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ANATOMY OF A SMALL CLAM, *ALVEINUS OJIANUS* (BIVALVIA: KELLIELLIDAE), WITH A DISCUSSION ON THE TAXONOMIC STATUS OF THE FAMILY

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ABSTRACT

The anatomy of the small bivalve *Alveinus ojianus* (Yokoyama, 1927) of 1.8–2.0 mm shell length from shallow bays of the northwestern Pacific was studied. The morphological features, in which *A. ojianus* differs from other bivalve species occurring in the shelf waters include: a reduced gill consisting of the inner demibranchs, the posterior filaments of which are replaced by a membrane lining the cloaca; one siphon, the walls of which consist of the cuticular epithelium lining the mantle cavity; the inner mantle fold of the adult is thickened and, in addition to the mantle gland, contains extracellular granules; the labial palps have no sorting ridges, and the gill flexure is without a food groove; the stomach has a thickened cuticular lining and a helicoid structure, which are homologues of the gastric shield of other bivalves; and there are no sorting areas, digestive pouch, caecum or dorsal hood in the stomach. Comparison of its internal morphological features with those of other bivalve taxa demonstrates the close similarity of the Kelliellidae to the deep-water Verticordiidae but not Veneroida, to which Kelliellidae are usually referred. However, comparison of Kelliellidae and Verticordiidae based on shell morphology shows that differences between them makes their relationship improbable. One of the reasons for these contradictions appears to be the paedomorphic development of *A. ojianus* and a mixed nature of the morphological features used for the taxonomy.

Key words: anatomy, mantle, extracellular granules, gill, stomach, paedomorphic features.

INTRODUCTION

The mollusks with a shell length no more than 3–5 mm hold a special position in the taxonomic systems of the Bivalvia. In their morphological features, they can be divided into two groups. One group is the miniature adult bivalves – many species of Propeamussiidae, Carditinae, Circinae and others – in which features are homologous to those of larger taxa, and which are usually included in a subfamily with those larger taxa (Habe, 1977; Dijkstra & Kastoro, 1997; Oliver & Zuschin, 2001). Small bivalves of the second group belong to families or superfamilies – Crenellidae, Montacutidae, Lasaeidae, Philobryidae, Condylocardiidae and others – in which the macroforms are usually absent (Habe, 1977; Morton, 1978; Morton & Scott, 1989; Middelfart, 2000). Their shell morphological features are usually characterized by hypoplasia, and among their internal organs there are structures that are unknown in macroforms (Oldfield, 1961; Morton, 1981; Mikkelsen & Bieler, 1989, 1992; Allen, 2000). As a result of this, in most cases the taxonomic features of the adult small forms are difficult to compare with those of the larger taxa, on which one of the most prevalent systems of Heterodonta is based (Cox, 1969; Keen, 1969). The taxonomic status and phylogenetic relationships some of them are still being discussed (Ockelmann, 1964; Cosel & Salas, 2001).

Alveinus ojianus (Yokoyama, 1927) belongs to the otherwise deep-water family Kelliellidae, a member of the second group of the small bivalves. In addition to *A. ojianus* and another species of this genus recently found in the Red and Arabian seas (Oliver & Zuschin, 2001), in the family there are 12–14 species of *Kelliella* mainly inhabiting the waters of the eastern and southern Pacific (Knudsen, 1970; Bernard, 1989). Allen (2001) has provided a detailed description of this genus, including internal morphology, as well as the taxonomic history of the Kelliellidae and its relationships with other deep-water taxa. In contrast to deep-water *Kelliella*, species of the genus *Alveinus* occur both in shallow bays and open parts of the coastal zone (Miyadi & Habe, 1957; Oliver & Zuschin, 2001).

Some data on biology of *A. ojianus* are to be found in general studies on the ecology and taxonomy of bivalves (Habe, 1950, 1973, 1977; Scarlato, 1981; Evseev, 2000). According to these works, *A. ojianus* is widely distributed in Peter the Great Bay and eastern part of the Sea of Japan, as well as off the Pacific coast of Japan and the South Kuril Islands. It is common in sandy mud at a depth of 2–22 m, where its density may exceed 1,000 specimens per m^2. The bivalves attach to the sand grains with 1–2 byssus threads. The shell length of *A. ojianus* rarely exceeds 2 mm. The mollusks are easily identified by their triangular, lustrous brownish shell.

In this study, we examined the anatomy of *A. ojianus*, no data on which were found in the literature. There is also no information on the phylogenetic relationships of the Kelliellidae with its sister families. In this connection, we also attempted to estimate the taxonomic and phylogenetic significance of the internal features of *A. ojianus* for their use as additional taxonomic characters for the family Kelliellidae, for which the taxonomy is almost completely based on shell morphology.

MATERIALS AND METHODS

The adult and juvenile specimens of *A. ojianus* from the Amursky Bay and Vostok Bay, as well as the open part of Peter the Great Bay, the Sea of Japan, were used in this study. The bivalves were collected with a dredge from the research vessel "Lugovoye" in September 1999 and sampled by SCUBA-diving to 12–14 m depth in July–September 2000–2001 and in March 2002. Most of the specimens investigated measured from 350–1,000 μm in length.

The anatomy was studied by means of serial histological sections. The mollusks were preliminarily fixed in 96% ethanol. The shell valves were removed with a fine needle. The specimens were embedded in paraffin using routine methods, but the holding time in alcohol, chloroform and paraffin was greatly reduced. The sections were made from 7–10 μm with a sliding microtome, mounted on glass slides and stained with Erlich and Boemer's haemotoxylin. A light microscope was used to examine the sections.

ABBREVIATIONS IN THE FIGURES

1	first cardinal tooth
3a	third anterior cardinal tooth
3b	third posterior cardinal tooth
aa	anterior adductor
abf	ascending branchial filaments
ag	apical gland of the foot
al	line of attachment of the inner demibranch to the visceral mass
an	anus
ar	anterior retractor
ba	branchial axis
bg	byssal gland
c	cloaca
cg	terminal cuticula of the gill
cls	cutucular lining of the stomach
cpg	cerebral-pleural ganglion
cso	crystalline style opening
ct	loose connective tissue
dd	digestive diverticula
ea	exhalant aperture
ec	excretory cells
eg	extracellular granules of the mantle lobe
f	foot
g	mantle gland
gg	extracellular granules of the apical gland
gh	gastric helicoid structure
gr	gastric ridges as "traffic circles" of the crystalline style
ia	inhalant aperture
ici	intracapillaceous inclusions
ice	inner ciliated epithelium
icg	intracellular granules
id	inner demibranch
ifc	interfilamentary connective
ig	intestinal groove
ip	inhalant sensory papillae
ipe	inner pavement epithelium
iue	inner unciliated epithelium
k	kidney
lc	branchial lateral cilia
lf	longitudinal muscle fibres
lfc	branchial latero-frontal cilia
lg	marginal groove of the lunule
li	pit of the internal ligament
lml	left mantle lobe
le	external ligament
lp	labial palps
mg	mid-gut
mm	mucous masses
mmf	middle mantle fold
n	nimpha
o	oesophagus
obc	opening of the byssogenous canal
omf	outer mantle fold
ose	outer stratified epithelium
ov	ovary
p	pericardium
pa	posterior adductor

pd	post-apertural dilatation of the mid-gut
pg	pedal ganglion
pj	posterior mantle junction
pp	posterior sensory papillae
pr	posterior retractor
ps	passage from the stomach to the post-apertural dilatation of mid-gut
pss	passage from the style sac to the post-apertural dilatation of mid-gut
pt1	posterior lateral tooth
pvj	postero-ventral mantle junction
r	rectum
rc	rotary cilia of the crystalline style sac
rml	right mantle lobe
rsw	right stomach wall
s	stomach
sc	statocyst capsule
si	exhalant siphon
skr	branchial skeletal rods
sla	slit-like aperture of the crystalline style sac
ss	crystalline style sac
st	statocyst
stl	statolith
t	testis
th	tooth of the gastric helicoid structure
ty	typhlosole
ucf	branchial unciliated filaments
vj	ventral mantle fusion
vsw	ventral stomach wall

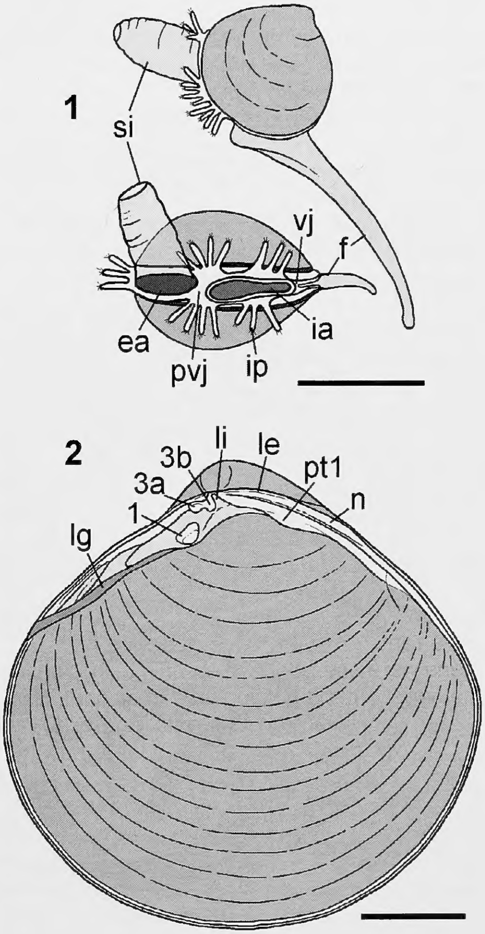
RESULTS

A general view, details of the right shell, and the internal topography of *A. ojianus* are shown in Figures 1–4.

Mantle

The mantle edge has three folds. The thin outer fold is located along the posterior, ventral and anterior shell margin. The thin middle fold fuses near the anterior adductor and ventrally (Fig. 1, *vj*) and forms a broad pedal-byssal gape occupying most of the ventral mantle edge. The inhalant aperture of the mantle cavity is separated from the exhalant aperture by the postero-ventral fusion of the fold (Fig. 1, *pvj*). The thickened edges of the inhalant aperture bear laterally three marginal sensory papillae each. There are one to three short guard cilia at the papillae tips.

Each side of the thickened, fused part of the middle mantle fold has four similar lateral papillae between the inhalant and exhalant apertures. The exhalant aperture terminates in a conic siphon with a smooth, tapering opening. Cuticular tissue forms very thin, semi-transparent walls of the siphon. Like the base of the inhalant aperture, the base of the siphon is thickened and its posterior edge bears three papillae. The total number of sensory papillae on both sides of the inhalant and exhalant apertures amounts to 17. In juveniles, there may be fewer papillae; for example, in a specimen of approximately 500 μm shell length, two pairs of papillae were found at the lateral edges of the inhalant aperture, two pairs of common papillae and one pair of short papillae were located between the inhalant and exhalant apertures. As in adults, three papillae were present dorsal to the siphon.



FIGS. 1, 2. *Alveinus ojianus*. FIG. 1. Lateral and ventral views of living specimen. Bar = 500 μm. FIG. 2. Internal view of right shell valve showing hinge teeth. Bar = 300 μm.

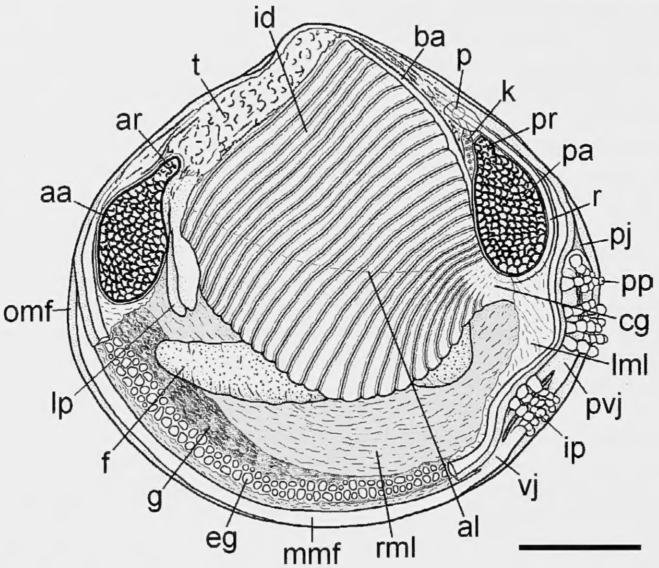


FIG. 3. Topography of internal organs as seen from left side with left shell valve and left mantle lobe removed. Bar = 200 μm.

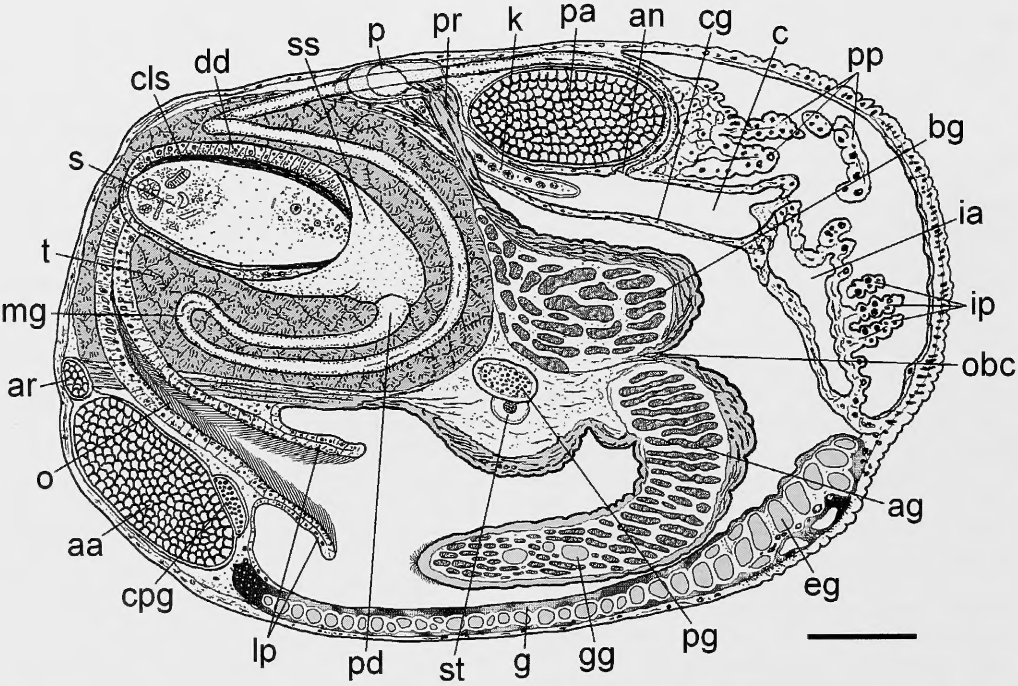
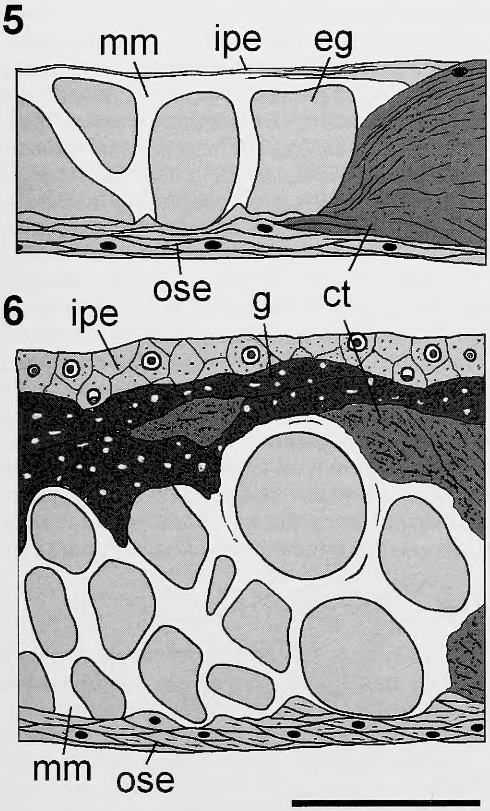


FIG. 4. Internal morphology and configuration as seen from left side (sagittal section). Bar = 100 μm.

The inner mantle fold of the adult is usually thickened (20–40 μm), whereas the thickness of the other proximal mantle part does not exceed 6–8 μm. In width, the thickened fold may vary from relatively narrow ridge to the crescent belt, which starts ventral to the anterior adductor, continues on either side of the pedal-byssal gape and ends close to the inhalant aperture.

Sections made near the posterior edge of the pedal-byssal gape (Fig. 5) and through the central part of the inner thickened fold (Fig. 6) show that the thickening and the proximal dilatation of this fold are formed by connective and glandular tissue, as well as by yellowish extracellular granules.

The surface of the inner wall of the mantle represents a smooth transparent epithelium consisting of polygonal pavement cells with marked nuclei and nucleoli. The wrinkled outer layer of the fold consists of a stratified semitransparent epithelium with large cells and clearly distinguishable nuclei. Within the thickened fold, there is a layer of deeply stained, vesicular floccular glandular tissue, under which the oval or oblong-angular grayish or yellowish granules are located.



FIGS. 5, 6. Extracellular granules of mantle. Bar = 50 μm. FIG. 5. Transverse section through posterior part of layer of granules. Fig 6. Diagonal section through central part of their layer.

The granules usually form one, sometimes two layers. They are enveloped in the homogeneous milk-white masses, which fuse into a single substance resembling the mucous secretion of the labial palps. Where granules form two layers, their size ranges from 20–30 μm in the upper layer and from 10–12 to 15–20 μm in the lower layer. If granules are in one layer, their length amounts to 35–40 μm, and they are large and roundly elongate. The granules are joined to the outer or inner epithelium by their short sides. At the same time, contacting sides of the granules are often free of the milk-white masses. The glandular tissue sometimes separates the granule layers.

The granules occur inside the mantle lobes in both males and females. In adults, the total number of granules is 60–80. On left and right lobes of the same individual, the arrangement may be asymmetrical and varying in shape, size and quantity of the granules. These appear to be different stages in their formation. In juveniles of 350–400 μm shell length, granules were not found. Adults 500–700 μm long collected in October–November have from 20–25 to 40–55 granules in the anterior part of the mantle cavity, where they were located in a single layer. No granules were found in bivalves sampled at the end of March.

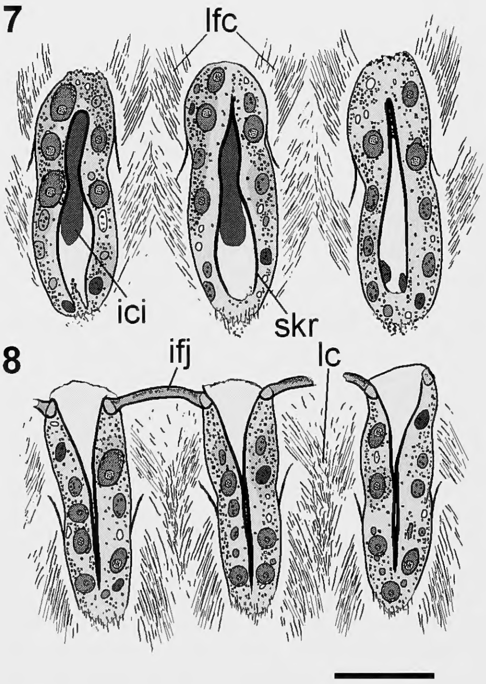
Muscular System

The anterior adductor is elongate and narrowed towards the retractor. The posterior adductor is larger and more rounded in shape. As in *Turtonia minuta* (Fabricius, 1780) and *Lasaea rubra* (Montagu, 1803) (Oldfield, 1955), both adductors consist of smooth, bundled muscle fibres (Figs. 3, 4). In other bivalves, muscle fibres of this type usually form the outer portion of adductor, which is responsible for maintaining valve closure (Yonge, 1936). An inner adductor component of "quick" cross-striated muscle fibres is lacking in *A. ojianus*.

A system of circular, longitudinal and diagonal muscle fibres is located within the foot. The longitudinal and diagonal fibres continue dorsally and form a pair of anterior and a pair of posterior pedal retractors, which do not differ from adductors in their color and structure. The other muscles are represented by smaller bundles and fine fibres scattered within the mantle and the visceral mass.

Gills

The subquadrate gills cover practically all the visceral mass. They consist of inner left and right demibranchs, each with long descending and short ascending lamellae. The descending lamellae extend from the branchial axes. The latter run almost parallel to the external ligament between the subumbonal enlargement of the visceral mass and the posterior adductor (Fig. 3, *ba*). The ascending lamella terminates dorsally in arcuate chitinous bridges attached to the visceral mass along a line between the adductors. The descending and ascending lamellae join ventrally in a flexure with one or two interlamellar connectives. Thin, rounded, chitinous interfilamentar connectives that join skeletal rods of adjacent filaments are rare and irregular.



FIGS. 7, 8. Branchial filaments. Bar = 30 μm. FIG. 7. Descending filaments. FIG. 8. Ascending filaments.

The homorhabdic gill filaments are oval in a transverse section, with two skeletal rods joining abfrontally (Figs. 7, 8, *skr*). The filament walls consist of a one-layer ciliary epithelium with indistinct cell borders. The blood vessels are without muscle septa. Rare blood cells and deeply stained organic inclusions, which appear to be bacterial in a nature, occur within some vessels. The interfilamentar space is filled with long cilia, of which the latero-frontal cilia are the most pronounced. Laterally, each filament bears symmetrical thick cilia (?) of unclear function, the orientation of which is opposite that of the remaining cilia. The former are similar to the “anomalous” latero-frontal cilia delimiting the water fluxes (Atkins, 1938) but differ from them in direction and location. The diameter of the filament is about 30–40 μm; the filament number varies from 17 to 22 in an adult demibranch.

