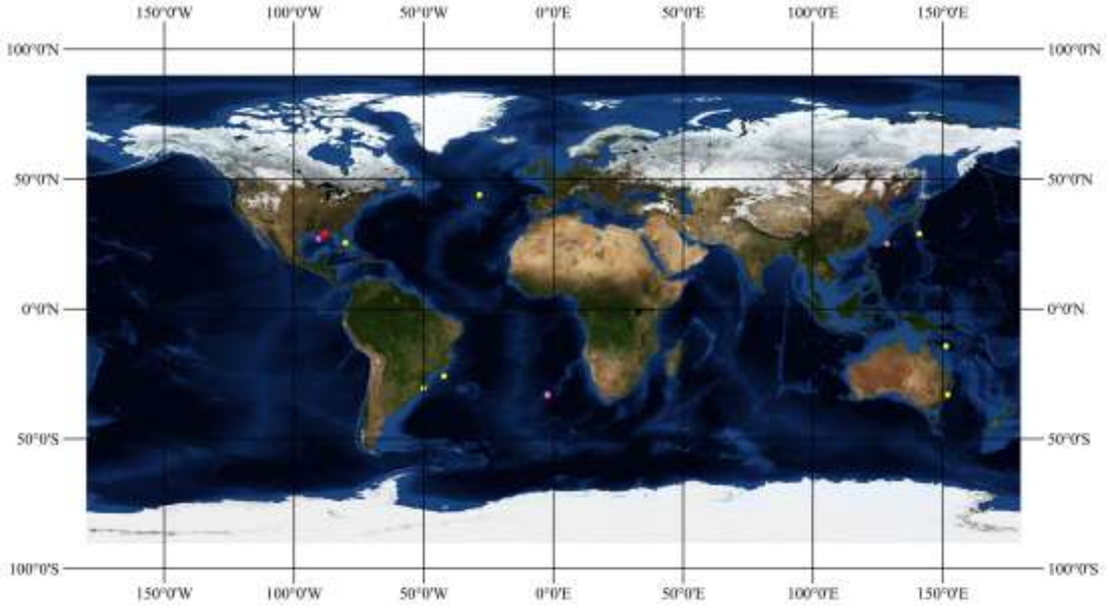

Figure 24. Specimen of *Isistius plutodus* (UF 232954) from the Gulf of Mexico.

Figure 25. Original photographs of original description of *Isistius plutodus* Garrick & Springer (1964): (A) ventral head of *I. plutodus*, (B) ventral head of *I. brasiliensis*, (C) caudal fin of *I. plutodus*, and (D) caudal fin of *I. brasiliensis*, showing the ventral dark collar and caudal morphological differences in the tail of both species. Kindly shared by Dr. George Burgess, FLMNH.

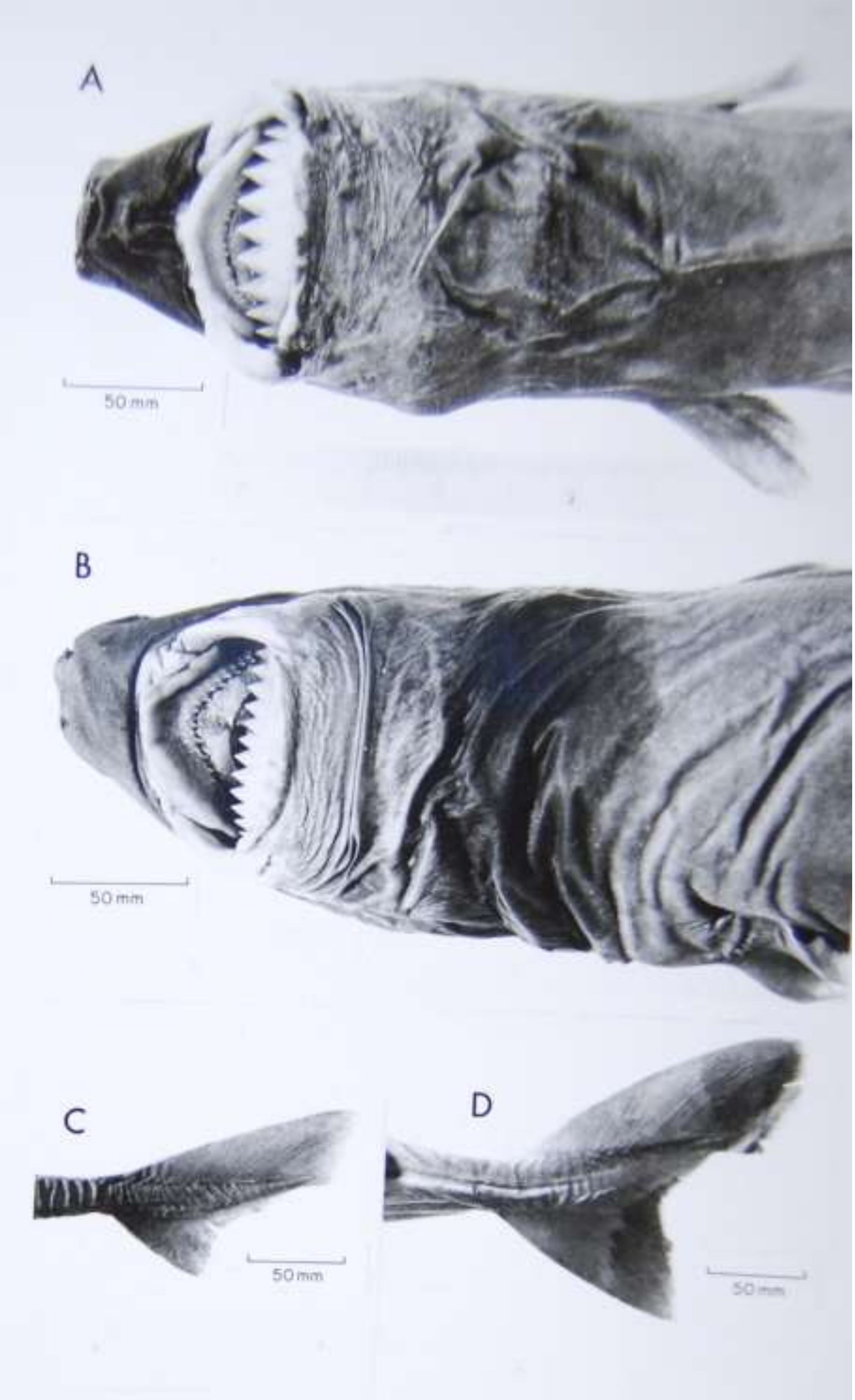

Figure 26. Specimen of *Dalatias licha* AM 3702 (holotype of the junior synonym *Scymnorhinus phillippsi*) from Great Australian Bight, Pacific Ocean. TL=1160 mm

Figure 27. Radiograph of *Dalatias licha* (SAIAB 189435) from Indian Ocean, with 38 monospondylous, 11 precaudal diplospondylous and 28 caudal diplospondylous vertebrae.

Figure 28. Upper teeth of an adult specimen (N/C) on top, and a juvenile on the bottom (NMMBA N/C) of *Dalatias licha*. On the left: Labial view, on the right: lingual view.

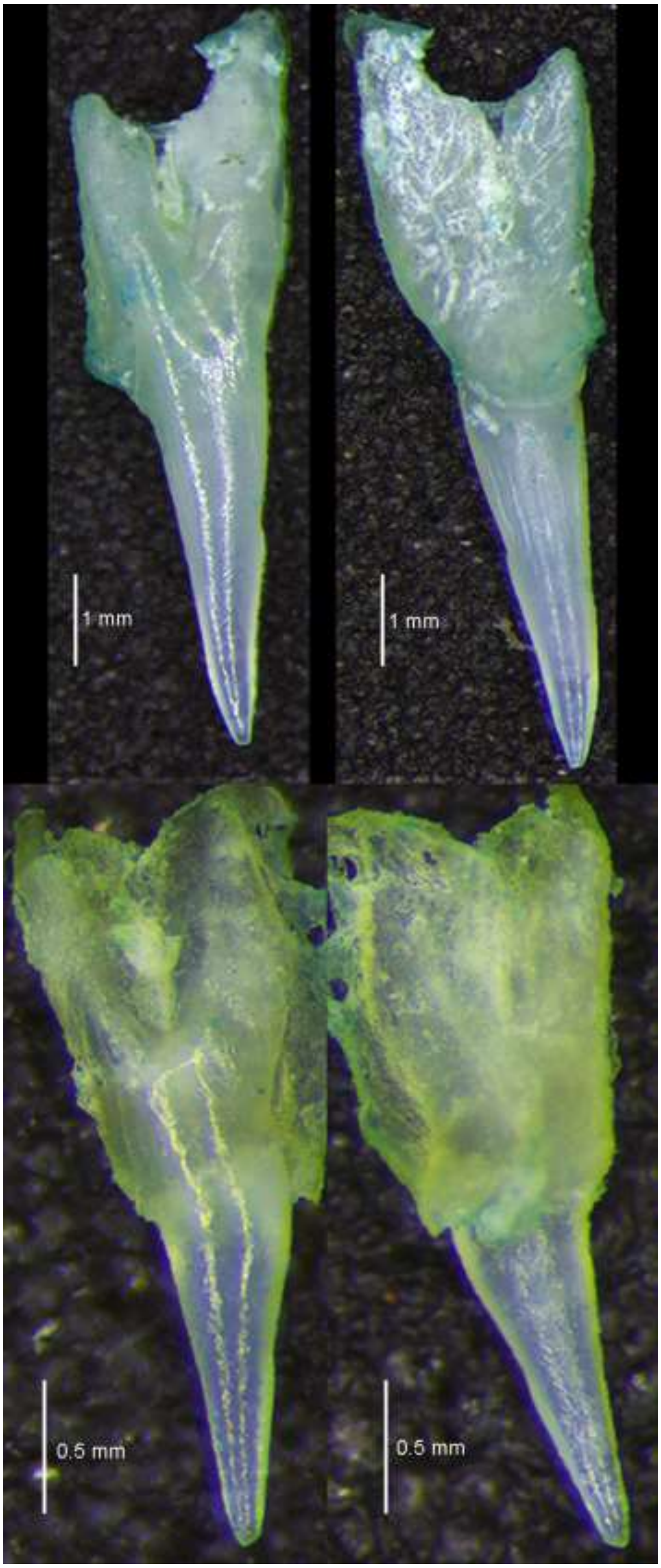

Figure 29. Specimen of *Dalatias licha* AM E.12876 (paratype) from Great Australian Bight, Pacific Ocean. TL = 496 mm

Figure 30. Dermal denticles of *Dalatias licha* from Pacific (NMMBA N/C) and Indian (SAIAB 189435) Oceans. Specimen NMMBA N/C on left (lateral region) and on right (anterior to second dorsal fin), and specimen SAIAB 189435 in the middle (abdominal region).

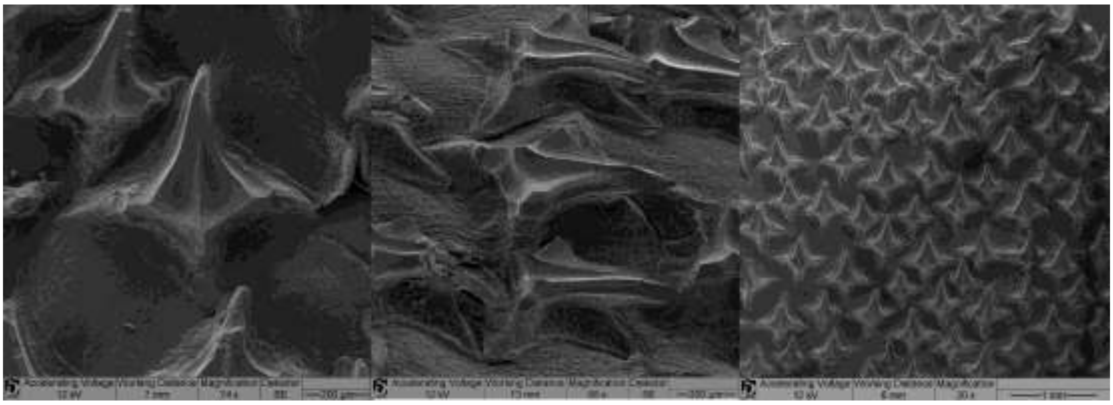

Figure 31. Distribution of *Dalatias licha* (yellow circles: analyzed specimens; red stars: analyzed holotype and paratype).

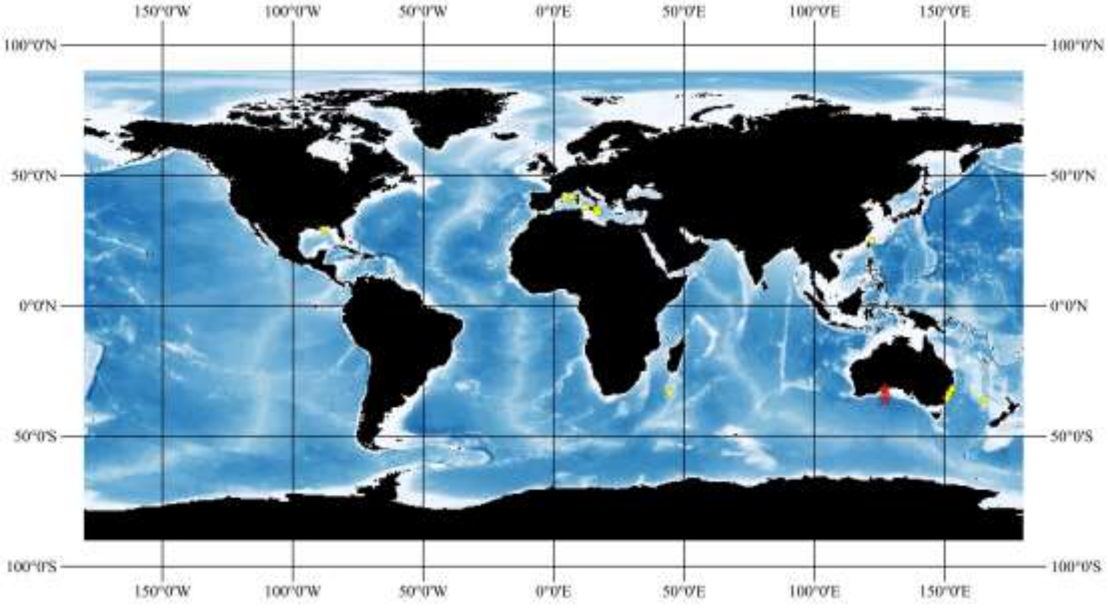

Figure 32. Specimen of *Squaliolus laticaudus* USNM 70259 (holotype) from Philippines, Pacific Ocean. TL=142.98 mm

Figure 33. Radiograph of the holotype of *Squaliolus laticaudus* (USNM 70259) from Northwestern Pacific Ocean, with 28 monospondylous, 17 precaudal diplospondylous and 15 caudal diplospondylous vertebrae.

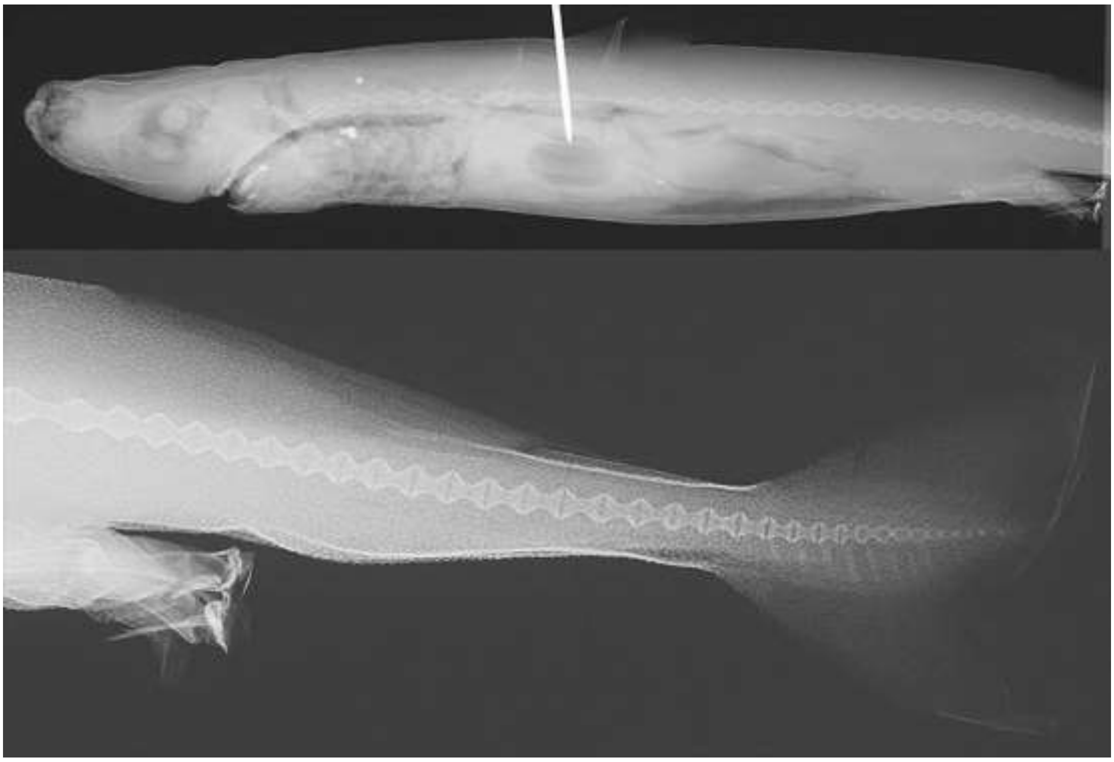

Figure 34. Image of the ventral side of *Squaliolus laticaudus* (MNRJ 30199). Photophores on top of and lateral to dermal denticles in an irregular pattern of distribution.

