**UNIVERSIDADE DE SÃO PAULO
INSTITUTO DE BIOCÊNCIAS DA USP**

**REVISÃO TAXONÔMICA DA SUBFAMÍLIA CRASSOSTREINAE
(BIVALVIA: OSTREIDAE)**

VANESSA SIMÃO DO AMARAL

ORIENTADOR: PROF. DR. LUIZ RICARDO LOPES DE SIMONE

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2014**

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Tese apresentada ao Instituto de
Biociências da Universidade de São Paulo
para obtenção do título de Doutor em
Zoologia.

**SÃO PAULO
2014**

Amaral, Vanessa Simão do

**Revisão taxonômica da subfamília Crassostreinae (Bivalvia:
Ostreidae)**

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**1. Revisão taxonômica 2. Morfologia comparada 3.
Crassostreinae 4. Ostreoidea**

Comissão Julgadora

Prof. Dr. Luiz Ricardo Lopes de Simone
Orientador

Suplentes

“Feci quod potui, faciant meliora potentes.”

*"Morre lentamente
Quem não viaja,
Quem não lê,
Quem não ouve música,
Quem não encontra graça em si mesmo
Morre lentamente
Quem destrói seu amor próprio,
Quem não se deixa ajudar.
Morre lentamente
Quem se transforma em escravo do hábito
Repetindo todos os dias os mesmos trajetos,
Quem não muda de marca,
Não se arrisca a vestir uma nova cor ou
Não conversa com quem não conhece.
Morre lentamente
Quem evita uma paixão e seu redemoinho de emoções,
Justamente as que resgatam o brilho dos
Olhos e os corações aos tropeços.
Morre lentamente
Quem não vira a mesa quando está infeliz
Com o seu trabalho, ou amor,
Quem não arrisca o certo pelo incerto
Para ir atrás de um sonho,
Quem não se permite, pelo menos uma vez na vida, Fugir dos conselhos sensatos...
Viva hoje!
Arrisque hoje!
Faça hoje!
Não se deixe morrer lentamente!
Não se esqueça de ser feliz."*

Pablo Neruda/ Marília Medeiros.

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<i>O. EQUESTRIS</i> (OEQ), <i>O. EDULIS</i> (OED), <i>O. PUELCHANA</i> (OPU), <i>P. NUMISMA</i> (PNUM), <i>P. MCGINTYI</i> (PMC), <i>H. HYOTIS</i> (HHY).....	187
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1. INTRODUÇÃO

A superfamília Ostreoidea Rafinesque, 1815 reúne bivalves marinhos e de águas salobras, adaptados à vida epifaunal sésil. O grupo é constituído por cerca de 100 espécies nas duas famílias atuais – Ostreidae e Gryphaeidae – e têm ampla distribuição geográfica, ocorrendo ao longo das praias de todos os continentes (exceto Antártida) e ilhas oceânicas (Huber, 2010). Quanto à distribuição batimétrica, ocorrem desde o mais alto nível das marés até 50-60 metros de profundidade (Boss, 1972).

A tolerância e resistência às variações ambientais permitem aos Ostreoidea a colonização de diferentes habitat marinhos como os de regiões costeiras com águas limpas e de alta salinidade, os de estuário cujas águas transportam muito sedimento em suspensão e têm salinidade variável, geralmente baixa (Quayle, 1981).

Contrastando com a grande importância econômica e ambiental dos bivalves, assim como sua enorme diversidade, o conhecimento filogenético, em particular, da classe Bivalvia é muito pobre. Embora a organização tradicional, usada na maioria dos catálogos (e.g., Newell, 1969; Rios, 1994, 2009; Diaz & Puyana, 1994; Redfern, 2001, Bouchet *et.al.*, 2010), empregue um cunho filogenético e com base puramente em morfologia, uma análise mais ampla e detalhada da classe ainda não foi feita.

Diversos estudos moleculares têm sido desenvolvidos com o intuito de investigar as relações filogenéticas existentes entre estes organismos e tentar elucidar os problemas taxonômicos existentes, produzindo bons resultados (Jozefowicz & Ó Foighil, 1998, Ignácio *et.al.*, 2000; Lapègue *et.al.*, 2002; Lazoski, 2004; Pie *et.al.*, 2006; Varela *et.al.* 2007; Cordes *et.al.*, 2008). Mas, diante da plasticidade, da falta de diagnóstico anatômico e generalizada translocação de espécies em todo o mundo, a sistemática mais acurada das ostras, em particular, tem sido difícil (Yamaguchi, 1994; Carlton & Mann, 1996; Kirkendale *et.al.*, 2004).

Hipóteses filogenéticas abordando dados de origem molecular e/ou morfológica possuem igualmente prós e contras e, embora estudos que utilizem dados moleculares e morfológicos juntos provejam geralmente hipóteses mais robustas, há inúmeras questões biológicas que só podem ser respondidas com a análise conjunta destas duas fontes de dados (Moritz & Hillis, 1996).

Em relação ao Meio Ambiente, o monitoramento de várias espécies de ostras em habitat naturais não é uma tarefa fácil, devido à dificuldade em discriminar diferentes espécies corretamente. Características morfológicas que seriam usadas na identificação, tais como forma, cor e estrutura da concha e do músculo adutor são altamente influenciadas pelas condições ambientais (Pie *et.al.*, 2006).

Apesar dos esforços de morfologistas e geneticistas para resolver as relações filogenéticas entre as ostras, ainda permanece uma confusão considerável sobre o reconhecimento entre as espécies mais xenomórficas de Ostreidae. Diferenças nas partes moles são consideradas poucas e oferecem baixa resolução para um problema já exacerbado pela plasticidade na forma da concha. Embora a variação geográfica tenha sido frequentemente usada para identificar espécies de ostras, estudos demonstram que algumas “espécies” cruzam originando híbridos, gerando uma progênie viável e fértil (Waller, 1998).

Várias espécies de ostras são cultivadas em diferentes partes do mundo e muitos países têm introduzido espécies não nativas, como o próprio Brasil, de tal forma que a distribuição geográfica tem cada vez menos credibilidade como uma característica definida (Littlewood, 1994). A hibridação entre táxons relacionados foi demonstrada em condições de laboratório, dificultando o estudo de populações naturais de ostras (Boudry *et.al.*, 2003). Nesse contexto, os marcadores moleculares demonstraram ser ferramentas para a identificação de espécies marinhas e sua distribuição geográfica.

Análises de DNA mitocondrial têm sido usadas com sucesso para o esclarecimento de dificuldades taxonômicas e estudos de estrutura populacional de ostras, uma vez que a classificação de ostras baseadas em características morfológicas externas é considerada insuficiente para sua identificação, pois, como dito acima, são altamente influenciadas pelas condições ambientais. Inúmeros estudos vêm sendo realizados para elucidar sua posição taxonômica através de marcadores moleculares (Boudry *et.al.*, 1998; Klinbunga *et.al.*, 2001; Boudry *et.al.*, 2003; Klinbunga *et.al.*, 2003; Lam & Morton, 2003; Morton *et.al.*, 2003; Kirkendale *et.al.*, 2004; Wang *et.al.*, 2004; Klinbunga *et.al.*, 2005; Lam & Morton, 2006; Reece *et.al.*, 2008; Wang & Guo, 2008; Wang *et.al.*, 2008; Xia *et.al.*, 2009).

1.1 Histórico: análises taxonômicas e anatômicas

Os principais estudiosos de ostras, como, Ranson (1943), Gunter (1950, 1951), Korringa (1952), Galtsoff (1964), Yonge (1966), Quayle (1981), entre outros, exibem uma composição da superfamília Ostreoidea como sendo constituída por uma única família, Ostreidae, com três gêneros básicos, *Ostrea* Linné, 1758, *Crassostrea* Sacco, 1897 e *Pycnodonte* Fischer de Waldheim, 1835, reunindo todas as ostras viventes, inclusive as classificadas como Gryphaeidae por Stenzel (1971) e Harry (1985).

Harry (1985) classificou as ostras em uma superfamília (Ostreoidea), dividida em duas famílias (Gryphaeidae e Ostreidae), quatro subfamílias (Pycnodonteinae, Lophinae, Ostreinae e Crassostreinae), 10 novas tribos, 24 gêneros e subgêneros, sendo 12 gêneros novos. Mais recentemente, a publicação do *Compendium of Bivalves*, de Huber (2011), diminui o número de gêneros e espécies, mas mantém a classificação estabelecida por Harry para as famílias, subfamílias e gêneros.

Os estudos anatômicos e funcionais só tiveram início no meio do século XX, com Nelson (1938), Shaw & Battle (1957), Galtsoff (1964) e Yonge (1966).

Poucos trabalhos analisaram anatomicamente as ostras, focando apenas em estruturas específicas e não a espécie como um todo, e.g., Ridewood (1903) se deteve na análise da estrutura e organização das brânquias de *Ostrea edulis* Linné, 1758; Kellogg (1915) verificou as correntes ciliares sobre as brânquias, palpo e manto de *Crassostrea virginica* Gmelin, 1791, e *Ostrea lurida* Carpenter, 1864; Shaw & Battle, (1957) descreveram a região do saco do estilete e intestino de *C. virginica*.

Yonge (1926) realizou um dos primeiros estudos mais abrangentes de anatomia geral e funcional de um ostreídeo, *Ostrea edulis*, com ênfase na fisiologia da digestão.

Atkins (1937a e 1937b) registrou os tipos de cílios e respectivos mecanismos ciliares de *O. edulis*, *C. virginica* e *C. angulata* (Lamarck, 1819).

Graham (1949) desenvolveu o estudo sobre a anatomia interna do estômago de vários moluscos e revisou a configuração desse órgão em *O. edulis*, com detalhes superiores vistos no trabalho de Yonge (1926).

Em suma, o conhecimento sobre anatomia e funcionamento do estômago dos ostreídeos é restrito aos estudos de Shaw & Battle, 1957 com *O. chilensis* Philippi, 1845, de Yonge (1926), Graham (1949), Purchon (1957) e Reid (1965) com *O. edulis*; de Purchon (1957) com *C. parasitica* (Simpson, 1889); e de Shaw & Battle (1957) e Galtsoff (1964) com *C. virginica*.

Shaw & Battle (1957), Nelson (1960) e Yonge (1966) abordaram ainda outros detalhes da morfologia e fisiologia do trato digestivo, mecanismos ciliares e estrutura e funcionamento do estômago, respectivamente, contribuindo para o conhecimento da anatomia dos ostreídeos.

Galtsoff (1964) abordou a taxonomia, o estudo detalhado da morfologia e estrutura da concha, funcionamento e fisiologia de praticamente todos os órgãos e

estruturas, a reprodução e o comportamento reprodutivo, a embriologia, desenvolvimento larval, fatores abióticos e bióticos que afetam as populações de *C. virginica*. É, portanto, um dos estudos mais completos e muito usado neste. Além destes, a revisão de Amaral & Simone, (2010) apresenta uma grande contribuição para a taxonomia do gênero *Crassostrea* do Brasil, a partir de comparações morfo-anatômicas.

1.1.1 Crassostreinae

A subfamília Crassostreinae Torigoe, 1981, foco de estudo neste trabalho, são ostreídeos de conchas de tamanho médio a grande, alongadas dorsoventralmente e ocasionalmente subcirculares. A valva esquerda, fixa ao substrato, é profundamente côncava, e a valva direita é plana e geralmente opercular. São três os gêneros englobados pela subfamília, os gêneros *Saccostrea* e *Striostrea* possuem os dentículos marginais nas valvas, denominados de “chomata”, já no gênero *Crassostrea* caracteristicamente esta estrutura é ausente. A impressão muscular é geralmente pigmentada em uma ou em ambas as valvas. A massa visceral possui a passagem promial, uma passagem entre o pericárdio e a massa visceral no lado direito. Essa passagem é característica de Crassostreinae, embora também esteja presente em Pycnodontinae (Gryphaeidae) (exceto *Hyotissa* que possui em ambos os lados), e é ausente nos demais grupos (Stenzel, 1971, Harry, 1985, Lawrence, 1995).

As espécies da subfamília Crassostreinae ocorrem preferencialmente em águas tropicais e subtropicais, mas algumas espécies suportam temperaturas mais baixas. São encontradas da zona entre marés até 50 metros de profundidade (Harry, 1985).

Crassostrea

De forma geral, o gênero *Crassostrea* Sacco, 1897 tem sido atribuído às espécies com a valva direita menor e plana, a valva esquerda mais côncava e aderida ao substrato. O resílio é longitudinalmente estriado. O exterior é geralmente cinza claro a branco, amarronzado e/ou púrpura. O interior é branco, com a cicatriz do músculo adutor e próxima ao centro, podendo estar pigmentada ou não. O ligamento é externo. O gênero apresenta indivíduos dióicos, sem dimorfismo sexual. a fêmea produz de 30 a 50 milhões de ovos por desova (Boss, 1982; Rios, 1994, 2009).

O atual número de espécies ainda é incerto. Na América do Sul o assunto ainda é polêmico (Absher, 1989). Alguns autores (e.g., Wakamatsu, 1973, Absher, 1989, Nascimento, 1991) têm usado o binômio *Crassostrea brasiliiana* (Lamarck, 1819) para espécimes de zonas sublitorâneas de costões rochosos; estas são principalmente distinguidas por seu maior tamanho. Por outro lado, o tamanho não é considerado um bom parâmetro taxonômico por vários autores (McLean, 1941; Abbott, 1974), já que o tamanho pode ser influenciado por fatores de desenvolvimento, ambientais, de alimentação, etc. Para outros autores, *C. brasiliiana* é geralmente menor, ocorre no Caribe, assim como entre as raízes de manguezais no Brasil (Lamy, 1929). Huber (2010) cita cerca de 30 espécies para o gênero *Crassostrea* amplamente distribuídos pelo mundo.

Analisando mais a fundo a taxonomia publicada do gênero *Crassostrea* das espécies citadas para o nosso litoral e que apresentam afinidades entre si, as maiores confusões taxonômicas ocorrem em relação à *C. rhizophorae*, *C. brasiliiana* e *C. virginica* (Gmelin, 1791), consideradas por muitos autores espécies válidas (e.g., Gunter 1950, 1951) e por outros, sinônimos (e.g., Weisbord 1964; Rios, 1994, 2009).

Singarajah (1980), ao descrever uma nova espécie da região, *C. parahibanensis*, diz ter encontrado “pelo menos três espécies muito distintas do gênero *Crassostrea*”,

onde se inclui a espécie nova descrita, assim como *C. brasiliana* e uma espécie desconhecida, denominada *C. sp.*. Aquele autor acredita que *C. rhizophorae* e *C. arborea* (Chemnitz, 1785) são sinônimos de *C. brasiliana*.

Absher (1989) verificou que *C. rhizophorae* ocorre em geral na zona entre marés e alcança um tamanho inferior a *C. brasiliana*, que normalmente ocorre na infralitoral em fundos consolidados. Ignácio *et.al.* (2000) analisaram populações simpáticas e alopáticas de duas espécies através de eletroforese de aloenzimas. As amostras foram coletadas no Paraná e no Rio de Janeiro e os resultados evidenciaram a presença de dois grupos de ostras, chamadas de *C. rhizophorae* e *C. brasiliana*, confirmando as observações feitas por Absher (1989).

Para Rios (1994, 2009) *C. rhizophorae* constitui a única espécie, sendo *C. brasiliana* (Lamarck, 1819), *C. arborea* (Chemnitz, 1785), *C. rhizophora praia* (Ihering, 1907) e *C. parahibanesis* (Singarajah, 1980) sinônimas.

Weisbord (1964) e Abbott (1974) também consideraram *Crassostrea brasiliana*, *C. virginica* e *C. rhizophorae* como sinônimas. Mas para outros autores como McLean (1941), Parodiz (1948), Mattox (1949), Gunter (1950, 1951), Popovici & Angelescu (1954), Ranson (1943, 1967), Warmke & Abbott (1962), Yonge (1966), Coomans (1969), Quayle (1981), Morton (1983), Rodriguez & Garcia-Cubas (1986), apregoam que *C. rhizophorae* e *C. virginica* são espécies distintas e válidas, mas divergem na opinião apenas sobre a distribuição geográfica de ambas. McLean (1941), Mattox (1949) e Galtsoff (1964) consideraram *C. rhizophorae* e *C. virginica* espécies distintas, e reconhecem que ambas apresentam características conquiliológicas diferentes, principalmente em relação ao tamanho da concha, sendo ainda mais espessa e com altura máxima de 400 mm em *C. virginica* e raramente tendo 100 mm de altura em *C. rhizophorae* (Timothy *et.al.*, 1988). *C. brasiliana* por sua vez é reconhecida como

espécie válida por Parodiz (1948), Ranson (1967), Quayle (1981), Mesquita (1993), Huber (2010), endêmica do litoral brasileiro.

Entretanto, diferenças em relação ao crescimento e à morfologia larval têm sido descritas entre *C. rhizophorae* e *C. brasiliana*, indicando que, certamente, são entidades biológicas distintas (Absher, 1989).

Christo & Absher (2008) desenvolveram um estudo de desenvolvimento larval em laboratório entre as espécies *C. rhizophorae* e *C. brasiliana*, nativas e, *C. gigas*, invasora, da costa do Paraná, diferenciando as espécies pelo tamanho das larvas e tempo de desenvolvimento.

Nascimento (1991) publicou a ocorrência das duas espécies, *C. rhizophorae* e *C. brasiliana* para a América do Sul e Central, comparando as características morfológicas, de desenvolvimento e reprodução.

Mesquita (1993) fundamentou-se na opinião de Métivier (Museu de História Natural de Paris), publicada por Santos (1978) e Fornasaro (1981), que os ostreídeos da região entre marés de manguezais, em particular da região de Cananéia, são identificados como pertencentes à espécie *C. rhizophorae*, resultados confirmados por Absher (1989) para as populações de ostras do norte do Paraná.

Recentemente, e como parte deste Projeto, a revisão taxonômica entre as ostras brasileiras foi realizada por Amaral & Simone, 2014 (anexo I), mostra que ocorrem três espécies no Brasil, *C. mangle* (espécie nova descrita), *C. brasiliana*, *C. praia* (espécie revalidada a partir da comparação dos sítipos encontrados no MZUSP com as demais espécies brasileiras). Em relação à *C. rhizophorae*, foram estudadas amostras da localidade tipo (Grenada, Carriacou), foram observadas diferenças anatômicas significantes em comparação com as amostras brasileiras permitindo que *C. rhizophorae* tenha a distribuição confirmada apenas para a região caribenha, e não como uma espécie de ampla distribuição para o Atlântico Oeste (e.g., Caribe até Uruguai -

Rios, 1994, 2009). Assim, ficou determinado que o que chamávamos de *C. rhizophorae* no Brasil passa a ser designado como *C. mangle*.

As demais espécies descritas para o gênero *Crassostrea*, que não ocorrem no Brasil, também apresentam grandes confusões de descrição e identificação. Restringe-se, então, este texto apenas às espécies que foram aqui estudadas.

Lucas (1982) elaborou a probabilidade que *C. angulata* era a espécie portuguesa estabelecida na Europa e *C. gigas* era a distinta espécie japonesa. No entanto, muitas importações, remessas e várias fases de cultivo durante os últimos 150 anos, fizeram que hoje elas fossem morfológica e geneticamente indistinguíveis.

Lam & Morton (2003) descreveram *C. hongkongensis* geneticamente e compararam com as demais espécies da China. Eles excluem a possibilidade desta ser geneticamente próxima a *C. nippona*, mas não excluem *C. ariakensis* (Fujita, 1913), *C. gigas*, *C. sikamea* (Amemiya 1928), *C. belcheri* (Sowerby, 1871) e *C. iredalei* (Sacco, 1932) (= *bilineata*) (Röding, 1798). Morfologicamente, *C. hongkongensis* é mais próxima à *C. bilineata*. *C. hongkongensis*, como o nome da espécie já diz, é conhecida na área de Hong Kong, e é endêmica. *C. bilineata* vive na mesma área, e também é cultivada juntamente com *C. belcheri*. No entanto, esta é consideravelmente grande, mais robusta e possui a impressão do músculo e margem internas brancas (Ranson, 1967, Huber, 2010).

C. corteziensis vem sendo sinonimizada com *C. columbiensis* por Harry (1985) e confirmada por Coan *et.al.* (2000).

Saccostrea

O gênero *Saccostrea* Dollfus & Dautzenberg, 1920 é caracterizado pela valva esquerda em forma de taça, com dentículos marginais e câmara promial. Este gênero está limitado às regiões tropicais e sub-tropicais (Atlântico oriental, Indo-Pacífico oeste

e Pacífico oriental, estando ausente no Atlântico oeste), em áreas salinas (mar aberto), mas ocasionalmente ocorrem em manguezais. A maioria das espécies vive exposta, fixada em rochas ou em corais (Harry, 1985). *Saccostrea* possui 9 espécies aceitas (Huber, 2010).

Trabalhos atuais que incluem as espécies de *Saccostrea* referem-se a dados de reprodução e desenvolvimento, população, caracterização e comparações molecular entre as espécies (e.g., Klibunga *et.al.*, 2002; Kakoi *et.al.*, 2008; Green *et.al.*, 2009; Parker *et.al.*, 2010; Dove & Connor, 2012). Em relação à morfologia, apenas descrições conquiliológicas são encontradas na literatura (e.g., Rao, 1987).

As espécies de *Saccostrea* apresentam grande confusão taxonômica entre as principais espécies e parecem apresentar complexos de espécies (Lam & Morton, 2009).

Por causa da plasticidade da concha, a taxonomia de *Saccostrea* vem sendo problemática. Para algumas “formas” de *Saccostrea cucullata* (Born, 1778) estão sendo usados diferentes nomes por diferentes autores, e.g., *S. echinata* (Quoy & Gaimard, 1835), *S. mordax* (Gould, 1850), *S. glomerata* (Gould, 1850) (Lam & Morton, 2004). Diversos trabalhos moleculares (e.g., Lam & Morton, 2004, 2006, 2009) estão sendo realizados a fim de tentar resolver tal confusão taxonômica e estabelecer a distribuição das mesmas, já que aparentemente elas ocorrem em diversas localidades do oceano Pacífico. Awati & Rai (1931) já reportavam a dificuldade de identificação por conta da grande variação do corpo, tamanho e coloração, sendo fácil a confusão entre as espécies. E confirmado por Lam & Morton, 2006: “A distribuição geográfica das linhagens de *Saccostrea* é algo incerto por causa da confusão taxonômica”.

Apenas como exemplo da confusão taxonômica, *S. commercialis* (Iredale & Roughley, 1933) e *S. mordax* tem sido consideradas como subespécies de *S. cucullata*, já que as duas apresentam caracteres de concha similares (Stenzel, 1971). Thomson (1954: 175, figs. 7.1-7.2) ilustra *Crassostrea* (*Saxostrea*) *amara* (Iredale, 1939) para a

Austrália, mas estas parecem *S. mordax* de Hong Kong; assim como as ilustrações de *S. cucullata* feitas por Morris (1985: 126, figs 3A–D). Lamprell & Healy (1998: 134, fig. 336), Yoosukh & Duangdee (1999: 336, fig. 6) e Slack-Smith (2000:271, fig. 6.15E) mostraram similaridades nos caracteres de concha de acordo com as ilustrações de Torigoe (1981:380-381, plate 17) e Qi & Choe (2000: 137, fig. 3C – E) para *S. mordax* (Lam & Morton, 2006). Bernard *et.al.* (1993) consideram que as últimas onze espécies nominais da China são sinônimas de *S. cucullata*.

A extrema extenuação dorsal, a forma “cornucopiae” (característica do gênero), é encontrada em várias espécies de *Saccostrea*, definitivamente em *S. cucullata* (Leste da África e Leste do oceano indiano) e *S. schyphophilla* (Peron & Lesueur, 1807) (Índia, Austrália e Japão), mas não é vista em *S. kegaki* (Torigoe & Inaba, 1981), *S. echinata*, *S. circumscuta* (Gould, 1850), *S. spathulata* (Lamarck, 18190), *S. malabonensis* (Faustino, 1932) ou nas panamenhas *S. tubulifera* (Dall, 1914) e *S. palmula* (Carpenter, 1857) (Huber, 2010).

S. glomerata é válida, espécie geneticamente isolada, restrita ao sudeste australiano e neozelandês, mas possivelmente é cultivada em qualquer lugar. *S. comercialis* não é distinguível morfolologicamente e geneticamente de *S. glomerata* (Huber, 2010). Anderson & Adlard (1994) obtiveram a sequência de ITS1 de *S. comercialis* de Sydney, Austrália, e *S. glomerata* da Nova Zelândia, mostrando serem sinônimas.

Estudos de sistemática molecular de *Saccostrea* são poucos, e a maioria não contribui com os problemas na taxonomia específica do gênero (Lam & Morton, 2005).

Nesse cenário, resta a pergunta: de acordo com as características de *Crassostrea* e *Saccostrea*, como podemos distingui-las de *Ostrea*, que também possui chomata? A maioria dos estudos sobre relações evolutivas entre Ostreidae é concentrada na distinção de *Crassostrea* e *Saccostrea* de *Ostrea* além dos estudos de genética de populações das

espécies de *Crassostrea* economicamente importantes (Buroker *et.al.*, 1979a, b; Singarajah, 1982; Rose, 1984; O'Foighil *et.al.*, 1995, 1998).

Brock (1990) aplicou técnicas de imuno-eletroforese para distanciar e diferenciar o gênero *Ostrea*, de *Crassostrea* e *Saccostrea*, e concluiu a proposta de Orton (1928) e Walne (1964) na separação dos gêneros *Ostrea* e *Crassostrea* e ainda na separação de *Crassostrea* de Stenzel (1971) do gênero *Saccostrea*.

Saccostrea tem sido caracterizada por exibir uma especial variação ecomorfológica, quanto à presença chomata e coloração (Tack *et.al.*, 1992). Todas as ostras do gênero *Saccostrea* na Tailândia foram previamente assumidas como sendo apenas *S. cucullata* (Visoothiviseth *et.al.*, 1998). Os resultados do estudo de Klibunga *et.al.* (2005) indicaram que mais do que uma espécie de *Saccostrea* é identificada em águas tailandesas, implicando em problemas com o uso para aquicultura pelos complexos de espécies.

Striostrea

O gênero *Striostrea* Vyalov, 1936, segundo a classificação de Harry (1985), é dividido em dois subgêneros, *Striostrea stritu sensu* (com duas espécies: *S. margaritacea* e *S. prismatica*) e *Striostrea (Parastriostrea) mytiloides* (Lamarck, 1819).

Todas essas espécies são caracterizadas por seu grande tamanho (até 200 mm), conchas normalmente alongadas dorsoventralmente, mas às vezes podem ser subcirculares, geralmente fixadas por toda área da valva esquerda. A valva direita não é plicada, mas o interior é distintamente subnacarado, iridescente e ocasionalmente branco, com muitas vezes manchado de marrom escuro, azul ou roxo. Os dentículos são largos, muitas vezes alongados, bem espaçados, normalmente se estendendo por ambas as margens das valvas, às vezes podem ser ausentes em conchas grandes (Harry, 1985; Huber, 2010).

Há poucos trabalhos que trabalharam com espécies do gênero *Striostrea*. Klibunga *et.al.* 2001 realizou um trabalho sobre a diversidade genética e marcadores moleculares dos gêneros *Crassostrea*, *Saccostrea* e *Striostrea* da Tailândia, onde mostra que as diferenças genéticas dentro de cada espécie do gênero *Crassostrea* foram muito menores do que aqueles dentro de cada espécie de *Saccostrea* e *Striostrea*. Os resultados corroboram com aqueles baseados em estudos morfológicos (Brock, 1990) e aloenzimáticos eletroforese (Buroker *et.al.*, 1979; Hedgecock, 1995; Visootiviset *et.al.*, 1998). Alta diversidade genética dentro cada ostra pode ter refletido correlação entre genética adaptação às variantes climáticas ou ambientais (Buroker, 1985).

1.1.2 Ostreinae

As subfamílias Ostreinae Rafinesque, 1815 e Lophinae Vyalov, 1936 incluem táxons mais bem conhecidos e estudados, como *Ostrea* Linnaeus 1758, *Dendostrea* Swainson, 1835 e *Lopha* Röding, 1798. Outros representantes menos conhecidos são incluídos nessas duas subfamílias, como *Alectryonella* Sacco, 1897, *Anomiotrea* Habe&Kosuge, 1966, *Myrakeena* (Harry, 1985) entre outros (sendo aqui estudado apenas *Alectryonella*).

Membros das duas subfamílias apresentam em comum a passagem promial ausente e hábito larvíparo; esses dois fenômenos são em muitas referências (e.g., Stenzel, 1971; Harry, 1985) funcionalmente associados um ao outro. A preferência batimétrica e a salinidade das duas subfamílias são as mesmas. Ostreinae tem regredido vários graus na quantidade da fusão mediana dos palpos externos, na presença e na forma do apêndice anal e nas plicas reduzidas nas conchas, mas eles mantiveram a habilidade de produzir depósitos calcários que em Lophinae foi perdido (Harry, 1985).

Os representantes da subfamília Ostreinae são caracterizados por conchas pequenas a grandes, subcirculares a subtriangulares a levemente alongadas dorsoventralmente, valva direita não plicada e plana ou apenas levemente convexa, manchadas por faixas radiais azuis, vermelhas ou roxas; a valva esquerda é mais inflada e com esculturas plicadas normalmente bem definidas (Stenzel, 1971, Harry, 1985).

Ostrea

O gênero *Ostrea*, Linnaeus, 1758, é caracterizado por ter conchas pequenas a grandes, (30 – 100 mm), subcirculares ou subtriangulares, raramente alongadas dorsoventralmente; valva direita quase plana e valva esquerda moderadamente inflada com pequenas plicas radiais. Os dentículos marginais (chomata) são muito pequenos, inconspícuos e limitados à margem próxima ao ligamento, ou ausentes em espécimes velhos (Harry, 1985).

O gênero *Ostreola* foi descrito por Monterosato, 1884 para a ostra italiana *O. stentina* e Harry (1985) aplicou tal classificação para 3 pequenas espécies similares: *Ostreola stentina*, *O. equestris* e *O. conchaphila* (= *lurida*), caracterizadas por serem conchas pequenas a médias, subcirculares irregulares as vezes alongadas dorsoventralmente e com a região não fixada da valva esquerda plicada, e com a chomata presente por toda vida se estendendo da região anterior até a posterior, e ocasionalmente por toda borda das valvas. Ainda restringe a ocorrência das espécies, estando ausentes para Indo-Pacífico oeste. Coan *et.al.*(2000) consideram *Ostrea* e *Ostreola* como sinônimos. Torigoe (2004) inclui novas espécies e as colocou os gêneros *Ostrea* e *Ostreola* como *incertae sedis*. Mais recentemente, Lapègue *et.al.*(2006) concluem que os dados obtidos favorecem a incorporação de *Ostreola* em *Ostrea*. Huber (2010) conclui que todos os gêneros, *Adontostrea*, *Eostrea*, *Tiostrea* (descritas por Harry, 1985) e *Ostreola* são sinônimos de *Ostrea*.

A espécie tipo, *Ostrea edulis* (Linnaeus, 1758), possui uma vasta literatura desde a biologia e desenvolvimento, morfologia e cultivo (e.g., Davaine 1853; Horst, 1883-1884; Younge, 1926; Fernando, 1931; Erdmann, 1935; Cole, 1938; Korringa, 1941, Millar, 1955; Gunter, 1950; Ranson, 1960; Carriker, 1961, Hickman & Gruffydd, 1971; Stenzel, 1971; Cranfield, 1973a, b, c, 1974; Waller, 1981, Chaparro *et.al.* 2001, entre outros), até atualmente com as análises moleculares (Launey *et.al.* 2002; Bénédikte *et.al.* 2006; Lapègue *et.al.* 2006, López-Flores *et.al.* 2010; Danic-Tchaleu *et.al.*, 2011).

O. equestris Say, 1834 foi estudada por Galtsoff & Merrill (1962) quanto a sua morfologia, crescimento e distribuição. Clavijo *et.al.* (2005) cita a ocorrência de *O. equestris* para a região estuarina do Uruguai, no período quaternário. Normalmente, *O. equestris* é listada de Maryland (nordeste dos Estados Unidos) até a Argentina com *O. spreta* e *O. 'cristata'* Dall & Simpson. 1901 como sinônimas (Torigoe, 2004). Há uma grande confusão quando se trata desta espécie, principalmente quanto à sua distribuição: Weisboard (1964) descreve duas novas espécies (*O. lixula* e *O. libella*) para a Venezuela, sendo espécies válidas. Por outro lado, *O. lixula* parece ser coespecífica com a espécie mais comum, *O. spreta* (= *O. equestris*). De acordo com o espécime tipo, *O. equestris*, no entanto, é um pouco menor, arroxeadas a esbranquiçadas, geralmente alongadas; a valva superior ou direita mais profunda, e comparativamente finas e frágeis. Em geral, é fortemente plicada e encontrada na região do médio e supralitoral.

O lectótipo e paralectótipos de *O. spreta* d'Orbigny, 1846 (BMNH n° 1846.12.4.821 e 1854.12.4.821, respectivamente) tem como localidade o Rio de Janeiro. Esta é sólida, oval, com interior tipicamente esverdeada e amarelada podendo ocorrer estrias arroxeadas, com uma grande cicatriz reniforme. De acordo com a distribuição e características apresentadas por Torigoe (2004), *O. spreta* continua sendo considerada sinônima de *O. equestris*.

1.1.3 Demais Ostreinae

Dentro da subfamília Ostreinae, são ainda incluídos os gêneros: *Cryptostrea*, *Teskeyostrea*, *Booneostrea*, *Pustulostrea*, *Undulostrea* e *Nanostrea*, todas descritas por Harry, 1985, e são monotípicas.

Cryptostrea permolis (Sowerby II, 1871) é caracterizada por iniciar o desenvolvimento pós-larval em esponjas (Forbes, 1964) e depois cimentar-se em substrato consolidado. Possuem conchas pequenas (30 mm de comprimento), muito finas, levemente infladas, inequivalves, subtriangular, subcircular ou levemente alongadas dorsoventralmente. Não possui linhas de crescimento, lamelas ou plicas. A coloração é uniforme, do castanho claro a um marrom escuro. Dentículos do tipo ostreine presentes se estendendo ao longo da margem anterior, mais que na margem posterior. O interior da concha é branco, não nacarado. Ocorre da zona intertidal até cerca de 150 metros de profundidade; no nordeste do México e ao largo da costa da Carolina do Norte (Harry, 1985).

O gênero *Teskeyostrea* foi descrito a partir da nova combinação sugerida por Harry, 1985 para a espécie *Ostrea weberi* Olsson, 1951. É caracterizado pelo pequeno tamanho (até 37 mm de altura), conchas finas, subcirculares, e com a coloração marrom dourada escura uniforme. A valva esquerda é completamente cimentada à rocha. A valva direita é levemente convexa, com extensões lamelares da camada prismática. Interior é aporcelanado, apresentando uma ou duas manchas esbranquiçadas de calcário. Os dentículos são do tipo ostreinae, pequenos e poucos ocorrem sobre ambas as margens, anterior e posterior, perto do ligamento.

Booneostrea subucula (Jousseaume in Lamy, 1925) apresenta conchas pequenas (até, 28 mm de altura), finas, frágeis, de formas variáveis, mas normalmente ovais alongadas dorsoventralmente; a valva direita é plana a levemente convexa; valva

esquerda é bastante inflada. Externamente, a valva direita é coberta por uma fina camada prismática branca ou brilhante. Já a valva esquerda é clara ou esbranquiçada, fixada no substrato por cimentação em cerca de 1/3 da área total da concha. Não possui plicas marginais. Internamente a superfície é porcelanada, esbranquiçada. Dentículos totalmente ausentes.

Pustulostrea australis (Lamarck, 1819), *Undulostrea megodon* (Hanley, 1846) e *Nanostrea fluctigera* (Jousseaume in Lamy, 1925) são espécies citadas em catálogos (e.g., Huber, 2010, Coan & Valentish-Scott, 2012), mas não possuem estudos além da descrição de Harry, 1985. Por serem gêneros monotípicos e de difícil identificação (com exceção de *B. megodon* que possui ondulações na borda bem características), mesmo exemplares desses gêneros são identificados, como a maioria, em nível de família (Ostreidae), ou como *Ostrea* sp.

1.1.4 Lophinae

A subfamília Lophinae é caracterizada por ostreídeos pequenos a grandes, normalmente com plicas em ambas as valvas, com grandes comissuras em zigzag na margem; interior metálico lustroso apresentando alguma cor além do branco (marrom, esverdeado, ou avermelhado). Estão incluídos nessa subfamília os gêneros: *Lopha* Röding, 1798, *Alectryonella* Sacco, 1897, *Dendostrea* Swainson, 1835 (tribo Lophinini), *Myrakeena* Harry, 1985 e *Anomiostrea* Habe & Kosuge, 1966 (tribo Myrakeenini).

Lopha

O gênero *Lopha* é caracterizado por conchas largas (acima de 100 mm de comprimento), forma subcircular a oval reniforme, com cerca de cinco plicas radiais

bem largas intercaladas, em ambas as valvas. As plicas são agudamente anguladas e os lados planos. Os dentículos estão presentes em ambas as valvas. Conchas finas, com a superfície interna normalmente metálica, bronze, raramente brancas.

É um gênero monotípico, inclui apenas *Lopha cristagalli* (Linnaeus, 1758), descrita originalmente como *Mytilus cristagalli*. Outras espécies eram incluídas neste gênero por Stenzel (1971), mas atualmente estão classificadas como *Dendostrea* (Harry, 1985). Torigoe (1981) também chegou a essa conclusão, diante as grandes diferenças conquiliológicas entre os gêneros. *Lopha cristagalli* é limitada aos trópicos do Indo-Pacífico oeste associadas a recifes de corais a poucos metros de profundidade, estendendo até a costa leste africana, Mar Vermelho e ilhas do Japão (Harry, 1985). Paulay (1996) reporta uma nova ocorrência para o Havaí.

São raros trabalhos que reportem a morfologia, biologia e taxonomia de *Lopha cristagalli*, e.g., Xiaoxu *et.al.* 1994, que foi publicado apenas em chinês.

Alectryonella

O gênero *Alectryonella* possui conchas de tamanho grande (até 110 mm de comprimento), subcirculares, levemente infladas, normalmente cimentadas até a metade da valva esquerda. Possuem numerosas costelas radiais (acima de 20) regulares presentes em ambas as valvas. Externamente possui coloração roxa ou marrom escura, mas pode ser totalmente branca. Interior é marrom escuro, submetálico. Dentículos do tipo ostreine estão presentes perto do ligamento, mas ocorre o tipo lophine no resto da margem da concha. A espécie monotípica *Alectryonella plicatula* (Gmelin, 1791) é rara e vive em baixas profundidades no Indo Pacífico leste, de Madagascar até as Filipinas (Harry, 1985).

A espécie é facilmente reconhecida pela cicatriz muscular se parecer com uma “impressão digital” escura, destacada na coloração bronze metálica internamente.

Dendostrea

O gênero *Dendostrea* apresenta poucos trabalhos abordando as espécies válidas (8 segundo Huber, 2010). Normalmente possuem espécies de tamanho pequeno a médio (até 85 mm), subcircular, irregulares a alongadas dorsoventralmente, conchas finas cimentadas em partes variadas, mas apresentam espinhos normalmente pequenos e ao longo do comprimento. Ambas as valvas podem ser convexas, a esquerda mais que a direita, e são geralmente plicadas, e as vezes podem apresentar plicas em pequenas regiões. As plicas são curtas, arredondadas e próximas uma das outras. Superfície externa sem pústulas, e normalmente lisa, raramente com pequenas lamelas de crescimento. Normalmente brancas, mas podem possuir cores azuis ou roxas com raros raios escuros. Internamente brancas, variando do verde claro a verde escuro. Chomata normalmente do tipo ostreine, limitado à margem do ligamento, mas pode ocorrer o tipo lophine na valva direita que se estende por toda margem ventral (Harry, 1985).

D. folium (Linnaeus, 1758), a espécie tipo, é caracterizada por conchas de tamanho médio (até 80 mm de altura), de forma orbicular a oval, subequivalve. Ambas as valvas côncavas, com costelas dicotômicas radiando do umbo e terminando ventralmente em um zig zag ou ondulação marginal arredondada. Apresentam dois morfos em relação à cor: amarelo escuro ou roxo escuro. Manchas roxas avermelhadas podem estar presentes em raios a partir do umbo. Dentículos podem ou não estar presentes, dos dois lados do ligamento e até a metade do comprimento da concha com pequenos tubérculos alongados. O interior da concha é branco lustroso com manchas verdes iridescentes, particularmente ao longo dos cumes formados pelas costelas (Lam & Morton, 2004).

Harry (1985), Torigoe (2004), Lam & Morton (2004) e Huber (2010) citam a distribuição da espécie no oceano Pacífico (Indo-Pacífico oeste, Austrália, Filipinas,

mares do sul e leste da China, Taiwan, Japão), na região do sub-litoral até os 50 m de profundidade sobre as rochas.

D. frons (Linnaeus, 1758) a concha é oval a alongada, com até 60 mm de altura. Charneira estreita, ampla área ligamentar, resilífero elevado. Ambas as valvas convexas. Escultura radial bem definida fazendo numerosas pregas ao longo de suas bordas. Superfície da valva esquerda com projeções tubulares alongados, que servem para prender as raízes de mangue ou ramos de gorgônias. Dentículos do tipo ostreine na margem interna, distribuídos por toda margem das valvas. Cicatriz do músculo adutor reniforme, localizado na região anteroposterior. Coloração marrom avermelhado ou marrom esverdeado externamente; interior roxo perolado, branco ou amarelado, com a borda interna marrom avermelhada ou roxa (Abbott, 1974, Castillo-Rodriguez, 1984). Distribuída da Flórida, Louisiana, Bermudas, Golfo do México e Caribe até o Brasil (Castillo-Rodriguez, 1984, Huber, 2010).

D. sandvichensis (Sowerby II, 1871), é tratada por Torigoe (2004), assim como Ranson (1967) *D. crenulifera* como sinônima de *D. sandvichensis*. Há certa confusão quanto a sua distribuição. Lamy (1930) concluiu que a espécie descrita por Küster (1868) como sp., do Havaí era na verdade *D. sandvichensis*. Huber (2010) cita a ocorrência par ao Japão ou para o Mar Vermelho. Coan & Valentish-Scott, (2012) citam a ocorrência de *D. cf. sandvichensis* para o sul da baixa Califórnia e México, pelas semelhanças com a espécie encontrada no Indo-Pacífico, sugerindo uma que seja uma espécie nova.

1.1.5 Gryphaeidae

Os grifeídeos são caracterizados por possuir a impressão muscular circular ou levemente plana dorsalmente. Duas de três subfamílias são extintas, Exogyrinae e

Gryphaeinae. Todos os grifeídeos vivos pertencem à subfamília Pycnodontinae (Stenzel, 1959). É característica a presença de vesículas internas nas valvas, nomeadas de “estrutura vesicular da concha”, e são ilustradas por Ranson (1967), Stenzel (1971), Torigoe (1981) e Harry (1985). A presença de chomata é dividida em 3 tipos de acordo com Harry (1985) que podem aparecer sozinhos ou combinados entre si (tipos descritos na lista de caracteres). Outra característica exclusiva dos táxons de Gryphaeidae é a aurícula lobada, e diferentemente do que ocorre em todos os Ostreídeos, o reto passa pelo ventrículo. *Hyotissa* apresenta a câmara promial aberta em ambos os lados, e *Parahyotissa* apresenta apenas do lado direito, como em *Crassostrea*.

Os trabalhos que abordam os grifeídeos são raros. Dados sobre distribuição são normalmente encontrados em catálogos, como Abbott (1974); Coan *et.al.* (2010). Os trabalhos que referem-se à morfologia e anatomia são Stenzel (1971) e Harry (1985). Atualmente, análises filogenéticas com dados moleculares incluem normalmente o gênero *Hyotissa* (Giribert & Wheeler, 2002; Bieler *et.al.*, 2014) como comparação entre os ostreídeos.

1.2 Histórico: análises moleculares

Vários trabalhos têm sido desenvolvidos em todo o mundo para determinar a variabilidade genética de ostras, através de marcadores nucleares e mitocondriais, para elucidação de táxons, melhoramento genético, manejo dos estoques naturais, cultivo e conservação (Huvet *et.al.*, 2000; Launey *et.al.*, 2002; Zhang *et.al.*, 2005; Hoover & Gaffney, 2005; Li *et.al.*, 2006; Galindo-Sanchez *et.al.*, 2007, 2008; Yu & Li, 2007; Yu *et.al.*, 2008; Taris *et.al.*, 2009; Varney *et.al.*, 2009).

Hedgecock & Okazaki (1984) analisaram a diversidade genética de oito populações da América Central de *C. virginica*, *C. rhizophorae* e *C. corteziensis* (Hertlein, 1951) através de técnicas eletroforéticas de enzimas.

Técnicas eletroforéticas de isoenzimas foram aplicadas por Absher (1989) com o propósito de encontrar parâmetros que permitissem identificar níveis de similaridade ou de distanciamento gênico entre as populações de ostras encontradas no infralitoral e de região entre marés no litoral sudeste do Brasil.

Boudry *et.al.* (1998) utilizaram a análise de restrição (RFLP) de fragmentos de DNA mitocondrial para determinar a diferenciação genética entre populações da ostra portuguesa (*Crassostrea angulata* Lamarck, 1819) e da ostra do Pacífico (*C. gigas*) introduzida no sul de Portugal e Espanha. Os resultados mostraram que as populações europeias de *C. angulata* agruparam-se com as de Taiwan, indicando que, provavelmente, são originárias daquele país. Boudry *et.al.* (2003) estudaram sequências de DNA mitocondrial (16S e COI) e DNA nuclear (28S) para determinar a variação em ostras, supostamente das espécies *C. gigas* e *C. angulata*, oriundas de diferentes regiões.

Klinbunga *et.al.* (2003) desenvolveram ferramentas para a identificação molecular de três espécies de ostras cultivadas na Tailândia, utilizando análises de restrição (RFLP) do DNA nuclear (18S) e do DNA mitocondrial (COI).

Wang & Guo (2008) investigaram o polimorfismo do comprimento do espaçador interno transcrito (ITS) entre genes do RNA ribossomal em 12 espécies de Ostreidae. Dois iniciadores (*primers*) foram desenhados para amplificação simultânea de ITS-1 e ITS-2 em uma única PCR. O método aplicado forneceu uma identificação efetiva, rápida e simples de *C. ariakensis* (Fujita, 1913) e outras espécies de ostra.

Análises filogenéticas baseadas em sequências do DNA nuclear (ITS) e mitocondrial (COI) foram realizadas por Reece *et.al.* (2008) para elucidar a taxonomia das ostras asiáticas do gênero *Crassostrea*. Xia *et.al.* (2009) distinguiram sete ostras do

gênero *Crassostrea* do sul da China usando análises de PCR-RFLP de fragmentos de genes mitocondriais (16S e COI) e nuclear (ITS-1).

Lapegue *et.al.* (2002) analisaram o polimorfismo do gene 16S do DNA mitocondrial através de sequenciamento e análises de PCR-RFLP de amostras de ostras da América do Sul e da África. Identificaram dois haplótipos, um deles foi atribuído a *C. rhizophorae* que só ocorre na América do Sul e o outro a *C. gasar* (Adanson, 1757) que ocorre tanto na costa atlântica da África como na costa brasileira. A constatação da ocorrência de *C. gasar* na América do Sul adicionou uma terceira espécie de *Crassostrea*, além de *C. brasiliana* e *C. rhizophorae*. Este autor verificou, ainda, que os cariótipos de *C. gasar* da África foram muito semelhantes aos do Brasil.

C. gasar distribui-se ao longo da costa ocidental da África, desde Senegal ate Angola, formando grandes aglomerados sobre as raízes dos mangues. Na America do Sul, esta espécie foi citada na Guiana Francesa e no Brasil por Lapegue *et.al.* (2002). Lazoski (2004) realizou estudos genéticos de cinco espécies do gênero *Crassostrea* que ocorrem ao longo da costa oeste do Atlântico, utilizando marcadores moleculares nucleares (aloenzimas e espaçadores ribossomais transcritos – ITS-2) e mitocondriais (citocromo oxidase I – COI e subunidade ribossomal maior – 16S). As espécies de *Crassostrea* spp. puderam ser separadas sem ambiguidade pelo sistema PCR/RFLP desenvolvido no trabalho. O autor constatou que *C. rhizophorae* e *C. brasiliana* foram as populações naturais mais abundantes na costa brasileira e que parecem geneticamente estruturadas, com uma separação clara de estoques ao longo da costa. Uma técnica simples de PCR-RFLP usando a endonuclease *Hae* III foi descrita por Pie *et.al.* (2006) para discriminar as espécies de ostras cultivadas no Brasil (*C. brasiliana*, *C. rhizophorae* e *C. gigas*).

Varela *et.al.* (2007) verificaram que a sequência da subunidade 16S do RNA ribossomal de *C. brasiliana* depositada no GenBank (DQ839413) por Pie *et.al.* (2006) é

idêntica a de *C. gasar* (AJ312937) estudada por Lapegue *et.al.* (2002), indicando que ambas pertencem a mesma espécie. Assim, esses autores referem-se a *C. brasiliiana* como *C. gasar*, uma vez que o último nome é precedente. Divergências sobre tal nome são discutidas em Amaral & Simone (2014).

Um estudo das relações filogenéticas através do sequenciamento de um fragmento do DNA mitocondrial (gene 16S RNAr) de 120 espécimes coletados ao longo da costa brasileira foi desenvolvido por Varela *et.al.* (2007). Os resultados identificaram duas espécies nativas de ostra, *C. gasar* e *C. rhizophorae*, e uma exótica do mesmo gênero, proximamente relacionada às ostras do Indo-Pacífico.

Melo *et.al.* (2010) analisaram sequências parciais do gene citocromo oxidase c subunidade 1 (COI) das espécies de ostras do gênero *Crassostrea* em 16 localidades da costa brasileira, do Estado do Pará a Santa Catarina. Os resultados revelaram a presença de *C. gasar* (= *C. brasiliiana*), *C. rhizophorae* e *Crassostrea* sp.. *C. gasar* foi encontrada do Estado do Pará até São Paulo e *C. rhizophorae* do Estado do Ceará até Santa Catarina. Ambas agruparam-se com *C. virginica*, indicando provavelmente um grupo monofilético do Atlântico. *Crassostrea* sp. só foi encontrada na Ilha de Canela, Pará, e mostrou maior similaridade com as ostras do indo-pacífico.

Melo *et.al.* (2010) constataram a presença de *C. gigas* em bancos naturais das espécies nativas na baía sul de Florianópolis e no litoral de Laguna, em Santa Catarina. Segundo esses autores, as populações de *C. gigas* encontradas, provavelmente, são originárias de fazendas marinhas e sua invasão foi facilitada, inicialmente, pelas águas frias encontradas no sul do país e ao longo do tempo a aclimação da espécie a temperaturas mais elevadas.

Com relação às características morfológicas e anatômicas das ostras da costa brasileira, alguns estudos recentes foram realizados por Alves (2004), Christo & Absher (2007), Amaral (2010), Amaral & Simone (2014) que corroboram com as análises

moleculares, demonstrando a distinção entre *C. rhizophorae* e *C. brasiliana*, consideradas por muitos anos como sinónímias.

Appleyard & Ward (2006) estudaram o nível e o padrão de variação genética em 4 linhagens de *C. gigas* oriundas da produção em laboratório. Para tanto, analisaram dados de aloenzimas e microsatélites de reprodutores selecionados e de indivíduos da 1ª, 3ª e 4ª gerações e compararam com populações naturais do Japão e da Austrália. Obtiveram dados de heterozigosidade, frequência alélica e mudanças temporais na diversidade genética de ostras cultivadas, demonstrando que há uma perda na variabilidade de linhagens selecionadas.

Li *et.al.* (2006) examinaram o polimorfismo de sete locos microsatélites em cinco populações cultivadas da ostra *C. gigas*, para avaliar os níveis de diversidade alélica e heterozigosidade dentro e entre populações. A variabilidade genética foi alta para os sete loci em todas as populações analisadas. As distancias genéticas mostraram uma clara separação entre três populações do norte e duas do sul da China, sugerindo que as populações cultivadas separadas geograficamente podem ser diferenciadas geneticamente.

Galindo-Sanchez *et.al.* (2007) avaliaram a diversidade genética da ostra americana (*C. virginica*) em Veracruz, México, através de marcadores microsatélites e constataram baixa variabilidade genética. Observaram diferenças genéticas entre as localidades e presença de estruturação das populações estudadas.

A diferenciação genética entre populações de *C. plicatula* e *C. gigas* da China foram analisadas por meio de marcadores microsatélites por Yu *et.al.* (2008). Os dados obtidos pelos autores mostraram que esses marcadores tem um grande potencial para diferenciar as populações dessas duas espécies, com importantes implicações para o manejo e a conservação deste recurso genético na China.

A diferenciação genética, por exemplo, de *Ostrea edulis* foi estudada ao longo da costa europeia por Launey *et.al.* (2002) por meio de 5 loci microssatélites. Os resultados mostraram um moderado, mas significativo isolamento por distância e uma tendência das populações do Atlântico ter uma menor variabilidade que as do Mediterrâneo, demonstrando uma independência relativa dos estoques locais.

Estudos filogenéticos moleculares são recentes e escassos quando se trata de Ostreoidea, as filogenias moleculares referem-se, normalmente, à Bivalvia como um todo. López-Flores (2004) analisou espécies de *Ostrea* e *Crassostrea* através de marcadores de microssatélites, avaliando a relação entre as espécies.

No geral, os trabalhos moleculares estão sendo importantes para a identificação das espécies e juntos com as análises moleculares podem trazer ótimos resultados, garantindo a identificação mais precisa.

2. METODOLOGIA

2.1 Análise morfo-anatômica

A lista de lotes estudados foi incluída na sequência da descrição de cada espécie. As amostras tiveram 4 diferentes origens: 1) material previamente depositado na coleção do Museu de Zoologia da USP (MZUSP); 2) material solicitado por empréstimo de outras instituições (tabela 1); 3) material coletado em atividades de campo, em vários pontos da costa brasileira (incluindo ilhas oceânicas), Caribe e Portugal, também depositado no MZUSP; 4) material doado por colegas do Brasil e estrangeiros, atendendo a solicitações por amostras de táxons ainda carentes de representantes.

Tabela 1– Lista de lotes emprestados.

Nº Lote	Espécie	Localidade	Preservação
USMN			
734199	<i>Ostrea palmula</i>	Miraflores Lock, Panamá Canal.	Dry
804411	<i>Ostrea edulis</i>	North Pacific Ocean, California Channel Is., Santa Catalina Is., Catalina Harbor,	70% eth.
806790	<i>Neopcyodontes cochlear</i>	Jeffs Reef, Florida	Dry
833923	<i>Dendostrea frons</i>	North Atlantic Ocean, Gulf Of Mexico, off Florida	70% eth.
833964	<i>Crassostrea virginica</i>	North Atlantic Ocean, Gulf Of Mexico, off Florida	70% eth.
836246	<i>Dendostrea folium</i>	North Atlantic Ocean, Gulf Of Mexico, Louisiana	70% eth.
843356	<i>Cryptostrea permolis</i>	Off. Florida	Dry
850792	<i>Ostrea equestris</i>	North Carolina Ocean	70% eth.
850796	<i>Ostrea permolis</i>	North Atlantic Ocean, South Carolina	70% eth.
850797	<i>Ostrea permolis</i>	North Atlantic Ocean, South Carolina	70% eth.
850798	<i>Ostrea permolis</i>	North Atlantic Ocean, South Carolina	70% eth.
852312	<i>Lopha cristagalli</i>	Saudi Arabia	Dry
856477	<i>Ostreola equestris</i>	North Atlantic Ocean, Gulf Of Mexico, off Florida	70% eth.
858434	<i>Saccostrea cucullata</i>	North Pacific Ocean, China, Hong Kong	70% eth.
886486	<i>Crassostrea cucullata</i>	South Pacific Ocean, New Zealand	70% eth.
1004295	<i>Dendostrea folium</i>	North Pacific Ocean, Colombia	70% eth.
FMNH			
16992	Ostreidae	California, La Jolla (on <i>Mytilus californianus</i>)	70% eth.
17210	<i>Crassostrea</i> sp.	Texas, Matagorda Bay	70% eth.
27226	<i>Ostrea palmula</i>	Panamá, Arraijan, Canal Zone,	70% eth.
49120	<i>Ostrea palmula</i>	Washington, Bay Center	70% eth.
223509	<i>Crassostrea rhizophorae</i>	Florida, Manatee	70% eth.
295705	<i>Ostrea equestris</i>	Florida, Monroe	70% eth.
314562	<i>Crassostrea virginica</i>	Florida, Monroe	70% eth.
Florida Museum			
24091	<i>Ostrea angasi</i>	New Zealand	Dry
43019	<i>Ostrea adriatica</i>	New Zealand	Dry
43020	<i>Ostrea angasi</i>	Mediterranean	Dry
43051	<i>Ostrea parasitica</i>	Cuba	Dry
43052	<i>Ostrea parasitica</i>	Cuba	Dry
157555	<i>Alectryonella plicatula</i>	Philippines	Dry
198964	<i>Ostrea sandwichensis</i>	Hawaii	Dry
245086	<i>Ostrea multistriata</i>	New Gorgona Is.	Dry
271410	<i>Ostrea iridescens</i>	Mexico	Dry

280263	<i>Alectryonella plicatula</i>	Indonesia	95% eth.
280380	Ostreidae		
280382	<i>Pycnodonte taniguchii</i>	Indonesia	95% eth.
282832	<i>Dendostrea folium</i>	Cook Is.	75% eth.
284793	<i>Saccostrea cucullata</i>	Mariana Is.	75% eth.
286145	<i>Ostrea subucula</i>	Oman	Dry
286693	<i>Ostrea equestris</i>	Florida	95% eth.
286695	<i>Lopha frons</i>	Florida	95% eth.
289623	<i>Dendostrea frons</i>	Panamá	95% eth.
290422	Ostreidae		
292925	Ostreidae		
294041	Ostreidae		
295089	Ostreidae		
295377	Ostreidae		
296246	<i>Saccostrea glomerata</i>		
296417	<i>Hyotissa hyotis</i>	Australia	95% Eth.
297300	Ostreidae		
297302	<i>Saccostrea echinata</i>	Mariana Is.	Dry
297605	<i>Ostrea subucula</i>	Oman	95% Eth.
297631	Ostreidae		
297649	Ostreidae		
298639	<i>Ostrea equestris</i>	Florida	95% Eth.
298644	<i>Teskeyostrea weberi</i>	Florida	95% Eth.
298646	<i>Teskeyostrea weberi</i>	Florida	95% Eth.
299446	Ostreidae		
299447	Ostreidae		
303012	<i>Saccostrea sp.</i>	Taiwan	95% Eth.
303671	<i>Saccostrea sp.</i>	Hawaii	95% Eth.
303677	<i>Saccostrea sp.</i>	Hawaii	95% Eth.
303686	<i>Dendostrea sandwichensis</i>	Hawaii	95% Eth.
304500	Ostreidae		
310047	Ostreidae		
310071	<i>Alectryonella plicatula</i>	Indonesia	95% Eth.
310073	<i>Ostrea tuberculata</i>	Indonesia	95% Eth.
310077	Ostreidae		
322404	<i>Lopha cristagalli</i>	Papua New Guine	95% Eth.
322470	<i>Lopha cristagalli</i>	Papua New Guine	95% Eth.
324260	<i>Striostrea mytiloides</i>	French Polynesia	Dry
324261	<i>Striostrea mytiloides</i>	French Polynesia	Dry
327379	<i>Pycnodonte taniguchii</i>	Papua New Guinea	Dry
327453	<i>Striostrea mytiloides</i>	Mariana Is.	Dry
327922	<i>Saccostrea sp.</i>	American Samoa	95% Eth.

327925	Ostreidae		
330846	<i>Dendostrea hawaiiensis</i>	Hawaiian Is.	Dry
334117	<i>Ostrea</i> sp.	Alaska	Dry
337489	<i>Crassostrea margaritacea</i>	South Africa	Dry
337654	<i>Ostrea iridescens</i>	Mexico	Dry
337668	<i>Crassostrea margaritacea</i>	South Africa	Dry
337668	<i>Ostrea megodon</i>	Mexico	Dry
338608	<i>Ostrea kauaia</i>	Hawaiian Is.	Dry
341293	Ostreidae		
350976	<i>Ostrea hanleyana</i>	Hawaiian Is.	Dry
351867	Ostreidae		
354728	<i>Ostrea columbiensis (corteziensis)</i>	Mexico	Dry
366014	Ostreidae		
366018	Ostreidae		
367470	<i>Parahyotissa mcgintyi</i>	Florida	95% Eth.
367484	<i>Ostrea equestris</i>	Florida	95% Eth.
367498	<i>Ostrea equestris</i>	Florida	95% Eth.
367502	<i>Ostrea equestris</i>	Florida	95% Eth.
367875	<i>Ostrea subucula</i>	Oman	95% Eth.
367888	<i>Saccostrea</i> sp.	Oman	95% Eth.
367977	<i>Ostrea subucula</i>	Oman	95% Eth.
367988	<i>Ostrea</i> sp.	Oman	95% Eth.
368004	Ostreidae		
378155	<i>Ostrea angélica</i>	Mexico	Dry
378156	<i>Ostrea corteziensis</i>	Panamá	Dry
382460	<i>Ostrea fischeri</i>	Panamá	Dry
389769	<i>Ostrea lutaria</i>	New Zealand	Dry
391533	<i>Ostrea tubulifera</i>	Costa Rica	Dry
400961	<i>Dendostrea sandwichensis</i>	French Polynesia	75% Eth.
413887	<i>Parahyotissa numisma</i>	Hawaiian Is.	95% Eth.
414099	<i>Dendostrea sandwichensis</i>	Hawaiian Is.	95% Eth.
423309	<i>Parahyotissa numisma</i>	Madagascar	95% Eth.
423309	<i>Parahyotissa numisma</i>	Madagascar	95% Eth.
423437	<i>Lopha cristagalli</i>	Madagascar	95% Eth.
423682	<i>Lopha cristagalli</i>	Madagascar	95% Eth.
423742	<i>Parahyotissa numisma</i>	Madagascar	95% Eth.
436152	<i>Parahyotissa numisma</i>	Florida	95% Eth.
437408	<i>Hyotissa mcgintyi</i>	Australia	75% Eth.

Amostras de outras espécies foram obtidas constituídas apenas por conchas. Essas amostras foram estudadas mas não foram incluídas na análise geral por carecerem de dados anatômicos. A lista das espécies adicionais estudadas foram relacionadas na tabela 2.

Tabela 2 – Lotes de espécies adicionais estudadas.

Nº Lote	Espécie	Localidade	Preservação
USMN			
806790	<i>Neopcyonodonte cochlear</i>	Jeffs Reef, Florida	Dry
Florida Museum			
24091	<i>Ostrea angasi</i>	New Zealand	Dry
43019	<i>Ostrea adriatica</i>	New Zealand	Dry
43020	<i>Ostrea angasi</i>	Mediterranean	Dry
43051	<i>Ostrea parasitica</i>	Cuba	Dry
43052	<i>Ostrea parasitica</i>	Cuba	Dry
198964	<i>Ostrea sandwichensis</i>	Hawaii	Dry
245086	<i>Ostrea multistriata</i>	New Gorgona Is.	Dry
271410	<i>Ostrea iridescens</i>	Mexico	Dry
286145	<i>Ostrea subucula</i>	Oman	Dry
324260	<i>Striostrea mytiloides</i>	French Polynesia	Dry
324261	<i>Striostrea mytiloides</i>	French Polynesia	Dry
327379	<i>Pycnodonte taniguchii</i>	Papua New Guinea	Dry
327453	<i>Striostrea mytiloides</i>	Mariana Is.	Dry
330846	<i>Dendostrea hawaiiensis</i>	Hawaiian Is.	Dry
334117	<i>Ostrea sp.</i>	Alaska	Dry
337489	<i>Crassostrea margaritacea</i>	South Africa	Dry
337654	<i>Ostrea iridescens</i>	Mexico	Dry
337668	<i>Crassostrea margaritacea</i>	South Africa	Dry
337668	<i>Ostrea megodon</i>	Mexico	Dry
338608	<i>Ostrea kuaia</i>	Hawaiian Is.	Dry
350976	<i>Ostrea hanleyana</i>	Hawaiian Is.	Dry
351867	Ostreidae		
354728	<i>Ostrea columbiensis (corteziensis)</i>	Mexico	Dry
378155	<i>Ostrea angélica</i>	Mexico	Dry
378156	<i>Ostrea corteziensis</i>	Panamá	Dry
382460	<i>Ostrea fischeri</i>	Panamá	Dry

389769	<i>Ostrea lutaria</i>	New Zealand	Dry
391533	<i>Ostrea tubulifera</i>	Costa Rica	Dry

Visava-se com as coletas de campo levantar dados ambientais, aumentar o número de espécimes e espécies na coleção do Museu de Zoologia, e obtenção de material fresco para estudo. A maior parte das coletas foram realizadas sob apoio financeiro da Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) e envolvia, principalmente, mergulhos livres e autônomos. Na costa brasileira, coletas foram realizadas em: Ceará, Rio Grande do Norte, Pernambuco, Fernando de Noronha, Alagoas, Bahia, Espírito Santo, Rio de Janeiro, São Paulo, Santa Catarina e Rio Grande do Sul. No Caribe, foram coletadas amostras em Grenada, Carriacou, Barbados e Panamá. E em Portugal, no Arquipélago dos Açores.

Nas coletas os animais foram fotografados *in situ* em seguida fixados em álcool 70% ou 90%.

Coleções de instituições foram também visitadas pessoalmente, sendo realizado contatos pessoais e levantamento de material preservado, que seria solicitado por empréstimo. No Brasil, as seguintes instituições foram visitadas: Laboratório do Mar - LABOMAR, Universidade Federal do Ceará; Museu Nacional da Universidade Federal do Rio de Janeiro – MNRJ; Universidade Estadual do Rio de Janeiro - UERJ; e Museu Oceanográfico da Universidade Federal de Rio Grande - MORG.

Para o estudo morfológico, o animal foi extraído de sua concha. Em espécies em que a extração era difícil, a concha foi quebrada. A dissecação ocorreu sob estereomicroscópio, com o espécime imerso preferencialmente em álcool 70%. A metodologia da dissecação seguiu técnicas tradicionais (e.g., Simone, 1997). Para a identificação e estudo do material foi utilizada Lupa estereoscópica Zeiss, modelo Stemi SV 11 ou SV 6 com câmara clara.

Para a representação gráfica dos exemplares inteiros, que apresentam grandes proporções, foi utilizada uma câmara clara apropriada sem a necessidade da lupa.

Primeiramente foi retirada a valva direita (superior), expondo o lobo do manto respectivo, os feixes musculares, o músculo adutor e em alguns casos, os a maioria dos órgãos do manto pode ser vista por transparência. Após a retirada completa do animal da concha, o lobo do manto é cortado, da base dos palpos até a junção pário-branquial, onde se fixa a linha de dorsal das brânquias, na região do capuz, e junto à massa gonadal, expondo as estruturas como, por exemplo, brânquias, palpos, pericárdio e gônadas.

Após a exposição dos órgãos, o lobo do manto retirado foi cortado longitudinalmente, para verificação do padrão das papilas da borda do manto. Também foi observada a posição, tamanho, espessura e textura do coração acessório localizado na câmara exalante.

Nos órgãos da cavidade do manto, foi observado o padrão das lamelas e feixes, tamanho, espessura e proporção das brânquias e palpos, através de cortes horizontais dos feixes. Posteriormente, o estômago foi aberto por um corte longitudinal expondo toda a área de seleção da porção oral até aboral.

Detalhes de todos os sistemas e órgãos foram investigados. Os desenhos foram obtidos com o auxílio de uma câmara clara, inicialmente a lápis e depois passados a limpo com nanquim e papel vegetal.

A nomenclatura anatômica, normalmente, seguiu os trabalhos principais que tratavam de cada grupo. Entretanto, muitos órgãos ou arranjos de órgãos inéditos foram encontrados, como por exemplo, capuz, localizado na junção dos lobos do manto. Nestes casos, uma nomenclatura meramente descritiva ou topológica foi usada. Em outros casos, a nomenclatura encontrada na literatura foi utilizada, a fim de manter o padrão para descrição dos bivalves (e.g., Stenzel, 1971).

Com o grande número de espécies estudadas e em cada uma havendo a necessidade de realizar descrição anatômica completa, acrescida de mudanças taxonômicas e discussão dos caracteres levantados em cada gênero, optou-se por incluir esses dados diretamente no presente texto dos táxons que ainda não foram publicados. Visando adiantar a publicação, as descrições dos táxons aqui foram feitas na língua inglesa. Encontram-se anexos os trabalhos já publicados diretamente ligados ao estudo e os manuscritos daqueles ainda não publicados, mas já encaminhados para tal. A intenção é facilitar alguma eventual consulta, pois boa parte da informação presente neste texto não é encontrada no restante da literatura.

2.2 Análise filogenética

Análises filogenéticas foram realizadas com NONA-Winclada (Nixon, 2002) e TNT (Goloboff et al., 2008). A estratégia de busca utilizada foi busca heurística, utilizando "*Tree Bisection and Reconnection*" (TBR) mais "branch swapping" em uma série de 1000 repetições aleatórias mantendo até 10 cladogramas por replicação. Para aplicação dos valores de K, e procura das árvores com maior *fit* utilizou-se o TNT. Posteriormente, as topologias oriundas do TNT são salvas em arquivos no modo "*treeview*" (.tre), para poderem ser lidas no ambiente Winclada. Utilizou-se otimizações conforme análise específica para cada caráter. As topologias resultantes foram posteriormente vetorizadas em Photoshop e PowerPoint.

A análise cladística tradicional, com a procura da(s) árvore(s) mais parcimoniosa(s), partindo do pressuposto que todos os caracteres apresentam o mesmo peso. Caso obtiver apenas uma árvore mais parcimoniosa, ela será retida como aquela que representa a evolução do grupo, segundo a distribuição mais parcimoniosa dos dados.

2.3 Grupo interno e enraizamento.

Partiu-se do princípio que para que uma filogenia possa apresentar uma boa resolução e acuidade, além de tornar válido o teste de monofiletismo de Crassostreinae, é necessário estudar outros ostreídeos, e por isso procurou-se representar toda a diversidade de ostreídeos. A base da escolha foi: a) proximidade filogenética já discutida na literatura; b) disponibilidade e facilidade de acesso de material fixado. No primeiro item podem-se incluir os táxons citados nos gêneros *Ostrea* e *Dendostrea*. Os espécimes utilizados no presente estudo e sua distribuição estão listados na em cada descrição das espécies.

O enraizamento foi feito em um táxon distante, *Barbatia candida* (Helbling, 1779) da Superfamília Arcoidea, um representante dimiário. Com este arranjo, as subfamílias de ostreídeos são tratados como grupos externos funcionais, mas operacionalmente analisados no grupo interno (*sensu* Waltrous & Wheeler, 1981).

Os demais táxons utilizados como grupo externo (*Spondylus americanus* Hermann, 1781, *Lima* sp., *Isognomon alatus* (Gmelin, 1791), *Plicatula gibbosa* Lamarck, 1801, *Plicatulostrea onca* Simone & Amaral, 2008, *Anomia simplex* d'Orbigny, 1853) fazem parte da subclasse Pteromorpha e são todos monomiários. Os representantes do grupo externo foram descritos em diversos trabalhos. *Barbatia candida*, foi estudada por Simone & Chichvarkhin, 2004; *Spondylus americanus*, *Anomia simplex*, *Plicatula gibbosa*, *Parahyotissa mcgintyi*, *Hyotissa hyotis* e *Isognomon alatus* foram estudadas por Simone *et. al.*, no prelo 2014; *Plicatulostrea onca* foi descrita por Simone & Amaral, 2008; *Lima caribea*, foi estudada em uma revisão de dois gêneros do Atlântico oeste por Mikkelsen & Bieler 2003. Tais publicações foram utilizadas aqui como referência para a comparação com o grupo

interno, Ostreidae. Apesar das referências, exemplares dessas espécies foram dissecados, visando complementar a comparação com o grupo interno.

2.4 Análises Moleculares

Todas as amostras analisadas anatômicamente foram utilizadas para as análises moleculares. O DNA de cada espécime incluído no estudo foi obtido a partir de uma porção (cerca de 25mg) do músculo adutor fresco ou preservado preferencialmente em álcool 70 - 95%. A não contaminação das amostras durante a retirada da porção de cada espécie foi realizada com a esterilização de pinças e tesouras com álcool 100% e água destilada.

Para a extração foi utilizado o kit de extração da marca Invitrogen® Genomic DNA kit, além de testes com os kits de extração da Macherey-Nagel – NucleoSpin® Tissue e Quiagen The QIAamp DNA Kit. Métodos de extração salina também foram utilizados, de acordo com a metodologia de Aljanabi & Martinez, 1997.

Os primers foram sintetizados pela Prodimol®, a partir das linhas F e R descritas na bibliografia (Palumbi *et.al.* 2001, Pie *et.al.*, 2006 – 16 S; Folmer *et. al.*, 1994 – COI; Dixon *et.al.* 1995, Hedgecock *et.al.* 1999, Wang & Guo, 2008a – ITS I e II; Klibunga *et.al.* 2003, 2005 - 18S; Kinkerdale *et.al.* 2004. - 28 S) além da consulta em diversos trabalhos gerais de invertebrados e/ou específicos para moluscos.

16S:

Forward: 16S.AR (5'-CGC CTG TTT ATC AAA AAC AT-3')

Reverse: 16S.BR (5'-CCG GTC TGA ACT CAG ATC ACG T-3')

COI:

Forward: LCO1490 (5'-GGT CAA CAA ATC ATA AAG ATA TTG G-3')

Reverse: HCO2198 (5'-TAA ACT TCA GGG TGA CCA AAA AAT CA-3')

Forward: COIbrF (5'-GGG TTT TGA GCA GTT TTA GCC GGG-3')

Reverse: COIbrR (5'-GGT CAT CCA GAA GTG TAC GTC C-3')

18S:

Forward: 18Sa2.0 (5'-ATG GTT GCA AAG CTG AAA C-3')

Reverse: 18Sbi (5'-GAG TCT CGT TCG TTA TCG GA-3')

ITS-1:

Forward: ITS-1A (5'-GGT TCT GTA GGT GAA CCT GC-3')

Reverse: ITS-1B (5'-CTG CGT TCT TCA TCG ACC C-3')

ITS-2:

Forward: PH19 (5'-CAT CGA CAC TT(T/C) GAA CGC A-3')

Reverse: ITS2 (5'-AAT CCT GGT TAG TTT CTT TTC CTC CGC T-3')

28 S:

Forward: 28Sa (5'-GAC CCG TCT TGA AAC ACG GA-3')

Reverse: 28Sb (5'-TCG GAA GGA ACC AGC TAC-3')

Além das soluções comuns para qualquer extração: DNTP, Proteinase K, Cloreto de Magnésio (MgCl₂), Taqs, entre outras, foi utilizada também uma super taq, Phusion High-Fidelity DNA Polymerase® da Thermo Scientific, aumentando as chances de resultados positivos.

A partir do DNA genômico extraído através do kit de extração da Invitrogen®, foram amplificados partes dos genes mitocondriais 16S rDNA e citocromo oxidase subunidade I (COX I), e dos nucleares, 28S e espaçador transcrito nuclear I e II (ITS I e II). Após a extração, fragmentos genômicos foram amplificados por PCR (*Polimerase Chain Reaction*) utilizando termociclador Touchgene Gradient (Techne, Inc), conforme protocolos padrão de PCR (e.g.. Folmer, 1994, Littlewood, 1994, Palumbi, 2001) e depois publicações que desenvolveram protocolos para cada *primer* (e.g. Pie *et.al.*2006) e subsequente otimização e adequação de rendimento com a variação de parâmetros de reação (e.g., temperatura de anelamento e concentração de Mg).

A qualificação e quantificação destas etapas, i.e., extração, amplificação e purificação, foram efetuadas por eletroforese em gel de agarose 2% e quando pertinente com o uso de espectrofotômetro e/ou quantificação no Nanodrop®. Finalmente, as reações de sequenciamento foram realizadas em sequenciador automático ABI 3100 (Applied Biosystems) enviados à Macrogen na Coreia. As sequências foram visualizadas, comparadas, alinhadas e manualmente editadas no BioEdit (versão 6.0). A árvore após a comparação das sequências foi gerada pelo Mega6® e Bioedit®.

Entretanto, os esforços despendidos para essa atividade foram praticamente infrutíferos. O problema não é necessariamente má conservação das amostras, já que algumas foram obtidas frescas e condizentemente fixadas, e sim a qualidade extração e amplificação das sequências de DNA.

Foram realizadas extrações iniciais no Laboratório de Genética de Organismos Aquáticos e Aquicultura – LAGOAA da Universidade de Mogi das Cruzes – UMC, sob os auspícios da Prof. Dr. Alexandre W. S. Hilsdorf com a Dra. Márcia S. N. Galvão (Instituto de Pesca de Santos – Centro de pesquisas do Pescado Marinho), utilizando um kit de extração da Macherey-Nagel – NucleoSpin® Tissue. Apesar da aplicação e desenvolvimento das técnicas de extração, não obtivemos sucesso na quantificação do

DNA para posterior PCR nas 34 amostras selecionadas. Outros kits foram testados (Quiagen- The QIAamp DNA Kit e Invitrogen – Kit for Tissue), e também não obtivemos resultados significativos para a finalização do processo.

Para tentar solucionar tais problemas, com auxílio do Laboratório de Genética de Peixes do Instituto de Biociências da USP, sob responsabilidade da Prof. Dra. Lurdes Foresti de Almeida Toledo e auxílio da Dra. Ana Cristina Vigliar Bondioli, foi utilizado com sucesso a extração salina nas 50 amostras selecionadas, de acordo com o protocolo publicado por Aljanabi & Martinez (1997). Tal extração apresentou resultados significativos na quantidade de DNA nos produtos da extração em pelo menos 80% das amostras analisadas. Os 20% restantes foram repetidos, modificando apenas a concentração das soluções, apresentando resultados um pouco melhores, mas que não apresentaram qualidade na leitura de concentração.

Finalmente, com a abertura do laboratório molecular do MZUSP, houve maior facilidade ao tempo dedicado às análises e à repetição dos procedimentos que apresentaram dados negativos e novos experimentos. Foram iniciadas novas extrações com o kit da Invitrogen Tissue DNA®, em amostras frescas e fixadas (45 amostras) com primers e reagentes novos, incluindo a adição do detergente CTAB (brometo de cetil-trimetil amônio) o que permite facilmente acomodar uma grande variação de quantidades iniciais de tecido, até mesmo miligramas de tecido mumificado, fossilizado ou herbarizado (Ferreira e Grattapaglia, 1998).. A extração do DNA continuou a apresentar dados negativos em algumas amostras, e as que tiveram resultado positivos foram enviadas para a purificação e sequenciamento na Coréia (Macrogen).

Ao receber as 31 sequências (Forward e Reverse) referentes aos dados positivos (Tabela 4), verificou-se a inconsistência das sequências verificadas através dos cromatogramas (Fig. 54 e 55 exemplo de cromatogramas). Sequências que deveriam apresentar uma continuidade de pelo menos 300-400 pares de bases (pb) (Fig. 56,

cromatograma consistente para análise), somente 90 pb são consistentes quanto ao alinhamento (Fig. 57). Este número baixo de coerências não permite que sejam utilizadas para qualquer análise.

Sequências não obtidas por falta de amostragem, ou que não apresentaram resultados positivos para comparação foram obtidas no GenBank®.

3. RESULTADOS

3.1 Descrições

Serão apresentadas nesta seção as descrições das espécies. Primeiramente as espécies do grupo em questão, subfamília Crassostreinae, e posteriormente as demais espécies incluídas no estudo, de acordo com a classificação de Harry, 1985 para ostreídeos e grifeídeos, e os demais representantes do grupo externo segundo a classificação geral para Bivalvia.

A classificação sugerida por Harry, 1985 é:

Superfamília OSTRAOIDEA Rafinesque, 1815

Família GRYPHAEIDAE Vyalov, 1936

Subfamília PYCNODONTINAE Stenzel, 1959

Tribo HYOTISSINI Harry, 1985

Gênero *HYOTISSA* Stenzel, 1971

Gênero *PARAHYOTISSA* Harry, 1985

Tribo NEOPYCNODONTINI Harry, 1985

Gênero *NEOPYCNODONTE* Stenzel, 1971

Família OSTREIDAE Rafinesque, 1815

Subfamília LOPHINAE Vyalov, 1936

Tribo LOPHINI Vyalov, 1936

Gênero *LOPHA* Röding, 1798

Gênero *ALECTRYONELLA* Sacco, 1897

Gênero *DENDOSTREA* Swainson, 1835

Tribo MYRAKEENINI Harry, 1985

Gênero *MYRAKEENA* Harry, 1985

Gênero *ANOMIOSTREA* Habe & Kosuge, 1966

Subfamília OSTREINAE Rafinesque, 1815

Tribo OSTREINI Rafinesque, 1815

Gênero *OSTREA* Linnaeus, 1758

Gênero *NANOSTREA* Harry, 1985

Gênero *PLANOSTREA* Harry, 1985

Tribo CRYPTOSTREINI Harry, 1985

Gênero *CRYPTOSTREA* Harry, 1985

Gênero *TESKEYOSTREA* Harry, 1985

Gênero *BOONEOSTREA* Harry, 1985

Tribo UNDULOSTREINI Harry, 1985

Gênero *UNDULOSTREA* Harry, 1985

Tribo PUSTULOSTREINI Harry, 1985

Gênero *PUSTULOSTREA* Harry, 1985

Subfamília CRASSOSTREINAE Torigoe, 1981

Tribo STRIOSTREINI Harry, 1985

Gênero *SACCOSTREA* Dolfuss & Dautzenberg, 1920

Gênero *STRIOSTREA* Vyalov, 1936

Tribo CRASSOSTREINI Torigoe, 1981

Gênero *CRASSOSTREA* Sacco, 1897

Vale lembrar que as descrições serão apresentadas na língua inglesa, visando à publicação da morfo-anatomia comparada.

SYSTEMATICS

Genus *Crassostrea* Sacco, 1897

Diagnosis. Shell usually large, ponderous, pleurothetic. Hinge line narrow; chromata absent. Right valve cup-shaped, with sub-umbonal space in some. Promyal chamber in right side present. Non-incubatory. Type by original designation: *Ostrea virginica* Gmelin, 1791.

For complete description and comparison between species *C. mangle*, *C. brasiliiana*, *C. rhizophorae*, *C. praia*, *C. virginica* and *C. gigas*, see Amaral & Simone (2014) annexed.

Crassostrea bilineata (Röding, 1798)

Plates 1 e 2 – Figs. A – M

Ostrea bilineata Röding 1798: 170; Lamy, 1925: 320, 1929: 107; Kuroda, 1930: 54;

Kuroda & Habe, 1952: 26.

Ostrea orientalis Dillwyn, 1817: 274; Hanley, 1856: 304; Küster, 1868: 69; Hidalgo,

1905: 387; Iwakawa, 1915: 14, 1918: 255.

Gryphaea angulata: Adams, 1858: 569 (*non* Lamarck, 1819).

Ostrea angulata: Sowerby, 1871: sp. 2.

Ostrea lugubris Sowerby, 1871: sp. 63; Hidalgo, 1905: 387; Lamy, 1929: 139; Blanco *et.al.*, 1951: 53 (*non* Conrad, 1857: 156).

Ostrea (Crassostrea) bilineata: Kuroda: 1930: 54; Takatsuki, 1949: 8; Kuroda, 1960: 1728.

Ostrea gigas: Kuroda, 1941: 1248.