Anteriorly, the demibranch is located between the labial palps. However, the ventral marginal food groove is indistinct. The height of the ascending lamella decreases posteriorly, and it is lacking behind the visceral mass. In its place, the descending lamella of the left demibranch joins the descending lamella of the right demibranch to form the reno-anal cavity (cloaca or suprabranchial cavity) (Pelseneer, 1906). Anteriorly, the lateral walls of the cloaca are formed by the distal limbs of the kidney. The posterior region of the lateral walls and the posterior wall of the cavity are lined internally with an elastic cuticular tissue (Figs. 3, 4, *cg*). The anus opens into the cloaca through the posterior wall; the cloaca communicates ventrally with the siphon through the exhalant aperture. The postero-ventral wall of the cloaca joins the inner fold of the mantle between the inhalant and exhalant apertures.

Foot

The elongate foot is comparatively large. Its middle part is cylindrical; the apical part is pointed and ciliated. At its base, the foot usually expands abruptly (Fig. 4). The postero-ventral part of the foot forms a well-marked heel. *In vivo*, the foot may greatly expand, becoming about twice or three times as long as the shell. In fixed specimens, the foot is usually directed towards the labial palps. The outer wrinkled surface of the foot is covered with a stratified epithelium.

There are two glands in the foot. The byssal gland (Fig. 4, *bg*) lies in the posterior part of the foot and consists of large, deeply stained cells forming the secreting lamellae. The latter are separated by narrow passages, which are filled with a homogeneous, poorly staining secretion. This system of the lamellae and passages converges ventrally to a broad byssogenous canal that opens anterior to the heel. The byssogenous canal is lined with one layer of similarly staining cells. The byssus threads are very thin (5–7 µm) and semi-transparent. Their proximal part is club-shaped; the distal tip bears a small terminal disc, which is attached to large grains of sand or gravel. There are usually one or two byssus threads.

The second apical gland (Fig. 4, *ag*) lies in the central and distal, or only in the distal parts of the foot. It is separated from the byssal gland by a layer of loose connective tissue and by a system of the blood lacunae, within which connective tissue islets and rare radial muscle fibres are scattered. The gland cells also form secreting lamellae, but these are narrower, more compact and less intensely stained in some places than the byssal gland cells. In the intercellular space of the apical gland, isometric or elongate homogenous, faintly stained granules sometimes occur. These are similar to the mantle cavity granules in shape and dimensions. Unlike the byssal gland cells, the cells of the apical gland are small and rare in some individuals. In others, the secreting cells may be absent, and only the axial part of the foot consists of relatively well-stained glandular tissue surrounded by numerous lacunae.

The byssal groove is not marked on the ventral side of the foot, and no openings are found in the distal and middle parts of the foot. The canal of the apical gland appears to open either in the byssogenous canal or in the short byssal slit.

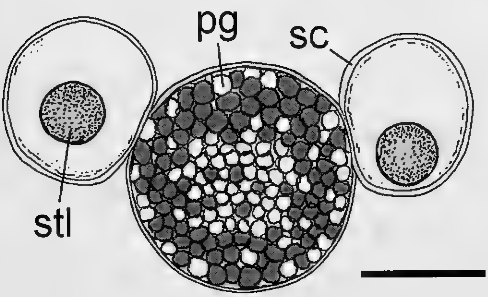


FIG. 9. Pedal ganglion and statocysts. Bar = 30 µm.

Statocysts

These are symmetrical sense organs represented by spherical capsules approximately 30 µm diameter. A spherical yellow or brownish statolith measuring up to 16–17 µm in diameter lies within each statocyst (Fig. 9). Cilia were not observed on the inner capsule walls. The statolith structure appears to be radial. A dark dot is sometimes seen in the center of statolith.

The capsules are located in the anterior part of the foot lateral to the pedal ganglion. They belong to the type B_2 occurring in the Anomalodesmata (Morton, 1985).

Labial Palps

These are parallel anterior and posterior lamellae attached dorsal to the visceral mass (Fig. 4, *lp*). The lamellae are ventrally elongated. Near their base is a broad funnel-shaped mouth that opens into a long oesophagus. The smooth inner surface of the palps and walls of the oesophagus are covered by long, dense cilia, which are inclined proximally. Sorting ridges on the palps are lacking. The ciliary area is usually covered with dense mucus. Under the ciliated epithelium there are scattered, intensely staining mucous gland cells, as well as loose connective tissue with numerous lacunae. The outer surface of the palps is unciliated.

In fixed adults, the length of the anterior palps, including bases, is 250–300 µm, whereas the length of the free ends does not usually exceed 100–150 µm. However, in living specimens the anterior palps are capable of expanding posteriorly up to 400–500 µm.

Alimentary Canal

A long oesophagus enters the stomach antero-ventrally (Fig. 4, *o*). The oesophageal walls consist of one layer of columnar ciliated epithelial cells, the long, dense cilia of which are directed towards the stomach. Mucous gland cells are scattered among the epithelial cells. Deep folds, three to four in number, may be seen in a transverse section of the oesophagus (Fig. 10).

The stomach is hemispherical (Fig. 4, *s*), consisting of anterior and posterior sections.

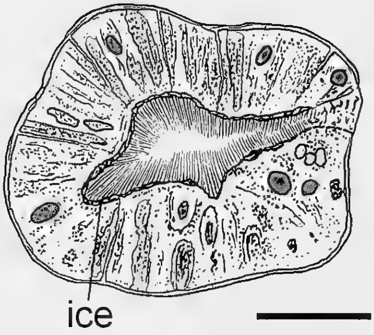


FIG. 10. Oesophagus (transverse section). Bar = 30 μm.

The lateral walls and antero-ventral section are thin and lined with the columnar digestive (?) epithelial cells containing numerous inclusions of different shape and density. The cell borders on the inside of stomach cavity are usually indistinct. Ciliated cells were not found. The dorsal and right-dorsal walls of the anterior section are composed of a thickened cuticular tissue (Fig. 4, *cls*) that is devoid of the inner covering of the digestive cells.

In the center of the anterior section of the stomach there is a cup-shaped organ 100 μm in diameter joined to the right-dorsal wall of the stomach (Fig. 11, *gh*). It is lined by the same thick cuticular tissue as the wall. In a transverse section, the organ is shaped like a convoluted or helicoid lamina. The initial bifurcated part appears to function as the erosive tooth of the gastric shield. The distal height of the wall of the helicoid structure is 30–40 μm. The antero-ventral wall of the helicoid structure is absent, and ventrally there are the curved ridges (Fig. 11, *gr*) running towards the intestinal groove.

The contents of the anterior section of the stomach consist of a mucous secretion and algae, among which the diatoms *Thalassiosira*, *Pyxidicula*, *Odantella* predominate. The diatoms are represented both by the whole

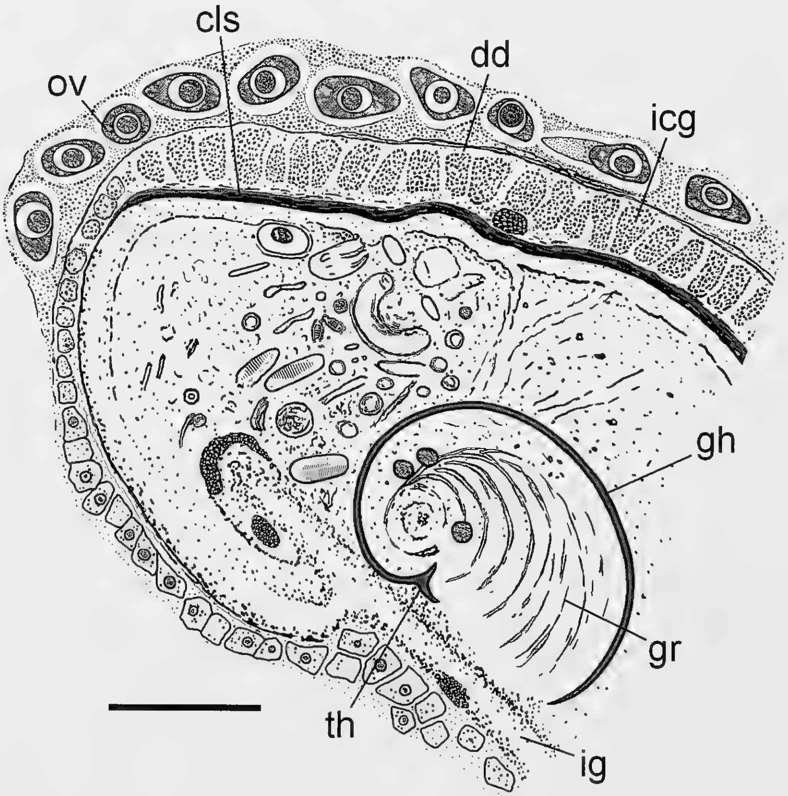


FIG. 11. Antero-dorsal wall of stomach and food contents (left view). Bar = 50 μm.

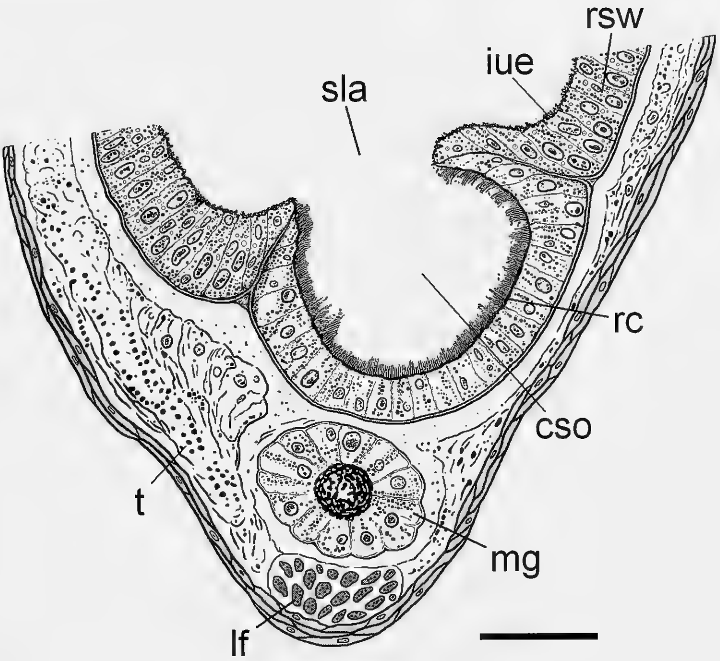


FIG. 12. Crystalline style sac. Transverse section through dorsal part. Bar = 50 μm.

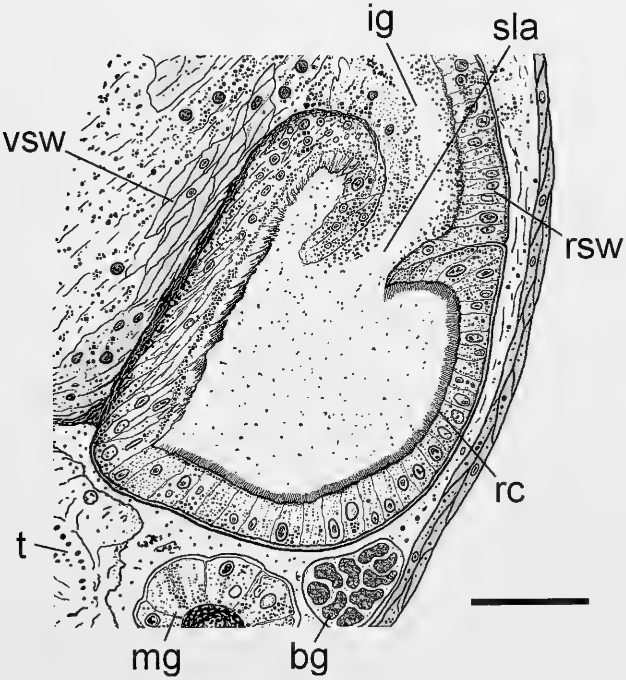


FIG. 13. Crystalline style sac. Transverse section through middle part and ventral wall of stomach. Bar = 50 μm.

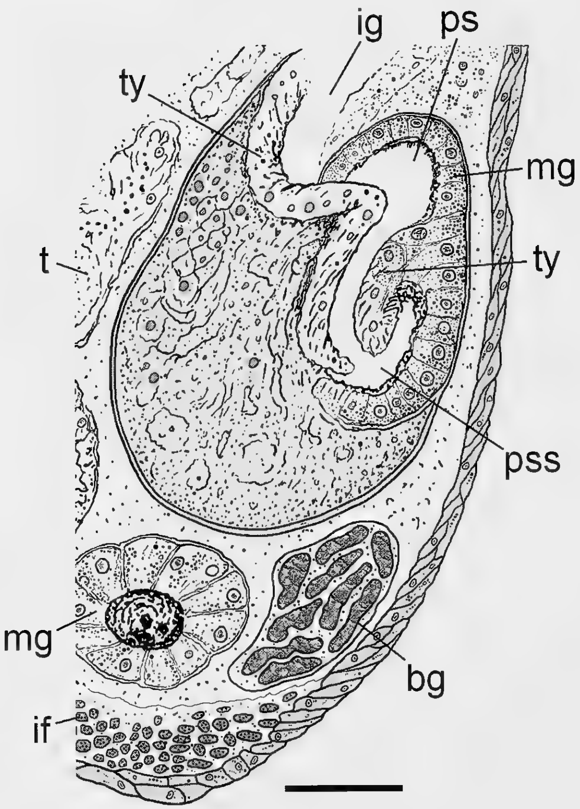


FIG. 14. Crystalline style sac. Transverse section through ventral wall and mid-gut opening. Bar = 50 μm.

thecas (25–30 μm length) and large fragments forming assemblages near the oesophagial opening. The small fragments forming two to three diffuse spots usually occur anterior to the helicoid structure, where one of the ducts of the digestive diverticula appears to be located.

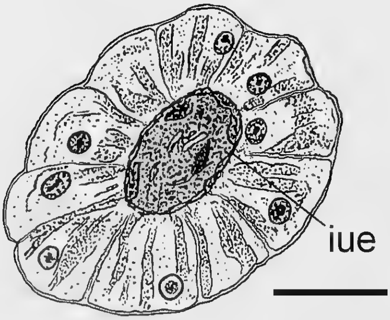


FIG. 15. Mid-gut (transverse section). Bar = 20 μm.

The relatively large crystalline style sac forms the posterior section of the stomach. The single layer of epithelial cells forming the sac walls has large nuclei and numerous inclusions (Figs. 12–14). The inner surface of the sac is densely lined with deeply staining cilia, which rotate the short thickened style clockwise. A thin membrane coat continuous with the similar coat of the stomach wall covers the outer surface of the sac.

The sac communicates with the stomach by means of a longitudinal slit-like aperture (Fig. 12, *sla*). The dorsal part of the aperture, where the style projects from the sac, is broad, whereas the middle part, to which the intestinal groove leads from the stomach, is narrower (Fig. 13, *sla*). In the middle part of the sac, the slit-like aperture is formed from the edges of the anterior sac wall, which are turned inward. Ventrally, the slit-like aperture extends to the bottom of the sac. In a transverse section through this area (Fig. 14), the left inward turned side of the aperture looks like the typhlosole, which is curved like a small tongue. It runs in a spiral along the posterior edge of the opening and the right wall of the sac into the post-apertural dilatation of the mid-gut. In other words, there are two passages that lead into the post-apertural dilatation of the gut. One of them (Fig. 14, *ps*) communicates gut with stomach via the intestinal groove. The other (Fig. 14, *pss*) leads from the sac cavity into the gut through the slit-like aperture.

The mid-gut runs from the bottom of the style sac towards the oesophagus (Fig. 4). At the anterior part of the visceral mass, it immediately loops and runs back to the base of the foot. Then the gut ascends dorsally along the posterior wall of the visceral mass to the pericardial cavity. The hindgut rounds the adductor not only on its dorsal side, as in all bivalves, but also to the ventral side. The rectum turns anteriorly and dorsally.

There are no differences in transverse sections of the gut immediately posterior to the stomach (Fig. 15) and across the ascending part (Figs. 12–14). The gut wall consists of a single layer of large cylindrical cells with distinct nuclei and transparent or stained cytoplasm. In diagonal and longitudinal sections, the cell aggregations look like twisted, intensely staining fibrous bands with the dense cytoplasmic inclusions. The outer wall of the gut is covered by a thin membrane. A similar membrane appears to line the inner gut wall. No cilia and no typhlosole were found in the lumen of the intestine.

The food wastes in the beginning of the mid-gut represent a thickened grayish mass consisting of fragments of algal thecas. Contents of the ascending section are brownish in color. Gaps outlining the borders of the pellets appear in the contents. There are isolated oval dark or brownish pellets in the hindgut.

The digestive diverticula consist of two lobes, which unite under the umbo and surround the stomach laterally. The lobes taper ventrally and extend almost to the base of the foot. In some individuals, large triangular-rounded cells of the diverticular gland together form oval rosettes. In sections transverse to the stomach wall, a branching net of canals located among the cell groups and converging towards the stomach wall can be observed. There are vacuoles, faintly staining nuclei and small dark cytoplasmic granules within the cells. In other individuals (Fig. 11), the thin gland has short broad canals and large cells, the borders of which are indistinct. This appears to be caused by autolysis. In this case, the gland cells contain numerous transparent brownish granules, among which the deeply stained granules form aggregations. Digestive ducts and tubules typical of most bivalves were not found.

Pericardium and Kidneys

The pericardial cavity lies anterior and dorsal to the posterior adductor (Figs. 3, 4). Within the cavity, there is a transparent ventricle, through which the rectum passes, and two thin-walled postero-ventral auricles. The kidney consists of two elongated distal limbs and lies posterior to the pericardium. Within the limbs, faintly staining floccular tissue and large excretory cells with the brownish or dark granules occur (Fig. 16). Each distal limb extends laterally to the terminal cuticula of the gill forming the cloaca and anteriorly to the posterior wall of the visceral mass. In the ven-

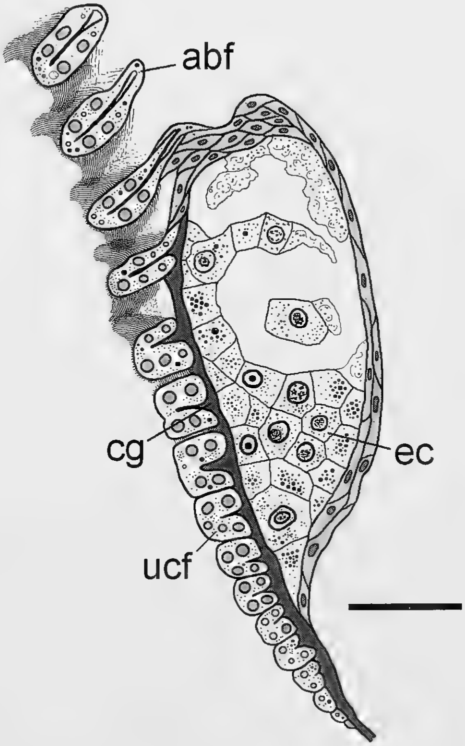


FIG. 16. Kidney. Transverse section through distal part of left limb and terminal cuticula of gill. Bar = 50 μm.

tral part of the cloaca, the kidney limbs only join the terminal cuticula of the gill, and the renal openings are located near the base of the exhalant siphon.

Reproductive System

The species is dioecious; it becomes mature at a shell length of approximately 0.8–1.0 mm. The ovary lies in the visceral mass and surrounds the digestive diverticula and the stomach laterally and posteriorly. The anterior part of the ovary is located in the subumbonal enlargement of the visceral mass. Ventrally, the ovary borders the base of the foot. The testis is similarly located in the visceral mass.

The walls of the follicle of the ovary or testis are very thin. In the ovary, the oval and oval-angular oocytes were predominant among the detached oocytes. The large growing oocytes of 30–40 μm, sometimes 45 μm, diameter with well-marked nuclei and nucleoli were attached to the follicle wall. No ripe oocytes were found in sections. Unlike the ovary, the testis was filled by both spermatocytes I and II and by nutritional cells. Ripe spermatozoa with the large heads occurred in center of the follicle. The largest spermatocytes were 6–7 μm in diameter. Their large nuclei were lightly stained, with small nucleoli and granules of chromatin. Gonial and nutritional cells were attached to the wall.

DISCUSSION

Alveinus ojianus is a member of the family Kelliellidae, which appears to consist of 3–4 genera and 23–25 species, including fossil taxa (Habe, 1953, 1977; Keen, 1969; Bernard, 1989; Hayami & Kase, 1993; Allen, 2001; Oliver & Zuschin, 2001). The taxonomic status and phylogenetic relationships of this family still remain insufficiently well-founded and this could be the result of poor data on the internal comparative and functional morphology both of this species and the family as a whole. As a result, the taxonomic significance of some internal features of the Kelliellidae that could also be useful phylogenetic characters is not yet determined.