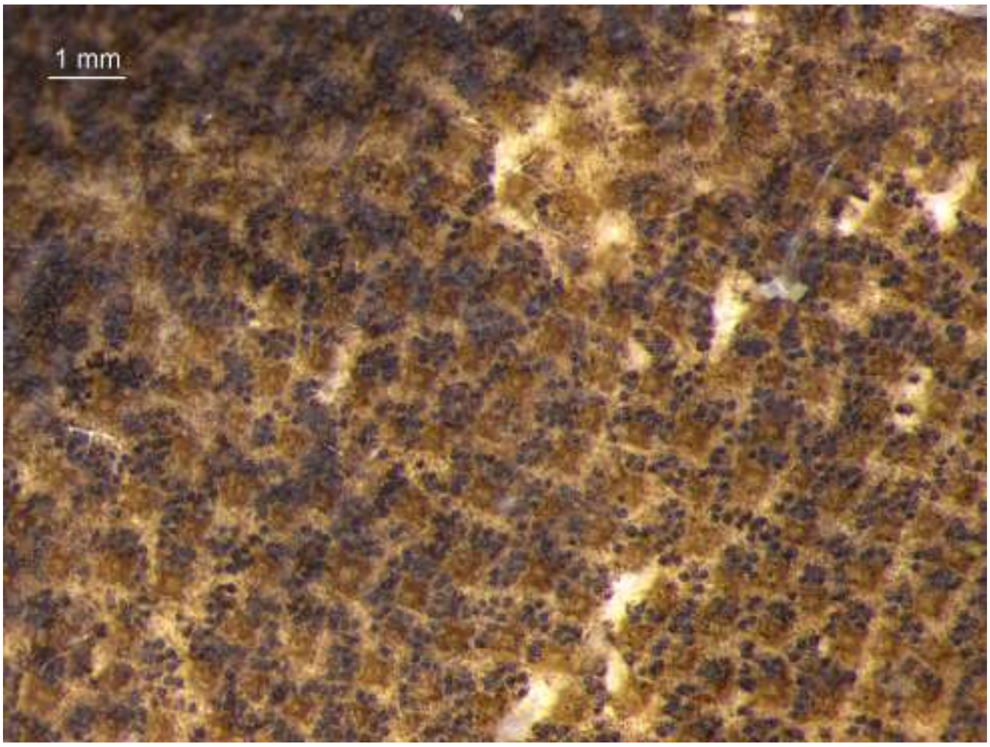

Figure 35. Distribution of *Squaliolus laticaudus* (yellow circles: analyzed specimens; red stars: analyzed holotype and paratype), and *Squaliolus aliae* (pink circles: analyzed specimens).

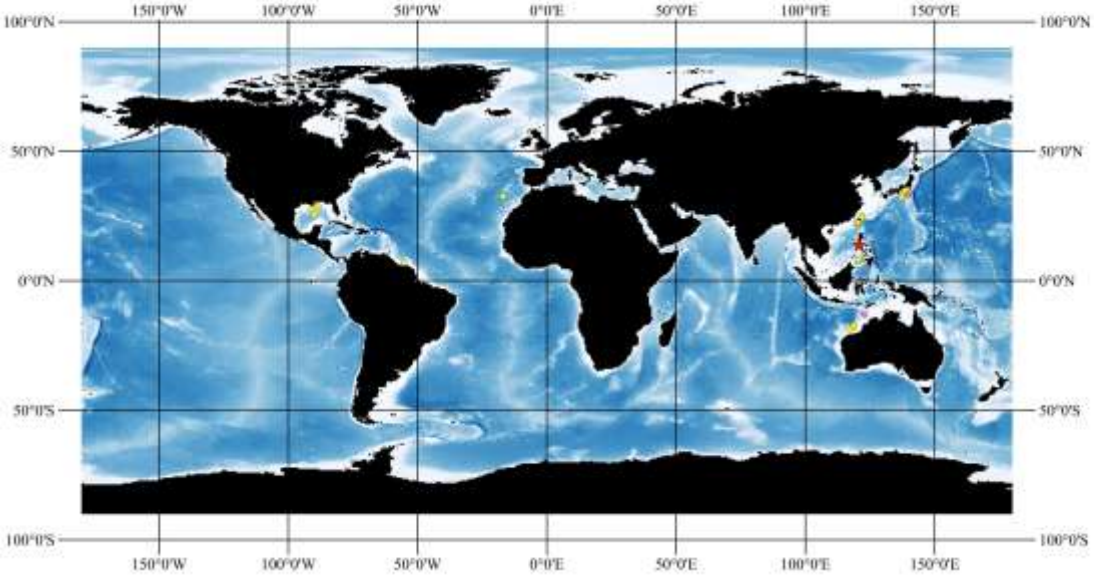

Figure 36. Specimen of *Squaliolus aliae* NSMT 77753.

Figure 37. Radiograph of the holotype of *Squaliolus aliae* (USNM 399935) from Northwestern Pacific Ocean, with 29 monospondylous, 17 precaudal diplospondylous and 11 caudal diplospondylous vertebrae.

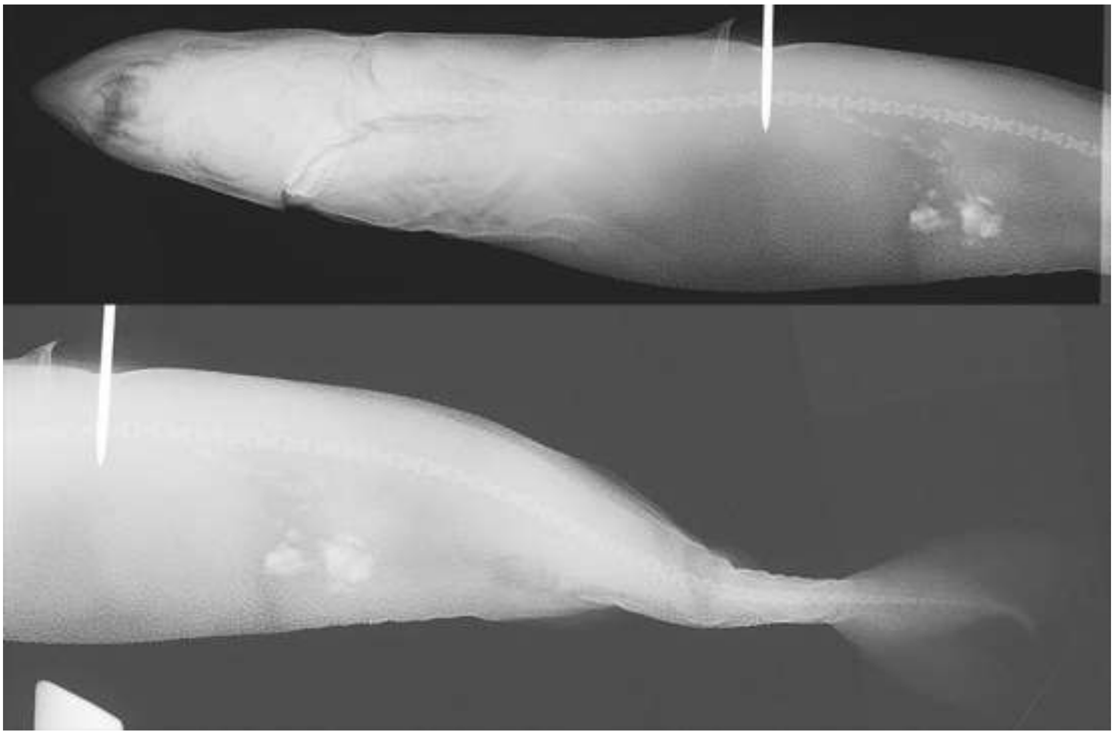

Figure 38. Dermal denticle of *Squaliolus aliae* from Pacific Ocean (HUMZ 119285), from Northwestern Pacific Ocean.

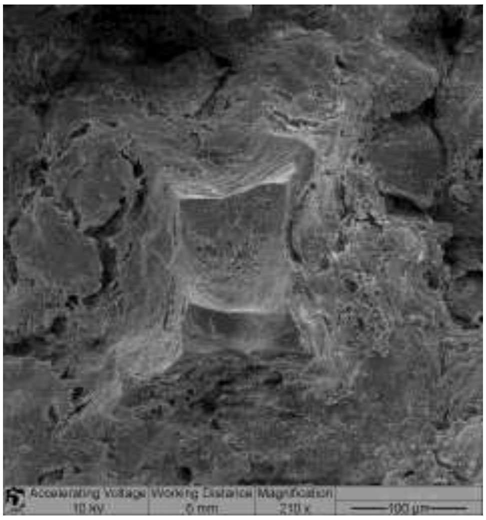

Figure 39. Top: holotype of *Euprotomicrus bispinatus* (MNHN 1216) from Mauritius, Indian Ocean. TL=194 mm. Bottom: specimen of *Euprotomicrus bispinatus* (UF 190031) from Midway Island, Pacific Ocean. TL = 240 mm.

Figure 40. Radiograph of the ventral portion of head and branquial region of *Euprotomicrus bispinatus* (USNM 164176) from the Northwestern Pacific Ocean. Darker structures on each side of branquial basket are the ventromedial branchial cartilages. 31 monospondylous, 16 precaudal diplospondylous and 15 caudal diplospondylous vertebrae.

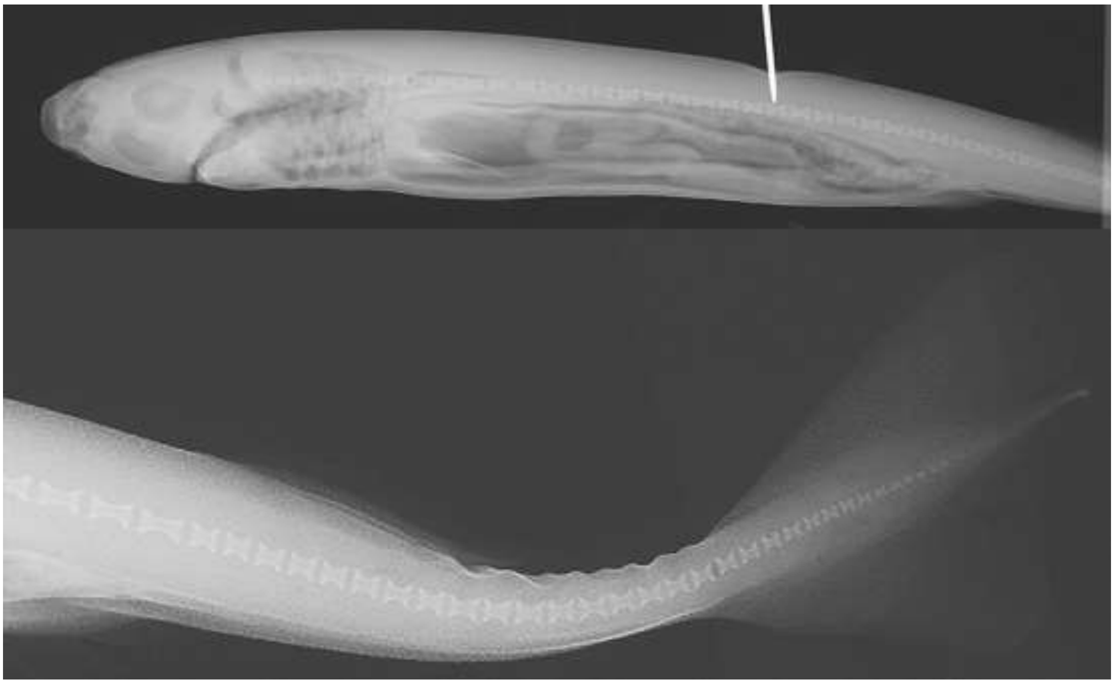

Figure 41. Dermal denticles of *Euprotomicrus bispinatus* from Pacific Ocean (BPBM 40404). At left and middle from dorsal region, and left left from lateral region.

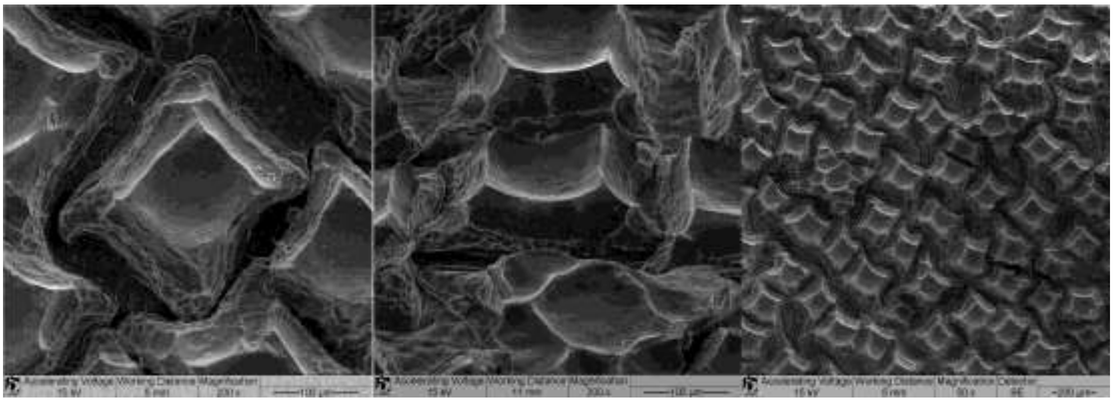

Figure 42. Images of the ventral side of *Euprotomicrus bispinatus* (BPBM 40404). Photophores are on top of and lateral to dermal denticles in an irregular pattern of distribution.

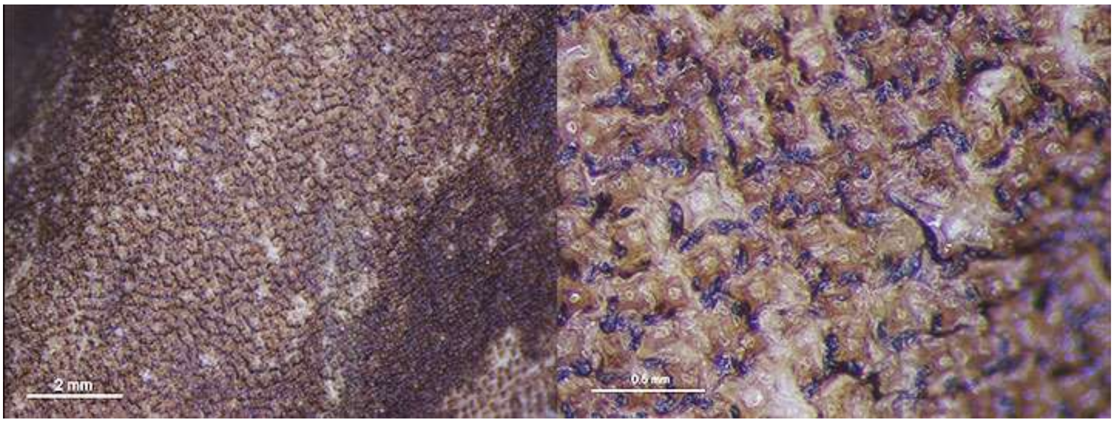

Figure 43. Distribution of *Euprotomicrus bispinatus* (yellow circles: analyzed specimens; red stars: analyzed holotype).

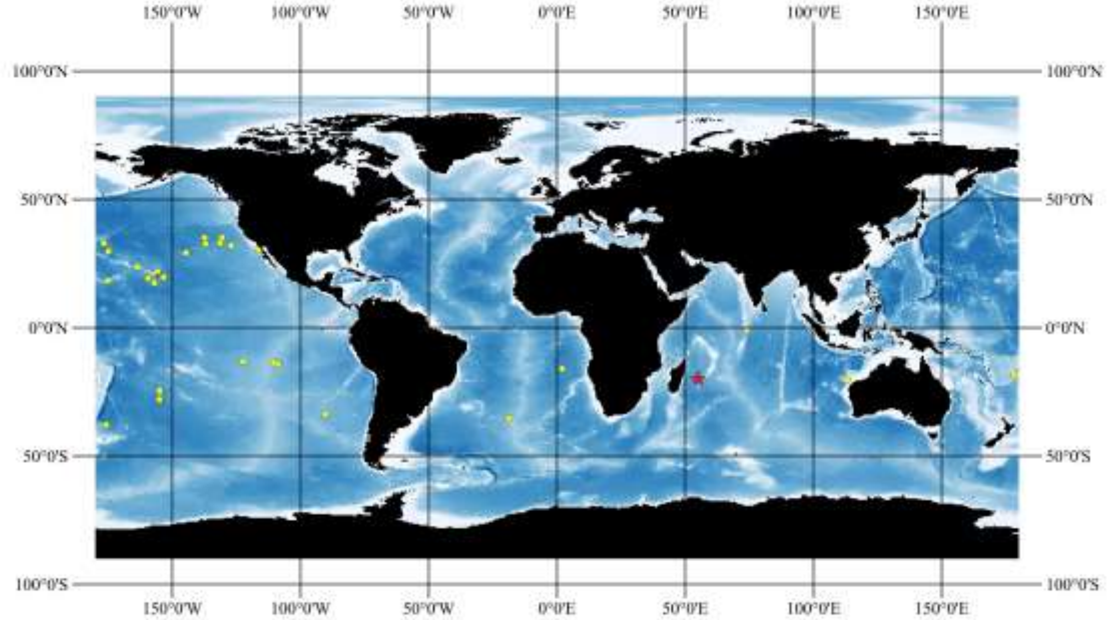

Figure 44. Specimens of *Heteroscymnoides marleyi* ANSP 53046 (holotype) on top from South Africa, Indian Ocean, and ZMH 108438 at bottom from South Atlantic Ocean. TL = 122.56 mm, and TL = 286.88 mm, respectively.