Ostrea benfica Bartsch, 1945: 1-2.

Crassostrea lugubris: Ranson, 1960: 17; 1967: 166 (*non* Conrad, 1857).

Ostrea (Saxostrea) iredalei: Kuroda, 1960: 1727.

Crassostrea gigas: Habe & Kosuge, 1967: 145; Xu, 1997: 93 (*non* Thunberg, 1793).

Crassostrea iredalei: Carreon, 1969: 109; Habe, 1977: 109; Rosell, 1991: 307.

Crassostrea lineate [*sic*]: Habe, 1977; Wu, 1980: 104, 1997: 94 (error for *bilineata*).

Saccostrea dactylena: Lamprell & Healy, 1998: 136

Types: *O. benfica* (Holotype USNM 254517; Paratype 573610) - Fig. 1.

Figura 1. Holotype. *O. benfica* (*C. bilineata*)

Shell (Figs. A, C): oval, with expansions in edges of valves; about 100 mm length. Color white to grayish brown. Right valve lightly concave, opercular, hinge not

protuberant. Left valve slightly larger and high than right valve. Umbonal cavity absent. Internally white with slight glossy edges. Adductor muscle impression pigmented, normally black or dark brown; located in posterodorsal region; shape oval with slight concavity in anterior region, occupying about 1/10 of valve surface. Scar of Quenstedt muscle oval-shaped, occupying 1/20 of size of adductor muscle.

Muscle system. Adductor muscle (Fig. B, D): position posterocentral. Transverse section oval shaped, occupying $\sim 1/4$ of shell length. **Quenstedt muscle** (Fig. J): thin and narrow, located in middle portion of length of palps.

Mantle (Figs. B, D, G): mantle lobes connected in hinge region along $\sim 1/3$ of body length; sub-umbonal region absent. Promyal chamber occupying $\sim 1/4$ of visceral mass. Mantle edge thick, color beige, unspotted. Middle fold with short and medium papillae fingerlike, up to four medium papillae between each short papilla. Internal fold with short and medium papillae elongated, with 1-4 medium papillae by 1-2 short papillae. Pallial muscles strong.

Gills (Fig. E, J): shape elongated, triangular, occupying $\sim 1/2$ of pallial cavity. Free anterior-dorsal gill end slightly arched, located between ventral margins of labial palps. Posterior region, free of visceral mass, of $\sim 1/2$ of total length of gill. Alimentary chamber thick, located in free margin of demibranchs, in entire length.

Visceral mass (Fig. D): occupying $\sim 1/2$ of total animal's size; located from ventral region of ligament to anterior surface of adductor muscle. Digestive diverticula in anterior and dorsal region of palps, occupying $\sim 1/4$ of visceral mass. Follicular gonads beige, occupying $\sim 1/2$ of visceral mass, covering digestive diverticula

externally. Renopericardial structures occupying $\sim 1/4$ of visceral mass, in posterior anterior-ventral region of adductor muscle.

Circulatory and excretory systems (Figs. F, G, J, L): Pair of accessory hearts, in posterior region of lobes, in exhalant chamber, (Figs. G, J), one branch, of short and large caliber, coming to height of adductor muscle. Heart located anteriorly to adductor muscle. Ventricle pyriform, walls with thin bundles of muscle fibers crossing ventricular lumen, two chambers incomplete. Auricles unpigmented. Walls of auricles thinner and lighter than those of ventricle, trabecular (Figs. G, L). Pair of kidneys triangular, tubular; mottled by light brown marks by translucence of visceral mass. Each kidney with direct communication with pericardium and gonad on medial side and laterally communicating by short chamber. Renal opening located on other side of cerebro-visceral connective.

Digestive system (Figs. H, I, J, K): ***Palps*** (Fig. H): collated in anterior-ventral region, occupying $\sim 1/6$ of animal's length. Hemipalps flattened, elongated, $\sim 50\%$ of total size of visceral mass, united throughout its length to visceral mass. Internal faces plicate, folds extending transversely to edge. External surface smooth, which irregular grooves and ridges. External hemipalps not fused. ***Esophagus*** (Fig. I, K): flattened dorso-ventrally, length $\sim 2/3$ of palps, slightly longer than large. ***Stomach*** (Fig. I, K): occupying $\sim 1/2$ of palps size. Selection area 1 (sa1) large and short; typhlosole starting in anterior portion of sa1. ***Intestine*** (Figs. K) and ***rectum*** (Fig. J) distinguished from distal end of style sac by 180° loop; afterwards passing through pericardium, following ovoid portion of visceral mass in 'U'-shaped loop, passing posteriorly to stomach, close to connection with esophagus, extending to right face of ovoid portion of visceral mass. Intestine changing course to ventral and posterior direction. Rectum not crossing

pericardium, running in contact with posterior face of adductor muscle; internal surface with well-developed typhlosole, with broad base and grooved free end up to anal opening. **Anus** (Fig. J): Sessile, surrounded by flat edge-shaped fold, bell-shaped; occupying 1/3 of height of adductor muscle.

Reproductive system (Figs. D, J): gonad formed by two lobes of follicular aspect, cream color, occupying ~1/4 of animal size. Genital opening located together with renal opening, on other side of cerebro-visceral connective.

Central nervous system (Fig. M): Cerebral ganglia located at base of labial palps, about 5% of esophagus transverse section. Cerebral commissure U-shaped, dorsally surrounding esophagus, 15 times longer than ganglia. Pair of visceral ganglia slightly ovoid, each with ~double size of cerebral ganglia, in depression formed by junction of rapid and slow components of adductor muscle. Circumpallial nerve travelling along mantle. Pedal ganglion absent.

Distribution and habitat: Indian and Pacific ocean, Yemen to China.

Examined material: THAILAND. MZUSP 54465, 4 specimens.

Plate 1- *Crassostrea bilineata*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista interna, valva esquerda com parte mole; Fig. C – Concha, vista interna, valva direita, detalhe para impressão muscular (im) pigmentada; Fig. D – Vista geral, lobo direito, detalhe para massa visceral (vm), pericárdio (pc) e músculo adutor (am); Fig. E – Brânquias (gi), detalhe para o canal alimentar (ac); Fig. F – Coração (he) em pericárdio (pc), ventrículo (ve) e aurículas (au); Fig. G – Manto (ma) e borda do manto (me), vista interna, detalhe para o coração acessório (ah) e músculos paliais (pm); Fig. H – Detalhe dos palpos (pa); Escalas A-G: 1 cm; Fig. I – Estômago (es) aberto pelo lobo direito, detalhe para o esôfago (Oe), área de seleção (sa1) e capuz dorsal (dh); escala: 1 mm.

Plate 2 – *Crassostrea bilineata*. Anatomia. Fig. J –Vista geral, lobo direito, detalhe para os palpos (pa), músculo de Quenstedt (qm), coração (he), reto (rt), ânus (na), músculo adutor (am), coração acessório (ah) e brânquias (gi); Fig. K –Estômago, vista lobo direito, detalhe para o esôfago (oe), área de seleção (sa1), capuz dorsal (dh), tiflossos (ty) e intestino (in); Fig. L – Coração (he) em pericárdio (pc), lobo direito, ventrículo (ve) e aurículas (au); Fig. M – Gânglio visceral, vista ventral. Escalas 1 cm.

Genus *Saccostrea* Dolfuss & Dautzenberg, 1920

Diagnosis. cup-shaped, marginal denticles and promial chamber in right side.

Distribution. restricted to Tropical and Subtropical (eastern Atlantic, Indo-West Pacific and eastern Pacific, while absent in the east Atlantic) in saline areas (open ocean), but occasionally occurring associated to mangroves. Most species living exposed, fixed on rocks or coral.

For complete description and comparison between species *S. cucullata*, *S. glomerata*, *S. echinata*, *S. mordax* and *S. palmula* see Amaral & Simone, submitted in annex II.

Genus *Striostrea* Vyalov, 1936

Diagnosis. Shell large size, to 200 mm or more high, usually elongated dorsoventrally, sometimes subcircular. Generally attached by nearly of left valve, especially in elongate shells. Right valve not plicate, brown, brittle lamellae, usually with closely spaced, very small radial riblets or striae continuous crossing them. Interior distinctly subnacreous, iridescent, occasionally white but more mottled and washed with dark brown, blue or purple. Chomata large, often elongate, widely spaced, usually extending far down both front and hind margins, but sometimes absent in large shells. One or both muscles scars often distinctively colored.

***Striostrea prismatica* (Gray, 1825)**

Plates 3 – 4: Figs. A – Q

Ostrea prismatica Gray, 1825: 139; Hanley, 1856: 302; Sowerby, 1871; Lamy, 1929: 146.

Ostrea iridescens Hanley, 1854: pl. 2; Carpenter, 1857a: 157, 1857b: 162, 226, 250, 312, 365; 1864: 621, 631; Olsson, 1961: 171; Galtsoff, 1964: 36; Keen, 1971: 84; Abbott, 1974: 456.

Ostrea panamensis Carpenter, 1863: 362, 1864: 552.

Ostrea sphenulata: Sowerby, 1871: 13 (*non* Lamarck, 1819).

Ostrea rufa Sowerby, 1871: 25 (*non* Lamarck, 1819).

Ostrea lucasiana Rochebrune, 1895: 241.

Ostrea turturina Rochebrune, 1895: 242.

Crassostrea iridescens: Rodriguez & García-Cubas, 1986: 268.

Striostrea prismatica: Hertlein & Strong, 1946a: 55; Olsson, 1961: 174; Keen, 1971: 84; Harry, 1985: 150-151; Poutiers, 1995: 161; Inaba *et.al.*, 2004: 32-33.

Type: Syntypes of *Ostrea rufa* in Museum of Genève n° 1089137 and in NMNH Paris, no number. (Fig. 2)

Figura 2 - Type of *O. rufa* (= *S. prismatica*)

Distinctive description

Shell. (Figs. A, B, C). Ovate to dorsoventrally elongate, heavy, thick, height to 190 mm. Left valve often broadly attached, but with raised margin, moderately to deep concave. Right valve flat to moderately convex. Resilifer long, narrow; chromata large, robust, few in number, usually 10 or more. Valves not plicate. Dense lamellae with broad undulations. External color brownish-purple. Inner white, iridescent, with olive-brown and gold patches. Left muscle scar purple, right scar lighter colored.

Main Muscle. Adductor muscle (Figs. D, H, M): Posterior region, crescent moon form, with anterior region convex, occupying about ½ of length of soft part. **Quenstedt muscle:** located in posterior region of palps base.

Mantle (Fig E, F, G): Mantle thick with abundant pallial muscles. Show a slight hood, not filled by palps. Mantle edge thick, well defined. Middle fold with medium and long papillae, digitiform, with 2-5 medium papillae intercalled with one long. Internal fold with medium papillae uniformly distributed. Accessory heart Y-shaped, fine gauge, with shorter portion surrounding adductor muscle, ~1/5 size of main branch.

Gills (Figs, I, M). Occupy 70% of length of animal. Alimentary chamber large, almost the same thickness of gill fold.

Visceral mass (Figs, D, M). Visceral mass occupying ~50% of length. Formed by gonads; yellowish, abundant digestive diverticula. Promial passage present only right

side, about $\frac{1}{4}$ of visceral mass size. Renopericardial structures occupying $\sim\frac{1}{6}$ of visceral mass, located in posterior anterior-ventral region of adductor muscle.

Circulatory system (Figs. L, O). Robust heart, auricles light color with some small bags beige; ventricle gray, also featuring bags on the outside wall, in greater number than in the auricle.

Digestive system. Palps (Fig. K, N). Large, elongated, flattened without handles on prior edges, occupying half size of visceral mass. External hemipalps not fused. **Esophagus** (Fig. P). flattened dorsoventrally, slightly long and wide, with half length of palps. **Stomach** (Fig. P). Selection area (sa1) thin and elongated, occupying $\frac{1}{3}$ of length of palps; tiflossoles beginning in posterior region in stomach. **Intestine and rectum** (Figs. J, P). Passing of posterior of stomach ending in rectum, occupying about $\frac{1}{3}$ of dorsal portion of adductor muscle. **Anus** (Figs. J, P). elongated, thin in anterior region and more robust in terminal portion, not pedunculate.

Reproductive system (Figs. D, M). Gonads massive independent of period of gonadal maturation. Acinus generally beige or yellow, involving entire visceral mass, including sometimes pyloric region. Genital opening located together with renal opening, on other side of cerebro-visceral connective.

Nervous system (Fig. Q). Visceral ganglia with two anterior projections, two lateral projections and three posterior, occupying about $\frac{1}{12}$ of size of adductor muscle.

Distribution and habitat: Baja California, Mexico to Peru. In intertidal zone, in exposed rocky areas.

Examined material: MEXICO. FLMNH 271410 – Mexico, 2 specimens. FLMNH 337654 1 specimenn. PANAMA. MZUSP 110478, 2 specimens;

Plate 3 – *Striostrea prismatica*. Fig. A – Concha, vista externa, valve direita; Fig. B – Concha, vista interna, valva esquerda, detalhe para coloração interna e impressão muscular (im) pigmentada; Fig. C – Concha, detalhe da chomata (ch) na porção anterior da valva esquerda; Fig. D – Vista geral, detalhes para a massa visceral (vm) e músculo adutor (am); Fig. E – Borda do manto (me), detalhe para a prega interna (if) e prega média (mf) papiladas. Escalas: 1 cm.

Plate 4 – *Striostrea prismatica*. Anatomia. Fig. M – Vista geral, lobo direito, detalhes para palpos (pa), brânquias (gi), coração acessório (ah), músculo adutor (am), ânus (an), reto (rt), coração (he), massa visceral (vm); Fig. N – Detalhe dos palpos (pa), vista ventral; Fig. O – Detalhe do coração (he), ventrículo (ve) e aurículas (au); Fig. P – Estômago, vista do lobo direito, detalhe para o esôfago (oe), área de seleção (sa1), capuz dorsal (dh), escudo gástrico (gs) e tiflossos (ty). Escalas: 1 cm.

Genus *Lopha* Röding, 1798

Shell large (to 100 mm high), profile subcircular to oval-reniform, with about five very large, interlocking, radial plicae on both valves; ridges and troughs of these plications acutely angled, sides flattened. Some low, rounded or quadrate pustules normally present, very small, arranged in radial rows, covering surface of both valves or present only in limited areas. Area of cementation generally small; clasper spines usually present, often long (to several cm) and irregularly recurved. Right valve usually with external distinct indentation on each spine of left valve. Walls thin, with inner surface usually iridescent, bronzed, rarely white. Chomata prominent, often extending to and around ventral margin; in both valves or on right valve only.

***Lopha cristagalli* (Linnaeus, 1758)**

Plates 5 – 6: Figs A – S

Mytilus crista galli Linnaeus, 1758: 704; 1764: 537; 1767: 1155; Born, 1778: 108; 1780: 122; Dillwyn, 1817: 299.

Ostrea crista-galli: Chemnitz, 1786: 150; Schumacher, 1817: 109; Lamarck, 1819: 213; Deshayes, 1830: 299; Küster, 1845: 80; Chenu, 1847: fig. 2-2a; Hanley, 1856: 308; Sowerby, 1871: fig. 22 a-b; Dautzenberg, 1891: 84; Pilsbry, 1985: 146, 184; Hedley, 1899: 495; Hidalgo, 1905:42; Lamy, 1909: 341; Hedley, 1909: 345; Lamy, 1924: 317; Lamy, 1925: 256; 1930: 254; Hirase, 1930: 19; Dodge, 1952: 190, 191, 205.

Lopha cristagalli: Röding, 1798, 168; Dall, 1898: 22; Iredale, 1939: 401; Habe, 1951: 92; Allan, 1959: 275; Kira, 1959: 128; 1962: 144; Habe & Kosuge, 1966: 144; Habe & Okutami, 1975: 237; Habe, 1977: 111; Cernohorsky, 1978: 181; Torigoe, 1981:

314; Abbott & Dance, 1982: 318; Harry, 1985: 135-137; Rodríguez & García-Cubas, 1986: 262; Springsteen & Leobrera, 1986: 315, 316; Matsukuma, 1986: 299; Okutani & Soyama, 1987: 152; Oliver, 1992: 87, 90; Li & Qi, 1994: 164; Xu, 1997: 98; Lamprell & Heally, 1998: 130; Hayami, 2000: 927.

Ostrea cristagalli: Cox, 1882: 131; Ranson, 1960: 25.

Type: in NHNM Paris – no number.

Distinctive description

Shell (Figs. A - D). Large size (up to 110 mm in length), usually almost square, ranging from globular to somewhat irregular. Valves convex, equivalve, 6-9 occasionally 12 plications, sharp, deep radial folds that continue from hinge to the farthest point from it. Surface area covered by both valves small rounded denticles, almost all of equal size, arranged in radial parallel rows. No scales imbricate growth. With hyote spines recurved, some of which in the left valve (bottom), as horns, serving to adhere to substrate. Internally, purple, brown, bronzed rarely white in margins.

Main muscles. Adductor muscle (Figs. G, N). Crescent moon form in section, occupying 1/5 of height of soft part. **Quenstedt muscle** (Fig. N). Located in anterior region of palps.

Mantle (Figs. G, E). Lobes thin, with pallial muscles more evident in posterior region. Mantle edge relatively thin, color light brown. Middle fold with short papillae, distributed uniformly. Internal fold with long and medium papillae, one long to 3-4 medium. Accessory heart with only one branch, thin to adductor muscle region, but not rounded. Promial passage not present.

Gills (Figs. F, N). Demibranchs occupying a 1/3 of total size. Alimentary chamber thin, about 1/6 of gill fold.

Visceral mass (Figs. G, N). Visceral mass occupying ~50% of length. Formed by gonads, yellowish, abundant digestive diverticula.

Circulatory system (Figs. H, P). Ventricle medium size, 1/4 of size of pericardium, whitish. Auricles medium size (1/4 of size of pericardium), brown color, with many bundles.

Digestive system. Palps (Figs. I, O). Rounded and small, about 1/2 of adductor muscle. External palps fused in 1/2 of length, with superior edge with folds. **Esophagus** (Figs. L, Q). Large and long, same size of palps. **Stomach** (Figs. L, Q). Occupying 2/3 of globular region length; selection area large. **Intestine** (Fig. Q). Passing behind anterior region of stomach. **Anus** (Figs. J, K, P). Pedunculated, with large expansion in shell form.

Nervous system (Figs. M, S). Visceral ganglia with two anterior, two posterior and two lateral projections, occupying about 1/10 of size of adductor muscle.

Distribution and habitat. Red Sea, Indian ocean to Japan.

Examined material: MADAGASCAR. FLMNH 423437, 2 specimens, FLMNH 42682, 3 specimens. PAPUA NEW GUINE. FLMNH 322404, 1 specimen, FLMNH 322470, 2 specimens. SAUDI ARABIA. USMN 852312, 3 specimens.

Plate 5 – *Lophocystis cristagalli*. Fig. A – Concha, vista ventral, detalhe para o zig zag da margem das valvas; Fig. B – Concha, valva esquerda, vista interna, detalhe para coloração dourada interna; Fig. C – Concha, valva direita, vista interna, detalhe para a coloração interna; Fig. D – Detalhe dos hyote spines (hs); Fig. E – Manto e borda do manto, detalhe para o coração acessório (ah) e músculos paliais; Fig. F – Brânquia, detalhe do canal alimentar (ac); Fig. G – Vista geral, detalhe para os músculos paliais (pm), massa visceral (vm) e borda do manto (me); Fig. H – Coração em pericárdio (pe), ventrículo (ve) e aurículas (au); Fig. I – Detalhe dos palpos (pa); Fig. J – Detalhe da porção terminal do ânus (an) papilado; Fig. K – Detalhe do reto (rt) e ânus (an); Fig. L – Estômago, detalhe para o esôfago (oe), tiflossoles (ty), intestino (in), capuz dorsal (dh), área de seleção (sa1); Fig.M – Detalhe do gânglio visceral. Escalas: 1 cm.

Plate 6 – *Lophocristagalli*. Anatomia. Fig. N – Vista geral, detalhe para os palpos (pa), músculos paliais (pm), brânquias (gi), coração acessório (ah), ânus (an), músculo adutor (am), reto (rt), coração (he), massa visceral (vm), e músculo de Quenstedt (qm); Fig. O – Detalhe dos palpos (pa); Fig. P – Detalhe do coração, ventrículo (ve) e aurículas m(au); Fig. Q – Estômago, vista lobo direito, detalhe para o esôfago (oe), área se seleção (sa1), capuz dorsal (dh), escudo gástrico (gs), tiflossos (ty) e intestino (in). Fig. R – Detalhe do ânus (an) papilado; Fig. S – Detalhe do gânglio cerebral. Escalas 1 cm.

Genus *Alectryonella* Sacco, 1897

Diagnosis. Large size, with to 150 mm long, subcircular, slightly inflate, usually cemented by half of left valve. Clasper spines rarely formed, usually adnate throughout their length. Numerous (up to 20) regular, rounded radial ribs on both valves. These plications roughened by closely spaced growth rests, no lamellae along them. Low, rounded pustules, closely spaced and irregularly arranged. Beaks moderately large, ligament shorter than long. Exterior surface usually uniformly white colored; dark bluish purple or brown sometimes present. Interior often dark brown, metallic. No chalk deposits. Chomata ostreine near hinge, typically lophine on rest of margin, becoming often prominent on both valves, or right one only. Small patches by narrow, thin, tips of brown deposited at any place on inner shell surface (rare on muscle scars); these bands closely spaced, mostly parallel to each other and chiefly normal to shell margin, especially near it, forming patten similar to human fingerprint.

***Alectryonella plicatula* (Gmelin, 1791)**

Plates 7 – 8: Figs. A – K

Ostrea orbicularis Linnaeus, 1758: 699; Chemnitz, 1785: 44; Schoröter, 1786: 362; Gmelin, 1791: 3334; Dillwyn, 1817: 278; Anton, 1839: 20; Hanley, 1855: 115; 1856: 310 (*nomen dubium*).

Ostrea plicata Chemnitz, 1785: 34; Schröter, 1786: 370; Dillwyn, 1817: 275; Hanley, 1856: 307; Weinkauff, 1867: 276; Küster, 1868: 79; Dunker, 1882: 249; Pilsbry, 1895: 146; Hidalgo, 1905: 387 (*non* Linnaeus, 1758)

Ostrea plicatula Gmelin, 1791: 3336; Lamarck, 1819: 211; Deshayes, 1831: 300; 1836: 232; Lamy, 1924: 237; 1925: 317; 1929: 82; 1936: 429; 1938: 288; Fischer & Fischer-Piette, 1938: 407.

Ostrea cumingiana Dunker, 1846: 48; Hidalgo, 1905: 386; Wada, 1953: 67; Ranson, 1960: 37; 1967: 247.

Ostrea solida Sowerby, 1871: sp. 28.

Ostrea lactea Sowerby. 1871: sp. 48.

Ostrea (Alectryonella) plicatula: Sacco, 1897: 99.

Ostrea (Lopha) cumingiana: Kuroda, 1930: 51; Hirase, 1932: 213; Hiro, 1936: 39; Wada, 1942: 71; Takatsuki, 1949: 7.

Dendostrea cumingiana: Habe, 1951: 93.

Ostrea (Dendostrea) cumingiana: Kuroda, 1960: sp 1717.

Alectryonella plicatula: Stenzel, 1971: N1160; Torigoe, 1981: 318, 340; Harry, 1985: 137; Xu & Hwang, 1993: 327; Hayami, 2000: 927.

Type material: *O. solida* Sowerby, 1871 - syntypes in BMNH 1989074 and 1989075.

Distinctive description

Shell (Figs. A – F): shape oval, size large, about 150 mm height, inflated. Regular, rounded radial ribs on both valves, up to 20, with rounded pustules, closely spaced and irregularly arranged (larger than *Lopha*). Beaks moderately large; ligament short. Exterior usually uniformly white colored, sometimes dark bluish purple or brown. Interior often dark brown and yellow metallic. No chalk deposits formed. Chomata ostreine near hinge, and lophine on rest. Small patches internally present, forming pattern similar to human fingerprint. Adductor muscle impression not pigmented

occupying ~1/10 of valve surface. Scar of Quenstedt muscle oval-shaped, occupying 1/22 of size of adductor muscle.

Muscle system. *Adductor muscle* (Figs. E, G, H): middle position of dorsal side. Transverse section triangular, occupying ~1/3 of shell length. **Quenstedt muscle** (Fig. H): thin and narrow, located in middle portion of length of palps.

Mantle (Figs. G, H): mantle lobes connected in hinge region by length equivalent to 1/4 of body length; sub-umbonal region present. Promyal chamber absent. Mantle edge thick, color cream and gray. Middle fold with short and medium papillae fingerlike, presenting up to four short papillae between one medium papilla. Internal fold with only medium papillae elongated. Pallial muscles strong and definite.

Gills (Figs. H): shape elongated, large, triangular, occupying up to 1/2 of pallial cavity. Free anterior-dorsal gill end slightly arched, located between ventral margins of labial palps. Posterior region, free of visceral mass, with 1/3 of total length of gill. Alimentary chamber thick, about 1/3 of demibranch's fold, located in free margin of demibranchs, in entire length.

Visceral mass (Fig. H): occupying ~1/3 of total animal's size; located from ventral region of ligament to anterior surface of adductor muscle. Digestive diverticula located in anterior and dorsal region of palps, occupying ~1/4 of visceral mass. Follicular gonads beige, occupying ~1/2 of visceral mass, covering digestive diverticula externally. Renopericardial structures occupying ~1/4 of visceral mass, located in posterior anterior-ventral region of adductor muscle.

Circulatory and excretory systems (Fig. H): Pair of accessory hearts, located in posterior region of lobes, in exhalant chamber, with one branch, long and thin caliber, coming to height of adductor muscle. Heart located anteriorly to adductor muscle. Ventricle pyriform, cream color. Auricles dark brown. Renal opening located on other side of cerebro-visceral connective.

Digestive system: Palps (Fig. I): located in anterior-ventral region, occupying ~1/5 of visceral mass length. Hemipalps flattened, elongated. Internal faces plicate, folds not extending transversely to edge, with free margin. External surface smooth, which irregular grooves and ridges. External hemipalps fused in 1/2 of total size. **Esophagus** (Fig. K): flattened dorso-ventrally, same length of palps, slightly longer than large. **Stomach** (Fig. K): occupying ~1/2 of visceral mass. Selection area 1 (sa1) thin and long; typhlosole starting in posterior portion of sa1. **Intestine** (Fig. K) and **rectum** (Fig. H). Distinguished from distal end of style sac by 180° loop; afterwards passing through pericardium, following ovoid portion of visceral mass in 'U'-shaped loop, passing posteriorly to stomach, close to connection with esophagus, extending to right face of ovoid portion of visceral mass. changing to ventral and posterior direction. Rectum crossing pericardium, running in contact with posterior face of adductor muscle; internal surface with well-developed typhlosole, with broad base and grooved free end up to anal opening. **Anus** (Fig. H): Sessile, surrounded by flat edge-shaped fold, bell-shaped; occupying total of height of dorsal region of adductor muscle.

Reproductive system (Fig. H): gonad formed by two lobes of follicular aspect, cream color, occupying ~1/4 of animal size. Genital opening located together with renal opening, light yellow color, on other side of cerebro-visceral connective.

Central nervous system (Fig. J): Cerebral ganglia located at base of labial palps, about 3% of esophagus cross section. Cerebral commissures U-shaped, dorsally surrounding esophagus 18 times longer than ganglia. Pair of visceral ganglia slightly ovoid, occupying about 1/12 of size of adductor muscle, with, two posterior nerves, two anterior and one lateral nerves; located in depression formed by junction of translucent and opaque parts of adductor muscle. Circumpallial nerve travelling along mantle. Pedal ganglion absent.

Distribution and habitat: Indo-west Pacific, Madagascar to Philippines

Examined material: INDONESIA. **Sulawesi Island.** UF 310071, 2 specimens; UF 310073, 3 specimens.

Plate 7 – *Alectryonella plicatula*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista interna, detalhe para chomata (ch) e “finger print” (fp); Fig. C – Concha, vista externa, valva esquerda, detalhe par ornamentação (or); Fig. D – Vista interna, valva esquerda, detalhes para coloração, depósito de cálcio (cd), “finger print” (fp) e cavidade umbonal (uc); Fig. E – Concha com parte mole, detalhe para o músculo adutor (am); Fig. F – Concha, detalhe das plicas marginais (pl) das valvas; Fig. G – Vista geral, detalhe para a borda do manto (me), músculos paliais (pm) e músculo adutor (am). Escalas 1 cm.

Plate 8 – *Alectryonella plicatula*. Anatomia. Fig. H – Vista geral, detalhes para os palpos (pa), brânquias (gi), borda do manto (me), coração acessório (ah), músculo adutor (am), ânus (an), reto (rt), coração (he), massa visceral (vm); Fig. I – Detalhe dos palpos (pa) e músculo de Quenstedt (qm); Fig. J – Detalhe do gânglio visceral; Fig. K – Estômago, detalhes para esôfago (oe), área se seleção (sa1), capuz dorsal (dh), escudo gástrico (gs), tiflosoles (ty) e intestino (in). Escalas 1 cm.

Genus *Dendostrea* Swainson, 1835

Diagnosis. Small to medium size (to 85 mm high), irregularly subcircular, to elongate dorsoventrally with thin shells cemented by variable part of the left valve, often with clasper spines which are usually short. Both valves may be convex, left more so than right, and generally plicate, although the right valve may have plications limited to a small region; the plications are small, rounded, closely spaced, with rounded grooves between. Shell margins are generally zigzag along some part, even when plications of the right valve are poorly developed. External surfaces without pustules, usually smooth often with a waxy texture, rarely with short lamellae at growth rests, which may form a few hyaline spines on both valves. Exterior often white, but usually blue or purple, sometimes rayed with darker stripes. Interior is often white, varying to light or dark green; chromata are usually only ostreine, limited to the margin near hinge, but occasionally supplemented by lophine chromata in right valve also, extending to the ventral margin.

***Dendostrea folium* (Linnaeus, 1758)**

Plates 9 – 10: Figs. A – M

Ostrea folium Linnaeus, 1758: 699; 1764: 534; 1767: 1148; Born, 1778: 97, 112; Chemnitz, 1785: 22; Schröter, 1786: 361; Gmelin, 1791: 3334; Dillwyn, 1817: 274; Lamarck, 1819: 211; Deshayes, 1836: 232; Hanley, 1856: 307; Küster, 1868: 76; Sowerby, 1871: sp. 40; Dunker, 1882: 249; Iwakawa, 1915: 13; Lamy, 1924: 236, 1930: 244; Hirase & Taki: 1951: pl. 7; Thompson, 1954: 146; Satyamurti, 1956: 69; Ranson, 1960: 23, 1967: 253.

Lopha folium: Röding, 1798: 169; Abbott, 1974: 457; Cernohorsky, 1978: 182.

Dendostrea folium: Swainson, 1835: 39; Habe & Okutani, 1975: 282; Habe, 1977: 110, 1981: 84; Torigoe, 1981: 315; Xu, 1997: 98; Lamprell & Healy, 1998: 132.

Dendostraea folium: Sowerby, 1839: 137; Iredale, 1939: 402; Habe, 1951: 92; Allan, 1959: 275; Habe, 1961: 120, 1964: 175.[sic]

More information about a systematic list, see Inaba *et.al.* 2004.

Type: In NMNH, no number.

Distinctive description

Shell (Figs. A-D). Ovate-elongate, small to medium size, to 50 mm; left valve flat to slightly convex, broadly attached; right valve convex, fitting on top of left valve; sculpture of strong radial plications that interlock; right valve with pustules, radial ribs near breaks in some, resiliifer long, narrow; weak chromata present in both sides of ligament, not present in all specimens; exterior color rose to purplish-red, sometimes erodes to cream; interior color white, light brown to rose on margins.

Main muscles. Adductor muscle (Figs. E, K). Oval shaped, occupying 1/3 of height of soft part. **Quenstedt muscle** (Fig. K). Located in middle of base of palps. Large and thick.

Mantle (Figs. F, G). Lobes thin, with pallial muscles broadly distributed more strong in posterior region. Mantle edge relatively thick, color cream. Middle fold with short and medium papillae, digitiform, with 2-6 short papillae for 1-3 medium papillae. Internal fold with only short papillae, uniformly distributed. Accessory heart with only one branch, thin, to the middle of mantle. Promial passage not present.

Gills (Figs. E, K). Demibranchs occupying a 1/2 of total size. Alimentary chamber thin, about of 1/10 of fold size.

Visceral mass (Figs. E, K). Visceral mass occupies a large part of the body of the animal, about 1/3 of length. Formed by the gonads, cream, abundant digestive diverticula.

Circulatory system (Fig. K). Ventricle small, whitish. Auricles small, brown color.

Digestive system. Palps (Fig. H). Rounded and very small, about 1/4 of visceral mass size. External palps fused for all length, with superior edge with folds. **Esophagus** (Fig. L). Short and large, occupying 1/3 of visceral mass. **Stomach** (Fig. L). Globular region occupying 2/3 of visceral mass size; selection area large and long. **Intestine** (Fig. L). Pass for anterior region of pericardium. **Anus** (Figs. J, K). pedunculated, with a large expansion in shell form, rounded an adductor muscle to 2/3 of dorsal side.

Nervous system (Figs. I, M). Visceral ganglia with two anterior, two posterior projections.

Distribution and habitat. Mexico, Panama, Costa Rica, Colombia, Ecuador. Attached to calcareous substrate, gorgonians, gastropods and corals, in 8-37 m.

Examined material: NEW ZEALAND. **Cook Is.** FLMNH 282832, 3 specimens; COLOMBIA. USMN 1004295, 2 specimens.

Plate 9 - *Dendostrea folium*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista interna, valva esquerda; Fig. C – Concha, vista lateral, detalhe para as plicas na borda das valvas; Fig. D – Concha, porção anterior, detalhe para chomata (ch) e impressão muscular (im); Fig. E – Vista geral, detalhe para a massa visceral (vm), músculo adutor (am) e brânquias (gi); Fig. F – Manto, detalhe para a borda do manto (me), músculos paliais (pm) e coração acessório (ah); Fig. G – Detalhe da borda do manto, prega interna (if) e prega média (mf) papiladas, e prega externa (ef) lisa; Fig. H – Detalhe dos palpos (pa) e brânquias (gi); Fig. I – Detalhe do manto; Fig. J – Detalhe do ânus (an) e reto (rt). Escalas 1 cm.

Plate 10 - *Dendostrea folium*. Anatomia. Fig. K – Vista geral, detalhes para os palpos (pa), brânquias (gi), borda do manto (me), coração acessório (ah), ânus (an), reto (rt), músculo adutor (am), coração (he), intestino (in), músculo de Quenstedt (qm); Fig. L – Estômago, detalhes para o esôfago (oe), área de seleção (sa1), capuz dorsal (dh), tiflossos (ty) e intestino (in); Fig. M – Detalhe do gânglio visceral. Escalas 1 cm.

***Dendostrea frons* (Linnaeus, 1758)**

Plates 11 – 12: Figs. A – M

Mytilus frons Linnaeus, 1758: 704; Born, 1778: 108; 1780:123; Gmelin, 1791:3350;
Dillwyn, 1817: 301.

Ostrea frons: Chemnitz, 1785: 3, 61; Hanley, 1856: 307; Küster, 1868: 82; Sowerby,
1871:sp.41; Dall, 1825: 23; Lamy, 1930: 248; Galtsoff, 1964:12; Ranson, 1967:257;
Warmke & Abbott, 1974: 173.

Lopha frons: Röding, 1798: 169; Abbott, 1974: 457; Rios, 1975:204; Abbott & Dance,
1982:318; Rodrigues & García-Cubas, 1986:263. *Ostrea rubella* Lamarck, 1819: 211:
Deshayes, 1836: 231; Lamy, 1924:236. *Ostrea folium*: d'Orbigny, 1853:365 (*non*
Linnaeus, 1758) *Ostrea cristata*: Dall, 1925: 23 (*non* Born, 1780) *Ostrea (Ostrea) frons*:
McLean, 1971:7 *Lopha folium*: Stenzel, 1971: N1023, N1024, N1157 (*non* Linnaeus,
1758) *Dendostrea frons*: Harry, 1985: 138.

Type: In MNHN, no number. Fig 3.

Figura 3 - Type of *D. frons*

Distinctive description.

Shell. (Figs. A-C). Elongate shell, to 60 mm high; both valves convex; sculpture of strong radial plications that interlock; right valve with pustules and radial ribs near

breaks in some; weak chromata present in both sides of ligament; exterior color brown-reddish or brown-greenish; interior color purple pearly, white or yellowish, with reddish brown or purple inner edge. Fixed normally in gorgonians.

Main muscles. Adductor muscle. (Figs. D, J). Oval or oval-elongated, occupying about 1/3 of height of soft part. **Quenstedt muscle.** (Figs. E, J). Located in anterior region of palps.

Mantle. (Figs. G, J). Lobes thin, with pallial muscles more evident in posterior region. Mantle edge thick, color light brown yellowish. Middle fold with short and medium papillae, 2 short for 1 medium. Internal fold with short papillae uniformly distributed. Accessory heart with only one branch, large, not rounded an adductor muscle.

Gills. (Fig. F). Demibranchs occupying a 1/2 of total size. Alimentary chamber thin, about 1/4 of fold size.

Circulatory system. (Fig. I). Ventricle small size, whitish. Auricles medium size, light brown color, with many bundles.

Digestive system. Palps. (Fig. E). Rounded, small size, 1/3 of adductor muscle size. External palps fused in 2/3 of length, with superior edge with folds. **Esophagus.** (Fig. K). Large and long, about same length of palps. **Stomach.** (Fig. K). Globular region occupying 2/3 of visceral mass. Selection area elongated. **Intestine.** (Fig. K). Pass behind a pericardium. **Rectum.** Rounded about 1/2 of concave region of

adductor muscle. **Anus.** (Figs. H, L). Pedunculated, with a large expansion in shell form.

Nervous system. (Fig. M). Visceral ganglia with two anterior, two posterior projections.

Distribution and habitat. Gulf of Mexico, Florida, Panamá to Venezuela. Associated with gorgonians.

Examined material: GULF OF MEXICO. USMN 833923, 5 specimens; PANAMA. FLMNH 289623, 6 specimens.

Plate 11 - *Dendostrea frons*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista interna, valva esquerda; Fig. C – Concha, vista interna, valva direita, detalhe para chomata (ch); Fig. D – Vista geral, detalhe para o pericárdio (pe) e músculo adutor (am); Fig. E – Palpos (pa) e músculo de Quenstedt (qm); Fig. F – Detalhe das brânquias (gi); Fig. G – Detalhe da borda do manto (me); Fig. H – Detalhe do ânus (an); Fig. I – Coração, ventrículo (ve) e aurículas (au). Escalas 1 cm.

Plate 12 – *Dendostrea frons*. Anatomia. Fig. J – Vista geral, detalhes para palpos (pa), borda do manto (me), brânquias (gi), coração acessório (ah), músculo adutor (am), ânus (an), reto (rt), massa visceral (vm) e músculo de Quenstedt (qm); Fig. K – Estômago, vista lobo direito, detalhe para esôfago (oe), área de seleção (sa1), escudo gástrico (gs), capuz dorsal (dh), tiflossoles (ty) e intestino (in); Fig. L – Detalhe do ânus papilado; Fig. M – Detalhe do gânglio visceral. Escalas 1 cm.

Dendostrea sp.1 (new species)

Plates 13 – 14: Figs A – L

Type: MZUSP 103122 - Holotype; FLMNH 286695 – Florida - Paratype

Distinctive description.

Shell (Figs. A, B). Ovate shell, to 80 mm high; right valve convex and left concave; edge plicate; chomata present in both sides of ligament in all edge shell; exterior color brown-reddish or brown-greenish; interior white or yellowish, with reddish brown inner edge. Fixed in hard substrate

Main muscles. Adductor muscle (Figs. C, J). Oval or oval-elongated, occupying about 1/4 of height of soft part. **Quenstedt muscle** (Figs. G, J). Located in posterior region of palps.

Mantle (Figs. D, E). Lobes thin, with pallial muscles more evident in posterior region. Mantle edge thick, color yellowish with spots brown. Middle fold with short and medium papillae, 4-10 short for 1 medium. Internal fold with short papillae uniformly distributed. Accessory heart with only one branch not rounded an adductor muscle.

Gills (Fig. E). Demibranchs occupying a 1/2 of total size. Alimentary chamber thin, about 1/3 of fold size.

Circulatory system (Figs. E, F, J). Ventricle small size, whitish. Auricles medium size, cream color, with many bundles.

Digestive system. Palps (Figs. G, J). Rounded, medium size, $\frac{1}{2}$ of adductor muscle size. External palps fused in $\frac{2}{3}$ of length, with superior edge with folds. ***Esophagus*** (Fig. L). Small and short, about same length of palps. ***Stomach*** (Fig. L). Globular region occupying $\frac{1}{3}$ of visceral mass. Selection area elongated, $\frac{1}{4}$ of length of globular region. ***Intestine*** (Fig. L). Pass behind a pericardium, like a other ostreids. ***Rectum*** (Fig. J). Rounded about totally region concave of adductor muscle. ***Anus*** (Figs. I, J). pedunculated, with a large expansion in shell form.

Nervous system (Figs. H, K). Visceral ganglia with one anterior, one posterior projections and one lateral.

Distribution and habitat. Florida, Panamá to Brazil. Only associated a hard substrate.

Examined material: GULF OF MEXICO. USMN 833923, 1 specimen; PANAMA. FLMNH 289623, 1 specimen. FLORIDA. FLMNH 286695, 2 specimens; BRASIL. **São Sebastião.** Arquipélago dos Alcatrazes, Saco do Funil. MZUSP 103122 – 2 specimens.

Plate 13 – *Dendostrea* sp.1 – Fig. A – Concha, vista interna, detalhe para chomata (ch); Fig. B – Concha, vista interna, detalhe das plicas na borda da concha (pl); Fig. C – Vista geral, detalhes para os palpos (pa), borda do manto (me), músculos paliais (pm), músculo adutor (am), pericárdio (pe) e massa visceral (vm); Fig. D – Detalhe da borda do manto (me); Fig. E – Detalhe do coração, ventrículo (ve) e aurículas (au); Fig. F – Detalhe dos palpos (pa) e músculo de Quenstedt (qm); Fig. G – Detalhe do gânglio visceral; Fig. H – Detalhe do ânus papilado (an). Escalas 1 cm.

Plate 14 – *Dendostrea* sp.1 – Anatomia. Fig. J – Vista geral, detalhes para os palpos (pa), brânquias (gi), músculos paliais (pm), borda do manto (me), coração acessório (ah), ânus (an), reto (rt), músculo adutor (am), pericárdio (pe), massa visceral (vm) e músculo de Quenstedt (qm). Escalas 1 cm.

Dendostrea sp.2 (new species)

Plates 15 – 16: Figs. A - R

Type: MZUSP 108585 – Holotype - Grenada, Grand Anse Bay

Distinctive description.

Shell (Figs. A - E). Ovate shell, to 50 mm high; right valve convex and left concave; edge plicate; chomata present in both sides of ligament in 1/3 of edge shell; exterior color brown-cream; inner white with spots greenish. Fixed in hard substrate or coral reef.

Main muscles. Adductor muscle (Fig. J, M). Oval-elongated, occupying about 1/3 of height of soft part. **Quenstedt muscle** (Figs. G, J, M). Located in medium region of palps.

Mantle (Fig. H). Lobes thin, with pallial muscles spaced. Mantle edge thin, color yellowish with spots brown. Middle fold with short and medium papillae, 4-6 short for 4 medium. Internal fold with short papillae uniformly distributed. Accessory heart thin, with only one branch not rounded an adductor muscle.

Gills (Fig. G). Demibranchs occupying a 1/2 of total size. Alimentary chamber thin, about 1/3 of fold size.

Circulatory system (Fig. I). Ventricle small size, cream color. Auricles large size, whitish color, with many bundles.

Digestive system. Palps (Figs. G, K). Rounded, small size, 1/6 of adductor muscle size. External palps fused in 1/2 of length, with superior edge without folds. ***Esophagus***. Small and short, about same length of palps. ***Stomach***. Globular region occupying 1/2 of visceral mass. Selection area elongated, 1/5 of length of globular region. ***Intestine***. Pass behind a pericardium, like a other ostreids. ***Rectum***. Rounded about totally region concave of adductor muscle. ***Anus*** (Fig. L). pedunculated, with a large expansion.

Nervous system. Visceral ganglia with two anterior, two posterior projections and one lateral.

Distribution and habitat. Caribbean sea.

Examined material: GRENADA. **Grand Anse Bay**. MZUSP 108585, 1 specimen.

Plate 15 – *Dendostrea* sp.2 Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista externa, valva esquerda; Fig. C – Concha, vista interna, valva direita, detalhe para impressão do músculo adutor e coloração esverdeada interna; Fig. D – Concha, vista interna, valva esquerda; Fig. E – Porção anterior da valva direita, vista interna, detalhe para chomata (ch); Fig. F – Porção posterior da valva direita, vista interna, detalhe para chomata (ch); Fig. G – Detalhe dos palpos (pa); Fig. H – Detalhe da borda do manto (me), músculos paliais (pm) e coração acessório (ah); Fig. I – Detalhe do coração em pericárdio, ventrículo (ve) e aurículas (au); Fig. J – Vista geral, detalhe para os palpos (pa), brânquias (gi), borda do manto (me), músculos paliais (pm), músculo adutor (am), pericárdio (pe) e músculo de Quenstedt (qm); Fig. K – Detalhe dos palpos; Fig. L – Detalhe do ânus papilado. Escalas 1 cm.

Plate 16 – *Dendostrea* sp.2 – Anatomia – Fig. M – Vista geral, detalhes para os palpos (pa), brânquias (gi), borda do manto (me), coração acessório (ah), músculo adutor (am), ânus (an), reto (rt), coração (he), massa visceral (vm) e músculo de Quenstedt (qm); Fig. N – Detalhe dos palpos (pa) e músculo de Quenstedt (qm); Fig. O – Detalhe do hemipalpos; Fig. P – Detalhe do coração em pericárdio, ventrículo (ve), aurículas (au) e reto (rt); Fig. Q – Estômago, detalhe para o esôfago (oe), área de seleção (sa1), capuz dorsal (dh), escudo gástrico (gs), tiflossoles (ty) e intestino (in); Fig. R – Detalhe do gânglio visceral. Escalas 1 cm.

Genus *Ostrea* Linnaeus, 1758

Diagnosis. Shells of moderate to large size, subcircular or subtriangular or rarely elongate dorsoventrally. The right valve nearly flat, very thin and brittle lamellae. The left valve is moderately inflated, with variable but usually distinct, small radial plicae, and a few growth rests which have only narrow, thick lamellae, or none at all. The interior is usually white occasionally washed with lavender or purple; similar color on the exterior of the shell. The chromata are very small, inconspicuous, ostreine type, limited to the margin bear the rings, and sometimes disappearing in older specimens. The species live in cool temperate, euryhaline waters, usually at several meters depth, but an occasional specimen may be found at low tide level.

Ostrea edulis Linnaeus, 1758

Plates 17 – 18: Figs. A – P

Ostrea edulis Linnaeus, 1758: 699; 1764: 534; Born, 1778: 99; 1780: 113; Dillwyn, 1817: 280; Turton, 1819: 133; Lamarck, 1819: 203; Deshayes, 1831: 288; 1836: 217; Hanley, 1856: 295; Adams, 1858: 568; Sowerby, 1859: pl. 8; Jeffreys, 1863: 38; 1869: 165. pl. 21; Weinkauff, 1867: 8; 1878: 63; 1884: 4; 1915: 8; Locard, 1886: 517; Lamy, 1924: 93; 1929: 16; Korringa, 1956: 6; Franc, 1960: 2086; Takatsuki, 1949: 15; Stenzel, 1971: 1139; Abbott & Dance, 1982: 318; Habe & Masuda, 1990: 99.

Ostrea rostrata Gmelin, 1791: 3336; Dillwyn, 1817: 279.

Ostrea cristata: Poli, 1795: 177. Pl. 28; Risso, 1826: 287; Philippi, 1836: 88; 1844: 63; Hanley, 1856: 297; Weinkauff, 1867: 273; Küster, 1868: 75 pl. 14; Hidalgo, 1870:

119; de Gregorio, 1883: 4; Monterosato, 1884: 4; Locard, 1886: 519. (*non* Born, 1778).

Ostrea denticulata: Poli, 1795: 178. (*non* Born, 1778)

Ostrea lamellosa Brocchi, 1814: 564; Risso, 1826: 288; Philippi, 1836: 88; 1844: 63; Hanley, 1856: 303; Weinkauff, 1867: 274; Küster, 1868: 70. Pl. 14; Sowerby, 1871: 54; Locard, 1886: 519.

Ostrea parasitica: Turton, 1819: 203; Deshayes, 1931: 288; 1836: 219; Haley, 1856: 296; Locard, 1886: 518; Lamy, 1924:93. (*non* Gmelin, 1791).

Type: not found, but the type of *O. cristata* (n° 1089124) in Museum of Natural History of Genève has a same characteristics of *O. edulis*.

Distinctive description

Shell. (Figs. A-C). Medium to large size (up to 100 mm), rounded, with external concentric layers, color brown-greenish. Have to 10 chomata in internal margin, not pigmented, show opalescent white. Muscle scar oval. Quenstedt muscle visible, rounded, located in median region of shell, in anterior region of shell, below a ligament.

Main Muscles. Adductor muscle. (Figs. D, L). Rounded or oval, occupying ¼ of height of soft part. Quenstedt muscle, thin, located in the middle portion of the base of the palps.

Mantle. (Figs. L, O). Thin, with pallial muscles slight, distributed uniformly, more concentrated in adductor muscle region. Hood not present. Mantle edge may be pigmented or not. Middle fold show short and medium papillae, 3-6 short for one

medium. Inner fold with only short papillae. Accessory heart with one branch, thin, rounded an adductor muscle.

Mantle cavity. (Fig. D). Promial chamber not present.

Gills. (Fig. G). Present a large alimentary chamber, 50% of size of folds.

Visceral mass. (Figs. B, L). Occupying same size of adductor muscle.

Circulatory System. (Figs. E, N). Ventricle large, with $\frac{2}{3}$ of size of auricles; translucent. Auricles more opaque, with more bundles than ventricle.

Digestive system. Palps. (Figs. H, N). Elongated, with anterior area free of folds, occupying $\frac{1}{4}$ of total size of adductor muscle. External hemipalps fused, about $\frac{1}{2}$ of total size. ***Esophagus.*** (Fig. J). Long and thin, about $\frac{1}{3}$ of adductor muscle size, with more striae in inferior region. ***Stomach.*** (Fig. J). Slightly flattened dorsoventrally, occupying $\frac{2}{3}$ of visceral mass, with more volume of digestive diverticula. More information of digestive system, see Yonge (1926), Graham (1949), Purchon (1957) e Reid (1965).

Nervous System. (Fig. K). Visceral ganglia with two anterior projections and tree posterior, occupying about $\frac{1}{8}$ of size of adductor muscle.

Distribution and habitat: Europe and Mediterranean.

Examined material: GREECE. USNM 804411, 3 specimens.

Plate 17 – *Ostrea edulis*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha com parte mole, vista interna, valva esquerda; Fig. C – Detalhe da porção anterior da valva direita, detalhe para chomata (ch) e impressão muscular; Fig. D – Detalhe da parte mole, porção posterior, detalhe para o músculo adutor (am); Fig. E – Detalhe do coração, ventrículo (ve) e aurícula (au); Fig. F – Detalhe da borda do manto (me) com músculos paliais (pm), detalhes para a prega interna (if), prega média (mf), papiladas, e preá externa sem papilas; Fig. G – Detalhe das brânquias; Fig. H – Detalhe dos palpos (pa); Fig. I – Detalhe do ânus papilado (an) e reto (rt); Fig. J – Estômago, detalhe para o esôfago (oe), área se seleção (sa1) e capuz dorsal (dh); Fig. K – Detalhe do gânglio visceral. Escalas 1 cm.

Plate 18 – *Ostrea edulis*. Anatomia. Fig. L – Vista geral, detalhes para os palpos (pa), brânquias (gi), músculos paliais (pm), coração acessório (ah), ânus (an), reto (rt), músculo adutor (am), coração (he) e massa visceral (vm); Fig. M – Detalhe dos palpos; Fig. N – Detalhe do coração, ventrículo (ve) e aurículas (au); Fig. O – Borda do manto (me) e coração acessório (ah); Fig. P – Detalhe do ânus. Escalas 1 cm.

***Ostrea puelchana* d'Orbigny, 1842**

Plates 19 – 18: Figs. A - L

Ostrea puelchana d'Orbigny, 1842: 672; Hanley, 1856:389; Sowerby, 1871: pl. 13;

Lamy, 1929: 99; McLean, 1941: 6; Rios, 1975: 204; 1994: 245, 2009: 500.

Ostrea (Eostrea) puelchana: Ihering, 1907: 42, 246, 426, 449; Harry, 1985: pl. 142.

Crassostrea brasiliiana: Ranson, 1960: 12; 1967: 158 (*non* Lamarck, 1819).

Ostrea (Ostrea) puelchana: Stenzel, 1971: N1139.

Type: Lectotype and Paralectotypes in BMNH n° 1854.12.4.822.

Distinctive description

Shell. (Figs. A, B). Elongated, medium size, about 70 mm of length. Slim concentric ornamentations in external surface. Color purple, white and yellowish. Show about 30 denticles in internal edge. Scar of adductor muscle presents a crescent moon form, not pigmented, and located in dorsal-posterior region, occupying about 1/5 of length of shell.

Main muscles. Adductor muscle. (Figs. C, J). Rounded or oval, occupying about 1/3 of length of soft part.

Mantle. (Figs. C, J). Lobes thin, with pallial muscles more abundant in posterior region rounded of adductor muscle. Mantle edge thick, pigmented with spots of cream or light brown. Middle fold and inner fold with long papillae uniformly distributed in both folds. Accessory heart with only one branch, thick, not rounded an adductor muscle.

Gill. (Fig. J). Occupying $\frac{1}{4}$ of total size. Alimentary chamber thick, about $\frac{1}{3}$ of folds size.

Circulatory system. (Fig. E). Ventricle and auricles thin, translucent. Connection between ventricle and auricles may presents a pigmentation cream opaque or yellowish.

Digestive system. Palps. (Figs. D, K). Triangular, elongated, about $\frac{1}{2}$ of adductor muscle size, superior margin with folds. Anterior area reduced free of folds. External hemipalps fused in $\frac{1}{3}$ of total size. **Esophagus.** (Figs. G, K). Elongated and narrow, $\frac{1}{2}$ of palps length. **Stomach.** (Figs. G, K). Two times larger than palps. Selection area short, ending in many grooves. **Intestine.** (Fig. K). Same for another species of *Ostrea*.

Nervous system. (Figs. H, L). Visceral ganglia with two anterior projections, two posterior and one lateral projection. Occupying about $\frac{1}{8}$ of size of adductor muscle.

Distribution and habitat: Rio de Janeiro, Brazil to Argentina.

Examined material: BRASIL. **Espírito Santo.** Vitória. MZUSP 87991, 3 specimens. **Rio de Janeiro,** Arraial do Cabo, MZUSP 48391, 2 specimens. Angra dos Reis, MZUSP 91752, 1 specimen. Ilha Grande, MZUSP 79323, 4 specimens; MZUSP79308, 3 specimens. Paraty, MZUSP 90963, 2 specimens. **São Paulo,** Ubatuba, Ilha Anchieta, MZUSP 46110, 3 specimens. MZUSP 86023, 5 specimens. São Sebastião, Arquipélago dos Alcatrazes, MZUSP 109285, 10 specimens; MZUSP 30874, 4 specimens; MZUSP 93288, 6 specimens. Santos, MZUSP 93161, 7 specimens. **Paraná.** Paranaguá. MZUSP 87740, 3 specimens; MZUSP 87741, 7 specimens. **Santa Catarina.** Itajaí, MZUSP 34617, 2 specimens. Florianópolis, MZUSP 36098, 1

specimen. **Rio Grande do Sul.** Imbé, MZUSP 111238, 4 specimens; Xangri-lá, MZUSP 112233. 5 specimens.

Plate 19 – *Ostrea puelchana*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista interna, valvas direita e esquerda; Fig. C – Vista geral, detalhe para a massa visceral (vm), músculos paliais (pm), músculo adutor (am) e borda do manto (me); Fig. D – Detalhe dos palpos (pa); Fig. E – Detalhe do coração, ventrículo (ve) e aurículas (au); Fig. F – Detalhe da borda do manto (me) e músculos paliais (pm); Fig. G – Estômago, detalhe para a área de seleção (sa1) e esôfago (oe); Fig. H – Detalhe do gânglio visceral; Fig. I – Detalhe do ânus (an) papilado e reto (rt). Escalas 1 cm.

Plate 20 – *Ostrea puelchana*. Anatomia. Fig. J – Vista geral, detalhe para os palpos (pa), músculo de Quenstedt (qm), brânquias (gi), borda do manto (me); coração acessório (ah), ânus (an), músculo adutor (am), reto (rt), coração (he), massa visceral (vm); Fig. K – Estômago, detalhe para os palpos (pa), esôfago (oe), área se seleção (sa1), escudo gástrico (gs), capuz dorsal (dh), tiflossoles (ty) e intestino (in); Fig. L – Detalhe do gânglio visceral. Escalas 1 cm.

***Ostrea equestris* Say, 1834**

Plates 21 – 22: Figs. A – P

Ostrea equestris Say, 1834: pl. 58; Tryon, 1873: 193; Dall, 1925: 23; Lamy, 1929: 82; Warmke & Abbott, 1961: 172; Galtsoff & Merrill, 1962: 235; Galtsoff, 1964: 12; Andrews, 1971: 170; Stenzel, 1971: N1038; Abbott, 1974: 455; Rios, 1975: 204; 1994: 245; 2009: 500.

Ostrea spreta d'Orbigny, 1842: 672; 1853: 365; Hanley, 1856: 310; Sowerby, 1871: sp.32; Lamy, 1929: 100

Ostrea (Ostreola) equestris: Dall, 1898: 672; Harry, 1985: 142

Ostrea cristata: Dall & Simpson, 1901 (*non* Born, 1778)

Ostrea (Eostrea) spreta: Ihering, 1907: 42, 450.

Type: Lectotype and Paralectotypes: *O. spreta* in BMNH n° 1854.12.4.821

Shell. (Figs. A- C). Small to medium size (to 50mm), normally oval, color purple, white and yellowish, arranged in spots not uniforms. Foliaceous layers in external edge. 10-15 denticles in internal edge. Right valve flat, slight concave, without plicae in edge. Left valve, slight convex with undulations in posterior portion of external valve. Internal predominantly white, slightly pearlescent. Adductor muscle scar rounded with anterior portion convex, normally with spots yellowish in region of scar, but not pigmented.

Main muscles. Adductor muscle. (Figs. D, F, N). Crescent moon form, ¼ of total size. **Quenstedt muscle.** (Figs. H, N). Located in anterior region of palps.

Mantle. (Figs. F, G, O). Lobes thick, with pallial muscles more evident in posterior region. Mantle edge is thin, color light brown. Middle fold with medium papillae, elongated or not, distributed uniformly. Inner fold with long and medium papillae interspersed. Accessory heart with only one branch, thick, to middle of lobe, not reaching adductor muscle.

Gills. (Fig. L). Occupying about $\frac{1}{2}$ of total size. Alimentary chamber large, same size of folds.

Circulatory system. (Figs. I, G, O). Ventricle small, color yellowish with abundant bundles. Auricles thin, translucent, with few bundles.

Digestive system. Palps. (Fig. H). Elongated and large, about $\frac{1}{6}$ of adductor muscle size, with superior and anterior edge with folds. External hemipalps fused in $\frac{1}{6}$ of total size. **Esophagus.** (Fig. K). Short and elongated, $\frac{1}{3}$ more elongated than palps. **Stomach.** (Fig. K). Occupying $\frac{1}{2}$ of globular region; selection area short, with several grooves in globular region. Gastric shield with iridescent color.

Nervous system. (Figs. M, P). Visceral ganglia with two anterior and tree posterior projections. occupying about $\frac{1}{6}$ of adductor muscle size.

Distribution and habitat. Florida to Argentina. In rock shores to 30 meters.

Examined material: **UNITED STATES. South Carolina.** USNM 850792, 1 specimen. **Florida.** Florida Museum 367484, 1 specimen; 367502, 2 specimen; 367498, 1 specimen; 298639, 3 specimens; 286693, 2 specimens. **MEXICO. Gulf of Mexico.** USNM 856477, 2 specimens. **BRASIL. Bahia.** Salvador, MZUSP 45084, 4 specimens. **Rio de Janeiro.** Ilha Grande, MZUSP 46099, 5 specimens. **São Paulo.** São Sebastião, Arquipélago dos Alcatrazes, MZUSP 109377, 3 specimens. **Santa Catarina.** Florianópolis, MZUSP 29049, 2 specimens.

Plate 21 – *Ostrea equestris*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista externa, valva esquerda; Fig. C – Concha, vista interna, valva direita, detalhe para a impressão do músculo adutor (im); Fig. D – Vista geral na valva esquerda, detalhe para o coração (he) e músculo adutor (am); Fig. F – Vista geral, detalhes para o coração (he), músculo adutor (am) e massa visceral (vm); Fig. G – Detalhe da borda do manto (me), músculos paliais (pm) e coração acessório (ah); Fig. H – Detalhe dos palpos (pa) e músculo de Quenstedt (qm); Fig. I – Detalhe do coração, ventrículo (ve) e aurículas (au); Fig. J- Corte longitudinal da borda do manto, detalhe para as pregas média (mf) e interna (if) papiladas, e prega externa lisa (ef); Fig. K – Estômago, detalhes para o esôfago (oe), área de seleção (sa1), capuz dorsal (dh) e tiflossoles (ty); Fig. L – Detalhe da brânquia e canal alimentar (ac); Fig. M – Detalhe do gânglio visceral. Escalas 1 cm.

Plate 22 – *Ostrea equestris*. Anatomia. Fig. N – Vista geral, detalhe para os palpos (pa), brânquias (gi), músculos paliais (pm), borda do manto (me), coração acessório (ah), ânus (an), músculo adutor (am), reto (rt), coração (he), massa visceral (vm) e músculo de Quenstedt (qm); Fig. O – Detalhe da borda do manto (me), músculos paliais (pm) e coração acessório (ah); Fig. P – Detalhe do gânglio visceral. Escalas 1 cm.

***Ostrea lurida* Carpenter, 1864**

Plates 23 – 24: Figs. A - O

Ostrea rufa Carpenter, 1857b: 226, 250; 1864: 552, 646 (*non* Lamarck, 1819).

Ostrea lurida Carpenter, 1864: 599, 606, 615, 645; Sowerby. 1871: sp.15; Dall, 1914: 2; Lamy, 1929: 39; Fitch, 1953: 38; Ranson, 1960: 32, Galtsoff, 1964: 11; Ranson, 1967: 233; Abbott, 1974: 455; Abbott & Dance, 1982: 318; García-Cubas, 1986: 277.

Ostrea conchaphila lurida: Stenzel, 1971: N1037

Ostreola conchaphila: Harry, 1985: 142

Type: Syntypes: *O. conchaphila* in BMNH n°. 1857.6.4.726

Shell. (Figs. A-D). Small size (up to 20mm), normally oval or subtriangular, color cream, white and yellowish, arranged in spots not uniforms. Foliate layers in external edge. About 10 denticles in internal edge. Right valve flat, slight concave, without plicae in edge. Left valve, slight convex. Internal predominantly white, slightly pearly. Adductor muscle scar reniform, not pigmented, occupying 1/3 of total size.

Main muscles. Adductor muscle. (Figs. E, K). Crescent moon elongated form, about 1/2 of total size. **Quenstedt muscle.** (Figs. F, K). Located in anterior region of palps.

Mantle. (Figs. E, K). Lobes thin, with pallial few muscles. Mantle edge is thin, not pigmented. Middle fold with medium papillae, digitiform, distributed uniformly.

Inner fold with short and medium papillae interspersed. Accessory heart with only one branch, thin, not reaching adductor muscle.

Gills. (Figs. E, K). Occupying 1/3 of total body length. Alimentary chamber thin, about the same size of folds.

Circulatory system. (Figs. J, M). Ventricle small, white color. Auricles large, thin, translucent, with few bundles.

Digestive system. Palps. (Figs. F, L). Robust and large, about 1/5 of visceral mass size; with superior margin with folds. External hemipalps fused in 1/2 of total size.

Esophagus. (Figs. I, N). Long and narrow, with 1/2 of palps size. **Stomach.** (Figs. I, N) The same size of pals; selection area large. Typhlosole begin in posterior region.

Nervous system. (Fig. O). Visceral ganglia with one anterior, tree posterior and one lateral projections. Occupying about 1/12 of adductor muscle size.

Distribution and habitat. California.

Examined material: UNITED STATES. Washington. FMNH 49120, 5 specimens. California. USNM 802721, 3 specimens; FMNH 16922, 4 specimens;

Plate 23 – *Ostrea lurida*. Fig. A – Concha, valva direita, vista externa; Fig. B – Concha, valva direita, vista interna; Fig. C – Concha, valva esquerda, vista interna, detalhe para chomata (ch); Fig. D – Concha, detalhe para a região do ligamento; Fig. E – Vista geral, detalhes para os palpos (pa), brânquias (gi), borda do manto (me), ânus (an), reto (rt), músculo adutor (am) e massa visceral (am); Fig. F – Detalhe dos palpos (pa) e músculo de Quenstedt; Fig. G – Detalhe da borda do manto (me) e músculos paliais (pm); Fig. H – Detalhe do reto (rt) e ânus (an); Fig. I – Estômago, detalhe para o esôfago (oe), área de seleção (sa1), capuz dorsal (dh) e intestino (in); Fig. J – Detalhe do coração e reto (rt), ventrículo (ve) e aurículas (au). Escalas 1 cm.

Plate 24 – *Ostrea lurida*. Anatomia. Fig. K – Vista geral, detalhes para músculo de Quenstedt (qm), palpos (pa), borda do manto (me), brânquias (gi), músculo adutor (ma), ânus (an), reto (rt), coração (he), massa visceral (vm); Fig. L Detalhe dos palpos (pa); Escalas: 1 cm; Fig. M – Detalhe do coração, ventrículo (ve) e aurículas (au); Fig. N – Estômago, vista do lobo direito, detalhe para o esôfago (oe), área de seleção (sa1), escudo gástrico (gs), tiflossoles (ty) e intestino (in); Fig. O – Detalhe do gânglio visceral (vg). Escalas 1 mm.

Genus *Cryptostrea* Harry, 1985

Imbedded in sponge in post-larval life, rather being cemented to firm substrate. The shells are small (about 30 mm high), very thin, only slightly inflate, inequivalve, but either valve may be the more inflate. The profile is subtriangular, subcircular or slightly elongate dorsoventrally; the beaks are of equal size, or the right one is smaller, and they are usually strongly twisted posterior, rarely orthogyrous; the ligament tends to be drawn out along the dorsal third or more of the posterior margin; the anterior shell margin forms a large, acute angle with the axis of the ligament, and the posterior forms a large obtuse angle, sometimes nearly a straight line. The outer shell layer is continuous over the surface, not interrupted by growth rests, and neither lamellose nor plicate, but often irregularly roughened. The color is uniformly light tan to darker brown. Small ostreine chromata are present, extending farther down along the anterior than the posterior margin. The interior of the shell is white, often slightly thickened with chalk deposit; it is not nacreous.

***Cryptostrea permolis* (Sowerby, 1871)**

Plates 25 – 26: Figs. A – L

Ostrea permolis Sowerby, 1871, *in* Reeve: pl.10, fig. 18a

Cryptostrea permolis: Harry, 1985: 144, fig. 23; Huber, 2010: 179.

Type: not found

Distinctive description

Shell (Figs. A - D): oval, small, to 50 mm. External color yellow, light brown. Right and left valve lightly, equivalve, concave, not protuberant in hinge. Umbonal cavity absent. Internally white, nacreous. Chomata absent. Adductor muscle scar not pigmented; located in posterodorsal region; reniform shape, occupying about 1/5 of valve surface. Scar of Quenstedt muscle oval-shaped, occupying 1/15 of size of adductor muscle.

Muscle system. Adductor muscle (Fig. E): reniform, posterior region, occupying 1/3 of total length. **Quenstedt muscle** (Fig. E, K): thin and narrow, located in middle portion of length of palps.

Mantle (Figs. E, G): mantle lobes connected in hinge region by length equivalent to 1/3 of body length; sub-umbonal region absent. Promyal chamber absent. Mantle edge thick, color beige, unspotted. Middle fold with short and medium papillae fingerlike, with 1 medium papillae for one short papilla. Inner fold with short papillae fingerlike, distributed uniformly. Pallial muscles thin, more concentrate in adductor muscle region.

Gills (Figs. E, G): shape elongated, occupying 1/3 of pallial cavity. Free anterior-dorsal gill end slightly arched, located between ventral margins of labial palps. Posterior region, free of visceral mass, has a 1/2 of total length of gill. Alimentary chamber thick, about 1/2 of fold size.

Visceral mass (Figs. E, J): occupying ~1/2 of total animal's size; located from ventral region of ligament to anterior surface of adductor muscle. Digestive diverticula

located in anterior and dorsal region of palps, occupying ~1/4 of visceral mass. Follicular gonads beige, occupying ~1/2 of visceral mass, covering digestive diverticula externally. Renopericardial structures occupying ~1/4 of visceral mass, located in posterior anterior-ventral region of adductor muscle.

Circulatory and excretory systems (Fig. J): Pair of accessory hearts, with one branch, short and thin caliber. Heart located anteriorly to adductor muscle. Ventricle pyriform, walls with thin bundles of muscle fibers. Auricles not pigmented. Walls of auricles thinner and lighter than those of ventricle, trabecular. Pair of kidneys triangular, tubular; mottled by light brown marks by translucence of visceral mass. Each kidney with direct communication with pericardium and gonad on medial side and laterally communicating by short chamber. Renal opening located on other side of cerebro-visceral connective.

Digestive system (Figs. H, J, K, L): ***Palps*** (Figs. H, K): located in anterior-ventral region, occupying ~1/8 of animal's length. Internal faces plicate, folds extending transversely to edge. External surface smooth, which irregular grooves and ridges. External hemipalps fused in 1/6 of length. **Esophagus** (Fig. L): flattened dorso-ventrally, length ~1/2 of palps, slightly larger than longer. **Stomach** (Fig. L): occupying same size of palps. Selection area 1 (sa1) long and narrow; typhlosole starting in anterior portion of sa1. **Intestine** (Figs. L) **and rectum** (Figs. J, I): Distinguished from distal end of style sac by 180 loop; afterwards passing through pericardium, following ovoid portion of visceral mass in 'U'-shaped loop, passing posteriorly to stomach, close to connection with esophagus, extending to right face of ovoid portion of visceral mass. It changes again course to ventral and posterior direction. Rectum crossing pericardium, running in contact with posterior face of adductor muscle; internal surface with well-

developed typhlosole, with broad base and grooved free end up to anal opening. **Anus** (Figs. I): Sessile, surrounded by flat edge-shaped fold, bell-shaped; occupying 1/4 of height of adductor muscle.

Reproductive system (Fig. I, J): gonad formed by two lobes of follicular aspect, cream color to dark yellow, occupying ~1/3 of animal size. Genital opening located together with renal opening, on other side of cerebro-visceral connective.

Central nervous system: Visceral ganglia not see.

Distribution and habitat: northeastern Gulf of Mexico and off coast of North Carolina. In “bread sponge”, the intertidal zone to 150 m depth.

Examined material: UNITED STATES. **North Carolina**. USNM 857098, 2 specimens.

Plate 25 – *Cryptostrea permolis*. Fig. A – Concha, valva direita, vista externa; Fig. B – Concha, valva esquerda, vista externa; Fig. C – Concha, valva direita, vista interna, detalhe para a impressão muscular; Fig. D – Concha, valva esquerda, vista interna, detalhe para a impressão muscular; Fig. E – Vista geral, detalhe para o músculo adutor (am), massa visceral (vm) e brânquias (gi); Fig. F – Porção anterior da valva direita, detalhe para chomata (ch); Fig. G – Detalhe da borda do manto, com prega interna (if) e prega média (mf), papiladas e prega externa (ef) lisa; Fig. H – Detalhe dos palpos e músculo de Quenstedt (qm); Fig. I – Detalhe do ânus (an) papilado e reto (rt). Escalas 1 cm.

Plate 26 – *Cryptostrea permolis*. Anatomia. Fig. J – Vista geral, detalhes para palpos (pa), brânquias (gi), músculos paliais (pm), músculo adutor (am), ânus (an), reto (rt), pericárdio (pe), coração (he), massa visceral (vm) e músculo de Quenstedt (qm); Fig. K – Detalhe dos palpos (pa) e músculo de Quenstedt (qm); Fig. L – Estômago, detalhes para os palpos (pa), esôfago (oe), área de seleção (sa1), capuz dorsal (dh), escudo gástrico (gs), tiflossos (ty) e intestino (in). Escalas 1 cm.

Genus *Teskeyostrea*

Diagnosis. Small size, thin, subcircular, of uniform dark golden brown color. The left valve is extensively cemented to rock, usually on the underside. The right valve is slightly convex, lamellose extensions of the prismatic layer at numerous growth rests; the interior is porcellaneous, often with one or two chalky pads. The chomata are ostreine, small, a few occurring on both anterior and posterior margins near the hinge.

***Teskeyostrea weberi* (Olson, 1951)**

Plates 27 – 28: Figs. A - I

Ostrea weberi Olsson, 1951: 6.

Ostrea permolis ecomorph *weberi*: Abbott, 1974: 455.

Teskeyostrea weberi: Harry, 1985: 145; Kinkerdale *et.al.*2004.

Type: not found

Distinctive description

Shell (Figs. A, B, C): oval shape, small size, about 30 mm length. Color dark golden brown. Right valve lightly convex, with lamellose extensions of the prismatic layer at numerous growth rests. Left valve extensively cemented to rock. Umbonal cavity absent. Internally porcellaneous, with one or two chalky pads. Chomata ostreine, in both, anterior and posterior, margin near hinge. Adductor muscle impression not pigmented, may with chalky depositions, occupying about 1/8 of valve surface. Scar of Quenstedt muscle oval-shaped, occupying 1/25 of size of adductor muscle.

Muscle system. Adductor muscle (Figs. D, G): position posterior. Transverse section oval shaped, occupying ~1/3 of shell length. **Quenstedt muscle** (Fig. D): thin and narrow, located in posterior portion of length of palps.

Mantle (Figs. D, G): mantle lobes connected in hinge region by length equivalent to 1/2 of body length; sub-umbonal region absent. Promyal chamber absent. Mantle edge thick, color dark yellow to brown. Middle fold with short and medium papillae fingerlike, presenting up to six small papillae between each medium papilla. Internal fold with short papillae. Pallial muscles thin.

Gills (Fig. G): shape elongated, triangular, occupying 2/3 of pallial cavity. Free anterior-dorsal gill end slightly arched, located between ventral margins of labial palps. Posterior region, free of visceral mass, has a 1/3 of total length of gill. Alimentary chamber thin, located in free margin of demibranchs, in all length.

Visceral mass (Figs. D, G): occupying ~1/2 of total animal's size; located from ventral region of ligament to anterior surface of adductor muscle. Digestive diverticula located in anterior and dorsal region of palps, occupying ~1/4 of visceral mass. Follicular gonads beige, occupying ~1/4 of visceral mass, covering digestive diverticula externally.

Circulatory and excretory systems (Figs. G, I): Accessory heart absent. Heart located anteriorly to adductor muscle. Ventricle pyriform, walls with thin bundles of muscle fibers crossing ventricular lumen, dividing it incompletely into two chambers. Auricles unpigmented. Walls of auricles thinner and lighter than those of ventricle, trabecular.

Digestive system (Figs. G, H): **Palps** (Figs. G): located in anterior-ventral region, occupying ~1/5 of animal's length. Hemipalps flattened, elongated, 50% of total size of visceral mass, united throughout its length to visceral mass. Internal faces plicate, folds extending transversely to edge. External surface smooth, which irregular grooves and ridges. External hemipalps fused in 1/3. **Esophagus** (Fig. H): flattened dorso-ventrally, almost same length of palps, longer than large. **Stomach** (Fig. H): occupying almost same palps size. Selection area 1 (sa1) thin and long; typhlosole starting in anterior portion of sa1. **Intestine** (Fig. H) **and rectum** (Figs. G, H): Distinguished from distal end of style sac by 180 loop; afterwards passing through pericardium, following ovoid portion of visceral mass in 'U'- shaped loop, passing posteriorly to stomach, close to connection with esophagus, extending to right face of ovoid portion of visceral mass. It changes again course to ventral and posterior direction. Rectum crossing pericardium, running in contact with posterior face of adductor muscle; internal surface with well-developed typhlosole, with broad base and grooved free end up to anal opening. **Anus** (Figs. G, H): Sessile, appendage not present, occupying 1/3 of height of adductor muscle.

Reproductive system (Fig. G): gonad formed by two lobes of follicular aspect, cream color, occupying ~1/4 of animal size. Genital opening located together with renal opening, on other side of cerebro-visceral connective.

Central nervous system: not seem.

Distribution and habitat: Florida

Examined material: UNITED STATES. **Florida.** Monroe Co. Grassy Key. UF 298644, 2 specimens.

Plate 27- *Teskeyostrea weberi*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista interna, valva direita, detalhe para os depósitos de cálcio (cd); Fig. C – Porção anterior da valva direita, vista interna, detalhe para chomata (ch); Fig. D – Vista geral, detalhe para o músculo adutor (am), borda do manto (me) e músculos paliais (pm); Escalas 1 cm. Fig. E – Detalhe da borda do manto (me) pigmentada; Fig. F – Detalhe da borda do manto com pregas média e interna papiladas, e músculos paliais (pm). Escalas 1 mm.

Plate 28. *Teskeyostrea weberi*. Anatomia. Fig. G – Vista geral, detalhes para os palpos (pa), borda do manto (me), brânquias (gi), músculo adutor (am), ânus (an), reto (rt), coração (he) e massa visceral (vm); Fig., H – Estômago, detalhes para os palpos (pa), esôfago (oe), área se seleção (sa1), capuz dorsal (dh), escudo gástrico (gs), intestino (in), reto (rt) e ânus (an). Escalas 1 cm. Fig. I – Detalhe do coração, ventrículo (ve) e aurículas (au). Escala 1mm.

Family Gryphaeidae Vyalov, 1936

Ostracea in which the adductor muscle scars are circular or only slightly flattened dorsally. Two of tree subfamilies are extinct: Gryphaeinae and Exogyrinae. Only Pycnodontinae include all living gryphaeid oysters.

Subfamily Pycnodontinae Stenzel, 1959

Gryphaeidae which vesicles, cavities in the edge shell, easily seen with magnification of 10 x or more. Vesicular shell structure is a termed illustrated in Ranson (1967), Stenzel (1971), Torigoe (1981) e Harry (1985). Chomata are always present, of three types: 1) vermiculate: small, rounded ridges, closely spaced, normal to the margin; always present near the ligament on the front and hind margins of both valves.; 2) neopycnodontinae: are modifications of the vermiculate type, having very pronounced ridges and troughs, with the vermiculate chromata greatly enlarged; this type is limited to the shell margin near of ligament; 3) lath: are elongated, straight, well defined ridges, spaced about as far apart as their widths, and normal to the margin. They occur in ventral to the vermiculate chromata, on both valves, but they seem to coincide rather than interlock, or alternate, with those of the opposite valve. These are present only in *Hyotissa hyotis*.

The mantle lobes are thin, transparent in smaller specimens, and probably not used to store glycogen; their inner surface is usually extensively papillate. The accessory heart not present. The outer labial palp is fused medially for most of its length. The right promial passage is broadly open, reaching from the adductor muscle nearly to the isthmian mantle. The bilobed ventricle of the heart is distinctly penetrated

by rectum. The auricles are fused to each other, irregularly out pocketed, appearing lobate. The gills appear to be more voluminous than those of the Ostreidae.

***Genus Hyotissa* Stenzel, 1971**

Type: *Ostrea hyotis* Linnaeus, 1758, in BMNH, no number.

Medium to very large shells (to 250 mm height or more), occasionally subcircular but usually oval, dorsoventrally elongate; both of the valves are thick, and both usually have a plications, from which semicylindrical lamellae may project as hyote spines. The marginal edge is usually zigzag, with vesicular chalky deposits developing internally in the troughs between plicae. The ventral margin of the adductor muscle scar is usually elevated. Lath chromata occasionally develop. The valve are colored, washed with red, blue, or purple. The inner with dark purple, almost black margins.

The promial chamber is open in both sides, but left is limited to the area of the pericardium and lower part of the visceral mass. The right passage extends from adductor muscle nearly to the hinge.

This genera is monotypic, but *Hyotissa hyotis* extends for a Indo-West Pacific tropics and north Atlantic ocean (records for Florida, USA).

The complete description and plates for this species see Simone *et.al. submitted* (Annex III).

Parahyotissa Harry, 1985

Type: *Ostrea thomasi* McLean 1941; Harry renamed for *Parahyotissa mcgintyi* to preserve a original honor to Thomas L. McGintyi (malacologist of Florida)

Shell smaller than *Hyotissa*, without lath chomata, but vermiculate chomata always present and restricted to the subligamentary margin. Plications and occasionally short hyote spines are potentially present on both valves. The valves are often washed with red or light purple, tending to be white inside. Left promyal passage are always closed.

For a complete description of *P. mcgintyi*, see Simone et. al. *submit*. (Annex III).

Plate 29: Figs. A – L for complement figures.

Plate 29 – *Parahyotissa mcgintyi*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista interna, valva direita; Fig. C – Vista geral, detalhe para o músculo adutor (am), manto (ma), brânquias (gi) e massa visceral (vm); Fig. D – Detalhe do chomata (ch) na porção anterior da valva; Fig. E, F – Detalhe das câmaras das valvas; Fig. G – Detalhe da borda do manto (me); Escalas: 1 cm. Fig. H – Detalhe dos palpos (pa); Fig. I – Coração em pericárdio, detalhe para ventrículo (ve) e aurículas (au) lobadas; Fig. J – Detalhe do rim (kd), lobo direito; Fig. K – Detalhe do gânglio visceral (vg); Fig. L – Detalhe do reto (rt) e ânus (an). Escalas 2 mm.

***Parahyotissa numisma* (Lamarck, 1819)**

Plates 30 – 31: Figs. A – M

Ostrea numisma Lamarck, 1819: 205; Deshayes, 1839: 222; 1863: 36; Hanley, 1856: 297; Lamy, 1924: 98; 1925: 256; 1929: 72.

Ostrea violacea Deshayes, 1863: 35

Ostrea lentiginosa Sowerby, 1871: sp. 58;

Ostrea cerata Sowerby, 1871: sp. 71

Ostrea inaequalvis Sowerby, 1871: sp. 82

Ostrea (Lopha) inaequalvis: Kuroda, 1928: sp. 38

Ostrea (Crassostrea) inaequalvis: Kuroda, 1930: 53; Hirase, 1932: 222; Takatsuki, 1949: 10

Ostrea sandvichensis: Dall, 1938: 113 (*non* Sowerby, 1871)

Ostrea thaanumi Dall, 1938: 114

Ostrea procles Iredale, 1939: 396; Allan, 1959: 275

Pycnodonta numisma: Ranson, 1949: 248-254; 1960: 6; 1967: 135

Dendostrea inaequalvis: Habe, 1951: 93; 1977: 110

Hyotissa inaequalvis: Torigoe, 1981: 302, 323; Xu, 1997: 92; Hayami, 2000: 923

Hyotissa numisma: Kliburn & Rippey, 1982: 170; Oliver, 1992: 89

Parahyotissa (Numismoida) numisma: Harry, 1985: 132; Lamprell & Healy, 1998: 130

Type: In MNHN, no number.