The mantle and apical glands as well as the extracellular mantle granules of *A. ojianus* are examples of such features of unclear taxonomic significance. A mantle gland that is structurally and topologically similar to that of *A. ojianus* is known not only in such sister families as the Vesicomyidae (Morton, 1986; Allen, 2001), but also in the more distant Hiatellidae, Crassatellidae, Carditidae, Thyasiridae and Verticordiidae (Pelseneer, 1906; Allen, 1968; Yonge, 1969, 1971; Allen & Turner, 1974). In these taxa, mucus secreted by the gland is used for pseudofaeces formation, for attaching sand grains to a shell and, probably in the Verticordiidae, for encapsulation of motile prey caught in the mantle cavity.

There are also species (for example, *Turtonia minuta*), in which only the female mantle gland takes part in the formation of brooding capsules (Oldfield, 1955, 1963). This species also has an apical gland. None of the above taxa, including *T. minuta*, contain extracellular granules, such as are found in the thickened inner mantle fold of *A. ojianus* and possibly in other species of Kelliellidae (Clausen, 1958).

These granules begin to form at the end of September or the beginning of October when the shell length of the juvenile *A. ojianus* exceeds 350–400 μm. In sections through the mantle of adults, the granules are located both on and under the mantle fold and on the epithelium. In some sections of the gland, there are “empty places”, which are similar to the granules in shape, size and location. Brooding, in which these granules might be used for nutrition of the young, as for instance in the eggs of some gastropods (Thorson, 1936), is absent in *A. ojianus*. In this species, there is no hypobranchial gland that can be used for nutrition of the brooded young (Owen, 1961; Morton, 1977, 1982). The pelagic larvae of *A. ojianus* occur in Peter the Great Bay in August and settle at a shell length about 230–240 μm. Formation of the granules at the beginning of the thermal minimum and their absence in spring indicate that the granules can be used as a food resource not for the young, but for the adult mollusk itself during the winter gametogenesis. Their presence is also independent of sex.

The stomach is another organ that is important in the taxonomy of *A. ojianus*. Its morphology noticeably differs from those in related families Arcticidae, Glossidae, Trapezidae and Veneridae (Purchon, 1960; Reid, 1965). There is no cuticular lining or helicoid structure in the stomachs of members of these families, but they possess digestive pouch, dorsal hood, caecum, gastric shield, and sorting areas consisting of ridges and grooves. The stomach of

Vesicomyidae has not been studied. But in a transverse section, the digestive tubules of large vesicomyids, for example *Calyptogena* (Morton, 1986), are similar to the tubules of most bivalves. The mid-gut, hindgut and rectum of *Calyptogena* differ from the gut of *A. ojianus* in having a folded, ciliated epithelium on the inner wall and in the presence of a typhlosole in the rectum or by absence of the anterior loop of the gut as, for instance, in *Isorropodon* (Cosel & Salas, 2001). The slit-like aperture of the style sac opening is not in the mid-gut, as in many bivalves, but in the posterior section of the stomach. It is a remarkable distinguishing feature of the alimentary canal of *A. ojianus* and, possibly, other members of Kelliellidae. Taking into account the general configuration and composition of functionally important sections of the stomach, which have been used as taxonomic characters of suborders or orders in the Bivalvia (Purchon, 1978, 1987; Starobogatov, 1992), as well as other internal features – siphons, papillae, mantle apertures, labial palps, terminal cuticula of the gill, foot and its glands (Table 1) – the inclusion of Kelliellidae in the same subdivision of the Veneroida as the above families may be considered as insufficiently founded.

On the other hand, some morphological features of *A. ojianus* that seem to be taxonomically important in comparison to veneroid families, occur in more distant phylogenetic lines. For instance, the cuticular lining of the stomach wall of *A. ojianus* and, possibly, other species of Kelliellidae is most similar either to that of more primitive Nucinellidae, Solemyiidae and Nuculidae, or of the specialized Verticordiidae, Poromyidae and Cuspidariidae (Starobogatov, 1992). A more detailed comparison shows that, like *A. ojianus*, the stomach of primitive taxa has no caecum, no digestive pouch, and no large ciliary fields, but has sorting ridges, large pouch-like digestive tubules, and small embayments in the right-dorsal wall resembling the dorsal hood (Purchon, 1956; Allen & Sanders, 1969). In addition to the cuticular lining occupying a small part of the stomach wall, a common gastric shield joined with the underlying columnar cells by means of pseudociliary cuticular connectives may also occur in stomach of the primitive mollusks (Halton & Owen, 1968). However, the cup-shaped helicoid structure is lacking, and the general configuration of the stomach of the primitive bivalve differs markedly from that of *A. ojianus* and other taxa, such that the former could be separated as a special subclass based on their morphology and digestion features alone (Purchon, 1987).

As in *A. ojianus*, the stomachs of specialized taxa (e.g., Verticordiidae) have no dorsal hood, caecum, sorting areas and digestive tubules similar to those of other bivalves (Allen & Turner, 1974). The cuticular (scleroprotein) lining may bear the irregular, almost parallel ridges covering the most part of the anterior section of the stomach or fan-like divergent curved ridges resembling those located at the bottom of the *A. ojianus* helicoid structure. The cuticular lining of the verticordiid stomach also has spiral structures (Allen & Turner, 1974: fig. 63), which are comparable with the helicoid structure of *A. ojianus* in shape and location. In addition to the dorsal opening, the style sac seems to have an anterior slit-like aperture that opens into the stomach, as in *A. ojianus* (Allen & Turner, 1974: figs. 19, 77). Other similarities to *A. ojianus* include a mid-gut consisting of columnar cells lacking cilia, although in some verticordiids a typhlosole may occur inside the gut. Also, the labial palps of the Verticordiidae are usually funnel-shaped and without the sorting ridges, but possess wing-shaped processes, buccal cavities or special glands used for capture and partial digestion of motile prey.

In addition to the above features, as well as valves and additional tentacles in the mantle apertures that are features concerned with nutritional specialization at specific or generic levels (Allen & Turner, 1974), the Verticordiidae have important characters at the familial level that are absent in *A. ojianus*. These are a thickened muscular wall surrounding the stomach and oesophagus, dilatation of the hindgut – an analogue of the “masticatory stomach” of Cephalaspidea (Ivanov, 1985) – a radial mantle gland consisting of separate islets, and a shell, which morphologically and structurally differs from the Kelliellidae, such that inclusion of these families within the same order is not possible.

Therefore, although there is no relationship between the Kelliellidae and the Verticordiidae, a similar evolutionary route can cause a high degree of likeness in the internal morphological features of these taxa (Table 1). One of the features of this evolutionary path is their small body size as, for instance, in many species of Kelliellidae, Verticordiidae, and Vesicomyidae, in which the average shell

TABLE 1. The internal morphological features of the Kelliellidae, Veneroida and Verticordiidae and their significance in the taxonomy and evolutionary development of Kelliellidae. (+) – feature present; (±) – feature may be absent; (-) – feature absent; (*) – feature has significance; (≠) – feature has no significance; (?) – significance of feature not determined.

	Taxa			Significance	
Morphological Features	Kelliellidae	Veneroida	Verticordiidae	Taxonomy	Paedo-morphosis
Mantle Organs					
Mantle gland	+	±	±	*	≠
Extracellular granules	+	-	-	*	*
Only exhalant siphon	+	-	+	≠	*
Apical siphonal papillae	-	+	-	≠	≠
Basal siphonal papillae	+	+	+	*	*
Ciliated mantle lobes	-	+	-	≠	?
Mantle Cavity Organs					
Inner and outer branchial lamellae differ in size	-	±	±	*	*
Only inner branchial lamellae	±	-	±	*	*
Ventral marginal food groove	±	+	±	*	?
Free posterior gill end	-	+	-	?	?
Homorhabdic branchial filaments	+	-	+	≠	*
Adductor consisting of one portion	±	-	±	*	*
Visceral Mass Organs					
Byssal gland	+	-	+	≠	?
Apical gland	+	-	-	*	≠
Ventral foot groove	-	-	±	*	≠
Ciliated foot	+	+	-	?	≠
Statocysts of B_2-type	+	?	+	≠	?
Alimentary Canal Organs					
Funnel-shaped labial palps	+	-	±	≠	*
Sorting ridges of labial palps	±	+	±	*	*
Labial muscle rim	-	+	-	≠	*
Cuticular lining of stomach	+	-	+	*	?
Gastric helicoid structure	+	-	?	*	?
Digestive pouch	-	+	-	≠	*
Dorsal hood	-	+	±	≠	*
Caecum of stomach	-	+	-	≠	*
Sorting areas of stomach	-	+	-	≠	*
Typhlosoles of stomach	±	+	±	*	?
Digestive tubules	±	+	+	?	*
Crystalline style sac combined with gut	-	±	?	≠	≠
Crystalline style sac combined with stomach	+	-	?	*	*
Typhlosole of gut	±	+	±	?	*
Dilatation of gut	-	-	±	≠	≠

length does not exceed 4–5 mm (Knudsen, 1970; Allen & Turner, 1974; Bernard, 1989; Warén, 1989; Hayami & Kase, 1993; Allen, 2001; Cosel & Salas, 2001). Mollusks of such a size usually have either only an inner demibranch or an inner and underdeveloped outer demibranch. The number of the gill branchial filaments rarely exceeds 22–23. At the same time, the branchial axis is located dorsally, and the posterior filaments are replaced by a membrane or differ from other filaments in their shape and ciliary system (Pelseneer, 1906). The adductors of these bivalves sometimes consist only of the outer portion of smooth muscle fibres, which in ontogenesis were previously the internal portion of cross-striated fibres (Oldfield, 1955). In these mollusks, the pedal gape of the mantle cavity may be not separated from the inhalant aperture (Clausen, 1958). In cases in which the pedal gape is separate, the inhalant siphon is usually absent, and the exhalant siphon represents a simple tube without the apical papillae, as in juvenile Veneridae (Ansell, 1962).

The alimentary canal is also characterized by such "juvenilization" (Table), that is, paedomorphosis (De Beer, 1958). The paedomorphic features include the funnel-shaped labial palps, the total or partial absence of the sorting ridges on the palps, the morphologically indistinct mouth without the labial muscle rim, the epithelium of the oesophagus covered with long cilia, which occurs in macroforms in the veliger or pediveliger stages, the absence of the digestive pouch, caecae and sorting areas as, for example, in Erycinidae and other bivalve families (Oldfield, 1955, 1963; Chanley & Andrews, 1971; Alatalo et al., 1984). These features as well as the underdeveloped gill and adductors, the primitive inhalant aperture without protection of the mantle cavity by valves; the unciliated epithelium of the mantle cavity and intestinal tract and cloaca, and the accelerated reproductive development, which in *A. ojianus* matures at a shell length of about 1 mm, suggest incomplete somatic development of not only the internal organ, but also the outer skeletal organ, the shell.

Thus, the Verticordiidae and the Kelliellidae are of different phylogenetic lines, but with a similar pattern of evolutionary development - paedomorphosis, in which the post-juvenile stages prove to be "cut" (De Beer, 1958; Gould, 1977) in taxa of both families. Therefore, based on internal morphological characters, an attempt to determine the place of Kelliellidae in the taxonomic system rested on the conchological features of adults, meets with failure. This is caused by insufficiently studied internal organs of bivalves as a whole. In conchological features, the family Kelliellidae appears to be among the most primitive Heterodonta, but it is impossible to determine its place more distinctly because of poorly studied juvenile stages of Heterodonta with morphological characters similar to those of adult kelliellids.

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MORPHOLOGICAL AND MOLECULAR ANALYSIS OF THE STATUS AND RELATIONSHIPS OF *OXYCHILUS PAULUCCIAE* (DE STEFANI, 1883) (GASTROPODA: PULMONATA: ZONITIDAE)

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ABSTRACT

Morphological data shows that *O. paulucciae* (De Stefani, 1883) belongs to *Oxychilus* (*s. str.*), *sensu* Giusti & Manganelli (1999), and is distinguished from sympatric, similarly shelled species, such as *O. draparnaudi* (Beck, 1837) and *O. meridionalis* (Paulucci, 1881), by its larger shell (diameter: 13.9–17.4 mm), smaller umbilicus (about 1/8 of shell diameter), narrow mid-penial region, internal ornamentation of proximal penis consisting of longitudinal pleats, and a less developed vaginal gland, often forming an incomplete ring around proximal vagina. DNA sequence data, analysing the ITS-1 region in two specimens of *O. paulucciae* and representatives of several other species occurring in Tuscany, *O. draparnaudi*, *O. majori* (Paulucci, 1886), *O. meridionalis*, *O. pilula* (Paulucci, 1886) and *O. uzielli* (Issel, 1873), indicates that *O. paulucciae* represents a well-differentiated evolutionary lineage and suggests it has close relationships with *O. meridionalis* and *O. uziellii*. Finally, analysis of morphological characters and DNA sequencing data demonstrates that *Oxychilus lanzai* Forcart, 1967, is a junior synonym of *O. paulucciae*.

Key words: Zonitidae, *Oxychilus paulucciae*, *Oxychilus lanzai*, systematics.

INTRODUCTION

During the 1960s, the leading Swiss malacologist L. Forcart received many specimens of Tuscan *Oxychilus*, most collected by Prof. B. Lanza (Museo Zoologico de "La Specola", Università di Firenze) in NW Tuscany (provinces of Massa Carrara, Lucca and Florence). Based on these specimens, Forcart (1967) produced a first revision of many taxa of the species group described from Tuscany in the nineteenth century (Table 1), and described a new species: *O.* (*Ortizius*) *lanzai* Forcart, 1967.

In the late 1960s, one of us (FG), together with M. Mazzini, was involved in the study of the malacofauna of the Apuan Alps (NW Tuscany) as part of a project promoted by the Società Italiana di Biogeografia (Giusti & Mazzini, 1971). The study of the *Oxychilus* material collected on this occasion led to revision of that studied by L. Forcart (1967, 1968). It became evident that Forcart, using diaphanized preparations of the whole distal genitalia mounted on glass slides, sometimes misinterpreted the internal structure of the penis, which was then considered very important for the diagnosis of subgenera: parallel rows of papillae for *Oxychilus s. str.*; parallel uninterrupted pleats for *Ortizius* Forcart, 1957. This happened for specimens from Tana di Magnano, Garfagnana, Province of Lucca, which he assigned to *O.* (*Oxychilus*) *paulucciae* (De Stefani, 1883), but when re-examined turned out to be a species of *Ortizius*, anatomically identical to that from the Grotta della Risvolta, Apuan Alps, which he assigned to *O. lanzai*.

Giusti & Mazzini (1971) declined to express formal synonymy between *O. lanzai* and *O. paulucciae*, because they realized that since Forcart did not have topotypical specimens of the classic Tuscan taxa for anatomical investigation, he based his study on spirit material with shells similar to those of the types, thus misinterpreting some classic species (shell shape is very rarely diagnostic in species of *Oxychilus*). They merely stated that the entire group of nominal species described for NW Tuscany required revision before the problem

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TABLE 1. Nominal taxa of the species group introduced for Tuscan *Oxychilus* (excluding those established for species living in the Tuscan Archipelago) (for syntypes kept in the Museo di Zoologia “La Specola”, the collection number is followed by the number of specimens).

Nominal taxon	Status
Zonites Uziellii Issel, 1872: 60–61. Type material: lectotype (MZUF 689) and one paralectotype (MZUF 11521) in Paulucci collection. Type locality: “Fra i detriti del Gombo, presso Pisa”, but see Manganelli & Giusti (2000).	*Oxychilus uziellii* (Issel, 1872) (Manganelli & Giusti, 1985, 1993, 2001)
Hyalina scotophila De Stefani, 1879: 38–39. Type material: 4 syntypes; one in Paulucci collection (MZUF 738) and three in Museo di Storia Naturale dell’Accademia dei Fisiocritici in Siena. Type locality: “Siena, in un profondo condotto sotterraneo”	probably junior synonym of *Oxychilus draparnaudi* (Beck, 1837) (Manganelli & Giusti, 2001)
Hyalinia meridionalis Paulucci, 1881: 78–79, pl. 1, fig. 6. Type material: lectotype (MZUF 13187) and 30 paralectotypes in Paulucci collection (781/12, 828/7, 829/1, 830/3, 832/2, 13188/5). MZUF 781, 829, 830, 832, 833 belong to other species (Manganelli & Giusti, 2001). Type locality: “Fabbriche presso i Bagni di Lucca”.	*Oxychilus meridionalis* (Paulucci, 1881) (Manganelli & Giusti, 2001)
Hyalinia Isseliana Paulucci, 1882: 165–168, pl. 9, fig. 13. Type material: lectotype (MZUF 687) and 4 paralectotypes (MZUF 688/3, 13346/1) in Paulucci collection (Manganelli & Giusti, 2001). Type locality: “Fabbriche presso i Bagni di Lucca (Lucca; Toscana)”.	junior synonym of *Oxychilus meridionalis* (Paulucci, 1881 (Manganelli & Giusti, 2001)
Hyalinia Guidoni De Stefani, 1883: 35, 1888: fig. 3. Type material: unknown. Type locality: “Forno Volasco, 480 [m]”.	nominal taxon in need of revision
Hyalinia Paulucciae De Stefani, 1883: 35–36, 1888: fig. 1. Type material: no syntype being known, a neotype was designated (Fig. 1). The neotype (a spirit specimen) is in the Museo Zoologico de “La Specola”, Sezione del Museo di Storia Naturale dell’Università di Firenze (Italy) (MZUF 17597) Type locality: “Alp. E. Vagli 850” (p. 36) and “Strada nazionale presso il Ponte di Ceserana” (caption of un-numbered plate). “Alp. E” is for “Pendici orientali delle Alpi Apuane dall’alveo del fiume Serchio e dell’Aulella fino alla crina” (p. 17). Following the designation of the neotype, the type locality becomes “Vagli di sopra, Valle Arnetola, 930 m asl (Vagli di sotto, Lucca), 32TPP0084”.	*Oxychilus paulucciae* (De Stefani, 1883) (this paper)
Hyalina scotophila var. *notha* Paulucci, 1886: 12–13, pl. 1, fig. 2. Type material: 27 syntypes (MZUF 788/4, 789/9, 790/5, 791/7, 792/1, 13347/1) in Paulucci collection. The shell MZUF 792 is that illustred by Paulucci (1886). Type locality: “alla Fonte dell’Appetito presso Porto Santo Stefano, presso la vetta del Telegrafo, sopra al Convento de’ Passionisti, in vicinanza delle scogliere di Calagrande ... All’isola del Giglio in una località denominata «Franco»“.	junior synonym of *Oxychilus draparnaudi* (Beck, 1837) (Giusti, 1968; Manganelli et al., 1995)

(Continues)

(Continued)

Nominal taxon	Status
Hyalinia nitidula var. *amiatae* Westerlund, 1886: 57. Type material: 33 syntypes in Paulucci collection (MZUF 807/12, 19290/10, 19291/11). Type locality: "Italien, M. Amiata" [in località La Scarpa].	junior synonym of *Oxychilus draparnaudi* (Beck, 1837) (Manganelli et al., 1995)
Hyalinia sylvicola Westerlund, 1886: 59. Type material: 8 syntypes in Paulucci collection (MZUF 805). Type locality: "Italien, Bosco di San Vittore in Toskana". [= Pozza delle Monache, Bosco di San Vettore].	nominal taxon in need of revision
Hyalinia blauneri var. *cloacarum* Westerlund, 1886: 61. Type material: 8 syntypes in Paulucci collection (MZUF 804) Type locality: "Italien b. Volterra" [= Fogna della Chiesa di Camporbiano].	nominal taxon in need of revision
Hyalina scotophila var. *dilatata* Westerlund, 1886: 61. Type material: 8 syntypes in Paulucci collection (MZUF 19289). Type locality: "Ital., San Martino b. Palma" [= San Martino alla Palma]	nominal taxon in need of revision
Oxychilus (*Ortizius*) *lanzai* Forcart, 1967: 114–115, fig. 1, pl. 1, fig.1. Type material: The holotype (spirit specimen, MZUF 462), seven paratypes (spirit specimens, MZUF 454/2, 463/5 from "Grotta del Buggine" and six paratypes (four spirit specimens, MZUF 683; two shells, MZUF 691) from "Grotta della Risvolta" are in the Museo Zoologico de "La Specola", Sezione del Museo di Storia Naturale dell'Università di Firenze (Italy). Four other paratypes from "Grotta del Buggine" (two spirit specimens, NMB 6562; two spirit specimens, MFP) are in the Naturhistorisches Museum Basel (Switzerland) and in the Museo "Felice Poey", La Habana (Cuba) respectively. Type locality: "Toskana, Prov. Lucca, Apuaner Alpen, Grotta del Buggine 315 m (N. 166 T.) bei Cardoso Stazzemese".	junior synonym of *Oxychilus paulucciae* (De Stefani, 1883) (this paper)
Oxychilus (*Ortizius*) *tongiorgii* Giusti, 1969: 367–369, figs. 1–2, 5A, pl. 1, figs. 1, 2. Type material: holotype and 9 paratypes in Giusti collection. Type locality: "Grotta dei Ladri (n. 262 T. Pi) Monti Pisani nei pressi di Asciano".	junior synonym of *Oxychilus meridionalis* (Paulucci, 1881) (Manganelli & Giusti, 2001)
Oxychilus (*Ortizius*) *forcartianus* Giusti, 1969a: 369–371, figs 3, 4, 5B, pl. 1, figs. 3, 4. Type material: holotype and 3 paratypes in Giusti collection. Type locality: "Grotta dei Fiorentini presso Pomarance (Grosseto)".	junior synonym of *Oxychilus meridionalis* (Paulucci, 1881) (Manganelli & Giusti, 2001)

of the relationships between *O. paulucciae* and *O. lanzai* could be tackled.