Figure 45. Radiograph of the holotype of *Heteroscymnoides zantedeschia* (ANSP 53046) from Southwestern Indian Ocean. 33 monospondylous, 18 precaudal diplospondylous, and 13 caudal diplospondylous vertebrae.

Figure 46. Distribution of *Heteroscymnoides marleyi* (yellow circles: specimens analyzed through photographs; red star: analyzed holotype).

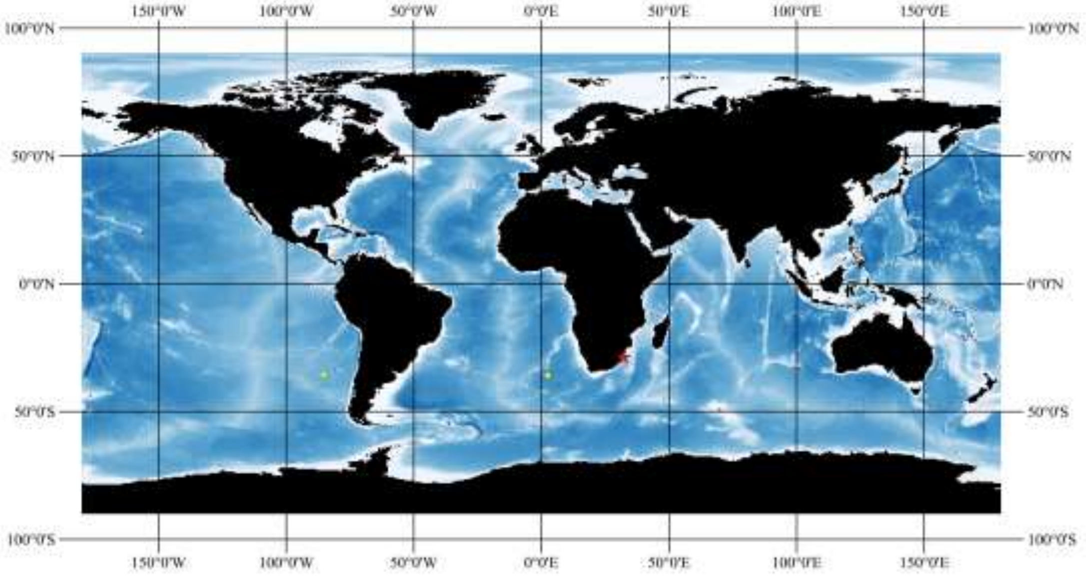

Figure 47. Specimen of *Mollisquama parini* ZIN 45988 (holotype) from Nazca Submarine Ridge, Pacific Ocean, and TU 203676 from Gulf of Mexico, Atlantic Ocean. TL = 400 mm, and TL = 145 mm, respectively. Photograph of holotype kindly shared by Spodareva Viktoria and Arcady V. Balushkin, Curator of Fishes of Zoological Institute Russian Academy of Sciences.

Figure 48. Distribution of *Mollisquama parini* (yellow circle: analyzed specimen; red star: holotype analyzed through photographs).

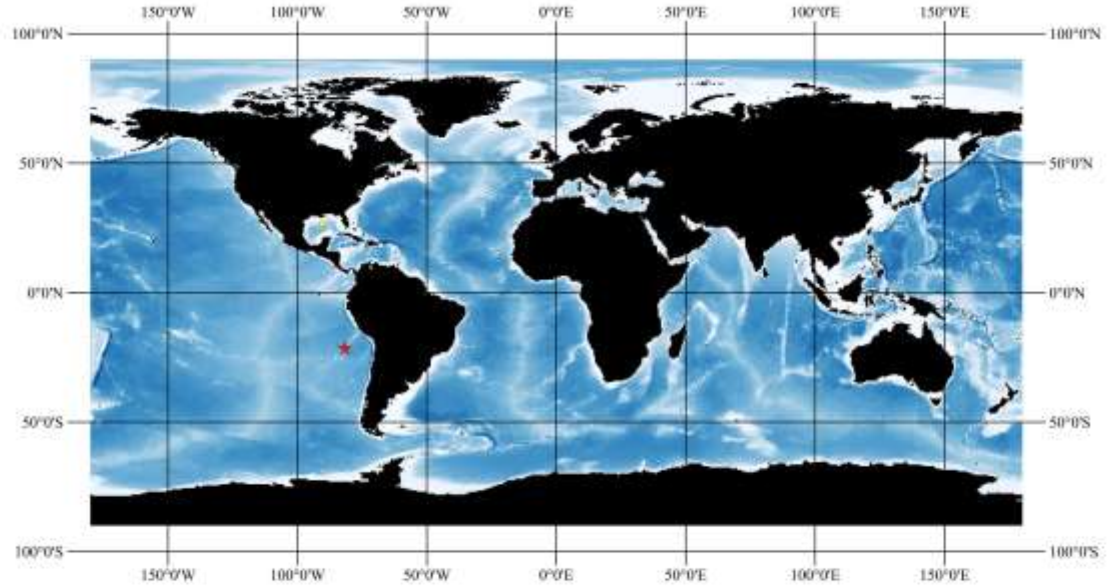

Figure 49. Specimen of *Euprotomicroides zantedeschia* SAM 23755 (holotype) from South Africa, Atlantic Ocean, and ZMH 114732 from Southeast of Brazil, Atlantic Ocean. TL = 176 mm, and TL = 377 mm, respectively. Photograph of holotype kindly shared by Michael Bougaardt, collection manager of Iziko: South African Museum.

Figure 50. Distribution of *Euprotomicroides zantedeschia* (yellow circle: specimen; red star: holotype). (Both specimens are the only ones ever collected and were analyzed through photographs).

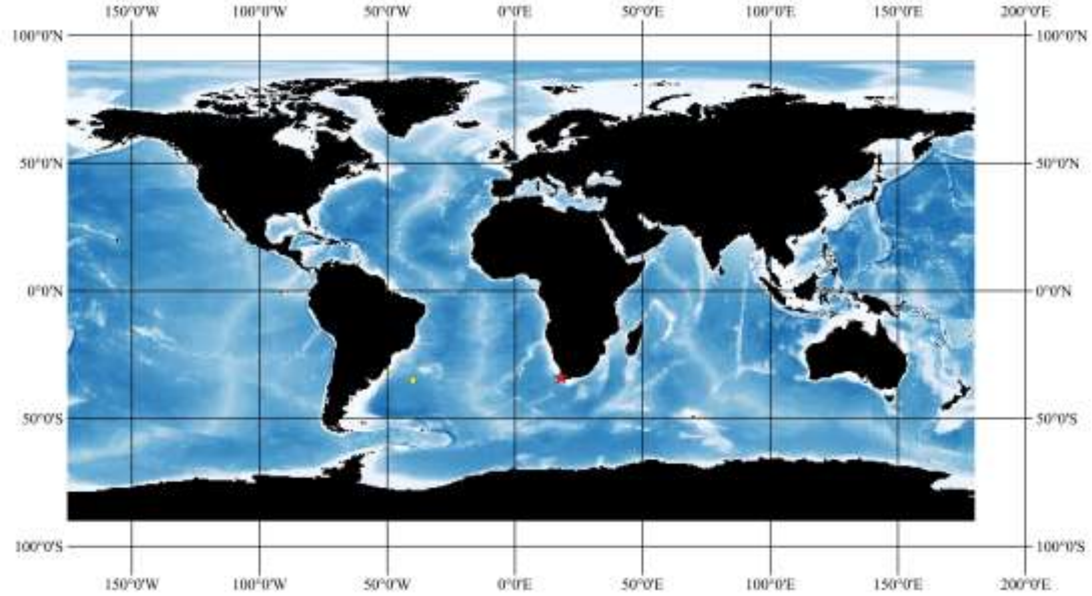

Figure 51. Radiograph of *Isistius brasiliensis* (USNM 190040) from Central Pacific Ocean with 40 monospondylous, 20 precaudal diplospondylous and 23 caudal diplospondylous vertebrae.

Figure 52. Drawings of the neurocranium of a specimen of *Isistius brasiliensis* (MZUSP N/C) in lateral, dorsal, and ventral views.

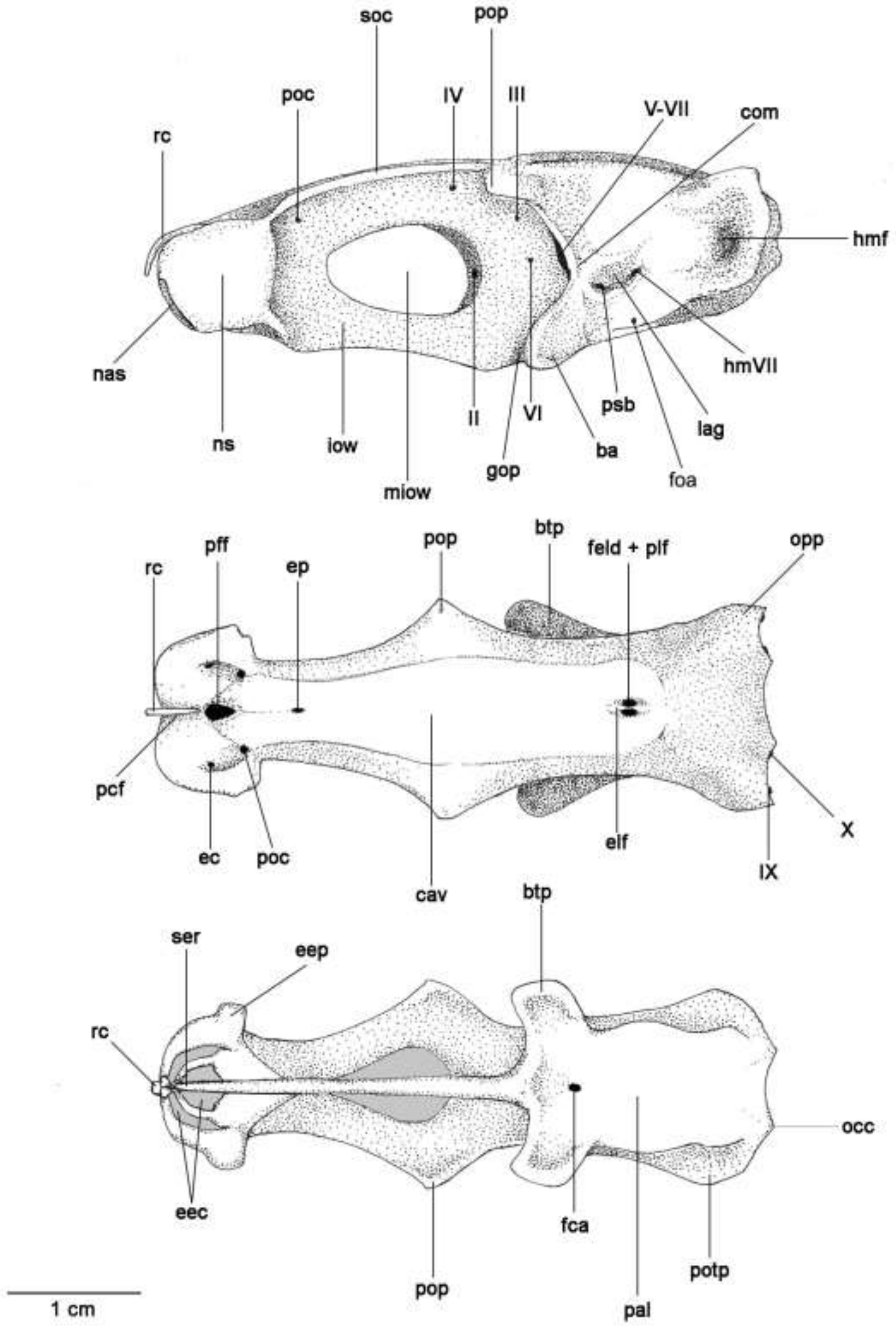

Figure 53. Mandibular and hyoid arches of a specimen of *Isistius brasiliensis* (MZUSP N/C). A: left lateral view of mandibular arch; B: dorsal view of mandibular and hyoid arches; C: anteropostero view of hyoid arch.

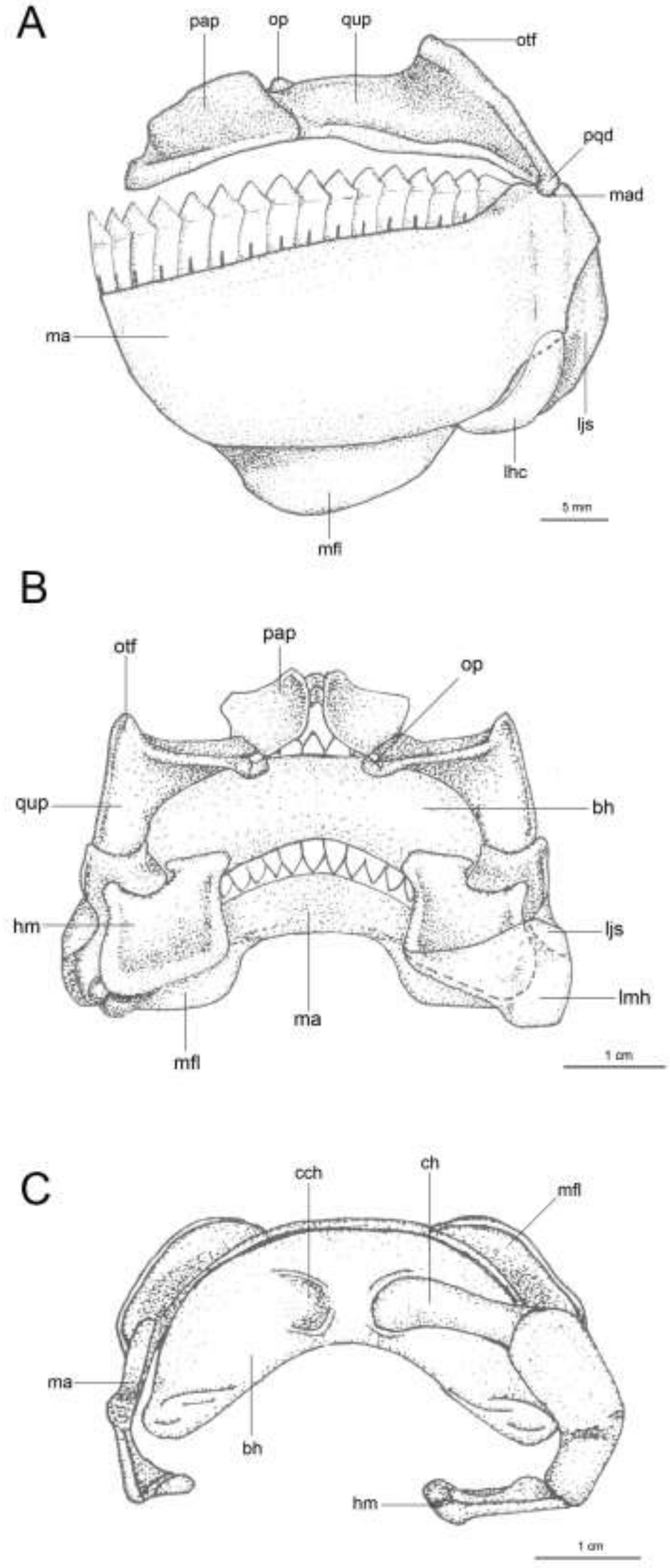

Figure 54. CT-scan of lateral view of *Isistius brasiliensis* (MNHN 1996-0465) showing the articulations between lower jaw and quadrate, and ceratohyal and hyomandibular cartilages.

Figure 55. CT-scan of a specimen of *Isistius brasiliensis* (MNHN 1996-0465) showing upper and lower tooth distribution, upper and lower labial cartilatilages articulation and a posterior upper labial cartilage.

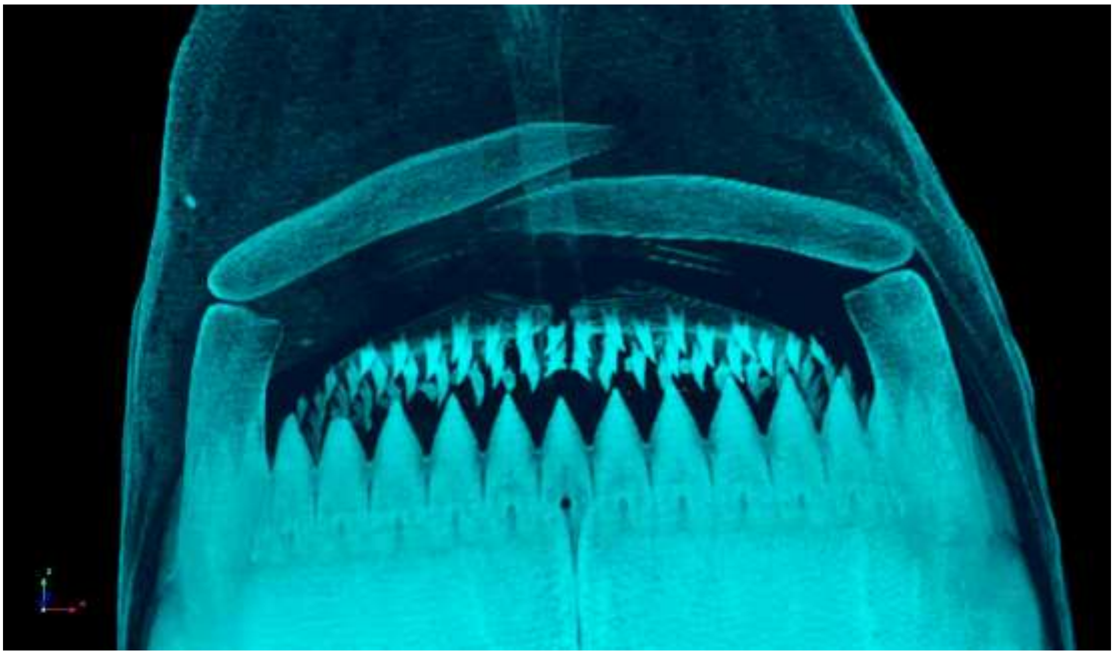

Figure 56. Dorsal view of hyoid and branchial arches of a clear and stained specimen of *Isistius brasiliensis* USNM 215948.