Distinctive description

Shell (Figs. A-C): oval-elongated shape, small to medium size, about 60 mm length. Color white. Inner with spots purple in edge of left valve. Right valve totally white. Left valve extensively cemented to rock. Umbonal cavity, plicae and spines absent. Chomata vermiculate. Adductor muscle scar not pigmented, occupying about 1/9 of valve surface. Scar of Quenstedt muscle oval-shaped, occupying 1/30 of size of adductor muscle. Vesicular shell structure present.

Muscle system. Adductor muscle (Figs. C, G, K): position posterior. Transverse section oval shaped, occupying ~1/5 of shell length. **Quenstedt muscle** (Fig. K): thin and narrow, located in posterior portion of length of palps.

Mantle (Figs. G, I): mantle thin, lobes connected in hinge region by length equivalent to 1/4 of body length; sub-umbonal region absent. Promyal chamber present only right side. Mantle edge thick, color dark brown, light brown and cream. Middle fold and inner fold with only short papillae fingerlike, uniformly distributed. Pallial muscles thin.

Gills (Figs. F, K): shape elongated, triangular, occupying 1/3 of pallial cavity. Free anterior-dorsal gill end slightly arched, located between ventral margins of labial palps. Posterior region, free of visceral mass, has a 1/2 of total length of gill. Alimentary chamber thick, about same size of filament.

Visceral mass (Fig. K): occupying ~1/2 of total animal's size; located from ventral region of ligament to anterior surface of adductor muscle. Digestive diverticula

located in anterior and dorsal region of palps, occupying $\sim 1/3$ of visceral mass. Follicular gonads beige, occupying $\sim 1/3$ of visceral mass, covering digestive diverticula externally.

Circulatory and excretory systems (Fig. J): Accessory heart absent. Heart located anteriorly to adductor muscle. Ventricle small, pyriform. Auricles lobate, grayish pigmented.

Digestive system (Figs. H, M): **Palps** (Figs. H): located in anterior-ventral region, occupying $\sim 1/6$ of animal's length. Hemipalps flattened, elongated, 50% of total size of visceral mass, united throughout its length to visceral mass. Internal faces plicate, folds not extending transversely to edge. External surface smooth, which irregular grooves and ridges. External hemipalps fused in $\frac{1}{2}$. **Esophagus** (Fig. M): flattened dorso-ventrally, almost same length of palps, as longer as large. **Stomach** (Fig. M): occupying almost $1/3$ of globular region. Selection area 1 (sa1) thin and long; typhlosole starting in anterior portion of sa1. **Intestine** (Figs. M) **and rectum** (Figs. K) Distinguished from distal end of style sac by 180 loop; afterwards passing through pericardium, following ovoid portion of visceral mass in 'U'- shaped loop, passing posteriorly to stomach. Rectum crossing by ventricle; internal surface with well-developed typhlosole, with broad base and grooved free end up to anal opening. **Anus** (Figs. K): Sessile, appendage not present, occupying $1/4$ of height of adductor muscle.

Reproductive system (Fig. K): gonad formed by two lobes of follicular aspect, cream color, occupying $\sim 1/3$ of animal size. Genital opening located together with renal opening, on other side of cerebro-visceral connective.

Central nervous system (Fig. L): Visceral ganglia with one anterior, one posterior and one lateral projections. Occupying about 1/20 of adductor muscle size.

Distribution and habitat: Indo-West Pacific, East Africa to Hawaii.

Examined material: MADAGASCAR. UF 423309, 1 specimen; UF 423742, 2 specimens.

Plate 30 – *Parahyotissa numisma*. Fig. A – Concha, vista externa, valva direita; Fig. B – Concha, vista interna, valva direita, detalhe para a impressão muscular (im); Fig. C – Vista geral da parte mole na valva esquerda, detalhe para o músculo adutor (am); Fig. D – Concha, vista interna, valva direita, porção anterior, detalhe para a impressão muscular (im); Fig. E – Concha, vista interna, valva esquerda, porção anterior, detalhe para a impressão muscular (im); Fig. F – Detalhe das brânquias; Fig. G – Vista geral, detalhe para o músculo adutor (ma) e a borda do manto (me); Fig. H – Detalhe dos palpos (pa); Fig. I – Detalhe da borda do manto (me), pregas média (mf) e interna (if) com papilas e prega externa (ef) lisa; Fig. J – Detalhe do coração no pericárdio, ventrículo (ve) e aurículas (au) lobadas. Escalas 1 cm.

Plate 31 – *Parahyotissa numisma*. Anatomia. Fig. K – Vista geral, detalhes para os palpos (pa), brânquias (gi), coração acessório (ah), músculos paliais (pm), anus (an), reto (rt), músculo adutor (am), coração (he), massa visceral, músculo de Quenstedt (qm); Fig.. L – Detalhe do gânglio visceral; Fig. M – Estômago, detalhes para o esôfago (oe), área de seleção (sa1), capuz dorsal (dh), escudo gástrico (gs) e tiflossos (ty). Escalas 1 cm.

3.2 Descrição dos caracteres

CONCHA

1. Concha

0 = fixada em substrato consolidado por bisso (*Isognomon*, *Barbatia*, *Lima*)

1 = fixada em substrato consolidado por cimentação (*Ostreidae*, *Gryphaeidae*, *Plicatula*, *Plicatulostrea*, *Spondylus*)

L = 1 CI = 100 RI = 100

Figura 4 - A) Fixação por bisso; b) fixação por cimentação

A maioria dos bivalves basais são adaptados para escavar o substrato infaunal (Harper *et.al.*, 2000; Giribet & Wheeler, 2002). Detalhes do processo de cimentação dos bivalves são discutidos por Yonge (1979) e Harper (1992) e exclusivamente de ostreídeos por Stenzel (1971). Os caracteres incluídos aqui são a fixação ao substrato duro por um bisso, não calcificado (e.g., *Barbatia*) e a cimentação ao substrato duro (e.g., *Crassostrea*, *Spondylus*). *Anomia simplex* (Fig. 5) é fixa, por um bisso calcificado, aqui codificado como 1.

Figura 5 - *Anomia*, fixação por bisso calcificado.

2. Fixação

0 = valva esquerda (Ostreidae, Gryphaeidae)

1 = valva direita (*Spondylus*, *Plicatula* e *Plicatulostrea*)

L = 3 CI = 66 RI = 80

Os ostreídeos normalmente se fixam ao substrato pela valva esquerda. *Spondylus* se fixa pela valva direita.

3. Forma da concha

0 = comprimento maior que altura (*Barbatia*, *Alectryonella*)

1 = altura maior que comprimento (*Lima*, *Isognomon*, *Plicatula*, *Plicatulostrea*, *Ostrea*, *Dendostrea*, *Lopha*, *Saccostrea*, *Striostrea*)

2 = altura maior que comprimento + forma de taça (*Crassostrea*)

L = 3 CI = 66 RI = 83

Figura 6 - Guia de orientação, retirado de Stenzel, 1971 (N957).

A variação intraespecífica das conchas de ostras, que é provavelmente maior do que em qualquer outro grupo de bivalves, impede a elaboração de uma chave taxonômica simples e inteligível. O formato aqui apresentado vai além de uma chave taxonômica, já que podemos excluir diversas “ostras” que imitam o formato das ostras verdadeiras (e.g., *Anomia*, *Plicatula*, *Spondylus*) (Harry, 1985).

4. Valvas

0 = equivalve (*Barbatia*, *Lima*, *Plicatula*, *Isognomon*)

1 = inequivalve (Ostreidae e Gryphaeidae)

L = 1 CI = 100 RI = 100

As conchas são geralmente pouco equilaterais, mas inequivalves, e a valva esquerda é geralmente mais côncava.

Figura 7 - A) *Lima caribea*, concha equivalve; B) *Crassostrea mangle*, concha inequivalve.

5. Ornamentação externa

0 = presente (*Barbatia*, *C. virginica*, *C. gigas*, *C. bilineata*, *Striostrea*, *Lopha*, *Alectryonella*, *D. frons*, *O. edulis*, *Hyotissa*, *Spondylus*, *Lima*, *Plicatula*)

1 = ausente (*C. mangle*, *C. brasiliiana*, *C. rhizophorae*, *Saccostrea*, *D. folium*, *D. sp1*, *D. cf. sandvichensis*, *O. equestris*, *O. puelchana*, *O. lurida*, *Cryptostrea*, *Teskeyostrea*, *Parahyotissa*, *Plicatulostrea*, *Anomia*)

L = 8 CI = 12 RI = 36

Figura 8– A) *C. gigas*, com ornamentação externa; B) *O. equestris*, sem ornamentação externa.

6. Ornamentação externa – presente:

0 = radial (*B. candida*, *A. plicatula*, *P. gibbosa*)

1 = concêntrica (*C. virginica*, *C. gigas*, *C. bilineata*, *O. edulis*)

2 = hyote spines (*H. hyotis*, *D. frons*)

3= escamas (*Lima*, *S. americanus*)

L = 9 CI = 33 RI = 0

Figura 9 – Tipos de ornamentação externa: A) radial, *A. plicatula*; B) concêntrica, *O. edulis*; C) hyote spines, *H. hyotis*; D) espinhos, *S. americanus*.

Barbatia e *Alectryonella* apresentam uma ornamentação radial (0), onde estruturas radiais finas são separadas por sulcos do mesmo tamanho. A ornamentação externa consiste do perióstraco, que pode ser contínuo, caracterizando uma superfície lisa, ou possuindo projeções lamelares (estado 1). Estas são normalmente juntas ou imbricadas, variando em extensão. Algumas vezes podem formar espinhos tubulares de tamanhos variados, chamados de “hyote spines” (encontrados em *Hyotissa hyotis* e *D. folium*-estado 2). No caso de *Spondylus* e *Lima*, tais estruturas são escamas modificadas, codificados aqui como estado 3. De acordo com o caráter 5, 0= ornamentação ausente (lisa) e 1 = ornamentação presente.

7. Borda externa das valvas

0 = lisa (*Barbatia*, *Anomia*, *Isognomon*, *Plicatulostrea*, *Spondylus*, *Cryptostrea*, *Teskeyostrea*, *Crassostrea* –exceto *C. virginica*, *Striostrea*, *P. numisma*)

1 = plicada (*Plicatula*, *Lima*, *Saccostrea*, *Dendostrea*, *Lopha*, *Alectryonella*, *Hyotissa*, *P. mcgintyi*, *Ostrea*).

L = 7 CI = 14 RI = 53

Figura 10– A) Borda externa lisa; B) Borda externa plicada.

As plicas comissurais tomam a forma de zigzag de ângulos agudos ou ondulações sinuosas na margem da concha em que as valvas opostas se encaixam umas as outras, quando fechadas. Todos os Lophinae possuem. *Hyotissa* comumente possui várias plicas em zigzag. As plicas com ângulos diversos com dentes sucessivos em uma

concha são desiguais e formam uma série graduada progressiva; o ângulo mais agudo de uma série é o único mais afastado do eixo de articulação e o menos agudo é o mais próximo. Em ostras plicadas que não são ou são pouco curvadas, a série graduada progride continuamente com ângulos decrescentes da charneira para a região do branchitellum (ponto posteroventral da margem da concha das ostras, perto da fusão paliobranquial). Entretanto os tamanhos dos ângulos das plicas diferem muito de uma plica para a seguinte, os flancos das plicas são curvas, a fim de acomodar a mudança sem interferir com a posição normal dos ângulos. Esta situação é perceptível em espécies com poucos dentes grandes em torno da periferia; em tais escudos um flanco é convexo e outro côncavo.

8. Tipo de plica

0 = simples (*Plicatula*, *Lima*, *Saccostrea*, *Dendostrea*, *Alectryonella*, *Hyotissa*, *P. mcgintyi*, *Ostrea*)

1 = angulosa (Autapomorfia de *Lopha*)

L = 1 CI = 100 RI = 100

Figura 11– A) Plicas simples, arredondadas, *Dendostrea*; B) Plicas angulosas, *Lopha*.

As plicas assumem a forma de zigzag arqueadas e anguladas ou ondulações sinuosas e arredondadas da margem de concha. A oposição das valvas se encaixa uma na outra, quando fechadas. Todos Lophinae, Ostreinae e Pycnodontinae comumente tem várias plicas em zigzag, em diferentes ângulos.

Os ângulos das plicas com várias pontas sucessivas são desiguais e formam uma série graduada progressiva de pontas; o ângulo mais agudo de uma série é o mais afastado do eixo de articulação e, o menos agudo é o mais próximo. Em ostras plicadas que possuem ângulos curvados, o ângulo das plicas é menor na região da charneira, aumentando gradualmente até a porção posterior. Como exemplo: (0) *D. frons*; (1) *L. cristagalli*. De acordo com o caráter 7: 0 = lisa; 1 = plicada.

9. Borda marginal interna das valvas

0 = compacto [Todos, exceto Pycnodontinae (Gryphaeidae)]

1 = com câmaras ocas (Sinapomorfia de Pycnodontinae)

L = 1 CI = 100 RI = 100

Figura 12– Estrutura vesicular.

Os grifeídeos apresentam depósitos de cálcio intercalados na matriz foliar da camada interna da concha apresentam vesículas ocas, cavidades subesféricas ou poliédricas, facilmente vistas em aumento superior a 10x, normalmente cheias de líquido ou ar. Estrutura vesicular da concha é o termo para a estrutura, ilustrado e descrito por Ranson, 1967, Stenzel, 1971 e Torigoe, 1981.

10. Coloração borda interna

0 = ausente (*B. candida*, *C. mangle*, *C. gigas*, *C. bilineata*, *S. echinata*, *D. folium*, *D. sp2*, *O. edulis*, *O. equestris*, *O. puelchana*, *O. lurida*, *C. permolis*, *T.*

weberi, *H. hyotis*, *P. mcgintyi*, *Spondylus*, *Lima* sp., *P. gibbosa*, *P. onca*, *A. simplex*)

1 = presente (*I. alatus*, *P. numisma*, *D. frons*, *D. sp.1*, *A. plicatula*, *L. cristagalli*, *S. prismatica*, *S. mordax*, *S. palmula*, *S. cucullata*, *S. glomerata*, *C. virginica*, *C. rhizophorae*, *C. brasiliana*).

L = 2 CI = 50 RI = 58

Figura 13– A) Borda da valva não pigmentada; B) borda da valva pigmentada

As ostras têm muitos padrões de pigmentação. Um exemplo comum são as estrias radiais de cores escuras sobre a face externa das valvas. Outro padrão comum encontrado em ostras tropicais é uma grande banda de cor escura (preto, marrom escuro ou roxo escuro) ao longo da margem internas das valvas. Ostras que vivem em regiões tropicais quentes possuem uma coloração mais escura, vívida, variada e mais cores que as que vivem em águas de climas frios (Stenzel, 1971).

11. Chomata

0 = ausente (*B. candida*, *I. bicolor*, *A. simplex*, *S. americanus*, *Lima*, *P. numisma*, *Crassostrea*)

1 = presente (*Ostrea*, *C. permolis*, *T. weberi*, *H. hyotis*, *P. mcgintyi*, *P. gibbosa*, *S. echinata*, *D. folium*, *D. sp1*, *D. frons*, *D. sp.2*, *A. plicatula*, *L. cristagalli*, *S. prismatica*, *S. mordax*, *S. palmula*, *S. cucullata*, *S. glomerata*)

L = 2 CI = 50 RI = 90

Figura 14 - valva esquerda – A) *Crassostrea*, sem chomata (retirado de Galtsoff, 1964); B) *Dendostrea*, com chomata (retirado de Stenzel, 1971).

A maioria das espécies de ostras possuem sulcos ou pústulas ao longo da margem interna das valvas. Estes são geralmente perto do ligamento, por vezes limitados a uma pequena linha, mas muitas vezes as pústulas se estendem sobre as margens anterior e posterior por uma distância variável, e até mesmo até a margem ventral. Estes dentículos marginais, chamados coletivamente de “chomata” por Stenzel (1971), são de importância sistemática.

12. Chomata

0 = presente somente na VD (*Saccostrea*, *Striostrea*, *Dendostrea*, *Cryptostrea*, *Anomia*)

1 = presente somente na VE (*Ostrea*, *Teskeyostrea*, *Plicatula*, *Plicatulostrea*)

2 = em ambas as valvas (*Lopha*, *Alectryonella*, *Hytotissa*, *Parahytotissa*)

L = 5 CI = 40 RI = 78

Neste caráter 12 existem duas otimizações igualmente parcimoniosas, o estado 1 pode embasar o nó 10 ou no nó 13. Na Figura (50; 51) foi escolhido o nó 10 com uma reversão no táxon *Dendostrea* sp.1.

13. Chomata - distribuição

0 = restrita a região anterior (*S. palmula*, *O. puelchana*, *O. lurida*, *C. permolis*, *T. weberi*, *H. hyotis*, *P. mcgintyi*, *P. numisma*)

1 = chegando à região mediana (*S. cucullata*, *S. prismatica*, *D. sp1*, *O. edulis*, *O. equestris*)

2 = por toda borda (*S. glomerata*, *S. mordax*, *S. echinata*, *L. cristagalli*, *A. plicatula*, *D. folium*, *D. frons*, *D. sp2*, *P. gibbosa*, *P. onca*).

Chomata ausente, codificada como (–): missing data.

L = 8 CI = 25 RI = 62

Figura 15 – A) Chomata apenas na região do ligamento, valva esquerda; B) Chomata até a região mediana, valva direita; C) Chomata por toda a borda da valva, valva direita.

14. Chomata – tipos

0 = não Ostreoidea (*P. gibbosa*, *P. onca*)

1 = Ostreoidea – Gryphaeidae (*H. hyotis*, *P. mcgintyi*, *P. numisma*)

2 = Ostreoidea - Ostreidae (*Saccostrea*, *Striostrea*, *Dendostrea*, *Ostrea*, *Cryptostrea*, *Teskeyostrea*, *Alectryonella*)

L = 3 CI = 66 RI = 92

Figura 16– Tipos de Chomata: A) não ostreoidea; B) Ostreoidea – Gryphaeidae; C) Ostreoidea – Ostreidae.

15. Chomata Ostreoidea - Gryphaeidae

0 = lath (*Parahyotissa*)

1 = vermicular + lath (*Hyotissa*)

L = 1 CI = 100 RI = 100

Figura 17– Chomata vermicular (vc) e chomata lath (lc). Retirado de Harry (1985).

Em Gryphaeidae (Pycnodontinae) chomata é sempre presente: Vermicular – os dentículos são pequenos, formando serras arredondadas, agregadas, normalmente na margem; eles são levemente retorcidos, afilados na região externa, variando de comprimento, ou se dividindo ou se fundindo. Estes são presentes perto do ligamento, na frente e posterior nas margens de ambas as valvas, essa oposição das valvas pode não ser interdigitado. Neopycnodonte – são modificações do tipo “vermicular”, tendo muitas ranhuras e calhas evidentes, com chomata vermicular com dentículos bem alargados na valva direita. Este tipo é limitado à margem da concha perto do ligamento. Este tipo de chomata é intermediário entre os tipos vermicular e ostreine. (0) Lath chomata – as pregas são alongadas, retilíneas, assemelhadas a costelas bem definidas, espaçadas umas das outras, normalmente na margem. Esta ocorre ventralmente a chomata vermiculate, em ambas as valvas, com costelas opostas umas às outras. Essa associação, (1) vermicular + lath está presente apenas em *Hyotissa hyotis*, entre as ostras viventes.

16. Tipo Ostreoidea – Ostreidae

0 = lophinae (*Dendostrea*)

1 = ostreine (*Ostrea*, *Saccostrea*, *Cryptostrea*, *Teskeyostrea*)

2 = ostreine + lophinae (*Lopha*, *Alectryonella*)

L = 4 CI = 50 RI = 50

Figura 18– A) Lophine chomata; B) Ostreine chomata. Figuras retiradas de Harry, 1985.C) Ostreine + lophine chomata.

Em Ostreidae, chomata pode estar ausente em toda vida em *Booneostrea* e *Crassostrea*, ou ocasionalmente perdida em conchas maiores e mais velhas em algumas espécies (*Ostrea*, *Striostrea* e *Pustulostrea*), ou ausente em alguns ecomorfos nas espécies em que geralmente ela estaria presente (*Saccostrea*). Chomata é presente na maioria das espécies de ostra, e pode ser dividida em dois tipos: (0) Lophine chomata – limitada a tribo Lophine; consiste de diminutas pústulas em linhas adjacentes que são normalmente encontrados na margem da concha, com uma ou muitas pústulas por linha. As linhas de pústulas estão manifestadas normalmente em bandas subjacentes a estrutura da concha. Lophine chomata tem a forma ampla, em bandas contínuas distribuídas por toda margem da concha, ou ocorre em poucos locais ao longo desta. Esse tipo de chomata pode estar presente em ambas as valvas, ou limitada somente à valva direita, mas em outros casos não apresentam a concavidade oposta na valva. (1) Ostreine chomata – consiste de pústulas, às vezes alongadas, normalmente na margem

da concha, e uma única linha paralela à margem; ocorre somente na valva direita possuindo concavidades que recebem estas na valva esquerda (Harry, 1985). Ocasionalmente, chomata tipo lophine e ostreine (2) podem ocorrer na mesma espécie (como de *Dendostrea* e *Alectryonella*), em casos que chomata ostreine é limitada à margem perto da charneira.

17. Chomata – disposição

0 = em uma linha (*Saccostrea*, *Dendostrea*, *Ostrea*, *Teskeyostrea*, *Cryptostrea*)

1 = em várias linhas (*Lopha*, *Alectryonella*, *Hyotissa*, *Parahyotissa*)

L = 2 CI = 50 RI = 75

Figura 19– A) disposição da chomata em uma linha; B) disposição da chomata em várias linhas.

18. Charneira

0 = taxodonte (*Barbatia*)

1 = heterodonte (*Spondylus*, *Lima*, *Plicatula*, *Plicatulostrea*)

2 = sem dentes (Ostreidae e Gryphaeidae)

L = 3 CI = 66 RI = 75

Figura 20– A) Charneira taxodonte (figura retirada de Brusca & Brusca, 2003); B) charneira heterodonte (figura retirada de Simone & Amaral, 2008); C) sem dentes (figura retirada de Stenzel, 1971).

A charneira do tipo taxodonte (0) apresenta dentes numerosos e de dimensões equivalentes, dispostos perpendicularmente à charneira ou em arco; a do tipo heterodonte (1) possui dois ou três dentes cardinais e dois dentes laterais. (2) Sem dentes apresenta somente o ligamento. É bom frisar que esses tipos de charneira foram codificados para formas adultas; outros tipos de charneira são encontrados em suas respectivas larvas (ver, e.g. Fuller *et.al.*, 1989, sobre *Anomia simplex*).

19. Componente do ligamento interno

0 = ausente

1 = presente, em forma de gota (*Spondylus*, *Lima*, *Plicatula*, *Plicatulostrea*)

2 = presente, em forma de linha (*Anomia*, *Isognomon*, *Ostreidae* e *Gryphaeidae*)

L = 2 CI = 100 RI = 100

20. Dentes laterais

0 = ausente (*Barbatia*, *Isognomon*, *Ostreidae*, *Gryphaeidae*)

1 = presente (*Lima*, *Spondylus*, *Plicatula*, *Plicatulostrea*)

L = 2 CI = 50 RI = 66

Figura 21– Dentes laterais (hi). Figura retirada de Simone & Amaral, 2008.

21. Cavidade umbonal

0 = ausente

1 = presente (Crassostreinae, exceto *Striostrea* e *Alectryonella*).

L = 2 CI = 50 RI = 91

Figura 22– Cavidade umbonal em *A. plicatula*.

Apenas a valva esquerda possui uma cavidade umbonal, que é uma câmara localizada mais posteriormente do que a charneira. Vários gêneros de ostras comumente possuem essa cavidade aberta sob a plataforma do ligamento e área ligamentar. A cavidade muda de formato e de tamanho durante o crescimento das ostras. Embora seja de tamanho variável, a cavidade umbonal é utilizada para a identificação de várias espécies em Ostreoidea (Stenzel, 1971).

Neste caráter 21 existem duas otimizações igualmente parcimoniosas, o estado 1 pode embasar o nó 6 ou no nó 8. Na Figura (50; 51) foi escolhido o nó 6 com uma reversão no táxon no nó 8.

22. Cavidade umbonal – Tamanho

0 = rasa, menor que 1/20 do volume interno (*A. plicatula*, *S. prismatica*, *S. echinata*, *S. palmula*)

1 = profunda, maior que 1/10 do volume interno (*Crassostrea*, *S. cucullata*, *S. glomerata*, *S. mordax*)

Neste caráter, de acordo com o item 22 (0 = ausente; 1 = presente), foi codificado como (-): missing data.

L = 2 CI = 50 RI = 66

23. Impressão muscular

0 = côncava (*Ostreidae*, *Barbatia*, *Spondylus*, *Isognonon*, *Lima*, *Plicatula*, *Plicatulostrea*, *Anomia*)

1 = convexa (*Gryphaeidae*)

L = 1 CI = 100 RI = 100

Figura 23– Tipos de impressão muscular: A) vermelho: côncava; porção anterior da impressão muscular côncava. B) azul: convexa, porção anterior da impressão muscular convexa. Figura retirada de Stenzel, 1971.

A forma da impressão muscular apresenta duas classes principais: as côncavas e as convexas ou orbiculares. A primeira tem margens dorsais côncavas ou quase retilíneas, podendo apresentar as formas: de lua crescente com pontas afiladas e cavidade profunda; semilunar ou em forma de meia lua, terminando afilada e com rasa concavidade; forma de vírgula termina afilada e concavidade profunda; forma de fita, muito longo e curvo; e reniforme.

A classe convexa ou de impressão esférica tem margens dorsais convexas. É característico de Gryphaeidae. Pode apresentar formas: circular, comprimento igual altura; altura superior à largura; oval, largura maior que altura.

24. Forma da impressão músculo adutor posterior

0 = elíptica (*Barbatia*, *Hyotissa*, *Parahyotissa*, *Spondylus*, *Lima*)

1 = reniforme (*Cryptostrea*, *Plicatula*, *Plicatulostrea*)

2 = em forma de lua com a borda ventral afilada (*Lopha*)

3 = em forma de lua com a borda ventral arredondada (*Crassostrea*, *Saccostrea*, *Dendostrea*, *Ostrea*, *Alectryonella*, *Teskeyostrea*)

L = 9 CI = 33 RI = 50

25. Coloração impressão muscular

0 = ausente

1 = presente (*P. numisma*, *A. plicatula*, *S. prismatica*, *S. mordax*, *S. glomerata*, *S. cucullata*, *C. virginica*, *C. gigas*, *C. bilineata*)

L = 4 CI = 25 RI = 66

Figura 24– Impressão muscular: A) sem coloração; B) com coloração.

A cor da impressão muscular apresenta-se ora fraca, ora altamente pigmentada, formando faixas geralmente na cor púrpura, lavanda, azul, marrom ou uma combinação dessas, em todas as espécies.

A cicatriz em uma ou ambas as valvas pode ser despigmentada, apresentando-se, então, esbranquiçada, ou apenas levemente colorida, o que é característico de populações de ostreídeos da região tropical (Harry, 1985).

26. Impressão músculo de Quenstedt

0 = ausente (*Barbatia*, *Spondylus*, *Lima*, *Isognomon*, *Plicatula*, *Plicatulostrea*, *Anomia*)

1 = presente (*Crassostrea*, *Saccostrea*, *Ostrea*, *Dendostrea*, *Lopha*, *Alectryonella*, *Teskeyostrea*, *Cryptostrea*, *Hyotissa*, *Parahyotissa*)

L = 1 CI = 100 RI = 100

Figura 25– Inserção do Músculo de Quenstedt. Figura retirada de Stenzel, 1971.

A impressão dos músculos de Quenstedt está localizada abaixo da área ligamentar, na altura da boca do animal, formando uma leve e pequena marca.

27. Forma impressão músculo de Quenstedt

0 = redonda (*Crassostrea*, *Saccostrea*, *Striostrea*, *O. lurida*, *Hytotissa*, *Parahytotissa*, *Cryptostrea*, *Teskeyostrea*)

1 = oval/ alongada (*Lopha*, *Alectryonella*, *Dendostrea*, *O. edulis*, *O. equestris*, *O. puelchana*)

L = 3 CI = 33 RI = 75

28. Linha Palial

0 = presente (*Barbatia*)

1 = ausente (todos exceto *Barbatia*)

L = 1 CI = 100 RI = 100

Figura 26– Linha palial (figura retirada de Marques, 2012).

A linha palial na face interna dos bivalves isomiários é contínua ou quase contínua, se estendendo da inserção de um músculo adutor até o outro. É originada pela coalescência das inserções dos músculos retratores paliais radiais. Os anisomiários possuem uma disjunção da linha palial. Estes músculos retratores do manto são inseridos nas valvas por meio de feixes de diferentes tamanhos, produzindo uma série de inserções musculares em linha na direção da inserção do músculo adutor até o outro.

MUSCULATURA

29. Músculo adutor anterior

0 = presente (*Barbatia*)

1 = ausente (Todos exceto *Barbatia*)

L = 1 CI = 100 RI = 100

Os músculos adutores têm sido reconhecidos como uma sinapomorfia de Bivalvia; estes músculos são primitivamente de tamanho equivalente. A presença e o tamanho dos músculos adutores têm sido utilizados em outros estudos comparativos (Yonge, 1953b; Gilmour, 1990; Giribet & Wheeler, 2002).

30. Localização do músculo adutor posterior

0= cerca de 1/10 distante da borda (*Crassostrea*, exceto *C. rhizophorae*, *S. mordax*, *S. palmula*, *S. echinata*, *Dendostrea* exceto *D. sp2*, *Ostrea*, *Parahyotissa*, *Spondylus*, *Plicatula*, *Plicatulostrea*, *Isognomon*)

1 = cerca de 1/6 distante da borda (*C. rhizophorae*, *S. cucullata*, *S. glomerata*, *S. prismatica*, *L. cristagalli*, *D. sp2*, *C. permolis*, *T. weberi*, *H. hyotis*, *A. simplex*, *Lima sp.*)

L = 8 CI = 12 RI = 30

31. Músculo de Quenstedt

0= ausente (*Barbatia*, *Spondylus*, *Lima*, *Anomia*, *Plicatula*, *Plicatulostrea*, *Isognomon*)

1= presente (Ostreidae e Gryphaeidae)

L = 1 CI = 100 RI = 100

Figura 27– Músculo de Quenstedt. A) esquema da origem na massa visceral e inserção nas conchas (figura retirada de Stenzel, 1971); B) foto do músculo.

Os músculos de Quenstedt (Quenstedt, 1867: 598), nomeados por Stenzel, 1971, são pequenos músculos protratores das brânquias. São geralmente bem evidentes em ostras, originado na superfície interna das conchas abaixo dos umbos, e apresentam uma leve impressão. Acredita-se que são remanescentes do músculo retrator do pé (Dall, 1880, Stenzel, 1971, Harry, 1985, Galtsoff, 1964).

32. Localização do músculo de Quenstedt

0 = região anterior dos palpos (*S. palmula*, *S. mordax*, *S. prismatica*, *L. cristagalli*, *D. sp1*, *O. equestris*, *P. mcgintyi*)

1 = região posterior dos palpos (*C. virginica*, *C. gigas*, *S. cucullata*, *S. glomerata*, *S. echinata*, *D. folium*, *D. sp2*, *D. frons*, *O. edulis*, *C. permolis*, *T. weberi*, *H. hyotis*)

2 = região mediana dos palpos (*P. numisma*, *O. lurida*, *O. puelchana*, *A. plicatula*, *C. bilineata*, *C. rhizophorae*, *C. brasiliiana*, *C. mangle*)

L = 11 CI = 18 RI = 30

Cada músculo é mais grosso na sua inserção na valva e afina dentro da massa visceral. Levanta-se em cerca de 50° a partir da sua inserção, passa perto do canal que

separa a dobra manto do palpo labial exterior, vira para a frente e divide-se principalmente entre os tecidos conjuntivos, entre as lamelas interior e exterior da demibrânquia externa na região dorsal ou final das brânquias. A inserção do músculo na valva é muito próxima da posição da boca do animal. Neste carácter 32 existem duas otimizações igualmente parcimoniosas, o estado 1 pode embasar o nó 7 ou o nó 9. Na Figura (50; 51) foi escolhido o nó 7 com uma reversão no nó 9.

PÉ E BISSO

33. Pé

0 = presente (*Barbartia*, *Spondylus*, *Lima*, *Isognomon*, *Plicatula*, *Plicatulostrea*, *Anomia*)

1 = ausente (Ostreidae e Gryphaeidae)

L = 1 CI = 100 RI = 100

Figura 28– Esquema de uma *Lima* (Limidae), detalhe para o pé (figura retirada de Mikkelsen & Bieler, 2003).

O pé é geralmente usado para escavar em bivalves, mas é reduzido em alguns táxons sésseis. No entanto, a perda do pé em bivalves sésseis não é uma regra absoluta; *Spondylus americanus*, por exemplo, é uma espécie cimentada, mas com pé distinguível. O pé está presente nas fases larvares de bivalves sésseis, notavelmente em

ostreídeos (Harry, 1985), que inclui *Hytissa*, e *Plicatula*, ambos sem o pé como adultos.

BORDA DO MANTO

34. Papilas da prega média

0 = ausente (*Barbatia*)

1 = presente (Todos, exceto *Barbatia*)

L = 1 CI = 100 RI = 100

Figura 29– Borda do manto; pregas média e interna com papilas.

Como a maioria dos bivalves, a borda do manto nos ostreídeos possui 3 pregas paralelas. A prega interna é moderadamente alta, bem suprida com músculos e seios sanguíneos com papilas na margem livre. A prega média apresenta papilas em até duas linhas. A prega externa é a prega da concha e é separada da prega média por um sulco periostracal; sem tentáculos.

Exposto ao ambiente, as bordas do manto apresentam vários tipos de receptores (mecânicos, fotorreceptor, ou estímulos químicos) conectados com o sistema nervoso. A presença de papilas, ou pequenos tentáculos, nas pregas do manto tem sido analisada em vários estudos comparativos (Waller, 1978, 1998; Gilmour, 1963, 1967; Giribet &

Wheeler, 2002), podendo ser utilizada como caráter para diversos bivalves, incluindo ostras.

35. Disposição das papilas – prega média

0 = uniforme (*D. sp1*, *O. puelchana*, *O. lurida*, *C. permolis*, *H. hyotis*, *P. numisma*, *Spondylus*, *Plicatula*, *Plicatulostrea*, *Anomia*, *Isognomon*)

1 = alternada (*Lima sp.*, *P. mcgintyi*, *T. weberi*, *O. equestris*, *O. edulis*, *D. sp2.*, *D. frons*, *D. folium*, *A. plicatula*, *L. cristagalli*, *Saccostrea*, *Crassostrea*, *Striostrea*)

L = 5 CI = 20 RI = 60

36. Papilas pequenas da prega média

0 = ausentes (*C. virginica*, *S. prismatica*, *O. equestris*, *O. lurida*, *Lima sp.*, *P. onca*, *I. alatus*)

1 = presentes (*Crassostrea* exceto *C. virginica*, *Saccostrea*, *O. edulis*, *O. puelchana*, *Dendostrea*, *Alectryonella*, *Lopha*, *Teskeyostrea*, *Cryptostrea*, *Hytissa*, *Parahytissa*, *P. gibbosa*, *Spondylus*, *Anomia*)

L = 7 CI = 14 RI = 0

Figura 30– Papilas pequenas na prega média.

37. Papilas médias da prega média

0 = ausentes (*C. mangle*, *S. cucullata*, *S. glomerata*, *S. echinata*, *L. cristagalli*, *D. folium*, *O. puelchana*, *H. hyotis*, *Parahyotissa*, *Spondylus*, *Lima*, *Anomia*, *Isognomon*)

1 = presentes (*Crassostrea*, exceto *C. mangle*, *S. palmula*, *S. mordax*, *Striostrea*, *Dendostrea* exceto *D. folium*, *Ostrea*, exceto *O. puelchana*, *Alectryonella*, *Teskeyostrea*, *Cryptostrea*, *Plicatula*, *Plicatulostrea*)

L = 8 CI = 12 RI = 46

Figura 31– Papilas médias na prega média.

38. Papilas longas da prega média

0 = ausentes (*C. rhizophorae*, *C. gigas*, *C. bilineata*, *S. mordax*, *A. plicatula*, *D. sp1*, *D. frons*, *O. edulis*, *O. equestris*, *O. puelchana*, *O. lurida*, *C. permolis*, *T. weberi*, *H. hyotis*, *P. mcgintyi*, *P. numisma*, *S. americanus*, *P. gibbosa*, *P. onca*)

1 = presentes (*C. mangle*, *C. brasiliiana*, *C. virginica*, *S. cucullata*, *S. glomerata*, *S. palmula*, *S. echinata*, *S. prismatica*, *L. cristagalli*, *D. folium*, *D. sp2*, *Lima sp.*, *A. simplex*, *I. alatus*)

L = 7 CI = 14 RI = 53

Figura 32– Papilas longas na prega média.

Este caráter é igualmente parcimonioso, sendo neste cenário uma sinapomorfia iniciada no nó 9, e diversas reversões nos táxons seguintes.

39. Papilas da prega interna

0 = ausentes (*Barbatia*, *Anomia*, *Lima*)

1 = presentes

L = 2 CI = 50 RI = 50

40. Papilas prega interna

0 = ausentes (*Crassostrea* exceto *C. bilineata*, *Saccostrea* exceto *S. glomerata*, *Dendostrea*, *Lopha*, *Alectryonella*, *O. edulis*, *O. equestris*, *Cryptostrea*, *Teskeyostrea*, *Hyotissa*, *Parahyotissa*, *Isognomon*)

1 = presentes (*C. bilineata*, *S. glomerata*, *S. prismatica*, *O. puelchana*, *O. lurida*, *Spondylus*, *Plicatula*, *Plicatulostrea*)

L = 6 CI = 16 RI = 28

Este caráter é igualmente parcimonioso, sendo aqui utilizado como sinapomorfia no nó 1, como convergência em *P. mcgintyi*, *Lopha* e no nó 7 e como reversão no nó 9 e no 11.

Neste caráter 12 existem duas otimizações igualmente parcimoniosas, o estado 1 pode embasar o nó 1, 7, 9, 11. Na Figura (50; 51) foi escolhido o nó 1 como

sinapomorfia, uma convergência em *P. mcgintyi* e *Lopha*, com uma reversão nos nós 9 e 11.

41. Papilas pequenas

0 = ausentes (*C. virginica*, *C. rhizophorae*, *C. brasiliana*, *S. echinata*, *O. equestris*, *D. sp1*, *Alectryonella*, *Isognomon*, *Plicatula*)

1 = presentes (*C. mangle*, *C. gigas*, *C. bilineata*, *Saccostrea* exceto *S. echinata*, *Striostrea*, *Lopha*, *D. folium*, *D. frons*, *D. sp2*, *O. edulis*, *O. puelchana*, *O. lurida*, *Cryptostrea*, *Teskeyostrea*, *Hyotissa*, *Parahyotissa*, *Spondylus*, *Plicatulostrea*)

L = 8 CI = 12 RI = 12

Figura 33– Papilas pequenas na prega interna.

42. Papilas médias

0 = ausentes (*Crassostrea* exceto *C. bilineata*, *Saccostrea* exceto *S. glomerata*, *Lopha*, *D. folium*, *D. frons*, *D. sp2*, *O. edulis*, *Hyotissa*, *Parahyotissa*, *Spondylus*, *Plicatula*, *Isognomon*)

1 = presentes (*C. bilineata*, *S. glomerata*, *S. prismatica*, *Alectryonella*, *D.sp1*, *Ostrea* exceto *O. edulis*, *Cryptostrea*, *Teskeyostrea*, *Plicatulostrea*)

L = 8 CI = 12 RI = 30

Figura 34– Papilas médias na prega interna.

43. Papilas longas

0 = ausentes (*C. mangle*, *C. gigas*, *C. bilineata*, *S. glomerata*, *S. palmula*, *S. mordax*, *Striostrea*, *Dendostrea*, *O. edulis*, *O. puelchana*, *O. lurida*, *Lopha*, *Alectryonella*, *Teskeyostrea*, *Cryptostrea*, *Hyotissa*, *Parahyotissa*, *Plicatula*, *Plicatulostrea*)

1 = presentes (*C. brasiliana*, *C. rhizophorae*, *C. virginica*, *S. cucullata*, *S. echinata*, *O. equestris*, *Spondylus*, *Isognomon*)

L = 6 CI = 16 RI = 28

Figura 35– Papilas longas na prega interna.

44. Borda do manto - coloração

0 = ausente (*Barbatia*, *C. bilineata*, *C. gigas*, *S. palmula*, *S. prismatica*, *Alectryonella*, *O. edulis*, *O. lurida*, *Cryptostrea*, *P. mcgintyi*, *Lima*, *Plicatula*, *Plicatulostrea*, *Anomia*)

1 = presente (*Crassostrea* exceto *C. bilineata*, *C. gigas*, *Saccostrea* exceto *S. palmula*, *Lopha*, *Dendostrea*, *O. equestris*, *O. puelchana*, *Teskeyostrea*, *Hytissa*, *P. numisma*, *Spondylus*, *Isognomon*)

L = 10 CI = 10 RI = 30

Figura 36– Coloração borda do manto: A) ausente; B) presente.

MANTO

45. Manto – espessura

0 = delgada (*Barbatia*, *C. mangle*, *C. brasiliana*, *C. rhizophorae*, *C. virginica*, *Saccostrea* exceto *S. mordax*, *Lopha*, *Alectryonella*, *Dendostrea*, *Ostrea* exceto *O. lurida*, *Teskeyostrea*, *Parahytissa*, *Plicatula*, *Plicatulostrea*, *Anomia*)

1= espessa (*C. gigas*, *C. bilineata*, *S. mordax*, *Striostrea*, *O. lurida*, *Cryptostrea*, *Hytissa*, *Spondylus*, *Lima*, *Isognomon*)

L = 8 CI = 12 RI = 22

Os lobos do manto podem ser delgados e transparentes em algumas, em outras espécies os lobos são grossos e opacos, e parecem ser usados para estoque de gordura (Galtsoff, 1964).

46. Manto – musculatura palial

0 = escassa (*Barbatia*, *C. virginica*, *C. gigas*, *S. cucullata*, *S. glomerata*, *S. palmula*, *L. cristagalli*, *Dendostrea*, *Ostrea*, *Cryptostrea*, *Teskeyostrea*, *Hyotissa*, *Parahyotissa*, *Plicatula*, *Plicatulostrea*, *Anomia*, *Isognomon*)

1 = abundante (*C. mangle*, *C. brasiliiana*, *C. rhizophorae*, *C. bilineata*, *S. mordax*, *S. echinata*, *S. prismatica*, *Alectryonella*, *Spondylus*, *Lima*)

L = 7 CI = 14 RI = 33

Figura 37– Músculos paliais: A) escassa; B) abundante.

As fibras musculares radiais servem como músculos paliais retratores e se estendem para dentro dos lóbulos do manto para as margens dos lobos do manto, onde alguns terminam em tentáculos sobre as dobras do manto. Cada uma destas vertentes musculares está cercada por um vaso de sangue pulsante. Perto da margem dos lóbulos do manto, em particular, as fibras e os seus seios sanguíneos circundantes tendem a mostrar como sulcos radiais na face externa dos lóbulos do manto. Algumas configurações da concha na borda das valvas podem ser causadas por estas nervuras (Jaworski, 1928).

47. Manto – câmara promial

0 = ausente (*Barbatia*, *Ostrea*, *Dendostrea*, *Alectryonella*, *Lopha*, *Teskeyostrea*, *Cryptostrea*, *Spondylus*, *Lima*, *Isognomon*, *Plicatula*, *Plicatulostrea*)

1 = presente (*Crassostrea*, *Saccostrea*, *Hyotissa*, *Parahyotissa*, *Anomia*)

L = 3 CI = 33 RI = 86

A passagem promial separa o lobo direito do manto da massa visceral na altura do pericárdio, e fica entre o músculo adutor e o ligamento. Essa passagem é um atalho que conecta diretamente a câmara suprabranquial exalante com a região dorsal do animal, sem passar pela câmara anal. Pode estar presente em ambos os lados (direito e esquerdo), como em *Hyotissa*, ou estar presente apenas no lado direito, como em *Crassostreinae* e *Pycnodontinae* e ausente em *Ostreinae* (Harry, 1985).

48. Par de corações acessórios

0 = ausente (*Barbatia*, *Teskeyostrea*, *Parahyotissa*, *Spondylus*, *Lima*, *Plicatula*, *Plicatulostrea*, *Anomia*, *Isognomon*)

1 = presente (*Crassostrea*, *Saccostrea*, *Striostrea*, *Dendostrea*, *Ostrea*, *Cryptostrea*, *Hyotissa*)

L = 3 CI = 33 RI = 77

Figura 38– Coração acessório (ah).

O par de corações acessórios é uma estrutura tubular pareada ao longo das faces internas dos lobos do manto direito e esquerdo, que juntos formam a câmara exalante. O

coração acessório das ostras não é simplesmente uma estrutura tubular como descrita por Hopkins (1934, 1936) e Elsey (1935), são pulsáteis e levam o sangue até as aurículas (Harry, 1985). Este consiste em três braços de quase mesmo tamanho, juntos por um centro comum, formando um Y, ou apenas um braço em algumas espécies. Este caráter é igualmente parcimonioso, sendo escolhido neste cenário, iniciando no nó 1 como sinapomorfia, com uma reversão em *Teskeyostrea* e neste nó (5).

49. Forma do coração acessório

0 = único (*C. rhizophorae*, *C. gigas*, *C. bilineata*, *S. mordax*, *S. echinata*, *Lopha*, *Alectryonella*, *Dendostrea*, *Ostrea*, *Hytissa*)

1 = bifurcado (*Striostrea*, *S. palmula*, *S. glomerata*, *S. cucullata*, *C. virginica*, *C. brasiliiana*, *C. mangle*)

L = 4 CI = 25 RI = 50

50. Posição do coração acessório

0 = não chega ao músculo adutor (*S. echinata*, *Dendostrea*, *O. equestris*, *O. lurida*, *Cryptostrea*)

1 = na altura do músculo adutor (*C. mangle*, *C. rhizophorae*, *C. bilineata*, *S. cucullata*, *S. glomerata*, *Lopha*, *Alectryonella*, *O. edulis*, *Hytissa*)

2 = contorna o músculo adutor (*C. brasiliiana*, *C. virginica*, *C. gigas*, *S. palmula*, *S. mordax*, *S. prismatica*, *O. puelchana*)

L = 11 CI = 18 RI = 30

51. Calibre do coração acessório

0 = fino, menor que uma prega branquial (*C. rhizophorae*, *S. echinata*, *Lopha*, *D. folium*, *D. frons*, *D. sp1*, *O. edulis*, *O. equestris*)

1= médio, do mesmo tamanho de uma prega branquial (*C. mangle*, *C. brasiliana*, *S. cucullata*, *S. glomerata*, *S. palmula*, *Striostrea*, *Alectryonella*, *O. puelchana*, *O. lurida*, *Cryptostrea*)

2 = grosso, maior que uma prega branquial (*C. virginica*, *C. gigas*, *C. bilineata*, *S. mordax*, *D. sp2*, *Hyotissa*)

L = 9 CI = 22 RI = 41

52. Espessura da parede do coração acessório

0 = fina (*C. virginica*, *C. bilineata*, *S. glomerata*, *S. echinata*, *Lopha*, *Dendostrea*, *O. edulis*)

1 = grossa (*C. mangle*, *C. rhizophorae*, *C. brasiliana*, *C. gigas*, *S. cucullata*, *S. palmula*, *S. mordax*, *Striostrea*, *Alectryonella*, *O. equestris*, *O. puelchana*, *O. lurida*, *Cryptostrea*, *Hyotissa*)

L = 7 CI = 14 RI = 33

Todas as espécies que não possuem coração acessório, foram codificadas nos caracteres 49 a 52 como (-) missing data.

BRÂNQUIAS

53. Tamanho da brânquia

0 = maior que 2/3 da área da valva (*Barbatia*, *C. brasiliana*, *C. rhizophorae*, *C. gigas*, *C. bilineata*, *Saccostrea*, *Striostrea*, *Alectryonella*, *Dendostrea*, *O. equestris*, *Parahyotissa*, *Spondylus*, *Lima*)

1 = cerca de 1/3 da área da valva (*C. mangle*, *C. virginica*, *Lopha*, *O. edulis*, *O. puelchana*, *O. lurida*, *Cryptostrea*, *Teskeyostrea*, *Hyotissa*, *Plicatula*, *Plicatulostrea*, *Anomia*, *Isognomon*)

L = 7 CI = 14 RI = 50

Uma brânquia camada típica ocupa uma área de 1/3 a 2/3 do tamanho total do animal. Discussões adicionais são encontradas em Yonge, 1939; Allen & Sanders, 1973; Waller, 1998; Simone, 2009.

54. Conexão entre os filamentos branquiais

0 = ciliar (*Barbatia*)

1 = tecidual (todos, exceto *Barbatia*)

L = 1 CI = 100 RI = 100

Este caráter trata da presença de conexões entre os filamentos, ou seja, das junções interfilamentais. Em táxons basais, bem como em outras classes de moluscos, junções interfilamentais são puramente ciliares. No entanto, em alguns táxons de bivalves, eles são formados de pontes estreitas de tecido, compondo uma estrutura reticulada, como nos ostreóideos, ou por meio de pontes grandes, como em vários bivalves sifonados (Simone, 2009).

55. Canal alimentar

0 = estreito (*Barbatia*, *C. rhizophorae*, *C. brasiliiana*, *C. virginica*, *C. gigas*, *S. cucullata*, *S. glomerata*, *S. palmula*, *S. mordax*, *Lopha*, *Alectryonella*, *Dendostrea*, *Ostrea*, *Cryptostrea*, *Teskeyostrea*, *Hytissa*, *Parahytissa*, *Spondylus*, *Plicatula*, *Plicatulostrea*, *Anomia*, *Isognomon*)

1 = largo (*C. mangle*, *C. bilineata*, *S. echinata*, *Striostrea*, *Lima*)

L = 5 CI = 20 RI = 0

Figura 39– A) canal alimentar estreito; B) canal alimentar largo.

Sulcos alimentares são modificações de bordas ventrais das demibrânquias para o transporte de partículas de alimentos filtrados para os palpos via correntes ciliares. Em alguns casos, existem ranhuras alimentares em outros locais nas brânquias, por exemplo, na região dorsal entre as demibrânquias, ou entre as demibrânquias e estruturas vizinhas (isto é, do manto); estes casos podem nem sempre ser detectados anatomicamente e são confirmados por análise *in vivo* (Yonge, 1969). A mesma abordagem é necessária para investigar a variedade e a atividade dos cílios branquiais; essas características têm sido aplicadas em várias análises comparativas em Bivalvia (Owen, 1966, 1978; Atkins, 1938; Giribet & Wheeler, 2002).

56. Inserção da brânquia em relação aos palpos

0 = junto à extremidade posterior dos palpos (*Barbatia*, *C. mangle*, *C. rhizophorae*, *C. bilineata*, *S. cucullata*, *S. glomerata*, *S. palmula*, *S. mordax*, *S. prismatica*, *Lopha*, *D. frons*, *O. edulis*, *Spondylus*, *Lima*, *Plicatula*, *Anomia*)

1 = cerca de ¼ mais anteriorizado do que a extremidade posterior dos palpos. (*C. brasiliiana*, *C. virginica*, *C. gigas*, *Alectryonella*, *D. sp1*, *S. sp2*, *O. equestris*, *O. puelchana*, *O. lurida*, *Cryptostrea*, *Teskeyostrea*, *Hyotissa*, *Plicatulostrea*, *Isognomon*)

2 = na metade dos palpos (*S. echinata*, *D. folium*, *Parahyotissa*)

L = 12 CI = 16 RI = 44

Figura 40– A) término da brânquia junto aos palpos; B) término da brânquia no primeiro quarto dos palpos; C) término da brânquia na metade dos palpos.

Neste caráter 56 existem duas otimizações igualmente parcimoniosas, o estado 1 pode embasar o nó 12 ou o nó 14. Na Figura (50; 51) foi escolhido o nó 12 com uma convergência nos táxons *S. echinata*, *C. virginica*, *C. gigas* e *C. brasiliiana*

ESTRUTURAS RENOPERICÁRDICAS

57. Aurículas

0 = simples (todos, exceto *Hyotissa* e *Parahyotissa*)

1 = lobadas (*Hyotissa*, *Parahyotissa*)

L = 1 CI = 100 RI = 100

Figura 41– A) Aurícula simples; B) aurícula lobada.

A aurícula multilobada é encontrada em algumas espécies (e.g., *Hyotissa*), e pode apresentar uma adaptação para aumentar o contato da parede auricular com a hemolinfa dentro do pericárdio. A superfície interior glandular possivelmente auxilia no metabolismo da hemolinfa, passando principalmente através da parede auricular na cavidade pericárdica.

58. Ventrículo e reto

0 = reto passa pelo ventrículo (*Barbatia*, *Spondylus*, *Lima*, *Anomia*, *Isognomon*, *Plicatula*, *Plicatulostrea*, *Hyotissa*, *Parahyotissa*)

1 = reto não passa pelo ventrículo (*Crassostrea*, *Saccostrea*, *Ostrea*, *Dendostrea*, *Lopha*, *Alectryonella*, *Cryptostrea*, *Teskeyostrea*)

L = 2 CI = 50 RI = 88

Figura 42- A) reto passa pelo ventrículo; B) reto não passa pelo ventrículo.

Na maioria dos bivalves o reto passa através do coração, mas em ostras o reto passa por não passa pelo coração, sendo localizado na região posterior do pericárdio, contornando o músculo adutor.

59. Rins

0 = facilmente visíveis na região posterior do músculo adutor posterior (*Barbatia*, *Striostrea*, *Spondylus*, *Plicatulostrea*)

1 = inconspícuos (todos, exceto *Barbatia*, *Striostrea*, *Spondylus*, *Plicatulostrea*)

L = 4 CI = 25 RI = 0

SISTEMA DIGESTIVO

60. Localização dos palpos

0 = na região lateral da massa visceral (*Barbatia*)

1 = perto da região anterior (todos, exceto *Barbatia*)

L = 1 CI = 100 RI = 100

Figura 43 A) Palpo lateral em *Barbatia*; B) Palpo na região anterior em *Crassostrea*.

61. Palpo como estrutura mais anteriorizada da massa visceral

0 = ausente (*Barbatia*, *Lima*)

1 = presente (todos, exceto *Barbatia* e *Lima*)

L = 1 CI = 50 RI = 0

O palpo, ou palpo labial é a primeira estrutura selecionadora de alimentos em bivalves filtradores. Essa importante estrutura se relaciona com a brânquia de forma a capturar o filtrado. O palpo costuma ser classificado conforme a associação que este apresenta juntamente à brânquia (Stasek, 1963).

62. Fusão entre os hemipalpos externos

0 = ausente (*Barbatia*, *Crassostrea*, *S. glomerata*, *S. cucullata*, *S. palmula*, *Plicatulostrea*, *Anomia*, *Isognomon*)

1 = fundidos a 1/3 (*S. mordax*, *Striostrea*, *D. sp2*, *Cryptostrea*, *Teskeyostrea*, *P. numisma*, *Spondylus*, *Lima*)

2 = fundidos até a metade (*S. echinata*, *Lopha*, *Alectryonella*, *D. folium*, *D. sp.1*, *D. frons*, *O. edulis*, *O. equestris*)

3 = fundidos a 2/3 (*O. puelchana*, *O. lurida*, *Hytissa*, *P. mcgintyi*, *Plicatula*)

L = 13 CI = 23 RI = 67

Figura 44– Fusão dos palpos.

Em muitas ostras há uma fusão dos hemipalpos externos, que formam um capuz sobre os hemipalpos internos; tal característica foi observada entre os Ostreinae e o grau de fusão pode ser usada para diferenciar as espécies. Este caráter é igualmente parcimonioso, sendo aqui iniciada no nó G e convergindo no nó 3.

63. Palpos – borda ventral

0 = com pregas (*Barbatia*, *C. virginica*, *C. gigas*, *C. bilineata*, *Saccostrea*, *Striostrea*, *D. frons*, *O. puelchana*, *O. lurida*, *Spondylus*, *Lima*, *Anomia*, *Isognomon*)

1 = livre de pregas (*C. mangle*, *C. brasiliana*, *C. rhizophorae*, *Lopha*, *Alectryonella*, *D. folium*, *D. sp1*, *D. sp2*, *O. edulis*, *O. equestris*, *Cryptostrea*, *Teskeyostrea*, *Hyotissa*, *Parahyotissa*, *Plicatula*, *Plicatulostrea*)

L = 4 CI = 25 RI = 81

Figura 45– A) Borda com pregas; B) borda livre de pregas.

64. Projeção dendrítica dos palpos

0 = ausente (todos, exceto *Spondylus*, *Plicatula*, *Plicatulostrea*)

1 = presente (*Spondylus*, *Plicatula*, *Plicatulostrea*)

L = 2 CI = 50 RI = 50

Figura 46– Projeção dendrítica dos palpos.

65. Esôfago – comprimento

0 = curto (menor que a metade do tamanho do palpo) (*Barbatia*, *C. virginica*, *S. glomerata*, *Alectryonella*, *D. folium*, *D. sp2*, *Cryptostrea*, *Teskeyostrea*, *Hytissa*, *P. numisma*, *Spondylus*, *Plicatulostrea*, *Isognomon*)

1 = longo (metade do tamanho do palpo) (*C. mangle*, *C. brasiliana*, *C. rhizophorae*, *C. gigas*, *C. bilineata*, *S. cucullata*, *S. palmula*, *S. mordax*, *S. echinata*, *Striostrea*, *Lopha*, *D. sp1*, *D. frons*, *Ostrea*, *P. mcgintyi*, *Lima*, *Plicatula*, *Anomia*).

L = 9 CI = 11 RI = 3

Figura 47– A) Esôfago curto; B) esôfago longo. Relação do tamanho do esôfago indicado pela linha vermelha.

66. Esôfago – largura

0 = estreita (menor que metade do comprimento do esôfago) (*Barbatia*, *Crassostrea*, *S. palmula*, *Dendostrea*, *Ostrea*, *Teskeyostrea*, *Hytissa*, *Spondylus*, *Anomia*, *Plicatula*, *Plicatulostrea*, *Isognomon*)

1 = larga (maior que a metade do comprimento do esôfago) (*S. cucullata*, *S. glomerata*, *S. mordax*, *S. echinata*, *Striostrea*, *Lopha*, *Alectryonella*, *Cryptostrea*, *Parahytissa*)

L = 5 CI = 20 RI = 55

Figura 48– A) Esôfago estreito; B) esôfago largo. Relação da largura do esôfago indicada pela linha vermelha.

67. Tamanho do capuz dorsal

0 = metade da área de seleção 1 (sa1) (*Barbatia*, *S. cucullata*, *S. glomerata*, *Lopha*, *D. folium*, *Ostrea*, *Teskeyostrea*, *Hytissa*, *Parahytissa*)

1 = menor que a metade da área de seleção 1 (sa1) (*Crassostrea*, *S. palmula*, *S. mordax*, *S. echinata*, *Alectryonella*, *D. sp1*, *D. frons*, *D. sp2*, *Cryptostrea*, *Spondylus*, *Lima*, *Anomia*)

2 = do mesmo tamanho que a área de seleção 1 (sa1) (*Striostrea*)

L = 7 CI = 28 RI = 58

Figura 49 – A) Capuz dorsal com metade do tamanho da área de seleção; B) capuz dorsal menor que a metade da área de seleção; C) capuz dorsal do mesmo tamanho que a área de seleção. Relação do tamanho entre a área de seleção e o capuz dorsal indicado pelas linhas vermelhas.

68. Posição do escudo gástrico

0 = junto a área de seleção (sa1) abaulando a mesma (*Barbatia*, *C*; *mangle*, *C. brasiliiana*, *C. virginica*, *C. gigas*, *S. cucullata*, *S. glomerata*, *S. mordax*, *S. echinata*, *Alectryonella*, *D. folium*, *D. sp1*, *O. equestris*, *Spondylus*, *Lima*)

1 = junto à área de seleção 1 (sa1), sem deformar a sa1 (*C. rhizophorae*, *C. bilineata*, *S. palmula*, *Lopha*, *O. edulis*, *O. puelchana*, *O. lurida*, *Cryptostrea*, *Teskeyostrea*, *P. numisma*)

2 = afastado da área de seleção 1 (sa1) (*Striostrea*, *D. frons*, *D.sp2*, *Hytissa*, *P. mcgintyi*, *Plicatulostrea*, *Anomia*, *Isognomon*)

L = 17 CI = 11 RI = 28

Figura 50– Posição do escudo gástrico; A) junto à área de seleção, deformando a mesma; B) junto à área de seleção, sem deformar; C) afastado da área de seleção.

Existe uma bolsa na parede esquerda do estômago que é revestida pelo escudo gástrico. Esta recebe um ou mais aberturas de divertículos digestivos. Esta bolsa esquerda pode ser profundo e compacto ou ser achatada e estendida.

69. Aro esofágico

0 = ausente (*Barbatia*, *Spondylus*, *Lima*, *Isognomon*)

1 = presente (Todos exceto *Barbatia*, *Spondylus*, *Lima*, *Isognomon*)

L = 2 CI = 50 RI = 66

70. Ânus

0 = não pedunculado (*Barbatia*, *Crassostrea*, *S. cucullata*, *S. glomerata*, *S. mordax*, *Striostrea*, *Teskeyostrea*, *Hyotissa*, *Parahyotissa*, *Spondylus*, *Plicatula*, *Plicatulostrea*, *Anomia*)

1 = pedunculado (*S. palmula*, *S. echinata*, *Lopha*, *Alectryonella*, *Dendostrea*, *Ostrea*, *Cryptostrea*, *Lima*, *Isognomon*)

L = 5 CI = 20 RI = 71

Figura 51– A) Ânus não pedunculado; B) Ânus pedunculado.

71. Distância entre o ânus e o gânglio visceral

0 = 1/3 (*Barbatia*, *Alectryonella*, *D. folium*, *D.sp2*, *Ostrea*, *Parahyotissa*, *Spondylus*)

1 = 1/2 (*D. sp1*, *D. frons*, *Lima*)

2 = 2/3 (*Crassostrea*, *Saccostrea*, *Striostrea*, *Lopha*)

L = 5 CI = 20 RI = 71

SISTEMA NERVOSO

72. Gânglio pedioso

0 = presente (*Barbatia*, *Lima*, *Spondylus*, *Plicatula*, *Plicatulostrea*, *Anomia*, *Isognomon*)

1 = ausente (Todos exceto *Barbatia*, *Lima*, *Spondylus*, *Plicatula*, *Plicatulostrea*, *Anomia*, *Isognomon*)

L = 1 CI = 100 RI = 100

73. Número de nervos anteriores – gânglio visceral

0 = 1 (*Barbatia*, *C. mangle*, *C. brasiliana*, *C. virginica*, *C. gigas*, *C. bilineata*, *Lopha*, *P. numisma*, *Plicatulostrea*, *Anomia*, *Isognomon*)

1 = 2 (*C. rhizophorae*, *S. cucullata*, *S. glomerata*, *S. palmula*, *S. echinata*, *Alectryonella*, *Dendostrea*, *O. equestris*, *O. puelchana*, *P. mcgintyi*, *Lima*, *Plicatula*)

2 = 3 (*S. mordax*, *Striostrea*, *O. edulis*, *O. lurida*, *Spondylus*)

L = 10 CI = 20 RI = 42

Figura 52– Nervos do gânglio visceral, vista ventral.

74. Número de nervos posteriores

0 = 3 (*Barbatia*, *Crassostrea*, *Saccostrea*, exceto *S. echinata*, *Striostrea*, *O. equestris*, *Plicatulostrea*, *Anomia*, *Isognomon*)

1 = 2 (*S. echinata*, *Lopha*, *Alectryonella*, *D.sp1*, *D. frons*, *D. sp2*, *O. edulis*, *O. puelchana*, *Parahyotissa*, *Spondylus*, *Plicatula*)

2 = 1 (*D. folium*, *O. lurida*)

L = 6 CI = 33 RI = 71

75. Número de nervos laterais

0 = 0 (*Barbatia*, *S. glomerata*, *S. echinata*, *O. edulis*, *Lima*, *Plicatula*, *Isognomon*)

1 = 1 (*Crassostrea* exceto *C. gigas*, *S. cucullata*, *S. palmula*, *S. mordax*, *Lopha*, *D. folium*, *D. sp1*, *D. sp2*, *O. puelchana*, *O. lurida*, *Parahyotissa*, *Plicatulostrea*, *Anomia*)

2 = 2 (*Striostrea*, *Alectryonella*, *D. frons*, *O. equestris*, *Spondylus*)

3 = 3 (*C. gigas*)

L = 13 CI = 23 RI = 9

O gânglio visceral é alocado junto ao músculo adutor posterior. Possivelmente devido à importância funcional da área posterior de bivalves – a região em que maior interação com o meio ambiente ocorre – os gânglios viscerais são tipicamente o maior par.

76. Gânglio cerebral

0 = distinguível do conectivo, localizado a base dos palpos (*Barbatia*, *O. puelchana*, *Spondylus*, *Lima*, *Plicatula*, *Plicatulostrea*, *Isognomon*)

1 = indistinguível do conectivo (todos, exceto *Barbatia*, *O. puelchana*, *Spondylus*, *Lima*, *Plicatula*, *Plicatulostrea*, *Isognomon*)

L = 3 CI = 33 RI = 66

3.3 Análise cladística

São apresentados aqui a matriz dos caracteres na tabela 3. Os representantes do grupo externo estão representados na cor rosa. Foram levantados 76 caracteres e seus diversos estados não ordenados.

A única árvore obtida é apresentada na figura 50. Detalhes da árvore são apresentadas nas figuras 51, 53 e 53. Discussão e considerações apresentadas no item 4.

Tabela 3– Matriz dos caracteres.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>Barbatia candida</i>	0	0	0	0	0	0	0	-	0	0	0	-	-	-	-	-	-	0	0	0	0	-	-	0	0	0
<i>Crassostrea mangle</i>	1	1	2	1	1	-	0	-	0	0	0	-	-	-	-	-	-	2	2	0	1	1	0	3	0	1
<i>Crassostrea brasiliiana</i>	1	1	2	1	1	-	0	-	0	1	0	-	-	-	-	-	-	2	2	0	1	1	0	3	0	1
<i>Crassostrea rhizophorae</i>	1	1	2	1	1	-	0	-	0	1	0	-	-	-	-	-	-	2	2	0	1	1	0	3	0	1
<i>Crassostrea virginica</i>	1	1	2	1	0	1	1	0	0	1	0	-	-	-	-	-	-	2	2	0	1	1	0	3	1	1
<i>Crassostrea gigas</i>	1	1	2	1	0	1	0	-	0	0	0	-	-	-	-	-	-	2	2	0	1	1	0	3	1	1
<i>Crassostrea bilineata</i>	1	1	2	1	0	1	0	-	0	0	0	-	-	-	-	-	-	2	2	0	1	1	0	3	1	1
<i>Saccostrea cucullata</i>	1	1	1	1	1	-	1	0	0	1	1	0	1	2	-	1	0	2	2	0	1	1	0	3	1	1
<i>Saccostrea glomerata</i>	1	1	1	1	1	-	1	0	0	1	1	0	2	2	-	1	0	2	2	0	1	1	0	3	1	1
<i>Saccostrea palmula</i>	1	1	1	1	1	-	1	0	0	1	1	0	0	2	-	1	0	2	2	0	1	0	0	3	1	1
<i>Saccostrea mordax</i>	1	1	1	1	1	-	1	0	0	1	1	0	2	2	-	1	0	2	2	0	1	1	0	3	1	1
<i>Saccostrea echinata</i>	1	1	1	1	1	-	1	0	0	0	1	0	2	2	-	1	0	2	2	0	1	0	0	3	0	1
<i>Striostrea prismatica</i>	1	1	1	1	0	1	0	-	0	1	1	0	1	2	-	1	0	2	2	0	1	0	0	3	1	1
<i>Lopha cristagalli</i>	1	1	1	1	1	-	1	1	0	1	1	2	2	2	-	2	1	2	2	0	0	-	0	2	0	1
<i>Alectryonella plicatula</i>	1	1	0	1	0	0	1	0	0	1	1	2	2	2	-	2	1	2	2	0	1	0	0	3	1	1
<i>Dendostrea folium</i>	1	1	1	1	1	-	1	0	0	0	1	0	2	2	-	0	0	2	2	0	0	-	0	3	0	1
<i>Dendostrea sp 1</i>	1	1	1	1	1	-	1	0	0	1	1	0	1	2	-	0	0	2	2	0	0	-	0	3	0	1
<i>Dendostrea frons</i>	1	1	1	1	0	2	1	0	0	1	1	0	2	2	-	0	0	2	2	0	0	-	0	3	0	1
<i>Dendostrea cf. sandvichensis</i>	1	1	1	1	1	-	1	0	0	0	1	0	2	2	-	0	0	2	2	0	0	-	0	3	0	1
<i>Ostrea edulis</i>	1	1	1	1	0	1	1	0	0	0	1	1	1	2	-	1	0	2	2	0	0	-	0	3	0	1
<i>Ostrea equestris</i>	1	1	1	1	1	-	1	0	0	0	1	1	1	2	-	1	0	2	2	0	0	-	0	3	0	1
<i>Ostrea puelchana</i>	1	1	1	1	1	-	1	0	0	0	1	1	0	2	-	1	0	2	2	0	0	-	0	3	0	1
<i>Ostrea lurida</i>	1	1	1	1	1	-	1	0	0	0	1	1	0	2	-	1	0	2	2	0	0	-	0	3	0	1
<i>Cryptostrea permolis</i>	1	1	1	1	1	-	0	-	0	0	1	0	0	2	-	1	0	2	2	0	0	-	0	1	0	1
<i>Teskeyostrea weberi</i>	1	1	1	1	1	-	0	-	0	0	1	1	0	2	-	1	0	2	2	0	0	-	0	3	0	1
<i>Hyotissa hyotis</i>	1	1	1	1	0	2	1	0	1	0	1	2	0	1	1	-	1	2	2	0	0	-	1	0	0	1
<i>Parahyotissa mcgintyi</i>	1	1	1	1	1	-	1	0	1	0	1	2	0	1	0	-	1	2	2	0	0	-	1	0	0	1
<i>Parahyotissa numissima</i>	1	1	1	1	1	-	0	-	1	0	1	2	0	1	0	-	1	2	2	0	0	-	1	0	1	1
<i>Spondylus americanus</i>	1	2	1	0	0	3	0	-	0	0	0	-	-	0	-	-	-	1	1	1	0	-	-	0	0	0
<i>Lima sp.</i>	0	0	1	0	0	3	1	-	0	0	0	-	-	0	-	-	-	1	1	1	0	-	-	0	0	0
<i>Plicatula gibbosa</i>	1	2	1	0	0	0	1	0	0	0	1	1	2	0	-	-	-	1	1	1	0	-	-	1	0	0
<i>Plicatuloostrea onca</i>	1	2	1	0	1	-	0	-	0	0	1	1	2	0	-	-	-	1	1	1	0	-	-	1	0	0
<i>Anomia simplex</i>	0	0	1	0	1	-	0	-	0	0	0	-	-	0	-	-	-	2	1	0	0	-	-	0	0	0
<i>Isognomon alatus</i>	0	0	1	0	1	-	0	-	0	1	0	-	-	0	-	-	-	2	1	0	0	-	-	2	0	0

Tabela. 3 – Continuação

27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	
-	0	0	0	0	-	0	0	-	-	-	-	0	-	-	-	-	0	0	0	0	0	-	-	-	-	0	0	0	0	0	
0	1	1	0	1	2	1	1	1	1	0	1	1	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	0	
0	1	1	0	1	2	1	1	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	2	1	1	0	1	0	1	0	
0	1	1	1	1	2	1	1	1	1	1	0	1	0	0	0	1	1	0	1	1	1	0	1	0	1	0	1	0	0	0	
0	1	1	0	1	1	1	1	1	0	1	1	1	0	0	0	1	1	0	0	1	1	1	2	2	0	1	1	0	1	0	
0	1	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1	0	1	1	0	2	2	1	0	1	0	1	0	
0	1	1	0	1	2	1	1	1	1	1	0	1	1	1	1	0	0	1	1	1	1	0	1	2	0	0	1	1	0	0	
0	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	0	0	1	1	1	1	1	1	0	1	0	0	0	
0	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	
0	1	1	0	1	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1	1	1	2	1	1	0	1	0	0	0	
0	1	1	1	1	0	1	1	1	1	1	0	1	0	1	0	0	1	1	1	1	1	0	2	2	1	0	1	0	0	0	
0	1	1	0	1	1	1	1	1	1	0	1	1	0	0	0	1	1	0	1	1	1	0	0	0	0	0	1	1	2	0	
0	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	0	0	1	1	1	1	1	2	1	1	0	1	1	0	0	
1	1	1	1	1	0	1	1	1	1	0	1	1	0	1	0	0	1	0	0	0	1	0	1	0	0	1	1	0	0	0	
1	1	1	0	1	2	1	1	1	1	1	0	1	0	0	1	0	0	0	1	0	1	0	1	1	1	0	1	0	1	0	
1	1	1	0	1	1	1	1	1	1	0	1	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	0	2	0
1	1	1	0	1	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	0	1	0
1	1	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	
1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	1	0	0	0	1	0	0	2	0	0	1	0	1	0	
1	1	1	0	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	
1	1	1	0	1	0	1	1	1	0	1	0	1	0	0	1	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	
1	1	1	0	1	2	1	1	0	1	0	0	1	1	1	1	0	1	0	0	0	1	0	2	1	1	1	1	0	1	0	
0	1	1	0	1	2	1	1	0	0	1	0	1	1	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	
0	1	1	0	1	1	1	1	0	1	1	0	1	0	1	1	0	0	1	0	0	1	0	0	1	1	1	1	0	1	0	
0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	0	1	0	0	0	0	-	-	-	-	1	1	0	1	0	
0	1	1	1	1	1	1	1	0	1	0	0	1	0	1	0	0	1	1	0	1	1	0	1	2	1	1	1	0	1	1	
0	1	1	0	1	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	1	0	-	-	-	-	0	1	0	2	1	
0	1	1	0	1	2	1	1	0	1	0	0	1	0	1	0	0	1	0	0	1	0	-	-	-	-	0	1	0	2	1	
-	1	1	0	0	-	0	1	0	1	0	0	1	1	1	0	1	1	1	1	0	0	-	-	-	-	0	1	0	0	0	
-	1	1	1	0	-	0	1	1	0	0	1	0	-	-	-	-	0	1	1	0	0	-	-	-	-	0	1	1	0	0	
-	1	1	0	0	-	0	1	0	1	1	0	1	1	0	0	0	0	0	0	0	0	-	-	-	-	1	1	0	0	0	
-	1	1	0	0	-	0	1	0	0	1	0	1	1	1	1	0	0	0	0	0	0	-	-	-	-	1	1	0	1	0	
-	1	1	1	0	-	0	1	0	1	0	1	0	-	-	-	-	0	0	0	1	0	-	-	-	-	1	1	0	0	0	
-	1	1	0	0	-	0	1	0	0	0	1	1	0	0	0	1	1	1	0	0	0	-	-	-	-	1	1	0	1	0	

Tabela 3 – Continuação.

58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1	1	1	1	0	1	1	0	0	1	0	1	0	2	1	0	0	1	1
1	1	1	1	0	1	1	0	0	1	0	1	0	2	1	0	0	1	1
1	1	1	1	0	1	1	0	0	1	1	1	0	2	1	1	0	1	1
1	1	1	1	0	0	0	0	0	1	0	1	0	2	1	0	0	1	1
1	1	1	1	0	0	1	0	0	1	0	1	0	2	1	0	0	3	1
1	1	1	1	0	0	1	0	0	1	1	1	0	2	1	0	0	1	1
1	1	1	1	0	0	1	0	1	0	0	1	0	2	1	1	0	1	1
1	1	1	1	0	0	0	0	1	0	0	1	0	2	1	1	0	0	1
1	1	1	1	0	0	1	0	0	1	1	1	1	2	1	1	0	1	1
1	1	1	1	1	0	1	0	1	1	0	1	0	2	1	2	0	1	1
1	1	1	1	2	0	1	0	1	1	0	1	1	2	1	1	1	0	1
1	0	1	1	1	0	1	0	1	2	2	1	0	2	1	2	0	2	1
1	1	1	1	2	1	1	0	1	0	1	1	1	1	1	0	1	1	1
1	1	1	1	2	1	0	0	1	1	0	1	1	1	1	1	1	2	1
1	1	1	1	2	1	0	0	0	0	0	1	1	0	1	1	2	1	1
1	1	1	1	2	1	1	0	0	1	0	1	1	0	1	1	1	1	1
1	1	1	1	2	0	1	0	0	1	2	1	1	0	1	1	1	0	1
1	1	1	1	1	1	0	0	0	1	2	1	1	0	1	1	1	1	1
1	1	1	1	2	1	1	0	0	0	1	1	1	0	1	2	1	0	1
1	1	1	1	2	1	1	0	0	0	0	1	1	0	1	1	0	2	1
1	1	1	1	3	0	1	0	0	0	1	1	1	0	1	1	1	1	0
1	1	1	1	3	0	1	0	0	0	1	1	1	0	1	2	2	1	1
1	1	1	1	1	1	0	0	1	1	1	1	1	-	1	?	?	?	1
1	1	1	1	1	1	0	0	0	0	1	1	0	-	1	?	?	?	1
0	1	1	1	3	1	0	0	0	0	2	1	0	-	1	?	?	?	1
0	1	1	1	3	1	1	0	1	0	2	1	0	0	1	1	1	1	1
0	1	1	1	2	1	0	0	1	0	1	1	0	0	1	0	1	1	1
0	0	1	1	2	0	0	1	0	1	0	0	0	0	0	2	1	2	0
0	1	1	0	2	0	1	0	0	1	0	0	1	1	0	1	-	0	0
0	1	1	1	3	1	1	1	0	-	1	1	0	0	0	1	1	0	0
0	0	1	1	0	1	0	1	0	-	2	1	0	0	0	0	0	1	0
0	1	1	1	0	0	1	0	0	1	2	1	0	0	0	0	0	1	1
0	1	1	1	0	0	0	0	0	-	2	0	1	0	0	0	0	0	0

Figura 53– Única árvore mais parcimoniosa. L = 372; CI = 27; RI = 58.

Figura 54– Detalhe da árvore, grupo externo. Nós A-G.

Figura 55– Detalhe da árvore; Ostreoidea, nós 1-16.

Figura 56– Detalhe da árvore, Crassostreinae. Nós 16-26.

3.4 Análise molecular

Um dos objetivos do presente trabalho é a obtenção de dados moleculares através de DNA mitocondrial e nuclear, 16S, 28S, COI, ITS I e II, para complementar a análise filogenética, suscitando uma comparação e confronto com os dados obtidos pela análise exclusivamente morfológica.

A partir dos resultados positivos na extração do DNA através da extração salina, foi realizado o PCR através dos protocolos estabelecidos para cada primer, mas infelizmente não apresentaram resultados positivos. Os passos (tempo de anelação, temperatura e quantidade de ciclos) e a concentração das soluções foram revisados, e alterados, consequentemente os ciclos foram repetidos mesmo assim os resultados não foram positivos.

Foram realizados testes com outras espécies de bivalves, polioplacóforos e gastrópodes, na tentativa de verificar a eficiência dos protocolos, mas os resultados foram semelhantes ao obtidos nas amostras de ostreídeos. Apenas algumas amostras foram amplificadas, mas não apresentam qualidade quanto ao sequenciamento para que possam ser analisadas e comparadas. Os resultados obtidos para esses genes impossibilitaram a condução de quaisquer análises de relação entre as espécies.

Tabela 4 – Lista de espécies com dados positivos de PCR para sequenciamento; 28S e 16S.

Lotes (código)	Identificação	Espécie	Primer
A1	PFR MZ01	<i>D. frons</i>	28S
A2	1 a	<i>C. brasiliiana</i>	28S
A3	2 a	<i>D. frons</i>	28S
A4	10	<i>P. mcgintyi</i>	28S
A5	11	<i>D. frons</i>	28S
A6	12	<i>S. glomerata</i>	28S
A7	15	<i>C. brasiliiana</i>	28S
A8	16	<i>O. puelchana</i>	28S
A9	17	<i>O. puelchana</i>	28S
A10	19	<i>S. cucullata</i>	28S
B1	1	<i>C. brasiliiana</i>	28S

B2	2	<i>D. frons</i>	28S
B3	7	<i>C. virginica</i>	28S
B4	8	<i>S. prismatica</i>	28S
B5	1'	<i>C. brasiliiana</i>	28S
B6	1"	<i>C. brasiliiana</i>	28S
B7	2'	<i>D. frons</i>	28S
B8	5	<i>C. bilineata</i>	28S
B9	6	<i>S. prismatica</i>	28S
B10	7	<i>C. virginica</i>	28S
C1	8'	<i>S. prismatica</i>	28S
C2	9	<i>C. mangle</i>	28S
D1	10 a	<i>P. mcgintyi</i>	16S
E1	18	<i>C. rhizophorae</i>	16S
E2	39	<i>D. frons</i>	16S
E3	41	<i>S. mordax</i>	16S
E4	42	<i>D. frons</i>	16S
E5	44	<i>S. cucullata</i>	16S
E7	4 a	<i>D. frons</i>	16S
E9	8 a	<i>S. prismatica</i>	16S
E10	9 a	<i>C. mangle</i>	16S

Figura 57– Exemplo de cromatograma 10 – 100 pb.

Figura 60– Trecho do alinhamento consistente, cerca de 90 pb.

Diante da maioria dos resultados negativos, foram analisadas sequências retiradas do GenBank® para 28S das espécies listadas na tabela 5.

Tabela 5 - Sequências 28S retiradas do GenBank®

Espécie/sigla	Numero de acesso
<i>C. rhizophorae</i> (cr1)	AF137049
<i>C. rhizophorae</i> (cr2)	Z29547
<i>C. rhizophorae</i> (cr3)	FJ544287
<i>C. brasiliiana</i> (cb1)	FJ544307
<i>C. gigas</i> (cg1)	AF137051
<i>C. virginica</i> (cv1)	KC429429
<i>C. virginica</i> (cv2)	AF137050
<i>S. cucullata</i> (sc1)	AJ344329
<i>S. commercialis</i>	Z29552
<i>D. frons</i> (dfr)	AF377039
<i>D. folium</i> (dfl)	AF137040
<i>A. plicatula</i> (apl)	AF137037
<i>L. cristagalli</i> (lcr)	AF137038
<i>O. equestris</i> (oeq)	DQ242425
<i>O. edulis</i> (oed)	AF137047
<i>O. puelchana</i> (opu)	AF137042
<i>P. numisma</i> (pnum)	AF137035
<i>P. mcgintyi</i> (pmc)	AY376596
<i>H. hyotis</i> (hhy)	AF137036

Todas as sequências listadas nas tabelas 5 e 6 foram alinhadas no BioEdit® e ClustralW®, a árvore gerada no Mega 6® (Tamura *et.al.*, 2013), analisando as sequências por Maximum Parsimony (500 replicações) (3 árvores) (Fig. 61 – Consenso) para o gene 28S e 3 árvores mais parcimoniosas por Maximum Parsimony (500 replicações) para o gene 16S (Fig. 62 – Consenso).