The oldest established Tuscan *Oxychilus* species – *Zonites uziellii* Issel, 1872; *Hyalinia meridionalis* Paulucci, 1881; and *Hyalinia isseliana* Paulucci, 1881 – have now been revised (Manganelli & Giusti, 1985, 1993, 2000, 2001), and it is therefore possible to revise *O. paulucciae*, to clarify its relationships with other Tuscan *Oxychilus* and to resolve the problem of its synonymy with *O. lanzai*.

The first problem with *Hyalinia paulucciae* is that its type-material has not been traced. The malacological collection of De Stefani, which remained in Pisa when he moved to Siena and then Florence, was irreparably damaged during the Second World War. In order to define this nominal taxon objectively, we have selected a neotype, because the "qualifying conditions", required for the designation of a neotype, exist (ICZN, 1999: Art. 75.3). The neotype, the shell and genitalia of which are shown in Figure 1 (shell) and Figures 3–4 (genitalia), is deposited in the Museo Zoologico de "La Specola", Sezione del Museo di Storia Naturale dell'Università di Firenze, Italy (catalogue no. 17597). It is a spirit specimen collected near Vagli, one of the two localities where De Stefani reported his species. Its shell matches the original description perfectly.

MATERIAL AND METHODS

Morphological Analysis

Whole shells were photographed under the light microscope (Wild M5A). All dimensions – NW number of whorls (Ehrmann, 1933: fig. 12), SD shell diameter, SH shell height and UD umbilicus diameter – were measured using a micrometer.

Live specimens were drowned in water, then fixed and preserved in 75% ethanol buffered with sodium carbonate. The bodies were isolated after crushing the shells and dissected under the light microscope (Wild M5A) using thin-pointed watchmaker's tweezers. Anatomical details were drawn using a Wild camera lucida. Some parts of the genital organs – duct of bursa copulatrix, distal vagina, epiphallus, flagellum, proximal portion of penis, "bottle-neck", distal penis and penial sheath – were measured by micrometer.

Radulae were extracted manually from buccal bulbs, washed in 75% ethanol, mounted on copper stubs with electronconductive glue, sputter-coated with gold and photographed using a Philips 505 SEM.

All specimens listed in material examined belong to anatomically determined populations. The material examined is listed as follows: locality, municipality and province names in parenthesis, UTM reference, collector(s), date, number of specimens in parenthesis (sp spirit preserved specimen/s, sh shell/s) and bibliographical reference, in parenthesis, if they are voucher specimens. Locality names and UTM references are according to the official 1:25,000 scale map of Italy (series M 891).

Key to museum and collection acronyms: FGC, collection F. Giusti, Dipartimento di Scienze Ambientali, University of Siena, Italy; NMB, Naturhistorisches Museum Basel, Switzerland; MFP, Museo "Felice Poey", La Habana, Cuba; MZUF, Museo Zoologico "La Specola", Sezione del Museo di Storia Naturale dell'Università di Firenze, Italy; SCC, S. Cianfanelli collection, Firenze, Italy.

Key to acronyms in figures: B, "bottle-neck"; BC, bursa copulatrix; BS, "bottle-neck" sheath; BW, body wall; DBC, duct of bursa copulatrix; DP, distal portion of penis; E, epiphallus; EO, epiphallus opening; F, flagellum; FO, free oviduct; POS, prostatic portion of ovispermiduct; PP, proximal portion of penis; PR, penial retractor; PS, penial sheath; UOS, uterine portion of ovispermiduct; V, vagina; VD, vas deferens; VG, vaginal gland.

Molecular Analysis

DNA Extraction, PCR and Sequencing

Two specimens of *O. paulucciae* and others of several species occurring in Tuscany – *O. draparnaudi* (Beck, 1837), *O. majori* (Paulucci, 1886), *O. meridionalis* (Paulucci, 1881), *O. pilula* (Paulucci, 1886), and *O. uzielli* (Issel, 1873) – were used for molecular analysis. One specimen of *O. paulucciae* (*O. paulucciae* 1) was collected in the type locality of this species and the other (*O. paulucciae* 2) in a cave where part of the type material of *O. lanzai* was collected. Collection sites and codes of the samples used for molecular analysis are indicated in Table 2. Total DNA was extracted from fresh foot muscle using standard phenol/chloroform and ethanol precipitation methods as described in Salomone et al. (2002). We amplified the ITS-1 region by PCR using the primer pair CS249 (5'TCGTAACAAGGTTTCCG3') and DT421 (5'GCTGCGTTCTTCATCG3') (Schlötterer et al., 1994). PCR amplification was performed in a reaction volume of 50 µl following a profile consisting of 25 cycles with temperatures of 95°C for 20", 55°C for 30" and 72°C for 30", plus a final extension step at 72°C for 5'. The products obtained using these conditions were very clean single bands, showing no evidence of double or ambiguous bands. After elimination of excess nucleotides and primers by gel separation and purification with Nucleospin Extract (Genenco) columns, both strands of the final products were sequenced using the two amplification primers. Sequencing reactions were performed at the core facility of MWG-BIOTECH, Ebersberg, Germany. All sequences were checked manually for sequencing errors and submitted to GenBank (Accession Nos. AY373635–AY373645).

TABLE 2. Material examined for DNA sequencing.

Taxon	Locality
Oxychilus draparnaudi 1	Castello di Brolio (Gaiole in Chianti, Siena), 32TPP9909, G. Manganelli & L. Manganelli leg. 01.10.2000
Oxychilus draparnaudi 2	Giglio Island: Giglio Castello (Isola del Giglio, Grosseto), 32TPM5692, V. Vignoli leg. 30.06.2000
Oxychilus majori	Monte Argentario: Grotta di Punta degli Stretti 250 T/GR (Monte Argentario, Grosseto), 32TPN7800, S. Cianfanelli & G. Manganelli leg. 07.10.2001
Oxychilus meridionalis 1	Capanno (Castelnuovo Berardenga, Siena), 32TPP9308, G. Manganelli & L. Manganelli leg. 28.05.2000
Oxychilus meridionalis 2	Passo della Calla (Santa Sofia, Forlì), 32TQP2060, S. Cianfanelli & G. Manganelli leg. 16.09.2001
Oxychilus meridionalis 3	Fabbriche di Bagni di Lucca (Bagni di Lucca, Lucca), 32TPP3175, S. Cianfanelli & E. Lori leg. 15.04.2003
Oxychilus paulucciae 1	Apuane Alps: Vagli di sopra, Valle Arnetola (Vagli di sotto, Lucca), 32TPP0084, S. Cianfanelli & M. Calcagno leg. 24.06.2000
Oxychilus paulucciae 2	Apuane Alps, Grotta della Risvolta 158T/LU (Stazzema, Lucca), 32TPP0372, S. Cianfanelli & M. Calcagno leg. 14.10.2001
Oxychilus pilula	Capraia Island: Il Laghetto (Capraia Isola, Livorno), 32TNN6665, F. Barbagli & S. Lotti leg. 22.06.2001
Oxychilus uziellii	Fosso delle Filicaie, San Giusto in Salcio (Gaiole in Chianti - Radda in Chianti, Siena), 32TPP9115, G. Manganelli & L. Manganelli leg. 28.05.2000
Retinella olivetorum	Fosso delle Filicaie, San Giusto in Salcio (Gaiole in Chianti - Radda in Chianti, Siena), 32TPP9115, G. Manganelli & L. Manganelli leg. 28.05.2000

Phylogenetic analysis

Sequences were aligned using Clustal W (Thompson et al., 1994) and slightly modified by eye. Boundaries of the ITS-1 region were estimated by comparison with those determined for *Albinaria caerulea* (Deshayes, 1835) (Genbank Acc. No. AF136012). Phylogenetic analyses were performed with PAUP* (version 4.0b10; Swofford, 2001) with *Retinella olivetorum* (Gmelin, 1791) as outgroup, using maximum parsimony (MP) and maximum likelihood (ML). MP reconstruction was performed by an exhaustive search of the most parsimonious tree(s) with equal weighting of all characters. Gaps were treated as missing data. For ML analysis, the appropriate substitution model of DNA evolution that best fitted the data set was determined by the likelihood ratio test and the Akaike information criterion (AIC; Akaike, 1974) with Modeltest 3.04 (Posada & Crandall, 1998). A ML heuristic search (Step-Add random; TBR branch swapping) was then run under the likelihood setting estimated by Modeltest. Support for individual nodes was evaluated by bootstrap analysis (heuristic search) with 1000 replications.

RESULTS

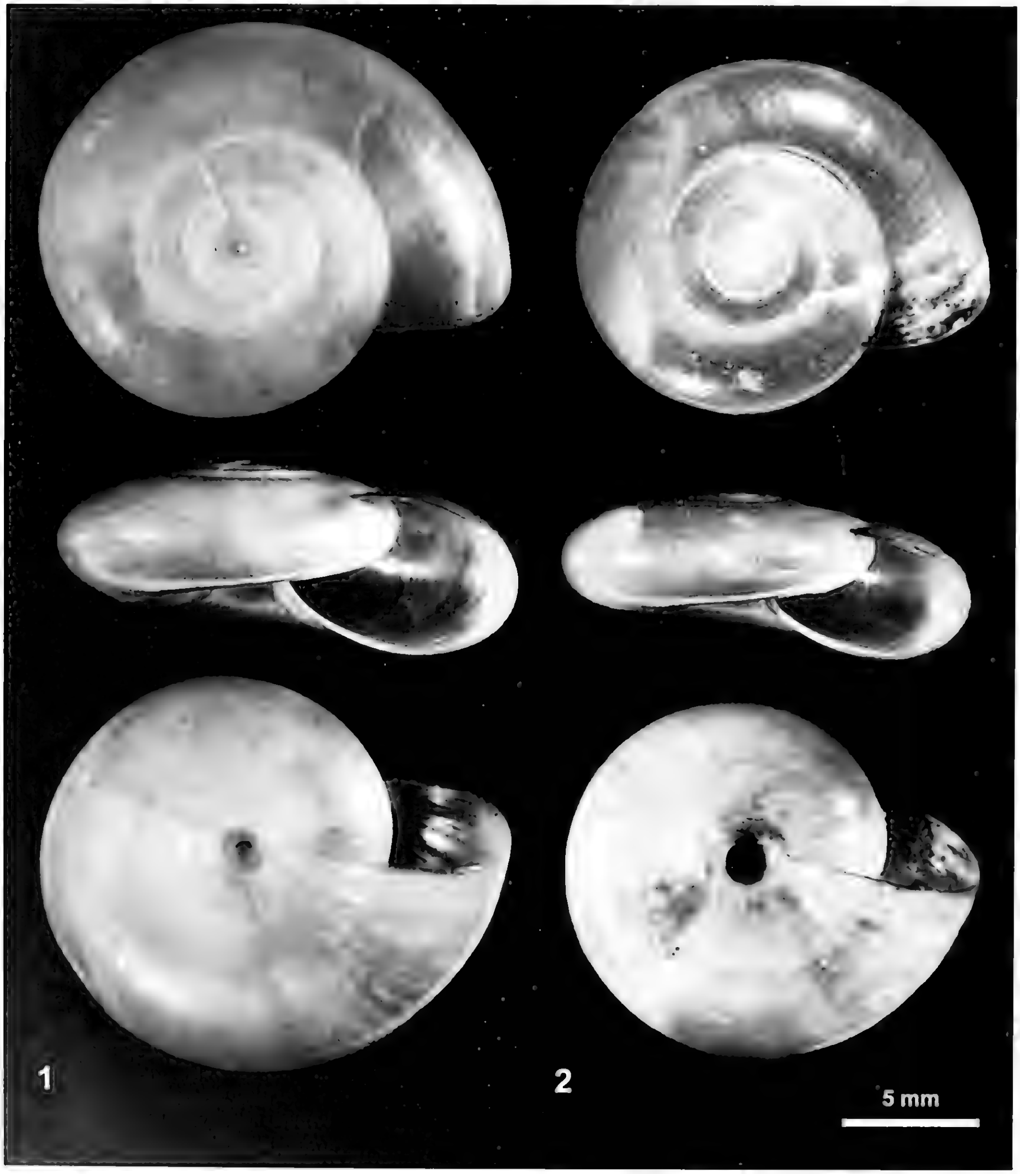
Redescription of *O. paulucciae* (De Stefani, 1883)

Identification

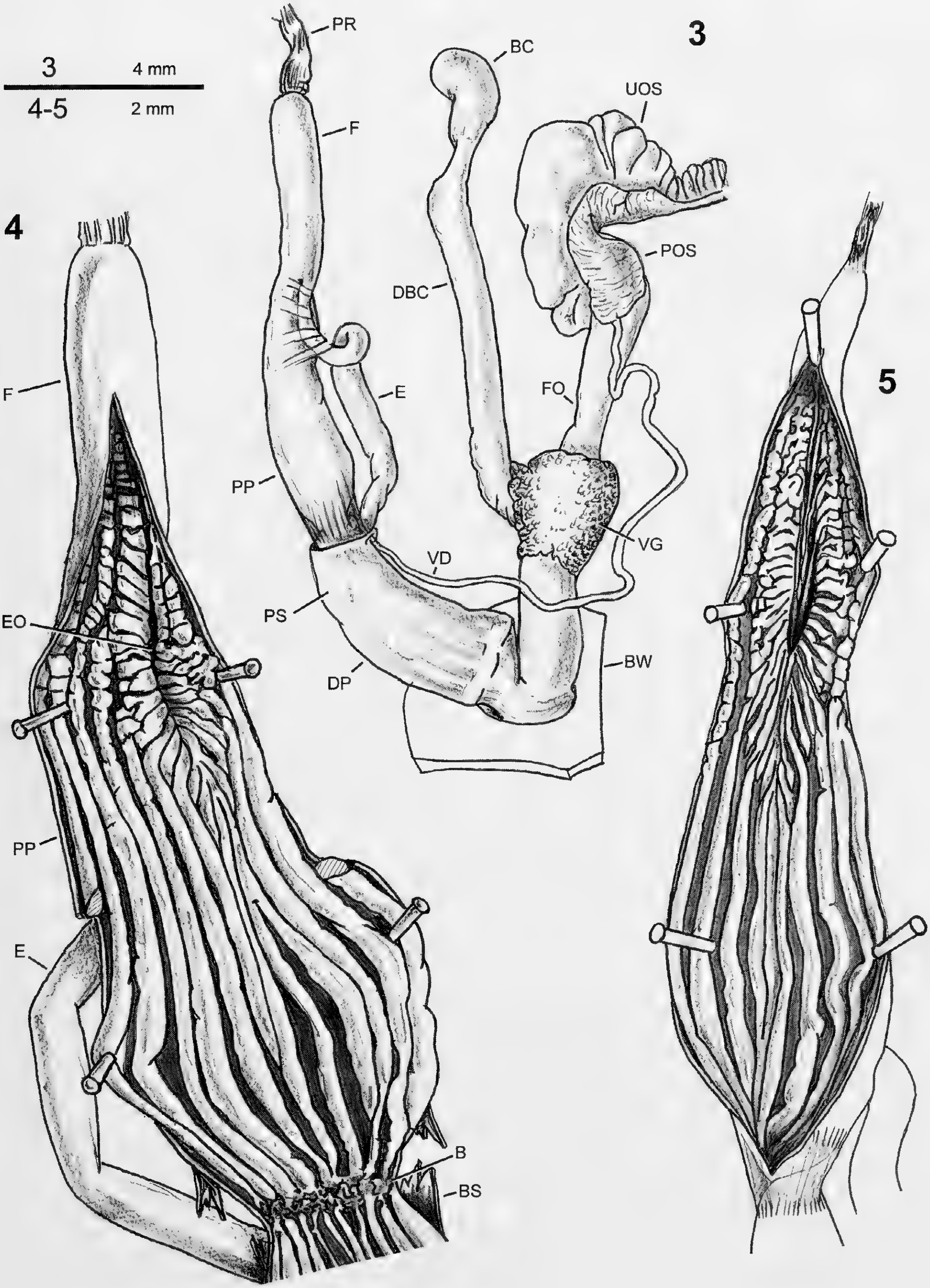
A medium-sized species of *Oxychilus* (*s. str.*), *sensu* Giusti & Manganelli (1999), a "subgenus" of *Oxychilus* characterized by: penis with flagellum; penial retractor inserted at apex of flagellum; internal ornamentation of proximal penis consisting of pleats or pleats and rows of papillae without apical thorns; epiphallus usually longer than proximal penis, its internal wall with slender longitudinal pleats; mucous gland mainly vaginal; long mesocone of central tooth). *Oxychilus paulucciae* is identified with respect to similar-shelled sympatric species (*O. draparnaudi* and *O. meridionalis*) by a larger shell (shell diameter: 13.9–17.4 mm) with small umbilicus (about 1/8 of shell diameter), narrow mid-penial region, internal ornamentation of proximal penis consisting of longitudinal pleats, and vaginal gland often forming incomplete ring around proximal vagina.

Description

Body pale gray in colour; neck and upper part of sides with variably wide areas with pits (with phylacites); foot slender, of aulacopod type, with sole longitudinally tripartite (central part whitish, lateral parts pale gray); eyes



FIGS. 1, 2. Two shells of *Oxychilus paulucciae* (De Stefani, 1883) from Vagli di sopra, Valle Arnetola, 930 m asl (Vagli di sotto, Lucca), 32TPP0084, S. Cianfanelli & M. Calcagno leg. 8.10.2000 (MZUF 17597, neotype) (FIG. 1) and Grotta della Risvolta, 220 m asl, no. 158T/LU (Stazzema, Lucca), 32TPP0372, M. Bodon & S. Cianfanelli leg. 9.11.1997 (FIG. 2).



FIGS. 3–5. Distal genitalia (FIG. 3) and internal ornamentation of flagellum and proximal penis (FIGS. 4, 5) in specimens of *Oxychilus paulucciae* (De Stefani, 1883) from Vagli di sopra, Valle Arnetola, 930 m asl (Vagli di sotto, Lucca), 32TPP0084, S. Cianfanelli & M. Calcagno leg. 8.10.2000 (MZUF 17597, neotype) (FIGS. 3–4) and S. Cianfanelli & M. Calcagno leg. 24.6.2000 (FIG. 5).

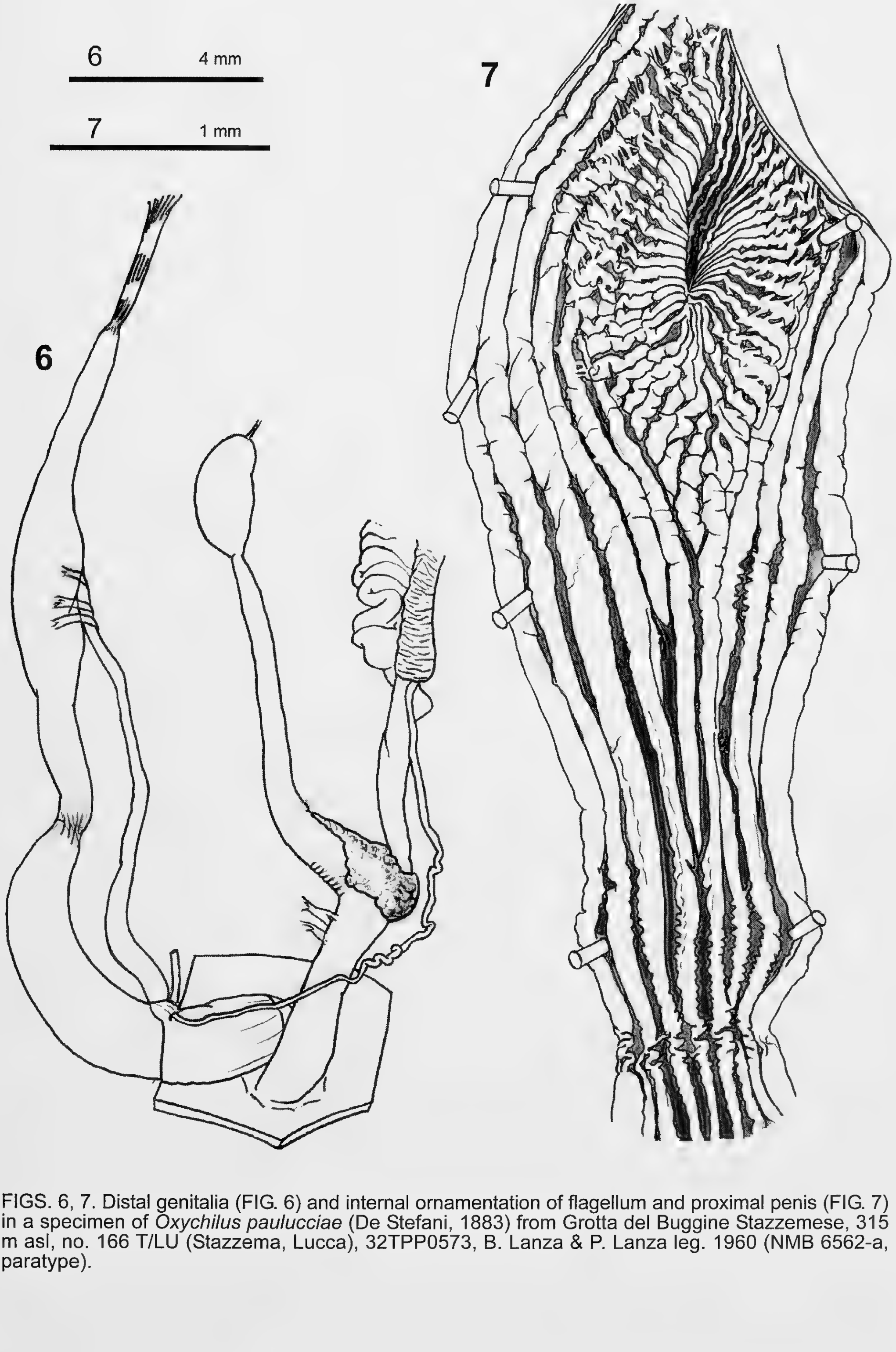
present, normal in size; kidney sigmurethrous; jaw oxygnathous.