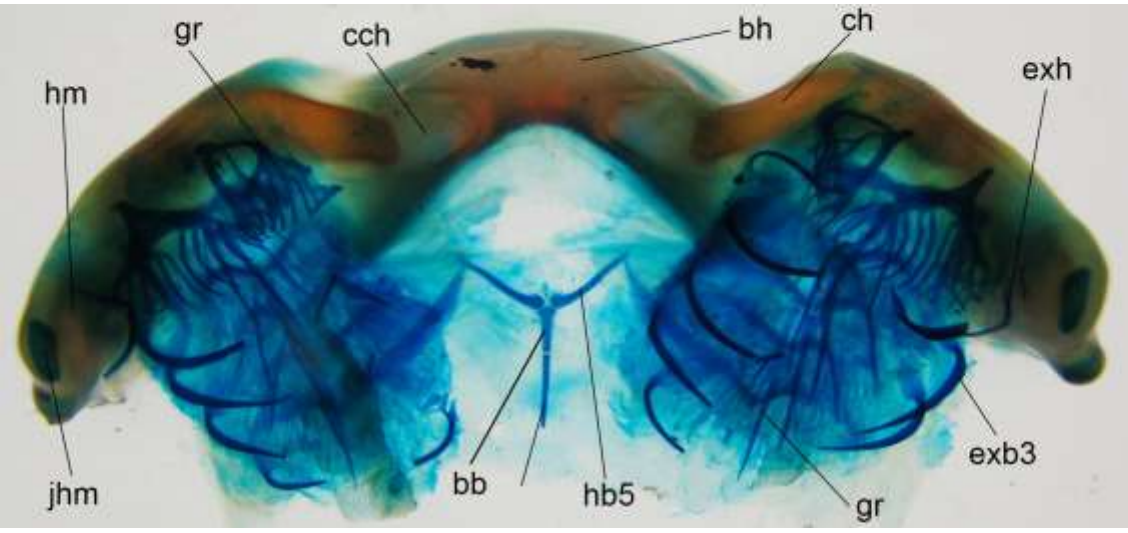

Figure 57. Ventral views (photograph and illustration) of hyoid and branchial arches of a specimen of *Isistius brasiliensis* (USNM 215948).

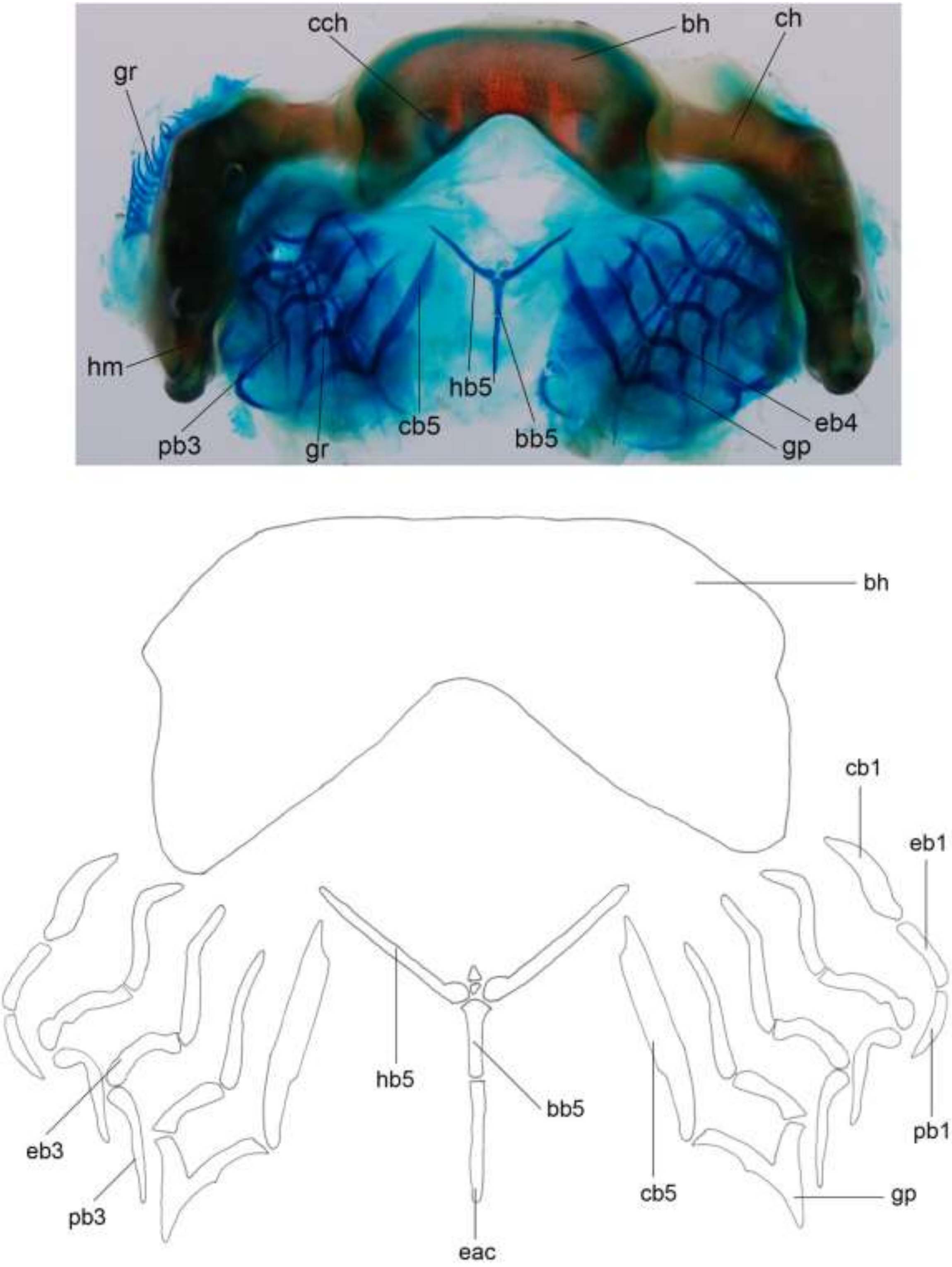

Figure 58. Medial-lateral view of anterior and posterior ventromedial branchial cartilages (vmbc) of a specimen of *Isistius brasiliensis* (MZUSP N/C). Anterior region to left, and dorsal to top.

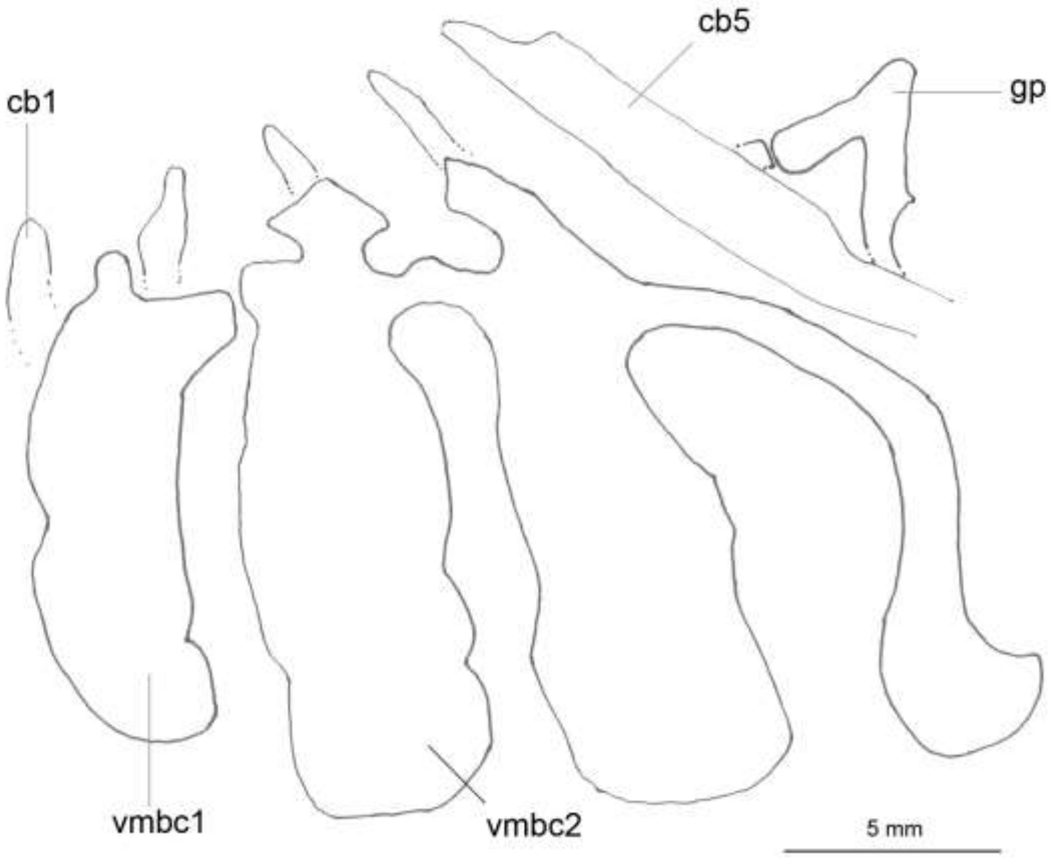

Figure 59. First (top) and second (bottom) dorsal fins of a specimen of *Isistius brasiliensis* (HUMZ 211104) from Northwestern Pacific Ocean.(anterior region to left).

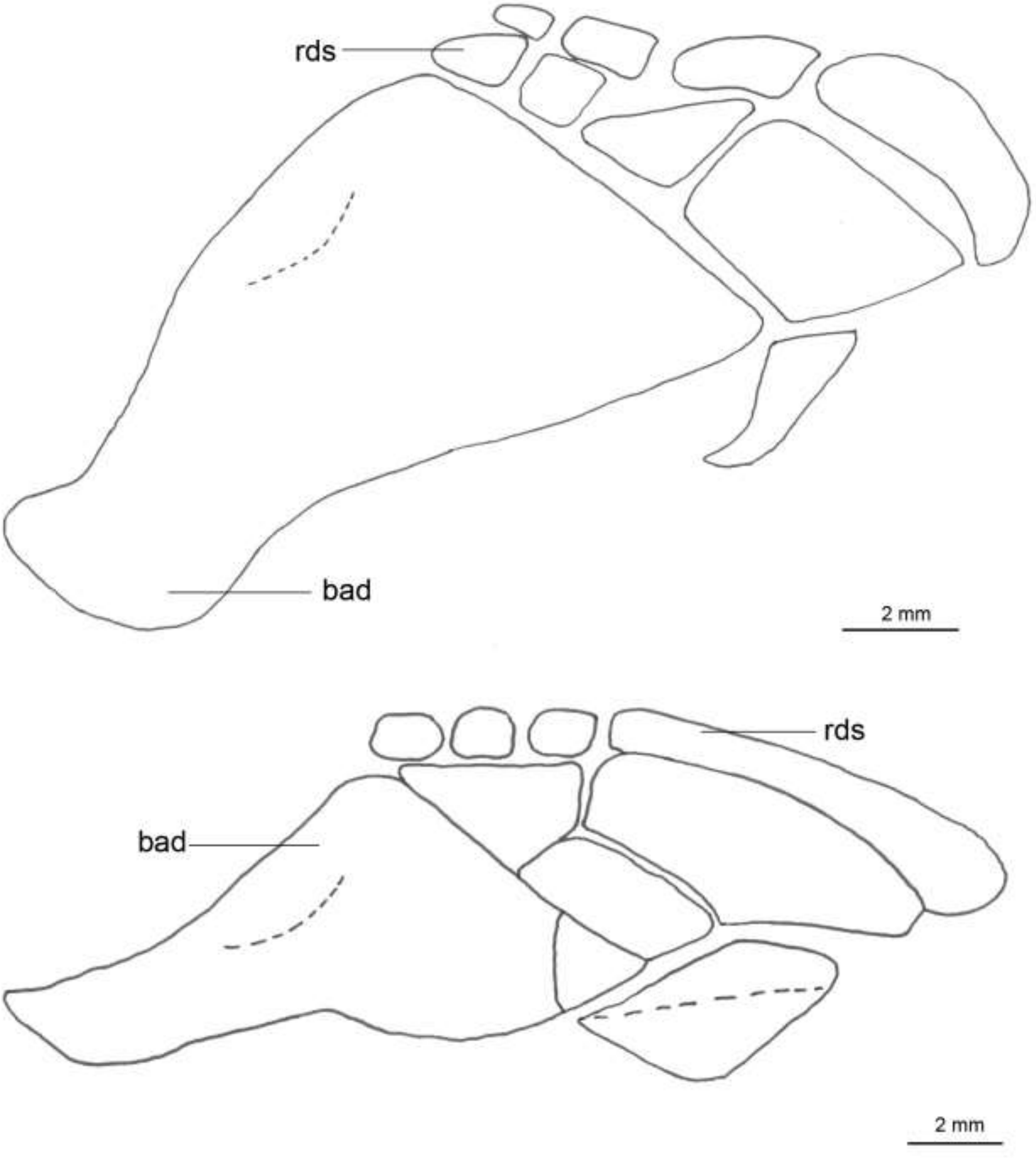

Figure 60. Pectoral girdle (A and B) and left pectoral fin (C) of a specimen of *Isistius brasiliensis* (MNHN 1996-0465). A: ventral view of pectoral girdle (anterior region at the bottom); B: anteroposterior view of pectoral girdle (dorsal region at the top); C: pectoral fin and its insertion on the girdle.

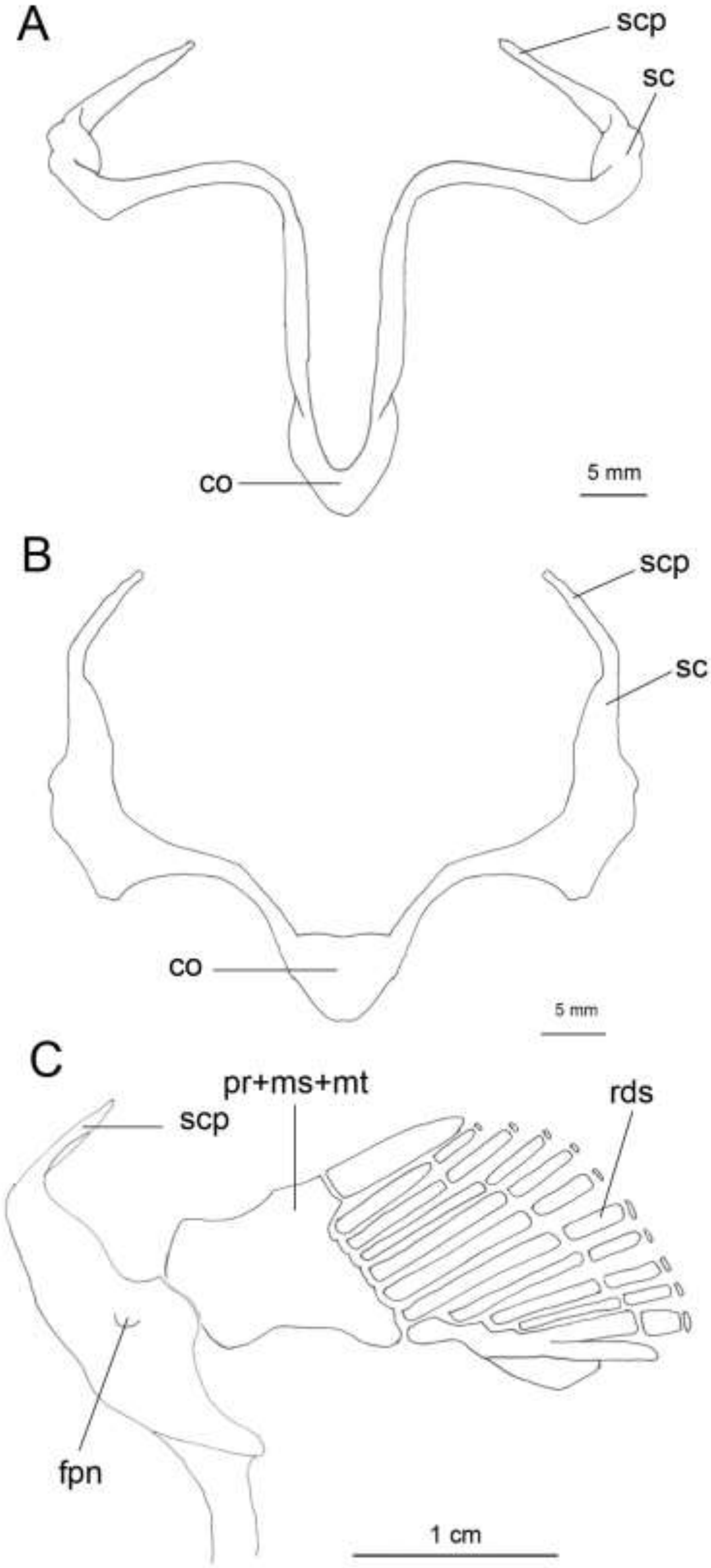

Figure 61. Ventral view of pelvic girdle and fin of a specimen of *Isistius brasiliensis* (USNM 215948).