Figura 61– Consenso de 3 árvores mais parcimoniosas – Maximum Parsimony – 28S. *C. virginica* (cv1), *C. virginica* (cv2), *C. rhizophorae* (cr1), *C. gigas* (cg1), *S. mararitacea* (smarg), *S. cucullata* (scu1), *C. rhizophorae* (cr2), *S. commercialis* (sco), *D. frons* (dfr), *C. brasiliiana* (cb1), *C. rhizophorae* (cr3), *O. equestris* (oeq), *P. mcgintyi* (pmc), *P. numisma* (pnum), *H. hyotis* (hhy), *O. edulis* (oed), *O. puelchana* (opu), *A. plicatula* (apl), *D. folium* (dfol), *L. cristagalli* (lcr).

O gene 16S também foi testado com as sequências depositadas no GenBank, listadas na tabela 6.

Tabela 6 - Sequências 16S retiradas do GenBank®.

Espécie/sigla	Numero de acesso
<i>C. rhizophorae</i> (cr2)	AJ312938
<i>C. brasiliiana</i> (cb1)	DQ839413
<i>C. gigas</i> (cg1)	AF280611
<i>C. virginica</i> (cv1)	AF092285
<i>C. angulata</i> (cang)	KC170322
<i>S. cucullata</i> (sc1)	EU815968
<i>S. cucullata</i> (sc2)	KC747111
<i>S. glomerata</i> (sglo)	AF353101
<i>S. palmula</i> (spalm)	FJ768524

<i>S. echinata</i> (sechin)	AF463493
<i>D. frons</i> (dfr)	AF052070
<i>D. folium</i> (dfl)	AF052069
<i>O. equestris</i> (oeq)	AF052074
<i>O. edulis</i> (oed)	DQ280032
<i>O. puelchana</i> (opu)	AF052073
<i>P. numisma</i> (pnum)	AY376598
<i>P. mcgintyi</i> (pmc)	AY376597
<i>H. hyotis</i> (hhy)	AY376599

Figura 62 – Consenso de 3 árvores mais parcimoniosas – Maximum Parsimony – 16 *S. C. rhizophorae* (cr2), *C. brasiliana* (cb1), *C. gigas* (cg1), *C. virginica* (cv1), *C. angulata* (cang), *S. cucullata* (sc1), *S. cucullata* (sc2), *S. glomerata* (sglo), *S. palmula* (spalm), *S. echinata* (sechin), *D. frons* (dfr), *D. folium* (dfl), *O. equestris* (oeq), *O. edulis* (oed), *O. puelchana* (opu), *P. numisma* (pnum), *P. mcgintyi* (pmc), *H. hyotis* (hhy).

4. DISCUSSÃO DOS CLADOGRAMAS

4.1 Morfo-anatômico

Na presente seção será discutido o cladograma obtido com base no estudo realizado (morfo-anatômico) e confrontados com dados de literatura, tanto sobre caracteres, quanto na sistemática.

Uma das características dos bivalves estudados, observada no decorrer do presente trabalho, é a enorme plasticidade fenotípica. Impressiona a quantidade e o grau de variação de estruturas homólogas e o número de homoplasias.

Tal plasticidade demanda, no mínimo, cuidados extras ao analisar dados alheios que, embora empregados neste estudo em vários pontos, como será visto a seguir, foram excluídos da lista de caracteres.

4.2 Caracteres extras não utilizados na análise

Alguns caracteres não foram utilizados na análise por se tratarem de características gerais de Bivalvia ou por serem autapomorfias.

A composição da concha, de aragonita, calcita ou ambas, é um caráter encontrado em diversas análises (e.g., Waller, 1990, 1998; Giribet & Weeler, 2002; Bieler *et.al.* 2014). Os Ostreoidea apresentam a composição de aragonita e calcita, também encontrada em Limoidea e Pectinoidea, mas é ausente em Arcoidea. Esse caráter é relacionado à estruturas foliares da concha, formando camadas subnacaradas, encontradas em Ostreoidea, Pectinoidea, Anomioidea e Limoidea.

Os depósitos de cálcio (chalky) são característicos de Ostreidae. São normalmente encontrados próximos ou na impressão do músculo adutor. A presença

desses depósitos fora da área da impressão muscular é autapomorfia do gênero *Teskeyostrea*.

Outra autapomorfia é facilmente reconhecida no gênero *Alectryonella*, são as “impressões digitais” (fingerlike impression) na face interna das valvas (Fig. 63). Tal característica não é encontrada em nenhum outro ostreídeo, e em nenhum dos representantes do grupo externo.

Figura 63 – Finger print em *Alectryonella plicatula*.

O umbo, normalmente contendo caracteres importantes nas filogenias de bivalves, aqui não foi incluído por ser inconspícuo em Ostreidae. Não apresenta padrões que possam ser codificados como nos demais bivalves (ortógiro, protógiro e opistógiro).

O tipo de ligamento também não foi incluído, pois todo grupo interno possui o ligamento do tipo alivincular (Carter, 1990a). De acordo com Waller, 1990, os bivalves equivalves normalmente possuem o componente externo do ligamento, e esta característica é plesiomórfica.

Outro caráter não incluído aqui se refere qual prega da borda do manto que secreta o perióstraco. Alguns estudos mostram que a secreção do perióstraco é feita pela prega média (Field, 1922; Morton, 2000a) em alguns bivalves. Em ostreídeos (e outros bivalves como em *Acanthocardia*) foi comprovado que a secreção é feita pela prega externa (Kessel, 1944; Brow, 1952; Beedham, 1958).

Entre os Pycnodontinae (*Hyotissa* e *Parahyotissa*), o músculo adutor possui a margem ventral mais elevada (Harry, 1985), sendo esta uma autapomorfia do grupo, não sendo utilizada aqui por ser uma característica variável.

Os tipos de estômago descritos por Purchon (1957) também não foram utilizados, pois todos os representantes aqui escolhidos apresentam um estômago do tipo III.

Além destas características, dados sobre a ontogenia e reprodução não foram incluídos. Alguns autores, e.g., Bandel (1988), Bandel et.al., (1997) e Riedel (2000), têm chamado a atenção para a importância dos caracteres larvais em análises comparativas, entretanto, um esforço nesse sentido mostrou-se infrutífero, uma vez que a maior parte do conhecimento atual é restrito à espécies economicamente importantes. A larva, ao se fixar no substrato, em ostreídeos, imediatamente perde o pé (Waller, 1998), sendo uma característica exclusiva de Ostreoidea. Na reprodução, os gêneros mais representativos, *Ostrea* e *Crassostrea* apresentam formas diferentes. *Ostrea* é caracterizada por ser incubatória, a fecundação ocorre nos espaços na massa visceral; já *Crassostrea* libera os gametas na água, como faz a maioria dos bivalves.

4.3 Espécies de ostreídeos utilizados como grupos externos funcionais.

A fim de provar o monofiletismo de Crassostreinae (*Saccostrea*, *Striostrea*, *Crassostrea*), foram utilizados 15 ostreídeos como grupo externo funcionais: *Cryptostrea permolis*, *Teskeyostrea weberi*, *Ostrea puelchana*, *Ostrea lurida*, *Ostrea edulis*, *Ostrea equestris*, *Dendostrea* sp.1, *Dendostrea* sp.2, *Dendostrea folium*, *Dendostrea frons*, *Lopha cristagalli*, *Alectryonella plicatula*, *Hyotissa hyotis*, *Parahyotissa mcgintyi*, *Parahyotissa numisma*.

Os Ostreinae (*Cryptostrea*, *Teskeyostrea*, *Ostrea* e *Dendostrea*) e Lophinae (*Lopha* e *Dendostrea*) são caracterizados, principalmente, pela ausência de câmara promial e presença de dentículos marginais. Essas duas características juntas, principalmente, os separam de Crassostreinae.

Os grifeídeos (*Hyotissa* e *Parahyotissa*) diferem dos demais ostreídeos pela presença de câmaras vesiculares nas valvas, além do caso especial de *Hyotissa* que apresenta a câmara promial nos ambos lobos.

4.4 Análise da árvore

Quase todos os caracteres utilizados para a obtenção do cladograma final (Fig. 53) foram extraídas da amostragem estudada, com pouca influência dos dados de literatura.

Na única árvore mais parcimoniosa obtida, os nós do grupo externo de A-G foram identificados. Os nós do grupo interno, Ostreidae, de 1-16 (Fig. 64). Serão discutidos aqui os principais caracteres de cada nó.

Os nomes apresentados em cada nó no grupo interno, referem-se à nomenclatura já utilizada entre os ostreídeos, e são apresentadas aqui algumas modificações quanto aos gêneros e novas tribos e subtribos.

No nó A, o enraizamento com *Barbatia candida* (Pteromorphia: Arcidae) foi escolhido por ser um representante dimiário bem distante do grupo interno.

O nó B representa os Pteriomorphia monomiários. Este nó é suportado por 11 sinapomorfias. Os caracteres 18 (charneira heterodonte) e 19 (ligamento interno em forma de gota) são os de maior destaque.

O nó C agrupa os táxons *Anomia* e *Isognomon*, suportado por 5 convergências. A charneira (caráter 18) sofre uma convergência, de uma charneira heterodonte para

uma charneira sem dentes, sendo o ligamento em forma de gota, o que os diferencia dos ostreídeos.

O nó D é suportado por 4 sinapomorfias. Os dentes laterais (caráter 20) são encontrados em *Lima*, *Spondylus*, *Plicatula* e *Plicatulostrea*. Este caráter é utilizado por Giribet & Wheeler (2002) e Bieler et. al. (2014). Tais autores, citam que os dentes laterais juntamente com os dentes cardinais, formam a definição de dentes heterodontes.

Figura 64– Árvore com nós A-G e 1-16.

A quantidade de feixes musculares (caráter 46) no nó D, é observada pela musculatura palial abundante (apresentando vários feixes musculares, grossos, por toda a extensão do manto mais concentrados na região do músculo adutor) e escassa (com poucos feixes musculares, normalmente finos e espaçados). Os táxons *Lima* e *Spondylus* possuem feixes abundantes por todo o manto.

A fusão dos hemipalpos externos (caráter 62), neste caso a extensão de 1/3, é bem comum em ostreídeos. Tal sinapomorfia é compartilhada com *Lima* e *Spondylus*, surgindo como convergência em diversos táxons do grupo interno, e corrobora com as observações de Harry (1985) quanto a variação na fusão dos hemipalpos externos.

A última sinapomorfia do nó refere-se ao número de nervos anteriores do gânglio visceral (caráter 73). Existe uma grande variação no número de nervos tanto no grupo externo quanto interno.

O nó E é suportado por 8 sinapomorfias. É neste nó que a fixação por cimentação ao substrato está em destaque [caráter 1 (1)] e, diferentemente dos representantes do grupo interno, se fixam pela valva direita [2 (1)]. Há uma exceção entre os ostreídeos, *Cryptostrea* que se fixa por ambas as valvas (Harry, 1985), mas normalmente é fixada pela esquerda. Neste cenário, o caráter 2 em *Cryptostrea* foi codificado como (2 – fixada pela valva esquerda). As papilas na prega interna, estado 1 (caráter 39), une *Spondylus*, *Plicatula* e *Plicatuloostrea* aos ostreídeos. *Lima*, *Anomia* e *Barbatia* não possuem papilas na prega interna. Em especial o gênero *Lima*, apresenta tentáculos e não papilas. Os tentáculos tem, por definição, normalmente superfície anelada que realiza a defesa e a captura de alimento (Yonge, 1957a), além de proporcionar a movimentação da água internamente, como as papilas nos ostreídeos. Aqui a presença de papilas na prega interna em *Lima* foi codificado como (-), não aplicável, por não serem papilas comparáveis aos demais táxons.

A posição do palpo como estrutura mais anteriorizada (caráter 61), os palpos estão localizados na região anterior, sendo uma das primeiras estruturas identificadas nas partes moles. Apenas *Barbatia* e *Lima* não apresentam os palpos como estrutura mais anteriorizada. Este caráter foi utilizado por Bieler *et.al.* (2014) como posição relativa dos palpos labiais (138, p.41).

A projeção dendrítica dos palpos (caráter 65), é uma estrutura localizada entre os palpos e é característico de Pectinoidea, mas a estrutura é presente em *Plicatula*, *Plicatulostrea* e em *Spondylus*.

O nó F agrupa *Spondylus* a *Plicatula*, suportado por 7 sinapomorfias não homoplásticas, 2 convergências e 2 reversões. Os caracteres 11, 12 e 13 referem-se à chomata. Os gêneros *Plicatula* e *Plicatulostrea* possuem chomata como os ostreídeos (exceto *Crassostrea*). O caráter 13 aqui é uma reversão do tipo de chomata, pois por mais que a estrutura tenha o mesmo nome para os ostreídeos, *Plicatula* e *Plicatulostrea* não possuem as divisões designadas por Stenzel (1971) e Harry (1985).

A forma da impressão muscular reniforme (caráter 24) é uma sinapomorfia de Plicatulidae também presente no gênero *Cryptostrea*. Na Fig. (50; 51) este caráter foi utilizado mostrando-o suportando o nó F com duas convergências, uma em *Teskeyostrea* e outra no nó C, e uma reversão no nó 4.

As papilas (caracteres 37, 43) são estruturas que se apresentam diferentemente entre os gêneros, até mesmo entre as espécies. Este caráter não é normalmente utilizado pela literatura, pois tais estruturas podem sofrer modificações de acordo com a contração do animal. Torigoe (1981) considera que o arranjo e tamanhos das papilas da borda do manto têm valor taxonômico dentre os ostreídeos. No presente trabalho, foram apresentados 3 tamanhos distintos (curtas, médias e longas) que se mostraram em um certo padrão entre as espécies.

A quantidade de feixes da musculatura palial, (caráter 46) já apresentado no nó D aqui aparece também como reversão. O tamanho que as brânquias ocupam em relação ao tamanho total do animal, neste caso, 2/3 do total (caráter 53). Esta convergência é compartilhada por vários táxons entre os ostreídeos. A presença de pregas até a borda dos palpos (caráter 63), aparecendo primeiro neste nó, mas converge em outros táxons do grupo interno. As pregas dos palpos, até o momento não foram utilizadas como caráter. Outra sinapomorfia importante é quanto a posição do escudo gástrico (caráter 68). De acordo com a descrição de Purchon (1957), o escudo gástrico pode estar localizado em diferentes alturas no assoalho estomacal, mas sempre está associado à dobras, perto da área de seleção, que auxiliam na fixação da estrutura para o processo de digestão.

O nó G é suportado por 7 sinapomorfias, sendo 5 convergências. Dentre as mais importantes estão as seguintes: As valvas sem ornamentação externa (caráter 5), característica esta compartilhada por ostreídeos, converge também com *Anomia* e *Isognomon* do grupo externo; o término das demibrânquias e relação aos palpos (caráter 56), é, neste caso, quando a demibrânquia termina no primeiro quarto entre os hemipalpos, característica compartilhada com *Isognomon* e representantes de quase todos os gêneros de Ostreidae. A inserção das brânquias nos palpos é uma característica utilizada em Tëmkin (2006: caráter 26) e por Bieler *et.al.* (2014). A fusão dos palpos (caráter 62) é uma característica levada em conta na maioria dos estudos anatômicos. O grau de fusão dos palpos é variável entre as espécies, corroborando com as observações de Harry (1985) para ostreídeos. .

A partir deste ponto serão discutidos os nós do grupo interno, de 1-25.

O nó 1 representa a família **Ostreidae**. Ele é bem suportado por 21 sinapomorfias, incluindo 3 convergências e 3 reversões. A sinapomorfia apresentada no caráter 2

agrupa todos que se fixam ao substrato pela valva esquerda. Segundo Harper (1992), hábito de cimentação nos bivalves aconteceu várias vezes na evolução de Bivalvia, mas o mecanismo de cimentação pós-larval é ainda obscuro. Igualmente ao caráter 2, o caráter 4 os agrupa pela forma inequivalve das valvas, sendo a valva esquerda (fixada ao substrato) maior e côncava, e a valva direita menor, normalmente opercular, levemente convexa ou plana. Tal característica é citada por diversos autores (e.g., Stenzel, 1971; Yonge, 1979; Harry, 1985), e utilizada como caráter em filogenias (e.g., Waller, 1998; Giribert & Weleer, 2002; Bieler *et.al.* 2014).

Chomata, no que se refere à distribuição e tipos, são codificados nos caracteres 13 e 14. A convergência no caráter 13, estado 0 (chomata presente até o primeiro terço) aparecem nos gêneros *Ostrea*, *Cryptostrea*, *Teskeyostrea*, *Hyotissa*, *Parahyotissa* e em *Saccostrea palmula*. Este caráter já foi citado como convergência no nó F (estado 2), de acordo com distribuição de chomata por toda a valva em *Plicatula* e *Plicatulostrea*. Os tipos de chomata (Gryphaeidae e Ostreidae) (caráter 14) foram determinados por Stenzel (1971) e aceitos por Harry (1985). Tal classificação separa a chomata diferentemente nas duas famílias, de acordo com a classificação proposta por Harry (1985) seguida aqui: Gryphaeidae e Ostreidae. A maioria dos táxons que representam Ostreidae neste estudo, possuem o tipo de chomata ostreidae, tendo as sinapomorfias 14 e 16 suportando este nó 1, normalmente dispostas em uma única linha (caráter 17), com exceção de Lophina e Hyotissina (novas subtribos aqui introduzidas e explicadas na discussão dos seus respectivos nós), que possuem chomata dispostas em várias linhas na margem das valvas.

Os dentes na charneira e a forma do ligamento (caracteres 18, 19 e 20) separam todo grupo interno dos grupos externos. Todos os ostreídeos não possuem dentes na charneira e o ligamento é em forma de linha. Táxons como *Anomia* e *Isognomon*, que

também não apresentam dentes na charneira (caráter 18) resultaram como uma convergência com o nó C. A presença de dentes laterais surge no nó D, mas desaparece nos ostreídeos, sendo aqui uma reversão do caráter 20.

Os ostreídeos são agrupados também em relação ao músculo de Quenstedt. A presença deste músculo (e sua impressão) (caracteres 26 e 31), é considerada por diversos autores (e.g., Stenzel, 1971; Harry, 1985) remanescente do retrator do pé. A posição que músculo de Quenstedt foi utilizado como caráter (32), sendo observada variação quanto a posição de inserção do músculo na massa visceral em relação à base dos palpos. A posição posterior, é aqui uma sinapomorfia do nó 1.

A ausência do pé (caráter 33) é aqui considerada outra sinapomorfia de Ostreidae. Na ontogenia, a perda do pé após a cimentação é típica de Ostreoidea (Harry, 1985, Waller, 1998). Este caráter foi utilizado em Giribet & Wheeler (2002) (caráter 116) e Bieler *et.al.* (2014) (caráter 70).

O coração acessório (caráter 48) é outra sinapomorfia encontrada em todos os ostreídeos, com algumas variações de tamanho, números de ramos e calibre.

As brânquias são eulamelibranquiais (filamentos adjacentes com lamelas fundidas por conexões teciduais, formando orifícios entre eles) e plicadas (muitos filamentos pequenos de tamanhos uniformes formando pontes entre os filamentos grandes e entre as dobras das plicas). Essa ligação tecidual é explorada pelo caráter 54 (1).

O reto, em bivalves, normalmente passa através do ventrículo, mas nas ostras o reto é livre do mesmo, passando por trás do pericárdio (caráter 58). A exceção é *Hyotissa* e *Parahyotissa* que possuem a condição plesiomórfica.

O nó 2, representa a subfamília Cryptostreinae. Esta nova subfamília aqui criada, agrupa os gêneros *Cryptostrea* e *Teskeyostrea* que foram classificados como Ostreinae - Cryptostrini por Harry (1985). Este nó é suportado por uma convergência (44) e uma

reversão (67). Por serem gêneros monotípicos e por não existirem trabalhos sobre a anatomia, morfologia, distribuição e dados moleculares, a posição destes ainda é incerta. *Teskeyostrea* apresenta externamente a forma de um anomídeo, mas com todas as características internas de um ostreídeo (e.g., chomata, músculo adutor, palpos entre outras). Os dois gêneros possuem uma autapomorfia em comum, a presença de depósitos de cálcio (chalky deposits) fora da área da impressão muscular.

O nó 3, que pela classificação de Harry (1985) é Pycnodontinae, é suportado por 1 sinapomorfia não homoplástica e duas convergências. As plicas na margem das valvas aparecem pela primeira vez neste nó (caráter 7), sendo característico também para os demais representantes de Ostreinae. Os gêneros *Hyotissa* e *Parahyotissa* eram, até o momento, classificados como Gryphaeidae-Pycnodontinae (Stenzel, 1959), as demais subfamílias revisadas por Stenzel (1971) e Harry & Dockery (1983), Gryphaeinae e Exogyrinae, são extintas (). Nesta análise tal agrupamento surgiu entre os Ostreidae, possuindo mais semelhanças com os Ostreidae do que diferenças significativas que fizessem tal grupo representar outra família. Uma vez que os táxons do gênero *Gryphaea* são fósseis, é impossível a comparação a nível anatômico para confirmar que ambos os gêneros viventes sejam mesmo identificados como Gryphaeidae. Dados de Stenzel (1971) sobre os grupos fósseis, as conchas largas, pesadas e que não apresentam chomata ou qualquer impressão dos mesmos entre os registros fósseis não corroboram com os táxons atuais, mesmo se comparados só as valvas ou impressões delas.

O nó 4, representa a tribo Hyotissini, já descrita por Harry (1985). é suportado 13 sinapomorfias, sendo 4 delas não homoplásticas, 5 convergências e 4 reversões. As mais representativas são: a presença de câmaras nas conchas (caráter 9), que é uma autapomorfia de Hyotissini, denominadas por Stenzel (1971) de estruturas vesiculares da concha. A presença de chomata em ambas as valvas (caráter 12), também é

característica, mas é compartilhada com Lophini (nó 12). Diante da classificação de chomata realizada por Harry (1985) para os grifeídeos, o caráter 14 é uma sinapomorfia deste nó pelas características de chomata. Chomata, de acordo com a disposição em várias linhas dos dentículos na borda das valvas (caráter 17) é aqui uma convergência, convergente também com os representantes de Lophini. De acordo com Stenzel (1971) todos os Pycnodontinae possuem chomata como caráter especial. No início, os gêneros primitivos possuíam espécies com dentículos baixos, estreitos e curtos, formando cumes com suas correspondentes depressões; esta característica é similar à encontrada em muitos Ostreinae; diferem apenas no número (apresentam cerca de 20 dentículos por centímetro) e quanto à distribuição entre as valvas direita e esquerda. A primeira organização de importância taxonômica em ostras foi feita por Fischer de Waldheim (1835) que estabeleceu o gênero *Pycnodonte* como base deste padrão. Posteriormente, diversos autores contribuíram na avaliação deste padrão de chomata dos grifeídeos sendo tratados como caracteres de valores taxonômicos (e.g., Douvillé, 1911; Ranson, 1939, 1941).

A partir desta observação, podemos dizer que os tipos de chomata característicos de ambas as famílias (aqui representadas como subfamílias) por Harry, podem ter uma única classificação para Ostreoidea, tendo apenas uma modificação encontrada nos representantes de Pycnodontinae. Esta característica corrobora com a posição de *Hytissa* e *Parahytissa* dentro de Ostreidae, uma vez que os representantes de Gryphaeinae e *Gryphaeostrea* (Exogyrinae) (ambos representantes fósseis) não apresentam dentículos (já discutidos acima) como também ocorre em *Crassostrea* (Stenzel, 1971).

De acordo com a classificação quanto às formas de impressão muscular denominadas por Stenzel (1959) os tipos são divididos entre os grifeídeos (classe

convexa) e os ostreídeos (classe côncava). A classe convexa (caráter 23) é sinapomorfia de Hyotissini.

A câmara promial aparece nesse nó como uma convergência (caráter 47), convergente com *Anomia*. *Hyotissa* apresenta a câmara promial de ambos os lados, sendo considerada a presença da câmara promial do lado esquerdo uma autapomorfia não utilizada neste cenário. De acordo com as observações de Stenzel (1971) gêneros que possuem a passagem promial não são incubatórias, característica esta que auxilia na distinção entre Crassostreinae (não incubatórias) e Ostreinae (incubatórias).

A aurícula lobada (caráter 57) também é uma sinapomorfia de Pycnodontinae. São caracterizadas pela formação de bolsas intercaladas dispostas por toda a aurícula. A reversão no caráter 58 refere-se ao reto passando pelo pericárdio, já comentado como sinapomorfia no nó 1.

A fusão entre os hemipalpos externos palpos à 2/3 (caráter 62: 3) é encontrada em *Hyotissa* e em *P. mcgintyi*. Esta característica é também encontrada como convergência no nó 7 e em *Plicatulostrea*. Como já dito anteriormente, a fusão dos palpos é variável, mas característica de cada espécie (Harry, 1985).

P. mcgintyi e *P. numisma* são táxons irmãos, suportados 5 sinapomorfias, sendo 1 sinapomorfia não homoplástica, 2 convergências e 2 reversões. Os dentículos do tipo lath, caracterizados por chomata alongados, normalmente até a região mediana das valvas, (caráter 15), é sinapomorfia entre os táxons irmãos. *Hyotissa* possui uma combinação de chomata vermicular e lath, sendo este último, exclusivo de *Parahyotissa*.

A ausência de coração acessório é apresentada neste nó por uma reversão do caráter 48. De acordo com Harry (1985), as primeiras estruturas neobranquiais em Hyotissini

(assim denominado pelo autor) não são expandidos e estendidos suficientemente a formar um coração acessório.

A altura do término das brânquias em relação aos palpos é aqui uma convergência (caráter 56), caráter já discutido no nó G. Tal caráter é utilizado por Tëmkin (2006: caráter 26) e por Bieler *et.al.* (2014).

Nota-se aqui que os táxons antes identificados como Gryphaeidae (= Pycnodontinae), são mais próximos dos Ostreinae (aqui = Eostreinae, Ostreinae e Ostreolinae) do que os táxons *Cryptostrea* e *Teskeyostrea* classificados como Ostreinae por Harry (1985). Aqui a nomenclatura utilizada por Harry foi mantida para subfamília dos táxons *Hyotissa* e *Parahyotissa*, transferindo-os para a família Ostreidae.

O nó 5, subfamília Eostreinae, subfamília nova, é suportada 4 sinapomorfias, sendo 1 sinapomorfia não homoplástica e 3 convergências. Os Ostreinae, com exceção de *Lopha*, possuem a impressão muscular em forma de lua com as extremidades arredondadas (27: 1). A forma alongada da impressão do músculo de Quenstedt é neste nó, outra sinapomorfia.

Os representantes de Eostreinae *O. puelchana* e *O. lurida* foram classificados por Harry (1985) como subespécie uma de *Ostrea* (*Eostrea*); aqui *Eostrea* é elevado à gênero, e os táxons irmãos, cujo nó é suportado por 5 sinapomorfias, sendo 4 convergências e 1 reversão.

O músculo de Quenstedt na posição mediana (caráter 32) agrupam os táxons *Eostrea puelchana* e *Eostrea lurida*, além da disposição das papilas (caráter 40), calibre do coração acessório (caráter 51), fusão dos palpos à 2/3 (caráter 62) e a presença de pregas até a margem ventral dos palpos (caráter 63).

O nó 6 representa a subfamília Ostreinae, já utilizada por Harry, 1985. Tal denominação é mantida uma vez que a espécie tipo de *Ostrea*, *O. edulis*, resultou no nó.

No momento esse parece ser o único representante do gênero *Ostrea*. Este ramo possui 4 sinapomorfias, sendo 1 sinapomorfia não homoplástica, 1 convergência e 2 reversões. A presença de chomata até a região mediana das valvas (caráter 13) é uma sinapomorfia homoplástica que suporta este nó. A convergência do caráter 35 (1) refere-se à alternância do tamanho das papilas na prega média em *Ostrea edulis*. Os caracteres 51 e 52 aparecem aqui como reversões, se referem ao coração acessório quanto ao calibre e quanto à espessura da parede da estrutura, ambos aqui observados como finos.

O nó 7, denominado aqui como tribo Ostreolini, nova tribo, em referência ao gênero *Ostreola*, criado por Harry (1985) para *O. equestris*, é suportado por 5 reversões. Tais reversões caracterizam a mudança nas estruturas entre as espécies dentro de Ostreinae.

O nó 8, subfamília sem nome, é suportada por 1 sinapomorfia não homoplástica e 3 convergências. *Dendostrea* sp.1 é normalmente identificada por diversos catálogos como *D. frons* de forma oval. Através das análises de comparação e, de acordo com a descrição original e o tipo estudado (Fig. 3), foi verificado que a forma oval de *D. frons*, mostra-se como uma nova espécie. A coloração escura da borda das valvas (caráter 10) é uma convergência, caráter não encontrado em *D. frons*. A presença de chomata apenas na valva esquerda e suas respectivas depressões na valva direita (caráter 12) é também uma convergência com *Ostrea* em todos os representantes do gênero *Dendostrea*. A sinapomorfia que representa o tipo Lophine de chomata (caráter 16), é também compartilhado por todas as *Dendostrea*.

O nó 9, representa a subfamília Lophinae (já denominada por Harry, 1985) suportada por 4 sinapomorfias, sendo 1 sinapomorfia não homoplástica, 1 convergência e 2 reversões. O caráter 13 agrupa os táxons dos nós seguintes, com exceção de *Striostrea* e *S. cucullata* em relação à distribuição de chomata pela borda das valvas até o terço mediano. A sinapomorfia 38 (1) refere-se a presença de papilas longas na prega

média, característica presente em *Lopha* e compartilhada com os táxons do nó 14. De acordo com a classificação sugerida por Harry (1985), Lophini e Dendostreini são todos da subfamília Dendostreinae. Aqui, esse parentesco foi confirmado, mas como 2 subfamílias

O nó **10** representa a tribo Lophini, já reconhecida por Harry (1985), é suportado por 6 sinapomorfias, sendo uma sinapomorfia não homoplástica, 4 convergências e uma reversão. O agrupamento desses táxons pelo tipo de chomata (caráter 16), que aqui são os únicos que apresentam a combinação ostreine+lophine. Este grupo também apresenta chomata em ambas as valvas (caráter 12) e em várias linhas (caráter 17) como no nó 4.

A forma do ânus, (caráter 70) que neste nó apresenta pedúnculo, é uma convergência, também aparece em *Isognomon*, *Lima* e *Cryptostrea*.

O nó **11**, denominado como subfamília Dendostreinae (subfamília nova, em referência ao gênero *Dendostrea* e aqui a presença da espécie tipo, *D. folium*), é suportado apenas por uma reversão. O caráter 42 é sinapomorfia no nó G revertendo em *O. edulis*, *Lopha*, no nó 4 e neste nó (13). Dentre os dois táxons terminais, *D. folium* é a espécie tipo do gênero, sendo demonstrado serem de fato *Dendostrea*. *Dendostrea* sp.2 é uma espécie nova, coletada no Caribe. As características desta espécie lembra *Dendostrea* cf. *sandvichensis* citada por Coan & Valentish-Scott (2012), mas, de acordo com a descrição original de *D. sandvichensis*, a espécie é pequena, até 30mm de altura, e ocorre no Oceano Pacífico. Ambos os táxons, *D. folium* e *D. sp.2*, compartilham 2 reversões, a coloração na borda interna das valvas ausente (caráter 10) e o esôfago curto (caráter 64).

O nó **12** é suportado por 3 sinapomorfias, sendo todas reversões. O caráter 56 apresenta o término das brânquias junto aos palpos, aqui em um estado plesiomórfico. O caráter 63 refere-se ao término das pregas nos palpos na borda superior já discutido no

nó F. A ausência de nervos laterais é também observada em *O. edulis*, *S. echinata*, *S. glomerata*.

O nó **13**, subfamília Crassostreinae, é suportado 6 sinapomorfias, sendo 1 sinapomorfia não homoplástica, 3 convergências e 2 reversões. Os dentículos do tipo ostreinae (caráter 17) é neste nó uma reversão, que também aparecem no nó 4. A cavidade umbonal é característica dos Crassostreinae. Aqui aparece como uma convergência entre ela e *Alectryonella*.

Nó **14**, nomeado aqui como tribo Saxostreini (gênero *Saxostrea* criado por Iredale, 1936 para espécies preteritamente consideradas *Saccostrea*) é suportado por 8 sinapomorfias, sendo uma sinapomorfia não homoplástica, 3 convergências e 4 reversões. A forma do coração acessório (caráter 49), o estado 1 (bifurcado) é uma sinapomorfia não homoplástica. A coloração da impressão muscular (caráter 25) é uma convergência. Este caráter é característico de populações tropicais (Stenzel, 1971; Mesquita, 1991). A ausência de fusão nos palpos é aqui uma reversão do caráter 62 que é uma característica compartilhada entre os táxons dos gêneros *Saccostrea* e *Crassostrea*. A fusão dos palpos é característica entre os Ostreinae (Harry, 1985).

O agrupamento entre os Saccostreini e Crassostreini é suportado por uma sinapomorfia e uma reversão. A cavidade umbonal (caráter 22) e o ânus não pedunculado (caráter 70) são características entre os Crassostreinae, com exceção dos táxons “*Saccostrea*” *palmula* e “*Saccostrea*” *echinata*.

Nó **15**, tribo Striostrini, já reconhecida por Harry (1985), é suportado por 2 convergências. A posição do músculo adutor a 1/6 da borda da valva está presente neste ramo (caráter 30:1), e compartilhada por *Lopha*, *Crassostrea rhizophorae*, *Hyotissa*, *Teskeyostrea* e *Lima*.

Nó **16** tribo Crassostreini, também já nomeada por Harry (1985), é suportado por 4 sinapomorfias, sendo uma sinapomorfia homoplástica e 3 reversões. O caráter 3 é sinapomorfia pela forma de taça que todas *Crassostrea* apresentam. A forma de taça é caracterizada pela concavidade profunda da valva esquerda. A borda das valvas sem plicas (7: 0) também é característica entre as espécies de *Crassostrea*, com exceção de *C. virginica*, que apresenta tipicamente a borda plicada ou ondulada, e aqui foi codificado como plicas presentes. A ausência de chomata (11: 0) é uma das características das valvas que permitem a diferenciação entre os gêneros *Saccostrea*, *Striostrea* e *Ostrea*, caráter esse utilizado por diversos autores como diagnose do gênero *Crassostrea* (e.g., Abbott, 1974; Stenzel, 1971, Harry, 1985).

5. DISCUSSÃO – ANÁLISES MOLECULARES

Muitos protocolos de extração genômica de DNA têm sido descritos para procariontes e eucariontes, para amostras de células a tecidos específicos (Sambrook *et.al.*, 1989). No entanto, é provado que o isolamento do DNA em moluscos é difícil por conta da presença de polissacarídeos presentes nos animais que co-precipitam com o DNA. Esses polissacarídeos inibem a atividade de muitas enzimas usadas na biologia molecular (Sokolov, 2000). A boa qualidade do DNA é essencial para alcançar bons resultados nos experimentos, especialmente no PCR, em que o excesso de células e proteínas pode inibir o processo de amplificação (Mullis *et.al.*, 1992).

Popa *et.al.* (2007) desenvolveram um estudo comparativo entre quatro métodos de extração de DNA em espécies bivalves de água doce. Dois entre os quatro métodos sugeridos pelo autor foram testados neste estudo (kit *NucleoSpin Tissue* da Macherey-Nagel e o kit *DNeasy Tissue*, da Qiagen Inc.), e somente o kit da Qiagen apresentou alguns resultados positivos.

Amostras de material, mesmo bem preservadas, porém antigas, não tem se mostrado propícias para extração de DNA, o que prejudicou na obtenção dos resultados, sendo então realizados testes com material fresco. E mesmo em materiais recentemente coletados, a extração por kits não apresenta resultados que garantem o sequenciamento.

Diversas técnicas genéticas tem sido usadas para a identificação de ostras, incluindo análises citogenéticas (Thiriot-Quévieux & Insua 1992, Li & Havenhand 1997, Leitão *et.al.*, 1999, Xu *et.al.*, 2001, Wang *et.al.*, 2004a), sequencia de DNA (Banks *et.al.*, 1993, Littlewood 1994, O'Foighil *et.al.*, 1995, O'Foighil *et.al.*, 1998, Wang *et.al.*, 2004b), RFPL, (Cordes *et.al.*, 2005, Klinbunga *et.al.*, 2005) e multiplex por PCR para espécies específicas (Wang & Guo, 2008). As análises citogenéticas tem revelado uma considerável variação entre as espécies, mas geralmente diferenças cromossômicas não

são usadas para identificação das espécies. A sequência de DNA oferece uma força não precedente para revelar as diferenças interespecíficas, mas nem sempre são acessíveis. Marcadores RFLP requerem uma digestão pós PCR com restrição de enzimas, que pode criar uma adicional restrição. Multiplex por PCR para espécies específicas é mais potente para um grande número de espécies, mas um método simples e efetivo para identificação de ostras ainda é preciso.

Apesar dos vastos dados na literatura e aqui testados, os resultados positivos são muito escassos para o confronto dos dados.

No caso do gene COI, desenhado por Folmer *et.al.*, 1994 para invertebrados, referindo ainda dados positivos para os gêneros *Crassostrea* e *Ostrea* em outros laboratórios (e.g. Melo *et.al.*, 2010), no presente trabalho nenhuma amostra apresentou resultados positivos.

Para o ITS (I e II), Wang & Guo (2008) afirmam que o tamanho de ITS1 e ITS2 é conservado entre as espécies de *Crassostrea*, mas variável entre algumas espécies. Entre as espécies, a variação no tamanho de ITS é claramente ligado às relações filogenéticas; algumas espécies-pares não podem ser diferenciadas pelo ITS, por serem muito próximas (*C. gigas/C. angulata*, *C. virginica/C. rhizophorae*, *S. echinata/S. glomerata*, *O. edulis/O. angasi*) (Littlewood, 1994), sendo consideradas como mesmas espécies por alguns autores. Nenhuma amostra aqui foi amplificada para este gene.

O poder das técnicas moleculares para a identificação de espécies foi inequivocamente demonstrado em muitas espécies. Apesar de sua eficácia comprovada, técnicas moleculares não são amplamente utilizadas para identificação de ostras. Isso porque a maioria dos métodos atuais ainda são muito trabalhosos ou complicados para uso comum (Wang & Guo, 2008).

A partir das sequências retiradas do GenBank®, para os genes 28S e 16S, foram geradas 2 árvores por consenso, ambas por máxima parcimônia.

A árvore mais parcimoniosa gerada, com as sequências do 28S não apresenta monofiletismo em relação aos Crassostreinae. Os táxons de *Crassostrea* do Brasil, clado 8 [aqui representados por cr3 (= *C. mangle*) e cb1] foram excluídas do clado 1, que agrupa os gêneros *Crassostrea*, *Saccostrea* e *Striostrea*.

O clado 2 apresenta a junção de vários táxons, sendo apenas o nó 9 monofilético, representado pelos Gryphaeidae.

O clado 3 agrupa os Ostreinae (exceto *O. equestris* e *Dendostrea frons*), representados pelos nós 10 (*O. edulis* e *O. puelchana*) e 11 (*A. plicatula*, *L. cristagalli* e *D. folium*). Estes gêneros são considerados por Harry (1985) como subfamília Ostreinae, e aqui não são considerados monofiléticos.

O clado 4, coloca *Striostrea* como táxon irmão das *Crassostrea*, que agrupadas no nó 5 representam as espécies do Atlântico Norte e Central e a espécie já considerada cosmopolita *C. gigas*.

O clado 6, representado aqui por *S. cucullata*, *S. glomerata* e *C. rhizophorae*, corrobora com relação apresentada por Littlewood (1994) (+ *C. virginica*) (Fig. 61).

Figura 65 – Árvore apresentada por Littlewood (1994) na análise do 28S para as relações entre as ostras.

Os Ostreinae (*Ostrea*, *Ostreola*, *Lopha*, *Alectryonella* e *Lopha*) também não são monofiléticos, sendo encontrados nos clados 2, 3 e 8. O clado 9 apresenta os representantes de Gryphaeidae (*Hyotissa* e *Parahyotissa*) como os únicos monofiléticos dessa análise.

Comparando a árvore do 28S (Fig. 62) com a árvore gerada pelas análises morfológicas (Fig. 61) , apenas a relação entre as espécies de *Crassostrea* do Brasil e o monofiletismo de Gryphaeidae (neste trabalho nomeado de tribo Hyotissini – nó 4, fig. 61) são correlacionadas.

De acordo com Littlewood (1994), apesar de demonstrar potencial nos dados moleculares para traçar uma origem evolucionária das ostras, esses dados precisam de caracteres morfológicos para ajudar na diferenciação das espécies. É essencial que os caracteres morfológicos junto com os caracteres não morfológicos, como por exemplo,

sequencias moleculares, sejam aplicados para que a sistemática e filogenia de Ostreidae seja bem entendido.

Um estudo filogenético molecular entre as espécies *P. mcgintyi*, *T. weberi* e *O. equestris* realizado por Kinkerdale *et.al.*, (2004) utilizou exemplares de Crassostreinae para mostrar a relação entre as espécies em questão. A árvore gerada através de análises do 28S (Fig. 63) mostram que Crassostreinae não é monofilético. As espécies do Atlântico são irmãs, assim como as espécies do Pacífico, separadas pelos representantes de *Saccostrea* e *Striostrea*. A relação entre as espécies *C. rhizophorae* e *C. virginica* corroboram com a árvore apresentada na figura 58, mas não corrobora em relação à *Saccostrea* e *Striostrea*.

Figura 66 - Árvore apresentada por Kinkerdale *et.al.* (2004) na análise do 28S para as relações entre as ostras.

Utilizando as sequências do gene 16S, a árvore gerada (Fig. 64) apresenta mais correlações com os dados morfológicos do que a árvore gerada com 28S. Apesar de Crassostreinae não ser monofilético nesta análise, os gêneros se apresentam monofiléticos. As espécies *C. rhizophorae* e *C. brasiliana* são novamente confirmadas como espécies irmãs, que juntamente com *C. virginica* formam um clado (5) com as espécies do Atlântico. *C. gigas* e *C. angulata* são apresentadas como espécies irmãs, agrupando as espécies do Pacífico, agrupando as espécies o gênero *Crassostrea*.

Figura 67– Árvore gerada a partir das sequências do 16S retiradas do GenBank®.

No clado 4, representado pelas espécies de *Saccostrea*, também formam um clado monofilético. Esse resultado, corrobora com os trabalhos realizados por Lapègue *et.al.* (2002) e Klibunga *et.al.* (2005) para o gene 16S.

Os táxons que representam Ostreinae neste clado, são monofiléticos, representadas pelo clado 6. O clado 2 agrupa a família Ostreidae separada da família Gryphaeidae, corroborando com dados morfológicos de Harry (1985) e Stenzel (1971), e com as filogenias moleculares de Lapègue *et.al.* (2002).

Nesta análise, os representantes de Gryphaeidae não são monofiléticos, diferente do apresentado para as análises moleculares do 28S e morfológicas.

6. CONCLUSÕES

O estudo morfológico e anatômico dos ostreídeos, com ênfase na subfamília Crassostreinae, aqui apresentado, mostra sua utilidade como dados para análise filogenética. Conclui-se que:

1. Baseado nos dados morfológicos, os três gêneros que correspondem à Crassostreinae possuem características que permitem diferenciação, por mais que a plasticidade fenotípica tenha grande influência na morfologia das valvas.
2. A análise anatômica provou ser útil na identificação e definição dos táxons, apesar de grande semelhanças, as diferenças (ou o conjunto delas) encontradas são características para cada espécie.
3. Crassostreinae é monofilético; O monofiletismo de Crassostreinae é suportado por 6 sinapomorfias e *Crassostrea* também monofilético, suportado por 4 sinapomorfias. *Saccostrea*, considerando a espécie tipo *S. cucullata*, é monofilético junto com *S. glomerata*. Mas considerando que as outras espécies pré-identificadas como *Saccostrea*, não são monofiléticas. A presença de *S. echinata* (8 sinapomorfias) e *S. palmula* (4 sinapomorfias) (clado Saxostreini) fora do clado da tribo Saccostreini, mostram que tais espécies podem se tratar de outros gêneros, pois cada táxon possui caracteres não compartilhados com os da tribo Saccostreini.

4. As relações entre os demais ostreídeos são parafiléticas, salvo algumas exceções entre os táxons terminais.
5. A família Gryphaeidae é aqui considerada como subfamília Pycnodontinae incluída em Ostreidae, visto que os táxons que deram o nome à família (*Gryphaea* e *Exogyra*) são fósseis e não apresentam os caracteres como as câmaras vesiculares e chomata como nas espécies viventes da subfamília Pycnodontinae (*Hyotissa*, *Parahyotissa* e *Pycnodonte*);
6. *Crassostrea* e *Saccostrea*, que normalmente são confundidas por sua semelhança conquiliológica, podem ser separadas pela presença de chomata em *Saccostrea*, além da ornamentação na borda das valvas, ambas características ausentes em *Crassostrea*. *Striostrea* pode ser considerada uma mescla entre os dois gêneros acima: possuem dentículos e camadas externas foliáceas mas a borda das valvas não possui ornamentação; apresenta uma característica única, a coloração metálica na face interna das valvas.
7. Diante dos demais representantes de ostreídeos na análise, os táxons aqui nomeados como tribo Hyotissini (família Gryphaeidae nas demais referências), tribo Lophinae subfamília Eostreinae e subfamília Dendostreinae apresentam-se monofiléticos.
8. Os dados moleculares corroboram quanto ao monofiletismo de *Crassostrea* e o parafiletismo de *Saccostrea*, *Ostrea* e *Dendostrea*.

RESUMO

Foram aplicadas técnicas de análise e comparação de anatomia detalhada, através de dissecções e por análises moleculares em um grupo altamente variável como os Ostreidae com objetivo de comprovar o monofiletismo de Crassostreinae. Por ser economicamente importante em todo o mundo, a diferenciação entre as espécies é fundamental, com aplicações até na produção.

Através de um estudo comparativo de morfologia detalhada, representantes de quase todos os gêneros de Ostreoidea foram analisados. Inicialmente, os representantes da subfamília Crassostreinae foram estudados isoladamente. Em cada uma foi realizada uma análise filogenética na procura de sua monofilia e de sua identidade básica. Os representantes de Ostreinae e Gryphaeidae foram utilizados como grupo-externo. Em seguida, alguns representantes de Pteriomorphia foram incorporados ao grupo-externo (Limidae, Spondylidae, Plicatulidae, Isognomonidae, Anomiidae) com enraizamento em Arcidae.

Foram estudados 73 caracteres, presentemente comentados e discutidos. Uma única árvore mais parcimoniosa foi obtida: (((((((Cryptostrea permolis (Teskeyostrea weberi ((Hyotissa hyotis (Parahyotissa mcgintyi - P. numisma)) ((Eostrea puelchana - E. lurida) (Ostrea edulis (Ostreola equestris ("Dendostrea" sp1 ((Lopha cristagalli - Alectryonella plicatula) ((Dendostrea folium - D. sp 2) ("Dendostrea" frons ("Saccostrea" echinata ("Saccostrea" palmula (((Saccostrea mordax - "Striostrea" prismatica) (Saccostrea cucullata - S. glomerata)) ((Crassostrea virginica (C. gigas - C. bilineata)) (C. mangle (C. brasiliiana - C. rhizophorae)))))))))) Plicatulostrea onca) Plicatula gibbosa) Spondylus americanus) Lima sp.) (Anomia simplex - Isognomon alatus)) Barbatia candida) tendo como índices: passos = 372, IC = 27 e IR = 58.

Nota-se que a monofilia de Crassostreinae foi comprovada e é suportada por 6 sinapomorfias, Crassostrea também é monofilético, suportado por 4 sinapomorfias. Saccostrea, considerando a espécie tipo S. cucullata, é monofilético junto com S. glomerata. Dados obtidos por análises moleculares, realizadas neste e dados do GenBank®, corrobora, em parte, com os dados anatômicos; Crassostrea é considerado monofilético em ambas análises.

As diferenças e semelhanças morfo-anatômicas encontradas em quase todas as estruturas foram suficientes para a separação e agrupamento entre os gêneros e respectivas espécies.

ABSTRACT

Techniques of analysis and comparison of detailed anatomy through dissections and molecular analysis were applied in a highly variable group as Ostreidae in order to prove the monophyly of Crassostreinae. Being economically important worldwide, differentiation between species is essential in applications to production.

Through a detailed comparative study of morphology, representatives of almost all genres of Ostreoidea were analyzed. Initially, the representatives of the subfamily Crassostreinae were studied in isolation. A phylogenetic analysis was performed in the search for your monophyly and their basic identity in each one. Representatives of Ostreinae Gryphaeidae and were used as-external. Then, some representatives of Pteriomorphia were incorporated into the group-external (Limidae, Spondylidae, Plicatulidae, Isognomonidae, Anomiidae) with rooting Arcidae.

73 characters presently commented and discussed were studied. A single most parsimonious tree was obtained: (((((((((Cryptostrea permolis (Teskeyostrea weberi ((Hyotissa hyotis (Parahyotissa mcgintyi - P. numisma)) ((Eostrea puelchana - E. lurida) (Ostrea edulis (Ostreola equestris ("Dendostrea" sp.1 ((Lopha cristagalli - Alectryonella plicatula) ((Dendostrea folium - D. sp.2) ("Dendostrea" frons ("Saccostrea" echinata ("Saccostrea" palmula (((Saccostrea mordax - "Striostrea" prismatica) (Saccostrea cucullata - S. glomerata)) ((Crassostrea virginica (C. gigas - C. bilineata)) (C. mangle (C. brasiliiana - C. rhizophorae)))))))))))))) Plicatulostrea onca) Plicatula gibbosa) Spondylus americanus) Lima sp.) (Anomia simplex - Isognomon alatus)) Barbatia candida) while indices: = 372 steps, CI = 27 and IR = 58.

We note that the monophyly of Crassostreinae been established and is supported by six synapomorphies, Crassostrea is also monophyletic, supported by four synapomorphies. Saccostrea, considering the type species S. cucullata, is monophyletic with S. glomerata. Data obtained by molecular analyzes, performed and this data GenBank® corroborates, in part, with the anatomical data; Crassostrea is considered to be monophyletic in both analyzes.

Differences and morphological, anatomical similarities found in almost all structures were sufficient for separating and grouping among genera and their species.

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ANEXO I – Amaral & Simone, 2014. Revision of genus *Crassostrea* of Brazil.

ANEXO II – Amaral & Simone, *submitt* – Comparative anatomy of five species of *Saccostrea* from Pacific and Indian Ocean.

Comparative anatomy of five species of *Saccostrea* (Bivalvia: Ostreidae) from Pacific Ocean.

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Running title: Anatomy of genus *Saccostrea*

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ABSTRACT

Ostreids are well known for their high intra-specific variation, which makes identification problematic. The present paper aims to provide a morpho-anatomical analysis of five species of Saccostrea, as well as some congeneric species from relevant areas in the Pacific Ocean. Saccostrea cucullata occurs in Africa, Indian Ocean and Arabian Sea, Red Sea and part of the Pacific, fixed on rocks and mangroves. S. glomerata occurs in the Pacific, New Zealand, Australia and Philippines, always associated with rocks. S. echinata, occurs from East Africa to Japan. S. palmula, occurs from Mexico to Peru, in the Pacific. S. mordax occurs in the Red Sea and Pacific. The wide distribution of these often sympatric species leads to confusion regarding their identity. Herein we describe several anatomical differences that allow a more precise identification, especially when they come from sympatric taxa.

ADDITIONAL KEYWORDS: oyster – morphology – systematics – food – cultivation - phenotypic plasticity.

INTRODUCTION

The superfamily Ostreoidea Rafinesque, 1815, includes marine and brackish water species adapted to sessile epifaunal communities attached to hard substrates. The taxon comprises ca. 80 species with a widespread distribution, which includes oceanic islands (Huber, 2010). Most of these species live in hot intertropical waters. Both tolerance and resistance to environmental variations allowed the Ostreoidea to colonize different marine habitats, from coastal regions with clear waters and high salinity levels, to estuarine environments with turbid waters and inconstant salinity levels (Quayle, 1981).

Harry (1985) classified the oysters within a superfamily (Ostreoidea), two families (Gryphaeidae and Ostreidae), four subfamilies (Pycnodonteinae, Lophinae, Ostreinae and Crassostreinae), 10 new tribes, 24 genera and subgenera, and 12 genera described then. The most recent revision by Huber (2010) reduced the number of genera and species, but retained the classification established by Harry (1985) for families, subfamilies and genera.

Species of the genus *Saccostrea* Dolfuss & Dautzenberg, 1920 are common oysters that live on rocky shores of the Indo-Pacific. The taxonomy of this genus is unclear, and the morphological plasticity makes identification problematic (Lam & Morton, 2006). They have small to medium shells, a left valve with a prominent ligamentary area showing clear, continuous and regular primes. The right valve is flat, bearing projections along its margin, with corresponding concavities on the left valve. The genus includes nine species (Huber, 2010): *Saccostrea cucullata* (Born, 1778) – the type species; *Saccostrea cirumsuta* (Gould, 1850); *Saccostrea echinata* (Quoy &

Gaimard, 1835); *Saccostrea glomerata* (Gould, 1850); *Saccostrea kegaki* Torigoe & Inaba, 1981; *Saccostrea malabonensis* (Faustino, 1932); *Saccostrea palmula* (Carpenter, 1857); *Saccostrea scyphophilla* (Peron & Lesueur, 1807) and *Saccostrea spatulata* (Lamarck, 1819).

S. cucullata occurs in Africa, Indian and Arabian Oceans, Red Sea and part of the Pacific Ocean, fixed on rocks and in mangrove areas. *S. glomerata*, occurs in the Pacific, New Zealand, Australia and Philippines, always associated with rocks. *S. echinata* occurs from East Africa to Japan. *S. palmula* occurs from Mexico to Peru, in the Pacific. *S. mordax* occurs in the Red Sea and the Pacific. The widespread, sometimes overlapping distribution of these species often makes identification problematic (Huber, 2010). Aiming to facilitate their identification, in this paper we carry out a detailed morpho-anatomical study of five *Saccostrea* species from the Pacific Ocean: *S. cucullata*, *S. glomerata*, *S. echinata*, *S. palmula* and *S. mordax*.

Studies including *Saccostrea* species usually refer to reproduction, development, population data and molecular characterization between species (e.g., Klibunga *et al.*, 2002; Kakoi *et al.*, 2008; Green *et al.*, 2009; Parker *et al.*, 2010; Dove & Connor, 2012). Few descriptions of shells and anatomy can be found in the literature (e.g., Awati & Rai, 1931; Rao, 1987).

Because of shell plasticity, the taxonomy of *Saccostrea* has become a troublesome matter; e.g., some "forms" of *S. cucullata* have been attributed to different names by different authors, such as *S. echinata*, *S. mordax*, *S. glomerata* (Lam & Morton, 2004). Molecular studies (e.g., Lam & Morton, 2004, 2006, 2009; Wuang & Guo, 2008a, 2008b) have been conducted as an attempt to resolve this taxonomic confusion and better understanding the genus' distribution, as it apparently occurs in several places along the Pacific Ocean. Reports on the difficulty in identifying the

species, because of the wide variation in body size and coloration are found in literature, which establish a very confusing scenario (Awati & Rai, 1931). This problem is further confirmed by Lam & Morton (2006): "The geographical distribution of lineages of *Saccostrea* is somewhat uncertain because of taxonomic confusion".

As an example of this confusing setup, *S. comercialis* (Iredale & Roughley, 1933) and *S. mordax* (Gould, 1850) have been considered subspecies of *S. cucullata*, because the two of them have similar shells (Stenzel, 1971). Thomson (1954: 175, pls. 7.1-7.2) illustrated *Crassostrea* (*Saxostrea*) *amara* (Iredale, 1939) from Australia, but it seems to be *S. mordax* from Hong Kong. Lamprell & Healy (1998: 134, Fig. 336) Yoosukh & Duangdee (1999: 336, fig. 6) and Slack-Smith (2000: 271, fig 6.15E) show similarities in the shell characters according to the graphics of Torigoe (1981: 380-381, plate 17) and Qi & Choe's (2000: 137, fig. 3C-E) for *S. mordax* (Lam & Morton, 2006). Bernard *et al.* (1993) consider the last eleven nominal species described from China to be synonyms of *S. cucullata*.

The dorsal extreme extenuation of form 'cornucopia' (typical of the genus), is found in several species of *Saccostrea*, definitely in *S. cucullata* (East African and East Indian Ocean) and *S. schyphophilla* (India, Australia and Japan), but is not seen in *S. kegaki*, *S. echinata*, *S. circumscuta*, *S. spathulata*, *S. malabonensis* or the Panamanian *S. tubulifera* and *S. palmula* (Huber, 2010).

S. glomerata is a valid, genetically isolated species, restricted to southeastern Australia and New Zealand, but may have established itself elsewhere. *S. comercialis* is not distinguishable morphologically and genetically from *S. glomerata* (Huber, 2010). Anderson & Adlard (1994) obtained the ITS1 sequence of *S. comercialis* from Sydney, Australia, and *S. glomerata* from New Zealand, showing that they are synonyms.

Molecular systematic studies of *Saccostrea* are few, and mostly restrained by the many issues regarding the genus' taxonomy (Lam & Morton, 2006). Moreover, it has been reported to display ecomorphological variation (Tack *et al.*, 1992). All oysters of the genus *Saccostrea* in Thailand were previously assumed to be only *S. cucullata* (Visoothiviseth *et al.*, 1998). The results of Klibunga *et al.* (2005) indicated that more than one species of *Saccostrea* may be present in Thai waters, which may result in problems regarding its commercial use.

MATERIALS AND METHODS

A list of the material examined is shown after each species description. The material was fixed in 70-99% ethanol. The specimens were immersed in preservative and dissected by standard techniques under a stereomicroscope (Simone, 1997, 2009, 2011). Details of all systems (mantle cavity, mantle edge, muscles, digestive, circulatory, excretory and nervous systems) and organs were investigated. The drawings were obtained with the aid of a camera lucida.

The studied samples are held at several institutional collections: Smithsonian Institute National Museum of Natural History (NMNH), Florida Museum of Natural History (USMN), Field Museum of Natural History (FMNH) and Museu de Zoologia da Universidade de São Paulo (MZUSP).

The following abbreviations are used in the figures: accessory heart (**ah**), adductor muscle (**am**), anus (**an**), auricles (**au**), chomata (**ch**), dorsal hood (**dh**), esophagus (**oe**), external fold (**ef**), gastric shield (**gs**), gills (**gi**), heart (**he**), hood (**ho**), inner fold (**if**), intestine (**in**), mantle edge (**me**), middle fold (**mf**), muscle scar (**im**), pallial muscles (**pm**), palps (**pa**), Quenstedt muscle (**qm**), rectum (**rt**), selection area

(**sa1**), typhlosole (**ty**), umbonal cavity (**uc**), undulations (**pl**), ventricle (**ve**), visceral ganglia (**vg**), visceral mass (**vm**).

SYSTEMATICS

Genus *Saccostrea* Dolfuss & Dautzenberg, 1920

Type species: *Ostrea saccellus*, Dujardim, 1835 = *O.cucullata*, Born, 1778

Diagnosis. Shell cup-shaped, with marginal denticles, promial chamber on right side.

Distribution. This genus is restricted to tropical and sub-tropical waters from Eastern Atlantic, Indo-West Pacific and Eastern Pacific, while absent in the Western Atlantic; in saline areas (open ocean), but occasionally occurring in mangrove areas. Most species live exposed, fixed on rocks or coral (Harry, 1985).

Saccostrea cucullata (Born, 1778)

Plates 1 – 2: Figs. A – O

Ostrea cuccullata [sic] Born, 1778: 100.

Ostrea cucullata Born, 1780: 114, pl. 6, figs. 11, 12; Dillwyn, 1817: 277; Smith, 1890: 322; Awati & Rai, 1931: 1-107.

Ostrea cornucopiae Gmelin, 1791: 3336; Küster, 1868: 77.

Lopha cornucopiae: Röding, 1798: 169.

Ostrea gibbosa Lamarck, 1819: 209; Hanley, 1856: 301.

Crassostrea cucullata Ranson, 1960: 20.

Saccostrea cucullata: Stenzel, 1971: N1134-N1135, fig. J106; Morris, 1985: 125-128, Pl. 3, figs. E-G; Lam & Morton, 2003: 110-112, pls. 11, 12; Lam & Morton, 2009: 482. fig. 1: 483.

Types: Born's type is located in Naturhistorisches Museum Vienna (Morris, 1985) – no additional data. **Examined:** Syntypes, *Ostrea cornucopiae* – Genève Museum n° 1089141 Lamarck Coll.

Description

Shell

Shell elongated, to 100 mm, generally cup-shaped, with left valve showing deep concavity in ligament region. Right valve (Fig. B) flat or slightly convex; ligament straight, of moderate size and devoid of teeth, characteristic of the subfamily. Umbonal cavity well-developed; Margins of both valves with well-developed angles (Figs. A, C); inner edge of right valve with small elongated denticles along (Fig. B) producing corresponding depressions on left valve. Adductor muscle scar reniform, occupying $\frac{1}{4}$ of total height (Fig. B), striate, color white or grayish. Color of outer surface of valves variable from white to gray, light or dark brown, green or purple. Inner surface of valves white, sometimes with purple stains.

Adductor muscle

Reniform or slightly oval, located in posterior region, occupying $\frac{1}{4}$ of total height (Fig. D, K, L).

Mantle

Mantle lobes thick, with well-defined pallial muscles mainly near adductor muscle, being are more abundant in this place (Figs. D, E). Hood formed by junction of anterior mantle lobes. Hood robust and well-defined, usually free or filled by gonad mass (Figs. D, K).

Mantle edge

Pleated and thick, dark, colored yellow with brown spots, bearing three similar-sized folds. Middle fold and internal fold with finger-like, uniformly-distributed papillae, one or two, short to long (Fig. E).

Gills

Gills occupy 50% of total height. Alimentary chamber of demibranchs moderately thick, ~1/3 of gill fold thickness (Fig. F, L).

Circulatory system

Ventricle large, walls thick, with internal beams crossing each other in various directions; opaque, white colored. Outer part of auricles thin, translucent, trabecular; external portion of auricles bearing small, saculiform structures (Fig. G). Pair of kidneys triangular, tubular; mottled by light brown marks by translucence of visceral mass. Each kidney with direct communication with pericardium and gonad on medial side and laterally communicating by short chamber. Renal opening located on other side of cerebro-visceral connective.

Digestive system

Palps large, $\frac{1}{4}$ of gills size, spatuliform; internal surface with pleats extending transversely to edge (Fig. F). The stomach is located in the globular region of the visceral mass, normally occupying $\frac{1}{4}$ of the animal's total size. Esophagus short, with $\frac{1}{2}$ of palps size, (Fig. M). Selection area of stomach (sa1) short ($\frac{1}{2}$ of palps size) and wide with tiflossoles beginning in posterior region of stomach (Fig. I, M). Intestine from style sac, returning in opposite direction, passing usually behind pericardium; surface, immersed in gonads; narrowest portion of intestine surrounding adductor muscle. Rectum long and thin, contouring adductor muscle almost until canopy-gill junction. Anus sessile, rounded a $\frac{1}{2}$ of adductor muscle, with single fold.

Reproductive system

Gonad formed by two lobes of follicular aspect, occupying $\frac{1}{4}$ of animal size. Dorsally and ventrally spread in left lobe and right lobe; shape indistinct from each other. Two pairs of separate systems of genital channels, as described above (excretory system).

Nervous system

Nervous system similar to other ostreid species, pair of cerebral ganglia in anterior region, near of palps, link at pair of visceral ganglia by connectives; visceral ganglia, occupying $\frac{1}{15}$ of adductor muscle size, with two pairs of branches in anterior region, three in posterior region and one laterally (Figs. J, N).

Distribution and habitat: Indo-West Pacific.

Material examined: CHINA. **Hong Kong.** North Pacific Ocean, USNM 858434, 3 specimens; NEW ZEALAND. South Pacific Ocean, USNM 886486, 5 specimens; THAILAND. **Chantaburi.** Kung Kraben Bay, MZUSP 55270, (L.R.Simone coll. 24/vii/2005), 6 specimens.

***Saccostrea glomerata* (Gould, 1850)**

Plates 3 – 4: Figs. A - L

Ostrea glomerata Gould, 1850: 346; 1852: 462; Sowerby, 1871: sp. 64.

Ostrea attenuata Sowerby, 1871: pl. 21.

Ostrea vitrefacta Sowerby, 1871: sp. 80; Lamy, 1929: 166; Île-Rodriguez, 1938: 289.

Ostrea mordax: Hutton, 1873b: 84 (*non* Gould, 1850).

Lopha glomerata: Finlay, 1928: 268.

Ostrea forskali var. *glomerata*: Lamy, 1929: 158.

Ostrea (Lopha) glomerata: Hiro, 1936: 36; Wada, 1942: 70.

Crassostrea cucullata: Ranson, 1967: 188; Nishimura *et al.*, 1998: 85 (*non* Born, 1778).

Saccostrea glomerata: Torigoe, 1981: 310, 332; Dinamani, 1991a: 335; Xu, 1997: 94.

Saccostrea cucullata: Oliver, 1992: 88; Nishimura *et al.* 1998: 86, 88 (*non* Born, 1778).

Types: Holotype USNM 5960 (examined); Paratypes USMN 612314, MCZC 178590, 178591.

Distinctive description

Shell

Rounded, to 50 mm; left valve concave, slightly larger than right valve, lacking well-developed umbonal cavity (Fig. A). Right valve slightly convex; ligament short with mild bulging in central region (Fig. B); margins of both valves with well-developed angles (Figs. A, B); color internally dark brown at edges, fading toward shell's median region. Right valve showing rounded denticles spread along entire edge, arranged in single row (Fig. B), with corresponding depressions on left valve. Adductor muscle scar reniform, occupying 1/5 of total height, located in median region, with

anterior portion normally pigmented gray/brown and posterior portion with pigmented lines; surface slightly pearlescent, white-colored; Quenstedt muscle scar roundish, occupying 1/20 of total size of adductor muscle scar, located in anterior-ventral region of valves (Fig. B).

Muscles

Adductor muscle reniform, occupying 1/3 of total height, with a convexity in posterior region (Fig. C, I).

Mantle

Mantle lobes slightly thick, with well-defined pallial muscles, mainly more abundant near adductor muscle (Fig. C, D).

Mantle edge thick, reddish; middle fold with 3-4 short to long, elongated papillae; internal fold with short, elongated to medium papillae, presenting 2-3 medium papillae for each short one (Fig. D).

Gills

Gills occupying 1/2 total body size. Alimentary channel narrow, ~1/5 as thick as gill fold (Fig. C).

Heart

Heart strong, ventricle relatively large with internal bundles crossing each other in different directions; color light beige. Auricles thin, with more abundant bundles, same texture and coloration, but more elongated than ventricle (Fig. E).

Digestive system.

Palps occupying $\sim 1/5$ of visceral mass, spatuliform, rounded; internal surface with plicae extending transversely to edge (Figs. H, J). Esophagus long and narrow; length $\sim 1/2$ palp length (Figs. G, K). Selection area (sa1) long and thin, with tiflossoles beginning in posterior region of stomach (Figs. G, K). Intestine passing behind pericardium, with narrowest portion surrounding adductor muscle. Rectum slightly long and thin, contouring adductor muscle at medial region of dorsal portion; anus with single fold (Fig. I).

Nervous system

Two pairs of branches in the anterior region and three in posterior region (Fig. L).

Distribution and habitat: India to Australia and New Zealand.

Material examined: FIJI. Nanuya-Lailai Island, Yasawa Group T. Moala. MZUSP 71454; 2 specimens.

***Saccostrea echinata* (Quoy & Gaimard, 1835)**

Plates 5 – 6: Figs. A – O

Ostrea mytiloides Lamarck, 1819: 207; Deshayes, 1836: 227; Hanley, 1856: 300;
Hidalgo, 1905: 387; Lamy, 1924: 155, 1929: 138 (*non* Gmelin, 1791).

Ostrea echinata Quoy & Gaimard, 1835: 455; Hanley, 1856: 302; Küster, 1858: 76;
Hidalgo, 1905: 387; Chen *et al.* 1980: 174.

Ostrea arakanensis Sowerby, 1871: sp. 83.

Ostrea nigromarginata Sowerby, 1871: sp. 85; Lamy, 1928: 140.

Ostrea cucullata: Pilsbry, 1895: 146 (*non* Born, 1778).

Crassostrea echinata: Thompson, 1954: 152; Carreon, 1969: 113.

Saxostrea mytiloides [sic]: Habe & Kosuge, 1966: 145 (*non* Gmelin).

Saccostrea echinata: Stenzel, 1971: N962; Torigoe & Inaba, 1981: 126; Torigoe, 1981:
308, 330; Li & Qi, 1994: 171; Hayami, 2000: 927.

Saccostrea cucullata: Morris, 1985: 125; Harry, 1985: 150; Oliver, 1992: 88, 91; Xu,
1997: 95 (*non* Born, 1778).

Types: Holotype in MNHN; examined.

Distinctive description

Shell

Elongated, ~ 60 mm, with slight ripples in margin of valves extending toward central region (Figs. A – C); left valve slightly larger than right valve, with deep umbonal cavity, lacking any major projections (Fig. B); internal color white/cream to

gray. Adductor muscle scar elongate-reniform, occupying $\sim \frac{1}{4}$ of total height, non-pigmented (Fig. C). Denticles present across edge of right valve (Fig. C), with corresponding depressions on left valve (Fig. B), distributed in various lines along posterior region, being elongated, rounded or both.

Muscles

Reniform, occupying $\sim \frac{1}{4}$ of total height, with a convexity in posterior region (Fig. D, J).

Mantle

Mantle edges delicate, with well-defined pallial muscles in all mantle surfaces. Hood filled with gonads (Figs. D, F, J).

Mantle edge

Mantle edge thick, with yellow and/or brown pigmentation. Papillae of middle fold alternately long and short; usually with a long papilla for each three short ones. Accessory heart with only one branch on both lobes, thin and translucent; both lobes not reaching the adductor muscle (Fig. F).

Gills

Gills occupying $\frac{1}{2}$ of total height. Alimentary chamber thick, $\sim \frac{1}{2}$ as thick as gill fold (Fig. F, J).

Circulatory system

Ventricle thin, usually translucent, auricles elongated, less cross-linked, non-pigmented (Figs. H, N).

Digestive system

Palps small, ~ ¼ of adductor muscle size, curved, sickle-shaped, with folds along anterior margin. External palps fused in middle region and overlying internal palps (Figs. E, K). Esophagus long (~1/3 of adductor muscle) and thin. Selection area of stomach (sa1) short (~ ½ of esophagus size) and wide, with tiflossoles (ty) beginning in posterior region of stomach (Fig. M). Intestine passing behind pericardium; narrowest portion circling adductor muscle. Rectum long and thin, contouring adductor muscle. Anus papillae shaped similarly to shell (Fig. J, I, L).

Nervous system

With three branches in anterior region and only one in posterior region (Figs. G, O).

Distribution and habitat: E. Africa to Japan.

Material examined: MARIANA IS. Guam UF 284793; 3 specimens.

***Saccostrea palmula* (Carpenter, 1857)**

Plates 7 – 8: Figs. A – K

Ostrea palmula Carpenter, 1857b: 163, 550; 1864: 538; Dall, 1914: 2; Lamy, 1929: 150; Keen, 1971: 84; Abbott, 1974: 456.

Ostrea plumula [sic] Carpenter, 1857b: 351, 353.

Ostrea amara Carpenter 1864a: 363; 1864: 541, 552, 621, 666; Lamy, 1930: 242.

Ostrea frons: Carpenter, 1864: 520 (*non* Linnaeus, 1758).

Ostrea mexicana Sowerby, 1871: sp. 35.

Ostrea cumingiana var. *Mexicana*: Dall, 1914: 2.

Ostrea conchaphila (pars): Abbott, 1974: 456 (*non* Carpenter, 1857).

Saccostrea palmula: Harry, 1985: 138.

Crassostrea palmula: Rodríguez & García-Cubas, 1986: 269.

Types: BMNH Syntypes n° 1857.6. 4.735, 1857.6. 4.736, 1857.6. 4.737; examined.

Description

Shell

Shell rounded with ~ 60 mm. Left valve larger than right valve, with small umbonal cavity and slight projection in ligament region; projections and evident ripples present along margin (Figs. A, B). Right valve smaller than left valve, opercular, following pattern of expansion of left valve (Fig. B). Color white/cream with purple spots on outer surface. Inner surface white, slightly nacreous; purple spots and lines sometimes present on inner surface. Adductor muscle scar well-defined, showing purple concentric lines in antero-ventral portion of valves, reniform (Figs. B, C) occupying 1/5 of total height.

Denticles rounded in anterior region, aligned uniformly distributed; corresponding depressions on right valve shallow, almost inconspicuous (Fig. B).

Muscles

Same morphology as other species, reniform (Figs. D, E, H), occupying ~ 1/5 of total height.

Mantle

Mantle lobes thin, with well-defined pallial muscles in posterior region (Fig. D, H); hood absent. Mantle edge thinner; color beige to cream. Papillae of middle fold small, finger-like, elongated, with medium to long length; two to five smaller papillae for each two larger ones (Fig. E). Accessory heart with three well-defined branches, reaching and circling adductor muscle in ventral region (Fig. E).

Gills

Gills occupying ~ 1/3 of total body size. Alimentary chamber narrow (Fig. F).

Heart

Ventricle elongated, slightly thick, reticulated and whitish. Auricles thin, small and non-pigmented (Fig. D, H).

Digestive system

Palps large, occupying ½ of adductor muscle size, thin, with folds on upper margin (Fig. F, I).

Nervous system

Visceral ganglia with two anterior expansions, two lateral and tree posterior (Figs. G, K).

Distribution and habitat: Mexico to Peru.

Material examined: PANAMA. **Miraflores Lock.** USNM 734199 2 specimens.

Arraijan. FMNH 27226 2 specimens.

***Saccostrea mordax* Gould, 1850**

Plates 9 – 10: Figs A – K

Ostrea mordax Gould, 1850: 346; 1852: 464; 1856: pl. 43; Sowerby, 1871: sp. 31;

Saville-Kent, 1891: 2; 1892: 65, 245; Hutton, 1937b: 84; Hirase & Taki, 1951: pl. 7.

Ostrea cornucopiae Saville-Kent, 1891: 3 (*non* Gmelin, 1791).

Ostrea mordax var. *cornucopiaeformis* Saville-Kent, 1893: 248.

Ostrea cucullata: Iwakawa, 1915: 15; 1919: 254; Hatai, 1941: 58; Wells & Bryce, 1988: 162.

Ostrea forskali var. *sueli*: Lamy, 1925: 192.

Ostrea (Lopha) cucullata: Kuroda, 1928: sp. 36; Hirase, 1930: 25; 1934: 5; Takatsuki, 1949: 5 (*non* Born, 1778).

Ostrea forskali var. *mordax*: Lamy, 1929: 158.

Ostrea (Lopha) mordax: Kuroda, 1930: 51; Tchang & Lo, 1956: 74.

Saxostrea amasa Iredale, 1939: 399; Allan, 1959: 273.

Ostrea glomerata: Blanco *et al.*, 1951: 52 (*non* Gould, 1850).

Crassostrea amasa: Thompson, 1954: 154; Carreon, 1969: 111.

Saxostrea mordax: Habe, 1951: 94; Kira, 1959: 127; 1962: 144; Taki, 1960: 192; Habe & Kosuge, 1966: 145; 1967: 137.

Saccostrea mordax: Habe & Okutani, 1975: 194; Habe, 1977: 109; 1981: 83; Torigoe, 1981: 306, 328; Okutani & Soyama, 1987: 152; Habe & Matsuda, 1990: 98; Xu, 1997: 95; Hayami, 2000: 925.

Saccostrea cucullata: Morris, 1985: 125; Li & Qi, 1994: 170; Lamprell & Healy, 1998: 134 (*non* Born, 1778).

Types: Syntype, NMNH 5958, examined.

Description

Shell

Shell elongated, ~ 40 mm, with undulations from entire edge of both valves up to ligamentary region (Fig. A). Left valve concave, umbonal cavity well-developed, with extensive anterior projection (Fig. C). Right valve flat or slightly convex, not opercular (Fig. B). Color beige/cream, with edges of valves dark purple. Denticles present in entire edges; rounded, relatively large and distributed in single row (Fig. B). Adductor muscle scar oval, colored grayish or non-pigmented (Fig. B).

Mantle

Mantle thick; pallial muscles more evident in adductor muscle region. Hood present, robust, filled by gonads and palps (Fig. D).

Mantle edge thin, color dark brown and yellow; middle fold with small and medium digitiform papillae; 2-4 smaller for each larger one. Internal fold with small, uniformly-distributed digitiform papillae. Accessory heart inverse T-shaped, well-marked and surrounding ventral region of adductor muscle (Fig. E, I).

Gills

Gills occupying ~ ½ of total size. Alimentary chamber narrow (Figs. F, I).

Circulatory system

Ventricle large, ~2/3 as large as auricles, with slight bundles more concentrated in posterior region; color whitish. Auricles translucent and elongated (Fig. G).

Digestive system

Palps large and thick, ~ ½ of adductor muscle size, superior edge with folds; external palps covers ~1/3 of internal palps (Figs. F, I). Esophagus long, two times more long than palps. Selection area of stomach 1 (sa1) long and narrow, ½ of esophagus height, typhlosole in terminal region of globular portion (Fig. J).

Nervous system

Visceral ganglia with tree nerves in anterior and posterior region and one laterally (Figs. H, K).

Distribution and habitat: Indo-West Pacific.

Material examined: CHINA. **Taiwan.** Taipei Co., Wanli, Yehliu., UF 303012, 3 specimens.

Discussion

Among the species studied here, the only one with a completely described anatomy is *S. cucullata*, by Awati & Rai (1931). The anatomy of the remaining species is mostly unknown, except for the shell (e.g., Lam & Morton, 2004, 2009). For a characterization of genus *Saccostrea* the comparison was taken with genus *Crassostrea* and others ostreids.

Shell

The shell of genus *Saccostrea* differs of genus *Crassostrea* basically for a presence of chomata and some species, the ornamentation of edge shells. Both genus have a medium a large shells, and occurs in same habitat, but *Saccostrea* are found only in Pacific and Indian Ocean. Between *Saccostrea* species, the taxonomy only for the shells characters is problematic, and this paper, show some anatomic differences to help a identification of species.

The shells of *Saccostrea cucullata* (Fig. xx) are elongated, normally cup-shaped, with a deeply concave left valve showing an expansion in the ligament area. The right valve is flat or slightly convex, like a lid. The umbonal cavity is well-defined, the edges of both valves are plicate, with folds laminated in defined angles. Small tubercles (elongated denticles) are present along the inner edge of the right valve (Fig. XX), with corresponding depressions on the left valve. The adductor muscle scar is reniform, striated, white or grayish, while the external surface of valves is variable in color, from pale white, light gray to dark brown, green or purple. The internal surface is white, and may present purple spots. These characteristics fittingly with those presented by Awati & Rai (1931).

The shell of *Saccostrea echinata* is more elongated, with slight undulations along the edge of the valves that stretch toward the central area. Its left valve is slightly larger, with an evident umbonal cavity lacking projections in the ligamentary area. It is colored white/cream to grayish. The adductor muscle scar is also reniform but more elongated and unpigmented. Denticles are present along the right valve's edge, with corresponding depressions on the left valve. These denticles are distributed in multiple lines in the posterior region, and may have an elongated or rounded contour.

The shell of *Saccostrea palmula* is rounded, with both valves laterally expanded; the left valve is larger than the right, with a small umbonal cavity and a light expansion in the ligamentary region; projections and undulations are evident along the edge; the right valve is small, opercular, following the pattern of expansions of the left valve. It is colored white/cream with purple spots externally. The internal surface is white and slightly nacreous; there may be purple spots in the region corresponding to the mantle edge in both valves. Differing from the above-mentioned species, the adductor muscle scar is defined by concentric purple lines in the antero-ventral portion of the valves, but it is also reniform. Both valves show more rounded denticles on the edge than those of *S. cucullata*, which are restricted to the anterior region, aligned and uniformly distributed; the corresponding depressions on the right valve are somewhat shallow.

Saccostrea mordax has a usually elongated shell, with undulations going from the margins to the ligamentary region; the left valve is concave, with a deep umbonal cavity and an extensive anterior projection of the ligamentary region; the right valve is almost flat or slightly convex, but it is not opercular as in the remaining species, and both valves have similar width. The color is cream in the centre, with dark purple colored in the margins. Both valves have denticles along their margins; they are rounded, relatively large and distributed in a single row. The adductor muscle scar is oval and

grayish, with concentric lines that may be pigmented. These characteristics fit with those described by Lam & Morton (2009).

The undulations of edge shells are characteristic in *Saccostrea*, and this character differs of genus *Crassostrea*, when present show this undulation only in posterior region and in follicular layers have this ornamentation.

All species of *Saccostrea* exhibit a slight Quenstedt muscle scar, a rounded mark located in the antero-ventral region of the valves.

Muscles

The adductor muscle (and scar) of Crassostreinae in general, not differs between genus, but have variations in species. This variation has been pointed out in the literature (Nascimento, 1991 for *C. rhizophorae*; Galtsoff, 1964 and Kennedy et al., 1996 for *C. virginica*), and possibly is associated with the high level of shell plasticity.

S. cucullata shows a normally reniform adductor muscle, which is sometimes oval, while *S. palmula* has a strictly reniform muscle. *S. echinata* also has a reniform adductor muscle, but with a convexity toward the posterior region (that of *S. cucullata* is anterior). *S. mordax* has an oval adductor muscle.

The pair of Quenstedt muscles has no differentiation regarding the origin on the shell and the insertion in the base of the palps in the five species,

Mantle

The mantle lobes in *S. cucullata* are thick, with well-defined pallial muscles, mainly around the adductor muscle. In *S. echinata* the mantle lobes are thin, with well-defined pallial muscles along the mantle's extension. *S. palmula* has a thick mantle with pallial muscles more evident around the adductor muscle.

S. cucullata has a robust, well-defined hood, normally free or filled by gonads. *S. echinata* has a smaller hood than *S. cucullata*. In *S. palmula* the hood is not present. *S. mordax* has a well-defined hood, filled by gonads and palps. In *S. glomerata* the mantle is slightly thick, with pallial muscles more evident in the adductor muscle region; the hood is absent.

The pallial muscles have some differences between species, in quantity, narrow and distributions. This data, corroborating with Amaral & Simone (2014), when the Quenstedt muscles in the *Crassostrea* species are not difficult to find, differently from what has been postulated in the literature (Galtsoff, 1964; Stenzel, 1971; Mesquita, 1993). From their origin on the shell, the muscles run through the anterior visceral mass up to the insertion in the base of the palps. This peculiar morphological arrangement shows improbable a homology with the anterior adductor muscle or any foot muscles (suggested by Galtsoff, 1964; Stenzel, 1971). They may retract the gills and the palps, helping in transferring particles to the mouth.

Mantle edge

S. cucullata has a thick edge, colored dark yellow with brown spots. The three folds have similar size. The middle and inner folds also have finger-like papillae, one or two short for each long one. *S. echinata* has a thick edge, colored yellow and/or brown; the papillae of the middle fold are alternately long and short, being three short for each long one. *S. palmula* has a thin edge, colored beige/cream; the finger-like papillae of the middle fold are small, elongated, alternately short and medium/long, usually two to five small papillae for each one or two long/medium ones. *S. mordax*, has a thin edge, colored dark brown and/or yellow; the middle fold bears medium and short finger-like papillae, at a ratio of two to four short papillae for each medium one; the internal fold

bears small, uniformly distributed finger-like papillae. *S. glomerata* has a thick mantle edge with reddish color; the middle fold has both short and long papillae, at a ratio of three to four short for each long one; the inner fold has short and medium papillae, usually two or three medium for each short one. This variation was found in Amaral & Simone (2014) for *Crassostrea* species, and here remained.