Shell (Figs. 1, 2; Forcart, 1967: pl. 1, fig.1, figs. 1, 1a–1c [as *O. lanzai*], figs. 4, 4a–4c) dextral, medium in size, discoidal, depressed, thin and fragile, subtransparent, glossy when fresh, whitish-yellow or pale greenish, sometimes opalescent below; surface smooth, with variably evident growth lines and microsculpture consisting of very fine wavy spiral lines; spire usually tectiform, 5 1/12–5 1/2 whorls, gradually increasing in size, last whorl dilated near aperture, its last quarter descending slightly or not at all, rarely slightly angled at periphery; sutures shallow; umbilicus small, about 1.4–2.6 mm wide (usually 1/8–1/9, rarely 1/7 and in only one case 1/5 of maximum shell diameter), sometimes eccentric; aperture oval, oblique; peristome interrupted, simple, not thickened or reflected, its superior vertex starting at, or slightly above, periphery of last whorl. Dimensions (30 shells measured). Number of whorls: 5 1/4 ± 1/6 (5–5 5/6); shell diameter: 15.5 ± 1.0 mm (13.9–17.4); height: 6.1 ± 0.6 mm (5.3–7.2); umbilicus diameter: 1.9 ± 0.2 mm (1.4–2.6).

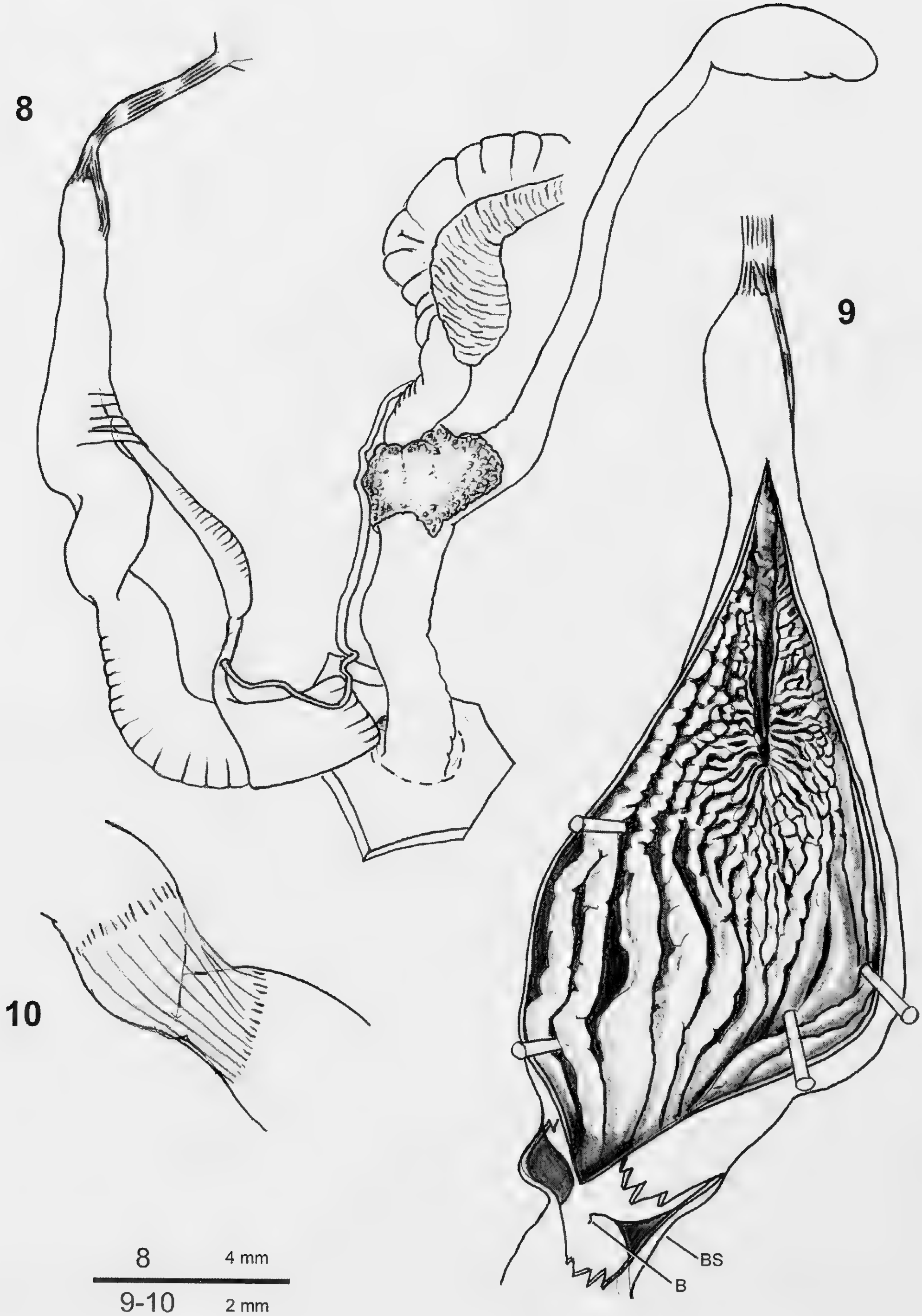
Genitalia (Figs. 3–12; Forcart, 1967: fig. 1 [as *O. lanzai*], fig. 3). General scheme of genitalia as in *Oxychilus* (*s. str.*), *sensu* Giusti & Manganelli (1999). Only distal genitalia are described here (a total of 21 adult specimens were dissected for study of genital structure during the various phases of the research). Female genitalia include free-oviduct, bursa copulatrix and its duct, and vagina. Distal free oviduct and most proximal vagina enveloped by muff of spongy glandular tissue forming vaginal gland; vaginal gland relatively undeveloped, sometimes enough to form continuous ring around wall of most proximal part of vagina, distal part of free oviduct and of duct of bursa copulatrix, sometimes reduced to cover only one side (that facing free-oviduct) of proximal vagina and of distal duct of bursa copulatrix (large portion of wall on opposite side is uncovered); in both cases, vaginal gland often envelopes one side (that facing free oviduct) of distal canal of bursa copulatrix; duct of bursa copulatrix long (7.5 mm; n: 2), initially moderately flared, narrowing before entering oval or pyriform bursa copulatrix; distal vagina (that without glandular muff) variably long (2.7–4.9 mm; n: 2) and wide, reducing in calibre slightly or not at all near genital atrium.

Male distal genitalia include vas deferens, epiphallus and penial complex (flagellum and penis). Epiphallus variably long (7.3–10.3 mm; n: 2) and slender, internal walls bearing series of very slender longitudinal pleats. Flagellum usually very long (3.7–4.7 mm; n: 2), with penial retractor muscle ending at apex (sometimes thin muscular branch extends on one side to end at about half flagellum length). Penis variably long (9.9–14.3 mm; n: 2) with clear distinction into proximal and distal parts due to "bottle-neck" (terminal, slender part of proximal penis: minimum caliber recorded 0.5–0.62 mm: n: 4), enveloped by thin, distinct, translucent sheath. Proximal penis rather short (5.4–5.9 mm; n: 2). Distal penis variable in length (4.5–8.4 mm; n: 2), enveloped by variably long (2.5–4.1 mm; n: 2) penial sheath, proximally very thin, traversed on one side by vas deferens, then slightly thicker for rest of length. Internal surface of flagellum and proximal penis surrounding opening of epiphallus into penis with many small radially disposed pleats, sometimes fragmented into rows of variably large papillae; lateral surface, and that opposite opening of epiphallus into penis, having slender longitudinal pleats with jagged sides, frequently fragmented into rows of variably large papillae. A variable number (9–12) of these pleats continues on rest of proximal penis, converging, fusing and reducing in number before continuing, with a more or less marked interruption at "bottle-neck", inside distal penis, where they are usually wider with jagged sides. Very short, thin-walled duct connects distal penis (level with where penial sheath originates) to genital atrium in which vagina also ends.

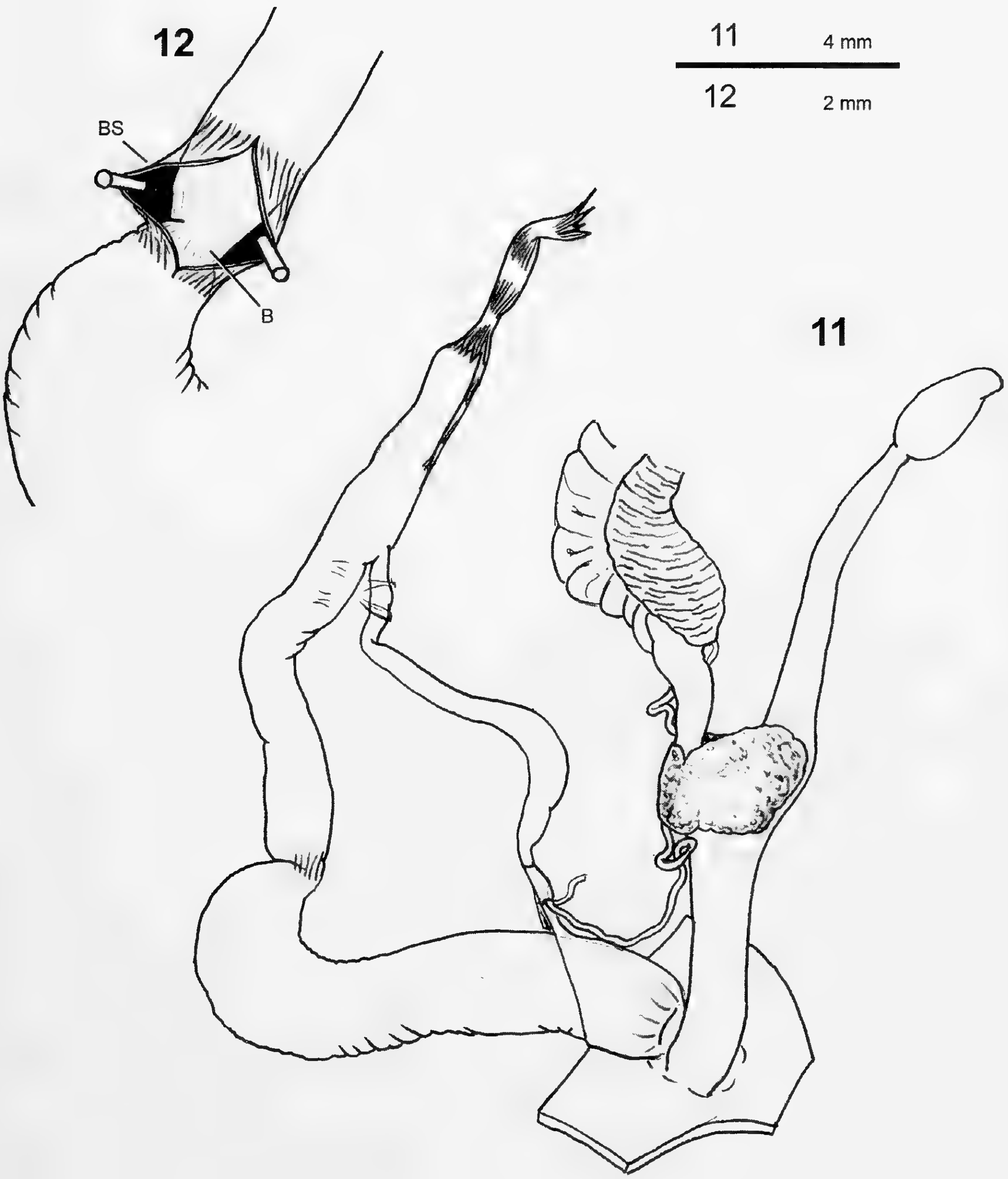
Radula consisting of many rows of about 31–35 teeth, according to formula: 11–13 M/1 + 0–1 LM/2 + 3–4 L/3 + C/3 + 3–4 L/3 + 0–1 LM/2 + 11–13 M/1 (6 specimens examined). Central teeth with well-developed basal plate, apical portion of which V-like, with pointed vertices; body of tooth wide, providing base for long, slender, pointed mesocone flanked by two very short ectocones. On both sides of each central tooth, three-four lateral tricuspid teeth, sometimes one latero-marginal bicuspid tooth and series of monocuspid marginal teeth in decreasing order of size.



FIGS. 6, 7. Distal genitalia (FIG. 6) and internal ornamentation of flagellum and proximal penis (FIG. 7) in a specimen of *Oxychilus paulucciae* (De Stefani, 1883) from Grotta del Buggine Stazzemese, 315 m asl, no. 166 T/LU (Stazzema, Lucca), 32TPP0573, B. Lanza & P. Lanza leg. 1960 (NMB 6562-a, paratype).



FIGS. 8–10. Distal genitalia (FIG. 8), internal ornamentation of flagellum and proximal penis (FIG. 9) and mid-penis region (FIG. 10) in a specimen of *Oxychilus paulucciae* (De Stefani, 1883) from Tana del Pollone di Magnano, 565 m asl, no. 1017 T/LU (Villa Collemandina, Lucca), 32TPP1592, B. Lanza leg. 30.4.72 (MZUF 15856).



FIGS. 11, 12. Distal genitalia (FIG. 11) and mid-penis region (FIG. 12) in a specimen of *Oxychilus paulucciae* (De Stefani, 1883) from Grotta della Risvolta, 220 m asl, no. 158 T/LU (Stazzema, Lucca), 32TPP0372, M. Bodon & S. Cianfanelli leg. 9.11.1997.

Material Examined

NP98 Buca della Freddana, 650 m asl, no. 230 T/MS (Massa, Massa Carrara), 32TNP9783, G. Comotti leg. 12.7.85 (1 sp, 2 sh, FGC).

PP07 Grotta del Buggine Stazzemese, 315 m asl, no. 166 T/LU (Stazzema, Lucca), 32TPP0573, no collector and date (2 sp, FGC), B. Lanza leg. 18.10.59 (2 sp [paratypes of *Oxychilus lanzai*], MZUF 454); B. Lanza & P. Lanza leg. 1960 (1 sp [holotype of *Oxychilus lanzai*], MZUF 462; 5 sp [paratypes], MZUF 463; 2 sp [paratypes of *Oxychilus lanzai*], NMB 6562-a). Grotta della Risvolta, 220 m asl, no. 158 T/LU (Stazzema, Lucca), 32TPP0372, B. Lanza leg. 23.7.61 (4 sp [paratypes of *Oxychilus lanzai*], MZUF 683; 2 sh [paratypes of *Oxychilus lanzai*], MZUF 691); B. Lanza leg. 15.3.64 (3 sp, FGC); B. Lanza leg. 21.12.69 (1 sp, FGC); M. Bodon & S. Cianfanelli leg. 9.11.97 (5 sp, 3 sh, SCC 8097/1742); S. Cianfanelli leg. 14.10.01 (1 sp, 29 sh, SCC 11647/2819).

PP08 Vagli di sopra, Valle Arnetola, 930 m asl (Vagli di sotto, Lucca), 32TPP0084, S. Cianfanelli & M. Calcagno leg. 24.06.2000 (2 sp, 2 sh, FGC; 22 sh, SCC 9328/2291; 7 sh, SCC 9330/2290; 1 sh, SCC 9485/2400), S. Cianfanelli & M. Calcagno leg. 8.10.2000 (1 sp, MZUF 17597 [neotype of *O. paulucciae*]; 7 sh SCC 9484/2399).

PP17 Buca delle Fate di San Rocco, 635 m asl, no. 362 T/LU (Pescaglia, Lucca), 32TPP1170, P. Magrini leg. 22.8.79 (1 sp, 3 sh, FGC).

PP19 Grotta della Faglia, Pania di Corfino (Villa Collemandina, Lucca), F. Utili leg. 24.11.63 (2 sp, FGC). Tana dei Gracchi di Sasso Rosso, 755 m asl, no. 289 T/LU (Villa Collemandina, Lucca), 32TPP1293, F. Utili leg. 22.11.63 (1 sp, FGC). Tana del Pollone di Magnano, 565 m asl, no. 1017 T/LU (Villa Collemandina, Lucca), 32TPP1592, B. Lanza leg. 30.4.72 (8 sp, MZUF 15856; 1 sp, MZUF 15858). Tana di Magnano, 635 m asl, no. 162 T/LU (Villa Collemandina, Lucca), 32TPP1592, B. Lanza & B. Malkin leg. 30.11.59 (1 sp det. *O. paulucciae* by Forcart, 1967, 1968, NMB 6561-a; 1 sp det *O. paulucciae* by Forcart, 1968, MZUF 445), F. Utili leg. 24.11.63 (5 sp, 1 sh, FGC), B. Lanza leg. 15.3.64 (2 sp, 2 sh, FGC), B. Lanza leg. 24.10.65 (1 sp, FGC), F. Utili leg. 5.12.65 (2 sp, 1 sh, FGC); P. Brignoli & A. Vigna Taglianti leg. 3.11.67 (3 sp, 3 sh, FGC); B. Lanza leg. 17.3.68 (11 sp, 20 sh, FGC).

PP28 Grotta dell'Iseretta, 650 m asl, no. 823 T/LU (Bagni di Lucca, Lucca), 32TPP2882, P. Magrini leg. 6.74 (2 sp, FGC).

Etymology

De Stefani (1883) named this species after the famous Italian malacologist, Marquise Marianna Paulucci (1835-1919) and Forcart (1967) after Prof. Benedetto Lanza, former director of the Museo Zoologico de "La Specola" (Florence), who collected the specimens used for the description.

Habitat

All the specimens of *O. paulucciae* were collected inside caves. The area inhabited by the species is karstic. The species is presumably adapted to subterranean life and may be defined as troglobie.

Geographical Distribution

Species with reduced distribution, limited to northwestern Tuscany (Fig. 13).

Status and Conservation

Not globally threatened. Despite its limited distribution, *O. paulucciae* does not seem to be under any particular threat at present.

Molecular Data

Sequence Data Analysis

The ITS-1 region ranged from 544 (*O. uziellii*) to 593 bp (*O. meridionalis* 1 and *O. meridionalis* 2) in length. After deletion of ambiguously aligned positions, the data-set included a total of 660 nucleotide positions, 61 of which were phylogenetically informative under the parsimony criterion. Uncorrected percentage sequence divergence (p-distance) between the two *O. paulucciae* specimens (1, Vagli di sopra; 2, Grotta della Risvolta) was 1.1%. *Oxychilus meridionalis* 1 (Capanno) and *O. meridionalis* 2 (Passo della Calla) are separated by a sequence divergence 0.3%, whereas a divergence of 2.3% distinguished them from *O. meridionalis* 3 (Bagni di Lucca). Sequence difference between *O. draparnaudi* 1 (Castello di Brolio) and *O. draparnaudi* 2 (Giglio Castello) was 1.3%. Genetic distances between morphologically defined species ranged from 2.5% (*O. meridionalis* 2 and *O. paulucciae* 2) to 7.9% (*O. draparnaudi* 2 and *O. majori*).

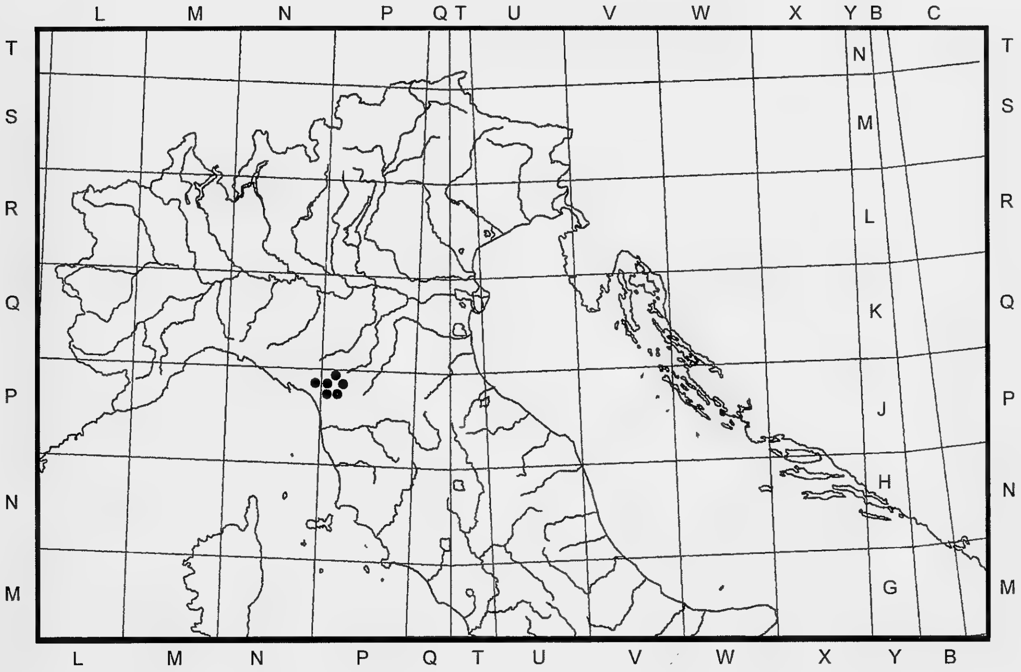


FIG. 13. The distribution of *Oxychilus paulucciae* (De Stefani, 1883) on UTM map of central-northern Italy.