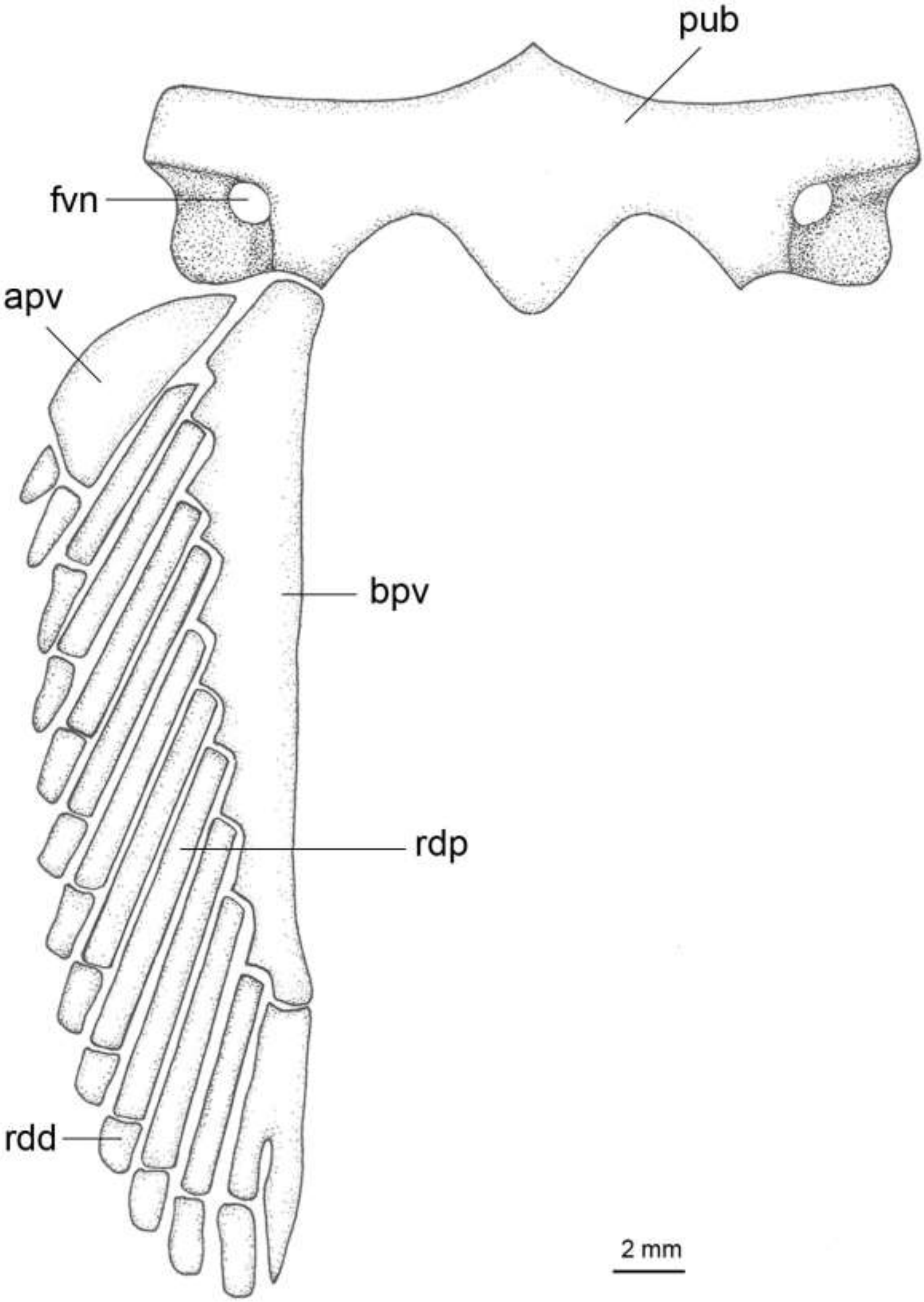

Figure 62. Ventral (left) and dorsal (right) views of the clasper skeleton of a specimen of *Isistius brasiliensis* (MNHN 1996-0465).

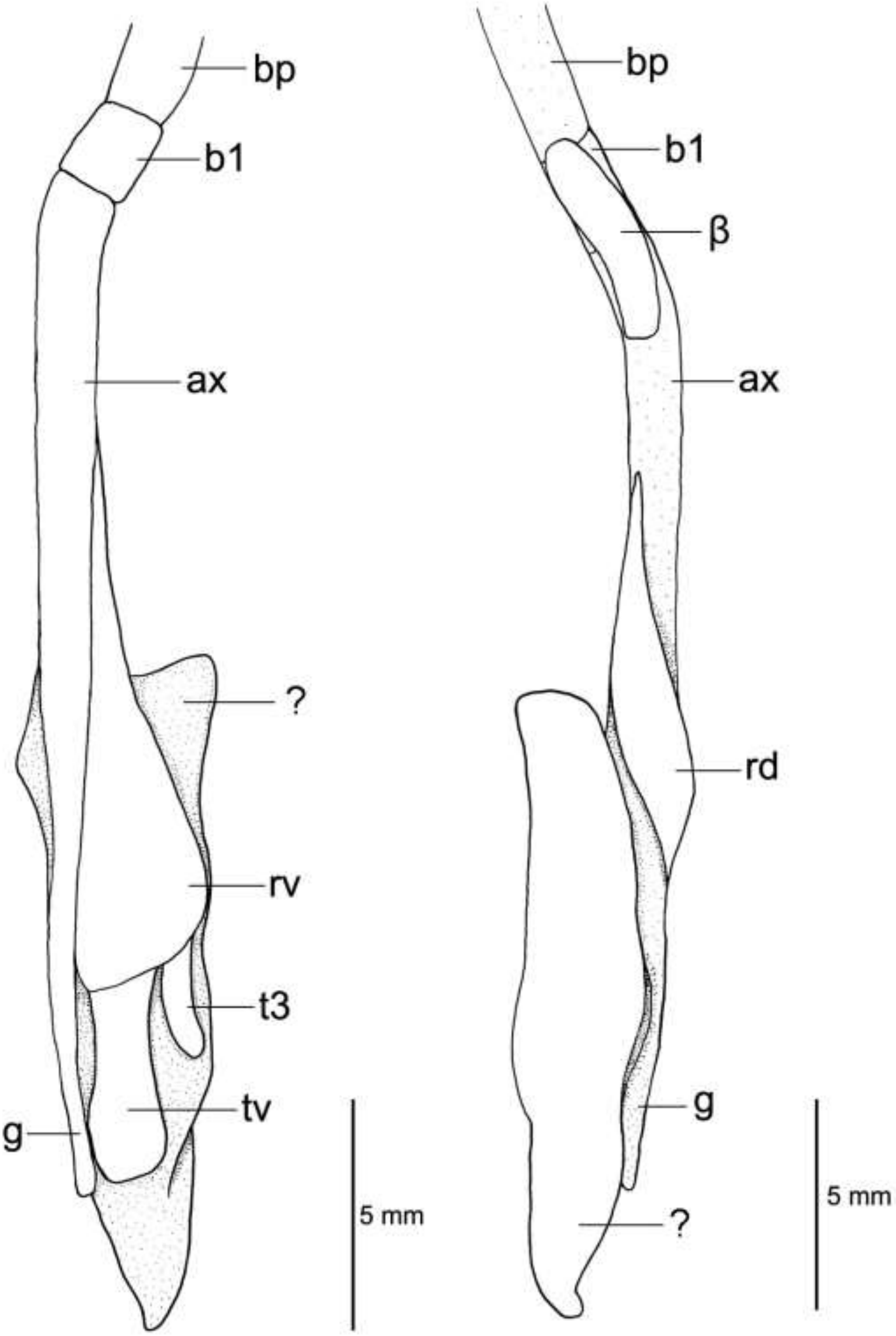

Figure 63. Left lateral view of the caudal fin of a specimen of *Isistius brasiliensis* (MZUSP N/C) from the Southwestern Atlantic Ocean.

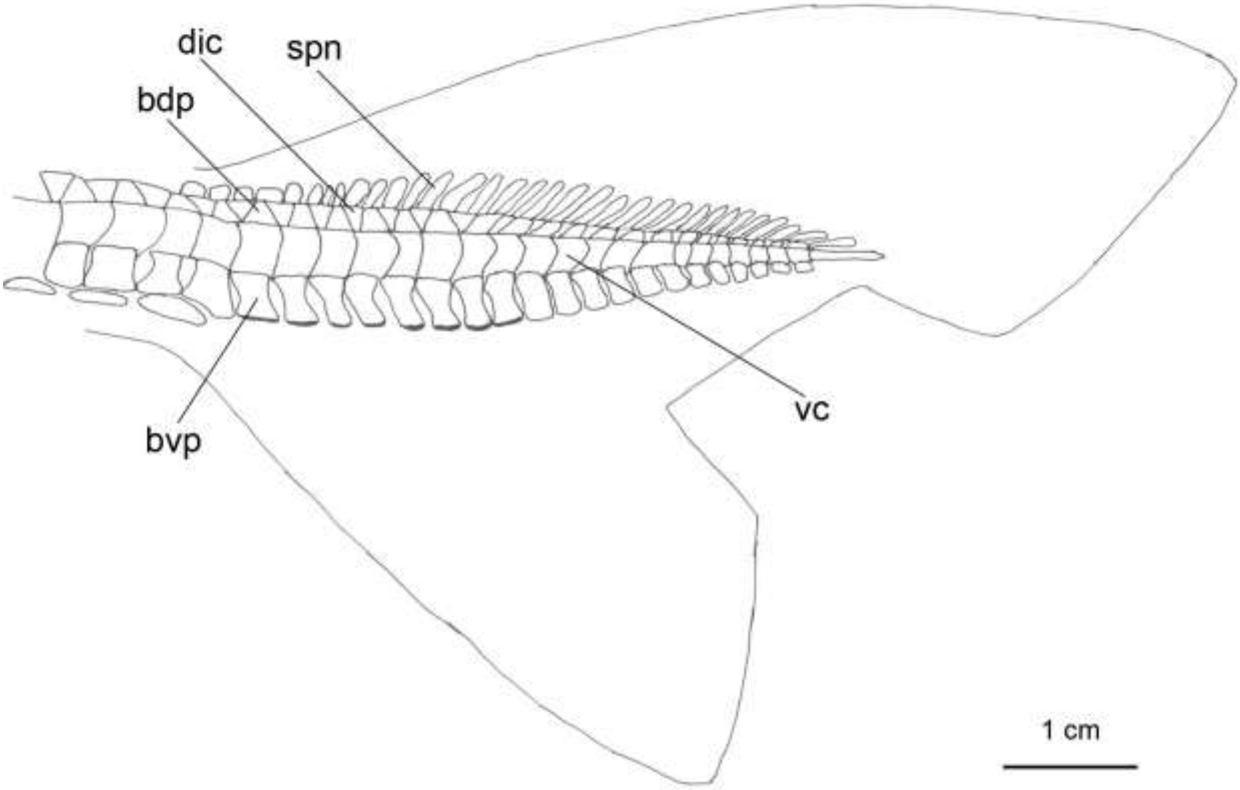

Figure 64. Mandibular, hyoid and partial hypobranchial musculature of *Isistius brasiliensis* (HUMZ 211104). A: lateral view; B: lateral view of muscles *adductor mandibulae* and *suborbitalis* in detail; C: ventral view; D, E: ventral views of muscles *intermandibularis*, *genio-coracoideus*, *coraco-hyoideus ventralis*, and *coraco-arculalis* in detail; F: lateral view showing the muscular bundle *genio-coracoideus externus*.

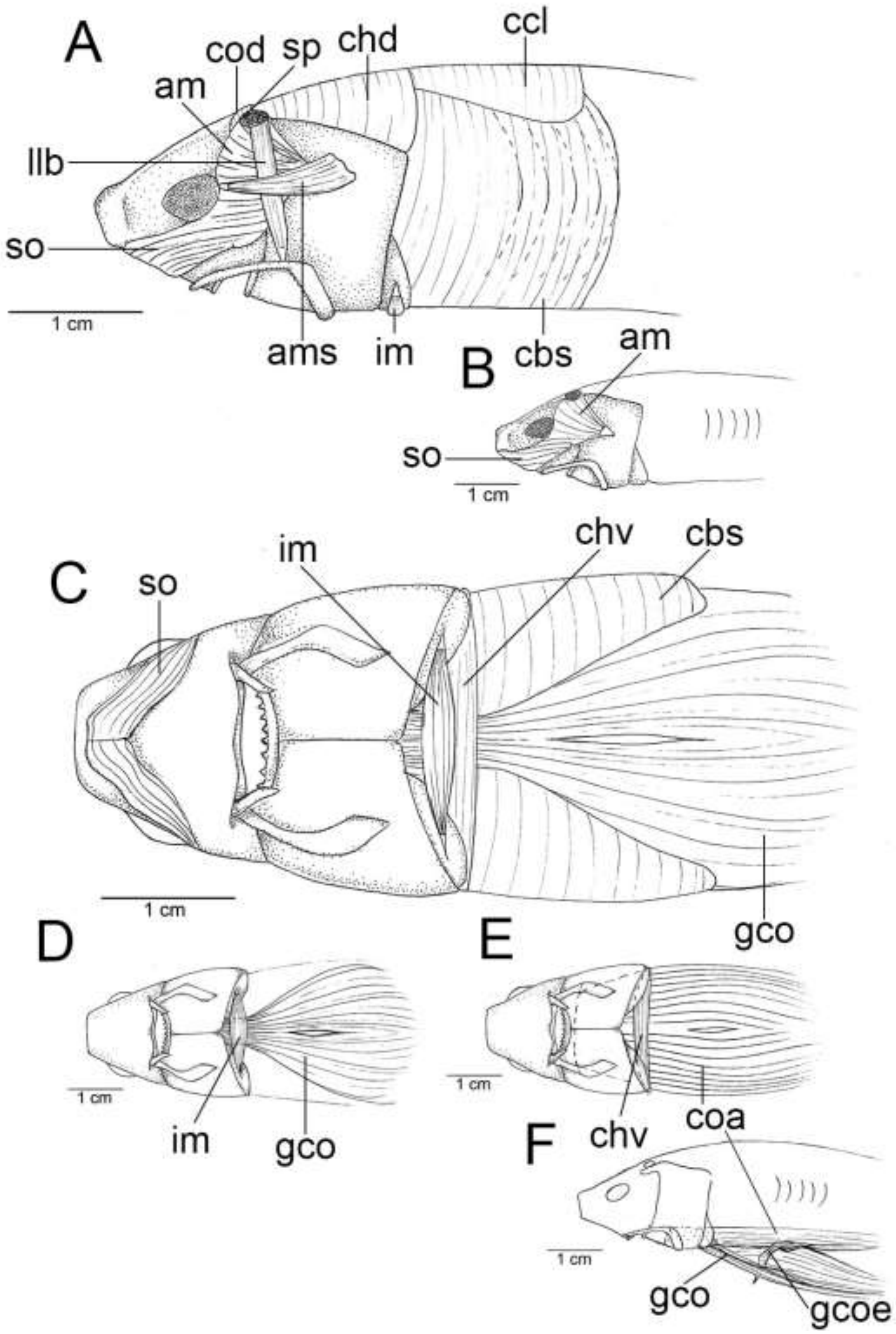

Figure 65. Pectoral fin musculature of a specimen of *Isistius brasiliensis* (HUMZ 211104) from Northwestern Pacific Ocean. A: lateral view; B: postero-anterior view; C: ventral view; D: dorsal view.

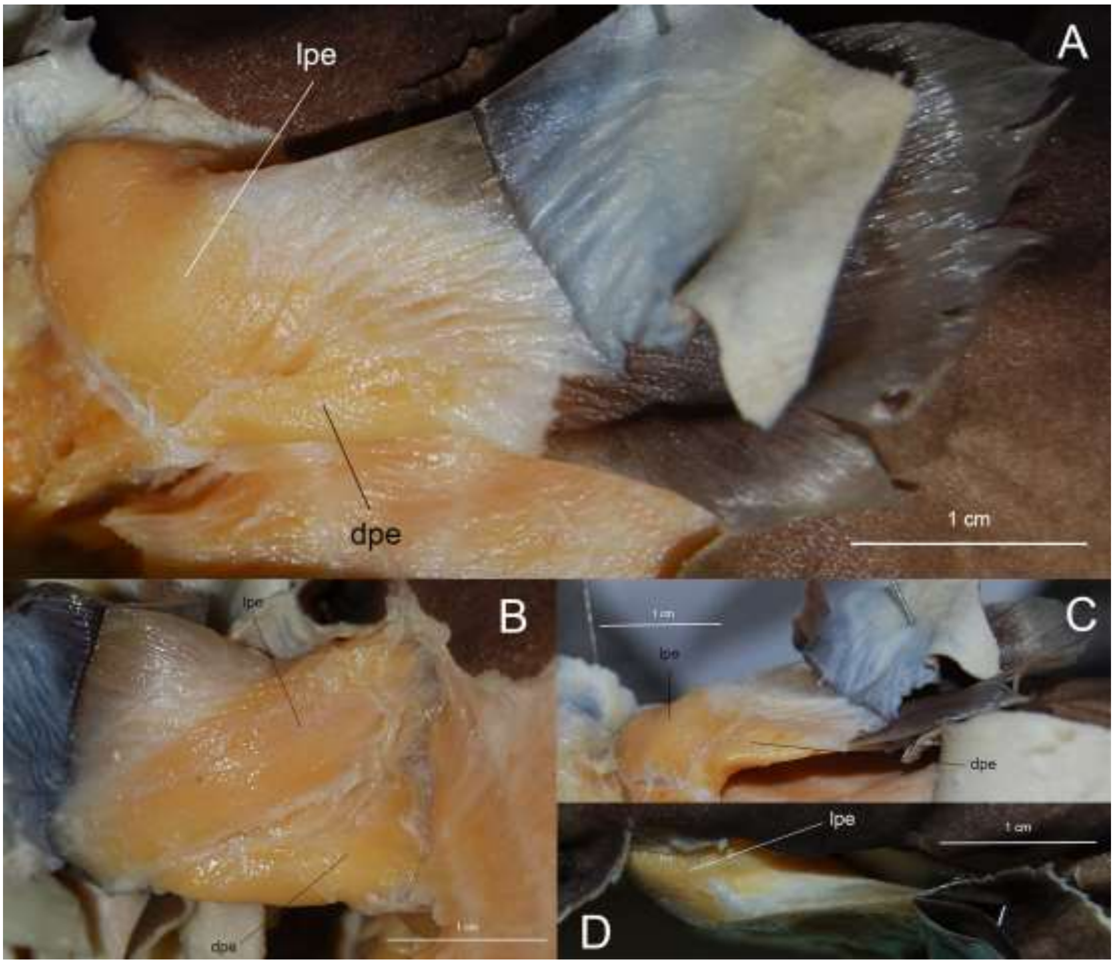

Figure 66. Pelvic fin musculature of a specimen of *Isistius brasiliensis* (BPBM 24471). Anterior region to the left; ventral view on top; left lateral view at the bottom.