The accessory heart in *S. cucullata* has three well-defined branches in the right lobe, forming a short y-shaped structure, while the left lobe shows only a single large branch. In *S. echinata* the accessory heart is slim, translucent, with thin walls, not reaching the adductor muscle in both lobes. In *S. palmula* it has tree branches that contour the adductor muscle. *S. mordax* has a different arrangement, forming a well-defined inverted T-shaped structure, and contouring the adductor muscle in the ventral region. *S. glomerata* has three branches in both lobes, forming a thick y-shaped structure, and one branch, about 1/3 thinner, which contours the adductor muscle.

Differently, *Crassostrea* genus has a tree branches in all species studied in Amaral & Simone (2014). This characteristic can be used for a differentiation for this genus.

Mantle Cavity

The promial passage is present in all *Saccostrea*. This is a characteristic of subfamily Crassostreinae. The promial passage has a variation in the size; in *Crassostrea* show in both sides a long chamber, the margin of the visceral mass to the base of the gills and in *Saccostrea*, the passage in the left lobe is open to half of the visceral mass.

Gills

The number of gill folds and filaments is a variable character, apparently increasing proportionally to the animal's size.

However, the numbers can be discrepant between individuals of similar size. Ridewood (1903) mentioned 9–12 filaments per fold in *O. edulis*, while Atkins (1937a) mentioned 8–17. Atkins (1937a) mentioned 8–17 in *C. virginica*; Nelson (1938) mentioned 8–15. Galtsoff (1964) mentioned 10–16 filaments per fold in *C. angulata*, while Atkins (1937a) referred to 15–16 and Nelson (1938) 8–14 filaments per fold. In Amaral & Simone (2014) was verified that the number of filaments per fold in *C. rhizophorae*, *C. mangle*, *C. brasiliiana* and *C. virginica* varies from 12 to 13, reaching 15 in *C. gigas*. Based on the proximity of the numbers, this parameter seems to be of little use in distinguishing the examined species. In all species of *Saccostrea* the variation is a 12-14 filaments per fold.

The gill of all species in this occupies about $\frac{1}{2}$ of the pallial cavity. *S. cucullata* has a medium-sized alimentary chamber, approximately $\frac{1}{3}$ as thick as the gill fold; *S. echinata* has a thick chamber, about $\frac{1}{2}$ as thick as the fold; *S. palmula*, *S. mordax* and *S. glomerata* have a narrow alimentary chamber, about $\frac{1}{5}$ as thick as the gill fold.

Visceral mass

The visceral mass extends from the ventral region of the ligament to the anterior surface of the adductor muscle. It is formed by normally yellowish-colored gonads, with abundant digestive diverticula and renopericardial structures, and occupies nearly $\frac{1}{4}$ of the total body size in all species.

Circulatory system

S. cucullata has a slightly large ventricle with thick walls, colored by opaque white; the auricles are thin-walled and translucent, and bear external saculiform structures. *S. echinata* has a thin ventricle, normally translucent, and two non-pigmented auricles, both more elongated than in *S. cucullata*. The ventricle is elongated in *S. palmula*, slightly thick and whitish; the auricles are small and non-pigmented. *S. mordax* has a large ventricle, about 2/3 the size of the auricles, with whitish coloration; the auricles are translucent and elongated. *S. glomerata* has a robust heart, with relatively large ventricle, colored light cream; the auricles are elongated, robust and have the color as the ventricle. The size and coloration of all Crassostreinae is variable into the species, and each has a pattern.

Digestive system

Palps

The palps of *S. cucullata* are large, spatuliform, having a folded anterior edge and a slightly arched ventral region. The palps of *S. echinata* are small, arched, sickle-shaped, with folds along the anterior margin. The external palps are fused in the middle, overlying the inner palps. In *S. palmula* the palps are larger than the remaining species, thin, with a superior margin bearing folds. *S. mordax* has large and thick palps, with folds in superior margin, as is the case in *S. echinata*, and the external palps overlie the inner palps for about 1/3 of their length.

Esophagus

The esophagus is dorsoventrally compressed in all species; in *S. cucullata* it is short and large, 1/2 of palps in size; in *S. echinata* it is long and thin, ~1/3 longer than palps length; in *S. palmula* it is elongated and thin, occupying 2/3 of palps size; in *S.*

mordax it is large and long, occupying the same size of palps; in *S. glomerata* it is long and narrow, $\sim\frac{1}{2}$ of palps size.

Stomach

Internally, the species normally differ in the selection area 1 (sa1), typhlosoles, gastric shield and dorsal hood. The sa1 in *S. cucullata* is short and large, with the typhlosole beginning in the posterior region of the stomach; *S. echinata* has a longer sa1, and the typhlosole begins more posteriorly than in *S. cucullata*. In *S. palmula* the sa1 is short and narrow, with typhlosole beginning laterally. The sa1 in *S. mordax* is long and narrow and the typhlosole is located more posteriorly than in *S. cucullata*.

Such an organ has been described as bagshaped, internally divided into a smaller anterior chamber and other larger posterior chamber, by means of a thick fold; such a fold is projected to the organ's lumen and seems to serve as a means to direct particles to the posterior region through a narrow channel (Shaw & Battle, 1957).

The dorsal hood length is nearly $\frac{1}{2}$ of the length of sa1 in *S. cucullata*. In *S. mordax*, the dorsal hood has about the same length as sa1. In *S. echinata* and *S. palmula* the dorsal hood is short and narrow, about $\frac{1}{2}$ the size of the others species.

All such stomach characters are similar to those of *O. edulis* (Yonge, 1926; Graham, 1949; Purchon, 1957; Reid, 1965), *C. parasitica* (Shaw & Battle, 1957) and *O. chilensis* (Purchon, 1957). Other details of the morphology and physiology of the ostreid digestive tract, such as ciliary mechanisms and stomach structure and operation, can be found in the literature (Shaw & Battle, 1957; Nelson, 1960; Reid, 1965; Yonge, 1966).

Intestine, rectum and anus

The intestine, before the style sac, passes behind the pericardium, immersed in the gonads in visceral mass. In *S. cucullata*, *S. echinata*, *S. mordax* and *S. glomerata* the intestine passes behind the pericardium; in *S. palmula*, behind the esophagus. The rectum of *S. cucullata* is long and thin, surrounding the adductor muscle in 2/3 of its concave region, with the anus bearing a single fold. *S. echinata* has a larger elongated rectum, with anus expansion in shell form; *S. palmula* is short and large, with anus ending with fold in bell shaped. *S. mordax* has a short and large rectum, and the anus bears a single fold.

Gonads

The gonads of all species are massive, apparently regardless of the gonadal maturation period, and surround the whole visceral mass, in some cases surrounding the region near the pyloric process. They are usually coloured beige or yellowish. The genital opening has been observed in *S. cucullata* in the kidney, and distinguishes itself from the opening by a brownish spot.

Nervous system

The nervous system is relatively simple, showing a pair of cerebral ganglia and a pair of visceral ganglia connected by commissures. The cerebral ganglia are somewhat inconspicuous because of their very small size and localization in the visceral mass. The visceral ganglia can be easily distinguished in the anterolateral region of the adductor muscle. *S. cucullata* and *S. glomerata* have two pairs of nerves in the anterior region and three in the posterior region; *S. echinata* presents two pairs in the anterior and posterior regions; *S. mordax* and *S. palmula* have three pairs in the anterior and posterior regions.

Legends

Plate 1. *Saccostrea cucullata*. Fig. A – General right view; Fig. B –Right valve, internal view; Fig. C – Ventral whole view; Fig. D – Whole soft parts, general view; Fig. E – Extracted mantle lobe and mantle edge and accessory heart; Fig. F – Palps, right-slightly ventral view, outer right hemipalp deplected; Fig. G – Heart isolated, showing a ventricle and auricles; Fig. H – Anus and rectum; Fig. I – Anterior region, right view, with exposure of digestive system; Fig. J – Visceral ganglia, ventral view, adjacent layer of tissues also shown. Scales 1 cm.

Plate 2 – *Saccostrea cucullata* anatomical features. Fig. K – General view of soft parts; Fig. L – general view, right mantle lobe removed; Fig. M – Stomach, right view, opened longitudinally; Fig. N – Visceral ganglia, ventral view. Fig. O – Detail for anus. Scales 1 cm.

Plate 3. *Saccostrea glomerata*. Fig. A – General right view; Fig. B – Right valve, internal view; Fig. C – General view of soft parts right view, right mantle lobe removed; Fig. D – Mantle lobe and edge; Fig. E – Heart, ventral view; Fig. F – Anterior region; Fig. G – Anterior region, right view, with Stomach opened longitudinally; Fig. H – Palps, right-slightly ventral view. Scales 1 cm.

Plate 4. *Saccostrea glomerata*. Fig. I – General right view of soft parts; Fig. J – Detail for a palps; Fig. K – Stomach opened longitudinally, right view; Fig. L – Visceral ganglia. Scales 1 cm.

Plate 5. *Saccostrea echinata*. Fig. A – External view; Fig. B – Internal view, left valve; Fig. C – Internal view right valve; Fig. D – General view of soft part; Fig. E – Anterior region; Fig. F – Mantle edge, detail for a pallial muscles and accessory heart; Fig. G – Visceral ganglia; Fig. H – Heart, and rectum; Fig. I – Anus with expansion and rectum. Scales 1 cm.

Plate 6. *Saccostrea echinata*. Fig. J – General view of soft part; Fig. K – Palps, detail for the median fusion of external hemipalps; Fig. L – Anus and rectum, detail for a expansion in anus; Fig. M – Stomach, right view; Fig. N – Heart in pericardium. Scales 1 cm.

Plate 7. *Saccostrea palmula*. Fig. A – External view; Fig. B – Internal view of left valve; Fig. C – Internal view of right valve; Fig. D – General view of soft parts; Fig. E – Posterior region, detail for a gills, mantle edge, accessory heart and adductor muscle; Fig. F – Detail for the palps; Fig. G – Visceral ganglia. Scales 1 cm.

Plate 8. *Saccostrea palmula*. Fig. H – General view of soft part; Fig. I – Detail for the palps; Fig. J – Stomach, right view; Fig. K – Visceral ganglia. Scales 1 cm.

Plate 9. *Saccostrea mordax*. Fig. A – External view; Fig. B – Internal view of right valve; Fig. C – Internal view of left valve, detail for a undulations of the edge valves and umbonal cavity; Fig D – General view of soft part; Fig. E – Mantle edge, detail for a accessory heart and pallial muscles; Fig. F – Detail of the palps and gills; Fig. G – Heart; Fig. H – Visceral ganglia. Scales 1 cm.

Plate 10. *Saccostrea mordax*. Fig. I – General view of soft parts; Fig. J – Stomach, right view; Fig. K – Visceral ganglia. Scales 1 cm.

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ANEXO III – Only descriptions of relationated taxon in: Simone et.al., subimitt - Comparative anatomy of selected marine bivalves from the florida keys, with notes on brazilian congeners (Mollusca: Bivalvia)

Family Gryphaeidae

***Parahyotissa mcgintyi* (Harry, 1985)**

Figs. 83–94

Synonymy

Le Bajet – Adanson, 1757: pl. 14, fig. 4. See also Fischer-Piette (1942: 295, pl. 12, fig. 2).

Mytilus roseus Gmelin, 1791: 3362 (based on Adanson's Le Bajet; see above). A forgotten name reinstated by Huber (2010: 616) under violation of Art. 23.9 and 23.11 of the ICZN (1999) Code. Prevailing usage of *Hyotissa mcgintyi* is here maintained; see Remarks.

Ostrea (Ostrea) thomasi McLean, 1941: 7, pl. 3, figs. 1–2, pl. 4, figs. 1–2 [Type locality: off Palm Beach, Florida] (non *Ostrea sellaeformis* var. *thomasi* “Conrad” Glenn, 1904).

Pycnodonte (Hyotissa) hyotis – Abbott, 1974: 457 [non *Mytilus hyotis* Linnaeus, 1758; see below].

Parahyotissa (Parahyotissa) mcgintyi Harry, 1985: 130 [replacement name for *O. thomasi* McLean, 1941, non Glenn, 1904].

Pycnodonte hiotis [sic] – Rios, 2009: 498, fig.

Parahyotissa macgintyi [sic] – Ardovini & Cossignani, 2004: 49.

Hyotissa mcgintyi – Kirkendale et al., 2004: 309 ff., fig. 2 [first record in the Florida Keys]; Bieler et al., 2004: 150–151, figs 1–2; Bieler & Mikkelsen, 2004: 513; Mikkelsen & Bieler, 2007: 114–117, 5 figs.

Description:

Shell (Figs. 83–85) rounded or D-shaped, reddish, thick; maximum SD $\approx$ 50 mm in material examined. Inner layer with vesicular structure most apparent marginally as foam-like or spongy, especially under magnification. LV cementing to and assuming shape of hard substrata; RV smaller, more planar. Outer surface highly irregular, covered by minute concavities; sometimes radially pleated. Valve margins undulating or irregularly plicated. Hinge plate edentulous; L $\approx$ 60% SD. Vermiculate chomata on shell margin on either side of ligament. Ligament occupying entire dorsal hinge plate, thicker in central third. Inner surface glossy white. Adductor muscle scar rounded, subcentral, slightly posterodorsal; A $\approx$ 7% of inner VA.

Main muscle system (Figs. 85, 88): Anterior adductor and pedal retractor muscles absent. Posterior adductor muscle (*pm*) very large, at approximate midpoint of posterior third of animal, clearly with 2 (“catch” and “quick”) portions of subequal A; anteriorly oval; posteriorly crescent-shaped (with concavity anterior); A $\approx$ 20% VA.

Foot: absent.

Mantle (Figs. 86, 90, 94): Mantle lobes almost totally free except for relatively narrow dorsal region adjacent to hinge area, and another very short area separating incurrent and excurrent apertures, composed of inner fold (Fig. 94: *um*). Outer fold of mantle edge thin, smooth, simple. Periostracum separating outer and middle folds.

Middle fold $T \approx 2$ outer fold T , $H \approx$ outer fold H , bearing series of papillae at edge (most of $H \approx 2$ fold base H); each papilla slender, relatively tall, pointed, with interspace $= 3$ papilla W ; papillar size and interspaces weakly variable. Inner fold L and $T =$ middle fold L and T , bearing series of very small papillae, with interspaces $= 3$ papilla W . Remaining areas of mantle inner surface almost totally covered by small papillae (Fig. 86), distributed randomly, variable in size, more concentrated in regions preceding edges and anteriorly preceding palps; narrow band lacking papillae at some distance from mantle edge (mostly probably a rejection tract); each papilla with whitish beige base and brown-stained tip. Pallial muscles relatively thick, originating at pallial line in inner edge of above-described smooth area. Pigmented papillae covering most structures of pallial cavity, including suprabranchial chamber, *pm*, and inner (dorsal) surface of gill.

Pallial cavity (Figs. 85, 87–88, 91–92, 94) on left side overlaying most of body surface, except *pm* and narrow visceral region close to hinge area. Visceral mass extending farther dorsally on right side, filling space between *pm* and hinge area. Infrabranchial chamber ventral to *pm* and visceral mass. Single right promyal passage (Fig. 88: *po*) as suprabranchial chamber passing through visceral mass on left, passing anteriorly to *pm*, and on both sides ventral to *pm*, also with region $= pm$ L toward posterior. Labial palp (*pp*) $L \approx 14\%$ of gill L , covering anterior end of gill (Fig. 87). Outer hemipalps connected, covering anterior ends of demibranchs, with longer region at level of inner demibranch. Inner surface of each outer hemipalp with series of arched, uniform, narrow folds, starting between demibranchs, running ventrally, arching medially; before midline, inner folds abruptly ending at same level, with smooth area uniting outer hemipalps in $A = 66\%$ of folded area A , Another narrow smooth area at

posterolateral ends of each hemipalp, broadly attaching to mantle at level posterior to anterior end of outer demibranch (*do*); taller region of each outer hemipalp bearing short, projecting, flattened flap. Inner hemipalp A $\approx$ 66% of outer hemipalp A, along midline from approximately same level of posterior end of outer hemipalp, adjacent only to inner surface of inner demibranch (*di*), posteriorly taller, decreasing gradually anteriorly; inner surface with transverse folds perpendicular to longitudinal body axis, ending ventrally close to ventral edge, with narrow ventral smooth inner edge. Remaining folds similar to those of outer hemipalps; folds ending approximately at same level as those of outer hemipalp, with smooth area preceding mouth. Gill A $\approx$ 66% of infrabranchial chamber A $\approx$ infrabranchial chamber L. Each demibranch subequal in size (Fig. 85); *di* with anterior end slightly more anterior than that of *do* (Fig. 87). Ventral demibranch edges narrow, each bearing shallow food groove; dorsally wide, with ascending and descending portions well-separated at base. Transverse inner septa (Figs. 88, 91: *gr*) uniting portions of each demibranch, between every 10–15 filaments; septa of all 4 demibranchs aligning transversely (Figs. 92, 94). Each septum connecting entire inner (dorsal) edge of filament, from ventral to dorsal ends, leaving suprabranchial chamber free; septum gradually becoming broader from ventral to dorsal, accompanying gill enlargement. Suprabranchial chamber totally covered by papillae similar to those on inner surfaces of mantle lobes, including surfaces of *pm* and visceral mass, and inner (dorsal) surface of gills and septa. Ctenidial vessels running along central connections between gills, also between connections of demibranchs (Fig. 91: *bv*). Tissue connections between gills along midline and between gills and mantle. Gill filaments connecting to neighboring filaments by transverse, narrow tissue connections. Anterior half of gills connecting to ventral surface of visceral mass; posterior half of gills supported by 3 suspensory stalks (Figs. 94: *do*, *di*), one at center

along union between gills, remaining 2 connecting to union of demibranchs of each gill. Origins of all 3 suspensory stalks on anteroventral surface of *pm* (leaving ventral surface free), slightly more posterior toward right. Posterior half of gills connecting via tissue to adjacent mantle along lateral edges, to mantle connection separating incurrent (*si*) and excurrent (*se*) apertures (Fig. 94: *um*).

Visceral mass (Figs. 85, 89, 92–93) filling entire space immediately ventral to umbones and hinge area; becoming narrower and restricted on right side after distance = 14% SH, keeping *po* anterior to *pm*, with space at right = W as suprabranchial chamber (Fig. 85). Stomach (Fig. 89: *st*; 93) filling anterodorsal region, immediately and entirely surrounded by greenish brown digestive diverticula. Gonad surrounding digestive diverticula and filling remaining subumbonal region plus short space in visceral mass at left of suprabranchial chamber, anterior to *pm* (Fig. 92). Pericardium anterodorsal to suprabranchial chamber; V $\approx$ 12% of visceral mass V.

Circulatory and excretory systems (Fig. 92): Pericardium relatively small, in dorsal region of visceral mass anterior to suprabranchial chamber, anterior to *pm*. Auricles (*au*) lobed, beige, V $\approx$ 25% of pericardial V; other characters of heart similar to that of *Hyotissa hyotis* (see below). Kidney (*ki*) internally hollow, compressed between remaining visceral mass and anterior surface of *pm*, filling left region adjacent to suprabranchial chamber; *ki* lobe V < 50% of inner *ki* V, restricted to ventral and left sides, bearing longitudinal, irregular folds, with dichotomies posteriorly, splaying across *pm* anterior surface.

Digestive system (Figs. 87, 89, 93–94): *Pp* as described above. Mouth (Fig. 87: *mo*) transverse, surrounded only by smooth areas; posterior lip $H \approx 66\%$ of anterior lip H . Esophagus (Fig. 89, 93: *es*) short, broad, in $L = 33\%$ of *pp* L ; inner surface covered by longitudinal, narrow, low folds well-separated. Stomach (Fig. 89: *st*; 93) oval; L and $W \approx 3$ *es* L and W . Dorsal hood (Fig. 89, 93: *dh*) $L \approx 2$ *st* $L \approx 50\%$ of *st* W , originating on anterior-right surface of *st*, just posterior to *es* opening, running left, immersed in visceral glands. Opening of conjoined style sac-intestine (Figs. 89, 93: *ss*, *in*) marked by abrupt constriction of posterior *st*, running posteriorly, weakly curving ventrally; $L = st$ L . Gastric inner surface (Fig. 93) with *es* folds abruptly ending in ventral, tall, broad gastric fold, running left along ventral surface of *dh*, decreasing at distal end of *dh*; also running toward right as pair of parallel folds, initially close, with anterior branch surrounding right gastric inner surface transversely, crossing dorsal surface, ending on opposite (left) side; posterior branch surrounding right edge of gastric shield (*gs*), diminishing into posterior *st*; another gastric fold in $W \approx 50\%$ W of previous fold W , running parallel and just posterior to ventral surface of *dh* main fold, anteriorly surrounding end of anterior branch of main gastric fold, curving perpendicularly posteriorly, running along *ss* as minor typhlosole; major typhlosole originating gradually on left edge of *gs*, running posteriorly next to minor typhlosole. Typhlosoles separating *in* (ventral) from *ss* (dorsal) (Fig. 93). *Gs* on posterior-right inner gastric surface (Fig. 93); $A \approx 16\%$ of inner gastric surface A . Ducts to digestive diverticula (Fig. 93: *dd*) between branches of right region of main gastric fold; *dd* as described above. *In* curving abruptly posterior to *ss* (Fig. 89, 93), running anteriorly close to *ss* to anterior-right region of *st*, making another ample loop in this region slightly away from gastric outer surface, then running posteriorly, obliquely, and sinuously from right side to closer to midline, at level of *pm*. Anus (Fig. 88: *an*) preceded by long, detached

(siphoned) portion of rectum, originating on posterior surface of *pm*, closer to left side; edge bearing few small folds on inner surface.

Reproductive system: Gonad as described above; genital aperture not observed.

Nervous system: not examined.

Material examined: USA, Florida Keys, FMNH 302069, 3 specimens (sta. FK-650; dissected: #1: 69 mm L, 55 mm H, 40 mm W; #2: 50 mm L, 39 mm H, 18 mm W; #3: 26 mm L, 25 mm H, 14 mm W); FMNH 317471, 3 shells (FK-260); FMNH 326538, 5 specimens (sta. FK-908/Bivatol-275); FMNH 333754, 6 specimens (sta. FK-991/Bivatol-450). BRAZIL, Bahia, off Alcobaça, 10–15 m, MZUSP 69725, 1 shell (iv/2002).

Distribution: Stated by Turgeon et al. (2009) to range from North Carolina to Texas, the Gulf of Mexico, Cuba, the tropical western Atlantic and the tropical eastern Pacific. A range to Bahia, Brazil, is here confirmed.

Remarks: Harry (1985) introduced the genus *Parahyotissa* with this species as the type species, distinguished from *Hyotissa* (type species *H. hyotis* – see below) by the promyal passage open only on the right side in *Parahyotissa* (here confirmed), and open on both sides in *Hyotissa*; The subsequent synonymy of *Parahyotissa* with *Hyotissa* is based on a molecular phylogeny advocated by Kirkendale *et al.* (2004); the material used in the molecular study is from the the same site ("Thunderbolt" wreck, off

Key Vaca) as the material here dissected. See also remarks under *H. hyotis*. No material from Brazil was available for dissection.

Parahyotissa mcgintyi is assumed to have amphiatlantic distribution (e.g., Harry, 1985; Carriker & Gaffney, 1996; Ardovini & Cossignani, 2004); unfortunately no anatomical or molecular data are available for eastern Atlantic specimens. Huber (2010: 614) synonymized this nominal species under *Parahyotissa rosea* (Gmelin, 1791), based on *Mytilus roseus* Gmelin, 1791, described from West Africa (not be confused with *Ostrea rosea* Gmelin, 1791, of the same work). As Huber's action appears to be in violation of ICZN (1999) Articles 23.9 and 23.11 (we have not located any prior post-1899 usage of *Mytilus roseus* as a valid name, whereas the name *P. mcgintyi* has been used frequently enough to fulfill the conditions of Art. 23.9.1.2) we are maintaining prevailing usage herein.

Parahyotissa mcgintyi, anatomy. FIG. I1: Labial palps and adjacent region of gill and mantle, ventral view, hemipalps deflected to show inner surface; FIG. I2: Suprabranchial chamber, lateral to right view, right mantle lobe removed, note promyal passage (po) anterior to adductor muscle (restricted to right side); FIG. I3: Digestive system *in situ*, dorsal view, topologies of some adjacent structures also shown; FIG. I4: Cross section of midportion of mantle lobe, in region close to mantle border; FIG. I5: Cross section through gills in midregion (anterior to adductor muscle); FIG. I6: Posterior region of visceral mass, dorsal view, left region of pericardium, renal membrane, and part of right mantle lobe removed,

showing inner renal structures and part of suprabranchial chamber anterior to adductor muscle; FIG. I7: Stomach, dorsal view, opened longitudinally; FIG. I8: Anal region of mantle cavity, right and slightly posterior view, right mantle lobe partially removed. Scale bars = 2 mm (FIGS. 88–91); 5 mm (FIGS. 92–94). an, anus; au, auricle; bv, “blood” vessel; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; dg, digestive diverticula; dh, dorsal hood; di, inner demibranch; do, outer demibranch; er, esophageal rim; es, esophagus; fg, food grooves; gf, gastric fold; gm, gill retractor muscle; go, gonad; gr, gill transverse septum in suprabranchial chamber; gs, gastric shield; gt, gill suspensory stalk; in, intestine; ip, inner hemipalp; kc, renal chamber; ki, kidney; mi, mantle border inner fold; mm, mantle border middle fold; mo, mouth; mp, mantle papillae; mt, mantle; mu, mantle border outer fold; op, outer hemipalp; pc, pericardium; pe, periostracum; pl, pallial muscles; pm, posterior adductor muscle; po, promyal passage of suprabranchial cavity; pp, labial palp; rt, rectum; sb, suprabranchial chamber; ss, style sac; st, stomach; su, supra-anal chamber of suprabranchial pallial cavity; um, fusion between left and right mantle lobes; vm, visceral mass.

Parahyotissa mcgintyi, shell morphology, FMNH 302069, 69 mm maximum D. FIG. I9: Articulated specimen, ventral view showing zigzag shell margin; FIG. I10: RV, interior view.

***Hyotissa hyotis* (Linnaeus, 1758)**

Figs. 95–104

Synonymy

Mytilus hyotis Linnaeus, 1758: 704 [Type locality: “Pelagi Gorgoniis” = in the Gorgonia corals of the sea].

Hyotissa hyotis – Harry, 1985: 128–131; Sevilla-H. *et al.*, 1998: 25–32, *figs 1–2*; Bieler *et al.*, 2004: 149–159, *figs 3–4*; Mikkelsen & Bieler, 2007: 118, 4 *figs*.

Description:

Morphology similar to that of *Hyotissa mcgintyi*, except as noted here.

Shell (Figs. 95–97) purplish black to magenta to violet-brown, with irregular sculpture of pleated ribs bearing hollow spines; maximum SL $\approx$ 180 mm in material examined. Interior bluish or yellowish white with black or brown stains; valve margins near ligament with both vermiculate and lath chomata.

Main muscle system (Fig. 101): Posterior adductor muscle (*pm*) more posterior, close to posterior mantle edge.

Mantle (Figs. 100–101, 103): Middle and inner folds of mantle edge dark brown, almost black, including connection between lobes (Fig. 100: *um*); separating excurrent (*se*) and incurrent (*si*) apertures. Three mantle border folds of subequal T and H, except for slightly thinner outer fold. Middle fold bearing series of papillae (Fig.

103: *mp*) along edge, most in $L < 50\%$ of remaining region of fold H; with 3 rows of papillae covering distal region of inner surface of fold to edge. Inner fold (Fig. 103: *mi*) bearing series of short, broad, dense papillae. Remaining areas of mantle inner surface lacking papillae, bearing only few bulging hemolymph sinuses in region close to mantle border folds. Promyal passage (Fig. 101: *po*) widely open on right side, narrow on left.

Pallial cavity (Figs. 98, 101): Suprabranchial chamber lacking papillae. Labial palps (Fig. 98: *op*, *ip*) with proportionally more internal folds.

Visceral mass (Fig. 99) anteroposteriorly longer. Gonad (*go*) pale cream-colored, surrounding greenish-beige digestive diverticula and remaining subumbonal region; with large space in visceral mass to left of suprabranchial chamber, anterior to *pm*. Connective tissue brown, surrounding most of digestive system, isolating it from surrounding *go*.

Circulatory and excretory systems (Figs. 99, 101): Pericardium (Fig. 101: *pc*) in $V \approx 25\%$ of visceral mass V , highly asymmetrical; right side $A \approx 2$ left side A . Ctenidial veins running along connection between demibranchs of each gill, connecting with T-shaped branch of ctenidial vein (Fig. 101: *cv*) running perpendicularly, originating between middle and anterior thirds of gill, running dorsally along *ca*. 50% of visceral H , bearing internal longitudinal, narrow, low folds. Ctenidial vein connecting to ventral end of auricle (*au*), marked by abrupt change in ST and color. *Au* multilobed (Fig. 99); right *au* $V \approx 130\%$ of left *au* V , placed more dorsally; walls thickly glandular, dark brown; *au* lobes covering most of pericardial posterior half, surrounding ventricle (*ve*). *Ve* thickly muscular, pyriform (Fig. 99); $L \approx 80\%$ of *pc* L , $V \approx 50\%$ of *pc* V . *Ve-au*

connections narrow, with unpigmented ducts at center of posterior *ve* slope; L and W $\approx$ 20% of *ve* L and W.

Digestive system (Figs. 101–102, 104): Inner surface of esophagus (*es*) covered by series of regular, broad, low, transverse folds, adjacent, abruptly ending in ventral gastric fold (Fig. 104); without distinct rim. Dorsal hood (Figs. 102, 104: *dh*) in V $\approx$ 12% of stomach V; inner surface with transverse folds. Gastric inner surface with pair of ventral, transverse folds (Fig. 104: *gf*) just posterior of *es* opening; aperture of *dh* between these folds; pair of narrow folds originating from right side of transverse folds, running posteriorly, penetrating conjoined style sac-intestinal opening; 2 pairs of ducts to digestive diverticula (Figs. 102, 104: *dd*) at midventral region of main gastric chamber, just posterior to *dh* and to origin of longitudinal gastric folds; left pair of ducts to *dd* separated by sharp, narrow fold. Gastric shield (Fig. 104: *gs*) on posterior-left side; A $\approx$ 25% of gastric inner surface A. Intestinal loops running more dorsally along dorsal wall of stomach-style sac. Anus (Fig. 101: *an*) preceded by short stalk; W $\approx$ 20% of *pm* W.

Material examined: USA, Florida Keys, FMNH 302010, 1 specimenn [sta. FK-717; dissected: 180 mm L, 145 mm H, ca. 48 mm W (without fouling organisms)].

Distribution: An Indo-Pacific species recently introduced to Florida. This species is not known from Brazil.

Remarks: The discovery of this specimenn, and hence the confirmed presence of this introduced Indo-Pacific species in South Florida, led to the tracking of this

potentially invasive species by the Florida Fish and Wildlife Commission in its Exotic Species Database. Tissue samples from this Florida Keys specimen were used in the molecular analyses of *Bieler et al.* (2004) and Tëmkin (2010).

This work provides the most complete anatomical descriptions of the two examined species of *Hyotissa* to date. They have similar anatomical features; however, a set of differences, detected here, facilitates the species-level distinction. The most readily perceived is the near-black mantle edges of *H. hyotis* (Fig. 100), in contrast to the pale beige or cream-colored ones of *P. mcgintyi* (Fig. 86). Another distinct feature is the greater development of pallial papillae in *P. mcgintyi*, covering the entire mantle lobes (Fig. 86), and some pallial structures, such as the surface of the posterior adductor muscle and the dorsal surface of the gills; this is not found in *H. hyotis*, in which these structures are smooth. Adult size appears to be another distinction, with *H. hyotis* typically reaching 3–4 times the size of *P. mcgintyi*. The extraordinary size and complexity of the auricles of *H. hyotis*, including the dark brown color, is less developed in *P. mcgintyi*. In the digestive system, *H. hyotis* has a shorter dorsal hood (Fig. 102) and anal papilla (Fig. 101), both of which are very long in *P. mcgintyi* (Figs. 89, 94); the inner organization of the stomach is also different (compare Figs. 93 and 104); the intestine of *H. hyotis* runs more dorsally than that of *P. mcgintyi* (Figs. 89, 102). On the other hand, the two species share some interesting and unusual features, such as the right promyal passage (Figs. 88, 101: *po*), the lobed auricles (Fig. 99), and the eulamellibranch gills with well-developed sequential septa reinforcing the filaments (Fig. 91: *gr*). The existence of a narrower left promyal passage in *H. hyotis* – a feature that led Harry (1985) to distinguish between the two genera *Hyotissa* and *Parahyotissa* (the latter with only the right passage) – was here confirmed (see comments above, under *P. mcgintyi*).

Hyotissa hyotis, anatomy, FMNH 302067. FIG. J1: Pallial cavity, ventral view, detail of anterior region, outer hemipalp (op) partially deflected; FIG. J2: Pericardial region, right view, right wall of pericardium removed, ctenidial vein (cv) opened longitudinally, including adjacent portion of auricle (au); FIG. J4: Mantle border, posterior view, detail of region between incurrent and excurrent flows. Scale bars = 5 mm; 2 mm. au, auricle; cv, ctenidial (efferent) vessel; di, inner demibranch; do, outer demibranch; go, gonad; in, intestine; ip, inner hemipalp; mb, mantle border; mo, mouth; op, outer hemipalp; pc, pericardium; sb, suprabranchial chamber; um, fusion between left and right mantle lobes; ve, ventricle.

Hyotissa hyotis, anatomy, FMNH 302067. FIG. J5: Pallial cavity, ventral view, detail of anterior region, outer hemipalp (op) partially deflected; FIG. J6: Pericardial region, right view, right wall of pericardium removed, ctenidial vein (cv) opened longitudinally, including adjacent portion of auricle (au); FIG. J7: Mantle border, posterior view, detail of region between incurrent and excurrent flows. Scale bars = 5 mm; 2 mm. au, auricle; cv, ctenidial (efferent) vessel; di, inner demibranch; do, outer demibranch; go, gonad; in, intestine; ip, inner hemipalp; mb, mantle border; mo, mouth; op, outer hemipalp; pc, pericardium; sb, suprabranchial chamber; um, fusion between left and right mantle lobes; ve, ventricle.

Family Spondylidae

Spondylus americanus Hermann, 1781

Figs. 119–135

Synonymy:

Spondylus americanus Hermann, 1781: 51 [Type locality: Santo Domingo]; Yonge, 1973: 177–188, figs. 2, 5, 9–11; Abbott, 1974: 450, pl. 21, fig. 5221; Rios, 1994: 250, pl. 86, fig. 1224; Viana & Rocha-Barreira, 2007: 815–819, figs. 1–4; Bieler & Mikkelsen, 2004: 520; Mikkelsen & Bieler, 2007: 154–155, 5 figs.; Rios, 2009: 508–509, fig.

Description:

Shell (Figs. 119–120) highly variable, thick, varying from white, yellow, orange, red, brown, to combination; SL $\approx$ 80 mm in material examined, SH = 1–2 SL. Valves highly asymmetrical; RV larger, cementing to and assuming shape of hard substratum, with tall, triangular auricles; free LV more planar. Sculpture most evident on LV and detached portion of RV, composed of 20–30 radial threads; interspace W = thread W; normal arrangement of smaller and larger threads intercalated, with smaller thread W $\approx$ 50% of larger thread W. Spines and long scales typically occurring along threads, directed externally and to periphery; disposition regular, aligning commarginally; spines of larger threads typically larger than those of smaller threads; spines variable, absent in some specimens. Outer shell surface opaque, delicately irregular. Ligament (Fig. 120: *li*) along entire horizontal dorsal hinge plate, centrally occupying 70–80% SL, with triangular expansion at midregion, along *ca.* 10% SL, running along auricles of each

valve, dividing them into 2 equal portions. Internal component of *li* extending at midregion of hinge plate along *ca.* 6% SH. Hinge plate occupying 70–80% SL and *ca.* 6% SH, symmetrical from internal component of *li*. RV with wide medial tooth and lateral socket on each side of *li*, each in $L \approx 15\%$ of hinge plate L; LV with medial socket and wide lateral tooth on each side of *li*; tooth with tip wider than base; tip bluntly bifid. Inner surface glossy white, except same color as external surface at valve margin (Fig. 120), colored band $H \approx 7\%$ SH at midventral edge, gradually diminishing toward hinge. Inner surface mostly smooth, except close to margin; latter with uniform denticles corresponding to external sculpture. Strong scar of adductor muscle subcentral, slightly posterodorsal; $A \approx 30\%$ of inner VA.

Main muscle system (Figs. 120, 124–125): Anterior adductor muscle absent. Posterior adductor muscle (*pm*) very large, circular in cross section, subcentral, slightly posterodorsal, in $A \approx 25\%$ of inner VA, divided into 2 semicircular, subequal (“catch” and “quick”) portions. No other well-developed muscles except T of visceral wall serving as pedal protractor muscles, thicker anteriorly, forming 2 lateral, anterior, dorsoventral folds (Fig. 124: *rr*).

Foot (Figs. 124–125: *ft*) well-developed, anteroventral, in form of wide bell, with relatively thick muscular walls and deep concavity; $V \approx 10\%$ $SV \approx 50\%$ of visceral mass portion ventral to *pm*. Outer surface smooth, pigmented by sparse, dark brown spots. Inner surface white, covered by uniform, low radial folds, originating in small, central, smooth area; each fold separated from others by narrow furrow and mostly dichotomizing at midlevel. Pair of deeper, wider furrows running, respectively, anteriorly and posteriorly. Byssus and byssal gland absent.

Mantle (Figs. 126–128): Mantle edge thickened, with 3 well-developed folds, mostly pigmented dark brown (rarely pale beige), with coalescent, broad, whitish spots, subcircular in some areas. Outer mantle fold thin ($T \approx 33\% ST$, $H \approx 2 T$), simple, white. Periostracum separating outer and middle folds. Middle fold $T \approx 3$ outer fold T , bearing large, tall papillae and eyes in following arrangement (Figs. 126–127): outer row of small, slender, pointed papillae; inner row of larger, taller papillae, fewer in number than smaller papillae of outer row; one eye between every one or 2 papillae. Each eye (Fig. 127–128: *ey*) on short eyestalk, containing large lens and dark retina contacting and covering basal and lateral sides of lens; cornea thin, occupying central tip; cornea surrounded by black integument. Ocular nerve thick, running from retina toward base of eyestalk, then as 8–10 nerves running radially along mantle lobes (Fig. 121: *nv*). Inner mantle fold very wide ($W \approx 20\% SH$), directed internally as pallial veil, contacting inner fold of opposing mantle lobe, especially high midventrally. Mantle muscles thick, originating at pallial line at some distance from shell margin, inserting along 3 folds, mostly in inner fold. Remaining mantle thin, translucent from pallial line to *pm*, bearing several iridescent, radial pallial nerves.

Pallial cavity (Fig. 123–124, 133) in $V \approx 33\%$ of body V , especially broader ventrally and anteriorly. Labial palps (Fig. 123–124: *pp*) dorsoventrally long, anteroposteriorly short; region between hemipalps attaching along anterior border of pallial cavity. Anterior ends of demibranchs ending between dorsal ends of hemipalps. Dorsal ends of hemipalps partially fused and situated as anterior cover of gill. Inner surfaces of hemipalps similar (Fig. 133), each with *ca.* 25 transverse folds, alternating on each hemipalp. Posterior end of each fold rounded, with narrow smooth area

preceding *pp* edge; posterior half of each fold slightly narrower than anterior half (gradually transitioning); anterior end gradually diminishing, with smooth furrow separating hemipalps. Inner surfaces of hemipalps abruptly changing ventrally (Figs. 123, 133), becoming longitudinal (perpendicular in relation to preceding folds), their distal ends curving toward *pp* edge, becoming tall and successively branching “lips,” each with dendritic projections (Figs. 123, 133: *dp*) protruding into flaps on inner surface of *pp* surrounding mouth. Smooth membrane as continuation of outer surface of *pp* surrounding dendritic external surface, little beyond them.

Gills (Fig. 130: *gi*) surrounding ventral surface of *pm*; $L = SL$, $V \approx 70\%$ of pallial cavity V . *Gi* filaments free (i.e., filibranch) and free from neighboring structures (mantle and visceral mass), connecting to latter by cilia. Each filament (Fig. 132) very narrow, long, without food grooves; ventral third of each demibranch descending and ascending lamellae connected; remaining part of lamellae free. Ctenidial vein running along *gi* base between demibranchs, surrounded by thin longitudinal muscle (Fig. 132); transverse muscle present ventral to it, also running in basal portion of each demibranch. Posterior projections of *gi* supported by suspensory stalk (Fig. 130: *gt*); each *gt* weakly muscular, laterally compressed, dorsoventrally tall; base of each *gt* originating at ventral *pm*, gradually tapering posteriorly; distal tip pointed; $L \approx 25\%$ of *gi* L . Inner demibranchs connecting by cilia along midline in posterior third of L .

Visceral mass (Figs. 124–125, 129) asymmetrical anterodorsally, accompanying asymmetry of umbonal region of shell valves; right portion taller and longer than left; taller portion very variable, mostly filled with connective tissue, ventrally compressed, extending posterior to *ft* and ventral to *pm*, protruding posteriorly as “heel” slightly

beyond *pm*. Stomach (Figs. 125: *st*; 129) mid-dorsal. Digestive diverticula greenish-brown, covering *st* almost totally and slightly beyond. Gonad cream-colored, covering digestive diverticula and extending dorsally into both umbonal regions, ventrally in compressed ventral region posterior to *ft*, and lateroposteriorly contacting *pm*. Pericardium just anterior to *pm*, compressed anteriorly by gonad.

Circulatory and excretory systems (Figs. 125, 131, 134–135): Pericardium (Fig. 125: *pc*) anteroposteriorly short, laterally broad; $W \approx pm\ W$, $V \approx 20\%$ of visceral mass V (including adductor). Ventricle (*ve*) massive, in central region, surrounding intestine crossing *pc*, with central portion narrower than lateral portions. *Ve* connection with auricles (*au*) narrow, in central region of lateral walls. *Au* lateral, each as large as *ve*; anterior surface of each connecting to pericardial wall; lateral end connecting to ctenidial vein. Anterior aorta broad, dichotomizing after short distance, running along surface of adjacent anterior portion of gonad, dorsal to intestine. Posterior aorta narrow, running ventral to intestine. Ctenidial vein narrow along entire L, connecting with *au* by short vein of same D between anterior and middle thirds of *gi*, just anterior to *pm*. Kidney (*ki*) brown, extending ventral to *pc* to posteroventral *pm*, posterodorsal to *ft*, mostly solid, containing tall transverse folds, coalescent and branching. Ventral wall of *ki* separating it from pallial cavity, thin, translucent, detached from renal tissue. Nephropore (Figs. 134–135: *ne*) small, at posterior end of renal chamber, at level of posteroventral *pm*. Genital structures bulging into posterior *ki* as described below.

Digestive system (Figs. 123, 125, 129–130, 133): *Pp* as described above. Mouth wide, located deep among dendritic lips of *pp* (Fig. 123, 133: *dp*). Esophagus (*es*) broad, conic, short ($L \approx 33\%$ of *pp\ L*); inner surface smooth; inserting into stomach (*st*)

anteroventrally. Gastric main chamber occupying *ca.* 33% of visceral portion anterior to *pm*, close to latter. Gastric inner surface (Fig. 129) with 3 transverse, mostly ventral, tall folds; anterior one close to *es* opening; middle one close to anterior fold; posterior one close to posterior end of *st*; relatively deep concavity between each successive ventral fold; anterior and posterior folds connecting by longitudinal, low, right fold; another tall longitudinal connection on left side uniting middle and posterior folds (Fig. 129: *gf*), with transverse furrow as sorting area. Ducts to digestive diverticula (Fig. 129: *dd*) relatively wide; one pair in concavity between anterior and middle ventral folds; another 3 ducts in ventral edge of longitudinal fold connecting anterior and posterior folds; another large duct in ventral edge of longitudinal fold uniting middle and posterior ventral folds. Gastric shield (*gs*) between posterior ventral fold and posterior end of *st*. Intestine (*in*) and style sac (*ss*) broadly conjoined, originating at midregion of concavity between middle and posterior ventral folds; opening relatively broad ($W \approx 33\%$ of *st* *W*), running posteroventrally, narrowing gradually to end of ventral, compressed region of visceral mass at posterior level of *pm*; *in* abruptly twisting in this region, running anterodorsally to *ss*, crossing to right of conjoined *ss-in* opening at right-ventral *st*; *in* running anteriorly beyond *st*, making wide loop dorsally, then running posteriorly, crossing *pc* and dorsal surface of *pm*, gradually running closer to LV. Anus (Fig. 130: *an*) simple, dorsoventrally compressed, preceded by long, free stalk, originating on left third of *pm* posterior surface; stalk base with pair of transverse folds, each originating from base of *gt*; right fold slightly more dorsal than left.

Reproductive system (Fig. 135): Gonad as described above, separated into 2 pairs of lobes; dorsal pair with terminal hollow chamber in anterior end of *ki*, in anteroventral visceral mass; this chamber separated from *ki* by membrane, latter

abruptly becoming tube-like (*ge*) at midventral surface; tube running posteriorly, opening at midventral region of other prerenal chamber. Ventral lobes without obvious terminal chambers, but also with terminal tube (*ge*) in $W \approx 2$ dorsal lobe *W*; terminal tube inserting into prerenal chamber in medial edge. Each prerenal chamber with thin walls, dorsoventrally compressed, in $A = 16\%$ of *ki* *A*; ventral surface attaching to walls separating renal and pallial chambers, also covering tube of dorsal gonadal lobes; dorsal surface free in renal chamber; anteroventral region of renal lobe bulging; aperture wide. Gametes apparently traversing these tubes and prerenal chamber, exiting at nephropores after crossing entire renal *L*.

Nervous system (Fig. 134): Paired anterior (pleural?; see Remarks) ganglia (*plg*) spherical, small ($A \approx 33\%$ of *es* *D*), adjacent, close to midline, just anterior to mouth; commissure $L \approx 50\%$ of single *plg* *L*. Paired pedal ganglia (*pg*) each in $V \approx 2$ single *plg* *V*, adjacent in posterodorsal region of visceral surface of *ft*; each *pg* with large anterior nerve running through pedal musculature. Paired visceral ganglia (*vg*) very large, just posterior to junction of visceral mass with ventral surface of *pm*, each in $V = 6-7$ single *plg* *V*. *Vg* forming 5-lobed structure; central lobe largest, with 2 lateral lobes, each in $V \approx 50\%$ of central lobe *V*, and 2 posterior lobes (cerebral ganglia?), each in $V \approx 25\%$ of central lobe *V*, bulging at anterior surface of this ganglionic mass, slightly away from midline. Pleurovisceral (?; see Remarks) connectives (*plv*) running through visceral glands, close to integument, surrounding *ft* base, joining with lateral region of posterior *vg* lobes. Cerebropedal connectives (*cn*) in $T \approx$ pleurovisceral connectives *T*, running ventral to latter, inserting medially into posterior visceral lobes. Thick pair of nerves inserting into lateral surface of *vg*, between posterior and lateral

lobes, with 2 branches each, one innervating gill stalks, other mantle border. Pallial eyes as described above. Abdominal sense organs not observed.

Material examined: USA, Florida Keys, FMNH 302065, 302066, 302068, 4 specimens [sta. FK-717; 2 dissected: #1: ca. 86 mm L, 103 mm H, 45 mm W (without spines); #2: ca. 80 mm L, 118 mm H, 46 mm W; Garden Key, Dry Tortugas, FMNH 177515 (84.9 mm L); FMNH 295736, 1 specimenn (= *S. ambiguus*) (sta. FK-048; dissected: ca. 67 mm L, 45 mm H, 41 mm W). BRAZIL. Pernambuco. Fernando de Noronha Archipelago, Conceição beach, 3°50'22.3"S, 32°24'55.8"W, 10 m, MZUSP 31402, 1 specimenn (vii/1999; dissected: 77.5 mm L, 72.2 mm H, 45.4 mm W). Bahia. Salvador; Itapuã beach, 12°57'13"S, 38°21'43"W, 2 m, MZUSP 28437, 1 specimenn (27/xi/1997; dissected, not measured). Espírito Santo. Off Guarapari, 45 m, MZUSP 70127, 1 specimenn (in lobster net, vi/2006), MZUSP 37381, 2 specimens, 1 shell (vi/2003; dissected, not measured). Rio de Janeiro. Conceição beach, 23°12'03.1"S, 44°37'36.8"W, 4 m, MZUSP 55737, 2 specimens (09/xii/2005; dissected, not measured), MZUSP 55739, 2 specimens (09/xii/2005; dissected, not measured); Ilha Comprida, 23°11'23.8"S, 44°37'23.9"W, MZUSP 55693, 1 specimenn (09/xii/2005; dissected, not measured); Lula beach, 23°11'38.5"S, 44°38'06.5"W, MZUSP 55812, 1 specimenn (10/xii/2005; dissected, not measured), 23°11'47.4"S, 44°37'44.1"W, MZUSP 58953, 1 specimenn (12/i/2006; dissected, not measured), Restaurante beach, 23°11'39.0"S, 44°37'32.2"W, 3 m, MZUSP 55775, 1 specimenn (10/xii/2005; dissected, not measured), Catimbau beach, 23°11'26.4"S, 44°37'25.5"W, 10 m, MZUSP 55945, 2 specimens (10/xii/2005; dissected, #1: 77.5 mm L, 69.0 mm H, 48.0 mm W; #2: 62.0 mm L, 64.0 mm H, 41.3 mm W), MZUSP 55944, 2 specimens (10/xii/2005; dissected, not measured); Ilha Grande; Imbuacica Is., MZUSP 79343, 2

specimens (20/viii/2006; dissected, not measured), Freguesia do Sul beach, MZUSP 23079, 1 specimen, 1 shell (24/vii/1966; dissected, not measured), Parcel do Aleijado, MZUSP 23080, 1 specimen (18/vii/1966; dissected, not measured). São Paulo. Queimada Grande Is., 24°28'57"S, 46°40'41"W, 8–25 m, MZUSP 35664, 2 specimens (28/vi/2002; dissected, not measured).

Distribution: Stated by Turgeon et al. (2009) to range from North Carolina to Quintana Roo (Mexico), the Gulf of Mexico outer banks, Brazil, and Bermuda. Its occurrence in Brazil to São Paulo is here confirmed.

Remarks: The anatomy described here agrees in all aspects with previous studies of spondylid anatomy (Dakin, 1928a, b, based mostly on Mediterranean *Spondylus gaederopus* Linnaeus, 1758; Yonge, 1973, based on *S. americanus* from Jamaica), including verifying two unusual features of the spondylid nervous system: (1) the very large visceral ganglionic complex (similar to that found in Pectinidae), and (2) the pedal ganglia joined via connectives with the latter (unique to Spondylidae). Watson (1930b) and Yonge (1973) postulated that the greater part of the cerebropleural ganglia are actually part of the visceral ganglionic complex (here as the two anterior bulges on the mass), evidenced by their connection with the pedal ganglia; if so, the anterior ganglia reported here are merely remnants, possibly only of the pleural ganglia. Further details of the pallial eyes of *S. americanus*, based on specimens from Brazil, were provided by Viana & Rocha-Barreira (2007).

This species shows a high degree of shell variation, due to phenotypic plasticity, incrustation, and moulding with the hard substratum. Logan (1974) explored the

functional morphology of this species in Bermuda, identifying five main modes of life, ranging from cementation on exposed deep reef walls to lying free in sediment pockets after having been dislodged from its substratum. In the Florida Keys, and elsewhere off both coasts of Florida, *Spondylus americanus* occurs in deeper water, on hard substrata (including shipwrecks) from *ca.* 25–30 m. It is replaced in shallower water by *S. ambiguus* Chenu, 1844 (in 1843–1845; previously known as *S. ictericus* Reeve, 1856, a synonym *teste* Lamprell, 2006; Finet & Lamprell, 2008), a morphospecies with brick-red shells (see Mikkelsen & Bieler, 2007: 156–157). [Both nominal species (*S. ictericus*, *S. ambiguus*) were recently synonymized under *S. tenuis* Schreibers, 1793, by Huber (2010: 628). Because the question of whether Schreibers' work can be accepted as binominal appears to be unresolved (see also Cox, 1929), we are using the name *S. ambiguus* herein]. In other parts of the western Atlantic, including Brazil and Bermuda, *S. americanus* also occurs in shallow water. *S. ambiguus* is also stated to occur in Brazil (Rios, 1994: 250, as *S. ictericus*), but no comparable anatomical differences were found by LRS in a study of extensive material that would justify a separation into two morphospecies within the Brazilian fauna. The *S. americanus* specimens from Florida and Brazil showed no anatomical differences. However, because the shells of *S. americanus* and *S. ambiguus* are clearly separable in Florida populations, we refrain from formally synonymizing the two species and await future molecular studies.

Spondylus americanus. FIG. 119: Shell morphology, articulated specimen, right view, FMNH 177515, 84.9 mm L. FIGS. 120–123: Anatomy, FMNH 302068, 98.0 mm maximum D; FIG. 120: Intact left view, LV and part of left mantle lobe removed; FIG. 121: Left mantle lobe, inner view; FIG. 122: Foot, opened longitudinally, exposing inner (ventral) surface; FIG. 123: Buccal region, ventral view, adjacent part of left labial palp (pp) also shown. Scale bars = 10 mm. dp, dentritic projection of lips and labial palps; ft, foot; gi, gill; li, ligament; mb, mantle border; mi, mantle border inner fold; mo, mouth; mp, mantle papillae; mu, mantle border outer fold; nv, nerves; pm, posterior adductor muscle; pp, labial palp; vm, visceral mass.

Spondylus americanus, anatomy. FIG. 124: Left overview, shell and part of left mantle lobe removed; FIG. 125: Same, digestive system *in situ*, topologies of some adjacent structures also shown; FIG. 126: Mantle border, cross section at midventral region; FIG. 127: Same, detail of outer and middle folds, ventral view; FIG. 128: Pallial eye, sectioned longitudinally; FIG. 129: Stomach, dorsal view, dorsal wall sectioned longitudinally and deflected. Scale bars = 10 mm (FIGS. 124–125); 1 mm (FIGS. 126–129). co, cornea; dd, ducts to digestive diverticula; er, esophageal rim; es, esophagus; ey, pallial eye; ft, foot; gc, gastric central pad; gf, gastric fold; gi, gill; go, gonad; gt, gill suspensory stalk; hf, hinge fold of mantle; in, intestine; ki, kidney; le, lens; mb, mantle border; mi, mantle border inner fold; mm, mantle border middle fold; mo, mouth; mp, mantle papillae; mu, mantle border outer fold; ne, nephropore; on, optical nerve; pc, pericardium; pl, pallial muscles; pm, posterior adductor muscle; pp, labial palp; re, retina; rr, pedal protractor muscle; rt, rectum; ss, style sac; st, stomach; su, supra-anal chamber of suprabranchial pallial cavity; vm, visceral mass; vo, mantle portion occupying umbonal cavity (in fixed valve only).

Spondylus americanus, anatomy. FIG. 130: Pallial cavity, detail of region posterior to posterior adductor muscle (pm), with gill deflected and mantle lobes removed; FIG. 131: Pericardial structures, dorsal view, dorsal region of pericardium removed; FIG. 132: Left gill, cross section in midregion; FIG. 133: Left labial palp, right-lateral view, outer hemipalp (op) deflected to show inner surface, short portion of adjacent region of gill (gi) and mantle (mt) also shown. Scale bars = 2 mm. aa, anterior aorta; an, anus; au, auricle; cv, ctenidial (efferent) vessel; di, inner demibranch; do, outer demibranch; dp, dentritic projection of lips and labial palps; gi, gill; gm, gill retractor muscle; gt, gill suspensory stalk; id, insertion of outer demibranch in mantle; im, insertion of inner demibranch in visceral mass; in, intestine; ip, inner hemipalp; ki, kidney; mt, mantle; op, outer hemipalp; pc, pericardium; pm, posterior adductor muscle; rt, rectum; ve, ventricle; vm, visceral mass.

Spondylus americanus, anatomy. FIG. 134: Nervous system *in situ*, ventral view, topologies of adjacent structures also shown, foot (ft) slightly deflected to left (at right in figure) and posterior region of visceral mass (vm) to right (at left in figure); FIG. 135: Left kidney and terminal reproductive structures, ventral view, topologies of adjacent structures also shown; ventral renal wall sectioned longitudinally; some inner structures exposed or seen by transparency. Scale bars = 1 mm. cn, cerebropedal connective; ft, foot; ge, genital ducts; gn, genital chamber; go, gonad; gt, gill suspensory stalk; im, insertion of inner demibranch in visceral mass; ki, kidney; mo, mouth; ne, nephropore; pg, pedal ganglion; plg, anterior (?pleural) ganglion; plv, pleurovisceral (?) connective; pn, pallial nerve from visceral ganglion; pp, labial palp; vg, visceral ganglia; vm, visceral mass.

Family Plicatulidae Gray, 1854

***Plicatula gibbosa* Lamarck, 1801**

Figs. 136–147

Synonymy:

Plicatula gibbosa Lamarck, 1801: 132 [no locality given]; *Yonge*, 1973: 188–197, *figs.* 14–23; Abbott, 1974: 450, *fig.* 5216, *pl.* 20, *fig.* 5216; Bieler & Mikkelsen, 2004: 519; Mikkelsen & Bieler, 2007: 158–159, 5 *figs.*

Description:

Shell (Figs. 136–138) oval to subtriangular, irregular, typically thick, white to brown, homogeneous to spotted; SL $\approx$ 9 mm in material examined. RV totally or partially cementing to hard substratum, fitting into surfaces even if irregular; periumbonally attaching to substratum in partially attached specimens. RV typically slightly more distorted and more concave than LV. Outer surface opaque, covered by pores, with 3–5 wide, irregular, radial undulations/plicae, producing undulating ventral and posterior margins (Fig. 137–138). Hinge plate of RV with medial pair of strong, symmetrical, divergent teeth, with corresponding medial sockets in LV; tooth L = 10–16% SH. Ligament central, between teeth. Inner surface smooth, translucent, glossy. Scar of adductor muscle circular, at mid-SH between middle and posterior thirds of SL; A $\approx$ 7% of inner VA.

Main muscle system (Figs. 138–139): Anterior adductor muscle absent. Posterior adductor muscle (*pm*) location and proportions as described above, clearly

possessing 2 (“catch” and “quick”) portions; anterior $A \approx 40\%$ of pm A. Pedal muscles absent.

Foot: absent.

Mantle (Figs. 139, 147):. Mantle lobes thin, translucent except at relatively thick borders; lobes free except for dorsal hinge fold; $H = 33\%$ SH. Pallial muscles connecting to pallial line, at distance from shell margin = 25–33% SH. Outer fold of mantle lobe (Fig. 147: *mu*) thin, simple; $T \approx 33\%$ ST, $H \approx 3$ T. Middle fold (Fig. 147: *mm*) in T and $H = 2$ outer fold T and H; papillae gradually appearing along entire posterior half of edge; each papilla $L \approx W$, at edges of fold, slightly internal; interspace $W = 2-3$ papilla W; longer papillae alternating with shorter papillae; shorter papilla $L \approx 50\%$ of longer papilla L. Inner mantle fold (Fig. 147: *mi*) of similar proportions to middle fold, except forming narrow pallial veil and having fewer and smaller papillae.

Pallial cavity (Figs. 138–139, 142–143, 145) in $V \approx 75\%$ of inner SV, except visceral mass from hinge area to midlevel of valves; cavity surrounding ventral, posterior, and dorsal sides of visceral mass. Labial palp $A \approx 2\%$ $VA \approx 25\%$ SL ventral to hinge plate. Palps (*pp*) covering anterior end of gills, extending *ca.* 12% SL anterior to gills. Hemipalps similarly shaped (Figs. 142–143) as 2 successive layers of bent flaps, in $L \approx 2$ H, narrowing gradually from anterodorsal to posterior. Outer hemipalps widely fused anteriorly; dendritic projection (Figs. 142–143: *dp*) with 3 papillae at ventral edge, located midway between outer hemipalps, in $H = 20\%$ of *pp* H; base slightly narrower than tip. Inner hemipalps widely connecting anteriorly, almost as tall as same regions of outer hemipalps, lacking dendritic projection. *Pp* inner surface with

5–7 wide transverse folds, successively shorter from anterior to posterior; each fold with rounded ventral end, leaving smooth ventral edge in $W \approx 12\%$ of pp W ; interspace $W = 50\%$ of fold W ; dorsal ends of folds connecting to dorsal furrow.

Gills (*gi*) not plicated, linear, lying along *ca.* 70% SL, in $H \approx 25\%$ SH in wider (anterior and middle) portions; anterior ends rounded; posterior ends tapering gradually. Gill suspensory stalks (Figs. 138–139: *gt*) inserting into posteroventral *pm*; base almost as wide as *pm*, gradually tapering to bluntly pointed tip; extending along (posterior) 50% of *gi*. *Gi* filaments connecting to one another and to adjacent structures only via cilia; each ascending lamella $L \approx 50\%$ of descending lamella L (Fig. 145); distal tip of these shorter lamellae bent laterally preceding ciliary connection (Fig. 145: *id*, *im*). Anterior ends of *gi* inserting between hemipalps along *ca.* 20% of posterior region (Figs. 142–143).

Visceral mass (Figs. 138–140, 144) along relatively narrow horizontal band between hinge area and *pm*; $V \approx 16\%$ SV, $L \approx 2$ H. Digestive system along central region; $V \approx 50\%$ of visceral mass V . Digestive diverticula greenish-cream, surrounding stomach; $V \approx 12\%$ of visceral mass V . Gonad greenish-cream, with clearly visible acini on nodular surface, filling entire remaining visceral mass V , including umbones. Renopericardial structures rectangular in section; $V \approx 16\%$ of visceral mass V just anterior to *pm* (Fig. 144).

Circulatory and excretory systems (Fig. 144–145): Size and location of renopericardial structures as described above. Ctenidial veins (Fig. 145: *cv*) running along central region of dorsal *gi* connections, with perpendicular component between

anterior and middle thirds, wider ventrally than dorsally, along 50% of visceral mass H, connecting with ventral ends of auricles. Auricles (*au*) subtriangular, attaching to posterolateral sides of pericardium (*pc*). Posterior wall of *au* bearing white, gland-like, middle protuberances in $L \approx 25\%$ of posterior wall T. Ventricle (*ve*) surrounding intestine as it traverses *pc*; $L \approx 20\%$ of *pc* L. *Ve* connection to *au* on posteroventral sides. Kidneys (*ki*) white, solid; $V \approx 10\%$ of *pc* V on ventral side. Nephropores minute, on anterior ends of *ki*.

Digestive system (Fig. 139–141, 146): *Pp* as described above. Esophagus (*es*) running dorsoventrally along *ca*. 70% of *pm* L, and similar distance ventral to hinge area; $W \approx 25\%$ of *pm* W. Stomach (*st*) conical, slightly perpendicular to *es*; main chamber $L \approx 2$ *es* L. Gastric inner surface with narrow, transverse *es* rim (Fig. 146: *er*); sorting area (*sa*) just dorsal to *es* opening, with wide, transverse, low folds. Gastric shield (*gs*) posterodoral; $A \approx 20\%$ of inner gastric surface A. Paired ducts to digestive diverticula (*dd*) ventral and at some distance from *es* opening, at ends of horseshoe-shaped furrow (with posterior concavity in $L \approx 25\%$ of main gastric chamber L); wide groove running longitudinally at right, edges gradually increasing in H, forming pair of typhlosoles (*ty*). Intestine (*in*) and style sac (*ss*) totally fused, separated only by pair of *ty*. *Ss* tapering gradually posteroventrally to ventral side of *pm*; $L \approx$ main gastric chamber L. *In* making 180° loop just posterior to *ss*, then performing wide, sinuous loop, running to right of *ss* and gastric main chamber, and along midline; total *in* $L \approx$ SL. Anus (Figs. 139–141: *an*) with blunt, weakly expanded edges, preceded by long portion of rectum detached from *pm*; $L \approx 50\%$ of *pm* L.

Reproductive system: Gonad as described above; genital aperture on *ki* not observed in detail.

Nervous system (Figs. 139–140): Paired cerebropleural ganglia (Figs. 140: *cg*) elliptical, located laterally close to posterior third of *pp*; $D \approx 16\%$ of *es* *D*. Cerebral commissure long, narrow. Pedal ganglia not observed. Paired visceral ganglia (Fig. 139: *vg*) elliptical, on middle of *pm* ventral side, very close; $V \approx 1.5$ *cg* *V*. Abdominal sense organs not observed.

Material examined: USA, Florida Keys, AMNH 298913, 1 specimenn (sta. FK-083; dissected : 8.9 mm L, 11.2 mm H).

Distribution: Stated by Turgeon et al. (2009) to range from North Carolina to Quintana Roo (Mexico), the Gulf of Mexico outer banks, the West Indies, Brazil and Bermuda.

Remarks: These anatomical results agree with those on *Plicatula australis* Lamarck, 1819, by Watson (1930a) and on *P. gibbosa* from Jamaica reported by Yonge (1973). There are many shell specimenn records from Brazil, but no anatomical material was available for dissection.

Plicatula gibbosa, anatomy. FIG. O1: Intact right view, RV and part of right mantle lobe removed; FIG. O2: Digestive system, right view, topologies of some adjacent structures also shown; FIG. O3: Detail of anus (an), right and slightly posterior view; FIG. O4: Labial palps, anterior and slightly right view, adjacent portion of gills (gi) and visceral mass (vm) also shown; FIG. O5: Same, outer hemipalp (op) sectioned along midline, right outer hemipalp deflected; FIG. O6: Pericardial region, right view, right pericardial wall removed, adjacent region of ctenidial vein (cv) also shown; FIG. O7: Gill, cross section in midregion; FIG. O8: Stomach, right view, sectioned longitudinally along dorsal region; FIG. O9: Mantle edge, cross section from midregion of posterior side. Scale bars = 1 mm. an, anus; au, auricle; cg, cerebropleural ganglion; ci, ciliary connection of gill; cp, cerebrovisceral connective; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; di, inner demibranch; do, outer demibranch; dp, dentritic projection of lips and labial palps; er, esophageal rim; es, esophagus; gi, gill; gm, gill retractor muscle; go, gonad; gs, gastric shield; gt, gill suspensory stalk; hf, hinge fold of mantle; hi, hinge; id, insertion of outer demibranch in mantle; im, insertion of inner demibranch in visceral mass; in, intestine; ip, inner hemipalp; li, ligament; mb, mantle border; mi, mantle border inner fold; mm, mantle border middle fold; mo, mouth; mp, mantle papillae; mu, mantle border outer fold; op, outer hemipalp; pc, pericardium; pl, pallial muscles; pm, posterior adductor muscle; pp, labial palp; rt, rectum; sa, gastric sorting area; sh, shell; ss, style sac; st, stomach; ty, typhlosole; ve, ventricle; vg, visceral ganglia; vm, visceral mass.

Plicatula gibbosa, shell morphology and anatomy, AMNH 298913, 8.9 mm L. FIG. O10: LV attached to shell of another bivalve, inner view; FIG. O11: RV, outer view; FIG. O12: Intact right view, RV and part of right mantle lobe removed. gi, gill; gt, gill suspensory stalk; hi, hinge; in, intestine; li, ligament; mb, mantle border; pc, pericardium; pm, posterior adductor muscle; pp, labial palp.

Family Anomiidae Rafinesque, 1815

Anomia simplex d'Orbigny, 1853

Figs. 148–165

Synonymy:

Anomia acontes J. E. Gray, 1850: 17 [Type locality: Jamaica]. A forgotten name reinstated by Huber (2010: 616) under violation of Art. 23.9 and 23.11 of the ICZN (1999) Code. Prevailing usage of *Anomia simplex* is here maintained; see Remarks.

Anomia simplex d'Orbigny, 1853: 367, pl. 28, figs. 31–33 [Type locality: Martinique, Cuba]. *Nomen protectum*.

Anomia simplex – Abbott, 1974: 451–452, fig. 5232, pl. 20, fig. 5232; Fuller et al., 1989: 83–94, figs. 1–26; Bieler & Mikkelsen, 2004: 510; Mikkelsen & Bieler, 2007: 162–163, 6 figs.

Anomia ephippium – Rios, 1994: 251 pl. 86, fig. 1227; 2009: 510, fig. (non Linnaeus, 1758; see Remarks).

Description

Shell (Figs. 148–150, 154–156) oval to circular, fragile, translucent, iridescent whitish to pale beige, orange, or brown, laterally very compressed; SL $\approx$ 15–20 mm in material examined, maximum SW $\approx$ 12% SD. Both valves (mainly RV) conforming to shape of substratum. LV simple, weakly convex; outer surface opaque smooth (Fig. 148) to glossy (Fig. 154); inner surface glossy, thinly iridescent; muscle scars restricted to infraumbonal region (Fig. 150), in A $\approx$ 16% of inner VA, W $\approx$ 2 L. Scar of posterior adductor muscle (*pm*) circular, in A $\approx$ 12% of total scar A, on posteroventral side of each valve. Scars of split posterior pedal retractor muscle anterior and dorsal to adductor

scar, inserting on LV only; one portion subequal in size and form to adductor scar, anterior to adductor scar; other portion (= byssal retractor of authors) circular, dorsal to posterior adductor scar; $A = 2 \text{ } pm \text{ scar } A$. Scar of anterior pedal retractor muscle (left only) in umbonal cavity, elongated; $A \approx 25\%$ of $pm \text{ scar } A$. RV with unclosed byssal orifice close to umbo, surrounding byssal portion of foot; $A \approx 6\%$ of LV A . Posterodorsal region of RV including hinge plate on thickened crurum; $pm \text{ scar}$ midway between orifice and posterior margin of valve (Fig. 155). Periostracum not evident. Hinge plate edentulous, composed only of dorsoventrally elongated internal ligament ($L \approx 5 \text{ } W \approx 20\% \text{ } SW$) on resilifer, preceded by thick, peduncular portion of RV (Fig. 156) and single concavity in LV (Figs. 150).

Main muscle system (Figs. 151–153, 157, 162): Anterior adductor muscle absent. Pm relatively small (Figs. 157, 162), approximately central on each valve, in $A \approx 5\%$ VA ; comprised of 2 (“catch” and “quick”) portions, one (darker) centrally, extending posteriorly, other (paler) surrounding lateral and anterior regions. Anterior pedal retractor muscle (Figs. 151–153, 157: *ar*) single (left), originating in umbonal cavity of LV, in $A = 50\%$ of ligament A , relatively long dorsoventrally; running directly posteriorly for distance = 25% SL , through wide portion of mantle tissue, laterally compressed, becoming slightly wider posteriorly; inserting along anterior byssal furrow in base of main pedal retractor muscle (origin in RV indicating probable homology with left anterior pedal retractor of more typical bivalves, with right anterior pedal retractor here lost). Posterior pedal retractor muscle single (left, *pr*), divided into 2 bundles. Anterior branch directly to left of byssal furrow (Figs. 151–152: *br*), originating on left surface of byssus, running short distance toward left, inserting at midanterior LV, in $A = 3 \text{ } pm \text{ } A$, approximately midway between pm and hinge area. Posterior branch

originating in posterior byssal furrow, running posteriorly and to left, surrounding posterior surface of anterior branch, gradually running away from anterior branch (Figs. 151–152: *pr*), inserting into LV just posterior to anterior branch, at some distance from it; insertion area between *pm* and anterior branch, displaced ventrally, slightly smaller than that of *pm*. Right posterior pedal retractor muscle absent.

Foot (Figs. 151–153, 157: *ft*) consisting of a thin, free shaft plus a massive, plug-like portion that produces calcified byssus. Pedal musculature as described above, with anterior projection in left *ar* (Fig. 157), and cylindrical, massive portion possessing both branches of *pr*. Byssal furrow (Figs. 152, 157: *bf*) wide, shallow, rimmed by thin walls, slightly smaller than insertion of anterior branch of *pr*. Both left pedal retractors originating from furrow, in anteroposterior alignment. *Ft* shaft just anterior to *bf*, turning right-anteriorly, in $L = ar$ L ; basal 66% comprising long, slender, cylindrical stalk; terminal third compressed, in $W \approx 3$ basal stalk W ; right surface concave, bearing byssal gland. Byssus solid, short, cylindrical, calcareous.

Mantle (Figs. 157, 161): Mantle lobes asymmetrical, thin, translucent, possessing whitish, coalescent spots. Left mantle lobe simple, as inner mold of generally compressed valve. Right mantle lobe forming arch surrounding byssal foramen to region close to hinge plate, maintaining narrow gap between foramen and hinge plate. Mantle edge with 3 folds (Fig. 161). Outer fold thin, smooth, simple, typically connecting to periostracum (*pe*) on inner surface. Middle fold with long, slender papillae except in region surrounding byssal foramen in right lobe. Papillae of middle fold organized in 3 layers; outer layer of short, aligned papillae; other 2 layers internal to outer layer, each with 3–4 times longer papillae; each papilla tall, slender;

interspace $W = 2-3$ papilla W ; papilla L not uniform, with longer and shorter papillae alternating; longer papilla $L \approx 5\%$ SL , shorter papilla $L \approx 25-33\%$ of longer papilla L . Inner fold smooth, simple, forming pallial veil; W and $T \approx 2$ outer fold W and T . Pallial muscles well developed, as radial, iridescent, mostly dichotomous fibers between edge of muscle area and mantle edge.

Pallial cavity (Figs. 157–158, 162–163) surrounding entire visceral mass, except dorsally; $V \approx 50\%$ SV . Promyal passage (Fig. 157: *po*) only on right side, connecting suprabranchial chamber with posterodorsal region, from anterior end of right gill, passing between *pm* and *ft*. Paired labial palps (Figs. 157, 162: *pp*) asymmetrical, long, surrounding midregion of byssal base of *ft*; left *pp* more ventral than right, connecting by oral groove on anterodorsal side of byssal base of *ft*. Hemipalps subequal, with smooth inner surfaces; inner folds inconspicuous. Gills (Fig. 162: *gi*) widely curved, in $L \approx SL \approx 8 T$; anterior third asymmetrical, with left *gi* more anterodorsal; middle and posterior thirds symmetrical, narrow, long. Inner demibranch of right *gi* connecting to right and left *pp* (Fig. 157); both demibranchs of left *gi* connecting to left *pp*. Inner (*di*) and outer (*do*) demibranchs similarly shaped. *Gi* suspensory stalk (Figs. 157, 163: *gt*) lying along 50% of *gi* L , narrow, weakly muscular. *Gi* filaments attaching to one another and to visceral mass and mantle via ciliary connections; right and left *gi* uniting posterior to visceral mass via tissue connections. *Do* with additional ventral prolongation along outer-dorsal edge of ascending branch (Fig. 158).

Visceral mass (Figs. 157, 162) strongly laterally compressed, more concentrated on left side, in dorsal and posterior regions around *ft*; $V \approx 25\%$ SV . Stomach and remaining digestive system central; remaining mostly filled by pale cream-colored

gonad. Pericardial region just posterior to *pm*; digestive diverticula greenish beige, anterior, surrounding stomach.

Circulatory and excretory systems (Figs. 157, 163): Pericardium (Fig. 157: *pc*) irregular, just posterior to *pm*, in $V = 10\text{--}12\%$ of visceral mass V ; auricles and ventricle not detected in any dissected specimen. Kidneys (Fig. 163: *ki*) solid, whitish, on both sides of posteroventral visceral mass, at base of each *gt*. Nephropores (Fig. 163: *ne*) as small papillae on both sides of *pm*, on internal surfaces of *gt* bases.

Digestive system (Figs. 157, 159–160, 162): *Pp* as described above. Esophagus (*es*) located *ca.* 16% SH below umbones; $L \approx pm\ L$, $W \approx 33\%$ of *pm\ W*. *Es* inner surface bearing 8–10 longitudinal, narrow, uniform folds. Stomach (*st*) elliptical; $L \approx 2\ W$, $V \approx 20\%$ of visceral mass V . Dorsal hood (*dh*) in posterior-right region; $A \approx 12\%$ of inner gastric surface A . Two pairs of ducts to digestive diverticula, simple, on posterodorsal gastric surface. Gastric inner surface (Fig. 160) with low *es* rim (*er*); *dh* preceded by pair of triangular adjacent folds, pointing in opposite directions. Gastric shield (*gs*) right-dorsal; $A \approx 16\%$ of gastric inner surface A . Large sorting area (*sa*) lying along posterodorsal gastric surface, with uniform, transverse, low folds; *sa* separating (on posterior-right side) intestinal (*in*) and style sac (*ss*) origins; transverse, tall, wide, arched fold separating *gs* from style sac opening. *Ss* totally separated from *in* (Fig. 157), narrow, very long, only slightly shorter than SH; making wide loop in posteroventral visceral mass, gradually passing from left to right side, weakly protruding into suprabranchial chamber; most regions $W \approx 16\%$ of main gastric chamber W , narrowing gradually distally to pointed tip just anterior to *pm*. *In* short ($L \approx 50\%$ of visceral mass L), at right of *ss* opening, running almost directly

posteroventrally, in $W \approx ss\ W$; *ca.* 33% of *in* L exposed in pallial cavity as anal stalk. *In* inner surface almost entirely with longitudinal typhlosole (Fig. 159: *ty*); *ty* tall, relatively thin, arching; remaining *in* inner surface with longitudinal, narrow, uniform folds. *In* passing anterior to (not through) *pc*. Anus preceded by relatively long free stalk; edges fringed; subterminal sphincter (Figs. 159: *sp*) very evident.

Reproductive system (Fig. 163) not observed in detail. Gonad filling most of visceral mass; genital ducts opening inside posteroventral *ki*.

Nervous system (Figs. 162, 164–165): Cerebropleural ganglia (*cg*) simple, triangular, well separated, connecting by long, narrow commissure (Fig. 164: *cc*) in $L \approx 5\ es\ D$; right *cg* more posterior than left; *cg* A $\approx 16\%$ of *es* D. Pedal ganglia not observed. Each visceral ganglion (*vg*) in $V \approx 5$ single *cg* V, on anteroventral surface of *pm*; broadly connected, with no visible commissure (Figs. 157, 165); weakly asymmetrical, with posterior nerves of left *vg* slightly more dorsal than those of right. Abdominal sense organs not observed.

Material examined: USA, Florida Keys, Florida Keys, MZUSP 36126, 1 specimenn (sta. FK-649); AMNH 298953, 3 specimens (sta. FK-352; 1 dissected, 23.6 mm maximum D); FMNH 301413, 1 specimenn (FK-629; dissected: 29 mm L, 30 mm H, 9 mm W); FMNH 314534, 1 specimenn (FK-287; dissected: 35.6 mm L, 29.2 mm H, 7.4 mm W). BRAZIL, Rio de Janeiro, Buzios, Ferradura beach, MZUSP 48466, 1 specimenn (19/iii/2005; dissected, not measured); Arraial do Cabo, Porcos Island, 22°57'53.5"S, 41°59'47.7"W, 8 m (18/iii/2005; dissected, not measured); Ilha Grande, Pau-Paulo beach, MZUSP 45890, 1 specimenn (22/vii/1966; dissected, not measured);

Paraty, Martinello Island, 23°11'15.6"S, 44°39'33.1"W, 3 m, MZUSP 83252, 3 specimens (26/i/2007; dissected, not measured). São Paulo, Anchieta Island (IO Bentos), Sul beach, MZUSP 23065, 15 specimens, MZUSP 23064, 6 specimens, (26/ii/1963; dissected, not measured), MZUSP 23063, 3 specimens (28/ii/1963; dissected, not measured); Ubatuba, MZUSP 26345, 2 specimens (1 dissected: 24.0 mm D, 22.2 mm H, 8.3 mm W); Enseada das Palmas (IO Bentos), MZUSP 23067, 5 specimens (13/ii/1963; 2 dissected: #1: 19.5 mm L, 19.1 mm H, 4.1 mm W; #2: 14.9 mm L, 9.9 mm H, 3.1 mm W), MZUSP 23068, 6 specimens (02/iii/1962; dissected, not measured), Andorinhas beach (IO Bentos), 1 m, MZUSP 23058, 1 specimen (23/i/1962; dissected, not measured), MZUSP 23060, 1 specimen (12/vii/1962; dissected, not measured), MZUSP 23066, 1 specimen (24/ii/1962; dissected, not measured), MZUSP 23059, 1 specimen (23/i/1962; dissected, not measured), Boqueirão (IO Bentos), 20 m, MZUSP 23061, 1 specimen (19/vii/1961; dissected, not measured), 32 m, MZUSP 23062, 1 specimen (14/vii/1962; dissected, not measured), Ponta do Navio, MZUSP 23069, 1 specimen (IO Bentos, 03/vii/1962; dissected, not measured); Ilha Bela, Garapucaia beach, MZUSP 45921, 2 specimens (04/iii/1967; dissected, not measured); Santos, Lage de Santos, 24°17'23"S, 46°11'57"W, 31–32 m, MZUSP 26285, 1 specimen (IO sta. 16, 23/iii/1961; dissected, not measured).

Distribution: Stated by Turgeon et al. (2009) to range from Massachusetts to Yucatan, the Gulf of Mexico outer banks, Cuba, Brazil, and Bermuda. Range in Brazil to São Paulo is here confirmed.

Remarks: For other details of the shell, see Mikkelsen & Bieler (2007: 162). The anatomy of *Anomia* (as reported here in agreement with earlier authors) is

extremely asymmetrical with some organs (e.g., pedal retractor muscle, adductor muscle, gonad; Yonge, 1980) represented only or mainly on one side. Yonge (1977) compared the anatomy of *Anomia* (including New England *A. simplex*) to other members of the family and superfamily, and pointed out that *Anomia* is distinct from other genera in Anomioidea in having a split posterior pedal retractor muscle, which results in three central muscle scars on the left valve. The foot is rotated, with a small free portion (used primarily for cleaning; Yonge, 1977; Prezant, 1984) and a bulbous portion that produces the calcified byssus rotated strongly to the right so that the byssus passes through the hole in the right valve. The labial palps literally wrap around the byssal portion of the foot, and the anterior portions of the demibranchs are asymmetrical in their association with the palps. Yonge (1977) wrote that three demibranchs are associated with the left palp, and only one demibranch with the right palp; this study confirmed this, however, each palp receives two demibranchs in *A. ephippium* Linnaeus, 1758 (S. Staubach, pers. comm., June 2012). Because there are no food grooves on the gills of *Anomia*, examinations of ciliary currents are needed to confirm these associations. According to Pelseneer (1911), the anomiid heart consists of a ventricle only, without auricles or a surrounding pericardium; Yonge (1977) indicated that the pericardium is absent and auricles are present and asymmetrical. A pericardium (?ventricle) was detected in these dissections but did not contain typical heart chambers; clearly the anomiid heart requires further investigation across the family. Purchon (1957) reported five ducts to the digestive diverticula in *A. ephippium*; only two were found here, but each duct branches soon after leaving the stomach, so this feature could be easily misinterpreted, or could vary among species. The visceral ganglia are on the anterior surface of the posterior adductor muscle, rather than the posterior surface as is true for most bivalves (Yonge, 1977).

Most striking as a result of this study is the presence of an apparent right promyal passage in *Anomia simplex*, similar to that characteristic of members of Gryphaeidae, not before recorded in Anomiidae.

Until recently, d'Orbigny's description of *Anomia simplex* was dated as 1842 but is now interpreted as having been published much later, between 1851 and 1853 (e.g., Mikkelsen & Bieler, 2007: 413; who adopted a 1853 date). *Anomia acontes* Gray, 1850, is an available older name. However, the name *A. simplex* d'Orbigny, 1853, has been in prevailing usage, with more than 25 usages in the last 50 years. By contrast, the name *A. acontes* apparently had not been used as valid since 1899 until Huber (2010: 616) reinstated it, thereby violating Art. 23.9 of the ICZN (1999) Code. Prevailing usage of *A. simplex* is here maintained.