Phylogenetic Analysis

Maximum parsimony analysis supported a single best tree shown in Figure 14 (tree length: 297, CI: 0.926, RI: 0.788). The likelihood ratio test and AIC from Modeltest supported the HKY+G model (Hasegawa et al., 1985, including among-site rate heterogeneity) as the best fit substitution model for the data. Parameters estimated for this model were: *Ti : Tv* ratio = 0.789, gamma shape parameter = 1.02 and base frequencies A = 0.1994, T = 0.2592, G = 0.26248, C = 0.2790. A ML analysis incorporating these parameters generated a tree with a likelihood score (-lnL) of 2193.43 (Fig. 15).

Parsimony and likelihood analyses produced essentially the same topologies. The clade grouping, in MP topology, the two *O. draparnaudi* specimens with *O. pilula* represents the only difference between the two reconstructions. In both topologies, all conspecific specimens grouped together in clades strongly supported by bootstrap values. The two reconstructions also suggest close phylogenetic relationships between *O. majori*, *O. paulucciae*, *O. uziellii* and *O. meridionalis*.

DISCUSSION

Hyalinia paulucciae and *Oxychilus lanzai*

Re-examination of the specimens from Grotta della Risvolta (Figs. 2, 11, 12) and Grotta del Buggine (Figs. 6, 7), which Forcart (1967) assigned to *O.* (*Ortizius*) *lanzai*, and those from Tana di Magnano, which Forcart (1967) assigned to *O.* (*Oxychilus*) *paulucciae*, confirmed that they belong to a single species. These specimens have the same characters as those collected near Vagli, the type locality of *O. paulucciae*. Similar conclusions were provided by molecular data. The two specimens (one from Grotta della Risvolta and one from Vagli) analysed were genetically very similar, forming a well differentiated evolutionary lineage with respect to all the other *Oxychilus* examined. The level of genetic divergence observed was correlated with geographic sampling and fall within the range observed for the other conspecific *Oxychilus*. The observed congruence between morphological and molecular data definitively demonstrates that *O. lanzai* is a junior synonym of *O. paulucciae*, as hypothesized by Giusti & Mazzini (1971) and Riedel (1980, 1997, 1998).

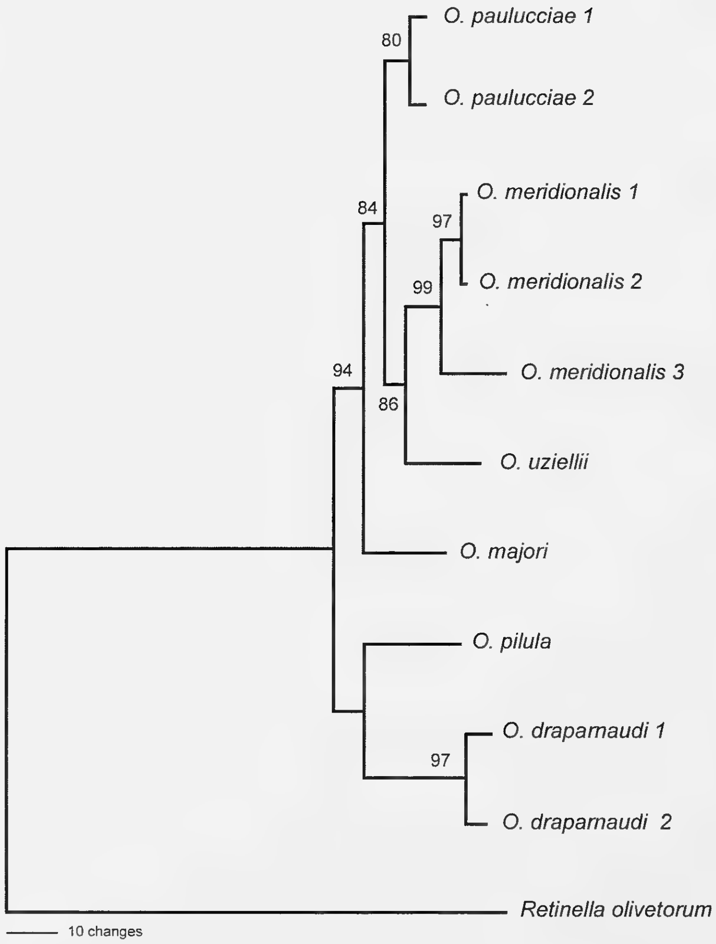


FIG. 14. Most parsimonious tree calculated from ITS-1 sequence data. Bootstrap values are indicated at nodes (1,000 replications).

Morphological Analysis

Oxychilus paulucciae belongs to *Oxychilus* (*s. str.*), *sensu* Giusti & Manganelli (1999), being characterized by: penis with flagellum; penial retractor inserted at apex of flagellum; internal ornamentation of penis consisting of pleats or rows of papillae without apical thorns; epiphallus long, usually longer than proximal penis; internal wall of epiphallus with slender longitudinal pleats; mucous gland mainly vaginal; long mesocone of central tooth.

Among *Oxychilus* (*s. str.*) species it holds an intermediate position, sharing a narrow mid-penial portion ("bottle-neck") enveloped by a thin sheath with *O. diductus* (Westerlund, 1886), *O. draparnaudi*, *O. majori*, *O. mortilleti* (Pfeiffer, 1859), *O. oglasicola* Giusti, 1968, and *O. oppressus* (Shuttleworth, 1878), but unlike them it has internal ornamentation of proximal penis consisting of longitudinal pleats very similar to that of *O. meridionalis* (*O. diductus*: Manganelli et al., 2002: figs. 7–11; *O. draparnaudi*: Giusti & Manganelli, 1997: figs. 15–30; Manganelli & Giusti, 1998: figs. 19–22; *O. majori*: figs. 4–8; *O. meridionalis*: Manganelli & Giusti, 2001: figs. 9–31; *O. mortilleti*: Manganelli & Giusti, 1998: figs. 5–17; *O. oglasicola*: Manganelli et al., 1999: figs 12–14; *O. oppressus*: Riedel, 1967: figs. 1, 2; personal unpublished data).

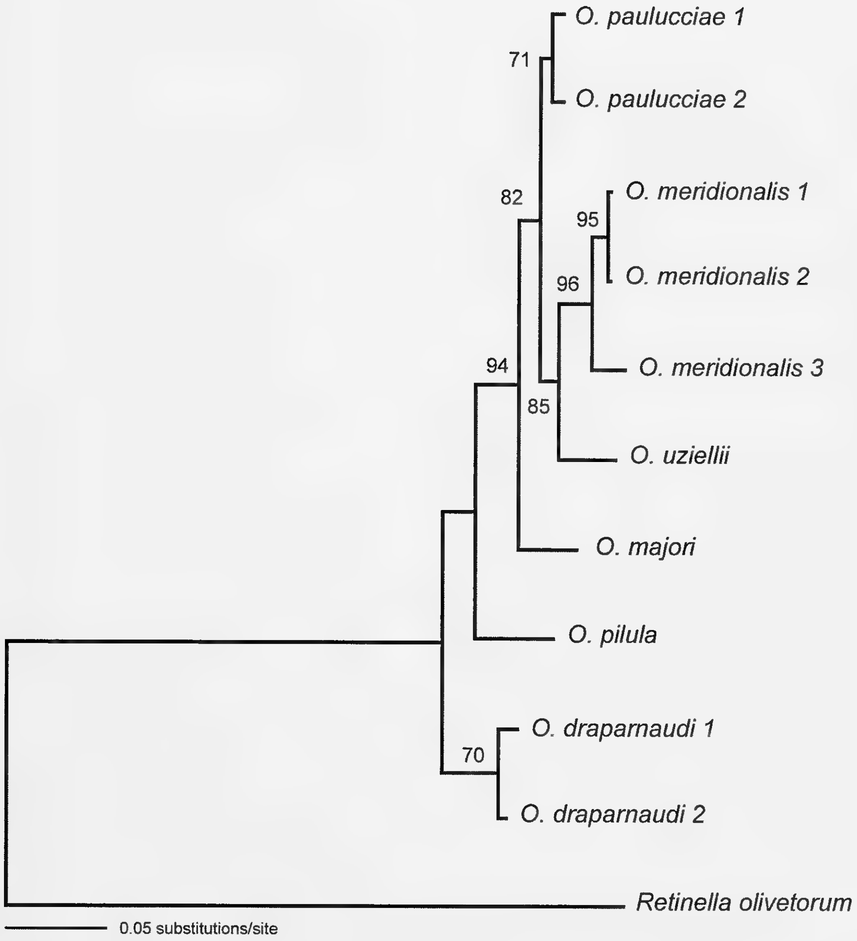


FIG. 15. Maximum likelihood tree calculated from ITS-1 sequence data. Bootstrap values are indicated at nodes (1,000 replications).

Consequently, internal ornamentation of the proximal penis consisting of longitudinal pleats readily distinguishes *O. paulucciae* from *O. diductus*, *O. draparnaudi*, *O. majori*, *O. mortilleti*, *O. oglasicola* and *O. oppressus*, and the narrow mid-penial region ("bottleneck") distinguishes it from *O. meridionalis*. Besides the structure of the mid-penial region, *O. paulucciae* can be distinguished from *O. meridionalis* by its pale grey body, larger shell (shell diameter: 15.5 ± 1.0 mm) with small umbilicus (about 1/8 of shell maximum diameter), and vaginal gland that often forms incomplete ring around proximal vagina (body slate blue in colour; smaller shell: shell diameter: 13.1 ± 2.0 mm, with larger umbilicus, about 1/6–1/7 of shell diameter; vaginal gland always forming complete ring around proximal vagina; for detailed description of *O. meridionalis*: Manganelli & Giusti, 2001).

Oxychilus paulucciae also shares the internal ornamentation of the proximal penis, consisting of longitudinal pleats, with the species traditionally assigned to *Ortizius* Forcart, 1957 (type species: *Hyalina* (*Polita*) *helvetica* Blum, 1881). Only one of the 28 species assigned by Riedel (1980, 1998) to this subgenus (Giusti & Manganelli, 2002: table 1) occurs within the area inhabited by *O. paulucciae*: *O. clarus* (Held, 1838). It is impossible to confuse the two species: *O. clarus* has a very small whitish shell (Kerney et al., 1983: pl. 10).

Phylogenetic Relationships

Our phylogenetic reconstructions indicate that the species analysed in this study do indeed represent well-differentiated evolutionary lineages. In particular, the three species for which multiple specimens were available always formed monophyletic clades supported by bootstrap analysis, suggesting good overall resolution of the data set. Molecular data also indicated that *O. paulucciae* is genetically close to *O. meridionalis*, the two taxa separated by a sequence divergence ranging from 2.5 to 3.7%. This result is congruent with morphological evidence, if it is admitted that the internal structure of proximal penis, not the narrow mid-penis region, supports taxonomic relationships within the genus. Another interesting finding of this study was the close relationship between *O. paulucciae*, *O. meridionalis, O. uziellii*, and *O. majori*, which supports the existence of a Tuscan radiation of the genus. The last two taxa, *O. uziellii*, and *O. majori,* are characterized by some highly derived features in the penial complex. This makes it difficult to unambiguously infer their systematic affinities based on morphological evidence. Morphologically derived taxa represent a challenge for systematics that can only be addressed by a molecular approach. Finally, molecular data indicated that *O. pilula* and *O. draparnaudi* are distantly related taxa with respect to the above species.

CONCLUSION

Both morphological and ITS-1 sequence data indicates that *O. paulucciae* is close, but distinct from *O. meridionalis*, a widespread Tuscan species. The molecular results also showed that *O. uziellii* and *O. majori*, two other morphologically highly derived Tuscan species, are closely related to *O. meridionalis* and *O. paulucciae* and distinct from the most common *O. draparnaudi.*

Combined morphological and molecular analysis of wider taxonomic sample, especially type species of the many subgenera of *Oxychilus*, will further clarify the taxonomy of the genus and the relationships within oxychiline zonitids.

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THE BIOLOGY AND FUNCTIONAL MORPHOLOGY OF *FOEGIA NOVAEZELANDIAE* (BIVALVIA: ANOMALODESMATA: CLAVAGELLOIDEA) FROM WESTERN AUSTRALIA

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ABSTRACT

As more representatives of the adventitious, tube-building anomalodesmatan Clavagelloidea are examined, a pattern of extraordinary adaptive radiation is being revealed. Despite its name, *Foegia novaezelandiae* is known only from the Holocene and Recent of Western Australia and is thus possibly very modern. A few tubes are held in the collections of the Western Australian Museum, Perth, and a single living individual has been collected from a hypoxic beach at Dampier, Western Australia. Like other clavagelloids, using a muscular pedal disc, *F. novaezelandiae* pumps interstitial water into its mantle cavity via the pedal gape, and hence the pedal slit and tubules of its anterior "watering pot" component of the adventitious tube.

Foegia novaezelandiae is similar to *Brechites vaginiferus* in being amyarian, except for minute anterior pedal retractor muscles in the latter. As with *B. vaginiferus* also, pallial retractor muscles effect siphonal and pedal disc retraction. The adventitious tube of *F. novaezelandiae* is more complex in that the shell valves are recessed and largely hidden externally by additional bulbous concretions of tube material secreted from anterior and posterior pallial crests. Also like *B. vaginiferus*, *F. novaezelandiae* pumps interstitial water into the mantle cavity, probably collecting interstitial bacteria and dissolved organic material as nutritional supplements. Unlike *B. vaginiferus*, however, *F. novaezelandiae* has an agglomeration of organic material and bacteria adhering to its highly convoluted periostracum anteriorly, particularly that of the pedal disc and thus inside the adventitious tube. Such bacteria may help detoxify the hydrogen sulphide contained in the interstitial water of the hypoxic sediment that *F. novaezelandiae* inhabits. However, *F. novaezelandiae* has a full complement of mantle cavity and intestinal organs for the processing of food filtered from the seawater above.

Key words: *Foegia novaezelandiae*, *Clavagelloidea*, adventitious tube formation, anatomy, tube function, watering-pot shell.

INTRODUCTION

The adventitious tubes of the diverse representatives of the Clavagelloidea d'Orbigny, 1843, constitute some of the weirdest and rarest bivalve structures. The most recent cladistic analysis of the Anomalodesmata by Harper et al. (2000) did not identify sister groups but noted that *Clavagella* and its allies first appeared in the Cretaceous, whereas *Brechites* and its allies are known from the Oligocene onwards. Savazzi (2000) also noted that representatives of the Clavagelloidea seem to fall into two groups comprising those that (i) have their left valve united into the fabric of an adventitious tube in the case of endobenthic (*Stirpulina*) and epibenthic (*Dianadema*) genera, or a crypt in the case of nestling and boring species (*Clavagella*, *Bryopa*), with the right valve free inside it, and (ii) those in which both valves are incorporated into the structure of an adventitious tube, again in the case of endobenthic (*Brechites*, *Foegia*) and epibenthic (*Humphreyia*) genera.

The anatomies of species of *Clavagella*, *Bryopa* and *Dianadema* have been described by Soliman (1971), Savazzi (1999, 2000) and Morton (1984a, 2003), respectively, and those of representatives of *Brechites* and *Humphreyia* by Morton (1984b, 2002a, b). Two of the above genera, that is, *Dianadema* and *Humphreyia,* are known only from Australia, and Smith (1971, 1976, 1998) and Lamprell & Healy (1998) catalogue the species recorded from that continent. These authors consider that in Australia the genus *Brechites* comprises three subgenera, that is, *Brechites, s.s.,* plus *Penicillus* and *Foegia*, the second subgenus being represented by *B.* (*P.*) *philippinensis* (Chenu, 1843) and the third by *B.* (*F.*) *novaezelandiae* (Bruguière, 1789) and *B.* (*F.*) *veitchi* Smith, 1971. *Brechites* (*F.*) *novaezelandiae* is the type species of *Foegia* but, as noted by Smith (1971), other than for a description of its adventitious tube, virtually nothing else is known about it and there are no extant specimens with tissues available for study.

During January 2000, a research trip was made to Western Australia and a single living individual of *Foegia novaezelandiae* was collected. On this and subsequent visits, the small collection of tubes of this species in the Western Australian Museum was examined. Observations on the living animal and the collection of examined tubes are herein reported upon to provide an insight into the biology and anatomy of one of the strangest species, of one of the strangest superfamilies (Clavagelloidea) within the Bivalvia (Morton, 1981a, 1985a).

MATERIALS AND METHODS

The specimen of *Foegia novaezelandiae* was collected from intertidal mud on the beach adjacent to the leased property of Dampier Salt Co. Ltd., Karratha, Western Australia. It was buried anterior end down, that is, the watering pot, with the posterior tube projecting just above the mud surface.

As described for *Brechites vaginiferus* (Chenu, 1843) by Morton (2002a), the anterior end only of the adventitious tube of *Foegia novaezelandiae* was placed within a transparent tub with a lid that had a central hole in it to hold the tube in place and containing a suspension of Ehrlich's haematoxylin in seawater. The whole animal and tub was then placed in a much larger, also transparent, container of filtered seawater and left overnight. The living animal was subsequently dissected and the ciliary currents of the organs of the mantle cavity studied by application, again, of a seawater suspension of Ehrlich's haematoxylin. The specimen was fixed in 5% formalin eventually and, following routine histological procedures, sectioned transversely at 6 µm and every tenth section retained. Alternate slides were stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome.

The nine specimens of *Foegia novaezelandiae* contained in the collections of the Western Australian Museum, Perth, were examined and the dimensions of all intact tubes measured to the nearest 1 mm. These were: greatest width, total length and length to the first growth (or possibly repair) increment.

ABBREVIATIONS USED IN FIGURES

AC	Anterior concretion
AN	Anus
APC	Anterior pallial crest
APCC	Anterior pallial crest cavity
AU	Auricle
CA	Ctenidial axis
CF	Cuticular fusion
CM	Circular muscle
CP	Ctenidial plica
C-P-V-CONN	Cerebro-pleural visceral connective
DD	Digestive diverticula
DK	Distal limb of the kidney
ES	Exhalant siphon
F	Foot
FPA	Fourth pallial aperture
H	Heart
HA	Haemocoel
HG	Hypobranchial gland
IBC	Infra-branchial chamber
ID	Inner demibranch
IE	Inner epithelium
ILP	Inner labial palp
IP	Inner layer of periostracum
IS	Inhalant siphon
K	Kidney
KC	Kidney concretion
KT	Kidney tubule
LM	Longitudinal muscle
LV	Left shell valve
MG	Mid gut
N	Nerve
O	Oesophagus
OA	Organic agglomeration
OD	Outer demibranch
OE	Outer epithelium
OLP	Outer labial palp
OP	Outer layer of periostracum
OS	Osphradium
OV	Ovary
P	Periostracum
PC	Posterior concretion

PD	Pedal disc
PE	Pericardium
PEG	Periostracal groove
PG	Pedal gape
PK	Proximal limb of the kidney
PL	Pallial line
PPC	Posterior pallial crest
PPCC	Posterior pallial crest cavity
PRM	Pallial retractor muscle
R	Rectum
RA	Renal aperture
RV	Right shell valve
S	Siphons
SA	Saddle
SBC	Supra-branchial chamber
SC	Sensory cell
SN	Siphonal nerve
SVI	Shell valve impression
TE	Testes
TMF	Transverse muscle fibres
V	Ventricle
VM	Visceral mass
VMG	Ventral marginal food groove

TAXONOMIC CONSIDERATIONS

Smith (1971) discussed the taxonomy of *Brechites* (*Foegia*) *novaezelandiae* (Bruguière, 1789). He regarded *Aspergillum agglutinans* Lamarck, 1818 (p. 430), and *A. novaehollandiae* Chenu, 1843 (p. 3, pl. 4, fig. 8), to be synonyms. *Penicillus novae Zelandiae* Bruguière, 1789 (p. 129–130), was based on an ambiguous illustration in Favanne de Montcervelle & Favanne de Montcervelle (1780: 642, plate 79, fig. E), and misattributed to New Zealand. A neotype may be needed to stabilize the concept, because the original material has not come to light. No type material of *A. agglutinans* has been found. Two syntypes of *Aspergillum novaehollandiae* Chenu, 1843, are held in the collections of the Natural History Museum, London (1968668), and these are figured here (Fig. 1).