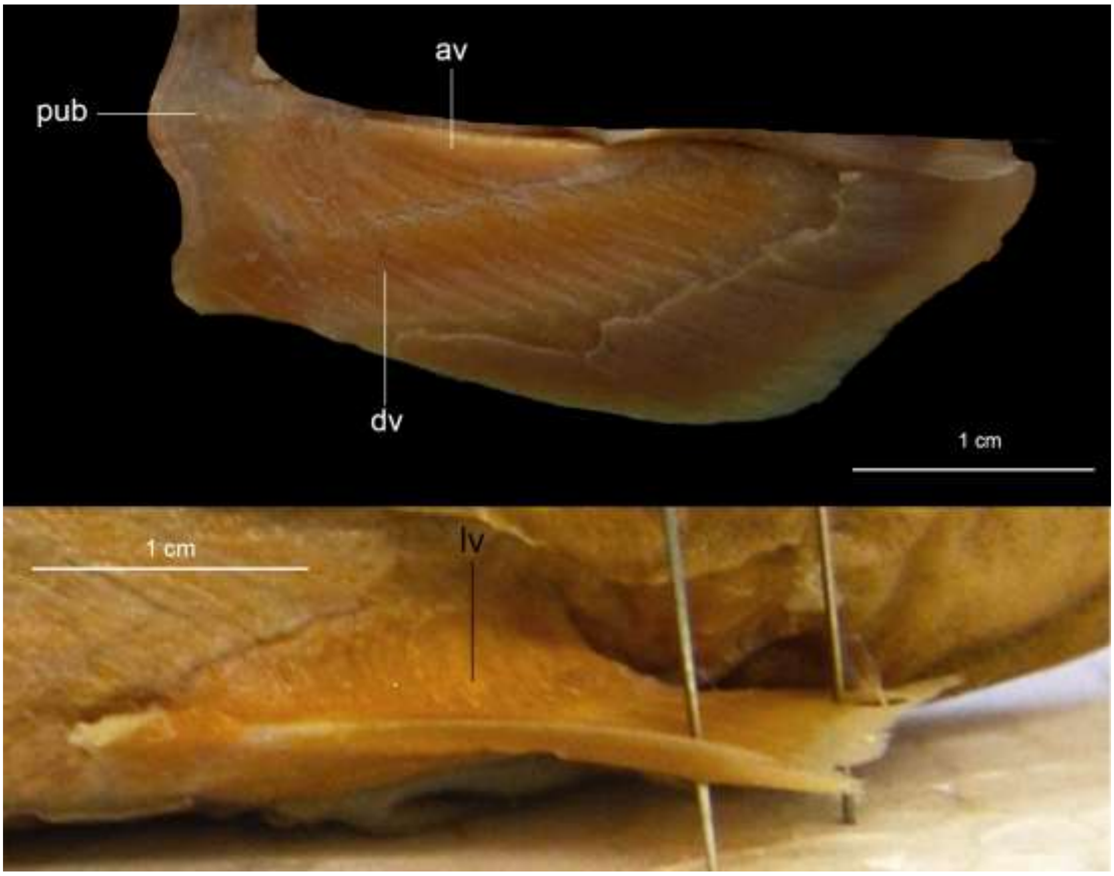

Figure 67. Clasper musculature of a specimen of *Isistius brasiliensis* (UFPB 2669). A: ventral view with siphon; B: ventral view without siphon; C: dorsal view; D: medial-lateral view.

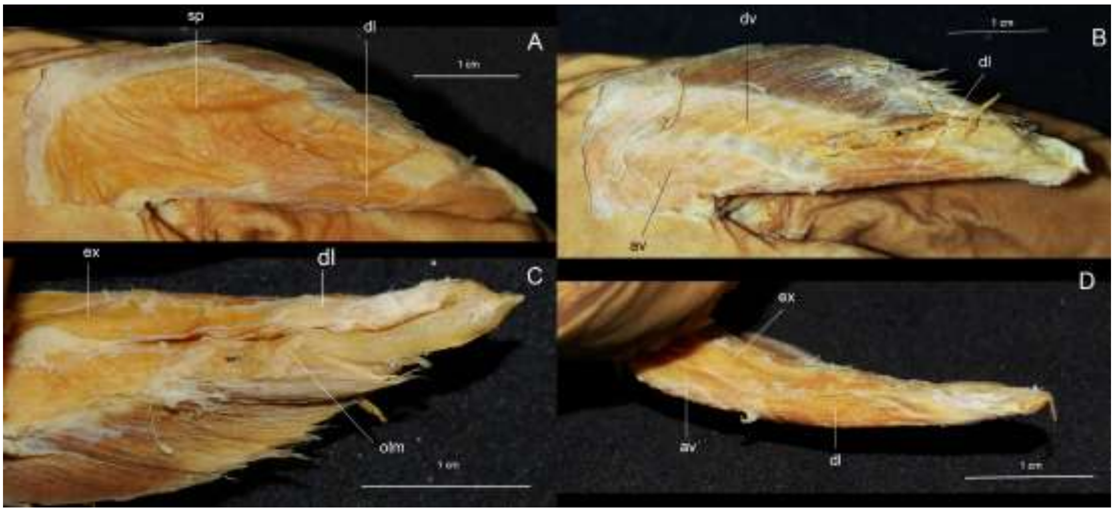

Figure 68. Dorsal fin musculature of a specimen of *Isistius brasiliensis* (HUMZ 157844) from Northwestern Pacific Ocean. Anterior region on the left; first dorsal fin at top; second dorsal fin at bottom.

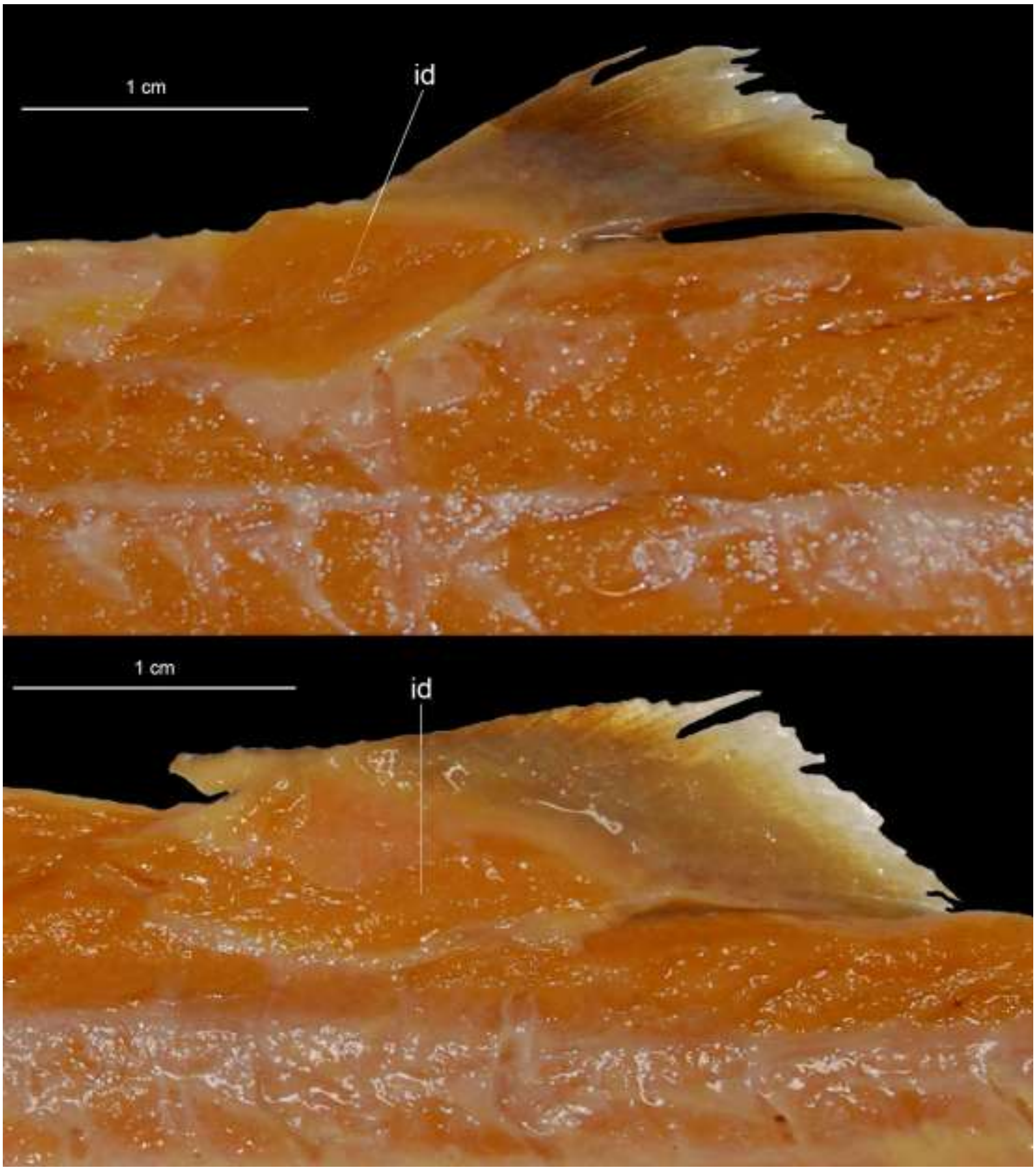

Figure 69. Left lateral view of caudal fin musculature of a specimen of *Isistius brasiliensis* (HUMZ 211104) from Northwestern Pacific Ocean.

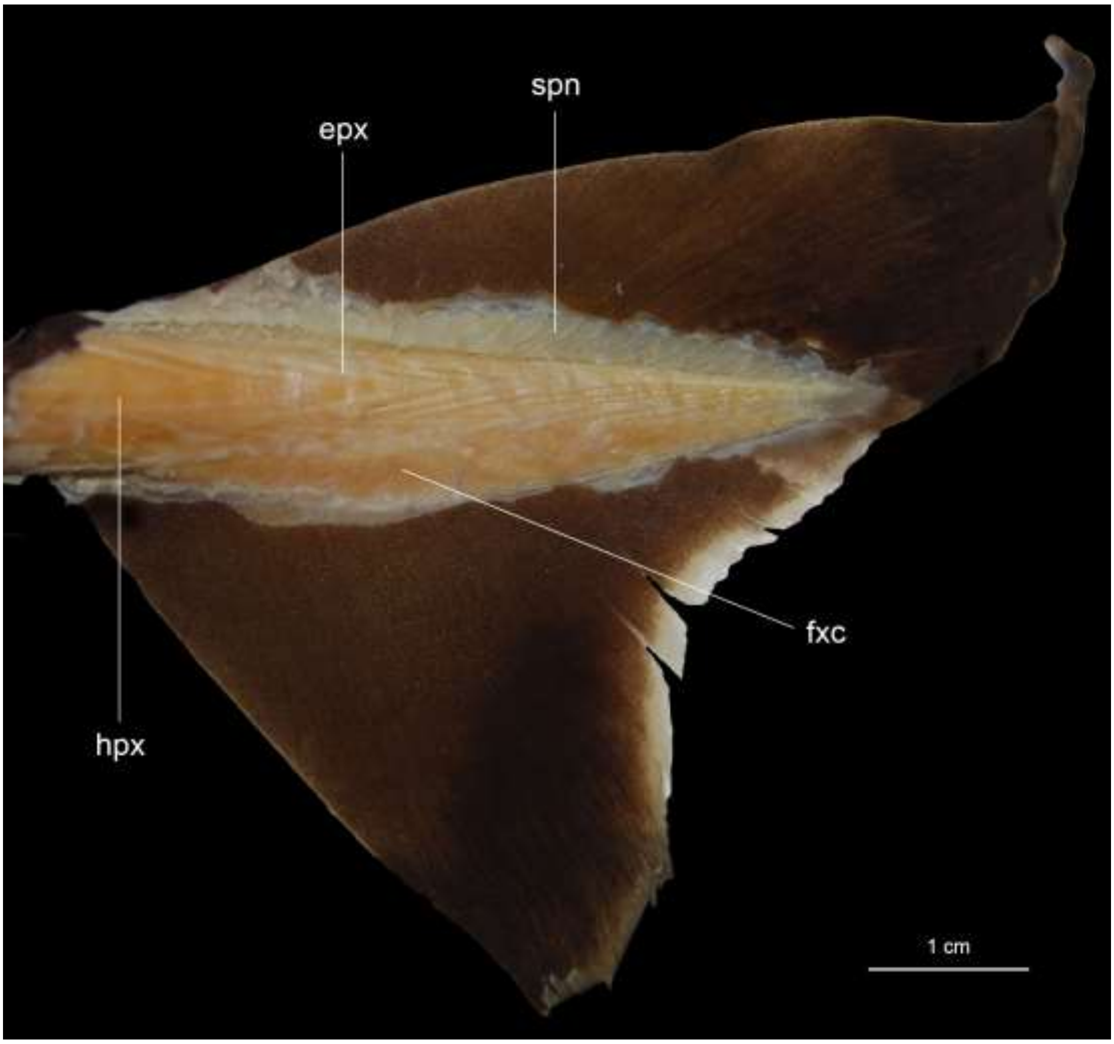

Figure 70. Dorsal view of lateral line canals of the head of *Isistius brasiliensis*.

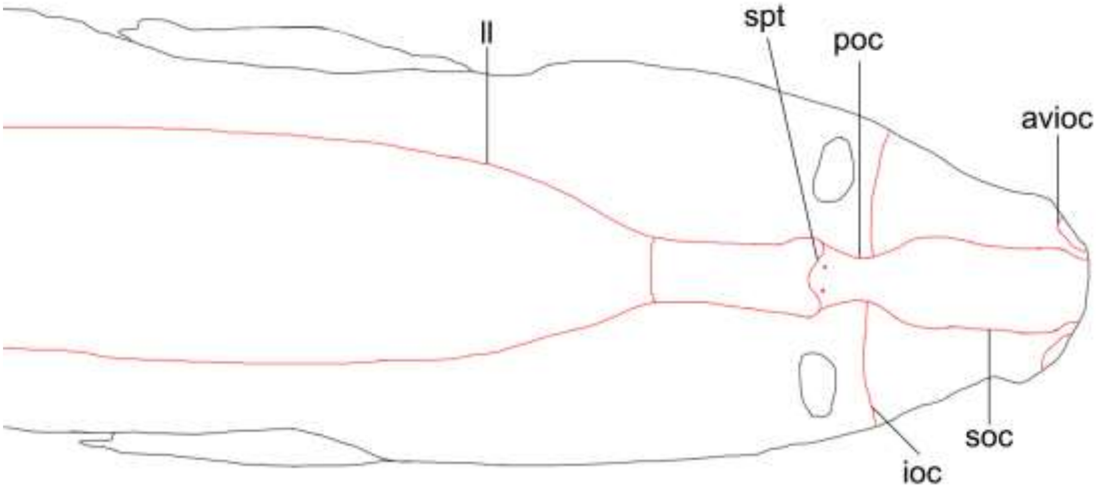

Figure 71. Lateral view of lateral line canals of the head of *Isistius brasiliensis*.

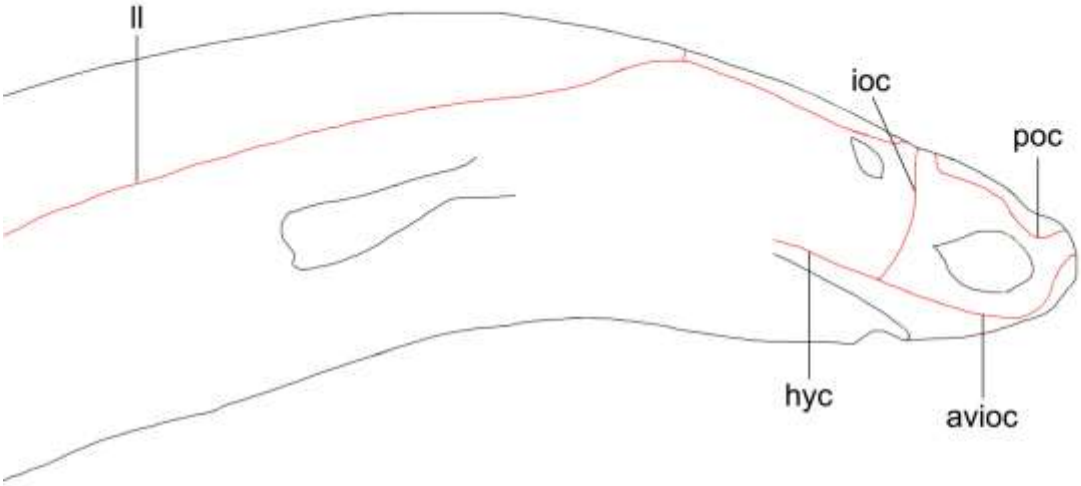

Figure 72. Ventral view of lateral line canals of the head of *Isistius brasiliensis*.