Some authors have considered *Anomia simplex* a synonym of Eastern Atlantic/Mediterranean *A. ephippium* Linnaeus, 1758, whereas others (e.g., Huber, 2011: 616) reported morphological differences. Additional research is needed.

Other studies of *Anomia simplex* from a variety of western Atlantic localities have included larval development and metamorphosis (Loosanoff, 1961; Loosanoff et al., 1966; reared from plankton from Long Island Sound), cardiac physiology (Navez, 1936, from Woods Hole, Massachusetts), and formation and mineralogy of the calcified byssus (Prezant, 1984, from Sanibel Island, Florida).

No morphological difference was found between Floridian and Brazilian specimens.

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Anomia simplex, anatomy. FIG. A1: Intact right view, RV and part of right mantle lobe removed; FIG. A2: Gills, cross section in midregion; FIG. A3: Rectum and anus, dorsal view, both longitudinally opened, typhlosole (ty) sectioned in distal third to show its profile; FIG. A4: Stomach, dorsal view, sectioned dorsally with inner surface exposed; FIG. A5: Mantle border, a portion extracted from the midventral region, with a portion of the periostracum still attached; FIG. A6: Intact right view, digestive system and nervous system *in situ*, topologies of some adjacent structures also shown. Scale bars = 1 mm. an, anus; ar, anterior pedal retractor muscle; bf, byssal furrow; cc, cerebral commissure; cg, cerebropleural ganglion; ci, ciliary connection of gill; cp, cerebrovisceral connective; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; dh, dorsal hood; di, inner demibranch; do, outer demibranch; er, esophageal rim; es, esophagus; ft, foot; gf, gastric fold; gi, gill; go, gonad; gs, gastric shield; gt, gill suspensory stalk; hf, hinge fold of mantle; in, intestine; mb, mantle border; mi, mantle border inner fold; mm, mantle border middle fold; mp, mantle papillae; mu, mantle border outer fold; pc, pericardium; pe, periostracum; pl, pallial muscles; pm, posterior adductor muscle; po, promyal passage of suprabranchial cavity; pp, labial palp; rt, rectum; sa, gastric sorting area; sl, crystalline style; sp, sphincter; ss, style sac; st, stomach; su, supra-anal chamber of suprabranchial pallial cavity; tg, integument; ty, typhlosole; vc, visceral mass gill connection; vg, visceral ganglia; vm, visceral mass.

Anomia simplex, anatomy. FIG. A7: Detail of posterior region of visceral mass, ventral-slightly right view, both gills deflected and only partially shown; FIG. A8: Right cerebropleural ganglion (cg) *in situ*, right view; FIG. A9: Visceral ganglia, ventral view. Scale bars = 0.5 mm. cc, cerebral commissure; cg, cerebropleural ganglion; ci, ciliary connection of gill; cp, cerebrovisceral connective; di, inner demibranch; es, esophagus; go, gonad; gt, gill suspensory stalk; ki, kidney; ne, nephropore; pm, posterior adductor muscle; sb, suprabranchial chamber.

Anomia simplex, shell morphology. AMNH 298953, 23.6 mm maximum D; FIG. A10: Left view; FIG. A11: Right view; FIG. A12: LV, inner view, detail of subumbonal region with muscular scars. FIG. A13: Left view; FIG. A14: Right view; FIG. A15: Ventral view; FIG. A16: MZUSP 23067, 19.5 mm D, left view; FIG. A17: Detail of hinge of RV; FIG. A18: Ventral view, RV deflected upward. Scale bars = 1 mm. ar, anterior pedal retractor muscle; bf, byssal furrow; br, byssal retractor muscle (derived from posterior pedal retractor muscle); ft, foot; pr, posterior pedal retractor muscle.

Family Isognomonidae Woodring, 1925 [1828]

***Isognomon alatus* (Gmelin, 1791)**

Figs. 72–82

Synonymy:

Ostrea alata Gmelin, 1791: 3339 [Type locality: Oceano americano = American Ocean].

Isognomon alatus – Abbott, 1974: 441, pl. 20, fig. 5124; Domaneschi & Martins, 2002: 621–624, fig. 9C; Bieler & Mikkelsen, 2004: 514; Tëmkin, 2006: 262, figs. 1A, 8A, 9B, 13A, 14A, 17C; Mikkelsen & Bieler, 2007: 98–99, 5 figs.; Wilk & Bieler, 2009: 1 ff., figs. 1–10.

Description

Shell (Figs. 72–73) quadrangular to oval, greenish pale brown or beige, with radial, narrow, irregular, dark brown spots, more evident close to margins; SL $\approx$ 20–60 mm in material examined, typically SW = SL, SW $\approx$ 0.1 SL (greatly compressed). Byssal notch narrow, in RV. Sculpture of series of low, thin, narrow, undulated, commarginal scales; generally irregularly lamellate close to shell margin; scales typically arranged in radial rows. Inner surface smooth; nacreous A = 66% VA, close to hinge, iridescent whitish-violet; remaining third along shell margin opaque, translucent, of same color as outer shell surface. Umbones low, terminal. Hinge line almost horizontal; ligament internal, with 6–8 resilia set in resilifers; each resilifer of regular L, of irregular W and disposition, more closely spaced anteriorly. Hinge plate with small subequal teeth near umbones, more evident in juveniles. Muscle scar in central nacreous portion, shallow, elliptical, in V $\approx$ 12% of inner VA; 66% of scar closest to hinge area

comprising posterior pedal retractor muscle (*pr*); remaining third narrowly crescent-shaped, comprising posterior adductor muscle (*pm*). Scars of anterior pedal retractor muscles (*ar*) small, circular, in $A \approx 5\%$ of *pm* A, close to hinge plate, between middle and posterior thirds.

Main muscle system (Fig. 77): Anterior adductor muscle absent. *Pm* central, crescent-shaped, with thicker anteroventral end, rounded, posterodorsal end tapering to point; $W \approx 50\%$ SW, $H \approx 20\%$ SH. Paired *ar* narrow, originating close to hinge plate, between middle and posterior thirds, running posteriorly close to ventral integument of visceral mass, inserting along anterior foot base. Paired anterior auxiliary pedal retractor muscles (*ap*) short, very narrow, in $L \approx 20\%$ of *ar* L, originating in umbonal cavity at distance = that between origin of *ar* and hinge plate; running posteromedially, inserting partly in middle of *ar*, partly in adjacent foot base. Paired *pr* acting as byssal retractors, very thick, broad, originating in wide, elliptical area just anterior to *pm*, closer to ventral end, in $L \approx 50\%$ of *pm* L, running anteroventrally, narrowing abruptly, inserting on middle and posterior foot base, just dorsal to byssal furrow.

Foot (Figs. 75–77) small, appendix-like, slender, narrowing gradually, with distal end broadly pointed; typically pigmented by dark brown, irregular, coalescent spots. Byssal furrow (Fig. 77: *bf*) deep, running along ventral surface and midline, unpigmented, very wide posteriorly, surrounding byssus; very shallow furrow also running along dorsal surface, diminishing close to foot base. Byssus (Figs. 75, 77: *by*) broad, thick, consisting of greenish-iridescent flattened strips connecting soon after exiting foot; dorsal to this, separating and organizing in uniform arrangement of 10–12

pairs of long strips, inserting along *pr*, close to their internal surface (Figs. 76–77). Hollow, flattened chamber between strips immersing in *pr*; *W* = strip *W* (Fig. 76).

Mantle (Figs. 74, 77, 79): Mantle border dark brown, paler near edge; outer fold thin, short, simple, weakly pigmented (Fig. 79). Periostracum attaching to inner surface of outer fold. Middle fold weakly taller and thicker than outer fold, with series of long, slender papillae (Figs. 74, 79: *mp*) mostly inserting subterminally along inner surface; distal papillar tips sharply pointed; interspace $W = 3 W$. Inner fold *T* and *H* each ≈ 2 middle fold *H*; edge with series of papillae, inserting terminally, with remaining characters similar to those of middle fold. Inner mantle fold forming pallial veil. Papillae of middle and inner folds longer in posteroventral half, gradually decreasing dorsally to mantle lobe fusion at hinge area. Low, narrow, transverse fold (Figs. 74, 77: *fd*) at distal end of gill between dorsal and posterior regions; broad ciliary strip running anteriorly from fold, surrounding mantle border. Pallial muscles narrow, thin, radiating from border to near *pm*. Two pairs of pallial glands (Fig. 74: *gl*) orange, visible as thickened mantle; one pair anterior, broad, $W \approx$ distance between *pm* and mantle edge; second pair narrow, surrounding *pm* and short distance beyond, with well-developed vessel (Fig. 74: *bv*) surrounding outer edge.

Pallial cavity (Figs. 74, 77, 80, 82) $A \approx 66\%$ *VA*, totally surrounding visceral mass except dorsally adjacent to hinge; very narrow in this region; laterally compressed. Labial palps (Fig. 77: *pp*, 80) $L \approx 16\%$ of gill *L*, $W \approx 50\%$ of gill *W*; each hemipalp elliptical. Anterior ends of demibranchs inserting into short portion between posterodorsal ends of hemipalps (Fig. 80). *Pp* posterior ends taller, with low projections; posterior edge weakly concave, preceded by short smooth inner region,

then as series of low, narrow folds perpendicular to dorsal border (Fig. 80); each fold with rounded ventral end, located near *pp* ventral edge, with narrow smooth inner border; dorsal ends of folds diminishing into dorsal furrow. Folds covering *ca.* 75% of *pp* L, diminishing subtly into remaining anterior region, with smooth inner surface preceding mouth, with thick walls (Fig. 80: *ll*), apparently glandular, yellowish, friable. Latter thicker region gradually decreasing preceding mouth. Gills (Fig. 77: *gi*) narrow; $L \approx 1.5$ visceral mass L. Short anterior base connecting to visceral mass for distance $\approx 25\%$ of gill L, remaining free, sustained by very long, muscular suspensory stalk (Fig. 77: *gt*). Gills dark brown in distal third. Demibranchs subequal (Fig. 77, 80: *do*, *di*). Food grooves (Fig. 82: *fg*) shallow, along ventral edge of each *di*. Each gill filament very narrow, connecting to neighboring filaments by regular ciliary bridges. Transverse septum (Fig. 82: *gq*) every 8–10 filaments, restricted to dorsal demibranch; each pair of septa connecting to *gt*, with short portion protruding dorsally, opposing connection to free portion of gill filament only at one dorsal and one ventral point; septa $W \approx 20\%$ of gill W, wider and taller toward anterior. *Do* connecting to mantle; *di* connecting to visceral mass anteriorly or to counterpart by cilia (Fig. 74: *ci*) along relatively wide bands.

Visceral mass (Figs. 77, 81) restricted to space between hinge area and *pm*, laterally compressed, mostly filled by yellowish gonad. Digestive diverticula surrounding stomach midanteriorly, of same color as gonad; $V \approx 25\%$ of visceral mass V. Posteroventrally greatly compressed by paired *pr*, with portion passing between them, bulging posterior to foot base. Pericardium (*pc*) posterodorsal, just anterior to dorsal half of *pm*, attaching directly to posterodorsal half of *pm*; $V \approx 20\%$ of visceral mass V.

Circulatory and excretory systems (Fig. 81): Pericardium (*pc*) as described above. Paired connections between ctenidial vein and auricles (*au*) narrow, long, surrounding anterior edge of *pr*, inserting into *au* at posterolateral ends. Narrow pallial vessel inserting just anterior and external to connection of *au* and ctenidial vein, coming from anterior mantle. Paired *au* totally fused externally, internally bearing several irregular transverse septa, apparently separating *au* lumens, each with subtriangular, posterior region, wide, curving (with ventral concavity), abruptly narrowing to ventricle connection. Ventricle (*ve*) small, anterior to *au*, internally with few transverse, irregular septa, connecting to *au* apparently with common aperture, protected by low internal, thin-walled, bicuspid valve, surrounding intestine, with main part dorsal. Common aorta very short, anterior to *ve*, contacting intestinal portion crossing anterior end of *pc*; anterior aorta (*aa*) running dorsally at right of this portion of intestine; posterior aorta (*ao*) $W \approx 4$ times narrower than *aa* W , running posteriorly, ventral to intestine. Kidneys inconspicuous, very small, surrounding anteroventral insertions of *pr*.

Digestive system (Figs. 77–78, 81): *Pp* as described above. Lips tall, thinner than preceding posterior regions. Esophagus (Figs. 77–78: *es*) broad, short, curving posterodorsally; $L \approx 33\%$ of *pp* L . Stomach (Fig. 77: *st*) oval; gastric chamber only slightly shorter and wider than *pp*. Large duct to digestive diverticula on right-anterior side, curving posteroventrally; inner gastric surface with longitudinal, broad folds; similar, slightly smaller duct on opposing (left) side, usually with another small duct just anterior to it. Gastric inner surface mostly smooth (Fig. 78). Gastric shield (Fig. 78: *gs*) thin, in anterodorsal gastric chamber. Conjoined style sac-intestine (Figs. 77–78: *ss-in*) weakly separated by pair of very low, longitudinal folds, running posteriorly,

forming wide curve ventrally to ventral end of *pm*. Intestine (Fig. 77: *in*) becoming free from *ss* posteroventrally, abruptly curving almost 360°, running initially left of distal *ss*, then surrounding posterior surface of *pm*, posterior surface of *pc*, performing wide, sigmoid loop. *In* running posteriorly after crossing dorsal surface of *pc* (Fig. 81), exiting to dorsal pallial cavity, running along midline attaching to posterior surface of *pm*; inner surface mostly smooth, except for broad, tall typhlosole, in $W \approx 25\%$ of intestinal W , running along entire L , on face of *pm*; typhlosole narrower at mid-*in*, wider in region running in pallial cavity; ending abruptly close to anus. Anus (Fig. 77: *an*) broad, with long, posterior anal papilla projecting from dorsal edge; anal papilla with flattened, sharply pointed distal end.

Nervous system (Fig. 77): Paired cerebropleural ganglia (*cg*) small, in lateral region just posterior to mouth, close to *ap*. Cerebropleural commissure long, slender, crossing anterior to *es* opening. Pedal ganglia not observed. Visceral ganglia (*vg*) $V \approx 3$ *cg* V , at ventral end on surface of *pm*, just anterior to *gt* origin; ganglia adjacent, close to midline; connective with *cg* running along ventral surface of visceral mass, contacting integument and foot base. Abdominal sense organs not observed.

Material examined: USA, Florida Keys, FMNH 295559, 4 specimens (sta. FK-223; 3 dissected: #1: 64.4 mm L , 65.0 mm H , 9.0 mm W ; #2: 59.0 mm L , 67.0 mm H , 10.7 mm W ; #3: 21.0 mm L , 22.5 mm H , 4.4 mm W); FMNH 311673–311687, 230 specimens (sta. FK-760); FMNH 311812–311813, 2 specimens (sta. FK-786); FMNH 311814–311815, 2 specimens (sta. FK-787). The material of Domaneschi & Martins (2002: 621) from Florida and the Caribbean was also examined.

Distribution: Stated by Turgeon et al. (2009) to range from Florida to Campeche Bank, northern South America to Brazil, the West Indies and Bermuda. *Isognomon alatus* has been reported from the Brazilian coast (Rios, 1994: 241). However, although specimens and further data about this record were intensely searched, no confirmation was obtained. Because the single species of the genus confirmed on the Brazilian coast is the invasive *I. bicolor* (C. B. Adams, 1845), the Brazilian reports have been removed from the synonymy herein as most probably referring to *I. bicolor*; Domaneschi & Martins (2002) also could not confirm previous records of *I. alatus* or *I. radiatus* (Anton, 1838).

Remarks: Shell morphology of *Isognomon alatus* was investigated by Domaneschi & Martins (2002) specifically for comparison with Brazilian specimens of *I. bicolor*; specimens from Florida, including several populations in the Florida Keys, were used in that study. The anatomy of *I. alatus* presented here agrees in most respects with that of the much more elongated species *I. isognomon* (Linnaeus, 1758) figured (but not extensively discussed) by Yonge (1968: fig. 8). The most complete earlier anatomical investigation was by Pelseneer (1911) for *I. perna* (Linnaeus, 1767) and *I. isognomum* (Linnaeus, 1758). The latter study, despite its very brief description, included figures of the gross anatomy, with details of the musculature, gills, labial palps, and digestive tract, which agree with the observations presented here. The one exception is the relationship to the heart and intestine, described by Pelseneer (1911) and Yonge (1968) with the intestine passing through the heart. Specimens studied here could be interpreted as such, but the main portion of the ventricle is ventral to the intestine, with weak, smaller portions of the ventricle passing up and around the intestine. The same condition occurs in members of the genus *Crassostrea* (Ostreidae;

L. Simone, unpubl. data), which is traditionally described as the intestine not passing through the heart. The sharply pointed distal end of the intestine was called "triangular anal funnel" by Tëmkin (2006: fig. 17C).

Various aspects of the biology of *Isognomon alatus* have been studied. Wilk & Bieler (2009) explored the ecophenotypic variation of this species across a tidal microhabitat gradient, based on specimens from Ramrod Key that were also included in the present study. Material from the same location was analysed in the morphological study by Tëmkin (2006), and specimens from the same and/or other Lower Florida Keys locations were used in the molecular analyses by Campbell et al. (1998) and Ó Foighil & Taylor (2000). Chromosome karyotypes of this species were studied by Wada (1978), based on specimens from Biscayne Bay, Florida (just north of the Florida Keys), and by Rodríguez et al. (1983) based on material from Veracruz, Mexico (with a diploid $[2n]$ number = 28). Veracruz specimens were also used in the study of chromosomal rearrangements (meiotic behavior) of *I. alatus* by Rodríguez-Romero et al. (1991). Specimens from Panama were investigated in a study of spermatozoan ultrastructural morphology by Introíni et al. (2009). Siung (1980) investigated its potential as a commercial species in Jamaica.

Isognomon alatus, anatomy. FIG. K1: Intact right view, RV and most of right mantle lobe removed, digestive system shown *in situ* as though visceral mass is transparent; cross sections of indicated levels of intestine (in) and posterior pedal retractor muscle (pr) also shown; FIG. K2: Stomach, right view, mostly opened longitudinally, including style sac (ss-in) and one duct to the digestive diverticula (dd); FIG. K3: Mantle border, section at midlevel of ventral region; FIG. K4: Right labial palp and some adjacent structures, right and slightly ventral view, outer hemipalp (op) deflected; FIG. K5: Pericardial region, right view, right region of pericardium removed; FIG. K6: Gill, cross section at midregion. Scale bars = 2 mm. aa, anterior aorta; an, anus; ao, posterior aorta; ap, auxiliary pedal retractor muscle; ar, anterior pedal retractor muscle; au, auricle; bf, byssal furrow; bv, "blood" vessel; by, byssus; ce, cerebral ganglion; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; di, inner demibranch; do, outer demibranch; es, esophagus; fd, fold; fg, food groove; ft, foot; gd, gill suspensory rod; gi, gill; gl, gland; gm, gill retractor muscle; gq, gill transverse reinforcement in suprabranchial chamber; gs, gastric shield; gt, gill suspensory stalk; hf, hinge fold of mantle; in, intestine; ip, inner hemipalp; ll, labial lips preceding mouth; mb, mantle border; mi, mantle border inner fold; mm, mantle border middle fold; mo, mouth; mp, mantle papillae; mu, mantle border outer fold; op, outer hemipalp; pc, pericardium; pe, periostacum; pl, pallial muscle(s); pm, posterior adductor muscle; pp, labial palp; pr, posterior pedal retractor muscle; sl, crystalline style; ss-in, conjoined style sac-intestine; st, stomach; ve, ventricle; vg, visceral ganglia; vm, visceral mass.

Isognomon alatus. FIGS. K6-K7: Shell morphology, RV, FMNH 295559, 64.4 mm L; FIG. K6: Inner view; FIG. K7: Outer view. FIGS. K8-K10: Anatomy; FIG. K8: Left mantle lobe, inner view; FIG. K9: Byssus, right view, its base in foot also shown; FIG. K10: Posterior pedal retractor muscle, cross section along its midregion, note dark spots corresponding to byssal gland. Scale bars = 5 mm. bv, “blood” vessel; ci, ciliary connection of gill; fd, fold; gl, glands; mb, mantle border; mp, mantle papillae; pm, posterior adductor muscle.

ANEXO IV – *Plicatulostrea*, a new genus of Plicatulidae (Molusca: Bivalvia) from Thailand.

Revision of genus *Crassostrea* (Bivalvia: Ostreidae) of Brazil

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The Ostreidae are well known for their high intra-specific variation, which makes identification problematic. The present paper aims to provide a morpho-anatomical and taxonomic review of the Brazilian species of Crassostrea, as well as some congeneric species from other relevant areas. The Brazilian species are Crassostrea mangle sp. nov. and Crassostrea brasiliana. The exotic species Crassostrea gigas, cultivated in the southern region of the country, is also included in this study. Additional species are: Crassostrea virginica, from the Atlantic coast of the USA, the type species, and Crassostrea rhizophorae, a south-eastern Caribbean species that is supposed to occur in Brazil, but is here understood as a different entity endemic to that region. Taking into account their economic importance, the differentiation between these species is critical, and is essential for a better planning of production and preservation strategies. We point out the differences in almost all structures amongst these species, which are formally redescribed herein. The occurrence of the African species Crassostrea gasar in Brazil is established as false. The voucher specimens of previous studies responsible for this assumption were examined, evidencing a misidentification for Crassostrea brasiliana from an estuarine environment. The geographical distribution of the studied species is recognized as follows: Crassostrea rhizophorae in the south-east Caribbean Sea; Crassostrea mangle sp. nov. from Pará to the Santa Catarina, only in mangroves; Crassostrea brasiliana from Paraíba to Santa Catarina, both in rocky shores and mangroves; Crassostrea virginica ranges from the Atlantic coast of Canada to the Caribbean; and Crassostrea gigas originates from the Indo-Pacific, but has been introduced in southern Brazil. This paper also deals with conchological aspects of the endemic species Crassostrea praia, from south Lagoa dos Patos, Rio Grande do Sul; after a more detailed definition, and considering the deleterious effects of the nearby port and construction sites, it can be classified as an endangered species.

Keywords: oyster, conchology, morphology, systematic, food, cultivation, phenotypic plasticity, bioinvasion

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INTRODUCTION

The superfamily Ostreoidea Rafinesque, 1815, includes marine and brackish water species adapted to the sessile epifaunal communities attached to hard substrates. The taxon comprises ~80 species with a widespread distribution, which includes oceanic islands (Huber, 2010). Most of these species live in hot intertropical waters. Both tolerance and resistance to environmental variations allowed the Ostreoidea to colonize different marine habitats, from coastal regions with clear waters and high salinity levels, to estuarine environments with turbid waters and variable salinity levels (Quayle, 1981).

The genus *Crassostrea* Sacco, 1897 includes several commercially important species (Rios, 1970, 1975, 1994, 2009; Abbott, 1974; Boss, 1982). Species in this genus show a characteristic attachment mark on the left valve resulting from the cementation on mangrove roots (Sowerby II, 1870–1871) or on offshore or coastlines. They also lack denticles (chomata) near the inner edge of the shell, which are characteristic of other ostreids, such as *Ostrea* Linnaeus, 1758, *Saccostrea* Dollfus & Dautzenberg, 1920 and *Striostrea* Vyalov, 1936.

In Brazil, *Crassostrea* species are popularly known as mangrove-oysters. They can form banks both in the intertidal

and subtidal zones, which are usually attached to rocky substrata and to the rhizomes of *Rhizophora mangle* Linnaeus, 1753, an estuarine tree (Absher, 1989). *Crassostrea rhizophorae* (Guilding, 1828) is sometimes reported as the only valid species of *Crassostrea* occurring in Brazil, allegedly from the southern Caribbean to Uruguay (Weisboard, 1964; Rios, 1994, 2009).

Individuals with a flat right valve and a wider, more convex left valve that is adhered to the substrate are commonly classified under the genus *Crassostrea*. The resilium is longitudinally striated. The outer surface of the shell is usually coloured light grey to white, brownish and/or purple. The inner surface is white, with an adductor muscle scar near the median region, which can be purple or non-pigmented (Harry, 1985). The genus is dioecious, without sexual dimorphism. Females produce from 30 to 50 million eggs per spawning (Boss, 1982).

The inconsistent identity of the species of *Crassostrea* occurring on the Brazilian coast is noteworthy (Absher, 1989). *Crassostrea rhizophorae* has been considered the single occurring species by some authors (e.g. Rios, 2009). Likewise, *C. brasiliana* has been considered the single occurring species by many others (e.g. Wakamatsu, 1973; Absher, 1989; Nascimento, 1991). Both species are also mentioned in different ways to designate estuarine or marine populations, without further explanations (e.g. Nascimento, 1991). On the other hand, the African species *C. gasar* (Dautzenberg, 1891) has been reported in the literature as occurring in Brazil (Lapégue *et al.*, 2002), and even *C. brasiliana* has been

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considered in its synonymy (Varela *et al.*, 2007). A detailed comparative morphological study on these species has never been performed before, and molecular studies are inconclusive (Littlewood, 1994; Jozefowicz & Ó'Foighil, 1998; Muchmore *et al.*, 1998; Canapa *et al.*, 2000; Ó'Foighil & Taylor 2000; Lapégue *et al.*, 2002; Martínez-Lage *et al.*, 2002; Klinbunga *et al.*, 2003; López-Flores *et al.*, 2004, 2010).

In the present paper we perform a detailed morpho-anatomical and taxonomic study of the *Crassostrea* species from Brazil, aiming at a better understanding of their identity. Specimens of the type species *C. virginica* and the invasive *C. gigas* are also investigated to widen the basis for reviewing the taxonomy and systematics of the genus in Brazil. Samples from the type locality of *C. rhizophorae* (Carriacou Island, Granada) are also studied in this manner for the first time. From this has arisen the necessity of describing the Brazilian species, previously considered to be *C. rhizophorae*, as a new species. So, herein we formally describe a new species *Crassostrea mangle* sp. nov., from Brazilian mangrove areas. Additionally, we provide an analysis of the currently available data and make environmental and geographical inferences focused on supporting complementary activities, such as oyster culturing.

MATERIALS AND METHODS

A list of the examined material is given after each species description. A significant part of the material belonged to the mollusc collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP). Additional samplings have been carried out aimed at obtaining fresh specimens allowing for better visualization of the mantle edge and cavity, as well as for *in vivo* analysis. The samplings were carried out along rocky seashores, mainly on the south-eastern Brazilian coast, near the Cananéia municipality (the largest oyster producing region in São Paulo state)—ESEC Tupiniquins, Peruibe—Juréia-Itatins Ecologic Station, Ilhabela, Paraty-RJ, in addition to specimens coming from the north-east region. The most important sampling was carried out in the type locality of *C. rhizophorae*, Carriacou, Grenada, in the south-east Caribbean Sea. Specimens of *C. gigas* cultivated in south-eastern Brazil were also purchased, reinforcing the comparison with the natural specimens.

The collected material was preserved in 70% or 90% ethanol and deposited in the mollusc collection of MZUSP. The specimens were immersed in ethanol and dissected by standard techniques, under a stereomicroscope (Simone, 1997, 2009, 2011). All systems (cavity of mantle, mantle edge, muscles, digestive, circulatory, excretory and nervous systems) and organs were investigated in detail. The drawings were obtained with the aid of a drawing tube.

In the figures, the following abbreviations are used: ah, accessory heart; ai, adductor muscle impression; am, adductor muscle; an, anus; at, artery; au, auricle; ba, branchial artery (ctenidial vein); bf, branchial filament; cs, crystalline style; db, demibranchs; dh, dorsal hood; e1, e2, e3, depressions of ducts of digestive diverticula; ef, outer mantle fold; fc, caecum selection area; fo, thick fold of stomach; ig1–ig2, portions of intestinal groove; if, inner mantle fold; gi, gill; gs, gastric shield; lb, left pouch; ma, mantle; mb, pallial muscles; me, medial portion of mantle border; mg, midgut opening; mf, middle mantle fold; mp, pallial muscles; oe, oesophagus;

pe, pericardium; pl, papillae of mantle border folds; qm, Quenstedt muscle; re, resilium; rs, resilifer; rt, rectum; sa2, selection area; ss, stylet sac; ty, higher typhlosole; tm, minor typhlosole; ve, ventricle.

SYSTEMATICS

Genus *Crassostrea* Sacco, 1897

DIAGNOSIS

Shell usually large, ponderous, pleurothetic. Hinge line narrow; chromate absent. Right valve cup-shaped, with subumbonal space in some. Promyal chamber in right side present. Non-incubatory. Type by original designation: *Ostrea virginica* Gmelin, 1791.

Crassostrea mangle, sp. nov.
(Figures 1, 2)

Crassostrea rhizophorae: Rios, 1970: 170–171; 1975: 204–205; 1994: 245 (pl. 85, figure 1202); 2009: 500–501 (figure); Oliveira *et al.*, 1981: 425; Singarajah, 1980: 833–847; Nascimento, 1991: 125–128; Ignacio *et al.*, 2000: 987–991; Pereira *et al.*, 2001: 19–28; Lapégue *et al.*, 2002: 232–242; Alvarenga, 2006: 163–169; Christo, 2006: 1–146; Varela *et al.*, 2007: 1–6; Pie *et al.*, 2006: 1598–1600; Christo & Absher, 2008: 71–77; Carranza *et al.*, 2008: 1–12 (*non* Guilding, 1828).

DIAGNOSIS

Size up to 120 mm; fixed in roots of mangroves, shape cupped; external colour varying from brown to reddish-brown, internal white opalescent; right valve concave, operculum-shaped; left valve larger in edge than right valve. Muscle impression not coloured; adductor muscle more central in postero dorsal region, occupying 1/2 of total size of animal. Accessory heart Y-shaped, composed of three branches of similar length, starting from a common centre. Internal faces of palps plicate, ending before edge, leaving free, narrow and smooth margins.

TYPES

Crassostrea mangle sp. nov.: MZSP 89462 (holotype) and MZSP 100495, MNRJ and USNM (paratypes).

DESCRIPTION

Shell

(Figure 1A–E) Cup shaped, size variable (both height and thickness) up to 120 mm long. Colour varying from white, yellowish, brown to purple. Right (upper) valve flat or concave, operculum-shaped and slightly protuberant near hinge to accommodate visceral portion. Left valve fixed to substrate, cupped and larger than right valve. Umbonal cavity of left valve. External coloration of shell highly variable: white, yellowish, brown, clear and opaque, background, mixed with miscellaneous pigments, forming irregular spots or bands across height of shell. Hinge massive and bulging, protruding from right valve and from respective shallow depression in left valve. Ligament alivincular. Inner surface of valves smooth. Interior of valves predominantly white, with little brightness or opaque. Purple pigmentation close to margin, in most inner regions, or absent. Scar of adductor muscle mostly located in posterocentral region, somewhat

Fig. 1. *Crassostrea mangle* sp. nov. (Holotype) shell and anatomy: (A) external view of shell, right valve (L 56 mm); (B) same, left valve; (C) internal view of shell, left valve, detail of sub-umbonal cavity; (D) same, right valve, detail of ligament; (E) same, detail of adductor muscle impression (ai); (F) right palp, right view, right hemipalp deflected (side 5 mm); (G) general view of right side, Quenstedt muscle in detail (qm) (L 60 mm); (H) gills, ventral edge, ventral view of middle portion, showing alimentary gutter (side 5 mm); (I) inner demibranch, longitudinal section at middle portion, showing internal filaments of folds (side 2 mm); (J) pericardium, right view, pericardial membrane removed (side 5 mm); (K) left mantle lobe, postero-dorsal region, inner view (side 10 mm), detail of accessory heart (ah); (L) right lobe, detail of medial portion of mantle border (me), showing papillae (pl) of median and internal fold (side 3 mm); (M) supra-branchial cavity, region dorsal to adductor muscle, detail of rectum (rt) and anus (an); scale 1 mm; (N) same portion, detail of anus (an) (side 1 mm).

central; form crescent to oval, with a concavity towards hinge; occupying about 1/4 shell height. Muscle scar sometimes strongly pigmented with purple, blue, brown bands or a combination (Figure 1E). Scar of Quenstedt muscle oval-shaped, marked by shallow and colourless depression; located in each valve, near to ventral inner edge of ligament area, occupying 1/8 size of adductor muscle.

Muscle system

Adductor muscle. (Figure 1G) Position posterocentral, slightly displaced to dorsal region. Comprised of two different portions, one dorsal, ovate, translucent, occupying 1/2 and 2/3 of total body. Other ventral, crescent shaped and of opaque white-milky aspect; very resistant.

Quenstedt muscle. (Figure 1G) Thin and narrow, fixed to valves close to ventral margin of ligament area or subcentral

to it. Fibres crossing mantle in direction to base of labial palps. Portion connected to valve enlarged, almost fan-shaped; becoming thinner through visceral mass.

Mantle

(Figures 1G, K, L, 2B, C) Mantle lobes connected in hinge region by length equivalent to half of valve length; anterior-ventral region forming deeper concavity named sub-umbonal region. Lobes fused to each other only by short portion at posterior end of gill, named pallio-branchial junction. Promyal chamber, or promyal passage, an extension of right epibranchial chamber, heading to posterior margin of body; limited from base of gill to portion of visceral mass, size ~1/3 of visceral mass. Inner surface of two side mantle lobes fixed to base of demibranch and coating adductor muscle, limiting other exhalant passage, cloacal passage. External fold devoid of papillae, exceeding margin of shell when extended. Middle

fold with two different types of fingerlike papillae: short with small diameter, and long (more than 1 mm) with enlarged base; arrangement of papillae not following regular pattern, normally presenting up to six short papillae between each two long papillae; both types of papillae of middle fold showing gradual increase in diameter and length from ventral region towards dorsal region. Internal fold with short papillae (Figures 1L, 2B, C). Edge pigmented in variable shades of brown or depigmented. Pallial muscles (Figures 1L, 2B) forming broad bundles around adductor muscle, fixed to visceral mass or to adductor muscle and extending towards free margin of mantle. Each bundle opening like a fan, ending inside three edge folds. Incurrent chamber located in anterior half, extending vertically. Excurrent chamber of $\sim 1/4$ size of shell. Anus and rectum located in dorsal–posterior region of body, close to posterior face of adductor muscle.

Gills

(Figures 1H, I) Gills shape elongated, triangular, becoming narrower in region surrounding ventral face of adductor muscle, until fusion to mantle lobes at pallial–branchial junction region. Free anterior–dorsal gill end slightly arched, located between ventral margins of labial palps. External demibranch ending between palp and marginal food groove, reaching base of external palp. Internal demibranch decreasing gradually in height anteriorly; marginal groove extending to base of internal hemipalp. Free margin of external demibranch, i.e. ascending lamella, attached to mantle. Septa of inter-lamellar junction, perpendicular to branchial axis, forming series of aqueous ducts. Gills transversally plicate; each fold ending at free margin of demibranchs, delimiting food groove. Folds comprising average of 13 filaments.

Visceral mass

(Figures 1G, 2A) Occupying $\sim 1/4$ total animal's size; located from ventral region of ligament to anterior surface of adductor muscle. Digestive diverticula located in anterior and dorsal region of palps, occupying $\sim 1/4$ of visceral mass. Follicular gonads beige, occupying $\sim 1/2$ of visceral mass, covering digestive diverticula externally. Renopericardial structures occupying $\sim 1/4$ of visceral mass, located in posterior anterior–ventral region of adductor muscle.

Circulatory and excretory systems

(Figures 1J, 2E) Arteries parallel to ventral margin, with several centripetal branches. Left and right circumpallial vessels united to each other in pallial–branchial junction. Pair of accessory hearts (Figures 1K, 2G) with three branches of similar length, starting from a common centre, forming 'Y', with basal branch leaning in ventral–posterior direction until its connection to pallial–branchial junction; basal branch bifurcating near adductor muscle, with branch extending towards rectum and anus, and other to epibranchial chamber. Pericardium (Figures 1J, 2E) located between visceral glands and adductor muscle. Two renopericardial channels opening at right and left sides of ventro-posterior wall of pericardium, providing direct communication with kidney. Heart located anteriorly to adductor muscle, with three chambers arranged obliquely in pericardium, connected by aortic root on one side and ctenidial veins on left side. Ventricle pyriform, walls with thin bundles of muscle fibres crossing ventricular lumen, dividing it incompletely into two

chambers. Auricles pigmented or depigmented, varying from yellowish-cream to brown. Walls of auricles thinner and lighter than those of ventricle, trabecular. Pair of kidneys triangular, tubular; mottled by light brown marks by translucence of visceral mass. Each kidney with direct communication with pericardium and gonad on medial side and laterally communicating by short chamber. Renal opening located on other side of cerebro-visceral connective.

Digestive system

(Figures 1F, 2D, G)

Palps. (Figures 1F, 2D) Located in anterior–ventral region, under sub-umbonal region of mantle, occupying $\sim 1/8$ of animal's body. Hemipalps flattened, elongated, base united throughout its length to visceral mass. Margins slightly arched anteriorly and ventrally free, converging towards ventral region to form apex. Internal faces plicate, folds extending transversely, ending in order to leave free, narrow and smooth margin. External surface smooth, with irregular grooves and ridges. External hemipalps dorsally united over mouth, forming arched dorsal lip. Internal hemipalps ventrally united, forming ventral mouth lip. Lips height similar to median part of hemipalps. Mouth slot-shaped.

Oesophagus. (Figure 2H) Dorso-ventrally flattened, length $\sim 1/8$ of that of palps, slightly longer than wide; insertion in stomach wide. Internal surface of distal end striated, with slight folds becoming more evident near stomach.

Stomach. (Figure 2H) Occupying $\sim 1/4$ of animal's size, laterally flattened, with irregular external invaginations. Stomach inner surface with small portion of posterior surface of stomach coated by gastric shield (gs), almost same area in transversal section of oesophagus; minor typhlosole (tm) projecting into stomach, ending after intestine opening; major typhlosole (ty) emerging as elbow-shaped structure, adjusting around intestinal opening, extending afterwards along left side of stomach floor; close to oesophageal opening, diverting almost 90° to right, penetrating into purse or caecum (fc). Caecum beginning in floor of anterior right gastric region, under oesophagus and going towards opening of intestine; major typhlosole penetrating deeply in distal end of ventral branch of caecum, returning along its left wall, penetrating and finishing into distal end of dorsal branch; two typhlosoles occupying $\sim 1/3$ of stomach length. Caecum (fc) composed of two branches, one longer and flattened, emerging laterally, under stomach floor; other branch smaller in length, projecting to posterior region, parallel and at left side of oesophagus, coiled in a spiral of about 1.5 turns; occupying $\sim 1/8$ of stomach width. Dorsal hood (dh) close to roof and on right side of stomach, inside which two thick, broad and slightly smooth folds beginning on right side of gastric wall, ascending to ceiling and invading dorsal hood; opening of ventral margin of dorsal hood protected by fold of gastric shield; right purse (rp) aligned to dorsal hood, consisting of two compartments, one in blind bottom, immediately ventral to dorsal hood opening, other deeper, located on floor of stomach, close to origin of ducts of digestive diverticula; upper edge of blind compartment coated by fold of gastric shield. Intestinal

Fig. 2. *Crassostrea mangle* sp. nov. Anatomy: (A) general right view, valve and mantle lobe removed (L 85 mm); (B) mantle border, inner view of median portion (side 5 mm); (C) transverse section at middle region of mantle border (side 5 mm); (D) detail of palps. (E) Detail of heart in pericardium, (ve) ventricle, (au) auricles; (F) detail of visceral ganglia; (G) posterior region of pallial cavity, posterior half of gills sectioned and deflected, showing accessory heart (ah) (side 40 mm) (adapted from Galtsoff, 1964); (H) stomach, dorsal view, opened longitudinally, showing inner surface, scale 1 mm.

groove (ig1) beginning near main opening of right purse, extending in anterior direction, along left side of major typhlosole, inside dorsal branch of caecum. Intestinal groove returning parallel to opposite face of major typhlosole, comprising 'ig' segment, extending inside initial portion of intestine, united to style sac. Style sac occupying $\sim 1/2$ of stomach length. Striated tissue in stomach floor beginning inside right purse, extending inside caecum, always right of intestinal groove (ig2), occupying $\sim 1/3$ of stomach length. Ducts to digestive diverticula opening inside right purse; additional diverticula originating in small depression (e1) in anterior wall of caecum, very close to its opening, occupying $\sim 1/16$ of stomach width. Second depression (e2) on left side of esophagus opening, larger and deeper than 'e1', where other ducts of digestive diverticula open. Another shallow depression (e3) wide, appearing on left wall, close to intestinal origin; also receiving ducts of digestive diverticula. Both, e1 and e3, occupying $\sim 1/8$ of stomach width; 'e1', 'e2' and 'e3' walls showing narrow folds advancing inside opening of ducts of digestive diverticula. Depression (h) located in stomach ceiling, posterior to dorsal hood, extending ventrally along right wall, forming deep trench (rt), ending at intestine

opening. Cylindrical portion of stomach emerging opposite to oesophagus insertion, represented by style sac and intestine. Intestine and style sac fused with each other, running up to ventral end of adductor muscle, surrounded by reproductive and excretory apparatus, forming pyloric process. Style sac walls transversally striated with $\sim 1/8$ of stomach width.

Intestine. (Figure 2A, H) Distinguished from distal end of style sac by 180° loop; afterwards passing through pericardium, following ovoid portion of visceral mass in 'U'-shaped loop, passing posteriorly to stomach, close to connection with esophagus, extending to right face of ovoid portion of visceral mass. It changes again course to ventral and posterior direction.

Rectum. (Figures 1M, N, 2G) Crossing pericardium, running in contact with posterior face of adductor muscle; internal surface with well-developed typhlosole, with broad base and grooved free end up to anal opening.

Anus. (Figures 1M, N, 2G) Sessile, surrounded by flat edge-shaped fold, bell-shaped, occupying $1/3$ of height of adductor muscle.

Reproductive system

(Figure 1G) Gonad formed by two lobes of follicular aspect, occupying $\sim 1/4$ of animal size. Dorsally and ventrally spread in left lobe and right lobe; shape indistinct from each other. Two pairs of separate systems of genital channels, as described above (excretory system).

Central nervous system

(Figure 2F) Cerebral ganglia located at base of labial palps, about 5% oesophagus. Cerebral commissure U-shaped, dorsally surrounding oesophagus 15 times longer than ganglia. Pair of visceral ganglia slightly ovoid, with projections; antero-ventral to adductor muscle, in depression formed by junction of translucent and opaque parts of adductor muscle, about $1/12$ of size of adductor muscle. Circumpallial nerve travelling along mantle. Pedal ganglion absent.

DISTRIBUTION AND HABITAT

Brazil, Pará to Santa Catarina, always associated with the mangroves.

EXAMINED MATERIAL

Brazil. Ceará: Fortaleza; Mangue da Foz do Rio Ceará, $3^{\circ}42'9''\text{S}$ $38^{\circ}35'31''\text{W}$, MZSP 101785, 50 specimens (V.S. Amaral col., 9 November 2011). Rio Grande do Norte: Ceará Mirim, Estuário do Rio Ceará Mirim, $05^{\circ}40'658''\text{S}$ $35^{\circ}13'578''\text{W}$, MZSP 107753, 50 specimens (M.D. Tavares col., 18/xi/2009). Paraíba: João Pessoa; Cabo da Ponta do Seixas, $07^{\circ}08'42.3''\text{S}$ $34^{\circ}48'12.2''\text{W}$ to $07^{\circ}08'46.5''\text{S}$, $34^{\circ}47'52.7''\text{W}$, MZSP 41344, 12 specimens (Simone col. 27 April 2004), $07^{\circ}08'43.3''\text{S}$ $34^{\circ}48'11.3''\text{W}$, MZSP 45287, 4 specimens, (Simone col. 14 January 2005). Pernambuco: Itamaracá, manguezal, MZSP 104522, 20 specimens (V.S. Amaral col., 27 February 2012). Alagoas: Maceió, lagoa de Mundaú, MZSP 46141, 3 specimens (José Geraldo Marques col., 23 September 1974); Barra de Camaragibe, estuary of Rio Camaragibe (M.D. Tavares *et al.*, col.), MZSP 89462, 30 specimens, MZSP 89518, 20 specimens (21 October 2008) (holotype), MZSP 100491, 15 specimens (8 January 2011), MZSP 100495, 40 specimens (8 January 2011) (paratype); MZSP 100497, 30 specimens (8 January 2011); MZSP 100498, 50 specimens (8 January 2011); MZSP 100499, 30 specimens (8 January 2011); MZSP 107743, 50 specimens (June 2011); MZSP 107746, 20 specimens (June 2011); MZSP 107758, 2 specimens (June 2011); MZSP 109156, 4 specimens (27 March 2010). Bahia: Salinas da Margarida, MZSP 46068, 9 specimens (Iracema Nascimento col.); Boipeba, $13^{\circ}38.528''\text{S}$ $038^{\circ}54.315''\text{W}$ MZSP 101849, 15 specimens (M.D. Tavares col., August 2011); Ilhéus, Olivença, MZSP 101553, 10 specimens, (M.D. Tavares col., 27 May 1994). Rio de Janeiro: São João da Barra, Praia de Manguinhos, MZSP 15286, 1 specimen, 1 valve ('Exp. Dep. Zool.; August 1963). São Paulo: São Sebastião, Araçá, $23^{\circ}48'54.89''\text{S}$ $45^{\circ}24'31.73''\text{W}$ MZSP 101922, 20 specimens (V.S. Amaral col., 18 August 2011), MZSP 106009, 8 specimens, (Simone col., 21 January 2012); Bertioga, MZSP 101984, 15 specimens (Francisca do Val col., May 2011); Praia Grande, Manguezal do Portinho, $23^{\circ}58'59''\text{S}$ $46^{\circ}24'53''\text{W}$ MZSP 101980, 15 specimens (Luiza Saad col., 19 July 2011); Cananéia, Cooperostra, MZSP 89670, 60 specimens (Fausto Campos Pires leg., March 2008); IPESCA, MZSP 89673, 3 specimens (Patrícia de Oliveira leg., June 2008); Portinho, MZSP 89676, 50 specimens (V.S.

Amaral col., 8 January 2009). Santa Catarina: Porto Belo, Ponta Norte da Praia de Porto Belo, MZSP 36319, 4 specimens (Cenemar col., 12 October 2002).

Crassostrea rhizophorae (Guilding, 1828)
(Figures 3, 4)

Ostrea rhizophorae Guilding, 1828: 542; Reeve, 1889: 9, 17a–b; Dall, 1889: 687; Lamy, 1929: 95–99, 100, 108, 135, 137, 139, 271; McLean, 1941: 5–7; Mattox, 1949: 339–356; Olsson & McGinty, 1958: 20.

Ostrea parasitica Mörch, 1878: 16; Arango & Molina, 1878: 273; Ihering, 1907: 359, 374, 426, 450; Richards, 1935: 236; Jaume & Farfante 1942: 38. (*auct. non* Gmelin, 1791)

Ostrea (*Crassostrea*) *rhizophorae* McLean, 1951: 25 (pl. 4, figure 6).

Crassostrea rhizophorae Gunter, 1950: 44–45; Abbott, 1974: 456 (figure 5273); Abbott, 1954: 374–375; Nowell & Usticke, 1959: 9; Warmke & Abbott, 1961: 173 (figure 35b); Buroker *et al.*, 1979a: 171–184; Buroker, 1984: 550–557; Castillo-Rodriguez & García-Cubas, 1984: 1–57; Hedgecock & Okazaki, 1984: 535–545; Angell, 1986: 1–37; Arakawa, 1990: 1–13; Márquez, 1992: 51–55; Littlewood, 1994: 221–229; Abbott & Dance 2000: 318 (figure 5); Wang *et al.*, 2004: 46–54; Vaisman *et al.*, 2005: 582–288; Erse & Bernardes, 2008: 57–93; Guimarães *et al.*, 2008: 118–122; Mikkelsen & Bieler, 2008: 112–113 (figure 1).

TYPES

Ostrea rhizophorae: NHMUK (possibly lost) (Carriacou, near Grenada).

DIAGNOSIS

Size up to 80 mm; fixed in roots of mangrove, shape cupped; colour varying from white, yellowish to brown; right valve operculum-shaped; left valve; larger and sling than right valve. Adductor muscle postero-dorsal located, occupying $1/15$ of total size of animal; mantle with several bundle of pallial muscles; colour of mantle edge brown or yellowish. Accessory heart with one only branch. Palps with folds extending transversally up to superior margin.

DISTINCTIVE REDESCRIPTION

Shell

(Figure 3A–D). Shape cupped, size up to 80 mm long. Colour varying from white, yellowish, to brown. Right (upper) valve flat or slightly concave, operculum-shaped, no protuberant near hinge to accommodate visceral portion. Left (lower) valve fixed to substrate, cupped and almost same width than right valve. Umbonal cavity on left valve small. Interior of valves predominantly white, with little brightness. Scar of adductor muscle unpigmented, mostly located in posterodorsal region, more lateralized; form oval, with a slightly concavity towards hinge; occupying about $1/15$ of valve surface. Scar of Quenstedt occupying $1/20$ of size of adductor muscle.

Muscle system

Adductor muscle. (Figure 3C, E) Posterodorsal elongated, close to dorsal region, occupying $1/15$ of total size body.

Quenstedt muscle. (Figure 3F) Thin and narrow, fixed to valves close to ventral margin of ligament or subcentral to it.

Fig. 3. *Crassostrea rhizophorae* shell and anatomy: (A) external view of right valve (L 65 mm); (B) right valve, internal view, detail of adductor muscle impression (ai); (C) view, detail of sub-umbonal region (sb) and adductor muscle (am); (D) left valve, lateral view; (E) general view of right side; (F) anterior view, detail of Quenstedt muscle; (G) right lobe, detail of accessory heart (ah); (H) right lobe: mantle edge (external, middle and internal folds with papillae) and pallial muscles; (I) right palp (pa), right view; (J) general view of digestory system; (K) gills, detail of alimentary chamber.

Mantle

(Figure 3E–H) Mantle lobes connected in hinge region by equivalent to $2/3$ of valve width–sub-umbonal region. Promyal passage, size $\sim 1/4$ visceral mass. External fold devoid of papillae, exceeding margin of shell when extended. Middle fold with two different types of fingerlike papillae: short with small diameter, and medium; arrangement of papillae not following clear regular pattern, normally presenting up to two short papillae for one medium papillae; both types of papillae of middle fold showing gradual increase in diameter and length from ventral region towards dorsal region. Internal fold with only elongate middle papillae. Edge pigmented in variable shades of brown. Anus and rectum located in dorsal–posterior region of body, close to middle face of adductor muscle.

Gills

(Figure 3K) Gills shape elongated, triangular, becoming narrower in region surrounding ventral face of adductor

muscle, until fusion to mantle lobes at pallial–branchial junction region. Gills transversally plicate; each fold ending at free margin of demibranchs, delimiting food groove. Folds comprising average of 13 filaments.

Visceral mass

(Figure 3E, I) Occupying $\sim 1/4$ of total animal size. Digestive diverticula located in anterior and dorsal region of palps, occupying $\sim 1/4$ of visceral mass. Follicular gonads beige, occupying $\sim 1/2$ of visceral mass, covering digestive diverticula externally. Renopericardial structures occupying $ca\ 1/6$ of visceral mass, located in posterior anterior–ventral region of adductor muscle.

Circulatory and excretory systems

Arteries parallel to ventral margin, with several centripetal branches. Left and right circumpallial vessels united to each other in pallial–branchial junction. Pair of accessory hearts (Figures 3G, 4A) with only one branch, connecting

pallial–branchial junction to near adductor muscle, not surrounding adductor muscle. Heart with ventricle elongate, auricle pyriform, walls formed by thin bundles of muscle fibres, dividing it incompletely into two chambers. Colour lacking or cream-yellowish (Figure 4C).

Digestive system

Palps. (Figures 3J, 4A, B) Located in anterior–ventral region, occupying $\sim 1/12$ of animal's body. Hemipalps flattened, elongated, base united throughout its anteroventral region to visceral mass; margins slightly arched anteriorly and ventrally free, converging towards ventral region to form apex; internal faces plicate, folds extending transversally up to superior margin; external surface smooth, which irregular grooves and ridges. External hemipalps dorsally united over mouth, forming arched dorsal lip. Internal hemipalps ventrally united, forming ventral mouth lip.

Oesophagus. (Figures 3J, 4E) Dorso-ventrally flattened, same length as palps, slightly longer than wide; insertion in stomach wide; internal surface of distal end striated, with slight folds becoming more evident near stomach.

Stomach. (Figures 3J, 4E) Occupying $\sim 1/6$ of animal's size. Two typhlosoles occupying $\sim 1/4$ of stomach length. Dorsal hood (dh) close to roof and on left side of stomach, inside which two thick, broad and slightly smooth folds beginning

on right side of gastric wall, ascending to ceiling and invading dorsal hood; opening of ventral margin of dorsal hood protected by fold of gastric shield; upper edge of blind compartment coated by fold of gastric shield. Style sac walls transversally striated occupying $\sim 1/8$ of stomach length.

Intestine. (Figures 3J, 4A, E) distinguished from distal end of style sac by 180° loop; afterwards passing through pericardium, following ovoid portion of visceral mass in 'S'-shaped loop, passing posteriorly to stomach, close to connection with esophagus, extending to right face of ovoid portion of visceral mass. Intestine and style sac fused with each other, running up to ventral end of adductor muscle, surrounded by reproductive and excretory apparatus, forming pyloric process.

Anus. (Figure 4A) Sessile, surrounded by flat edge-shaped fold, occupying $1/4$ of height of adductor muscle.

Reproductive system

(Figures 3E, 4A) Gonad formed by two lobes of follicular aspect, occupying $\sim 1/4$ of animal's size. Dorsally and ventrally spread in left lobe and right lobe; shape indistinct from each other.

Central nervous system

Cerebral ganglia, almost 10% of area of oesophagus. Cerebral commissure U-shaped, dorsally surrounding esophagus, 30

Fig. 4. *Crassostrea rhizophorae* anatomy: (A) general right view, valve and mantle lobe removed; (B) detail of palps, internal view; (C) detail of heart, ventricle and auricles; (D) visceral ganglia in detail; (E) stomach, dorsal view, opened longitudinally showing inner surface.

times more long of cerebral ganglia. Pair of visceral ganglia (Fig. 4D) slightly ovoid, with two anterior projections, one lateral and three posterior projections; antero-ventral to adductor muscle, in depression formed by junction of translucent and opaque parts of adductor muscle, occupying about 1/30 of size of adductor muscle.

DISTRIBUTION AND HABITAT

Caribbean, always associated with mangroves.

EXAMINED MATERIAL

Grenada. Carriacou: Tyrrel Bay, Oyster Bay, 12°27'51.51"N 61°45'18.67"W, MZSP108492, 50 specimens (Amaral & Simone col., 9 October 2012) (type locality).

Crassostrea brasiliana (Lamarck, 1819)
(Figures 5, 6)

Ostrea brasiliana Lamarck, 1819: 205; Maury, 1936:283; Ranson, 1967: 189–191; Bianchi, 1969: 3–40; Figueiras & Sicardi, 1979: 107–161.

Crassostrea parahibanensis Singarajah, 1980: 5 (figures 2–3): (new synonym). Harry, 1981:44.

Crassostrea brasiliana: Singarajah, 1980: 833–847; Muniz *et al.*, 1986: 77–138; Nascimento, 1991: 125–134; Galvão *et al.*, 2000: 147–462; Ignacio *et al.*, 2000: 987–991; Pereira *et al.*, 2000: 49–62; Pereira *et al.*, 2001: 85–95; Lâpegue *et al.*, 2002: 232–242; Machado *et al.*, 2002: 13–18; Lazoski, 2004: 197–212; Christo, 2006: 1–146; Pie *et al.*, 2006: 1598–1600; Christo & Absher, 2008: 71–77; Carranza *et al.*, 2008: 1–12; Guimarães *et al.*, 2008: 118–122; Christo *et al.*, 2010: 645–650; Lazoski *et al.* 2011: 197–212.

Crassostrea parahibensis: Rios, 1994: 245 (err).

Crassostrea gasar Lâpegue *et al.*, 2002: 232–242; Varela *et al.*, 2007: 1–6; Melo *et al.*, 2007: 1; Carranza *et al.*, 2008: 1–14. (*non* Dautzenberg, 1891).

TYPES

Ostrea brasiliana: Syntype: MNHN no number (figure 82). *Crassostrea parahibanensis*: Holotype: NHMUK 1978114; Paratypes: NHMUK 1978115, MNRJ 3815–3816 [Paraíba River estuary, Brazil] (figures 80, 81) (all examined).

DIAGNOSIS

Size up to 130 mm; fixed in roots of mangrove submerge and in rock; shape cupped or oval; colour varying from white, brown, purple to greenish; right valve slightly operculum-shaped; left valve, fixed in substrate, more larger than right valve. Muscle impression is purple and adductor muscle, oval central in posterior region. Adductor muscle postero-dorsal located, occupying 1/5 of total size of animal; hood present and fully filled by palps and gonads; colour of mantle edge usually brown. Accessory heart of three branches of similar length, starting from common centre, forming 'Y'. Palps with margin superior free.

DISTINCTIVE DESCRIPTION

Shell

(Figure 5A–D) Ovoid, wide and thin, height 50–130 mm. Colour greenish to brownish with white bands. Right (upper) valve opercular and wide. Left (lower) valve shallow cupped with slight depression under umbo (um). Ornamentation present or absent on external face of valves (since directly influenced by tidal action). Internal portion

white, smooth, with little brightness, sometimes showing orange pigmentation on edge. Adductor muscle impression (ai) located in posterior–dorsal region, always rounded in shape, proportionally larger, occupying ~1/6 of shell size. Purple pigmentation sometimes present. Light Quenstedt muscle impression located just below ligament area, ~1/10 of size of adductor muscle impression.

Muscle system

Adductor muscle. (Figures 5E, 6A) Section rounded, dorsal portion ovoid, translucent, vertical portion crescent shaped with opaque white-milky aspect. Occupying ~1/5 of animal size.

Quenstedt muscle. (Figure 6A) Widened origin in portion linked to shell and anteriorly directed towards inside of visceral mass, inserted in base of palps. Size ~1/10 of adductor muscle.

Mantle

(Figures 5F, L, 6B, E) Blood vessels wide, apparent in pallial muscles (me), near palp. Sub-umbonal region (sb) filled by palps and gonads. Mantle edge (me) usually brown pigmented. External fold devoid of papillae, height similar (~2% of pallial lobe height). Middle fold with long, medium and short papillae (pl), two last finger-like from 2 to 4 medium or short papillae to one long papilla. Papillae uniform in size and distribution, 2–3 times more numerous in middle fold than in internal fold. Internal fold with long papillae, more concentrated in pallial–branchial junction of mantle lobes, sometimes pigmented (Figures 5F, 6B). Pallial muscles evident, with more abundant bundles near adductor muscle, forming fan. Radial muscles fainter throughout length of mantle border; occupying ~30% of mantle lobe surface. Circumpallial veins well-developed. Accessory heart (ah) (Figures 5L, 6E) of left lobe with thicker tissue, smaller in diameter than *C. mangle*, bifurcating around adductor muscle towards gills. Portion around muscle reduced or absent. Accessory heart of right lobe devoid of bifurcations comprised a single vessel ending in branchial artery.

Gills

(Figure 5I, J) Similar to anterior species in size and number of lamellae, having 12–13 bundles. Marginal alimentary groove wide, with ~1/2 width mantle border plicae.

Visceral mass

(Figures 5E, 6A) Occupying ~1/5 of animal total volume. Located in ventral region of ligament to anterior surface of adductor muscle. Digestive diverticula, located at dorsal region of palps, occupying about half of significant part of visceral mass volume. Gonads beige-yellowish, covering whole visceral mass, including digestive diverticula, externally. Renopericardial structures occupying ~1/6 of visceral mass, located in antero-ventral posterior region of adductor muscle.

Circulatory and excretory systems

(Figure 5H) Pericardium wide, anteriorly and ~1/2 size of adductor muscle. Ventricle (ve) thin, reticulate, usually translucent. Auriculas (au) thin, less reticulate and non-pigmented than ventricle. Excretory organ (renal opening and kidneys) occupying same position as *C. mangle*, over each side of visceral mass. Pigmented mark absent.

Fig. 5. *Crassostrea brasiliiana* shell and anatomy: (A) external view of shell, right valve; (B) same, left valve; (C) internal view, right valve, detail of muscle impression; (D) same, left valve (L 65 mm); (E) general view of right side, valve and mantle lobe removed; (F) right lobe, middle portion of mantle border (side 20 mm), detail of papillae of internal and middle folds; (G) right palp, right view, outer hemipalp deflected; (H) pericardium, right view, pericardial membrane removed; (I) gill, detail of ventral edges of demibranchs, ventral view, showing alimentary chamber; (J) same, longitudinal section of median portion of internal demibranch, showing internal filaments and folds; (K) supra-branchial cavity, region dorsal to adductor muscle, detail for a rectum and anus; (L) left mantle lobe, postero-dorsal region, internal view, showing accessory heart (ah). Scales: 1 mm.

Digestive system

(Figures 5G, 6C, D) Same as *C. mangle*, except for mouth accompanying animal's size, oesophageal plicae following to straight and wide esophagus.

Palps. (Figures 5G, 6C) Located under sub-umbonal region of mantle filling free space, occupying $\sim 1/6$ of animal size. Slightly flattened, sickle-shaped, joined throughout length of their base to visceral mass. Free margins, anterior and ventral, slightly ventrally arched forming apex. Internal faces intensively plicate; upper internal face of palps showing free region. External faces smooth or with slight striations and irregular grooves. Anterior and posterior portions wide and devoid of plicae. Dorsally united external palps over mouth covering inner palps.

Oesophagus. (Figure 6D) Slightly long, longer than wide, reaching stomach; inner surface striated, with striations becoming fainter near stomach.

Stomach. (Figure 6D) Same as *C. mangle*, except for longer selection area (sa2) ending near base of major typhlosole. Shorter selection caecum (fc), not completing one and a half turn.

Intestine. Narrow in portion surrounding adductor muscle ventrally; internal structures similar to *C. mangle*.

Reproductive system

(Figures 5E, 6A) Gonad composed of abundant follicular formations, beige coloured, covering mantle and between digestive diverticula, comprising visceral mass and extending ventrally to end of pyloric process, where they open to mantle cavity. Genital opening located at terminal level of style sac, ventral of adductor muscle.

DISTRIBUTION AND HABITAT

On rocky coasts, but may appear in mangroves (including cultures, e.g. Cooperostra, 2009- Cananeia, SP). It occurs on rocky coasts and in mangroves (subtidal).

Fig. 6. *Crassostrea brasiliana* anatomy: (A) general right view, valve and mantle lobe removed (L 62 mm); (B) mantle border, internal view of median portion (L 5 mm); (C) palps, right-slightly ventral view (L 30 mm); (D) posterior region of pallial cavity, with posterior half of gill longitudinally cut and deflected showing accessory heart (ah) (am, adductor muscle; rt, rectum; an, anus; me, mantle edge; gi, gill), scale 1 mm (adapted from Galtsoff, 1964); (E) stomach opened longitudinally, dorsal view, inner surface (L 20 mm).

EXAMINED MATERIAL

Brazil. Paraíba: Conde, Mouth of Rio Gramame (beach), 07°14'07.0"S 34°48'14.7"W, MZSP 45372, 2 specimens (Simone col.; 12 January 2005), (mangrove), 07°14'13.2"S 34°48'23.2"W, MZSP 45395, 1 specimen (Simone col., 11 January 2005). Rio Grande do Norte: Nísia Floresta, Praia de Búzios, MZSP 32656, 7 valves, (Simone & Souza col., 27 July 1999); Natal, Balsa, 05°47'46.44"S 35°13'45.02"W, MZSP 79689, 10 specimens (Simone col., August 2006); Praia da Ponta Negra, 05°53'04.68"W 35°09'52.73"W, MZSP 79690, 3 specimens, 1 valve, MZSP 79692, 4 specimens; Barra da Praia de Canhaú, MZSP 89672, 4 specimens (C.M. Cunha leg., purchased in Búzios beach, 20 October 2007). Alagoas: Maceió, Lagoa Mundaú, Canal do Calunga, close to sea, MZSP 46129, 6 specimens (J.B. Pereira-Barros col., 12 June 1970). Espírito Santo: MZSP 87473, 2 specimens, (G.H.P. Filho & F. Corteleti col.; 25 March 2008). Rio de Janeiro: Búzios, Praia da Ferradura, MZSP 48451, 30 specimens, (Exp. IMP, 19 March 2005); Arraial do Cabo, Praia do Forno, 3 m deep, MZSP 50375, 1 specimen, 5 valves, (Exp. IMP, 17 March 2005); São João da Barra, Praia de Manguinhos, MZSP 15286, 1 specimen, 1 valve (Exp. Dep. Zool.; August 1963); Niterói, MZSP 26349, 6 specimens; Angra dos Reis, Praia Grande do Frade, MZSP 46126, 10

specimens (Exp. Dep. Zool.; 24 July 1966); Ilha dos Coqueiros, MZSP 46231, 1 specimen (Exp. Dep. Zool.; 5 July 1966); Baía de Ilha Grande, MZSP 46090, 25 valves, (Exp. Dep. Zool.; 27 April 1966); Praia dos Meros, MZSP 86222, 1 specimen, [seed collector (cultivation of *Nodipecten nodosus*, 3° PET)]; Paraty, Trindade, Caixa d'áço, natural pool, 23°21'35.05"S 44°43'55.87"W, MZSP 55644, 2 specimens ('Exp. IMP', 8 December 2005); Praia da Lula, 23°11'38.5"S 44°38'06.5"W, MZSP 55827, 2 specimens, MZSP 55937, 1 specimen (10 December 2005), 55937, 2 specimens (10 December 2005); Praia do Catimbau, 23°11'26.4"S 44°37'25.5"W, MZSP 55946, 2 specimens (Exp. IMP, 10 December 2005; in *Cymatium pathernopeum* and *Spondylus americanus*). São Paulo: Ubatuba, Rio Puruba, MZSP 91799, 20 specimens (Beto Chagas col., March 2009); Ilhabela, Praia da Vila, 0–3 m, MZSP 41743, 3 specimens (Simone *et al.*, col., 5 May 2004); Praia de Barra Velha, MZSP 81167, 2 specimens (Simone, 27 October 1996); Praia do Sino, MZSP 89675, 40 specimens (V.S. Amaral col., 1 December 2008); São Sebastião, Praia de Boissucanga, 13 m deep, MZSP 46133, 12 valves ('Emília', 20 April 1959); Bertioga, MZSP 89674, 3 specimens, (E.P. Gonçalves col., May 2008); Praia de Indaiá, MZSP 46111, 8 specimens, (Isabel Cristina N. dos Santos col., March 1999); Santos, Ponta da Praia, MZSP 90847, 20

specimens (C.M. Cunha col., April 2009); São Vicente, Ilha de Urubuqueçaba, intertidal, MZSP 85718, 1 specimen (C.H. Guimarães col., 24 February 2007); Praia Grande, Praia do Forte, MZSP 82576, 1 specimen, (Simone col., 1990); Peruíbe, Estação Ecológica Juréia-Itatins, lade of Rio Perequê, Marina, 24°21'39.2"S 46°58'49.5"W, MZSP 86030, 15 specimens (V.S. Amaral col., 4 September 2007); Ponta da Juréia, adjacent to Praia do Rio Verde, MZSP 26992, 30 specimens (A.E. Migotto, 5 October 1982); Cananéia, Cooperostra, MZSP 91800, 20 specimens (V.S. Amaral leg., January 2009), Ilha do Castilho, 0–9 m deep, ESEC Tupiniquins, 25°16'17.3"S 47°57'31.6"W, MZSP 83306, 13 specimens, MZSP 83309, 6 specimens, MZSP 83335, 2 specimens (C.H. Guimarães *et al.*, 26 January 2007); Ilha Comprida, 23°10'16.45"S 44°40'41.62"W, MZSP 86972, 10 specimens (C.M. Cunha *et al.*, col.; 18 January 2008). Paraná: Paranaguá, 40–50 m, MZSP 37135, 1 specimen (Barco de Camaroneiro col., C.M. Cunha leg., May 2000); Iate Club de Paranaguá, MZSP 87739, 10 specimens (M. Galvão leg., 2008). Santa Catarina: Arvoredo, MZSP 46088, 1 specimen (Manoelito Ribas col., 'Dalila', 17 June 1960).

Crassostrea virginica (Gmelin, 1791)
(Figures 7, 8)

Synonymy in: Rodriguez & García-Cubas (1984: pp. 28–29)

Complement:

Ostrea elongata Lightfoot, 1786: 151 (*non* Born, 1778).
Ostrea virginica Gmelin, 1791: 3336; Galtsoff, 1937: 356, 1938a: 461–486, 1938b: 75; 1940: 117–135; Walzl, 1937: 125–140; Nelson, 1938: 1–61, 1960: 163–203; Lunz, 1938: 367; Medcof, 1939: 287–301, 1944: 209–216; Loosanoff, 1939: 177–178; 1949: 122; Taylor, 1941: 278–281; Medcof & Needler, 1941: 253–257; Menzel, 1955: 69–153; Numachi, 1962: 211–217.
Ostrea (*Crassostrea*) *virginica*: Sacco, 1897: 23 (pl. 15).
Crassostrea virginica: McLean, 1941: 8 (pl. 1, figures 1–4); Warmke & Abbott, 1962: 173; Galtsoff, 1964: 1–458; Stenzel, 1971: 967–1172; Abbott, 1974: 456 (figure 5274); Brusca & Ardill, 1974: 111–131; Menzel, 1974: 453–456; Ahmed, 1975: 357–397 (figure 6); Andrew, 1979: 293–335; Haley & Newkirk, 1982: 399–401; Buroker, 1983: 99–112, 1984: 550–557; Castillo-Rodriguez & García-Cubas, 1984: 1–57; Hedgecock & Okazaki, 1984: 535–545; Harry, 1985: 152; Quayle, 1981: 1–241; Arakawa, 1990: 1–13; Brock, 1990: 59–63; Reeb & Avise, 1990: 397–406; Márquez, 1992: 51–55; Hu *et al.*, 1993: 471–496; Lawrence, 1994: 185–202; Littlewood, 1994: 221–229; Kennedy *et al.*, 1996: 1–734; Beninger & Veniot, 1999: 179–188; Leitão *et al.*, 1999: 175–186; Coan *et al.*, 2000: 218 (pl. 38); Wang *et al.*, 2004: 46–54; López-Flores *et al.*, 2004: 181–188; Wang *et al.*, 2008: 489–493.

DIAGNOSIS

Size up to 130 mm; fixed in rocks; shape cupped elongate; colour varying between white and purple; right valve slightly operculum-shaped; left valve, fixed in substrate, more larger than right valve with ornamentation in edge shell. Muscle impression is elongated and pigmented purple bands. Adductor muscle postero-dorsal located, occupying 1/6 of total size of animal; sub-umbonal region present and free; colour of mantle edge normally brown or orange. Accessory heart in left lobe is bifurcate around adductor muscle reduced, but thick. Right lobe presenting only one branch of accessory heart. Palps superior margin with plicae.

DISTINCTIVE DESCRIPTION

Shell

(Figures 7A–D) Large, ~130 mm, thick, with well-defined cupped shape. Surface ornamented with waves and layered lamellae. Right valve opercular and protruding near hinge. Left valve slightly larger than right valve, with high umbo. External coloration variable, from white to purple, with orange or brownish spots on borders. Inner portion of valves predominantly white, sometimes opalescent brightness like in other species. Adductor muscle impression oval, not elongated, located in postero-dorsal region, concavity towards hinge, occupying ~1/6 of valve area. Muscular impression highly pigmented, forming purple bands. Quenstedt muscle impression oval, marked by slightly deep and colourless depression, located in middle of anterior quadrant, occupying ~1/20 of size of adductor muscle impression.

Muscle system

Adductor muscle. (Figure 7F) Rounded in section.

Quenstedt muscle. Inserting in most basal portion of palps, near gill.

Mantle

(Figures 7F–H, 8B) Thin, with well-defined and abundant pallial muscles. Sub-umbonal region free, not filled by palps. Pallial muscles mainly located around adductor muscle. Accessory heart of left lobe with thin walls, with wide diameter. Bifurcation around adductor muscle reduced, but thick. Other branch leaves pallial branchial junction and follows towards gills, like in *C. mangle*. Right lobe presenting only one branch of accessory heart. Mantle borders slightly pigmented, brownish or orange. Middle fold with uniformly distributed medium to long papillae. Internal fold with well distributed long papillae.

Gills

(Figure 7E) Similar to other species in size or number of lamellae. Margin of alimentary groove thinner, with ~1/2 size of alimentary channel of *C. brasiliensis*.

Visceral mass

(Figure 7F) Occupying ~1/4 of animal's size. Located from ventral region of ligament to anterior surface of pericardium. Digestive diverticula, located in dorsal region of palps, occupying ~1/4 of visceral mass.

Circulatory and excretory systems

(Figure 7I) Ventricle large, reticulated, sometimes pigmented. Auricles slightly thinner and less reticulated, devoid of pigmentation. A pair of kidneys occupying relatively same position of other species.

Digestive system

(Figure 8A, C)

Palps. (Figure 8A) Somewhat small, ~1/5 size of animal. Palps located under mantle in sub-umbonal region, not filling whole free space of sub-umbonal region. Thin, sickle-shaped, joined throughout length of its base towards visceral mass. Upper margin with plicae over border of palps. Anterior and posterior portions reduced, but devoid of plicae. Internal

Fig. 7. *Crassostrea virginica* shell and anatomy: (A) external view, right valve; (B) left valve, sub-umbonal cavity, internal view (L 36 mm); (C) same, detail of adductor muscle impression; (D) same, external view, detail of ornamentation of the shell edge; (E) gill, internal surface of middle portion; (F) general view of right side, shell and mantle lobe removed (L 48 mm); (G) mantle border, middle portion (side 5 mm); (H) pallial cavity, postero-dorsal region, right view, showing accessory heart (ah) (L 30 mm); (I) pericardium and heart, right view, pericardial membrane removed. Scales: 1 mm.

faces intensively plicate, plicae thinner than in other species. External face smooth, but striations may be present.

Oesophagus. (Figure 8C) Short, $\sim 1/6$ size of palps; internal surface intensively striated.

Stomach. (Figure 8C) Same as other species, except for smaller globose region with $\sim 1/8$ of animal's size, laterally flattened, with numerous irregular external and internal invaginations. Style sac and intestine separated by thinner pyloric process, slightly longer than in other species. Digestive diverticula well distributed and not very abundant.

Intestine. Thin in portion between adductor muscle and gills; internally similar to other species. Minor and major typhlosoles thin. Rectum shorter, not surrounding curved portion of muscle.

Reproductive system

(Figure 7F) Gonads abundant, occupying $\sim 1/5$ of animal's height. Genital opening not observed.

DISTRIBUTION AND HABITAT

From western Canada to Florida and Mexican Gulf (Abbott, 1974; Mikkelsen & Bieler, 2008). Only on rocky coasts.

EXAMINED MATERIAL

USA. Florida: Wabasso, Sand and flat on rest area, on causeway, state route 512, $27^{\circ}49.3'N$ $80^{\circ}25.257'W$, MZSP 46930, 1 specimen (Simone col.; 5 August 2004); Fort Pierce, sand bar on north side of Fort Pierce Inlet, and of Little Jim Island, $27^{\circ}28.147'N$ $80^{\circ}18.503'W$, MZSP 46961, 3 specimens (Simone col., 6 August 2004); Monroe, Field Museum of Natural History FMNH 314566, 1 specimen (D. Gonsalves-Jackson, 4 August 1999); Off Florida, Gulf of Mexico, USMN 833964, 1 specimen (CSA for MMS, 9 December 1984).

Fig. 8. *Crassostrea virginica* anatomy: (A) palps and adjacent structures, right-slightly ventral view, adapted from Galtsoff (1954); (B) pallial cavity, posterior region, with posterior half of gill cut and deflected, detail for an accessory heart (ah) (adapted from Galtsoff, 1964); (C) stomach opened longitudinally, dorsal view showing internal structures. Scale: 1 mm.

Crassostrea gigas (Thünberg, 1793)
(Figures 9, 10)

Ostrea gigas Thünberg, 1793: 140–142 (pl. 6, figures 1–3); Lischke 1896: 174.

Ostrea (Crassostrea) gigas: Hirase, 1930: 49–55.

Crassostrea gigas Ahmed & Sparks, 1967: 2155–2158; Abbott, 1974: 456 (figure 5276); Menzel, 1974: 453–456; Ahmed, 1975: 375 (figure 10); Andrew, 1979: 293–335; Buroker *et al.*, 1979a: 157–169; Buroker *et al.*, 1979b: 171–184; Torigoe, 1981: 304–305, 325 (pl. 2, figure 1); Castillo-Rodriguez & García-Cubas, 1984: 1–57; Harry, 1985: 152; Arakawa, 1990: 1–13; Brock, 1990: 59–63; Littlewood, 1994: 221–229; Li, 1989: 239–255; Banks *et al.*, 1994; Boudry *et al.*, 1998: 279–291; Ó’Foighil, *et al.*, 1998: 497–503; Abbott & Dance, 2000: 318 (figure 7); Coan *et al.*, 2000: 217 (pl. 37); Hayami, 2000: 925; Yu *et al.*, 2003: 31–37; Christo, 2006: 101–110; Pie *et al.*, 2006: 1598–1600; Camara *et al.*, 2008: 313–322; Christo & Absher, 2008: 71–77; Xia *et al.*, 2009: 1–8.

DIAGNOSIS

Size up to 140 mm; fixed in rocks; shape cupped elongate, with crenulations and ornamentation in edge shells; colour varying from white, brown, purple to yellowish spots; right valve and left valve almost of same size; left valve cupped-shaped. Adductor impression purple and is oval. Adductor muscle postero-dorsal located, occupying 1/4 of total size of animal; sub-umbonal region present and usually free; mantle edge unpigmented. Accessory heart of left lobe thick, bifurcated portion around adductor muscle very reduced; in right lobe with single branch. Palps with margin superior with plicae.

DISTINCTIVE DESCRIPTION

(More information and figures in Galtsoff (1964).)

Shell

(Figure 9A–C) Large, ~140 mm, thick and with well-defined, elongated cupped shape. Surface ornamented by waves in borders and many layered lamellae in upper shell surface. Right valve almost same size as left valve, presenting a

protruding area near hinge. Left valve cupped-shaped, a little larger than right valve, with internal depression that advances under a deep umbo. External coloration variable, sometimes with white, brown and yellowish spots. Inner portion of valves predominantly white, with opalescent brightness sometimes present like other species. Adductor muscle impression (ai) oval, slightly elongated, located in postero-dorsal region, concavity towards hinge; highly pigmented with purple bands. Quenstedt muscle impression located in middle of anterior portion of valves.

Muscle system

Adductor muscle. (Figure 9F) Outline ovoid. Distinction of quick and slow portions clear, of similar size.

Mantle

(Figures 9D–F, H, J, 10A) Thick, with well-defined pallial muscles, stronger around adductor muscle. Accessory heart

(Figures 9H, 10A) of left lobe thick, diameter varying from narrow to wide. Bifurcated portion around adductor muscle very reduced. Other branches leaving pallio–branchial junction towards gills, like preceding species. Accessory heart of right lobe with single branch. Mantle border unpigmented. External fold almost two times larger than middle and internal folds. Middle fold with small and middle finger-like, uniformly distributed papillae, more numerous than those of internal fold. Internal fold with small and uniform papillae (Figure 9J). Sub-umbonal region not filled by palp.

Gills

(Figure 9I) Same as other *Crassostrea* in size. Number of filaments of lamellae ~15. Marginal alimentary groove thin.

Visceral mass

(Figure 9F) Occupying ~1/6 of animal's size. Located from ventral region of ligament to anterior surface of pericardium.

Fig. 9. *Crassostrea gigas* shell and anatomy: (A) external view, right valve; (B) left valve, inner partial view (L 97 mm); (C) same, detail of adductor muscle impression; (D) same, detail of sub-umbonal region at anterior portion; (E) same, detail of postero-ventral mantle edges showing pallial muscles; (F) general right view, valve removed (L 85 mm); (G) palps, anterior—slightly ventral view (side 20 mm); (H) edge of right lobe, middle-ventral portion, showing papillae of middle and internal folds (side 6 mm); (I) left mantle lobe, detail of postero-dorsal region, internal view, detail for a accessory heart (ah) (side 20 mm); (J) gill, internal surface of middle portion; (K) detail for a rectum (rt) and anus (an). Scale: 1 mm.

Digestive tubes located in anterior region, posterior to palps, occupying $\sim 1/4$ of visceral mass, with diverticula. Gonads yellowish, covering digestive diverticula externally.

Circulatory and excretory systems

Ventricle triangular-shaped, very reticulated, usually unpigmented. Auricles thinner and less reticulated, unpigmented.

Digestive system

(Figures 9G, 10B) Alimentary channel fully involved by gonads, diverticula of digestive gland and kidneys. All structures as in preceding species.

Palps. (Figure 9G) Large, located under mantle sub-umbonal region, of free space of sub-umbonal region. Thick, wide sickle-shaped, joined throughout length of their base to visceral mass. Anterior and posterior portions wide and devoid of plicae. Anterior and ventral free margins slightly arched in ventrally to form apex. Internal faces intensively plicate, including upper region of palps. External faces smooth, in which there may be striations and irregular grooves.

Oesophagus. (Figure 10B) Oesophagus dorso-ventrally flattened, relatively longer than short. Internal surface intensively striated.

Stomach. (Figure 10B) Same as other species. Selection wall portion shorter than *C. mangle* and *C. brasiliensis*. Digestive diverticula fewer than in other species, with fewer connections to stomach. Selection area (sa2) smaller than other species.

Reproductive system

(Figure 9F) Gonads abundant, occupying $\sim 1/4$ of animal's height.

DISTRIBUTION AND HABITAT

Crassostrea gigas is the most cultivated species around the world, but it appears naturally in estuaries and rocky coasts of Japan and south-eastern Asia. It is usually found from the intertidal to subtidal zones (NIMPIS 2002). In Brazil, it is largely cultivated in the Southern region of the country. It appears only on rocky coasts.

EXAMINED MATERIAL

Brazil. Santa Catarina: Florianópolis, cultivation, MZSP 89671, 12 specimens (Simone leg., August 2008).

Crassostrea praia (Ihering, 1907) (revalidated)
(Figure 11A, B)

Ostrea (*Crassostrea*) *parasitica praia* Ihering, 1907: 426 [not figured].

Crassostrea rhizophora praia: Rios, 1970: 171; 1975: 205 (in syn.); 1994: 245 (in syn.); 1985: 229 (in syn.).

Crassostrea rhizophorae praia: Rios, 2009: 501 (in syn.)

DIAGNOSIS

Size up to 100 mm; left valve shape cupped elongate and thick, with crenulations and ornamentation on entire shells; colour varying from white to purple. Muscle impression purple. Adductor muscle oval-elongate, occupying $2/3$ of height of shell. Sub-ligamentary area long; sling umbonal cavity present.

TYPES

Syntypes MZSP 10916 (figures 81, 82).

DIFFERENTIAL DESCRIPTION

Shell

(Figure 11A, B) Shape cupped, elongate, up to 100 mm long. Colour varying from white to purple, with longitudinal bands of these. Right valve not seen. Umbonal cavity of left valve sling. Interior of valves predominantly white, with little brightness or opaque. Purple pigmentation close to

Fig. 10. *Crassostrea gigas* anatomy: (A) pallial cavity, posterior region, posterior half of the gills sectioned from each other and deflected (H 55 mm), detail of accessory heart (ah) (adapted from Galtsoff, 1964); (B) stomach opened longitudinally, dorsal view, inner surface exposed, scale 1 mm.