Gray (1858a: 313) differentiated *Foegia* Gray, 1847 (p. 188), from other genera in his Aspergillidae Gray, 1858, a junior synonym of the Clavagellidae Orbigny, 1844, in several important respects: "Umbo more or less covered with a swollen prominence in front; the whole of the valves except the umbo or nucleus enclosed in the tube; fringe indistinct, formed like the hole in the disk, of short thick separate tubes". The above description is generally correct, and because of other anatomical differences, I agree with Gray (1858a) that the genus *Foegia* is valid. It is possible that *Foegia* might date from Gray (1842: 77), where there is a definition but no named species. In any event, the type species of *Foegia* is *Penicillus novae Zelandiae* Bruguière, 1789, by monotypy in Gray (1847). The species under consideration is, therefore, *Foegia novaezelandiae* (Bruguière, 1789).

FIG. 1. *Foegia novaezelandiae*. The two syntypes of *Aspergillum novaehollandiae* (NHM London 1968668).

DISTRIBUTION

In the collection of the Department of Earth and Planetary Sciences of the Western Australian Museum are a number of local Holocene subfossils of *Foegia novaezelandiae*:

1. Kwinana (south of Perth). Dredged from Cockburn Sound, 3 specimens (WAM 69.1070a, b, c).
2. Fremantle. Dredged from a fishing anchorage, 1 specimen (WAM 70.2034).

In the collection of Recent Mollusca in the Western Australian Museum are 16 specimens of *Foegia novaezelandiae* collected from either Cockburn Sound, South Fremantle, Woodman's Point or Leighton Beach, all locations again just south of Perth. One was dredged from 1–2 fathoms (2–4 m), and all were dead when collected. Only nine tubes are intact.

Smith (1971) records that *Foegia novaezelandiae* occurs along "The central and south west coast of Western Australia and two specimens from the north coast of Queensland" (p. 152). Cotton (1961) does not record the species from South Australia, nor do Wells & Bryce (2000) from Western Australia, presumably because of its rarity. Smith (1976) illustrates (p. 201, map 3) the range of *F. novaezelandiae*. Lamprell & Healy (1998) agree with this distribution pattern and report that the species occurs from depths of 3–22 m in sand. The record herein, from Dampier, though intertidal, is within the distribution range described, and therefore *F. novaezelandiae* is a Southern Hemisphere, warm temperate-tropical species.

BIOLOGY

The single specimen from the Dampier Salt Co. Ltd. lease at Karratha, Western Australia, was collected from the intertidal of an unnamed muddy beach, the landward drainage onto which has been restricted by construction of a bund to create solar salt pond "0". The seaward remnant of the original creek which drained onto the beach, lies opposite and is divided into two outlets by West Intercourse Island. Mangroves fringe the beach: an *Avicennia* forest to the seaward is followed landward, in succession, by *Rhizophora* scrub, *Avicennia* scrub, and (locally) *Ceriops-Avicennia* heath grading into a salt flat. The main water influence here is the tides because the hypersaline (salinities > 40‰), drainage from the land, as reported upon by Morton (2002a) for this part of Western Australia, has been halted by construction of the bund and causeway for pond "0". This has thus in turn adversely impacted not only beach dynamics but also interstitial water character. Whether

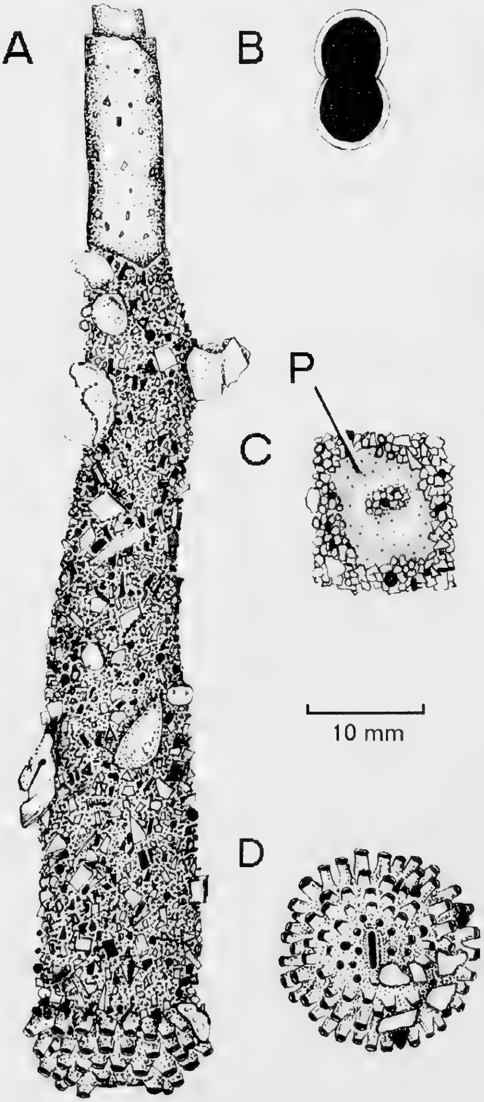

FIG. 2. *Foegia novaezelandiae*. A. The adventitious tube; B. the siphonal tube as seen from the posterior aspect; C. a closer view of the tube showing the calcareous tube and periostracum beneath the adhering detritus and D, the watering pot as seen from the anterior aspect. Note the dorso-ventrally aligned pedal slit (for abbreviations see pp. 38–39).

natural or perturbed, the substratum of sandy-mud in this *Foegia novaezelandiae* habitat is hypoxic, and the specimen was oriented vertically in it with the posterior end of the tube projecting above the sediment surface by some 10 mm. Semeniuk & Wurm (1987) describe in broad terms the characteristics of the shore seaward of pond "0" and provide basic maps (figs. 21, 22) of the area.

ANATOMY

Adventitious Tube

The nine tubes of *Foegia novaezelandiae* in the collections of the Western Australian Museum range in total length from 69–98 mm and in maximum width from 13–16 mm. The living individual from Dampier was 130 mm long and 15 mm wide. Some tubes in the collection have either a single growth increment or a repair at a length ranging from 80–94 mm. The Dampier individual has two (Fig. 2A). The relationships between tube width and total tube length and length to the first growth increment or repair are illustrated in Figure 3. Where there is no growth increment, the two measurements are the same. Although the correlations are poor, the lines of best fit are similar. Four individuals, each with one growth or repair mark on the tube, lie on the right side of the plot suggesting that any such increment occurs at a length of between ~ 85–100 mm. The above implies that the adventitious tube is secreted but once when the contained animal becomes an adult, but that it can be subsequently extended or repaired posteriorly, as in *Brechites vaginiferus* (Morton, 2002a).

The tube of the living *Foegia novaezelandiae* is illustrated in Figure 2. The main shaft of the tube (Fig. 2A) is covered in sand grains and other hard detritus, except posteriorly and anteriorly at the watering pot disc. Posteriorly, there are two growth (or repair) increments, both secreted internal to the preceding one. These are covered sparsely in detritus and raised above the sediment surface. Viewed from the posterior aspect (Fig. 2B), the tube aperture is 8-shaped in cross-section matching the configuration of the siphons, which project up into it. In places, the shell debris is worn away from the tube beneath exposing the calcareous tube with a thin adhering film of periostracum (Fig. 2C). Seen from the anterior end (Fig. 2D), the watering pot disc has

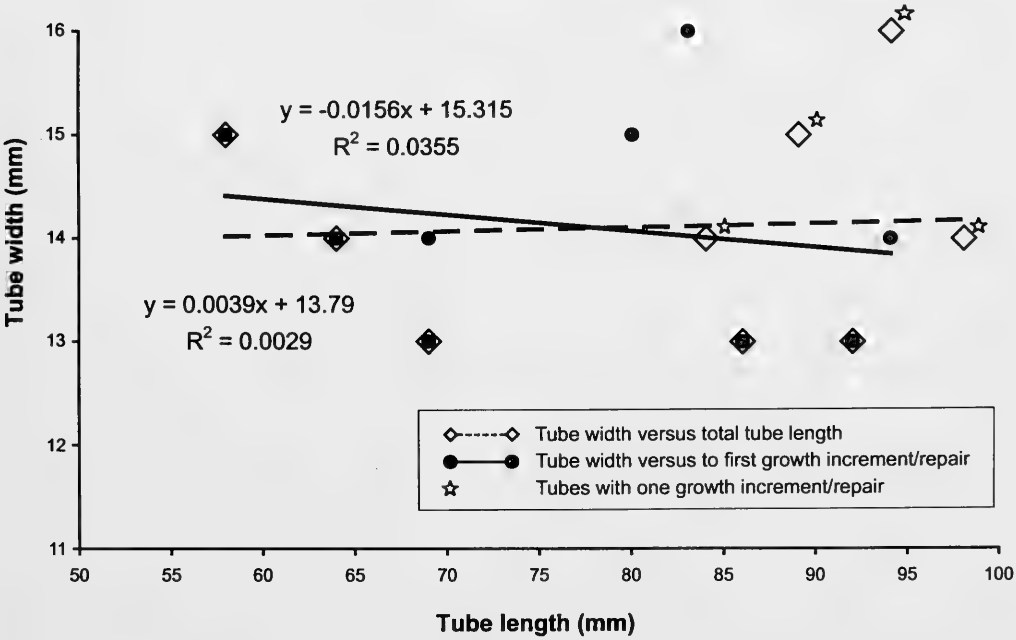

FIG. 3. *Foegia novaezelandiae*. The relationship between adventitious tube width and (i), total length and (ii), length to the first growth (or repair) increment.

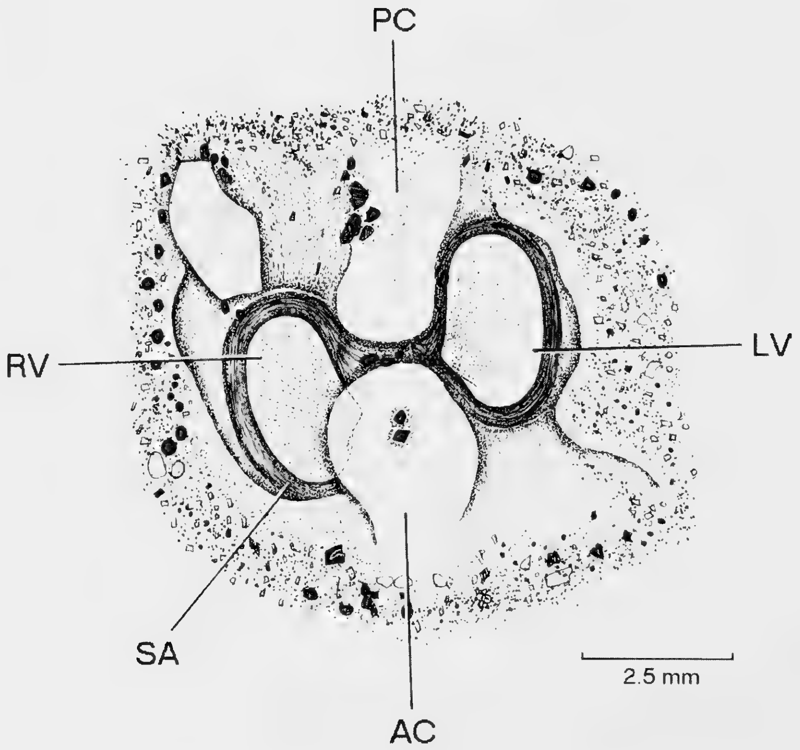

FIG. 4. *Foegia novaezelandiae*. A view of the dorsal surface of the adventitious tube showing the true shell valves and enclosing anterior and posterior bulbous projections (for abbreviations see pp. 38–39).

a dorso-ventrally aligned pedal slit and an array of open tubules which, as shown by Gray (1858a), do not have a distinct "fringe" separating it from the tube's shaft, as is the case in *Brechites vaginiferus* and where it is identified as a distinct "line" (Morton, 2002a: fig. 1).

Tube Function

When the watering pot of the living individual of *Foegia novaezelandiae* was placed in a suspension of Ehrlich's haematoxylin in seawater, the animal clarified it within 12 hours. Thus, as with *Brechites vaginiferus* (Morton, 2002a), *F. novaezelandiae* pumps interstitial water into the mantle cavity through the pedal slit and tubules that constitute the watering pot.

Shell

As noted by Gray (1858a), the shell of *Foegia novaezelandiae* is covered by two, anterior and posterior, bulbous secretions and is generally hidden within the fabric of the adventitious tube. However in one specimen in the Western Australian Museum collection (from Cockburn Sound, (i) of (iv) specimens collected in 1965; broken base only; S 14232), the shell valves are partly visible. This specimen was cleaned carefully with dilute nitric acid, to remove sand grains and other debris and is illustrated in Figure 4. The two shell valves have parted and are ~ 3 mm long. They are equivalve and inequilateral, that is, anteriorly foreshortened and posteriorly elongate, and thus of the same general form as in all clavagelloids hitherto described, for example, *Brechites vaginiferus*, *Humphreyia strangei* and *Dianadema multangularis* (Morton, 2002a, b, 2003). The umbones are slightly pointed, and there is a trace of a radial sculpture of periostracal spinules, similar to those described for *Lyonsia hyalina* by Prezant (1979a) and for the clavagelloids listed above. Around

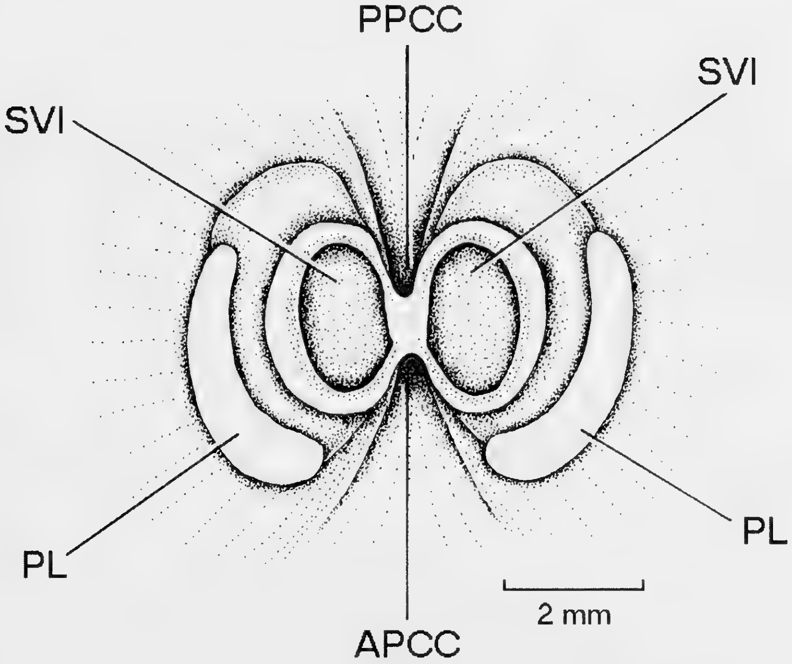

FIG. 5. *Foegia novaezelandiae*. An internal view of the adventitious tube showing the positions of the true shell valves and pallial line lying below the saddle (for abbreviations see pp. 38–39).

the two shell valves and uniting them, is a "saddle" of secondarily secreted shell which has fine concentric growth lines also seen in other clavagelloids (see above). Shell and saddle are sunk into the general fabric of the adventitious tube. A thick, bulbous concretion covers the antero-dorsal region of the right valve, and a second, similarly bulbous concretion is present posteriorly.

Internally, the shell, saddle and adventitious tube of the Dampier specimen (Fig. 5) are united and covered by a smooth calcareous concretion. The positions of the valves appear as depressions surrounded by raised borders of secondarily and internally secreted calcium carbonate. Pockets where anterior and posterior pallial crests are inserted above the valves to create the bulbous secretions covering them are also evident. Two crescentric pallial-line scars encircle the antero-lateral sides of the shell valve impressions. The Pilbarra region of Western Australia is mineral rich and the internal surface of the anterior watering pot was stained brown with iron oxide.

Internal Anatomy

The living animal of *Foegia novaezelandiae* was removed from its tube and is illustrated in Figure 6A–C. The siphons have contracted. The entire body is enclosed in periostracum secreted by the general mantle epithelium. Covering the mantle immediately beneath the true shell and, therefore, approximately encompassing the pericardium, the periostracum is a transparent skin (this is illustrated as a light stippling in Figure 6C). Elsewhere, covering siphons, pedal disc and the general mantle surface, the light brown periostracum is thick and wrinkled. From the dorsal view (Fig. 6A), the pericardium contains a heart, which comprises a central ventricle, penetrated by the rectum, and lateral auricles. Posteriorly, there are paired kidneys, over which the rectum passes. Anteriorly, the visceral mass contains the digestive diverticula and the paired ovaries. From what is the crescentric remnant of a pallial line, pallial retractor muscles pass into the mantle in anterior, ventral and posterior directions to effect

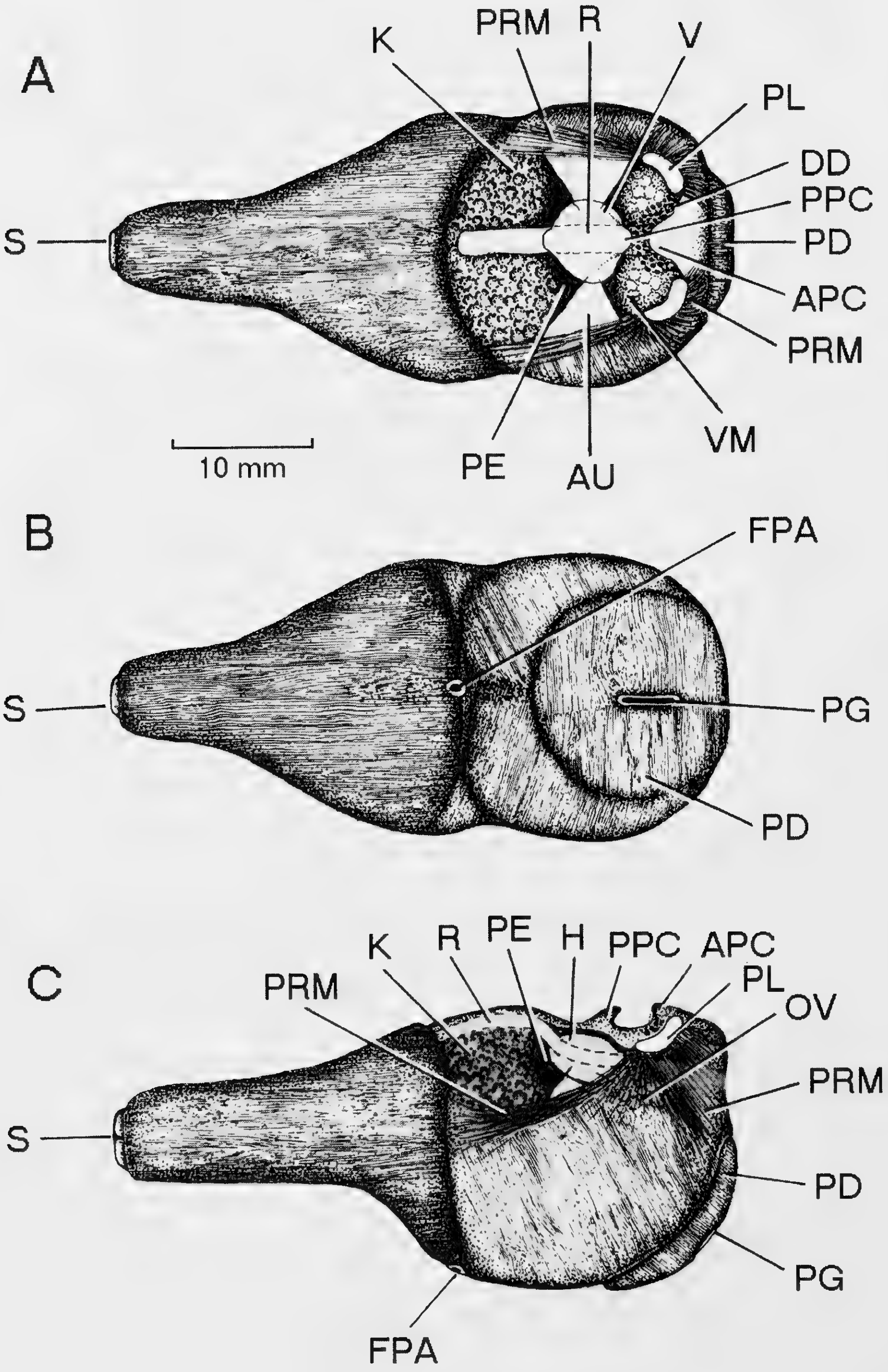

FIG. 6. *Foegia novaezelandiae*. A generalized picture of the anatomy, as seen from A, dorsal; B, ventral and C, right lateral aspects. Note that in C the periostracum surrounding the pericardium is illustrated with a light stippling as in Figure 2C: elsewhere the periostracum is brown, thick and wrinkled (for abbreviations see pp. 38–39).