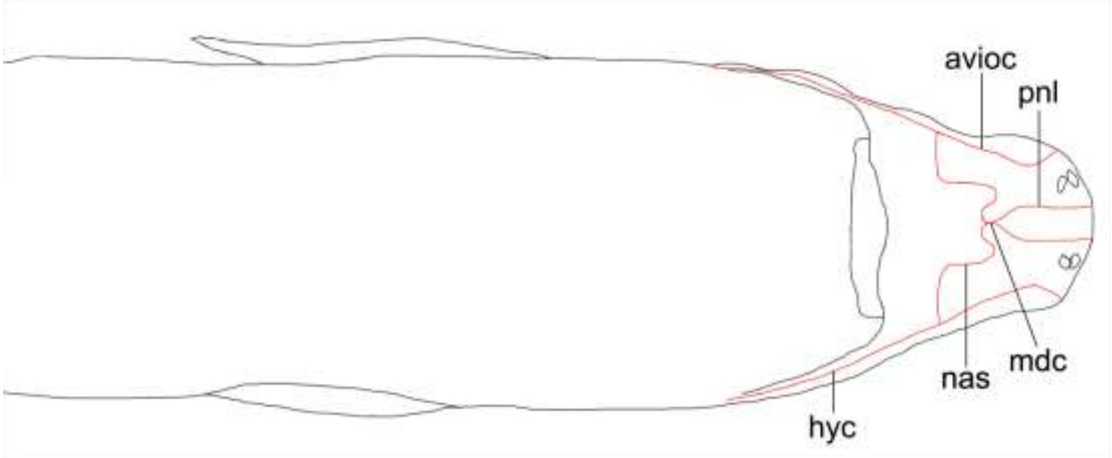

Figure 73. Radiograph of the holotype of *Isistius plutodus* (USNM 188386) from the Gulf of Mexico, with 43 monospondylous, 24 precaudal diplospondylous and 24 caudal diplospondylous vertebrae.

Figure 74. Neurocranium of a specimen of *Isistius plutodus* (ZUEC 8333) in lateral, dorsal, and ventral views.

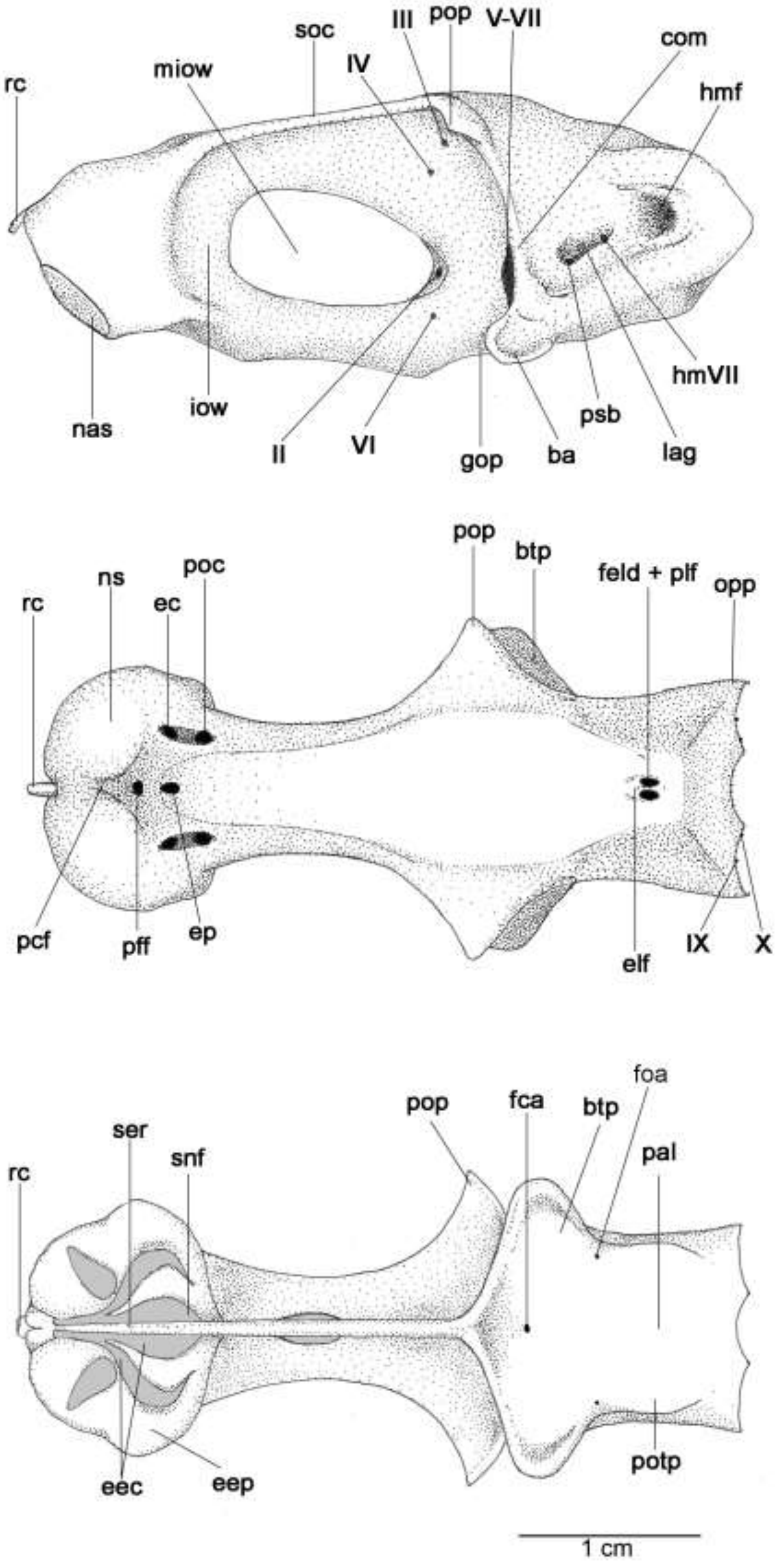

Figure 75. CT-scan of lateral view of *Isistius plutods* (ZUEC 8332) showing the articulation between lower jaw and quadrate.

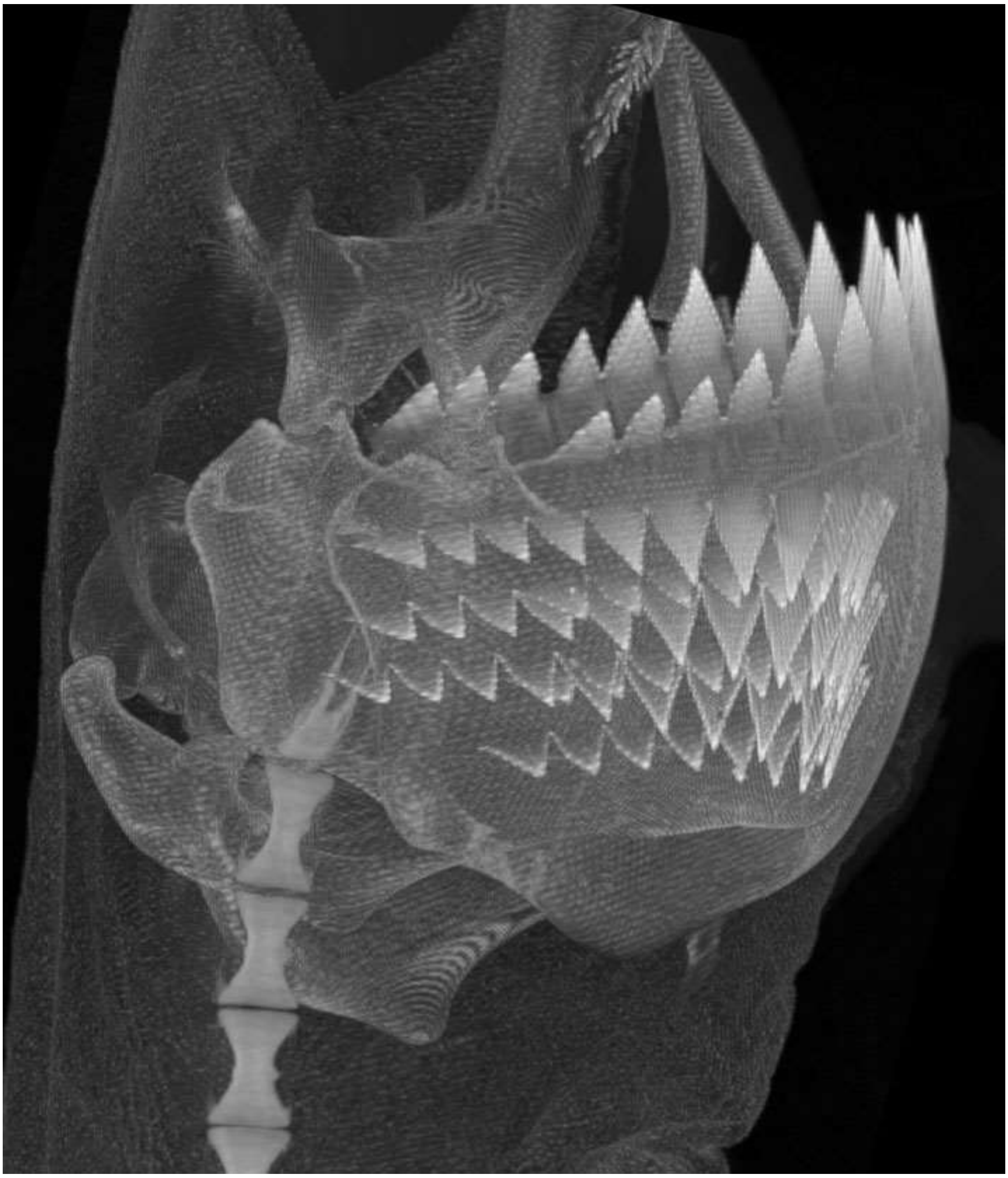

Figure 76. First (top) and second (bottom) dorsal fins of a specimen of *Isistius plutodus* (ZUEC 8333) from the Southwestern Atlantic Ocean. (anterior region to the left)

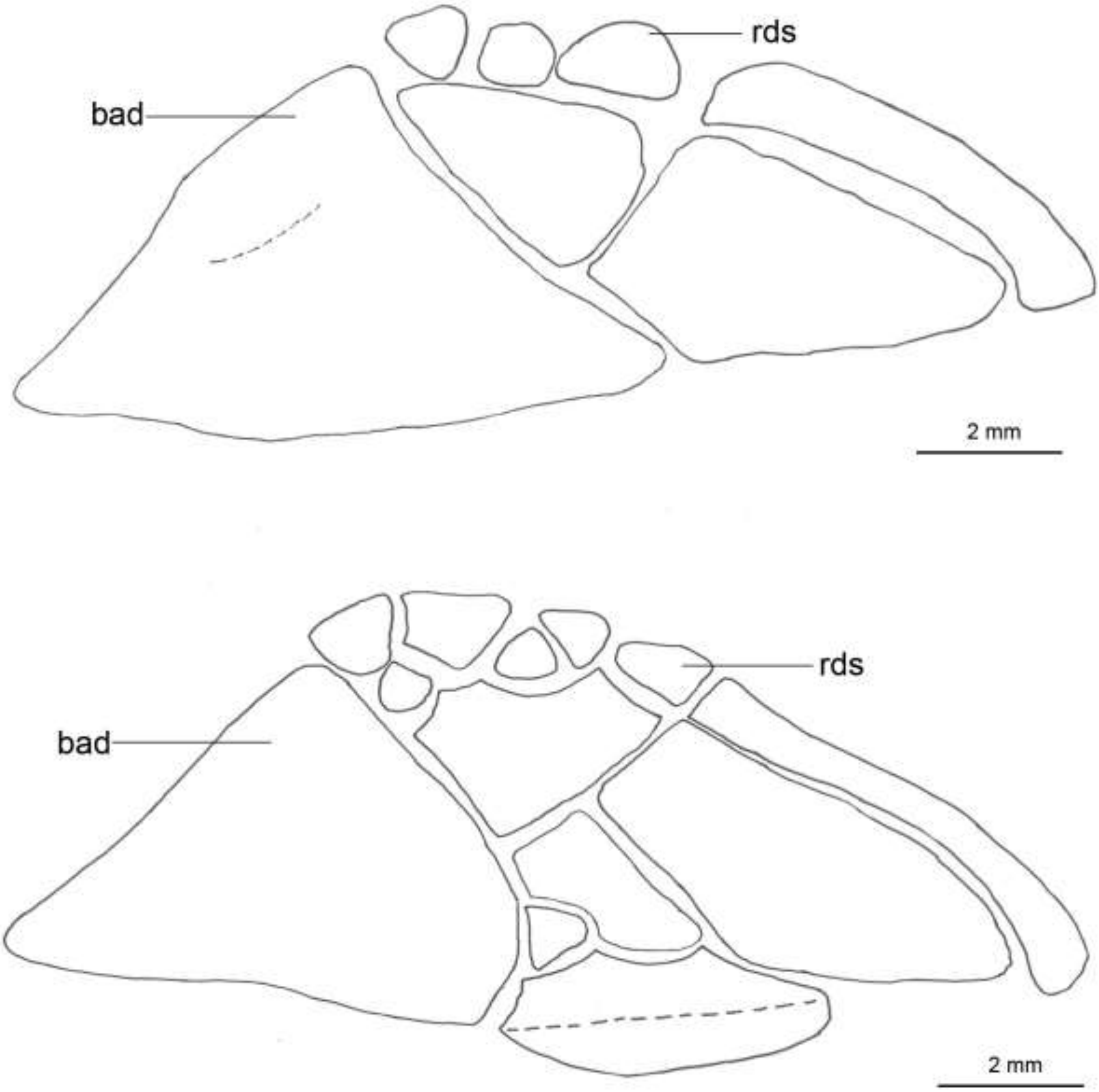

Figure 77. Left lateral view of the caudal fin of *Isistius plutodus* (ZUEC 8333) from Southwestern Atlantic Ocean..

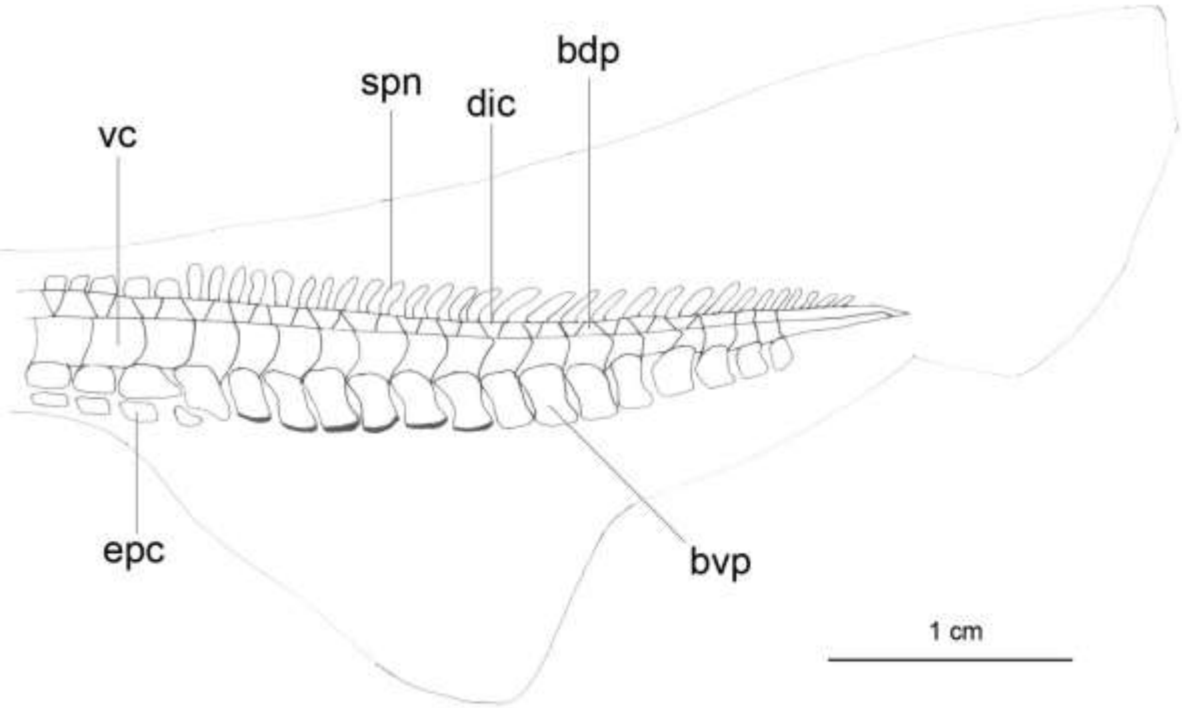

Figure 78. Lateral view of mandibular musculature of *Isistius plutodus* (ZUEC 8332) from Southwestern Atlantic Ocean showing the abscence of the muscle *levator labialis* in between the sheets of *adductor mandibulae* and *adductor mandibulae superficialis*.