Fig. 11. Types. *Crassostrea praia* shell type MZSP 10916: (A) left valve, detail of ornamentation; (B) same, external view, inner view (H 80 mm). *Crassostrea parahibanensis* shell paratype. MNRJ 3815; (C) left valve, external view, detail of ornamentation; (D) same, inner view (H 220.5 mm). *Crassostrea brasiliiana* syntype; (E) right valves, inner view.

margin, in most inner regions. Scar of adductor muscle mostly located in anterocentral region, somewhat middle; form long crescent, occupying about 2/3 of shell height. Muscle scar sometimes strongly pigmented with purple, brown bands or a combination.

DISCUSSION

The new species described herein, *Crassostrea mangle*, has been referred to in Brazil as *C. rhizophorae*. A comparison with specimens of *C. rhizophorae* from the type locality (Carriacou) revealed significant differences, which endorse the specific separation. The introduction of a new species was necessary, as no previous name was available. *Ostrea arborea* Dillwyn 1817, a possible name for the Brazilian species, is considered herein a *nomen dubium*, as neither the too brief description nor the locality (Atlantic and Indian Oceans, Moluccas Island and Curaçao) were precise enough to allow for its recognition (Dillwyn, 1817; Rios, 1970). The type specimen has not been found. Therefore, *O. arborea* is here understood as a senior synonym of *C. rhizophorae*. Furthermore, Parodiz (1948) described the morphological differences between *O. arborea*, *O. spreta* d'Orbigny, 1845 and *O. puelchana* d'Orbigny, 1842 (Parodiz, 1948; Castellanos, 1968), and highlighted the confusion involving these taxa.

Another previously described name and possible synonym, *Ostrea parasitica praia* Ihering, 1907, occurs in Rio Grande do Sul State (Parodiz, 1948). The shell characteristics differ from

those of *C. mangle* and *C. rhizophorae* (more information below). *Crassostrea praia* is available according to ICZN Art. 12 (Bouchet, 2013, personal communication)

Shell

The shells of the Caribbean *C. rhizophorae* are generally the smallest, up to 60 mm long, cup-shaped and thicker; the colour varies from brown, yellowish to white, with intermediary shades (Figure 2E, F). *Crassostrea mangle* shells are also cup-shaped, with an average of 70 mm long, and a more elongated outline (Figure 1A–C). *Crassostrea brasiliiana* is large, with an average length of 100 mm and a more rounded outline when occurring in open sea, or cup-shaped in mangroves (Figure 4B, C). *Crassostrea praia* are elongated but not as large as *C. gigas*, average 100 mm (Figure 9E, F). *Crassostrea virginica* has an ornamented shell, with foliaceous layers and undulations, which externally distinguishes it from the other species (Galtsoff, 1964; Abbott, 1974) (Figures 5L, 6A, B). *Crassostrea gigas* has a larger (with average of 120 mm) and a thicker shell, ornamented by foliaceous layers coupled with undulating margins (Figure 7F, G). The exterior of the valves is ornamented by projections of the prismatic layer forming foliaceous blades with variable number of folds or scales, low and short, arranged radially in *C. brasiliiana*, *C. virginica* and *C. gigas* (Galtsoff, 1964). In *C. brasiliiana* and *C. mangle*, such ornamentation can be inconspicuous or absent, depending on the environment (Nascimento, 1991). In contrast, *C. rhizophorae* presents small folds on the right

valve. In *C. praia* the ornamentation consists of longitudinal undulations.

The outer colour is highly variable in all species; it may vary in *C. rhizophorae*, *C. mangle* and *C. brasiliiana* from brown, yellow, white to purple, including a combination of these colours. *Crassostrea virginica* and *C. praia* have shades of purple and brown, with white spots. *Crassostrea gigas* varies from brown to orange with white spots. Natural erosive agents may cause fading, especially in the older specimens (Harry, 1985).

The right valve of *C. mangle* and *C. rhizophorae* is flattened or slightly arched (convex), opercular, and in *C. mangle* it is slightly protuberant towards the hinge (it accommodates the visceral portion of the oyster's body). In *C. brasiliiana*, *C. virginica* and *C. gigas*, the right valve is arched-convex, opercular and very protuberant towards the hinge. The right valve of *C. praia* was not observed in the present study.

The left valve of *C. rhizophorae*, *C. mangle*, *C. brasiliiana*, *C. virginica*, *C. gigas* and *C. praia*, as is the case in any ostreoid, is fixated to the substrate. It is cup-shaped, and particularly much larger than the right valve (Figures 1D, 2E, 4C, 5L, 7F, 9E). All of them have a deeper umbonal cavity, which may be shallower (Gunter, 1950; Thompson, 1954; Galtsoff, 1964; Yonge, 1966) in some specimens.

The internal surface of the six species is usually glossy, but some specimens have it opaque. The pallial line is absent in ostreids (Morton, 1983), possibly due to the fibres of radial muscles being fixed directly to the region surrounding the adductor muscle and to the visceral mass, and not to the region close to the shell border, as is the case in most bivalves (Galtsoff, 1964). The Quenstedt muscles scar is very small, marked by a shallow and colourless depression, close to the internal ventral margin of the ligamentary area; it is similar in position and size in all species. The adductor muscle impressions of *C. mangle* (Figure 1D) and *C. brasiliiana* (Figure 4B, C) may be pigmented or unpigmented; it is unpigmented in *C. rhizophorae* (Figure 2G). The different pigmentation has been mentioned in the literature as a distinguishing feature between species (Nascimento, 1991), however, this proves to be inaccurate according to our findings, as a high degree of variation is present. A pigmented adductor muscle scar is also commonly found in *C. praia* (Figure 11B), *C. virginica* (Figure 7C) and *C. gigas* (Figure 9C). The free margin of the shell and the cavity that comprises the visceral mass in *C. rhizophorae*, *C. mangle*, *C. brasiliiana* and *C. praia*, can be coloured light purple (Weisboard, 1964; this study), which has been regarded as a characteristic of tropical populations (Harry, 1985).

Musculature

ADDUCTOR MUSCLE

The adductor muscle of *C. rhizophorae* (Figure 3C, D), *C. mangle* (Figure 1E), *C. brasiliiana* (Figure 5C), *C. virginica* (Figure 7C) and *C. gigas* (Figure 9C) show variable outlines among specimens, including crescent, oval, oval–elongated in cross-section. This variation has been pointed out in the literature (Nascimento, 1991 for *C. rhizophorae*; Galtsoff, 1964 and Kennedy *et al.*, 1996 for *C. virginica*), and possibly is associated with the high level of shell plasticity.

The loss of the post-larval anterior adductor muscle and the enlargement of the posterior adductor muscle are

characteristic of the ostreids. These are obviously related features. In *Gryphaea* Lamarck, 1801 the fibres of the opaque portion of the adductor muscle occupy about 30% of the adductor cross-section area (Thompson, 1954); this contrasts with more than 50% in *Ostrea* and is significantly reduced in *Pycnodonte* Waldheim, 1835. This proportion has been considered in the diagnosis of the three genera (*Ostrea*, *Pycnodonte* and *Gryphaea*) (Stenzel, 1971). However, the diagnostic value of such character is not applicable in *Crassostrea*, since *C. rhizophorae*, *C. brasiliiana* and *C. virginica* show individual variations in the proportions of the opaque and translucent parts. The opaque part may be found in proportions higher than 30%, but is always smaller than the translucent portion (Galtsoff, 1964 and Kennedy *et al.*, 1996 for *C. virginica*; this study).

QUENSTEDT MUSCLES

The pair of Quenstedt muscles has no differentiation regarding the origin on the shell and the insertion in the base of the palps in the five species; they are thicker in the portion connected to the shell in *C. mangle* (Figure 1G), *C. rhizophorae* (Figure 3F) and *C. brasiliiana* (Figure 5E) if compared to *C. virginica* and *C. gigas*. The Quenstedt muscles in the five species are not difficult to find, differently from what has been postulated in the literature (Galtsoff, 1964; Stenzel, 1971; Mesquita, 1993). The direct observation of the muscle is possible mainly in large (>40 mm) specimens. From their origin on the shell, the muscles run through the anterior visceral mass up to the insertion in the base of the palps. This peculiar morphological arrangement shows improbable a homology with the anterior adductor muscle or any foot muscles (suggested by Galtsoff, 1964; Stenzel, 1971). They may retract the gills and the palps, helping in transferring particles to the mouth.

Pallial structures

MANTLE

The mantle lobes in *C. mangle* (Figure 1L), *C. rhizophorae* (Figure 3H), *C. brasiliiana* (Figure 5F) and *C. gigas* (Figure 9F) are very similar. They are robust, with evident blood vessels mainly near the palps. The pallial musculature is strong in all species, clustering near the adductor muscle. *C. virginica* (Figure 7F) differs by having thin mantle lobes (Galtsoff, 1964).

The sub-umbonal region in *Crassostrea* is formed by the anterior junction of the mantle lobes; it is actually an inner mould of the depth of the apex of the left valve. In *Ostrea*, this structure is not present, since the shells are not cup-shaped. The sub-umbonal region may be completely filled by the anterior region of the palps, as is the case in *C. brasiliiana* (Figure 5E), or free, not filled by palps, as in *C. mangle* (Figure 1G), *C. rhizophorae* (Figure 3E), *C. virginica* (–Figure 7F) and *C. gigas* (Figure 9D).

The mantle edges of *C. rhizophorae* are thick and pigmented; the external fold is devoid of papillae and may exceed the shell margins in length when extended (Figure 3H). The middle fold has two different kinds of fingerlike papillae: short and thin, and long (more than 1 mm) with an enlarged base. The papillae are arranged normally presenting up to six short papillae alternated by two longer ones; both types of papillae show a gradual increase in diameter and length

from the ventral region towards dorsal region. The edge is pigmented in various shades of brown or depigmented. In *C. mangle*, the mantle edge is thick, and can be pigmented or unpigmented; the three folds have similar sizes; the middle fold has sparsely distributed, short and long papillae; the successive arrangement may be two long papillae and up to six short papillae; the internal fold has evenly distributed papillae (Mesquita, 1993; this study) (Figure 1L). The mantle edges of *C. brasiliiana* are always brown coloured; the middle fold has long, medium and short papillae, having from 2 to 4 medium or short papillae for each long one (Figure 5F). In *C. virginica* the mantle edge can be brown or orange coloured; the middle fold shows intercalated medium and long papillae; the internal fold has evenly distributed, long papillae, intercalated with the middle fold papillae (Figure 7G). The mantle edge of *C. gigas* is pigmented; the middle fold shows medium and small papillae; the internal fold has small digitiform folds. In general, the internal fold of the mantle margin is extensible and highly vascularized (Figure 9J).

PROMYAL PASSAGE

One of the outstanding characters of *Crassostrea* is the promyal passage on the right side of the visceral sac. This additional opening significantly improves the cleaning mechanisms on the animal's dorsal side, providing a wide area closer to the hinge from which the water can be expelled. Additionally, as it is closer to the support between the valves, the water leaving by the promyal chamber can be ejected more vigorously, by using the same intensity of the adductor contraction (Nelson, 1938). The promyal passage was first described in *C. virginica* by Kellogg (1892), and has been pointed out as associated with the higher capacity of growth and survival of *C. gigas* when compared to the sympatric and promyal-wanting *Ostrea lurida* Carpenter, 1864 by Elsey (1935).

Otherwise, and beyond the promyal passage, the oysters with a cup-shaped left valve, such as *Crassostrea*, have a more efficient cleaning mechanism of the pallial cavity, which allows for the establishment of populations close to river mouths. In such environment, the turbidity is higher and the suspended sediment is significant enough to preclude the survival of oysters not provided with a promyal passage. Galtsoff (1964) did not agree with the opinion of Nelson (1938), stating that 'nothing is known about the adaptive meaning of such [promyal] passage, in addition to the fact that it provides an additional way for the water flowing through the gills'. The positioning and function of the promyal passage undoubtedly characterize a more effective water flowing mechanism, besides preventing the accumulation of particles in the pallial cavity.

GILLS

The gills of all species are similar to each other, with the number of lamellae increasing with the animal's size. The general shape of the gills of all species studied herein is similar to that described for *Ostrea edulis* Linné, 1758, *C. virginica* and *C. angulata* in the literature (Ridewood, 1903; Yonge, 1926, 1966; Atkins, 1937a, b, 1938; Nelson, 1938; Galtsoff, 1964). The gills of the studied species differ only by the thickness of the marginal food channel. *Crassostrea mangle* (Figure 1H), *C. rhizophorae* (Figure 3K) and *C. brasiliiana* (Figure 5I) have a broader food channel, while *C. virginica* (Figure 7E) and *C. gigas* have a narrower one. In all examined

species, the gills reach ~80% of the specimen's length. The presence of a ventral particle groove is another particularity of an adult pseudolamellibranch gill (the Pectinidae do not possess such a groove) (Cannuel & Beninger, 2006).

The number of gill folds and filaments is a variable character, apparently increasing proportionally to the animal's size. However, the numbers can be discrepant between individuals of similar size. Ridewood (1903) mentioned 9–12 filaments per fold in *O. edulis*, while Atkins (1937a) mentioned 8–17. Atkins (1937a) mentioned 8–17 in *C. virginica*; Nelson (1938) mentioned 8–15. Galtsoff (1964) mentioned 10–16 filaments per fold in *C. angulata*, while Atkins (1937a) referred to 15–16 and Nelson (1938) 8–14 filaments per fold. In the present paper we verified that the number of filaments per fold in *C. rhizophorae*, *C. mangle*, *C. brasiliiana* and *C. virginica* varies from 12 to 13, reaching 15 in *C. gigas*. Based on the proximity of the numbers, this parameter seems to be of little use in distinguishing the examined species.

The mucous secretion of the gill plays an important role in the selection mechanisms. It has been verified that, in *O. edulis* Linnaeus, 1758, the common filaments have twice more mucous cells than the main ones, concluding that the material reaches the front face of the common filaments and has twice the chance of causing sufficient mucous secretion for its rejection when reaching the palps (Nelson, 1960). Those characteristics have been observed in *C. mangle*, *C. brasiliiana*, and *C. gigas* in the analyses of functional anatomy performed here.

Circulatory system

HEART

The hearts of the analysed species differ in colour, arrangement and thickness of the ventricular and auricular fibres. The ventricle of *C. rhizophorae* is elongate and thicker than the auricles; the auricle walls are formed by thin bundles of muscle fibres crossing the ventricular cavity, dividing it incompletely in two chambers. The colour varies from cream-yellowish to depigmented (Figure 4C). *Crassostrea mangle* has a more developed, thick-walled ventricle, with internal fibres crossing in several directions; the auricles can be pigmented or unpigmented; it has a thinner external tissue, with also thinner fibres, forming a trabecular structure (Figure 1J). *Crassostrea brasiliiana* has a thin, well-reticulated, usually translucent ventricle; the two auricles are less reticulated and unpigmented (Figure 5H). *Crassostrea virginica*, as reported by Galtsoff (1964) (Figure 7I) and *C. gigas* have a broad, reticulated ventricle, either pigmented or unpigmented; the auricle, in contrast, has fewer fibres and is colourless.

Accessory heart

The accessory heart, present symmetrically in both mantle lobes, is characteristic of the genus, and shows significant differences between the four species. The primary function of the accessory hearts is to promote the blood circulation inside the mantle and facilitate the gaseous exchanges (Galtsoff, 1964). In *C. rhizophorae*, the accessory heart has a single branch, and lies near the adductor muscle on both sides (Figure 3G). In *C. virginica*, it has three long and well-defined branches (Y-shaped) on both lobes, as described by Galtsoff (1964) and Stenzel (1971) for *C. virginica* (Figure 7H). In *C. mangle* (Figure 1K), *C. brasiliiana* (Figure 5L) and *C. gigas*

(Figure 9H), the branch surrounding the adductor muscle towards the anus on the left lobe is reduced or absent; while the left lobe has a single vessel. Additionally, in all species, the accessory heart also varies concerning the gauge of vessels and tissue thickness, as stressed in the descriptions.

Digestive system

PALPS

The labial palps are evident organs, located fully or partially inside the mantle's sub-umbonal region. The palps of *C. mangle* are flattened and elongated, slightly arched anteriorly, with ventral free margins; the internal surfaces have folds, which extend themselves transversally. The joining of the palps constitutes a ventral lip (Figures 1F, 2D). In *C. rhizophorae* the palps are flattened, elongated, the base is united throughout its length to the visceral mass; the margins are slightly arched anteriorly and ventrally free, converging towards the ventral region to form the apex; the internal faces are plicate, the inner folds extend transversally, ending in the free, narrow and smooth inner margin (Figures 3I, 4B). The palps of *C. brasiliiana* are slightly flattened and sickle-shaped; the superior margin of the folds are free and smooth (Figures 5G, 6C). In *C. virginica* (Figure 8A), the palps are thinner and smaller than in the prior species, and have no free upper margin such as in *C. brasiliiana*. In *C. gigas* (Figure 9G), the palps are large and thick and lack a free upper margin, such as those of *C. virginica* and *C. rhizophorae*.

The arrangement of the palps of *C. mangle* is similar to the palps of *Ostrea* and *Crassostrea* described above, but there are significant differences concerning their functionality. The currents in the smooth (external) surface of the four hemipalps are similar to each other and work in order to lead all particles towards the ventral (aboral) margin of the palps.

OESOPHAGUS

The oesophagus is dorso-ventrally flattened in all species. It varies only concerning the length and width: in *C. mangle* (Figure 2A, H), *C. brasiliiana* (Figure 6D), and in *C. rhizophorae* (Figures 3J, 4E) it is slightly longer than wide; in *C. virginica*, the oesophagus is clearly the shortest (Figure 8C); and in *C. gigas* it is slightly longer than short. In all species the oesophagus have similar internal striae (Figure 10B).

STOMACH

The stomach is slightly flattened dorsal-ventrally in all species. It is located in the globular region of the visceral mass, and shows a higher number of ducts to digestive diverticula in some species (*C. rhizophorae* and *C. brasiliiana*) or a smaller number in others (*C. mangle*, *C. gigas* and *C. virginica*). Besides the general quantity, these structures are abundant in the globular region. The stomach ducts to the digestive diverticula are much reduced, ~50% in *C. gigas* when compared to the other species.

The internal structures of the stomach are similar among the species, only differing by some details. The selection area of *C. brasiliiana* (Figure 6D) is longer than that of *C. mangle* (Figure 2H) and *C. rhizophorae* (Figure 4E), ending closer to the base of the typhlosoles on the stomach floor. The caecum of the selection area of *C. brasiliiana* is shorter than that of *C. rhizophorae*, not completing 1.5 turns

(Mesquita, 1993; present study). In *C. virginica*, the style sac and the intestine are surrounded by a thinner pyloric process and are slightly longer than that of the other species. In *C. gigas*, the selection area is shorter than that of *C. rhizophorae* and *C. brasiliiana*.

The stomach of *C. virginica* has been additionally studied based on latex or resin moulds (Shaw & Battle, 1957; Galtsoff, 1964). Such an organ has been described as bag-shaped, internally divided into a smaller anterior chamber and other larger posterior chamber, by means of a thick fold; such a fold is projected to the organ's lumen and seems to serve as a means to direct particles to the posterior region through a narrow channel. Shaw & Battle (1957) saw the caecum organization in *C. virginica* and named the ventral branch as 'posterior appendix of the caecum' and the dorsal branch as 'anterior appendix'. Purchon (1957) named such set of bags with a blind bottom in *C. parasitica* as 'food sorting caecum - fc'. In *C. rhizophorae*, *C. mangle* and *C. brasiliiana*, the base of such fold on the floor can be strong, with grooves that extend to the distal region, or it can be almost smooth. This grooved area corresponds to the sorting area (sa2).

All such stomach characters are similar to those of *O. edulis* (Yonge, 1926; Graham, 1949; Purchon, 1957; Reid, 1965), *C. parasitica* (Shaw & Battle, 1957) and *O. chilensis* (Purchon, 1957). Other details of the morphology and physiology of the ostreid digestive tract, such as ciliary mechanisms and stomach structure and operation, can be found in the literature (Shaw & Battle, 1957; Nelson, 1960; Reid, 1965; Yonge, 1966). In this scenario, the internal anatomy of the stomach of *C. rhizophorae*, *C. mangle*, *C. brasiliiana*, *C. virginica* and *C. gigas* has the same essential characteristics described by Purchon (1957) for *C. parasitica*, but the author did not mention the anatomy and the currents of the cylindrical portion (style bag and early intestine) of the stomach of that species. Purchon (1957) did not disclose in his schemes the existence of folds on the walls of the recesses of *C. parasitica*, but in *C. rhizophorae*, *C. mangle*, *C. brasiliiana* and *C. gigas* the structures were very conspicuous. Regardless, the locality of the specimens studied by Purchon (1957) was not mentioned.

When comparing the globular region of the stomach of *C. mangle* and *O. edulis* (Yonge, 1926; Graham, 1949), a general morphological similarity was detected, with a few exceptions. The caecum of selection in *Ostrea edulis* has only a ventral branch (= posterior appendix of Shaw & Battle, 1957), where the largest typhlosole penetrates and ends; two evaginations are missing in the anterior wall of the stomach, as well as the isolated opening of the digestive duct on the right wall, appearing in *C. mangle* and *C. brasiliiana*. Graham (1949) mentioned the existence of a series of folds and grooves with an irregular arrangement on the right wall and close to the intestine opening of *O. edulis*; these were considered similar to the folds that constitute the well-developed area of the posterior sorting in *Glycymeris glycymeris* (Linné, 1758). In this same position, irregular plicae and grooves can be observed in the stomach of *C. rhizophorae* and *C. brasiliiana*, which lies inside the dorsal hood.

Yonge (1926) considered the sorting mechanisms inside the selection caecum of *O. edulis* less complex than that of *Modiolus* (Lamarck, 1799) and *Mya* (Linné, 1758), and attributed such simplicity to the higher development of the selection mechanisms of the gills and palps.

INTESTINE

The intestine is individualized from the style sac distal end; it returns in the opposite direction, extending behind the pericardium, superficially immersed in the gonads in the visceral mass. In *C. brasiliiana*, the portion surrounding the adductor muscle is narrower than in *C. mangle*. In *C. virginica* it is thinner, like in *C. brasiliiana* and *C. rhizophorae*, and its typhlosoles are also thinner. The rectum of *C. virginica* is shorter than that of the other species, keeping the adductor muscle free. *C. gigas* has a similar to that of *C. mangle* and *C. brasiliiana*.

Genital system

The gonads of all species are massive, apparently regardless of the gonadal maturation period, and surround the whole visceral mass, in some cases surrounding the region near the pyloric process. They are usually coloured beige or yellowish. The genital opening has been observed in *C. mangle* and *C. brasiliiana* in the kidney, and distinguishes itself from the opening by a brownish spot.

Nervous system

The relatively simple nervous system of the four species is similar, displaying variations in the size of the commissures in relation to the animal size. The cerebral ganglia are interestingly inconspicuous, because of their small size and deep location in the visceral mass, showing no remarkable differences.

Habitat and distribution

We confirm *C. rhizophorae* occurs in salty mangroves in the south-east Caribbean Sea; *C. mangle* has been reported only

in mangroves and *C. brasiliiana* in both environments—open sea, rocky shores and mangroves. *Crassostrea gigas* has been observed forming banks in the Indo-Pacific Ocean and has been introduced in Southern Brazil (Orensanz *et al.*, 2002; Ruesink *et al.*, 2005).

Larval development (survival) and incrustation of *Crassostrea* are associated with high salinity levels (27–37‰) (Sandison 1966; Nascimento, 1991; Lemos *et al.*, 1994; Marques-Silva *et al.*, 2006). *Crassostrea brasiliiana* and *C. mangle* have a quick development and growth in low salinities, but *C. brasiliiana* tends to be more tolerant to salinity fluctuations (8–34‰) than *C. mangle* (7–28‰) (Nascimento, 1991); *C. rhizophorae* tolerates salinities of 37–44‰ (Mattox, 1949; Ladrón de Guevara *et al.*, 1996); and *C. virginica* of 19–25‰ (Castillo-Rodríguez & García-Cubas, 1984). This explains the presence of *C. brasiliiana* in both estuarine and open sea regions, and *C. mangle*'s restriction to mangroves.

The struggle for space in the environment causes distortions in the shell shape, as described by several authors (e.g. Galtsoff, 1964), precluding the immediate visual identification. According to Stenzel (1971), the 'spatuliform' or 'semi-tubular' shells (Mesquita, 1993) are characteristic of overpopulated substrates. This is intuitive and confirmed in the presently studied samples.

Importation and culture of exotic species have gradually obscured nature's long-term patterns of adaptation and evolution (Andrews, 1979).

Despite some authors having considered *Crassostrea mangle*, wrongly named as *C. rhizophorae*, as the single species of this genus occurring in Brazil (e.g. Rios, 2009); some studies have restricted its occurrence to mangroves, while the name *C. brasiliiana* has been applied to forms restricted to intertidal environments (Absher, 1989; Galvão *et al.*, 2000). This landscape is only partially confirmed here.

Fig. 12. Identification key.

As *C. brasiliiana* also occurs in estuarine environments, this concept must change. Further distinction between both species (once more, considering the misidentification of *C. mangle* as *C. rhizophorae*) has also been based on biological and ecological differences (Mattox, 1949; Galtsoff, 1964; Timothy *et al.*, 1988), and growth and larval morphology (Absher, 1989; Christo & Absher, 2008, including *C. gigas*).

Even though *Crassostrea praia* is endemic to Lagoa dos Patos, Rio Grande do Sul, no records (old or recent) were found in the MORG (Museu Oceanográfico do Rio Grande—‘Prof. Eliéser de Carvalho Rios’). Lagoa dos Patos is under severe influence of the nearby port, as well as the construction of a dam; it may be that the species is already extinct due to environmental changes. A comparison of the syntypes (left valves, strongly elongated with characteristic ornamentation) with other examples found on the Brazilian coast, suggests the specific separation between *C. praia* and *C. rhizophorae* (= *C. mangle*).

Some recent papers (Ignácio, 2002; Lèpegue *et al.*, 2002; Varela *et al.*, 2007) have considered the occurrence of *Crassostrea gasar*, an African species identified as a synonym of *C. brasiliiana*, in north-eastern and south-eastern Brazil. Based on the anatomical studies made with the voucher material of Varela *et al.* (2007), identified as *C. gasar*, we verified that specimens are, in fact, *C. brasiliiana*. In a study on the molecular phylogeny of the Brazilian mangrove oysters, Varela *et al.* (2007) assume that Brazilian oysters identified as *C. gasar* are *C. brasiliiana*, based on identical sequences of 16S rRNA. Until further studies with reliable African samples of *C. gasar* are carried out, we assume that the species does not occur in Brazil, being restricted to Africa, and all citations of *C. gasar* in Brazil must be interpreted as *C. brasiliiana*. A comparative molecular work of this species (and others species) will be included in a future revision of Crassostreinae.

CONCLUSIONS

The comparative and detailed anatomy of the species *Crassostrea rhizophorae*, *C. mangle*, *C. brasiliiana*, *C. gigas* and *C. virginica*, as well as the conchology of *C. praia*, allow for the following conclusions.

1. As stated in the descriptions and discussion, important anatomical differences have been found in almost all structures, allowing for the discernment of the species and their identification. This includes the type species of *Crassostrea*.
2. The distinction between the *Crassostrea* species based only on shell characters is complicated but not impossible (see Figure 12 and Table 1), since their structure shows phenotypic plasticity and may be subject to environmental influence.
3. Based on conchological, anatomical and geographical differences, *C. rhizophorae*, has been separated from the supposed conspecific population in Brazil. A new species, *C. mangle*, is introduced in order to settle the Brazilian entity.
4. In reference to the environment, two of the studied species native to Brazil, *C. mangle* occurs in mangroves and *C. brasiliiana* occurs in open sea and mangroves. The Indo-Pacific species, *C. gigas*, has been introduced in Southern Brazilian

Table 1. Characteristics of species, morphological and anatomical.

	<i>Crassostrea rhizophorae</i>	<i>Crassostrea mangle</i>	<i>Crassostrea brasiliiana</i>	<i>Crassostrea praia</i>	<i>Crassostrea virginica</i>	<i>Crassostrea gigas</i>
Shell inner smooth	X	X	X	X	X	X
Shell ornamentation	Little folds	Absent	Radial or absent	Longitudinal undulations	Radial	Radial
Shell shape cupped	X	X	X	X	X	X
Right valve operculum shaped	Slightly opeccular shaped	Slightly opeccular shaped	Fully opeccular shaped	No data	Present	Present
Left valve—deep protuberant near hinge	Absent	Present	Present	Present	Absent	Absent
Umbonal cavity in left valve	Slightly	Deep	Deep	Deep	Slightly	Slightly
Inner valve pigmented in edge	Present	Absent	Present	Present	Present	Absent
Scar of muscle adductor—form	Oval	Crescent to oval	Oval	Crescent much elongated	Crescent elongated	Crescent
Scar of muscle adductor—pigmentation	Absent	Absent or present	Absent or present	Present	Present	Present
Muscle adductor—form	Oval	Crescent oval	Oval	No data	Crescent	Crescent
Mantle edge—pigmentation	Pigmented	Pigmented	Pigmented	No data	Pigmented	Slightly pigmented
Accessory heart—form	Only one branches in both sides	Three branches in right side and one branch in left side	Three branches in right side and reduced in left side	No data	Three branches in both sides	Three branches in right side and reduced in left side
Hood—free or full	Free	Free	Fully	No data	Free	Free
Palps—anterior margins	Free	Free	Free	No data	No free	No free

seashores, mainly in open sea. *Crassostrea praia* occurs, apparently, only in Southern Brazil.

5. The occurrence of the African species, *C. gasar*, in Brazil has not been confirmed. The examination of testimonial material allowed us to assert that it is misidentified, and is, in fact, *C. brasiliiana*.
6. The geographical distribution of the studied species is the following: *C. rhizophorae* occurs in mangrove areas in the south-eastern Caribbean Sea; *C. mangle* occurs from Pará to Santa Catarina, only in mangroves; *C. brasiliiana* from Maranhão to Santa Catarina, in mangroves and open sea rocky shores; *C. virginica* occurs from the Atlantic coast of Canada to the Caribbean; *C. gigas* is originated from the Indo-Pacific; and *C. praia* is restricted to Rio Grande do Sul. The latter is here understood as a probably extinct endangered species.

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ANEXO II – Amaral & Simone, *submitt* – Comparative anatomy of five species of *Saccostrea* from Pacific and Indian Ocean.

Comparative anatomy of five species of *Saccostrea* (Bivalvia: Ostreidae) from Pacific Ocean.

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Running title: Anatomy of genus *Saccostrea*

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ABSTRACT

Ostreids are well known for their high intra-specific variation, which makes identification problematic. The present paper aims to provide a morpho-anatomical analysis of five species of Saccostrea, as well as some congeneric species from relevant areas in the Pacific Ocean. Saccostrea cucullata occurs in Africa, Indian Ocean and Arabian Sea, Red Sea and part of the Pacific, fixed on rocks and mangroves. S. glomerata occurs in the Pacific, New Zealand, Australia and Philippines, always associated with rocks. S. echinata, occurs from East Africa to Japan. S. palmula, occurs from Mexico to Peru, in the Pacific. S. mordax occurs in the Red Sea and Pacific. The wide distribution of these often sympatric species leads to confusion regarding their identity. Herein we describe several anatomical differences that allow a more precise identification, especially when they come from sympatric taxa.

ADDITIONAL KEYWORDS: oyster – morphology – systematics – food – cultivation - phenotypic plasticity.

INTRODUCTION

The superfamily Ostreoidea Rafinesque, 1815, includes marine and brackish water species adapted to sessile epifaunal communities attached to hard substrates. The taxon comprises ca. 80 species with a widespread distribution, which includes oceanic islands (Huber, 2010). Most of these species live in hot intertropical waters. Both tolerance and resistance to environmental variations allowed the Ostreoidea to colonize different marine habitats, from coastal regions with clear waters and high salinity levels, to estuarine environments with turbid waters and inconstant salinity levels (Quayle, 1981).

Harry (1985) classified the oysters within a superfamily (Ostreoidea), two families (Gryphaeidae and Ostreidae), four subfamilies (Pycnodonteinae, Lophinae, Ostreinae and Crassostreinae), 10 new tribes, 24 genera and subgenera, and 12 genera described then. The most recent revision by Huber (2010) reduced the number of genera and species, but retained the classification established by Harry (1985) for families, subfamilies and genera.

Species of the genus *Saccostrea* Dolfuss & Dautzenberg, 1920 are common oysters that live on rocky shores of the Indo-Pacific. The taxonomy of this genus is unclear, and the morphological plasticity makes identification problematic (Lam & Morton, 2006). They have small to medium shells, a left valve with a prominent ligamentary area showing clear, continuous and regular primes. The right valve is flat, bearing projections along its margin, with corresponding concavities on the left valve. The genus includes nine species (Huber, 2010): *Saccostrea cucullata* (Born, 1778) – the type species; *Saccostrea cirumsuta* (Gould, 1850); *Saccostrea echinata* (Quoy &

Gaimard, 1835); *Saccostrea glomerata* (Gould, 1850); *Saccostrea kegaki* Torigoe & Inaba, 1981; *Saccostrea malabonensis* (Faustino, 1932); *Saccostrea palmula* (Carpenter, 1857); *Saccostrea scyphophilla* (Peron & Lesueur, 1807) and *Saccostrea spatulata* (Lamarck, 1819).

S. cucullata occurs in Africa, Indian and Arabian Oceans, Red Sea and part of the Pacific Ocean, fixed on rocks and in mangrove areas. *S. glomerata*, occurs in the Pacific, New Zealand, Australia and Philippines, always associated with rocks. *S. echinata* occurs from East Africa to Japan. *S. palmula* occurs from Mexico to Peru, in the Pacific. *S. mordax* occurs in the Red Sea and the Pacific. The widespread, sometimes overlapping distribution of these species often makes identification problematic (Huber, 2010). Aiming to facilitate their identification, in this paper we carry out a detailed morpho-anatomical study of five *Saccostrea* species from the Pacific Ocean: *S. cucullata*, *S. glomerata*, *S. echinata*, *S. palmula* and *S. mordax*.

Studies including *Saccostrea* species usually refer to reproduction, development, population data and molecular characterization between species (e.g., Klibunga *et al.*, 2002; Kakoi *et al.*, 2008; Green *et al.*, 2009; Parker *et al.*, 2010; Dove & Connor, 2012). Few descriptions of shells and anatomy can be found in the literature (e.g., Awati & Rai, 1931; Rao, 1987).

Because of shell plasticity, the taxonomy of *Saccostrea* has become a troublesome matter; e.g., some "forms" of *S. cucullata* have been attributed to different names by different authors, such as *S. echinata*, *S. mordax*, *S. glomerata* (Lam & Morton, 2004). Molecular studies (e.g., Lam & Morton, 2004, 2006, 2009; Wuang & Guo, 2008a, 2008b) have been conducted as an attempt to resolve this taxonomic confusion and better understanding the genus' distribution, as it apparently occurs in several places along the Pacific Ocean. Reports on the difficulty in identifying the

species, because of the wide variation in body size and coloration are found in literature, which establish a very confusing scenario (Awati & Rai, 1931). This problem is further confirmed by Lam & Morton (2006): "The geographical distribution of lineages of *Saccostrea* is somewhat uncertain because of taxonomic confusion".

As an example of this confusing setup, *S. comercialis* (Iredale & Roughley, 1933) and *S. mordax* (Gould, 1850) have been considered subspecies of *S. cucullata*, because the two of them have similar shells (Stenzel, 1971). Thomson (1954: 175, pls. 7.1-7.2) illustrated *Crassostrea* (*Saxostrea*) *amara* (Iredale, 1939) from Australia, but it seems to be *S. mordax* from Hong Kong. Lamprell & Healy (1998: 134, Fig. 336) Yoosukh & Duangdee (1999: 336, fig. 6) and Slack-Smith (2000: 271, fig 6.15E) show similarities in the shell characters according to the graphics of Torigoe (1981: 380-381, plate 17) and Qi & Choe's (2000: 137, fig. 3C-E) for *S. mordax* (Lam & Morton, 2006). Bernard *et al.* (1993) consider the last eleven nominal species described from China to be synonyms of *S. cucullata*.

The dorsal extreme extenuation of form 'cornucopia' (typical of the genus), is found in several species of *Saccostrea*, definitely in *S. cucullata* (East African and East Indian Ocean) and *S. schyphophilla* (India, Australia and Japan), but is not seen in *S. kegaki*, *S. echinata*, *S. circumscuta*, *S. spathulata*, *S. malabonensis* or the Panamanian *S. tubulifera* and *S. palmula* (Huber, 2010).

S. glomerata is a valid, genetically isolated species, restricted to southeastern Australia and New Zealand, but may have established itself elsewhere. *S. comercialis* is not distinguishable morphologically and genetically from *S. glomerata* (Huber, 2010). Anderson & Adlard (1994) obtained the ITS1 sequence of *S. comercialis* from Sydney, Australia, and *S. glomerata* from New Zealand, showing that they are synonyms.

Molecular systematic studies of *Saccostrea* are few, and mostly restrained by the many issues regarding the genus' taxonomy (Lam & Morton, 2006). Moreover, it has been reported to display ecomorphological variation (Tack *et al.*, 1992). All oysters of the genus *Saccostrea* in Thailand were previously assumed to be only *S. cucullata* (Visoothiviseth *et al.*, 1998). The results of Klibunga *et al.* (2005) indicated that more than one species of *Saccostrea* may be present in Thai waters, which may result in problems regarding its commercial use.

MATERIALS AND METHODS

A list of the material examined is shown after each species description. The material was fixed in 70-99% ethanol. The specimens were immersed in preservative and dissected by standard techniques under a stereomicroscope (Simone, 1997, 2009, 2011). Details of all systems (mantle cavity, mantle edge, muscles, digestive, circulatory, excretory and nervous systems) and organs were investigated. The drawings were obtained with the aid of a camera lucida.

The studied samples are held at several institutional collections: Smithsonian Institute National Museum of Natural History (NMNH), Florida Museum of Natural History (USMN), Field Museum of Natural History (FMNH) and Museu de Zoologia da Universidade de São Paulo (MZUSP).

The following abbreviations are used in the figures: accessory heart (**ah**), adductor muscle (**am**), anus (**an**), auricles (**au**), chomata (**ch**), dorsal hood (**dh**), esophagus (**oe**), external fold (**ef**), gastric shield (**gs**), gills (**gi**), heart (**he**), hood (**ho**), inner fold (**if**), intestine (**in**), mantle edge (**me**), middle fold (**mf**), muscle scar (**im**), pallial muscles (**pm**), palps (**pa**), Quenstedt muscle (**qm**), rectum (**rt**), selection area

(**sa1**), typhlosole (**ty**), umbonal cavity (**uc**), undulations (**pl**), ventricle (**ve**), visceral ganglia (**vg**), visceral mass (**vm**).

SYSTEMATICS

Genus *Saccostrea* Dolfuss & Dautzenberg, 1920

Type species: *Ostrea saccellus*, Dujardim, 1835 = *O.cucullata*, Born, 1778

Diagnosis. Shell cup-shaped, with marginal denticles, promial chamber on right side.

Distribution. This genus is restricted to tropical and sub-tropical waters from Eastern Atlantic, Indo-West Pacific and Eastern Pacific, while absent in the Western Atlantic; in saline areas (open ocean), but occasionally occurring in mangrove areas. Most species live exposed, fixed on rocks or coral (Harry, 1985).

Saccostrea cucullata (Born, 1778)

Plates 1 – 2: Figs. A – O

Ostrea cuccullata [sic] Born, 1778: 100.

Ostrea cucullata Born, 1780: 114, pl. 6, figs. 11, 12; Dillwyn, 1817: 277; Smith, 1890: 322; Awati & Rai, 1931: 1-107.

Ostrea cornucopiae Gmelin, 1791: 3336; Küster, 1868: 77.

Lopha cornucopiae: Röding, 1798: 169.

Ostrea gibbosa Lamarck, 1819: 209; Hanley, 1856: 301.

Crassostrea cucullata Ranson, 1960: 20.

Saccostrea cucullata: Stenzel, 1971: N1134-N1135, fig. J106; Morris, 1985: 125-128, Pl. 3, figs. E-G; Lam & Morton, 2003: 110-112, pls. 11, 12; Lam & Morton, 2009: 482. fig. 1: 483.

Types: Born's type is located in Naturhistorisches Museum Vienna (Morris, 1985) – no additional data. **Examined:** Syntypes, *Ostrea cornucopiae* – Genève Museum n° 1089141 Lamarck Coll.

Description

Shell

Shell elongated, to 100 mm, generally cup-shaped, with left valve showing deep concavity in ligament region. Right valve (Fig. B) flat or slightly convex; ligament straight, of moderate size and devoid of teeth, characteristic of the subfamily. Umbonal cavity well-developed; Margins of both valves with well-developed angles (Figs. A, C); inner edge of right valve with small elongated denticles along (Fig. B) producing corresponding depressions on left valve. Adductor muscle scar reniform, occupying $\frac{1}{4}$ of total height (Fig. B), striate, color white or grayish. Color of outer surface of valves variable from white to gray, light or dark brown, green or purple. Inner surface of valves white, sometimes with purple stains.

Adductor muscle

Reniform or slightly oval, located in posterior region, occupying $\frac{1}{4}$ of total height (Fig. D, K, L).

Mantle

Mantle lobes thick, with well-defined pallial muscles mainly near adductor muscle, being are more abundant in this place (Figs. D, E). Hood formed by junction of anterior mantle lobes. Hood robust and well-defined, usually free or filled by gonad mass (Figs. D, K).

Mantle edge

Pleated and thick, dark, colored yellow with brown spots, bearing three similar-sized folds. Middle fold and internal fold with finger-like, uniformly-distributed papillae, one or two, short to long (Fig. E).

Gills

Gills occupy 50% of total height. Alimentary chamber of demibranchs moderately thick, ~1/3 of gill fold thickness (Fig. F, L).

Circulatory system

Ventricle large, walls thick, with internal beams crossing each other in various directions; opaque, white colored. Outer part of auricles thin, translucent, trabecular; external portion of auricles bearing small, saculiform structures (Fig. G). Pair of kidneys triangular, tubular; mottled by light brown marks by translucence of visceral mass. Each kidney with direct communication with pericardium and gonad on medial side and laterally communicating by short chamber. Renal opening located on other side of cerebro-visceral connective.

Digestive system

Palps large, $\frac{1}{4}$ of gills size, spatuliform; internal surface with pleats extending transversely to edge (Fig. F). The stomach is located in the globular region of the visceral mass, normally occupying $\frac{1}{4}$ of the animal's total size. Esophagus short, with $\frac{1}{2}$ of palps size, (Fig. M). Selection area of stomach (sa1) short ($\frac{1}{2}$ of palps size) and wide with tiflossoles beginning in posterior region of stomach (Fig. I, M). Intestine from style sac, returning in opposite direction, passing usually behind pericardium; surface, immersed in gonads; narrowest portion of intestine surrounding adductor muscle. Rectum long and thin, contouring adductor muscle almost until canopy-gill junction. Anus sessile, rounded a $\frac{1}{2}$ of adductor muscle, with single fold.

Reproductive system

Gonad formed by two lobes of follicular aspect, occupying $\frac{1}{4}$ of animal size. Dorsally and ventrally spread in left lobe and right lobe; shape indistinct from each other. Two pairs of separate systems of genital channels, as described above (excretory system).

Nervous system

Nervous system similar to other ostreid species, pair of cerebral ganglia in anterior region, near of palps, link at pair of visceral ganglia by connectives; visceral ganglia, occupying $\frac{1}{15}$ of adductor muscle size, with two pairs of branches in anterior region, three in posterior region and one laterally (Figs. J, N).

Distribution and habitat: Indo-West Pacific.

Material examined: CHINA. **Hong Kong.** North Pacific Ocean, USNM 858434, 3 specimens; NEW ZEALAND. South Pacific Ocean, USNM 886486, 5 specimens; THAILAND. **Chantaburi.** Kung Kraben Bay, MZUSP 55270, (L.R.Simone coll. 24/vii/2005), 6 specimens.

***Saccostrea glomerata* (Gould, 1850)**

Plates 3 – 4: Figs. A - L

Ostrea glomerata Gould, 1850: 346; 1852: 462; Sowerby, 1871: sp. 64.

Ostrea attenuata Sowerby, 1871: pl. 21.

Ostrea vitrefacta Sowerby, 1871: sp. 80; Lamy, 1929: 166; Île-Rodriguez, 1938: 289.

Ostrea mordax: Hutton, 1873b: 84 (*non* Gould, 1850).

Lopha glomerata: Finlay, 1928: 268.

Ostrea forskali var. *glomerata*: Lamy, 1929: 158.

Ostrea (Lopha) glomerata: Hiro, 1936: 36; Wada, 1942: 70.

Crassostrea cucullata: Ranson, 1967: 188; Nishimura *et al.*, 1998: 85 (*non* Born, 1778).

Saccostrea glomerata: Torigoe, 1981: 310, 332; Dinamani, 1991a: 335; Xu, 1997: 94.

Saccostrea cucullata: Oliver, 1992: 88; Nishimura *et al.* 1998: 86, 88 (*non* Born, 1778).

Types: Holotype USNM 5960 (examined); Paratypes USMN 612314, MCZC 178590, 178591.

Distinctive description

Shell

Rounded, to 50 mm; left valve concave, slightly larger than right valve, lacking well-developed umbonal cavity (Fig. A). Right valve slightly convex; ligament short with mild bulging in central region (Fig. B); margins of both valves with well-developed angles (Figs. A, B); color internally dark brown at edges, fading toward shell's median region. Right valve showing rounded denticles spread along entire edge, arranged in single row (Fig. B), with corresponding depressions on left valve. Adductor muscle scar reniform, occupying 1/5 of total height, located in median region, with

anterior portion normally pigmented gray/brown and posterior portion with pigmented lines; surface slightly pearlescent, white-colored; Quenstedt muscle scar roundish, occupying 1/20 of total size of adductor muscle scar, located in anterior-ventral region of valves (Fig. B).

Muscles

Adductor muscle reniform, occupying 1/3 of total height, with a convexity in posterior region (Fig. C, I).

Mantle

Mantle lobes slightly thick, with well-defined pallial muscles, mainly more abundant near adductor muscle (Fig. C, D).

Mantle edge thick, reddish; middle fold with 3-4 short to long, elongated papillae; internal fold with short, elongated to medium papillae, presenting 2-3 medium papillae for each short one (Fig. D).

Gills

Gills occupying 1/2 total body size. Alimentary channel narrow, ~1/5 as thick as gill fold (Fig. C).

Heart

Heart strong, ventricle relatively large with internal bundles crossing each other in different directions; color light beige. Auricles thin, with more abundant bundles, same texture and coloration, but more elongated than ventricle (Fig. E).

Digestive system.

Palps occupying $\sim 1/5$ of visceral mass, spatuliform, rounded; internal surface with plicae extending transversely to edge (Figs. H, J). Esophagus long and narrow; length $\sim 1/2$ palp length (Figs. G, K). Selection area (sa1) long and thin, with tiflossoles beginning in posterior region of stomach (Figs. G, K). Intestine passing behind pericardium, with narrowest portion surrounding adductor muscle. Rectum slightly long and thin, contouring adductor muscle at medial region of dorsal portion; anus with single fold (Fig. I).

Nervous system

Two pairs of branches in the anterior region and three in posterior region (Fig. L).

Distribution and habitat: India to Australia and New Zealand.

Material examined: FIJI. Nanuya-Lailai Island, Yasawa Group T. Moala. MZUSP

71454; 2 specimens.

***Saccostrea echinata* (Quoy & Gaimard, 1835)**

Plates 5 – 6: Figs. A – O

Ostrea mytiloides Lamarck, 1819: 207; Deshayes, 1836: 227; Hanley, 1856: 300;
Hidalgo, 1905: 387; Lamy, 1924: 155, 1929: 138 (*non* Gmelin, 1791).

Ostrea echinata Quoy & Gaimard, 1835: 455; Hanley, 1856: 302; Küster, 1858: 76;
Hidalgo, 1905: 387; Chen *et al.* 1980: 174.

Ostrea arakanensis Sowerby, 1871: sp. 83.

Ostrea nigromarginata Sowerby, 1871: sp. 85; Lamy, 1928: 140.

Ostrea cucullata: Pilsbry, 1895: 146 (*non* Born, 1778).

Crassostrea echinata: Thompson, 1954: 152; Carreon, 1969: 113.

Saxostrea mytiloides [sic]: Habe & Kosuge, 1966: 145 (*non* Gmelin).

Saccostrea echinata: Stenzel, 1971: N962; Torigoe & Inaba, 1981: 126; Torigoe, 1981:
308, 330; Li & Qi, 1994: 171; Hayami, 2000: 927.

Saccostrea cucullata: Morris, 1985: 125; Harry, 1985: 150; Oliver, 1992: 88, 91; Xu,
1997: 95 (*non* Born, 1778).

Types: Holotype in MNHN; examined.

Distinctive description

Shell

Elongated, ~ 60 mm, with slight ripples in margin of valves extending toward central region (Figs. A – C); left valve slightly larger than right valve, with deep umbonal cavity, lacking any major projections (Fig. B); internal color white/cream to

gray. Adductor muscle scar elongate-reniform, occupying $\sim \frac{1}{4}$ of total height, non-pigmented (Fig. C). Denticles present across edge of right valve (Fig. C), with corresponding depressions on left valve (Fig. B), distributed in various lines along posterior region, being elongated, rounded or both.

Muscles

Reniform, occupying $\sim \frac{1}{4}$ of total height, with a convexity in posterior region (Fig. D, J).

Mantle

Mantle edges delicate, with well-defined pallial muscles in all mantle surfaces. Hood filled with gonads (Figs. D, F, J).

Mantle edge

Mantle edge thick, with yellow and/or brown pigmentation. Papillae of middle fold alternately long and short; usually with a long papilla for each three short ones. Accessory heart with only one branch on both lobes, thin and translucent; both lobes not reaching the adductor muscle (Fig. F).

Gills

Gills occupying $\frac{1}{2}$ of total height. Alimentary chamber thick, $\sim \frac{1}{2}$ as thick as gill fold (Fig. F, J).

Circulatory system

Ventricle thin, usually translucent, auricles elongated, less cross-linked, non-pigmented (Figs. H, N).

Digestive system

Palps small, ~ ¼ of adductor muscle size, curved, sickle-shaped, with folds along anterior margin. External palps fused in middle region and overlying internal palps (Figs. E, K). Esophagus long (~1/3 of adductor muscle) and thin. Selection area of stomach (sa1) short (~ ½ of esophagus size) and wide, with tiflossoles (ty) beginning in posterior region of stomach (Fig. M). Intestine passing behind pericardium; narrowest portion circling adductor muscle. Rectum long and thin, contouring adductor muscle. Anus papillae shaped similarly to shell (Fig. J, I, L).

Nervous system

With three branches in anterior region and only one in posterior region (Figs. G, O).

Distribution and habitat: E. Africa to Japan.

Material examined: MARIANA IS. Guam UF 284793; 3 specimens.

***Saccostrea palmula* (Carpenter, 1857)**

Plates 7 – 8: Figs. A – K

Ostrea palmula Carpenter, 1857b: 163, 550; 1864: 538; Dall, 1914: 2; Lamy, 1929: 150; Keen, 1971: 84; Abbott, 1974: 456.

Ostrea plumula [sic] Carpenter, 1857b: 351, 353.

Ostrea amara Carpenter 1864a: 363; 1864: 541, 552, 621, 666; Lamy, 1930: 242.

Ostrea frons: Carpenter, 1864: 520 (*non* Linnaeus, 1758).

Ostrea mexicana Sowerby, 1871: sp. 35.

Ostrea cumingiana var. *Mexicana*: Dall, 1914: 2.

Ostrea conchaphila (pars): Abbott, 1974: 456 (*non* Carpenter, 1857).

Saccostrea palmula: Harry, 1985: 138.

Crassostrea palmula: Rodríguez & García-Cubas, 1986: 269.

Types: BMNH Syntypes n° 1857.6. 4.735, 1857.6. 4.736, 1857.6. 4.737; examined.

Description

Shell

Shell rounded with ~ 60 mm. Left valve larger than right valve, with small umbonal cavity and slight projection in ligament region; projections and evident ripples present along margin (Figs. A, B). Right valve smaller than left valve, opercular, following pattern of expansion of left valve (Fig. B). Color white/cream with purple spots on outer surface. Inner surface white, slightly nacreous; purple spots and lines sometimes present on inner surface. Adductor muscle scar well-defined, showing purple concentric lines in antero-ventral portion of valves, reniform (Figs. B, C) occupying 1/5 of total height.

Denticles rounded in anterior region, aligned uniformly distributed; corresponding depressions on right valve shallow, almost inconspicuous (Fig. B).

Muscles

Same morphology as other species, reniform (Figs. D, E, H), occupying ~ 1/5 of total height.

Mantle

Mantle lobes thin, with well-defined pallial muscles in posterior region (Fig. D, H); hood absent. Mantle edge thinner; color beige to cream. Papillae of middle fold small, finger-like, elongated, with medium to long length; two to five smaller papillae for each two larger ones (Fig. E). Accessory heart with three well-defined branches, reaching and circling adductor muscle in ventral region (Fig. E).

Gills

Gills occupying ~ 1/3 of total body size. Alimentary chamber narrow (Fig. F).

Heart

Ventricle elongated, slightly thick, reticulated and whitish. Auricles thin, small and non-pigmented (Fig. D, H).

Digestive system

Palps large, occupying ½ of adductor muscle size, thin, with folds on upper margin (Fig. F, I).

Nervous system

Visceral ganglia with two anterior expansions, two lateral and tree posterior (Figs. G, K).

Distribution and habitat: Mexico to Peru.

Material examined: PANAMA. **Miraflores Lock.** USNM 734199 2 specimens.

Arraijan. FMNH 27226 2 specimens.

***Saccostrea mordax* Gould, 1850**

Plates 9 – 10: Figs A – K

Ostrea mordax Gould, 1850: 346; 1852: 464; 1856: pl. 43; Sowerby, 1871: sp. 31;

Saville-Kent, 1891: 2; 1892: 65, 245; Hutton, 1937b: 84; Hirase & Taki, 1951: pl. 7.

Ostrea cornucopiae Saville-Kent, 1891: 3 (*non* Gmelin, 1791).

Ostrea mordax var. *cornucopiaeformis* Saville-Kent, 1893: 248.

Ostrea cucullata: Iwakawa, 1915: 15; 1919: 254; Hatai, 1941: 58; Wells & Bryce, 1988: 162.

Ostrea forskali var. *sueli*: Lamy, 1925: 192.

Ostrea (Lopha) cucullata: Kuroda, 1928: sp. 36; Hirase, 1930: 25; 1934: 5; Takatsuki, 1949: 5 (*non* Born, 1778).

Ostrea forskali var. *mordax*: Lamy, 1929: 158.

Ostrea (Lopha) mordax: Kuroda, 1930: 51; Tchang & Lo, 1956: 74.

Saxostrea amasa Iredale, 1939: 399; Allan, 1959: 273.

Ostrea glomerata: Blanco *et al.*, 1951: 52 (*non* Gould, 1850).

Crassostrea amasa: Thompson, 1954: 154; Carreon, 1969: 111.

Saxostrea mordax: Habe, 1951: 94; Kira, 1959: 127; 1962: 144; Taki, 1960: 192; Habe & Kosuge, 1966: 145; 1967: 137.

Saccostrea mordax: Habe & Okutani, 1975: 194; Habe, 1977: 109; 1981: 83; Torigoe, 1981: 306, 328; Okutani & Soyama, 1987: 152; Habe & Matsuda, 1990: 98; Xu, 1997: 95; Hayami, 2000: 925.

Saccostrea cucullata: Morris, 1985: 125; Li & Qi, 1994: 170; Lamprell & Healy, 1998: 134 (*non* Born, 1778).

Types: Syntype, NMNH 5958, examined.

Description

Shell

Shell elongated, ~ 40 mm, with undulations from entire edge of both valves up to ligamentary region (Fig. A). Left valve concave, umbonal cavity well-developed, with extensive anterior projection (Fig. C). Right valve flat or slightly convex, not opercular (Fig. B). Color beige/cream, with edges of valves dark purple. Denticles present in entire edges; rounded, relatively large and distributed in single row (Fig. B). Adductor muscle scar oval, colored grayish or non-pigmented (Fig. B).

Mantle

Mantle thick; pallial muscles more evident in adductor muscle region. Hood present, robust, filled by gonads and palps (Fig. D).

Mantle edge thin, color dark brown and yellow; middle fold with small and medium digitiform papillae; 2-4 smaller for each larger one. Internal fold with small, uniformly-distributed digitiform papillae. Accessory heart inverse T-shaped, well-marked and surrounding ventral region of adductor muscle (Fig. E, I).

Gills

Gills occupying ~ ½ of total size. Alimentary chamber narrow (Figs. F, I).

Circulatory system

Ventricle large, ~2/3 as large as auricles, with slight bundles more concentrated in posterior region; color whitish. Auricles translucent and elongated (Fig. G).

Digestive system

Palps large and thick, ~ ½ of adductor muscle size, superior edge with folds; external palps covers ~1/3 of internal palps (Figs. F, I). Esophagus long, two times more long than palps. Selection area of stomach 1 (sa1) long and narrow, ½ of esophagus height, typhlosole in terminal region of globular portion (Fig. J).

Nervous system

Visceral ganglia with tree nerves in anterior and posterior region and one laterally (Figs. H, K).

Distribution and habitat: Indo-West Pacific.

Material examined: CHINA. **Taiwan.** Taipei Co., Wanli, Yehliu., UF 303012, 3 specimens.

Discussion

Among the species studied here, the only one with a completely described anatomy is *S. cucullata*, by Awati & Rai (1931). The anatomy of the remaining species is mostly unknown, except for the shell (e.g., Lam & Morton, 2004, 2009). For a characterization of genus *Saccostrea* the comparison was taken with genus *Crassostrea* and others ostreids.

Shell

The shell of genus *Saccostrea* differs of genus *Crassostrea* basically for a presence of chomata and some species, the ornamentation of edge shells. Both genus have a medium a large shells, and occurs in same habitat, but *Saccostrea* are found only in Pacific and Indian Ocean. Between *Saccostrea* species, the taxonomy only for the shells characters is problematic, and this paper, show some anatomic differences to help a identification of species.

The shells of *Saccostrea cucullata* (Fig. xx) are elongated, normally cup-shaped, with a deeply concave left valve showing an expansion in the ligament area. The right valve is flat or slightly convex, like a lid. The umbonal cavity is well-defined, the edges of both valves are plicate, with folds laminated in defined angles. Small tubercles (elongated denticles) are present along the inner edge of the right valve (Fig. XX), with corresponding depressions on the left valve. The adductor muscle scar is reniform, striated, white or grayish, while the external surface of valves is variable in color, from pale white, light gray to dark brown, green or purple. The internal surface is white, and may present purple spots. These characteristics fittingly with those presented by Awati & Rai (1931).

The shell of *Saccostrea echinata* is more elongated, with slight undulations along the edge of the valves that stretch toward the central area. Its left valve is slightly larger, with an evident umbonal cavity lacking projections in the ligamentary area. It is colored white/cream to grayish. The adductor muscle scar is also reniform but more elongated and unpigmented. Denticles are present along the right valve's edge, with corresponding depressions on the left valve. These denticles are distributed in multiple lines in the posterior region, and may have an elongated or rounded contour.

The shell of *Saccostrea palmula* is rounded, with both valves laterally expanded; the left valve is larger than the right, with a small umbonal cavity and a light expansion in the ligamentary region; projections and undulations are evident along the edge; the right valve is small, opercular, following the pattern of expansions of the left valve. It is colored white/cream with purple spots externally. The internal surface is white and slightly nacreous; there may be purple spots in the region corresponding to the mantle edge in both valves. Differing from the above-mentioned species, the adductor muscle scar is defined by concentric purple lines in the antero-ventral portion of the valves, but it is also reniform. Both valves show more rounded denticles on the edge than those of *S. cucullata*, which are restricted to the anterior region, aligned and uniformly distributed; the corresponding depressions on the right valve are somewhat shallow.

Saccostrea mordax has a usually elongated shell, with undulations going from the margins to the ligamentary region; the left valve is concave, with a deep umbonal cavity and an extensive anterior projection of the ligamentary region; the right valve is almost flat or slightly convex, but it is not opercular as in the remaining species, and both valves have similar width. The color is cream in the centre, with dark purple colored in the margins. Both valves have denticles along their margins; they are rounded, relatively large and distributed in a single row. The adductor muscle scar is oval and

grayish, with concentric lines that may be pigmented. These characteristics fit with those described by Lam & Morton (2009).

The undulations of edge shells are characteristic in *Saccostrea*, and this character differs of genus *Crassostrea*, when present show this undulation only in posterior region and in follicular layers have this ornamentation.

All species of *Saccostrea* exhibit a slight Quenstedt muscle scar, a rounded mark located in the antero-ventral region of the valves.

Muscles

The adductor muscle (and scar) of Crassostreinae in general, not differs between genus, but have variations in species. This variation has been pointed out in the literature (Nascimento, 1991 for *C. rhizophorae*; Galtsoff, 1964 and Kennedy et al., 1996 for *C. virginica*), and possibly is associated with the high level of shell plasticity.

S. cucullata shows a normally reniform adductor muscle, which is sometimes oval, while *S. palmula* has a strictly reniform muscle. *S. echinata* also has a reniform adductor muscle, but with a convexity toward the posterior region (that of *S. cucullata* is anterior). *S. mordax* has an oval adductor muscle.

The pair of Quenstedt muscles has no differentiation regarding the origin on the shell and the insertion in the base of the palps in the five species,

Mantle

The mantle lobes in *S. cucullata* are thick, with well-defined pallial muscles, mainly around the adductor muscle. In *S. echinata* the mantle lobes are thin, with well-defined pallial muscles along the mantle's extension. *S. palmula* has a thick mantle with pallial muscles more evident around the adductor muscle.

S. cucullata has a robust, well-defined hood, normally free or filled by gonads. *S. echinata* has a smaller hood than *S. cucullata*. In *S. palmula* the hood is not present. *S. mordax* has a well-defined hood, filled by gonads and palps. In *S. glomerata* the mantle is slightly thick, with pallial muscles more evident in the adductor muscle region; the hood is absent.

The pallial muscles have some differences between species, in quantity, narrow and distributions. This data, corroborating with Amaral & Simone (2014), when the Quenstedt muscles in the *Crassostrea* species are not difficult to find, differently from what has been postulated in the literature (Galtsoff, 1964; Stenzel, 1971; Mesquita, 1993). From their origin on the shell, the muscles run through the anterior visceral mass up to the insertion in the base of the palps. This peculiar morphological arrangement shows improbable a homology with the anterior adductor muscle or any foot muscles (suggested by Galtsoff, 1964; Stenzel, 1971). They may retract the gills and the palps, helping in transferring particles to the mouth.

Mantle edge

S. cucullata has a thick edge, colored dark yellow with brown spots. The three folds have similar size. The middle and inner folds also have finger-like papillae, one or two short for each long one. *S. echinata* has a thick edge, colored yellow and/or brown; the papillae of the middle fold are alternately long and short, being three short for each long one. *S. palmula* has a thin edge, colored beige/cream; the finger-like papillae of the middle fold are small, elongated, alternately short and medium/long, usually two to five small papillae for each one or two long/medium ones. *S. mordax*, has a thin edge, colored dark brown and/or yellow; the middle fold bears medium and short finger-like papillae, at a ratio of two to four short papillae for each medium one; the internal fold

bears small, uniformly distributed finger-like papillae. *S. glomerata* has a thick mantle edge with reddish color; the middle fold has both short and long papillae, at a ratio of three to four short for each long one; the inner fold has short and medium papillae, usually two or three medium for each short one. This variation was found in Amaral & Simone (2014) for *Crassostrea* species, and here remained.

The accessory heart in *S. cucullata* has three well-defined branches in the right lobe, forming a short y-shaped structure, while the left lobe shows only a single large branch. In *S. echinata* the accessory heart is slim, translucent, with thin walls, not reaching the adductor muscle in both lobes. In *S. palmula* it has tree branches that contour the adductor muscle. *S. mordax* has a different arrangement, forming a well-defined inverted T-shaped structure, and contouring the adductor muscle in the ventral region. *S. glomerata* has three branches in both lobes, forming a thick y-shaped structure, and one branch, about 1/3 thinner, which contours the adductor muscle.

Differently, *Crassostrea* genus has a tree branches in all species studied in Amaral & Simone (2014). This characteristic can be used for a differentiation for this genus.

Mantle Cavity

The promial passage is present in all *Saccostrea*. This is a characteristic of subfamily Crassostreinae. The promial passage has a variation in the size; in *Crassostrea* show in both sides a long chamber, the margin of the visceral mass to the base of the gills and in *Saccostrea*, the passage in the left lobe is open to half of the visceral mass.

Gills

The number of gill folds and filaments is a variable character, apparently increasing proportionally to the animal's size.

However, the numbers can be discrepant between individuals of similar size. Ridewood (1903) mentioned 9–12 filaments per fold in *O. edulis*, while Atkins (1937a) mentioned 8–17. Atkins (1937a) mentioned 8–17 in *C. virginica*; Nelson (1938) mentioned 8–15. Galtsoff (1964) mentioned 10–16 filaments per fold in *C. angulata*, while Atkins (1937a) referred to 15–16 and Nelson (1938) 8–14 filaments per fold. In Amaral & Simone (2014) was verified that the number of filaments per fold in *C. rhizophorae*, *C. mangle*, *C. brasiliiana* and *C. virginica* varies from 12 to 13, reaching 15 in *C. gigas*. Based on the proximity of the numbers, this parameter seems to be of little use in distinguishing the examined species. In all species of *Saccostrea* the variation is a 12-14 filaments per fold.

The gill of all species in this occupies about $\frac{1}{2}$ of the pallial cavity. *S. cucullata* has a medium-sized alimentary chamber, approximately $\frac{1}{3}$ as thick as the gill fold; *S. echinata* has a thick chamber, about $\frac{1}{2}$ as thick as the fold; *S. palmula*, *S. mordax* and *S. glomerata* have a narrow alimentary chamber, about $\frac{1}{5}$ as thick as the gill fold.

Visceral mass

The visceral mass extends from the ventral region of the ligament to the anterior surface of the adductor muscle. It is formed by normally yellowish-colored gonads, with abundant digestive diverticula and renopericardial structures, and occupies nearly $\frac{1}{4}$ of the total body size in all species.

Circulatory system

S. cucullata has a slightly large ventricle with thick walls, colored by opaque white; the auricles are thin-walled and translucent, and bear external saculiform structures. *S. echinata* has a thin ventricle, normally translucent, and two non-pigmented auricles, both more elongated than in *S. cucullata*. The ventricle is elongated in *S. palmula*, slightly thick and whitish; the auricles are small and non-pigmented. *S. mordax* has a large ventricle, about 2/3 the size of the auricles, with whitish coloration; the auricles are translucent and elongated. *S. glomerata* has a robust heart, with relatively large ventricle, colored light cream; the auricles are elongated, robust and have the color as the ventricle. The size and coloration of all Crassostreinae is variable into the species, and each has a pattern.

Digestive system

Palps

The palps of *S. cucullata* are large, spatuliform, having a folded anterior edge and a slightly arched ventral region. The palps of *S. echinata* are small, arched, sickle-shaped, with folds along the anterior margin. The external palps are fused in the middle, overlying the inner palps. In *S. palmula* the palps are larger than the remaining species, thin, with a superior margin bearing folds. *S. mordax* has large and thick palps, with folds in superior margin, as is the case in *S. echinata*, and the external palps overlie the inner palps for about 1/3 of their length.

Esophagus

The esophagus is dorsoventrally compressed in all species; in *S. cucullata* it is short and large, 1/2 of palps in size; in *S. echinata* it is long and thin, ~1/3 longer than palps length; in *S. palmula* it is elongated and thin, occupying 2/3 of palps size; in *S.*

mordax it is large and long, occupying the same size of palps; in *S. glomerata* it is long and narrow, $\sim\frac{1}{2}$ of palps size.

Stomach

Internally, the species normally differ in the selection area 1 (sa1), typhlosoles, gastric shield and dorsal hood. The sa1 in *S. cucullata* is short and large, with the typhlosole beginning in the posterior region of the stomach; *S. echinata* has a longer sa1, and the typhlosole begins more posteriorly than in *S. cucullata*. In *S. palmula* the sa1 is short and narrow, with typhlosole beginning laterally. The sa1 in *S. mordax* is long and narrow and the typhlosole is located more posteriorly than in *S. cucullata*.

Such an organ has been described as bagshaped, internally divided into a smaller anterior chamber and other larger posterior chamber, by means of a thick fold; such a fold is projected to the organ's lumen and seems to serve as a means to direct particles to the posterior region through a narrow channel (Shaw & Battle, 1957).

The dorsal hood length is nearly $\frac{1}{2}$ of the length of sa1 in *S. cucullata*. In *S. mordax*, the dorsal hood has about the same length as sa1. In *S. echinata* and *S. palmula* the dorsal hood is short and narrow, about $\frac{1}{2}$ the size of the others species.

All such stomach characters are similar to those of *O. edulis* (Yonge, 1926; Graham, 1949; Purchon, 1957; Reid, 1965), *C. parasitica* (Shaw & Battle, 1957) and *O. chilensis* (Purchon, 1957). Other details of the morphology and physiology of the ostreid digestive tract, such as ciliary mechanisms and stomach structure and operation, can be found in the literature (Shaw & Battle, 1957; Nelson, 1960; Reid, 1965; Yonge, 1966).

Intestine, rectum and anus

The intestine, before the style sac, passes behind the pericardium, immersed in the gonads in visceral mass. In *S. cucullata*, *S. echinata*, *S. mordax* and *S. glomerata* the intestine passes behind the pericardium; in *S. palmula*, behind the esophagus. The rectum of *S. cucullata* is long and thin, surrounding the adductor muscle in 2/3 of its concave region, with the anus bearing a single fold. *S. echinata* has a larger elongated rectum, with anus expansion in shell form; *S. palmula* is short and large, with anus ending with fold in bell shaped. *S. mordax* has a short and large rectum, and the anus bears a single fold.

Gonads

The gonads of all species are massive, apparently regardless of the gonadal maturation period, and surround the whole visceral mass, in some cases surrounding the region near the pyloric process. They are usually coloured beige or yellowish. The genital opening has been observed in *S. cucullata* in the kidney, and distinguishes itself from the opening by a brownish spot.

Nervous system

The nervous system is relatively simple, showing a pair of cerebral ganglia and a pair of visceral ganglia connected by commissures. The cerebral ganglia are somewhat inconspicuous because of their very small size and localization in the visceral mass. The visceral ganglia can be easily distinguished in the anterolateral region of the adductor muscle. *S. cucullata* and *S. glomerata* have two pairs of nerves in the anterior region and three in the posterior region; *S. echinata* presents two pairs in the anterior and posterior regions; *S. mordax* and *S. palmula* have three pairs in the anterior and posterior regions.

Legends

Plate 1. *Saccostrea cucullata*. Fig. A – General right view; Fig. B –Right valve, internal view; Fig. C – Ventral whole view; Fig. D – Whole soft parts, general view; Fig. E – Extracted mantle lobe and mantle edge and accessory heart; Fig. F – Palps, right-slightly ventral view, outer right hemipalp deplected; Fig. G – Heart isolated, showing a ventricle and auricles; Fig. H – Anus and rectum; Fig. I – Anterior region, right view, with exposure of digestive system; Fig. J – Visceral ganglia, ventral view, adjacent layer of tissues also shown. Scales 1 cm.

Plate 2 – *Saccostrea cucullata* anatomical features. Fig. K – General view of soft parts; Fig. L – general view, right mantle lobe removed; Fig. M – Stomach, right view, opened longitudinally; Fig. N – Visceral ganglia, ventral view. Fig. O – Detail for anus. Scales 1 cm.

Plate 3. *Saccostrea glomerata*. Fig. A – General right view; Fig. B – Right valve, internal view; Fig. C – General view of soft parts right view, right mantle lobe removed; Fig. D – Mantle lobe and edge; Fig. E – Heart, ventral view; Fig. F – Anterior region; Fig. G – Anterior region, right view, with Stomach opened longitudinally; Fig. H – Palps, right-slightly ventral view. Scales 1 cm.

Plate 4. *Saccostrea glomerata*. Fig. I – General right view of soft parts; Fig. J – Detail for a palps; Fig. K – Stomach opened longitudinally, right view; Fig. L – Visceral ganglia. Scales 1 cm.

Plate 5. *Saccoostrea echinata*. Fig. A – External view; Fig. B – Internal view, left valve; Fig. C – Internal view right valve; Fig. D – General view of soft part; Fig. E – Anterior region; Fig. F – Mantle edge, detail for a pallial muscles and accessory heart; Fig. G – Visceral ganglia; Fig. H – Heart, and rectum; Fig. I – Anus with expansion and rectum. Scales 1 cm.

Plate 6. *Saccoostrea echinata*. Fig. J – General view of soft part; Fig. K – Palps, detail for the median fusion of external hemipalps; Fig. L – Anus and rectum, detail for a expansion in anus; Fig. M – Stomach, right view; Fig. N – Heart in pericardium. Scales 1 cm.

Plate 7. *Saccoostrea palmula*. Fig. A – External view; Fig. B – Internal view of left valve; Fig. C – Internal view of right valve; Fig. D – General view of soft parts; Fig. E – Posterior region, detail for a gills, mantle edge, accessory heart and adductor muscle; Fig. F – Detail for the palps; Fig. G – Visceral ganglia. Scales 1 cm.

Plate 8. *Saccoostrea palmula*. Fig. H – General view of soft part; Fig. I – Detail for the palps; Fig. J – Stomach, right view; Fig. K – Visceral ganglia. Scales 1 cm.

Plate 9. *Saccoostrea mordax*. Fig. A – External view; Fig. B – Internal view of right valve; Fig. C – Internal view of left valve, detail for a undulations of the edge valves and umbonal cavity; Fig D – General view of soft part; Fig. E – Mantle edge, detail for a accessory heart and pallial muscles; Fig. F – Detail of the palps and gills; Fig. G – Heart; Fig. H – Visceral ganglia. Scales 1 cm.

Plate 10. *Saccoostrea mordax*. Fig. I – General view of soft parts; Fig. J – Stomach, right view; Fig. K – Visceral ganglia. Scales 1 cm.

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ANEXO III – Only descriptions of relationated taxon in: Simone et.al., subimitt - Comparative anatomy of selected marine bivalves from the florida keys, with notes on brazilian congeners (Mollusca: Bivalvia)

Family Gryphaeidae

***Parahyotissa mcgintyi* (Harry, 1985)**

Figs. 83–94

Synonymy

Le Bajet – Adanson, 1757: pl. 14, fig. 4. See also Fischer-Piette (1942: 295, pl. 12, fig. 2).

Mytilus roseus Gmelin, 1791: 3362 (based on Adanson's Le Bajet; see above). A forgotten name reinstated by Huber (2010: 616) under violation of Art. 23.9 and 23.11 of the ICZN (1999) Code. Prevailing usage of *Hyotissa mcgintyi* is here maintained; see Remarks.

Ostrea (Ostrea) thomasi McLean, 1941: 7, pl. 3, figs. 1–2, pl. 4, figs. 1–2 [Type locality: off Palm Beach, Florida] (non *Ostrea sellaeformis* var. *thomasi* “Conrad” Glenn, 1904).

Pycnodonte (Hyotissa) hyotis – Abbott, 1974: 457 [non *Mytilus hyotis* Linnaeus, 1758; see below].

Parahyotissa (Parahyotissa) mcgintyi Harry, 1985: 130 [replacement name for *O. thomasi* McLean, 1941, non Glenn, 1904].

Pycnodonte hiotis [sic] – Rios, 2009: 498, fig.

Parahyotissa macgintyi [sic] – Ardovini & Cossignani, 2004: 49.

Hyotissa mcgintyi – Kirkendale et al., 2004: 309 ff., fig. 2 [first record in the Florida Keys]; Bieler et al., 2004: 150–151, figs 1–2; Bieler & Mikkelsen, 2004: 513; Mikkelsen & Bieler, 2007: 114–117, 5 figs.

Parahyotissa rosea – Huber, 2010: 615.

Description:

Shell (Figs. 83–85) rounded or D-shaped, reddish, thick; maximum SD $\approx$ 50 mm in material examined. Inner layer with vesicular structure most apparent marginally as foam-like or spongy, especially under magnification. LV cementing to and assuming shape of hard substrata; RV smaller, more planar. Outer surface highly irregular, covered by minute concavities; sometimes radially pleated. Valve margins undulating or irregularly plicated. Hinge plate edentulous; L $\approx$ 60% SD. Vermiculate chomata on shell margin on either side of ligament. Ligament occupying entire dorsal hinge plate, thicker in central third. Inner surface glossy white. Adductor muscle scar rounded, subcentral, slightly posterodorsal; A $\approx$ 7% of inner VA.

Main muscle system (Figs. 85, 88): Anterior adductor and pedal retractor muscles absent. Posterior adductor muscle (*pm*) very large, at approximate midpoint of posterior third of animal, clearly with 2 (“catch” and “quick”) portions of subequal A; anteriorly oval; posteriorly crescent-shaped (with concavity anterior); A $\approx$ 20% VA.

Foot: absent.

Mantle (Figs. 86, 90, 94): Mantle lobes almost totally free except for relatively narrow dorsal region adjacent to hinge area, and another very short area separating incurrent and excurrent apertures, composed of inner fold (Fig. 94: *um*). Outer fold of mantle edge thin, smooth, simple. Periostracum separating outer and middle folds. Middle fold $T \approx 2$ outer fold T , $H \approx$ outer fold H , bearing series of papillae at edge (most of $H \approx 2$ fold base H); each papilla slender, relatively tall, pointed, with interspace = 3 papilla W ; papillar size and interspaces weakly variable. Inner fold L and $T =$ middle fold L and T , bearing series of very small papillae, with interspaces = 3 papilla W . Remaining areas of mantle inner surface almost totally covered by small papillae (Fig. 86), distributed randomly, variable in size, more concentrated in regions preceding edges and anteriorly preceding palps; narrow band lacking papillae at some distance from mantle edge (mostly probably a rejection tract); each papilla with whitish beige base and brown-stained tip. Pallial muscles relatively thick, originating at pallial line in inner edge of above-described smooth area. Pigmented papillae covering most structures of pallial cavity, including suprabranchial chamber, *pm*, and inner (dorsal) surface of gill.

Pallial cavity (Figs. 85, 87–88, 91–92, 94) on left side overlaying most of body surface, except *pm* and narrow visceral region close to hinge area. Visceral mass extending farther dorsally on right side, filling space between *pm* and hinge area. Infrabranchial chamber ventral to *pm* and visceral mass. Single right promyal passage (Fig. 88: *po*) as suprabranchial chamber passing through visceral mass on left, passing anteriorly to *pm*, and on both sides ventral to *pm*, also with region = *pm* L toward posterior. Labial palp (*pp*) $L \approx 14\%$ of gill L , covering anterior end of gill (Fig. 87). Outer hemipalps connected, covering anterior ends of demibranchs, with longer region

at level of inner demibranch. Inner surface of each outer hemipalp with series of arched, uniform, narrow folds, starting between demibranchs, running ventrally, arching medially; before midline, inner folds abruptly ending at same level, with smooth area uniting outer hemipalps in $A = 66\%$ of folded area A. Another narrow smooth area at posterolateral ends of each hemipalp, broadly attaching to mantle at level posterior to anterior end of outer demibranch (*do*); taller region of each outer hemipalp bearing short, projecting, flattened flap. Inner hemipalp $A \approx 66\%$ of outer hemipalp A, along midline from approximately same level of posterior end of outer hemipalp, adjacent only to inner surface of inner demibranch (*di*), posteriorly taller, decreasing gradually anteriorly; inner surface with transverse folds perpendicular to longitudinal body axis, ending ventrally close to ventral edge, with narrow ventral smooth inner edge. Remaining folds similar to those of outer hemipalps; folds ending approximately at same level as those of outer hemipalp, with smooth area preceding mouth. Gill $A \approx 66\%$ of infrabranchial chamber $A \approx$ infrabranchial chamber L. Each demibranch subequal in size (Fig. 85); *di* with anterior end slightly more anterior than that of *do* (Fig. 87). Ventral demibranch edges narrow, each bearing shallow food groove; dorsally wide, with ascending and descending portions well-separated at base. Transverse inner septa (Figs. 88, 91: *gr*) uniting portions of each demibranch, between every 10–15 filaments; septa of all 4 demibranchs aligning transversely (Figs. 92, 94). Each septum connecting entire inner (dorsal) edge of filament, from ventral to dorsal ends, leaving suprabranchial chamber free; septum gradually becoming broader from ventral to dorsal, accompanying gill enlargement. Suprabranchial chamber totally covered by papillae similar to those on inner surfaces of mantle lobes, including surfaces of *pm* and visceral mass, and inner (dorsal) surface of gills and septa. Ctenidial vessels running along central connections between gills, also between connections of demibranchs (Fig.

91: *bv*). Tissue connections between gills along midline and between gills and mantle. Gill filaments connecting to neighboring filaments by transverse, narrow tissue connections. Anterior half of gills connecting to ventral surface of visceral mass; posterior half of gills supported by 3 suspensory stalks (Figs. 94: *do*, *di*), one at center along union between gills, remaining 2 connecting to union of demibranchs of each gill. Origins of all 3 suspensory stalks on anteroventral surface of *pm* (leaving ventral surface free), slightly more posterior toward right. Posterior half of gills connecting via tissue to adjacent mantle along lateral edges, to mantle connection separating incurrent (*si*) and excurrent (*se*) apertures (Fig. 94: *um*).

Visceral mass (Figs. 85, 89, 92–93) filling entire space immediately ventral to umbones and hinge area; becoming narrower and restricted on right side after distance = 14% SH, keeping *po* anterior to *pm*, with space at right = W as suprabranchial chamber (Fig. 85). Stomach (Fig. 89: *st*; 93) filling anterodorsal region, immediately and entirely surrounded by greenish brown digestive diverticula. Gonad surrounding digestive diverticula and filling remaining subumbonal region plus short space in visceral mass at left of suprabranchial chamber, anterior to *pm* (Fig. 92). Pericardium anterodorsal to suprabranchial chamber; $V \approx 12\%$ of visceral mass V.

Circulatory and excretory systems (Fig. 92): Pericardium relatively small, in dorsal region of visceral mass anterior to suprabranchial chamber, anterior to *pm*. Auricles (*au*) lobed, beige, $V \approx 25\%$ of pericardial V; other characters of heart similar to that of *Hyotissa hyotis* (see below). Kidney (*ki*) internally hollow, compressed between remaining visceral mass and anterior surface of *pm*, filling left region adjacent to suprabranchial chamber; *ki* lobe $V < 50\%$ of inner *ki* V, restricted to ventral and left

sides, bearing longitudinal, irregular folds, with dichotomies posteriorly, splaying across *pm* anterior surface.

Digestive system (Figs. 87, 89, 93–94): *Pp* as described above. Mouth (Fig. 87: *mo*) transverse, surrounded only by smooth areas; posterior lip $H \approx 66\%$ of anterior lip H . Esophagus (Fig. 89, 93: *es*) short, broad, in $L = 33\%$ of *pp* L ; inner surface covered by longitudinal, narrow, low folds well-separated. Stomach (Fig. 89: *st*; 93) oval; L and $W \approx 3$ *es* L and W . Dorsal hood (Fig. 89, 93: *dh*) $L \approx 2$ *st* $L \approx 50\%$ of *st* W , originating on anterior-right surface of *st*, just posterior to *es* opening, running left, immersed in visceral glands. Opening of conjoined style sac-intestine (Figs. 89, 93: *ss*, *in*) marked by abrupt constriction of posterior *st*, running posteriorly, weakly curving ventrally; $L = st$ L . Gastric inner surface (Fig. 93) with *es* folds abruptly ending in ventral, tall, broad gastric fold, running left along ventral surface of *dh*, decreasing at distal end of *dh*; also running toward right as pair of parallel folds, initially close, with anterior branch surrounding right gastric inner surface transversely, crossing dorsal surface, ending on opposite (left) side; posterior branch surrounding right edge of gastric shield (*gs*), diminishing into posterior *st*; another gastric fold in $W \approx 50\%$ W of previous fold W , running parallel and just posterior to ventral surface of *dh* main fold, anteriorly surrounding end of anterior branch of main gastric fold, curving perpendicularly posteriorly, running along *ss* as minor typhlosole; major typhlosole originating gradually on left edge of *gs*, running posteriorly next to minor typhlosole. Typhlosoles separating *in* (ventral) from *ss* (dorsal) (Fig. 93). *Gs* on posterior-right inner gastric surface (Fig. 93); $A \approx 16\%$ of inner gastric surface A . Ducts to digestive diverticula (Fig. 93: *dd*) between branches of right region of main gastric fold; *dd* as described above. *In* curving abruptly posterior to *ss* (Fig. 89, 93), running anteriorly close to *ss* to

anterior-right region of *st*, making another ample loop in this region slightly away from gastric outer surface, then running posteriorly, obliquely, and sinuously from right side to closer to midline, at level of *pm*. Anus (Fig. 88: *an*) preceded by long, detached (siphoned) portion of rectum, originating on posterior surface of *pm*, closer to left side; edge bearing few small folds on inner surface.

Reproductive system: Gonad as described above; genital aperture not observed.

Nervous system: not examined.

Material examined: USA, Florida Keys, FMNH 302069, 3 specimens (sta. FK-650; dissected: #1: 69 mm L, 55 mm H, 40 mm W; #2: 50 mm L, 39 mm H, 18 mm W; #3: 26 mm L, 25 mm H, 14 mm W); FMNH 317471, 3 shells (FK-260); FMNH 326538, 5 specimens (sta. FK-908/Bivatol-275); FMNH 333754, 6 specimens (sta. FK-991/Bivatol-450). BRAZIL, Bahia, off Alcobaça, 10–15 m, MZUSP 69725, 1 shell (iv/2002).

Distribution: Stated by Turgeon et al. (2009) to range from North Carolina to Texas, the Gulf of Mexico, Cuba, the tropical western Atlantic and the tropical eastern Pacific. A range to Bahia, Brazil, is here confirmed.

Remarks: Harry (1985) introduced the genus *Parahyotissa* with this species as the type species, distinguished from *Hyotissa* (type species *H. hyotis* – see below) by the promyal passage open only on the right side in *Parahyotissa* (here confirmed), and open on both sides in *Hyotissa*; The subsequent synonymy of *Parahyotissa* with

Hyotissa is based on a molecular phylogeny advocated by Kirkendale *et al.* (2004); the material used in the molecular study is from the the same site ("Thunderbolt" wreck, off Key Vaca) as the material here dissected. See also remarks under *H. hyotis*. No material from Brazil was available for dissection.

Parahyotissa mcgintyi is assumed to have amphiatlantic distribution (e.g., Harry, 1985; Carriker & Gaffney, 1996; Ardovini & Cossignani, 2004); unfortunately no anatomical or molecular data are available for eastern Atlantic specimens. Huber (2010: 614) synonymized this nominal species under *Parahyotissa rosea* (Gmelin, 1791), based on *Mytilus roseus* Gmelin, 1791, described from West Africa (not be confused with *Ostrea rosea* Gmelin, 1791, of the same work). As Huber's action appears to be in violation of ICZN (1999) Articles 23.9 and 23.11 (we have not located any prior post-1899 usage of *Mytilus roseus* as a valid name, whereas the name *P. mcgintyi* has been used frequently enough to fulfill the conditions of Art. 23.9.1.2) we are maintaining prevailing usage herein.

Parahyotissa mcgintyi, anatomy. FIG. I1: Labial palps and adjacent region of gill and mantle, ventral view, hemipalps deflected to show inner surface; FIG. I2: Suprabranchial chamber, lateral to right view, right mantle lobe removed, note promyal passage (po) anterior to adductor muscle (restricted to right side); FIG. I3: Digestive system *in situ*, dorsal view, topologies of some adjacent structures also shown; FIG. I4: Cross section of midportion of mantle lobe, in region close to mantle border; FIG. I5: Cross section through gills in midregion (anterior to adductor muscle); FIG. I6: Posterior region of visceral mass, dorsal view, left region of pericardium, renal membrane, and part of right mantle lobe removed,

showing inner renal structures and part of suprabranchial chamber anterior to adductor muscle; FIG. 17: Stomach, dorsal view, opened longitudinally; FIG. 18: Anal region of mantle cavity, right and slightly posterior view, right mantle lobe partially removed. Scale bars = 2 mm (FIGS. 88–91); 5 mm (FIGS. 92–94). an, anus; au, auricle; bv, “blood” vessel; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; dg, digestive diverticula; dh, dorsal hood; di, inner demibranch; do, outer demibranch; er, esophageal rim; es, esophagus; fg, food grooves; gf, gastric fold; gm, gill retractor muscle; go, gonad; gr, gill transverse septum in suprabranchial chamber; gs, gastric shield; gt, gill suspensory stalk; in, intestine; ip, inner hemipalp; kc, renal chamber; ki, kidney; mi, mantle border inner fold; mm, mantle border middle fold; mo, mouth; mp, mantle papillae; mt, mantle; mu, mantle border outer fold; op, outer hemipalp; pc, pericardium; pe, periostracum; pl, pallial muscles; pm, posterior adductor muscle; po, promyal passage of suprabranchial cavity; pp, labial palp; rt, rectum; sb, suprabranchial chamber; ss, style sac; st, stomach; su, supra-anal chamber of suprabranchial pallial cavity; um, fusion between left and right mantle lobes; vm, visceral mass.

Parahyotissa mcgintyi, shell morphology, FMNH 302069, 69 mm maximum D. FIG. 19: Articulated specimen, ventral view showing zigzag shell margin; FIG. 110: RV, interior view.

***Hyotissa hyotis* (Linnaeus, 1758)**

Figs. 95–104

Synonymy

Mytilus hyotis Linnaeus, 1758: 704 [Type locality: “Pelagi Gorgoniis” = in the Gorgonia corals of the sea].

Hyotissa hyotis – Harry, 1985: 128–131; Sevilla-H. *et al.*, 1998: 25–32, *figs 1–2*; Bieler *et al.*, 2004: 149–159, *figs 3–4*; Mikkelsen & Bieler, 2007: 118, 4 *figs*.

Description:

Morphology similar to that of *Hyotissa mcgintyi*, except as noted here.

Shell (Figs. 95–97) purplish black to magenta to violet-brown, with irregular sculpture of pleated ribs bearing hollow spines; maximum SL $\approx$ 180 mm in material examined. Interior bluish or yellowish white with black or brown stains; valve margins near ligament with both vermiculate and lath chomata.

Main muscle system (Fig. 101): Posterior adductor muscle (*pm*) more posterior, close to posterior mantle edge.

Mantle (Figs. 100–101, 103): Middle and inner folds of mantle edge dark brown, almost black, including connection between lobes (Fig. 100: *um*); separating excurrent (*se*) and incurrent (*si*) apertures. Three mantle border folds of subequal T and H, except for slightly thinner outer fold. Middle fold bearing series of papillae (Fig.

103: *mp*) along edge, most in $L < 50\%$ of remaining region of fold H; with 3 rows of papillae covering distal region of inner surface of fold to edge. Inner fold (Fig. 103: *mi*) bearing series of short, broad, dense papillae. Remaining areas of mantle inner surface lacking papillae, bearing only few bulging hemolymph sinuses in region close to mantle border folds. Promyal passage (Fig. 101: *po*) widely open on right side, narrow on left.

Pallial cavity (Figs. 98, 101): Suprabranchial chamber lacking papillae. Labial palps (Fig. 98: *op*, *ip*) with proportionally more internal folds.

Visceral mass (Fig. 99) anteroposteriorly longer. Gonad (*go*) pale cream-colored, surrounding greenish-beige digestive diverticula and remaining subumbonal region; with large space in visceral mass to left of suprabranchial chamber, anterior to *pm*. Connective tissue brown, surrounding most of digestive system, isolating it from surrounding *go*.

Circulatory and excretory systems (Figs. 99, 101): Pericardium (Fig. 101: *pc*) in $V \approx 25\%$ of visceral mass V , highly asymmetrical; right side $A \approx 2$ left side A . Ctenidial veins running along connection between demibranchs of each gill, connecting with T-shaped branch of ctenidial vein (Fig. 101: *cv*) running perpendicularly, originating between middle and anterior thirds of gill, running dorsally along *ca*. 50% of visceral H , bearing internal longitudinal, narrow, low folds. Ctenidial vein connecting to ventral end of auricle (*au*), marked by abrupt change in ST and color. *Au* multilobed (Fig. 99); right *au* $V \approx 130\%$ of left *au* V , placed more dorsally; walls thickly glandular, dark brown; *au* lobes covering most of pericardial posterior half, surrounding ventricle (*ve*). *Ve* thickly muscular, pyriform (Fig. 99); $L \approx 80\%$ of *pc* L , $V \approx 50\%$ of *pc* V . *Ve-au*

connections narrow, with unpigmented ducts at center of posterior *ve* slope; L and W $\approx$ 20% of *ve* L and W.

Digestive system (Figs. 101–102, 104): Inner surface of esophagus (*es*) covered by series of regular, broad, low, transverse folds, adjacent, abruptly ending in ventral gastric fold (Fig. 104); without distinct rim. Dorsal hood (Figs. 102, 104: *dh*) in V $\approx$ 12% of stomach V; inner surface with transverse folds. Gastric inner surface with pair of ventral, transverse folds (Fig. 104: *gf*) just posterior of *es* opening; aperture of *dh* between these folds; pair of narrow folds originating from right side of transverse folds, running posteriorly, penetrating conjoined style sac-intestinal opening; 2 pairs of ducts to digestive diverticula (Figs. 102, 104: *dd*) at midventral region of main gastric chamber, just posterior to *dh* and to origin of longitudinal gastric folds; left pair of ducts to *dd* separated by sharp, narrow fold. Gastric shield (Fig. 104: *gs*) on posterior-left side; A $\approx$ 25% of gastric inner surface A. Intestinal loops running more dorsally along dorsal wall of stomach-style sac. Anus (Fig. 101: *an*) preceded by short stalk; W $\approx$ 20% of *pm* W.

Material examined: USA, Florida Keys, FMNH 302010, 1 specimenn [sta. FK-717; dissected: 180 mm L, 145 mm H, ca. 48 mm W (without fouling organisms)].

Distribution: An Indo-Pacific species recently introduced to Florida. This species is not known from Brazil.

Remarks: The discovery of this specimenn, and hence the confirmed presence of this introduced Indo-Pacific species in South Florida, led to the tracking of this

potentially invasive species by the Florida Fish and Wildlife Commission in its Exotic Species Database. Tissue samples from this Florida Keys specimen were used in the molecular analyses of *Bieler et al.* (2004) and Tëmkin (2010).

This work provides the most complete anatomical descriptions of the two examined species of *Hyotissa* to date. They have similar anatomical features; however, a set of differences, detected here, facilitates the species-level distinction. The most readily perceived is the near-black mantle edges of *H. hyotis* (Fig. 100), in contrast to the pale beige or cream-colored ones of *P. mcgintyi* (Fig. 86). Another distinct feature is the greater development of pallial papillae in *P. mcgintyi*, covering the entire mantle lobes (Fig. 86), and some pallial structures, such as the surface of the posterior adductor muscle and the dorsal surface of the gills; this is not found in *H. hyotis*, in which these structures are smooth. Adult size appears to be another distinction, with *H. hyotis* typically reaching 3–4 times the size of *P. mcgintyi*. The extraordinary size and complexity of the auricles of *H. hyotis*, including the dark brown color, is less developed in *P. mcgintyi*. In the digestive system, *H. hyotis* has a shorter dorsal hood (Fig. 102) and anal papilla (Fig. 101), both of which are very long in *P. mcgintyi* (Figs. 89, 94); the inner organization of the stomach is also different (compare Figs. 93 and 104); the intestine of *H. hyotis* runs more dorsally than that of *P. mcgintyi* (Figs. 89, 102). On the other hand, the two species share some interesting and unusual features, such as the right promyal passage (Figs. 88, 101: *po*), the lobed auricles (Fig. 99), and the eulamellibranch gills with well-developed sequential septa reinforcing the filaments (Fig. 91: *gr*). The existence of a narrower left promyal passage in *H. hyotis* – a feature that led Harry (1985) to distinguish between the two genera *Hyotissa* and *Parahyotissa* (the latter with only the right passage) – was here confirmed (see comments above, under *P. mcgintyi*).

Hyotissa hyotis, anatomy, FMNH 302067. FIG. J1: Pallial cavity, ventral view, detail of anterior region, outer hemipalp (op) partially deflected; FIG. J2: Pericardial region, right view, right wall of pericardium removed, ctenidial vein (cv) opened longitudinally, including adjacent portion of auricle (au); FIG. J4: Mantle border, posterior view, detail of region between incurrent and excurrent flows. Scale bars = 5 mm; 2 mm. au, auricle; cv, ctenidial (efferent) vessel; di, inner demibranch; do, outer demibranch; go, gonad; in, intestine; ip, inner hemipalp; mb, mantle border; mo, mouth; op, outer hemipalp; pc, pericardium; sb, suprabranchial chamber; um, fusion between left and right mantle lobes; ve, ventricle.

Hyotissa hyotis, anatomy, FMNH 302067. FIG. J5: Pallial cavity, ventral view, detail of anterior region, outer hemipalp (op) partially deflected; FIG. J6: Pericardial region, right view, right wall of pericardium removed, ctenidial vein (cv) opened longitudinally, including adjacent portion of auricle (au); FIG. J7: Mantle border, posterior view, detail of region between incurrent and excurrent flows. Scale bars = 5 mm; 2 mm. au, auricle; cv, ctenidial (efferent) vessel; di, inner demibranch; do, outer demibranch; go, gonad; in, intestine; ip, inner hemipalp; mb, mantle border; mo, mouth; op, outer hemipalp; pc, pericardium; sb, suprabranchial chamber; um, fusion between left and right mantle lobes; ve, ventricle.

Family Spondylidae

Spondylus americanus Hermann, 1781

Figs. 119–135

Synonymy:

Spondylus americanus Hermann, 1781: 51 [Type locality: Santo Domingo]; *Yonge*, 1973: 177–188, figs. 2, 5, 9–11; Abbott, 1974: 450, pl. 21, fig. 5221; Rios, 1994: 250, pl. 86, fig. 1224; Viana & Rocha-Barreira, 2007: 815–819, figs. 1–4; Bieler & Mikkelsen, 2004: 520; Mikkelsen & Bieler, 2007: 154–155, 5 figs.; Rios, 2009: 508–509, fig.

Description:

Shell (Figs. 119–120) highly variable, thick, varying from white, yellow, orange, red, brown, to combination; SL $\approx$ 80 mm in material examined, SH = 1–2 SL. Valves highly asymmetrical; RV larger, cementing to and assuming shape of hard substratum, with tall, triangular auricles; free LV more planar. Sculpture most evident on LV and detached portion of RV, composed of 20–30 radial threads; interspace W = thread W; normal arrangement of smaller and larger threads intercalated, with smaller thread W $\approx$ 50% of larger thread W. Spines and long scales typically occurring along threads, directed externally and to periphery; disposition regular, aligning commarginally; spines of larger threads typically larger than those of smaller threads; spines variable, absent in some specimens. Outer shell surface opaque, delicately irregular. Ligament (Fig. 120: *li*) along entire horizontal dorsal hinge plate, centrally occupying 70–80% SL, with triangular expansion at midregion, along *ca.* 10% SL, running along auricles of each

valve, dividing them into 2 equal portions. Internal component of *li* extending at midregion of hinge plate along *ca.* 6% SH. Hinge plate occupying 70–80% SL and *ca.* 6% SH, symmetrical from internal component of *li*. RV with wide medial tooth and lateral socket on each side of *li*, each in $L \approx 15\%$ of hinge plate L; LV with medial socket and wide lateral tooth on each side of *li*; tooth with tip wider than base; tip bluntly bifid. Inner surface glossy white, except same color as external surface at valve margin (Fig. 120), colored band $H \approx 7\%$ SH at midventral edge, gradually diminishing toward hinge. Inner surface mostly smooth, except close to margin; latter with uniform denticles corresponding to external sculpture. Strong scar of adductor muscle subcentral, slightly posterodorsal; $A \approx 30\%$ of inner VA.

Main muscle system (Figs. 120, 124–125): Anterior adductor muscle absent. Posterior adductor muscle (*pm*) very large, circular in cross section, subcentral, slightly posterodorsal, in $A \approx 25\%$ of inner VA, divided into 2 semicircular, subequal (“catch” and “quick”) portions. No other well-developed muscles except T of visceral wall serving as pedal protractor muscles, thicker anteriorly, forming 2 lateral, anterior, dorsoventral folds (Fig. 124: *rr*).

Foot (Figs. 124–125: *ft*) well-developed, anteroventral, in form of wide bell, with relatively thick muscular walls and deep concavity; $V \approx 10\%$ $SV \approx 50\%$ of visceral mass portion ventral to *pm*. Outer surface smooth, pigmented by sparse, dark brown spots. Inner surface white, covered by uniform, low radial folds, originating in small, central, smooth area; each fold separated from others by narrow furrow and mostly dichotomizing at midlevel. Pair of deeper, wider furrows running, respectively, anteriorly and posteriorly. Byssus and byssal gland absent.

Mantle (Figs. 126–128): Mantle edge thickened, with 3 well-developed folds, mostly pigmented dark brown (rarely pale beige), with coalescent, broad, whitish spots, subcircular in some areas. Outer mantle fold thin ($T \approx 33\% ST$, $H \approx 2 T$), simple, white. Periostracum separating outer and middle folds. Middle fold $T \approx 3$ outer fold T , bearing large, tall papillae and eyes in following arrangement (Figs. 126–127): outer row of small, slender, pointed papillae; inner row of larger, taller papillae, fewer in number than smaller papillae of outer row; one eye between every one or 2 papillae. Each eye (Fig. 127–128: *ey*) on short eyestalk, containing large lens and dark retina contacting and covering basal and lateral sides of lens; cornea thin, occupying central tip; cornea surrounded by black integument. Ocular nerve thick, running from retina toward base of eyestalk, then as 8–10 nerves running radially along mantle lobes (Fig. 121: *nv*). Inner mantle fold very wide ($W \approx 20\% SH$), directed internally as pallial veil, contacting inner fold of opposing mantle lobe, especially high midventrally. Mantle muscles thick, originating at pallial line at some distance from shell margin, inserting along 3 folds, mostly in inner fold. Remaining mantle thin, translucent from pallial line to *pm*, bearing several iridescent, radial pallial nerves.

Pallial cavity (Fig. 123–124, 133) in $V \approx 33\%$ of body V , especially broader ventrally and anteriorly. Labial palps (Fig. 123–124: *pp*) dorsoventrally long, anteroposteriorly short; region between hemipalps attaching along anterior border of pallial cavity. Anterior ends of demibranchs ending between dorsal ends of hemipalps. Dorsal ends of hemipalps partially fused and situated as anterior cover of gill. Inner surfaces of hemipalps similar (Fig. 133), each with *ca.* 25 transverse folds, alternating on each hemipalp. Posterior end of each fold rounded, with narrow smooth area

preceding *pp* edge; posterior half of each fold slightly narrower than anterior half (gradually transitioning); anterior end gradually diminishing, with smooth furrow separating hemipalps. Inner surfaces of hemipalps abruptly changing ventrally (Figs. 123, 133), becoming longitudinal (perpendicular in relation to preceding folds), their distal ends curving toward *pp* edge, becoming tall and successively branching “lips,” each with dendritic projections (Figs. 123, 133: *dp*) protruding into flaps on inner surface of *pp* surrounding mouth. Smooth membrane as continuation of outer surface of *pp* surrounding dendritic external surface, little beyond them.

Gills (Fig. 130: *gi*) surrounding ventral surface of *pm*; $L = SL$, $V \approx 70\%$ of pallial cavity V . *Gi* filaments free (i.e., filibranch) and free from neighboring structures (mantle and visceral mass), connecting to latter by cilia. Each filament (Fig. 132) very narrow, long, without food grooves; ventral third of each demibranch descending and ascending lamellae connected; remaining part of lamellae free. Ctenidial vein running along *gi* base between demibranchs, surrounded by thin longitudinal muscle (Fig. 132); transverse muscle present ventral to it, also running in basal portion of each demibranch. Posterior projections of *gi* supported by suspensory stalk (Fig. 130: *gt*); each *gt* weakly muscular, laterally compressed, dorsoventrally tall; base of each *gt* originating at ventral *pm*, gradually tapering posteriorly; distal tip pointed; $L \approx 25\%$ of *gi* L . Inner demibranchs connecting by cilia along midline in posterior third of L .

Visceral mass (Figs. 124–125, 129) asymmetrical anterodorsally, accompanying asymmetry of umbonal region of shell valves; right portion taller and longer than left; taller portion very variable, mostly filled with connective tissue, ventrally compressed, extending posterior to *ft* and ventral to *pm*, protruding posteriorly as “heel” slightly

beyond *pm*. Stomach (Figs. 125: *st*; 129) mid-dorsal. Digestive diverticula greenish-brown, covering *st* almost totally and slightly beyond. Gonad cream-colored, covering digestive diverticula and extending dorsally into both umbonal regions, ventrally in compressed ventral region posterior to *ft*, and lateroposteriorly contacting *pm*. Pericardium just anterior to *pm*, compressed anteriorly by gonad.

Circulatory and excretory systems (Figs. 125, 131, 134–135): Pericardium (Fig. 125: *pc*) anteroposteriorly short, laterally broad; $W \approx pm\ W$, $V \approx 20\%$ of visceral mass V (including adductor). Ventricle (*ve*) massive, in central region, surrounding intestine crossing *pc*, with central portion narrower than lateral portions. *Ve* connection with auricles (*au*) narrow, in central region of lateral walls. *Au* lateral, each as large as *ve*; anterior surface of each connecting to pericardial wall; lateral end connecting to ctenidial vein. Anterior aorta broad, dichotomizing after short distance, running along surface of adjacent anterior portion of gonad, dorsal to intestine. Posterior aorta narrow, running ventral to intestine. Ctenidial vein narrow along entire L, connecting with *au* by short vein of same D between anterior and middle thirds of *gi*, just anterior to *pm*. Kidney (*ki*) brown, extending ventral to *pc* to posteroventral *pm*, posterodorsal to *ft*, mostly solid, containing tall transverse folds, coalescent and branching. Ventral wall of *ki* separating it from pallial cavity, thin, translucent, detached from renal tissue. Nephropore (Figs. 134–135: *ne*) small, at posterior end of renal chamber, at level of posteroventral *pm*. Genital structures bulging into posterior *ki* as described below.

Digestive system (Figs. 123, 125, 129–130, 133): *Pp* as described above. Mouth wide, located deep among dendritic lips of *pp* (Fig. 123, 133: *dp*). Esophagus (*es*) broad, conic, short ($L \approx 33\%$ of *pp\ L*); inner surface smooth; inserting into stomach (*st*)

anteroventrally. Gastric main chamber occupying *ca.* 33% of visceral portion anterior to *pm*, close to latter. Gastric inner surface (Fig. 129) with 3 transverse, mostly ventral, tall folds; anterior one close to *es* opening; middle one close to anterior fold; posterior one close to posterior end of *st*; relatively deep concavity between each successive ventral fold; anterior and posterior folds connecting by longitudinal, low, right fold; another tall longitudinal connection on left side uniting middle and posterior folds (Fig. 129: *gf*), with transverse furrow as sorting area. Ducts to digestive diverticula (Fig. 129: *dd*) relatively wide; one pair in concavity between anterior and middle ventral folds; another 3 ducts in ventral edge of longitudinal fold connecting anterior and posterior folds; another large duct in ventral edge of longitudinal fold uniting middle and posterior ventral folds. Gastric shield (*gs*) between posterior ventral fold and posterior end of *st*. Intestine (*in*) and style sac (*ss*) broadly conjoined, originating at midregion of concavity between middle and posterior ventral folds; opening relatively broad ($W \approx 33\%$ of *st* *W*), running posteroventrally, narrowing gradually to end of ventral, compressed region of visceral mass at posterior level of *pm*; *in* abruptly twisting in this region, running anterodorsally to *ss*, crossing to right of conjoined *ss-in* opening at right-ventral *st*; *in* running anteriorly beyond *st*, making wide loop dorsally, then running posteriorly, crossing *pc* and dorsal surface of *pm*, gradually running closer to LV. Anus (Fig. 130: *an*) simple, dorsoventrally compressed, preceded by long, free stalk, originating on left third of *pm* posterior surface; stalk base with pair of transverse folds, each originating from base of *gt*; right fold slightly more dorsal than left.

Reproductive system (Fig. 135): Gonad as described above, separated into 2 pairs of lobes; dorsal pair with terminal hollow chamber in anterior end of *ki*, in anteroventral visceral mass; this chamber separated from *ki* by membrane, latter

abruptly becoming tube-like (*ge*) at midventral surface; tube running posteriorly, opening at midventral region of other prerenal chamber. Ventral lobes without obvious terminal chambers, but also with terminal tube (*ge*) in $W \approx 2$ dorsal lobe *W*; terminal tube inserting into prerenal chamber in medial edge. Each prerenal chamber with thin walls, dorsoventrally compressed, in $A = 16\%$ of *ki* *A*; ventral surface attaching to walls separating renal and pallial chambers, also covering tube of dorsal gonadal lobes; dorsal surface free in renal chamber; anteroventral region of renal lobe bulging; aperture wide. Gametes apparently traversing these tubes and prerenal chamber, exiting at nephropores after crossing entire renal *L*.

Nervous system (Fig. 134): Paired anterior (pleural?; see Remarks) ganglia (*plg*) spherical, small ($A \approx 33\%$ of *es* *D*), adjacent, close to midline, just anterior to mouth; commissure $L \approx 50\%$ of single *plg* *L*. Paired pedal ganglia (*pg*) each in $V \approx 2$ single *plg* *V*, adjacent in posterodorsal region of visceral surface of *ft*; each *pg* with large anterior nerve running through pedal musculature. Paired visceral ganglia (*vg*) very large, just posterior to junction of visceral mass with ventral surface of *pm*, each in $V = 6-7$ single *plg* *V*. *Vg* forming 5-lobed structure; central lobe largest, with 2 lateral lobes, each in $V \approx 50\%$ of central lobe *V*, and 2 posterior lobes (cerebral ganglia?), each in $V \approx 25\%$ of central lobe *V*, bulging at anterior surface of this ganglionic mass, slightly away from midline. Pleurovisceral (?; see Remarks) connectives (*plv*) running through visceral glands, close to integument, surrounding *ft* base, joining with lateral region of posterior *vg* lobes. Cerebropedal connectives (*cn*) in $T \approx$ pleurovisceral connectives *T*, running ventral to latter, inserting medially into posterior visceral lobes. Thick pair of nerves inserting into lateral surface of *vg*, between posterior and lateral

lobes, with 2 branches each, one innervating gill stalks, other mantle border. Pallial eyes as described above. Abdominal sense organs not observed.

Material examined: USA, Florida Keys, FMNH 302065, 302066, 302068, 4 specimens [sta. FK-717; 2 dissected: #1: ca. 86 mm L, 103 mm H, 45 mm W (without spines); #2: ca. 80 mm L, 118 mm H, 46 mm W; Garden Key, Dry Tortugas, FMNH 177515 (84.9 mm L); FMNH 295736, 1 specimenn (= *S. ambiguus*) (sta. FK-048; dissected: ca. 67 mm L, 45 mm H, 41 mm W). BRAZIL. Pernambuco. Fernando de Noronha Archipelago, Conceição beach, 3°50'22.3"S, 32°24'55.8"W, 10 m, MZUSP 31402, 1 specimenn (vii/1999; dissected: 77.5 mm L, 72.2 mm H, 45.4 mm W). Bahia. Salvador; Itapuã beach, 12°57'13"S, 38°21'43"W, 2 m, MZUSP 28437, 1 specimenn (27/xi/1997; dissected, not measured). Espírito Santo. Off Guarapari, 45 m, MZUSP 70127, 1 specimenn (in lobster net, vi/2006), MZUSP 37381, 2 specimens, 1 shell (vi/2003; dissected, not measured). Rio de Janeiro. Conceição beach, 23°12'03.1"S, 44°37'36.8"W, 4 m, MZUSP 55737, 2 specimens (09/xii/2005; dissected, not measured), MZUSP 55739, 2 specimens (09/xii/2005; dissected, not measured); Ilha Comprida, 23°11'23.8"S, 44°37'23.9"W, MZUSP 55693, 1 specimenn (09/xii/2005; dissected, not measured); Lula beach, 23°11'38.5"S, 44°38'06.5"W, MZUSP 55812, 1 specimenn (10/xii/2005; dissected, not measured), 23°11'47.4"S, 44°37'44.1"W, MZUSP 58953, 1 specimenn (12/i/2006; dissected, not measured), Restaurante beach, 23°11'39.0"S, 44°37'32.2"W, 3 m, MZUSP 55775, 1 specimenn (10/xii/2005; dissected, not measured), Catimbau beach, 23°11'26.4"S, 44°37'25.5"W, 10 m, MZUSP 55945, 2 specimens (10/xii/2005; dissected, #1: 77.5 mm L, 69.0 mm H, 48.0 mm W; #2: 62.0 mm L, 64.0 mm H, 41.3 mm W), MZUSP 55944, 2 specimens (10/xii/2005; dissected, not measured); Ilha Grande; Imbuacica Is., MZUSP 79343, 2

specimens (20/viii/2006; dissected, not measured), Freguesia do Sul beach, MZUSP 23079, 1 specimen, 1 shell (24/vii/1966; dissected, not measured), Parcel do Aleijado, MZUSP 23080, 1 specimen (18/vii/1966; dissected, not measured). São Paulo. Queimada Grande Is., 24°28'57"S, 46°40'41"W, 8–25 m, MZUSP 35664, 2 specimens (28/vi/2002; dissected, not measured).

Distribution: Stated by Turgeon et al. (2009) to range from North Carolina to Quintana Roo (Mexico), the Gulf of Mexico outer banks, Brazil, and Bermuda. Its occurrence in Brazil to São Paulo is here confirmed.

Remarks: The anatomy described here agrees in all aspects with previous studies of spondylid anatomy (Dakin, 1928a, b, based mostly on Mediterranean *Spondylus gaederopus* Linnaeus, 1758; Yonge, 1973, based on *S. americanus* from Jamaica), including verifying two unusual features of the spondylid nervous system: (1) the very large visceral ganglionic complex (similar to that found in Pectinidae), and (2) the pedal ganglia joined via connectives with the latter (unique to Spondylidae). Watson (1930b) and Yonge (1973) postulated that the greater part of the cerebropleural ganglia are actually part of the visceral ganglionic complex (here as the two anterior bulges on the mass), evidenced by their connection with the pedal ganglia; if so, the anterior ganglia reported here are merely remnants, possibly only of the pleural ganglia. Further details of the pallial eyes of *S. americanus*, based on specimens from Brazil, were provided by Viana & Rocha-Barreira (2007).

This species shows a high degree of shell variation, due to phenotypic plasticity, incrustation, and moulding with the hard substratum. Logan (1974) explored the

functional morphology of this species in Bermuda, identifying five main modes of life, ranging from cementation on exposed deep reef walls to lying free in sediment pockets after having been dislodged from its substratum. In the Florida Keys, and elsewhere off both coasts of Florida, *Spondylus americanus* occurs in deeper water, on hard substrata (including shipwrecks) from *ca.* 25–30 m. It is replaced in shallower water by *S. ambiguus* Chenu, 1844 (in 1843–1845; previously known as *S. ictericus* Reeve, 1856, a synonym *teste* Lamprell, 2006; Finet & Lamprell, 2008), a morphospecies with brick-red shells (see Mikkelsen & Bieler, 2007: 156–157). [Both nominal species (*S. ictericus*, *S. ambiguus*) were recently synonymized under *S. tenuis* Schreibers, 1793, by Huber (2010: 628). Because the question of whether Schreibers' work can be accepted as binominal appears to be unresolved (see also Cox, 1929), we are using the name *S. ambiguus* herein]. In other parts of the western Atlantic, including Brazil and Bermuda, *S. americanus* also occurs in shallow water. *S. ambiguus* is also stated to occur in Brazil (Rios, 1994: 250, as *S. ictericus*), but no comparable anatomical differences were found by LRS in a study of extensive material that would justify a separation into two morphospecies within the Brazilian fauna. The *S. americanus* specimens from Florida and Brazil showed no anatomical differences. However, because the shells of *S. americanus* and *S. ambiguus* are clearly separable in Florida populations, we refrain from formally synonymizing the two species and await future molecular studies.

Spondylus americanus. FIG. 119: Shell morphology, articulated specimen, right view, FMNH 177515, 84.9 mm L. FIGS. 120–123: Anatomy, FMNH 302068, 98.0 mm maximum D; FIG. 120: Intact left view, LV and part of left mantle lobe removed; FIG. 121: Left mantle lobe, inner view; FIG. 122: Foot, opened longitudinally, exposing inner (ventral) surface; FIG. 123: Buccal region, ventral view, adjacent part of left labial palp (pp) also shown. Scale bars = 10 mm. dp, dentritic projection of lips and labial palps; ft, foot; gi, gill; li, ligament; mb, mantle border; mi, mantle border inner fold; mo, mouth; mp, mantle papillae; mu, mantle border outer fold; nv, nerves; pm, posterior adductor muscle; pp, labial palp; vm, visceral mass.

Spondylus americanus, anatomy. FIG. 124: Left overview, shell and part of left mantle lobe removed; FIG. 125: Same, digestive system *in situ*, topologies of some adjacent structures also shown; FIG. 126: Mantle border, cross section at midventral region; FIG. 127: Same, detail of outer and middle folds, ventral view; FIG. 128: Pallial eye, sectioned longitudinally; FIG. 129: Stomach, dorsal view, dorsal wall sectioned longitudinally and deflected. Scale bars = 10 mm (FIGS. 124–125); 1 mm (FIGS. 126–129). co, cornea; dd, ducts to digestive diverticula; er, esophageal rim; es, esophagus; ey, pallial eye; ft, foot; gc, gastric central pad; gf, gastric fold; gi, gill; go, gonad; gt, gill suspensory stalk; hf, hinge fold of mantle; in, intestine; ki, kidney; le, lens; mb, mantle border; mi, mantle border inner fold; mm, mantle border middle fold; mo, mouth; mp, mantle papillae; mu, mantle border outer fold; ne, nephropore; on, optical nerve; pc, pericardium; pl, pallial muscles; pm, posterior adductor muscle; pp, labial palp; re, retina; rr, pedal protractor muscle; rt, rectum; ss, style sac; st, stomach; su, supra-anal chamber of suprabranchial pallial cavity; vm, visceral mass; vo, mantle portion occupying umbonal cavity (in fixed valve only).

Spondylus americanus, anatomy. FIG. 130: Pallial cavity, detail of region posterior to posterior adductor muscle (pm), with gill deflected and mantle lobes removed; FIG. 131: Pericardial structures, dorsal view, dorsal region of pericardium removed; FIG. 132: Left gill, cross section in midregion; FIG. 133: Left labial palp, right-lateral view, outer hemipalp (op) deflected to show inner surface, short portion of adjacent region of gill (gi) and mantle (mt) also shown. Scale bars = 2 mm. aa, anterior aorta; an, anus; au, auricle; cv, ctenidial (efferent) vessel; di, inner demibranch; do, outer demibranch; dp, dentritic projection of lips and labial palps; gi, gill; gm, gill retractor muscle; gt, gill suspensory stalk; id, insertion of outer demibranch in mantle; im, insertion of inner demibranch in visceral mass; in, intestine; ip, inner hemipalp; ki, kidney; mt, mantle; op, outer hemipalp; pc, pericardium; pm, posterior adductor muscle; rt, rectum; ve, ventricle; vm, visceral mass.

Spondylus americanus, anatomy. FIG. 134: Nervous system *in situ*, ventral view, topologies of adjacent structures also shown, foot (ft) slightly deflected to left (at right in figure) and posterior region of visceral mass (vm) to right (at left in figure); FIG. 135: Left kidney and terminal reproductive structures, ventral view, topologies of adjacent structures also shown; ventral renal wall sectioned longitudinally; some inner structures exposed or seen by transparency. Scale bars = 1 mm. cn, cerebropedal connective; ft, foot; ge, genital ducts; gn, genital chamber; go, gonad; gt, gill suspensory stalk; im, insertion of inner demibranch in visceral mass; ki, kidney; mo, mouth; ne, nephropore; pg, pedal ganglion; plg, anterior (?pleural) ganglion; plv, pleurovisceral (?) connective; pn, pallial nerve from visceral ganglion; pp, labial palp; vg, visceral ganglia; vm, visceral mass.

Family Plicatulidae Gray, 1854

***Plicatula gibbosa* Lamarck, 1801**

Figs. 136–147

Synonymy:

Plicatula gibbosa Lamarck, 1801: 132 [no locality given]; *Yonge*, 1973: 188–197, *figs.* 14–23; Abbott, 1974: 450, *fig.* 5216, *pl.* 20, *fig.* 5216; Bieler & Mikkelsen, 2004: 519; Mikkelsen & Bieler, 2007: 158–159, 5 *figs.*

Description:

Shell (Figs. 136–138) oval to subtriangular, irregular, typically thick, white to brown, homogeneous to spotted; SL $\approx$ 9 mm in material examined. RV totally or partially cementing to hard substratum, fitting into surfaces even if irregular; periumbonally attaching to substratum in partially attached specimens. RV typically slightly more distorted and more concave than LV. Outer surface opaque, covered by pores, with 3–5 wide, irregular, radial undulations/plicae, producing undulating ventral and posterior margins (Fig. 137–138). Hinge plate of RV with medial pair of strong, symmetrical, divergent teeth, with corresponding medial sockets in LV; tooth L = 10–16% SH. Ligament central, between teeth. Inner surface smooth, translucent, glossy. Scar of adductor muscle circular, at mid-SH between middle and posterior thirds of SL; A $\approx$ 7% of inner VA.

Main muscle system (Figs. 138–139): Anterior adductor muscle absent. Posterior adductor muscle (*pm*) location and proportions as described above, clearly

possessing 2 (“catch” and “quick”) portions; anterior $A \approx 40\%$ of pm A. Pedal muscles absent.

Foot: absent.

Mantle (Figs. 139, 147):. Mantle lobes thin, translucent except at relatively thick borders; lobes free except for dorsal hinge fold; $H = 33\%$ SH. Pallial muscles connecting to pallial line, at distance from shell margin = 25–33% SH. Outer fold of mantle lobe (Fig. 147: *mu*) thin, simple; $T \approx 33\%$ ST, $H \approx 3$ T. Middle fold (Fig. 147: *mm*) in T and $H = 2$ outer fold T and H; papillae gradually appearing along entire posterior half of edge; each papilla $L \approx W$, at edges of fold, slightly internal; interspace $W = 2\text{--}3$ papilla W; longer papillae alternating with shorter papillae; shorter papilla $L \approx 50\%$ of longer papilla L. Inner mantle fold (Fig. 147: *mi*) of similar proportions to middle fold, except forming narrow pallial veil and having fewer and smaller papillae.

Pallial cavity (Figs. 138–139, 142–143, 145) in $V \approx 75\%$ of inner SV, except visceral mass from hinge area to midlevel of valves; cavity surrounding ventral, posterior, and dorsal sides of visceral mass. Labial palp $A \approx 2\%$ $VA \approx 25\%$ SL ventral to hinge plate. Palps (*pp*) covering anterior end of gills, extending *ca.* 12% SL anterior to gills. Hemipalps similarly shaped (Figs. 142–143) as 2 successive layers of bent flaps, in $L \approx 2$ H, narrowing gradually from anterodorsal to posterior. Outer hemipalps widely fused anteriorly; dendritic projection (Figs. 142–143: *dp*) with 3 papillae at ventral edge, located midway between outer hemipalps, in $H = 20\%$ of *pp* H; base slightly narrower than tip. Inner hemipalps widely connecting anteriorly, almost as tall as same regions of outer hemipalps, lacking dendritic projection. *Pp* inner surface with

5–7 wide transverse folds, successively shorter from anterior to posterior; each fold with rounded ventral end, leaving smooth ventral edge in $W \approx 12\%$ of pp W ; interspace $W = 50\%$ of fold W ; dorsal ends of folds connecting to dorsal furrow.

Gills (*gi*) not plicated, linear, lying along *ca.* 70% SL, in $H \approx 25\%$ SH in wider (anterior and middle) portions; anterior ends rounded; posterior ends tapering gradually. Gill suspensory stalks (Figs. 138–139: *gt*) inserting into posteroventral *pm*; base almost as wide as *pm*, gradually tapering to bluntly pointed tip; extending along (posterior) 50% of *gi*. *Gi* filaments connecting to one another and to adjacent structures only via cilia; each ascending lamella $L \approx 50\%$ of descending lamella L (Fig. 145); distal tip of these shorter lamellae bent laterally preceding ciliary connection (Fig. 145: *id*, *im*). Anterior ends of *gi* inserting between hemipalps along *ca.* 20% of posterior region (Figs. 142–143).

Visceral mass (Figs. 138–140, 144) along relatively narrow horizontal band between hinge area and *pm*; $V \approx 16\%$ SV, $L \approx 2$ H. Digestive system along central region; $V \approx 50\%$ of visceral mass V . Digestive diverticula greenish-cream, surrounding stomach; $V \approx 12\%$ of visceral mass V . Gonad greenish-cream, with clearly visible acini on nodular surface, filling entire remaining visceral mass V , including umbones. Renopericardial structures rectangular in section; $V \approx 16\%$ of visceral mass V just anterior to *pm* (Fig. 144).

Circulatory and excretory systems (Fig. 144–145): Size and location of renopericardial structures as described above. Ctenidial veins (Fig. 145: *cv*) running along central region of dorsal *gi* connections, with perpendicular component between

anterior and middle thirds, wider ventrally than dorsally, along 50% of visceral mass H, connecting with ventral ends of auricles. Auricles (*au*) subtriangular, attaching to posterolateral sides of pericardium (*pc*). Posterior wall of *au* bearing white, gland-like, middle protuberances in $L \approx 25\%$ of posterior wall T. Ventricle (*ve*) surrounding intestine as it traverses *pc*; $L \approx 20\%$ of *pc* L. *Ve* connection to *au* on posteroventral sides. Kidneys (*ki*) white, solid; $V \approx 10\%$ of *pc* V on ventral side. Nephropores minute, on anterior ends of *ki*.

Digestive system (Fig. 139–141, 146): *Pp* as described above. Esophagus (*es*) running dorsoventrally along *ca*. 70% of *pm* L, and similar distance ventral to hinge area; $W \approx 25\%$ of *pm* W. Stomach (*st*) conical, slightly perpendicular to *es*; main chamber $L \approx 2$ *es* L. Gastric inner surface with narrow, transverse *es* rim (Fig. 146: *er*); sorting area (*sa*) just dorsal to *es* opening, with wide, transverse, low folds. Gastric shield (*gs*) posterodoral; $A \approx 20\%$ of inner gastric surface A. Paired ducts to digestive diverticula (*dd*) ventral and at some distance from *es* opening, at ends of horseshoe-shaped furrow (with posterior concavity in $L \approx 25\%$ of main gastric chamber L); wide groove running longitudinally at right, edges gradually increasing in H, forming pair of typhlosoles (*ty*). Intestine (*in*) and style sac (*ss*) totally fused, separated only by pair of *ty*. *Ss* tapering gradually posteroventrally to ventral side of *pm*; $L \approx$ main gastric chamber L. *In* making 180° loop just posterior to *ss*, then performing wide, sinuous loop, running to right of *ss* and gastric main chamber, and along midline; total *in* $L \approx$ SL. Anus (Figs. 139–141: *an*) with blunt, weakly expanded edges, preceded by long portion of rectum detached from *pm*; $L \approx 50\%$ of *pm* L.

Reproductive system: Gonad as described above; genital aperture on *ki* not observed in detail.

Nervous system (Figs. 139–140): Paired cerebropleural ganglia (Figs. 140: *cg*) elliptical, located laterally close to posterior third of *pp*; $D \approx 16\%$ of *es* D. Cerebral commissure long, narrow. Pedal ganglia not observed. Paired visceral ganglia (Fig. 139: *vg*) elliptical, on middle of *pm* ventral side, very close; $V \approx 1.5$ *cg* V. Abdominal sense organs not observed.

Material examined: USA, Florida Keys, AMNH 298913, 1 specimenn (sta. FK-083; dissected : 8.9 mm L, 11.2 mm H).

Distribution: Stated by Turgeon et al. (2009) to range from North Carolina to Quintana Roo (Mexico), the Gulf of Mexico outer banks, the West Indies, Brazil and Bermuda.

Remarks: These anatomical results agree with those on *Plicatula australis* Lamarck, 1819, by Watson (1930a) and on *P. gibbosa* from Jamaica reported by Yonge (1973). There are many shell specimenn records from Brazil, but no anatomical material was available for dissection.

Plicatula gibbosa, anatomy. FIG. O1: Intact right view, RV and part of right mantle lobe removed; FIG. O2: Digestive system, right view, topologies of some adjacent structures also shown; FIG. O3: Detail of anus (an), right and slightly posterior view; FIG. O4: Labial palps, anterior and slightly right view, adjacent portion of gills (gi) and visceral mass (vm) also shown; FIG. O5: Same, outer hemipalp (op) sectioned along midline, right outer hemipalp deflected; FIG. O6: Pericardial region, right view, right pericardial wall removed, adjacent region of ctenidial vein (cv) also shown; FIG. O7: Gill, cross section in midregion; FIG. O8: Stomach, right view, sectioned longitudinally along dorsal region; FIG. O9: Mantle edge, cross section from midregion of posterior side. Scale bars = 1 mm. an, anus; au, auricle; cg, cerebropleural ganglion; ci, ciliary connection of gill; cp, cerebrovisceral connective; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; di, inner demibranch; do, outer demibranch; dp, dentritic projection of lips and labial palps; er, esophageal rim; es, esophagus; gi, gill; gm, gill retractor muscle; go, gonad; gs, gastric shield; gt, gill suspensory stalk; hf, hinge fold of mantle; hi, hinge; id, insertion of outer demibranch in mantle; im, insertion of inner demibranch in visceral mass; in, intestine; ip, inner hemipalp; li, ligament; mb, mantle border; mi, mantle border inner fold; mm, mantle border middle fold; mo, mouth; mp, mantle papillae; mu, mantle border outer fold; op, outer hemipalp; pc, pericardium; pl, pallial muscles; pm, posterior adductor muscle; pp, labial palp; rt, rectum; sa, gastric sorting area; sh, shell; ss, style sac; st, stomach; ty, typhlosole; ve, ventricle; vg, visceral ganglia; vm, visceral mass.

Plicatula gibbosa, shell morphology and anatomy, AMNH 298913, 8.9 mm L. FIG. O10: LV attached to shell of another bivalve, inner view; FIG. O11: RV, outer view; FIG. O12: Intact right view, RV and part of right mantle lobe removed. gi, gill; gt, gill suspensory stalk; hi, hinge; in, intestine; li, ligament; mb, mantle border; pc, pericardium; pm, posterior adductor muscle; pp, labial palp.

Family Anomiidae Rafinesque, 1815

Anomia simplex d'Orbigny, 1853

Figs. 148–165

Synonymy:

Anomia acontes J. E. Gray, 1850: 17 [Type locality: Jamaica]. A forgotten name reinstated by Huber (2010: 616) under violation of Art. 23.9 and 23.11 of the ICZN (1999) Code. Prevailing usage of *Anomia simplex* is here maintained; see Remarks.

Anomia simplex d'Orbigny, 1853: 367, pl. 28, figs. 31–33 [Type locality: Martinique, Cuba]. *Nomen protectum*.

Anomia simplex – Abbott, 1974: 451–452, fig. 5232, pl. 20, fig. 5232; Fuller et al., 1989: 83–94, figs. 1–26; Bieler & Mikkelsen, 2004: 510; Mikkelsen & Bieler, 2007: 162–163, 6 figs.

Anomia ephippium – Rios, 1994: 251 pl. 86, fig. 1227; 2009: 510, fig. (non Linnaeus, 1758; see Remarks).

Description

Shell (Figs. 148–150, 154–156) oval to circular, fragile, translucent, iridescent whitish to pale beige, orange, or brown, laterally very compressed; SL $\approx$ 15–20 mm in material examined, maximum SW $\approx$ 12% SD. Both valves (mainly RV) conforming to shape of substratum. LV simple, weakly convex; outer surface opaque smooth (Fig. 148) to glossy (Fig. 154); inner surface glossy, thinly iridescent; muscle scars restricted to infraumbonal region (Fig. 150), in A $\approx$ 16% of inner VA, W $\approx$ 2 L. Scar of posterior adductor muscle (*pm*) circular, in A $\approx$ 12% of total scar A, on posteroventral side of each valve. Scars of split posterior pedal retractor muscle anterior and dorsal to adductor

scar, inserting on LV only; one portion subequal in size and form to adductor scar, anterior to adductor scar; other portion (= byssal retractor of authors) circular, dorsal to posterior adductor scar; $A = 2 \text{ } pm \text{ scar } A$. Scar of anterior pedal retractor muscle (left only) in umbonal cavity, elongated; $A \approx 25\%$ of $pm \text{ scar } A$. RV with unclosed byssal orifice close to umbo, surrounding byssal portion of foot; $A \approx 6\%$ of LV A . Posterodorsal region of RV including hinge plate on thickened crurum; $pm \text{ scar}$ midway between orifice and posterior margin of valve (Fig. 155). Periostracum not evident. Hinge plate edentulous, composed only of dorsoventrally elongated internal ligament ($L \approx 5 \text{ } W \approx 20\% \text{ } SW$) on resilifer, preceded by thick, peduncular portion of RV (Fig. 156) and single concavity in LV (Figs. 150).

Main muscle system (Figs. 151–153, 157, 162): Anterior adductor muscle absent. Pm relatively small (Figs. 157, 162), approximately central on each valve, in $A \approx 5\%$ VA ; comprised of 2 (“catch” and “quick”) portions, one (darker) centrally, extending posteriorly, other (paler) surrounding lateral and anterior regions. Anterior pedal retractor muscle (Figs. 151–153, 157: *ar*) single (left), originating in umbonal cavity of LV, in $A = 50\%$ of ligament A , relatively long dorsoventrally; running directly posteriorly for distance = 25% SL , through wide portion of mantle tissue, laterally compressed, becoming slightly wider posteriorly; inserting along anterior byssal furrow in base of main pedal retractor muscle (origin in RV indicating probable homology with left anterior pedal retractor of more typical bivalves, with right anterior pedal retractor here lost). Posterior pedal retractor muscle single (left, *pr*), divided into 2 bundles. Anterior branch directly to left of byssal furrow (Figs. 151–152: *br*), originating on left surface of byssus, running short distance toward left, inserting at midanterior LV, in $A = 3 \text{ } pm \text{ } A$, approximately midway between pm and hinge area. Posterior branch

originating in posterior byssal furrow, running posteriorly and to left, surrounding posterior surface of anterior branch, gradually running away from anterior branch (Figs. 151–152: *pr*), inserting into LV just posterior to anterior branch, at some distance from it; insertion area between *pm* and anterior branch, displaced ventrally, slightly smaller than that of *pm*. Right posterior pedal retractor muscle absent.

Foot (Figs. 151–153, 157: *ft*) consisting of a thin, free shaft plus a massive, plug-like portion that produces calcified byssus. Pedal musculature as described above, with anterior projection in left *ar* (Fig. 157), and cylindrical, massive portion possessing both branches of *pr*. Byssal furrow (Figs. 152, 157: *bf*) wide, shallow, rimmed by thin walls, slightly smaller than insertion of anterior branch of *pr*. Both left pedal retractors originating from furrow, in anteroposterior alignment. *Ft* shaft just anterior to *bf*, turning right-anteriorly, in $L = ar$ L ; basal 66% comprising long, slender, cylindrical stalk; terminal third compressed, in $W \approx 3$ basal stalk W ; right surface concave, bearing byssal gland. Byssus solid, short, cylindrical, calcareous.

Mantle (Figs. 157, 161): Mantle lobes asymmetrical, thin, translucent, possessing whitish, coalescent spots. Left mantle lobe simple, as inner mold of generally compressed valve. Right mantle lobe forming arch surrounding byssal foramen to region close to hinge plate, maintaining narrow gap between foramen and hinge plate. Mantle edge with 3 folds (Fig. 161). Outer fold thin, smooth, simple, typically connecting to periostracum (*pe*) on inner surface. Middle fold with long, slender papillae except in region surrounding byssal foramen in right lobe. Papillae of middle fold organized in 3 layers; outer layer of short, aligned papillae; other 2 layers internal to outer layer, each with 3–4 times longer papillae; each papilla tall, slender;

interspace $W = 2-3$ papilla W ; papilla L not uniform, with longer and shorter papillae alternating; longer papilla $L \approx 5\%$ SL , shorter papilla $L \approx 25-33\%$ of longer papilla L . Inner fold smooth, simple, forming pallial veil; W and $T \approx 2$ outer fold W and T . Pallial muscles well developed, as radial, iridescent, mostly dichotomous fibers between edge of muscle area and mantle edge.

Pallial cavity (Figs. 157–158, 162–163) surrounding entire visceral mass, except dorsally; $V \approx 50\%$ SV . Promyal passage (Fig. 157: *po*) only on right side, connecting suprabranchial chamber with posterodorsal region, from anterior end of right gill, passing between *pm* and *ft*. Paired labial palps (Figs. 157, 162: *pp*) asymmetrical, long, surrounding midregion of byssal base of *ft*; left *pp* more ventral than right, connecting by oral groove on anterodorsal side of byssal base of *ft*. Hemipalps subequal, with smooth inner surfaces; inner folds inconspicuous. Gills (Fig. 162: *gi*) widely curved, in $L \approx SL \approx 8 T$; anterior third asymmetrical, with left *gi* more anterodorsal; middle and posterior thirds symmetrical, narrow, long. Inner demibranch of right *gi* connecting to right and left *pp* (Fig. 157); both demibranchs of left *gi* connecting to left *pp*. Inner (*di*) and outer (*do*) demibranchs similarly shaped. *Gi* suspensory stalk (Figs. 157, 163: *gt*) lying along 50% of *gi* L , narrow, weakly muscular. *Gi* filaments attaching to one another and to visceral mass and mantle via ciliary connections; right and left *gi* uniting posterior to visceral mass via tissue connections. *Do* with additional ventral prolongation along outer-dorsal edge of ascending branch (Fig. 158).

Visceral mass (Figs. 157, 162) strongly laterally compressed, more concentrated on left side, in dorsal and posterior regions around *ft*; $V \approx 25\%$ SV . Stomach and remaining digestive system central; remaining mostly filled by pale cream-colored

gonad. Pericardial region just posterior to *pm*; digestive diverticula greenish beige, anterior, surrounding stomach.

Circulatory and excretory systems (Figs. 157, 163): Pericardium (Fig. 157: *pc*) irregular, just posterior to *pm*, in $V = 10\text{--}12\%$ of visceral mass V ; auricles and ventricle not detected in any dissected specimen. Kidneys (Fig. 163: *ki*) solid, whitish, on both sides of posteroventral visceral mass, at base of each *gt*. Nephropores (Fig. 163: *ne*) as small papillae on both sides of *pm*, on internal surfaces of *gt* bases.

Digestive system (Figs. 157, 159–160, 162): *Pp* as described above. Esophagus (*es*) located *ca.* 16% SH below umbones; $L \approx pm\ L$, $W \approx 33\%$ of *pm\ W*. *Es* inner surface bearing 8–10 longitudinal, narrow, uniform folds. Stomach (*st*) elliptical; $L \approx 2\ W$, $V \approx 20\%$ of visceral mass V . Dorsal hood (*dh*) in posterior-right region; $A \approx 12\%$ of inner gastric surface A . Two pairs of ducts to digestive diverticula, simple, on posterodorsal gastric surface. Gastric inner surface (Fig. 160) with low *es* rim (*er*); *dh* preceded by pair of triangular adjacent folds, pointing in opposite directions. Gastric shield (*gs*) right-dorsal; $A \approx 16\%$ of gastric inner surface A . Large sorting area (*sa*) lying along posterodorsal gastric surface, with uniform, transverse, low folds; *sa* separating (on posterior-right side) intestinal (*in*) and style sac (*ss*) origins; transverse, tall, wide, arched fold separating *gs* from style sac opening. *Ss* totally separated from *in* (Fig. 157), narrow, very long, only slightly shorter than SH; making wide loop in posteroventral visceral mass, gradually passing from left to right side, weakly protruding into suprabranchial chamber; most regions $W \approx 16\%$ of main gastric chamber W , narrowing gradually distally to pointed tip just anterior to *pm*. *In* short ($L \approx 50\%$ of visceral mass L), at right of *ss* opening, running almost directly

posteroventrally, in $W \approx ss\ W$; *ca.* 33% of *in* L exposed in pallial cavity as anal stalk. *In* inner surface almost entirely with longitudinal typhlosole (Fig. 159: *ty*); *ty* tall, relatively thin, arching; remaining *in* inner surface with longitudinal, narrow, uniform folds. *In* passing anterior to (not through) *pc*. Anus preceded by relatively long free stalk; edges fringed; subterminal sphincter (Figs. 159: *sp*) very evident.

Reproductive system (Fig. 163) not observed in detail. Gonad filling most of visceral mass; genital ducts opening inside posteroventral *ki*.

Nervous system (Figs. 162, 164–165): Cerebropleural ganglia (*cg*) simple, triangular, well separated, connecting by long, narrow commissure (Fig. 164: *cc*) in $L \approx 5\ es\ D$; right *cg* more posterior than left; *cg* A $\approx 16\%$ of *es* D. Pedal ganglia not observed. Each visceral ganglion (*vg*) in $V \approx 5$ single *cg* V, on anteroventral surface of *pm*; broadly connected, with no visible commissure (Figs. 157, 165); weakly asymmetrical, with posterior nerves of left *vg* slightly more dorsal than those of right. Abdominal sense organs not observed.

Material examined: USA, Florida Keys, Florida Keys, MZUSP 36126, 1 specimenn (sta. FK-649); AMNH 298953, 3 specimens (sta. FK-352; 1 dissected, 23.6 mm maximum D); FMNH 301413, 1 specimenn (FK-629; dissected: 29 mm L, 30 mm H, 9 mm W); FMNH 314534, 1 specimenn (FK-287; dissected: 35.6 mm L, 29.2 mm H, 7.4 mm W). BRAZIL, Rio de Janeiro, Buzios, Ferradura beach, MZUSP 48466, 1 specimenn (19/iii/2005; dissected, not measured); Arraial do Cabo, Porcos Island, 22°57'53.5"S, 41°59'47.7"W, 8 m (18/iii/2005; dissected, not measured); Ilha Grande, Pau-Paulo beach, MZUSP 45890, 1 specimenn (22/vii/1966; dissected, not measured);

Paraty, Martinello Island, 23°11'15.6"S, 44°39'33.1"W, 3 m, MZUSP 83252, 3 specimens (26/i/2007; dissected, not measured). São Paulo, Anchieta Island (IO Bentos), Sul beach, MZUSP 23065, 15 specimens, MZUSP 23064, 6 specimens, (26/ii/1963; dissected, not measured), MZUSP 23063, 3 specimens (28/ii/1963; dissected, not measured); Ubatuba, MZUSP 26345, 2 specimens (1 dissected: 24.0 mm D, 22.2 mm H, 8.3 mm W); Enseada das Palmas (IO Bentos), MZUSP 23067, 5 specimens (13/ii/1963; 2 dissected: #1: 19.5 mm L, 19.1 mm H, 4.1 mm W; #2: 14.9 mm L, 9.9 mm H, 3.1 mm W), MZUSP 23068, 6 specimens (02/iii/1962; dissected, not measured), Andorinhas beach (IO Bentos), 1 m, MZUSP 23058, 1 specimen (23/i/1962; dissected, not measured), MZUSP 23060, 1 specimen (12/vii/1962; dissected, not measured), MZUSP 23066, 1 specimen (24/ii/1962; dissected, not measured), MZUSP 23059, 1 specimen (23/i/1962; dissected, not measured), Boqueirão (IO Bentos), 20 m, MZUSP 23061, 1 specimen (19/vii/1961; dissected, not measured), 32 m, MZUSP 23062, 1 specimen (14/vii/1962; dissected, not measured), Ponta do Navio, MZUSP 23069, 1 specimen (IO Bentos, 03/vii/1962; dissected, not measured); Ilha Bela, Garapucaia beach, MZUSP 45921, 2 specimens (04/iii/1967; dissected, not measured); Santos, Lage de Santos, 24°17'23"S, 46°11'57"W, 31–32 m, MZUSP 26285, 1 specimen (IO sta. 16, 23/iii/1961; dissected, not measured).

Distribution: Stated by Turgeon et al. (2009) to range from Massachusetts to Yucatan, the Gulf of Mexico outer banks, Cuba, Brazil, and Bermuda. Range in Brazil to São Paulo is here confirmed.

Remarks: For other details of the shell, see Mikkelsen & Bieler (2007: 162). The anatomy of *Anomia* (as reported here in agreement with earlier authors) is

extremely asymmetrical with some organs (e.g., pedal retractor muscle, adductor muscle, gonad; Yonge, 1980) represented only or mainly on one side. Yonge (1977) compared the anatomy of *Anomia* (including New England *A. simplex*) to other members of the family and superfamily, and pointed out that *Anomia* is distinct from other genera in Anomioidea in having a split posterior pedal retractor muscle, which results in three central muscle scars on the left valve. The foot is rotated, with a small free portion (used primarily for cleaning; Yonge, 1977; Prezant, 1984) and a bulbous portion that produces the calcified byssus rotated strongly to the right so that the byssus passes through the hole in the right valve. The labial palps literally wrap around the byssal portion of the foot, and the anterior portions of the demibranchs are asymmetrical in their association with the palps. Yonge (1977) wrote that three demibranchs are associated with the left palp, and only one demibranch with the right palp; this study confirmed this, however, each palp receives two demibranchs in *A. ephippium* Linnaeus, 1758 (S. Staubach, pers. comm., June 2012). Because there are no food grooves on the gills of *Anomia*, examinations of ciliary currents are needed to confirm these associations. According to Pelseneer (1911), the anomiid heart consists of a ventricle only, without auricles or a surrounding pericardium; Yonge (1977) indicated that the pericardium is absent and auricles are present and asymmetrical. A pericardium (?ventricle) was detected in these dissections but did not contain typical heart chambers; clearly the anomiid heart requires further investigation across the family. Purchon (1957) reported five ducts to the digestive diverticula in *A. ephippium*; only two were found here, but each duct branches soon after leaving the stomach, so this feature could be easily misinterpreted, or could vary among species. The visceral ganglia are on the anterior surface of the posterior adductor muscle, rather than the posterior surface as is true for most bivalves (Yonge, 1977).

Most striking as a result of this study is the presence of an apparent right promyal passage in *Anomia simplex*, similar to that characteristic of members of Gryphaeidae, not before recorded in Anomiidae.

Until recently, d'Orbigny's description of *Anomia simplex* was dated as 1842 but is now interpreted as having been published much later, between 1851 and 1853 (e.g., Mikkelsen & Bieler, 2007: 413; who adopted a 1853 date). *Anomia acontes* Gray, 1850, is an available older name. However, the name *A. simplex* d'Orbigny, 1853, has been in prevailing usage, with more than 25 usages in the last 50 years. By contrast, the name *A. acontes* apparently had not been used as valid since 1899 until Huber (2010: 616) reinstated it, thereby violating Art. 23.9 of the ICZN (1999) Code. Prevailing usage of *A. simplex* is here maintained.

Some authors have considered *Anomia simplex* a synonym of Eastern Atlantic/Mediterranean *A. ephippium* Linnaeus, 1758, whereas others (e.g., Huber, 2011: 616) reported morphological differences. Additional research is needed.

Other studies of *Anomia simplex* from a variety of western Atlantic localities have included larval development and metamorphosis (Loosanoff, 1961; Loosanoff et al., 1966; reared from plankton from Long Island Sound), cardiac physiology (Navez, 1936, from Woods Hole, Massachusetts), and formation and mineralogy of the calcified byssus (Prezant, 1984, from Sanibel Island, Florida).

No morphological difference was found between Floridian and Brazilian specimens.

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Anomia simplex, anatomy. FIG. A1: Intact right view, RV and part of right mantle lobe removed; FIG. A2: Gills, cross section in midregion; FIG. A3: Rectum and anus, dorsal view, both longitudinally opened, typhlosole (ty) sectioned in distal third to show its profile; FIG. A4: Stomach, dorsal view, sectioned dorsally with inner surface exposed; FIG. A5: Mantle border, a portion extracted from the midventral region, with a portion of the periostracum still attached; FIG. A6: Intact right view, digestive system and nervous system *in situ*, topologies of some adjacent structures also shown. Scale bars = 1 mm. an, anus; ar, anterior pedal retractor muscle; bf, byssal furrow; cc, cerebral commissure; cg, cerebropleural ganglion; ci, ciliary connection of gill; cp, cerebrovisceral connective; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; dh, dorsal hood; di, inner demibranch; do, outer demibranch; er, esophageal rim; es, esophagus; ft, foot; gf, gastric fold; gi, gill; go, gonad; gs, gastric shield; gt, gill suspensory stalk; hf, hinge fold of mantle; in, intestine; mb, mantle border; mi, mantle border inner fold; mm, mantle border middle fold; mp, mantle papillae; mu, mantle border outer fold; pc, pericardium; pe, periostracum; pl, pallial muscles; pm, posterior adductor muscle; po, promyal passage of suprabranchial cavity; pp, labial palp; rt, rectum; sa, gastric sorting area; sl, crystalline style; sp, sphincter; ss, style sac; st, stomach; su, supra-anal chamber of suprabranchial pallial cavity; tg, integument; ty, typhlosole; vc, visceral mass gill connection; vg, visceral ganglia; vm, visceral mass.

Anomia simplex, anatomy. FIG. A7: Detail of posterior region of visceral mass, ventral-slightly right view, both gills deflected and only partially shown; FIG. A8: Right cerebropleural ganglion (cg) *in situ*, right view; FIG. A9: Visceral ganglia, ventral view. Scale bars = 0.5 mm. cc, cerebral commissure; cg, cerebropleural ganglion; ci, ciliary connection of gill; cp, cerebrovisceral connective; di, inner demibranch; es, esophagus; go, gonad; gt, gill suspensory stalk; ki, kidney; ne, nephropore; pm, posterior adductor muscle; sb, suprabranchial chamber.

Anomia simplex, shell morphology. AMNH 298953, 23.6 mm maximum D; FIG. A10: Left view; FIG. A11: Right view; FIG. A12: LV, inner view, detail of subumbonal region with muscular scars. FIG. A13: Left view; FIG. A14: Right view; FIG. A15: Ventral view; FIG. A16: MZUSP 23067, 19.5 mm D, left view; FIG. A17: Detail of hinge of RV; FIG. A18: Ventral view, RV deflected upward. Scale bars = 1 mm. ar, anterior pedal retractor muscle; bf, byssal furrow; br, byssal retractor muscle (derived from posterior pedal retractor muscle); ft, foot; pr, posterior pedal retractor muscle.

Family Isognomonidae Woodring, 1925 [1828]

***Isognomon alatus* (Gmelin, 1791)**

Figs. 72–82

Synonymy:

Ostrea alata Gmelin, 1791: 3339 [Type locality: Oceano americano = American Ocean].

Isognomon alatus – Abbott, 1974: 441, pl. 20, fig. 5124; Domaneschi & Martins, 2002: 621–624, fig. 9C; Bieler & Mikkelsen, 2004: 514; Tëmkin, 2006: 262, figs. 1A, 8A, 9B, 13A, 14A, 17C; Mikkelsen & Bieler, 2007: 98–99, 5 figs.; Wilk & Bieler, 2009: 1 ff., figs. 1–10.

Description

Shell (Figs. 72–73) quadrangular to oval, greenish pale brown or beige, with radial, narrow, irregular, dark brown spots, more evident close to margins; SL $\approx$ 20–60 mm in material examined, typically SW = SL, SW $\approx$ 0.1 SL (greatly compressed). Byssal notch narrow, in RV. Sculpture of series of low, thin, narrow, undulated, commarginal scales; generally irregularly lamellate close to shell margin; scales typically arranged in radial rows. Inner surface smooth; nacreous A = 66% VA, close to hinge, iridescent whitish-violet; remaining third along shell margin opaque, translucent, of same color as outer shell surface. Umbones low, terminal. Hinge line almost horizontal; ligament internal, with 6–8 resilia set in resilifers; each resilifer of regular L, of irregular W and disposition, more closely spaced anteriorly. Hinge plate with small subequal teeth near umbones, more evident in juveniles. Muscle scar in central nacreous portion, shallow, elliptical, in V $\approx$ 12% of inner VA; 66% of scar closest to hinge area

comprising posterior pedal retractor muscle (*pr*); remaining third narrowly crescent-shaped, comprising posterior adductor muscle (*pm*). Scars of anterior pedal retractor muscles (*ar*) small, circular, in $A \approx 5\%$ of *pm* A, close to hinge plate, between middle and posterior thirds.

Main muscle system (Fig. 77): Anterior adductor muscle absent. *Pm* central, crescent-shaped, with thicker anteroventral end, rounded, posterodorsal end tapering to point; $W \approx 50\%$ SW, $H \approx 20\%$ SH. Paired *ar* narrow, originating close to hinge plate, between middle and posterior thirds, running posteriorly close to ventral integument of visceral mass, inserting along anterior foot base. Paired anterior auxiliary pedal retractor muscles (*ap*) short, very narrow, in $L \approx 20\%$ of *ar* L, originating in umbonal cavity at distance = that between origin of *ar* and hinge plate; running posteromedially, inserting partly in middle of *ar*, partly in adjacent foot base. Paired *pr* acting as byssal retractors, very thick, broad, originating in wide, elliptical area just anterior to *pm*, closer to ventral end, in $L \approx 50\%$ of *pm* L, running anteroventrally, narrowing abruptly, inserting on middle and posterior foot base, just dorsal to byssal furrow.

Foot (Figs. 75–77) small, appendix-like, slender, narrowing gradually, with distal end broadly pointed; typically pigmented by dark brown, irregular, coalescent spots. Byssal furrow (Fig. 77: *bf*) deep, running along ventral surface and midline, unpigmented, very wide posteriorly, surrounding byssus; very shallow furrow also running along dorsal surface, diminishing close to foot base. Byssus (Figs. 75, 77: *by*) broad, thick, consisting of greenish-iridescent flattened strips connecting soon after exiting foot; dorsal to this, separating and organizing in uniform arrangement of 10–12

pairs of long strips, inserting along *pr*, close to their internal surface (Figs. 76–77). Hollow, flattened chamber between strips immersing in *pr*; $W = \text{strip } W$ (Fig. 76).

Mantle (Figs. 74, 77, 79): Mantle border dark brown, paler near edge; outer fold thin, short, simple, weakly pigmented (Fig. 79). Periostracum attaching to inner surface of outer fold. Middle fold weakly taller and thicker than outer fold, with series of long, slender papillae (Figs. 74, 79: *mp*) mostly inserting subterminally along inner surface; distal papillar tips sharply pointed; interspace $W = 3 W$. Inner fold *T* and *H* each ≈ 2 middle fold *H*; edge with series of papillae, inserting terminally, with remaining characters similar to those of middle fold. Inner mantle fold forming pallial veil. Papillae of middle and inner folds longer in posteroventral half, gradually decreasing dorsally to mantle lobe fusion at hinge area. Low, narrow, transverse fold (Figs. 74, 77: *fd*) at distal end of gill between dorsal and posterior regions; broad ciliary strip running anteriorly from fold, surrounding mantle border. Pallial muscles narrow, thin, radiating from border to near *pm*. Two pairs of pallial glands (Fig. 74: *gl*) orange, visible as thickened mantle; one pair anterior, broad, $W \approx$ distance between *pm* and mantle edge; second pair narrow, surrounding *pm* and short distance beyond, with well-developed vessel (Fig. 74: *bv*) surrounding outer edge.

Pallial cavity (Figs. 74, 77, 80, 82) $A \approx 66\%$ *VA*, totally surrounding visceral mass except dorsally adjacent to hinge; very narrow in this region; laterally compressed. Labial palps (Fig. 77: *pp*, 80) $L \approx 16\%$ of gill L , $W \approx 50\%$ of gill W ; each hemipalp elliptical. Anterior ends of demibranchs inserting into short portion between posterodorsal ends of hemipalps (Fig. 80). *Pp* posterior ends taller, with low projections; posterior edge weakly concave, preceded by short smooth inner region,

then as series of low, narrow folds perpendicular to dorsal border (Fig. 80); each fold with rounded ventral end, located near *pp* ventral edge, with narrow smooth inner border; dorsal ends of folds diminishing into dorsal furrow. Folds covering *ca.* 75% of *pp* L, diminishing subtly into remaining anterior region, with smooth inner surface preceding mouth, with thick walls (Fig. 80: *ll*), apparently glandular, yellowish, friable. Latter thicker region gradually decreasing preceding mouth. Gills (Fig. 77: *gi*) narrow; $L \approx 1.5$ visceral mass L. Short anterior base connecting to visceral mass for distance $\approx 25\%$ of gill L, remaining free, sustained by very long, muscular suspensory stalk (Fig. 77: *gt*). Gills dark brown in distal third. Demibranchs subequal (Fig. 77, 80: *do*, *di*). Food grooves (Fig. 82: *fg*) shallow, along ventral edge of each *di*. Each gill filament very narrow, connecting to neighboring filaments by regular ciliary bridges. Transverse septum (Fig. 82: *gq*) every 8–10 filaments, restricted to dorsal demibranch; each pair of septa connecting to *gt*, with short portion protruding dorsally, opposing connection to free portion of gill filament only at one dorsal and one ventral point; septa $W \approx 20\%$ of gill W, wider and taller toward anterior. *Do* connecting to mantle; *di* connecting to visceral mass anteriorly or to counterpart by cilia (Fig. 74: *ci*) along relatively wide bands.

Visceral mass (Figs. 77, 81) restricted to space between hinge area and *pm*, laterally compressed, mostly filled by yellowish gonad. Digestive diverticula surrounding stomach midanteriorly, of same color as gonad; $V \approx 25\%$ of visceral mass V. Posteroventrally greatly compressed by paired *pr*, with portion passing between them, bulging posterior to foot base. Pericardium (*pc*) posterodorsal, just anterior to dorsal half of *pm*, attaching directly to posterodorsal half of *pm*; $V \approx 20\%$ of visceral mass V.

Circulatory and excretory systems (Fig. 81): Pericardium (*pc*) as described above. Paired connections between ctenidial vein and auricles (*au*) narrow, long, surrounding anterior edge of *pr*, inserting into *au* at posterolateral ends. Narrow pallial vessel inserting just anterior and external to connection of *au* and ctenidial vein, coming from anterior mantle. Paired *au* totally fused externally, internally bearing several irregular transverse septa, apparently separating *au* lumens, each with subtriangular, posterior region, wide, curving (with ventral concavity), abruptly narrowing to ventricle connection. Ventricle (*ve*) small, anterior to *au*, internally with few transverse, irregular septa, connecting to *au* apparently with common aperture, protected by low internal, thin-walled, bicuspid valve, surrounding intestine, with main part dorsal. Common aorta very short, anterior to *ve*, contacting intestinal portion crossing anterior end of *pc*; anterior aorta (*aa*) running dorsally at right of this portion of intestine; posterior aorta (*ao*) $W \approx 4$ times narrower than *aa* W , running posteriorly, ventral to intestine. Kidneys inconspicuous, very small, surrounding anteroventral insertions of *pr*.

Digestive system (Figs. 77–78, 81): *Pp* as described above. Lips tall, thinner than preceding posterior regions. Esophagus (Figs. 77–78: *es*) broad, short, curving posterodorsally; $L \approx 33\%$ of *pp* L . Stomach (Fig. 77: *st*) oval; gastric chamber only slightly shorter and wider than *pp*. Large duct to digestive diverticula on right-anterior side, curving posteroventrally; inner gastric surface with longitudinal, broad folds; similar, slightly smaller duct on opposing (left) side, usually with another small duct just anterior to it. Gastric inner surface mostly smooth (Fig. 78). Gastric shield (Fig. 78: *gs*) thin, in anterodorsal gastric chamber. Conjoined style sac-intestine (Figs. 77–78: *ss-in*) weakly separated by pair of very low, longitudinal folds, running posteriorly,

forming wide curve ventrally to ventral end of *pm*. Intestine (Fig. 77: *in*) becoming free from *ss* posteroventrally, abruptly curving almost 360°, running initially left of distal *ss*, then surrounding posterior surface of *pm*, posterior surface of *pc*, performing wide, sigmoid loop. *In* running posteriorly after crossing dorsal surface of *pc* (Fig. 81), exiting to dorsal pallial cavity, running along midline attaching to posterior surface of *pm*; inner surface mostly smooth, except for broad, tall typhlosole, in $W \approx 25\%$ of intestinal W , running along entire L , on face of *pm*; typhlosole narrower at mid-*in*, wider in region running in pallial cavity; ending abruptly close to anus. Anus (Fig. 77: *an*) broad, with long, posterior anal papilla projecting from dorsal edge; anal papilla with flattened, sharply pointed distal end.

Nervous system (Fig. 77): Paired cerebropleural ganglia (*cg*) small, in lateral region just posterior to mouth, close to *ap*. Cerebropleural commissure long, slender, crossing anterior to *es* opening. Pedal ganglia not observed. Visceral ganglia (*vg*) $V \approx 3$ *cg* V , at ventral end on surface of *pm*, just anterior to *gt* origin; ganglia adjacent, close to midline; connective with *cg* running along ventral surface of visceral mass, contacting integument and foot base. Abdominal sense organs not observed.

Material examined: USA, Florida Keys, FMNH 295559, 4 specimens (sta. FK-223; 3 dissected: #1: 64.4 mm L , 65.0 mm H , 9.0 mm W ; #2: 59.0 mm L , 67.0 mm H , 10.7 mm W ; #3: 21.0 mm L , 22.5 mm H , 4.4 mm W); FMNH 311673–311687, 230 specimens (sta. FK-760); FMNH 311812–311813, 2 specimens (sta. FK-786); FMNH 311814–311815, 2 specimens (sta. FK-787). The material of Domaneschi & Martins (2002: 621) from Florida and the Caribbean was also examined.

Distribution: Stated by Turgeon et al. (2009) to range from Florida to Campeche Bank, northern South America to Brazil, the West Indies and Bermuda. *Isognomon alatus* has been reported from the Brazilian coast (Rios, 1994: 241). However, although specimens and further data about this record were intensely searched, no confirmation was obtained. Because the single species of the genus confirmed on the Brazilian coast is the invasive *I. bicolor* (C. B. Adams, 1845), the Brazilian reports have been removed from the synonymy herein as most probably referring to *I. bicolor*; Domaneschi & Martins (2002) also could not confirm previous records of *I. alatus* or *I. radiatus* (Anton, 1838).

Remarks: Shell morphology of *Isognomon alatus* was investigated by Domaneschi & Martins (2002) specifically for comparison with Brazilian specimens of *I. bicolor*; specimens from Florida, including several populations in the Florida Keys, were used in that study. The anatomy of *I. alatus* presented here agrees in most respects with that of the much more elongated species *I. isognomon* (Linnaeus, 1758) figured (but not extensively discussed) by Yonge (1968: fig. 8). The most complete earlier anatomical investigation was by Pelseneer (1911) for *I. perna* (Linnaeus, 1767) and *I. isognomum* (Linnaeus, 1758). The latter study, despite its very brief description, included figures of the gross anatomy, with details of the musculature, gills, labial palps, and digestive tract, which agree with the observations presented here. The one exception is the relationship to the heart and intestine, described by Pelseneer (1911) and Yonge (1968) with the intestine passing through the heart. Specimens studied here could be interpreted as such, but the main portion of the ventricle is ventral to the intestine, with weak, smaller portions of the ventricle passing up and around the intestine. The same condition occurs in members of the genus *Crassostrea* (Ostreidae;

L. Simone, unpubl. data), which is traditionally described as the intestine not passing through the heart. The sharply pointed distal end of the intestine was called "triangular anal funnel" by Tëmkin (2006: fig. 17C).

Various aspects of the biology of *Isognomon alatus* have been studied. Wilk & Bieler (2009) explored the ecophenotypic variation of this species across a tidal microhabitat gradient, based on specimens from Ramrod Key that were also included in the present study. Material from the same location was analysed in the morphological study by Tëmkin (2006), and specimens from the same and/or other Lower Florida Keys locations were used in the molecular analyses by Campbell et al. (1998) and Ó Foighil & Taylor (2000). Chromosome karyotypes of this species were studied by Wada (1978), based on specimens from Biscayne Bay, Florida (just north of the Florida Keys), and by Rodríguez et al. (1983) based on material from Veracruz, Mexico (with a diploid $[2n]$ number = 28). Veracruz specimens were also used in the study of chromosomal rearrangements (meiotic behavior) of *I. alatus* by Rodríguez-Romero et al. (1991). Specimens from Panama were investigated in a study of spermatozoan ultrastructural morphology by Introíni et al. (2009). Siung (1980) investigated its potential as a commercial species in Jamaica.

Isognomon alatus, anatomy. FIG. K1: Intact right view, RV and most of right mantle lobe removed, digestive system shown *in situ* as though visceral mass is transparent; cross sections of indicated levels of intestine (in) and posterior pedal retractor muscle (pr) also shown; FIG. K2: Stomach, right view, mostly opened longitudinally, including style sac (ss-in) and one duct to the digestive diverticula (dd); FIG. K3: Mantle border, section at midlevel of ventral region; FIG. K4: Right labial palp and some adjacent structures, right and slightly ventral view, outer hemipalp (op) deflected; FIG. K5: Pericardial region, right view, right region of pericardium removed; FIG. K6: Gill, cross section at midregion. Scale bars = 2 mm. aa, anterior aorta; an, anus; ao, posterior aorta; ap, auxiliary pedal retractor muscle; ar, anterior pedal retractor muscle; au, auricle; bf, byssal furrow; bv, "blood" vessel; by, byssus; ce, cerebral ganglion; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; di, inner demibranch; do, outer demibranch; es, esophagus; fd, fold; fg, food groove; ft, foot; gd, gill suspensory rod; gi, gill; gl, gland; gm, gill retractor muscle; gq, gill transverse reinforcement in suprabranchial chamber; gs, gastric shield; gt, gill suspensory stalk; hf, hinge fold of mantle; in, intestine; ip, inner hemipalp; ll, labial lips preceding mouth; mb, mantle border; mi, mantle border inner fold; mm, mantle border middle fold; mo, mouth; mp, mantle papillae; mu, mantle border outer fold; op, outer hemipalp; pc, pericardium; pe, periostacum; pl, pallial muscle(s); pm, posterior adductor muscle; pp, labial palp; pr, posterior pedal retractor muscle; sl, crystalline style; ss-in, conjoined style sac-intestine; st, stomach; ve, ventricle; vg, visceral ganglia; vm, visceral mass.

Isognomon alatus. FIGS. K6-K7: Shell morphology, RV, FMNH 295559, 64.4 mm L; FIG. K6: Inner view; FIG. K7: Outer view. FIGS. K8-K10: Anatomy; FIG. K8: Left mantle lobe, inner view; FIG. K9: Byssus, right view, its base in foot also shown; FIG. K10: Posterior pedal retractor muscle, cross section along its midregion, note dark spots corresponding to byssal gland. Scale bars = 5 mm. bv, “blood” vessel; ci, ciliary connection of gill; fd, fold; gl, glands; mb, mantle border; mp, mantle papillae; pm, posterior adductor muscle.