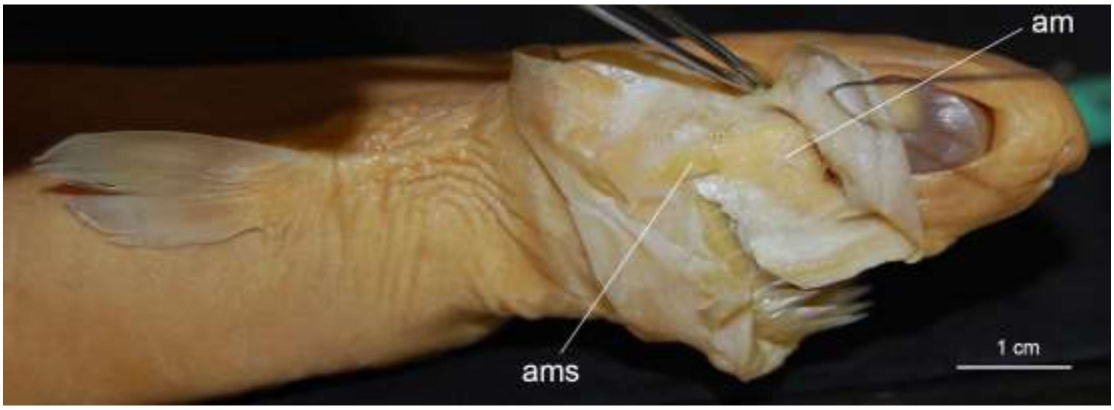

Figure 79. Dorsal view of lateral line canals in the head of *Isistius plutodus*

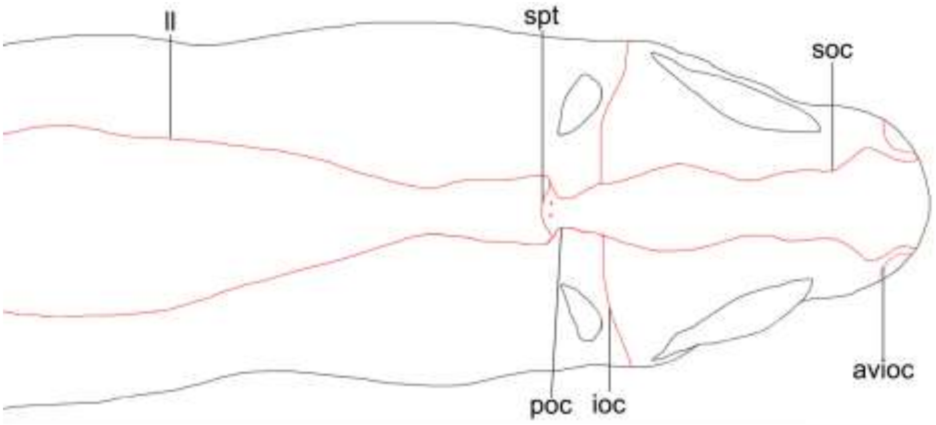

Figure 80. Ventral view of lateral line canals in the head of *Isistius plutodus*.

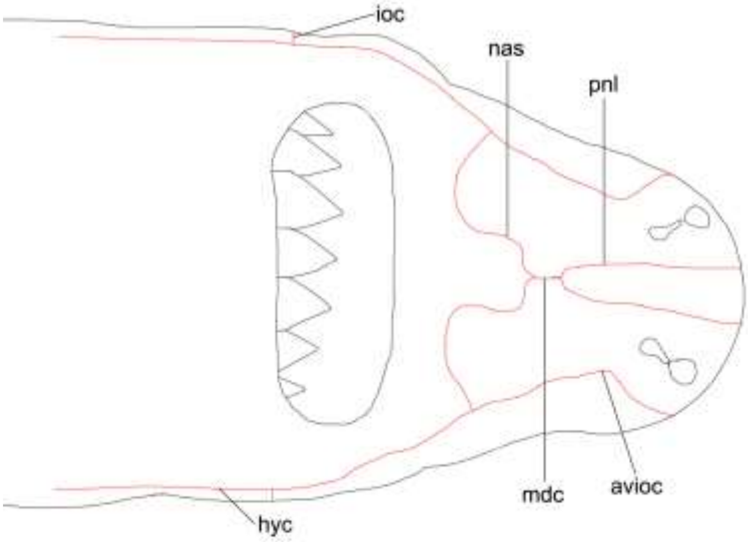

Figure 81. Lateral view of lateral line canals in the head of *Isistius plutodus*.

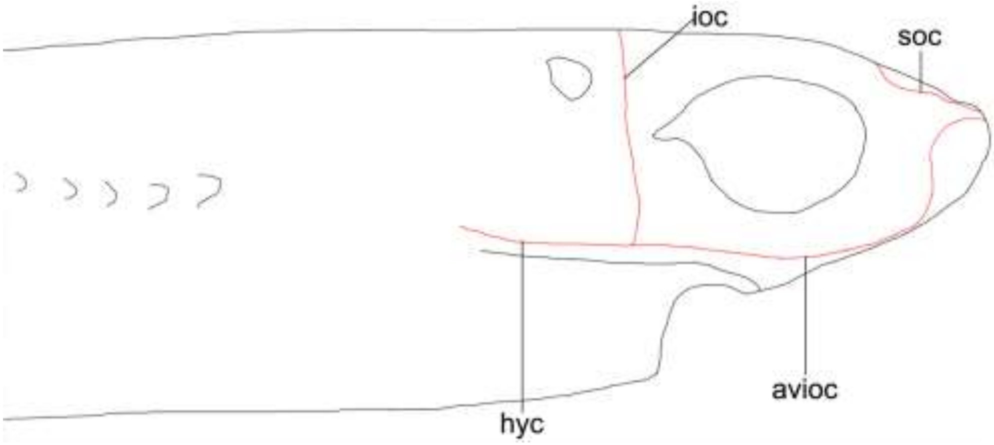

Figure 82. Dorsal view of lateral line canals in the head of *Dalatias licha*.

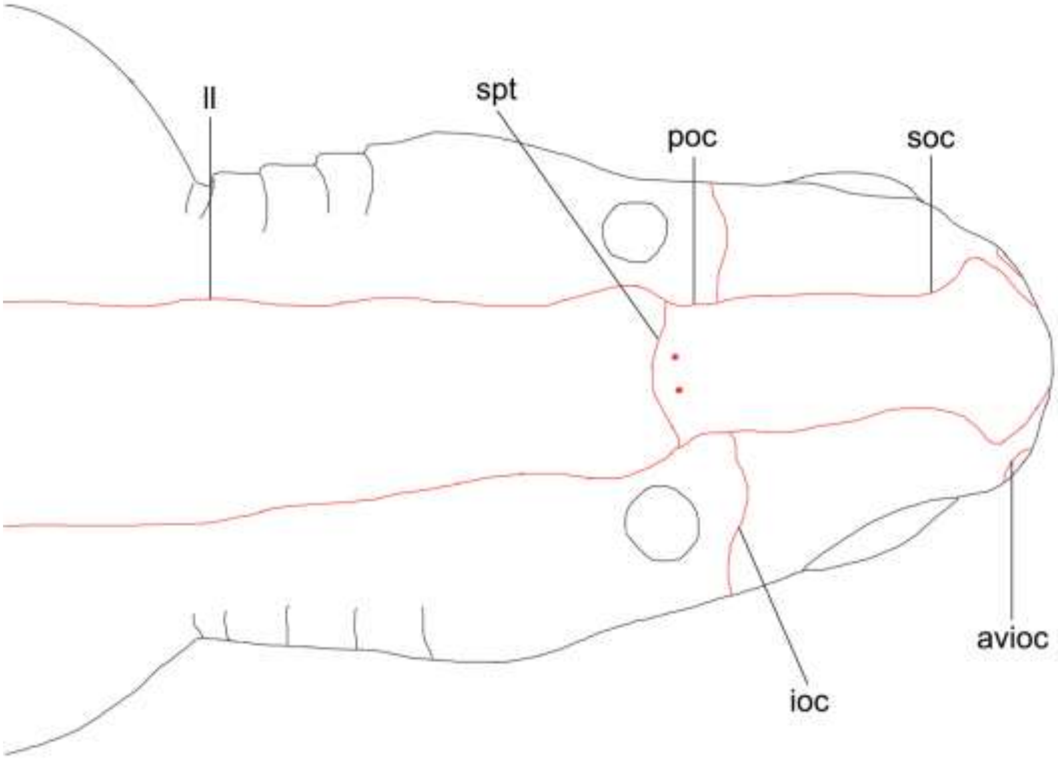

Figure 83. Ventral view of lateral line canals in the head of *Dalatias licha*.

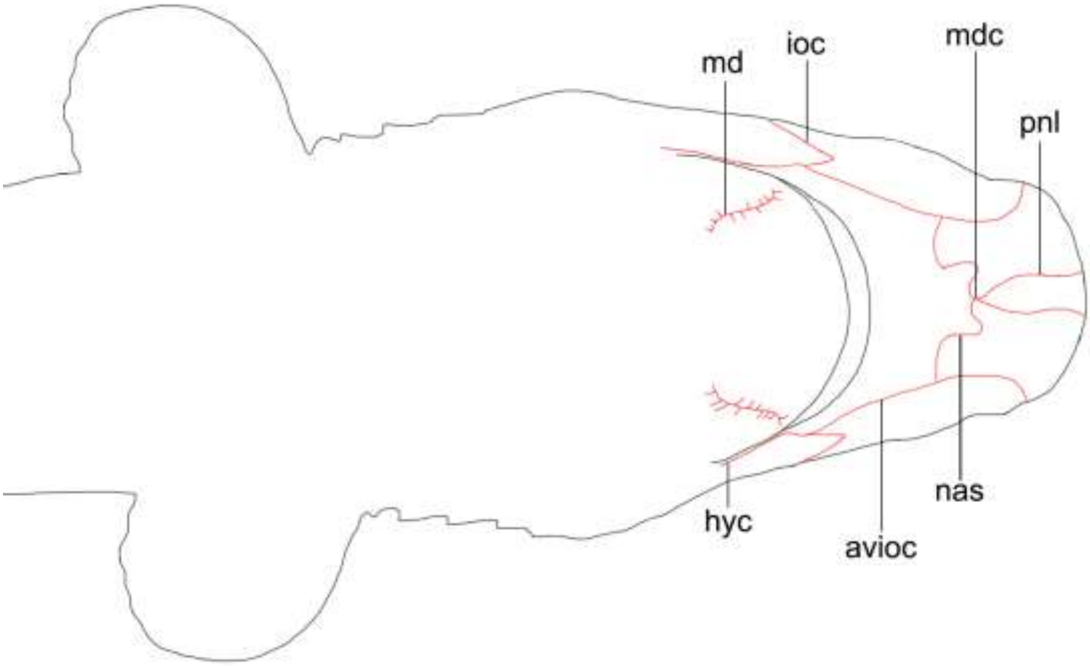

Figure 84. Radiograph of the ventral portion of head and branquial region of *Isistius brasiliensis* (UFPB 2669) from the Southeast coast of Brazil. Darker structures on each side of branquial basket are the ventromedial branquial cartilages.

Figure 85. Radiograph of the ventral portion of head and branquial region of *Isistius plutodus* (ZUEC 8333) from the Southeast coast of Brazil. Darker structures on each side of branquial basket are the ventromedial branquial cartilages.

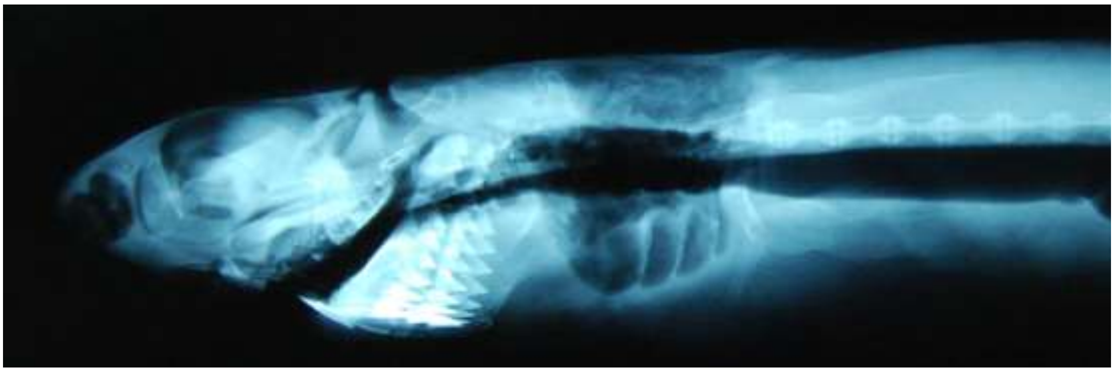

Figure 86. Ventral view of the pigmentation difference between the dark collar (ventral portion) and the rest of ventral side of the body (dorsal portion) of *Isistius brasiliensis* (MNHN 1996-0465).

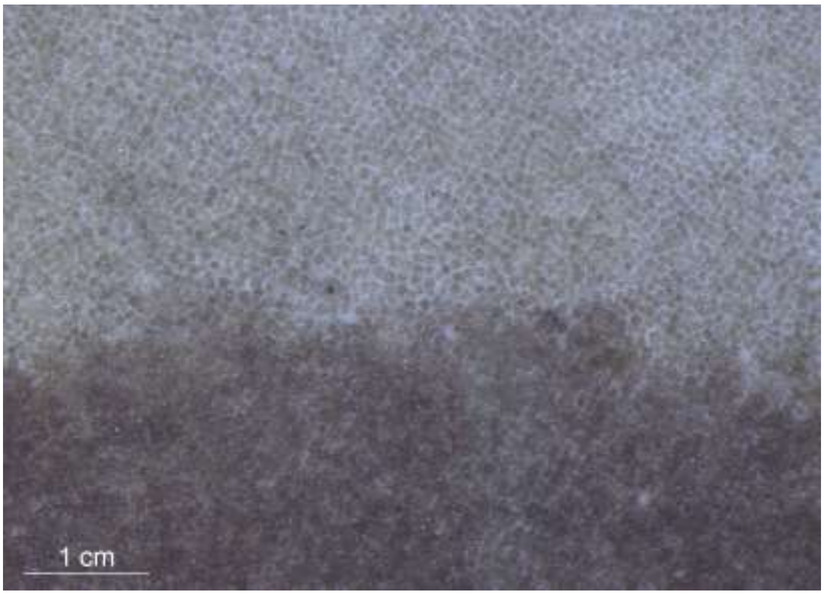

Figure 87. Stomach contents of a specimen of *Isistius brasiliensis* (UW 21895) from the Northwestern Pacific Ocean.

Figure 88. Stomach contents of a specimen of *Isistius brasiliensis* (LACM 46046) from Hawaii, with lower teeth markings of the piece of flesh.

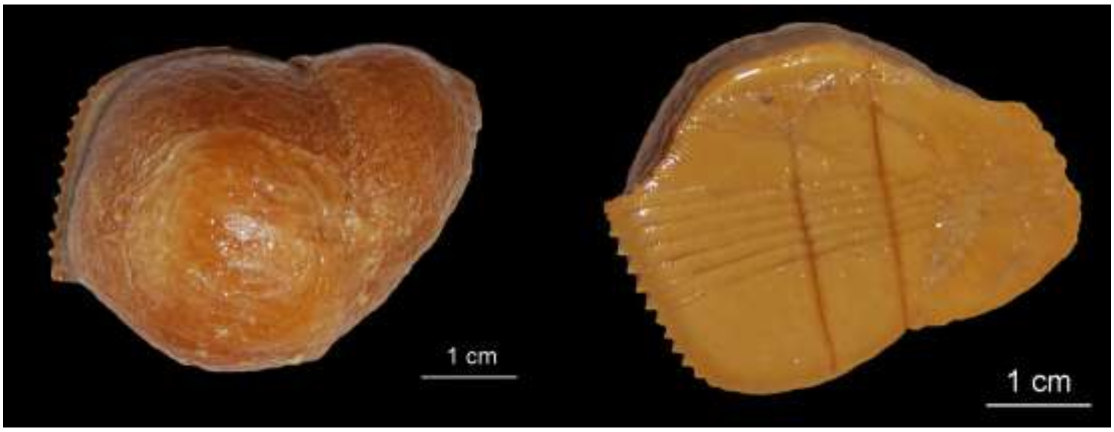

Figure 89. Bite wounds by *Isistius* on a specimen of *Regalecus glesne* SIO – not catalogued, that appeared on the beach at California, Northeastern Pacific Ocean.

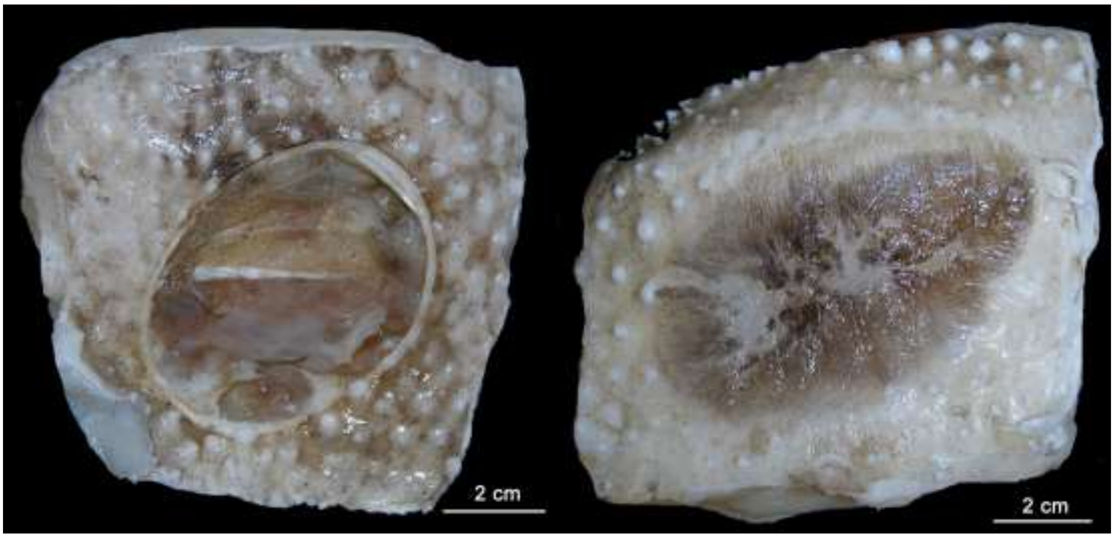

Figure 90. Radiograph of *Isistius brasiliensis* (MCZ 58096) from Western Atlantic Ocean, with lower teeth in stomach.