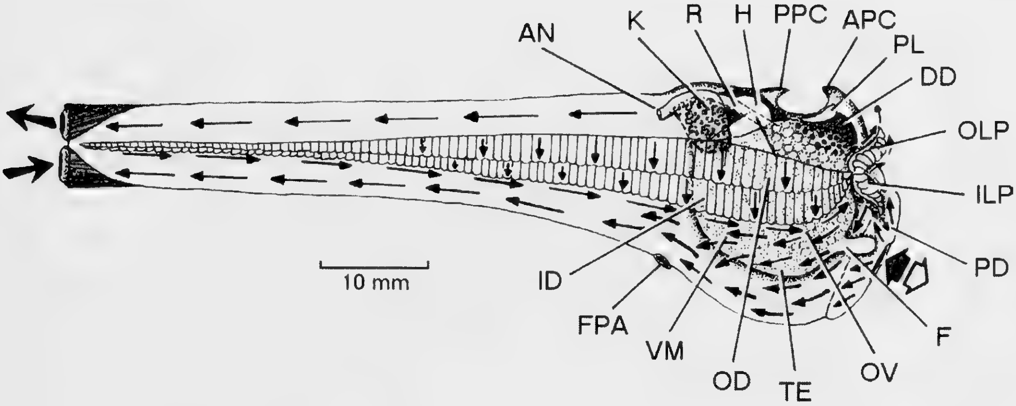

FIG. 7. *Foegia novaezelandiae*. An interval view of the organs and ciliary currents of the mantle cavity as seen from the right side (for abbreviations see pp. 38–39).

contraction of the body within its adventitious tube. There are no other muscles. Also seen dorsally, above the visceral mass, are anterior and posterior pallial crests.

From the ventral view (Fig. 6B), the periostracum-covered pedal disc lies antero-ventrally, and in its centre is a dorso-ventrally aligned pedal gape. Where the siphons meet the remainder of the mantle, there is a mid-ventral fourth pallial aperture. The animal, as seen from the right side (Fig. 6C), shows the heart within the pericardium and the rectum passing over the kidneys, the pallial retractor muscles and the anterior pedal disc and gape. Also seen are the fourth pallial aperture and the anterior and posterior pallial crests.

Organs and Ciliary Currents of the Mantle Cavity

The extended body of *Foegia novaezelandiae* is shown in Figure 7 after being opened on the right side. The most obvious feature is the long paired ctenidia, each of which consists of a complete inner demibranch and the dorsally directed descending lamella only of the outer. The ctenidia extend into the apex of the siphons and thus separate supra- from infra-branchial chambers. The ciliary currents of the ctenidia are of Type E (Atkins, 1937a) and pass collected particles anteriorly towards the mouth in the ctenidial axis and in the ventral marginal food groove of the inner demibranch via small labial palps.

The visceral mass is small with a little foot antero-ventrally. No statocysts have been identified, although they occur in most anomalodesmatans (Morton, 1985b), but were similarly not seen in *Dianadema multangularis* (Morton, 2003). Their absence in this specimen may be because only every 10th transverse section was kept but this would mean any missed statocysts would be very small, that is, < 60 µm in length. Within the visceral mass, dorsal ovaries are separate from ventral testes.

The ciliary currents of the visceral mass are directed towards its postero-ventral edge where unwanted particles fall onto the mantle mid-ventrally. As in *Brechites vaginiferus* (Morton, 2002a), the ciliary currents on the internal surface of the pedal disc radiate outwards and downwards from the pedal gape. The ciliary currents on the internal surface of the mantle are downward, complementing those of the visceral mass but, mid-ventrally, strong ciliary currents transfer unwanted material posteriorly, where it is ejected from the inhalant siphon as pseudofaeces There are also posteriorly directed ciliary currents in the supra-branchial chamber and which presumably help to transfer faeces to the exhalant aperture because the anus is located deep inside the siphons on the posterior surface of the paired kidneys.

Musculature

Foegia novaezelandiae has no adductor and pedal retractor muscles. The pallial line is short, ~ 3 mm, on each side of the body and from it arise pallial retractor muscles that extend anteriorly, ventrally and posteriorly. The attachment of the pallial retractor muscles to the adventitious tube, at the pallial line, is shown in transverse section in Figure 8.

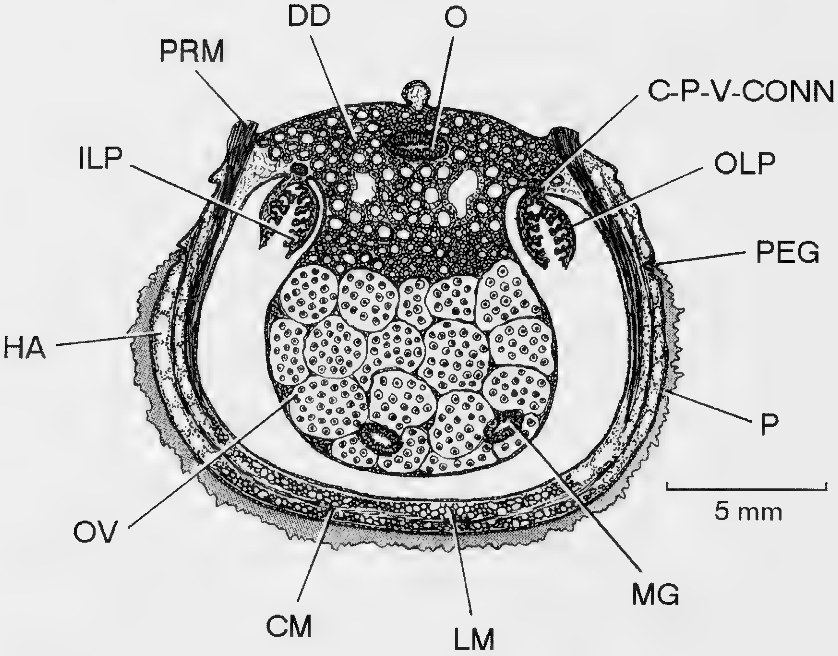

FIG. 8. *Foegia novaezelandiae*. A transverse section through the visceral mass and mantle (for abbreviations see pp. 38–39).

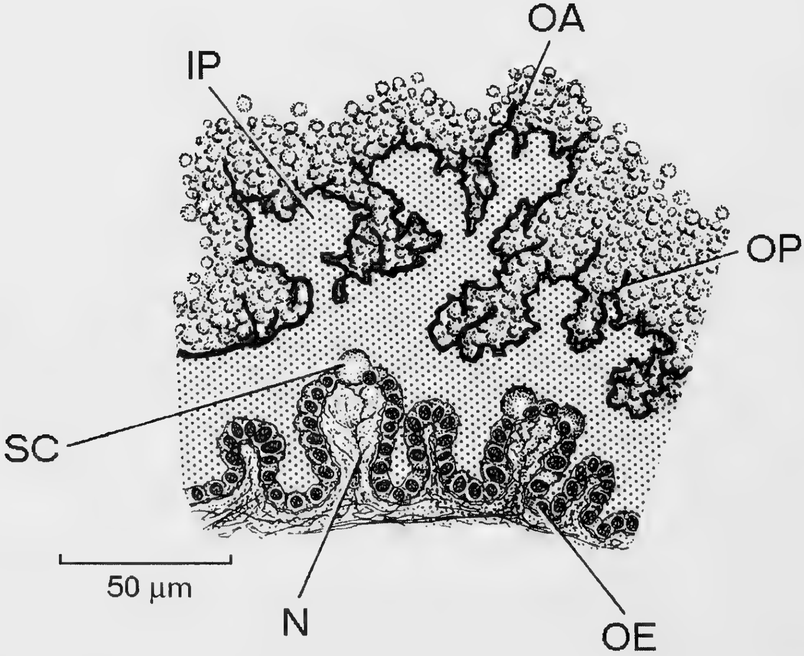

FIG. 9. *Foegia novaezelandiae*. A transverse section through the outer mantle epithelium of the pedal disc showing the periostracum and agglomeration of adhering organic material and bacterial cells (for abbreviations see pp. 38–39).

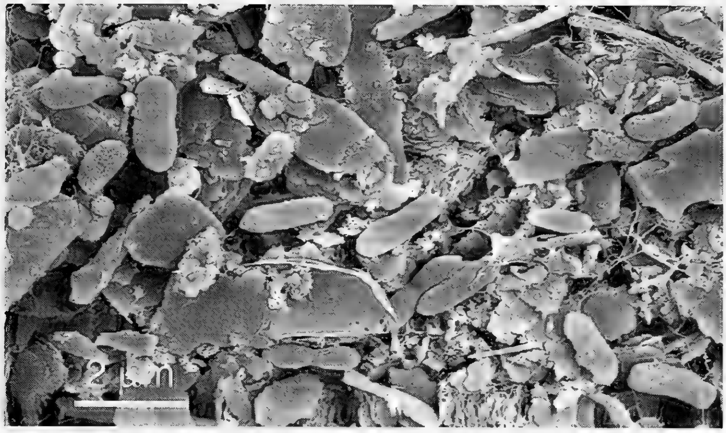

FIG. 10. *Foegia novaezelandiae*. A SEM micrograph of the outer surface of the pedal disc, that is, inside the adventitious tube, showing attached inorganic and organic detritus and rod-shaped bacteria.

Mantle

The mantle margin of *Foegia novaezelandiae* is shown in transverse section in Figure 8. Mantle fusion is of Type C (Yonge, 1982), that is, inner, middle and inner surfaces of the outer mantle folds, so that virtually everywhere the outer surface of the general mantle is enclosed in thick periostracum. The pallial retractor muscles extend into the mantle (Fig. 7) and posteriorly form longitudinal fibres that retract the siphons. Laterally, the mantle has a capacious haemocoel and circular muscles from both the left and right assist in pallial contraction.

The mantle of the pedal disc is shown in transverse section in Figure 9. The outer epithelium is thrown into many folds and at the apex of each pleat there is a swollen cell ~ 8 μm in diameter which is innervated by tiny subepithelial nerves. The epithelium also secretes the periostracum, which comprises two layers. The inner is thick, up to 50 μm and stains blue in Masson's trichrome. It is probably mucoid. The outer layer is thin (2 μm), stains red in Masson's trichrome and is thrown into complex fibrous folds and strands. Around the pedal disc but diminishing towards the siphons, the outer surface of the periostracum is covered in an agglomeration of organic material. Within this are slightly curved, rod-shaped bacteria, ~ 1.5–2 μm in length, and which do not stain in either Masson's trichrome or Ehrlich's haematoxylin, but shine a bright yellow-green. This agglomeration of organic material and bacteria attached to the pedal disc, being inside the adventitious tube, is in darkness. It is not present in the similarly endobenthic *Brechites vaginiferus* (Morton, 1984a: fig 16a). The agglomeration of inorganic and organic detritus with the bacteria attached to the pedal disc, as seen under the SEM, is illustrated in Figure 10.

Siphons

As is typical of all clavagelloids studied hitherto (Morton, 1984a, b, 2002a, b, 2003), and for other anomalodesmatans (Prezant, 1979b; Morton, 1981b), radial mantle glands at the apices of the siphons of *F. novaezelandiae* produce a secretion which attaches sand grains and other detritus to the thick periostracum of their outer surfaces to camouflage them. The siphons are shown in transverse section in Figure 11A. Internally, there are 16 pallial nerves that, in other clavagelloids, for example, *Brechites vaginiferus* (Morton, 2002a) relate to the number of sensory papillae, which surround the siphonal orifices.

The siphonal wall is illustrated in greater detail in Figure 11B. Externally, are outer and inner layers of the periostracum. Internal to the outer epithelium is a haemocoel and internal to this are successive layers of longitudinal, circular, longitudinal and circular muscles. Criss-crossing the longitudinal muscle blocks are transverse and oblique fibres that must create the tonus which extends and contracts the siphons, in cooperation with the other

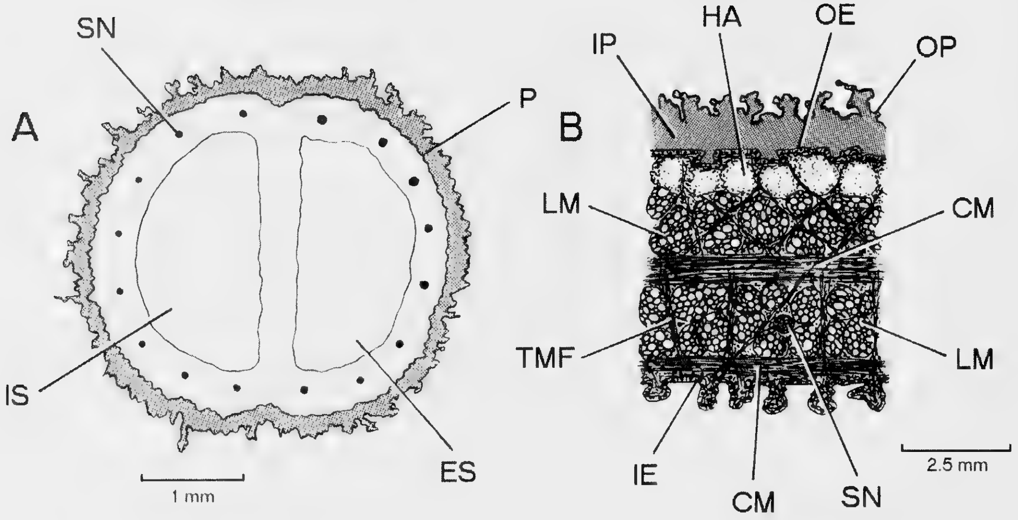

FIG. 11. *Foegia novaezelandiae.* Transverse sections through A, the siphons showing the thick periostracum and pallial nerves and B, the siphonal wall in greater detail (for abbreviations see pp. 38–39).

muscles and blood-filled haemocoels of the mantle. In terms of its muscular complexity, the siphons of *Foegia novaezelandiae* are very similar to those of *Brechites vaginiferus* (Morton, 1984a: fig.14) and *Humphreyia strangei* (Morton, 2002b: fig.12).

Ctenidia

The long, homorhabdic ctenidia (Fig. 7) are also illustrated diagrammatically in transverse section in Figure 12. Approximately five plicae make up the descending lamella of the outer demibranch and about eight both lamellae of the inner. There is a ventral marginal food groove in the latter. Each plica comprises a maximum of 20 filaments anteriorly, but only two as the ctenidia decline in size posteriorly (Fig. 7).

As in other clavagelloids, for example, *Brechites vaginiferus* (Morton, 1984a, 2002a), the epithelium ventral to the kidneys and which forms the dorsal surface of the supra-branchial chamber of the outer demibranch is modified into a hypobranchial gland. The descending lamella of the outer demibranch attaches to the visceral mass by a cuticular junction, as does the ascending lamella of the inner (Atkins, 1937b). This was first described for an anomalodesmatan, that is, *Laternula truncata*, by Morton (1973) and is considered characteristic of all representatives.

Medially, adjacent to the cuticular junction is an osphradium that has not hitherto been described for any anomalodesmatan, although it has been reported in other bivalves, for example, *Corbicula fluminea* (Kraemer, 1981). Left and right osphradia (Fig. 12) extend from the labial palps to the posterior end of the visceral mass. In transverse section (Fig. 13), each osphradium lies between the cuticular junction of the outer demibranch with the visceral mass and the hypobranchial gland. It comprises a central core of cells between which nerve fibres pass towards the periphery. The outer epithelium is thin (4 μm) but periodically along its margin there are swollen sensory cells ~ 8 μm tall and towards which the nerves are oriented.

Pericardium and Kidneys

The pericardium and kidneys are illustrated in Figure 6A and C and in transverse section in Figure 12. The rectum is enclosed by the ventricle of the heart (in turn surrounded by the pericardium) but lies dorsal to the paired kidneys. Each kidney comprises a capacious distal limb and a bag-like proximal limb that opens into the supra-branchial chamber of the inner demibranch at ciliated renal apertures (Fig. 12). There are no pericardial proprioreceptors such as occur in *Humphreyia strangei* and *Dianadema multangularis*

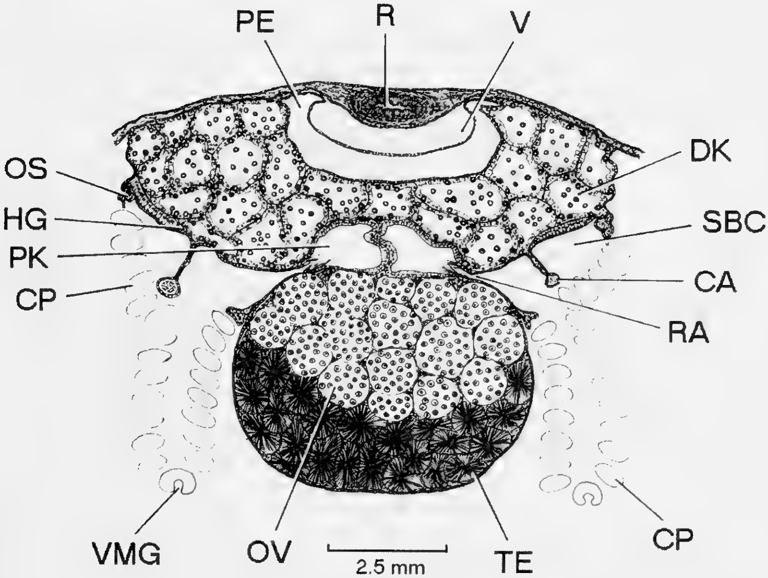

FIG. 12. *Foegia novaezelandiae*. A transverse section through the paired kidneys showing the renal apertures, the ctenidia and the position of the paired hypobranchial glands and osphradia within the supra-branchial chamber of the outer demibranch (for abbreviations see pp. 38–39).

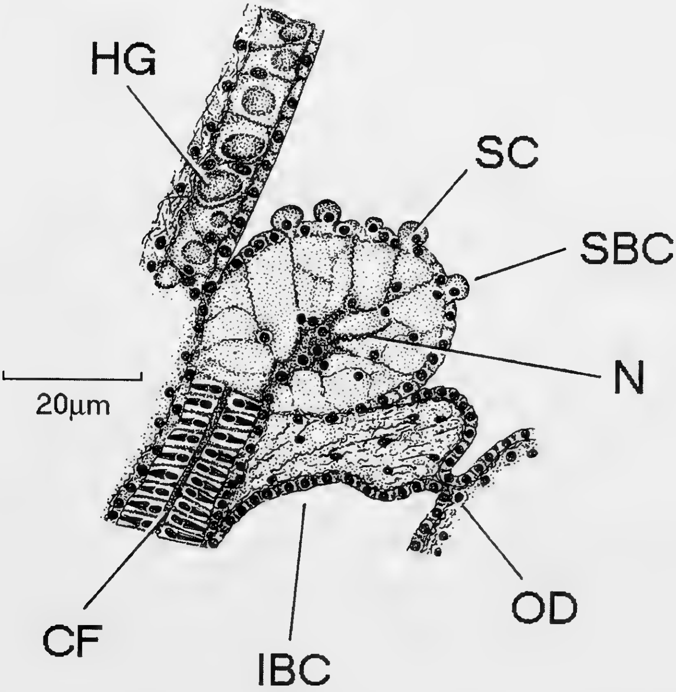

FIG. 13. *Foegia novaezelandiae*. A transverse section through the hypobranchial gland and osphradium in the supra-branchial chamber of the outer demibranch (for abbreviations see pp. 38–39).

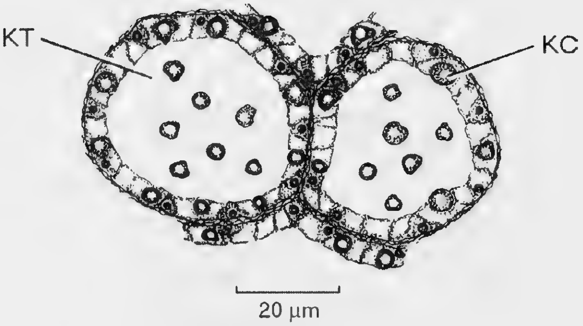

FIG. 14. *Foegia novaezelandiae*. A transverse section through two distal limb tubules of the kidney showing the contained concretions (for abbreviations see pp. 38–39).

(Morton, 2002b, 2003) probably because there are no remnants of the posterior pedal retractor muscles as in *Brechites vaginiferus*, which similarly does not have such sense organs (Morton, 2002a).

Distal kidney tubules are illustrated in transverse section in Figure 14. The cells are some 10 µm tall, largely vacuolated, and contain approximately spherical concretions, between 6–8 µm in diameter and which stain blue in Masson's trichrome but with a lighter staining core. Such concretions also occur in the lumina of the distal limb tubules.

DISCUSSION

The first, detailed description of a tube-dwelling clavagelloid (*Aspergillum dichotomum*) was by Lacaze-Duthiers (1883). Three-quarters of a century later, Purchon (1956, 1960) described *Brechites penis* and, later, Smith (1971, 1976, 1998) produced simple illustrations of Australian species, but not *Foegia novaezelandiae*. Subsequently, Morton (1984a, 2002a, b) described *Brechites vaginiferus* and the cemented *Humphreyia strangei*. Clavagelloids that unite only the left valve into the fabric of a crypt (*Clavagella* and *Bryopa*) have been described by Owen (1835), Soliman (1971) and Morton (1984b). The strange, cemented species, *Dianadema multangularis*, with tubules that form a crown over the dorsal part of the shell and adventitious tube, was described by Morton (2003) and suggested to be similar functionally to the North American, Late Cretaceous *Ascaulocardium armatum* (Pojeta & Sohl, 1987).

Savazzi (1982, 1999) described adaptations of clavagelloids to a tube-dwelling mode of life, and Carter (1978) described how the tubes of gastrochaenids are formed. The gastrochaenids *Cucurbitula* and *Eufistulana* (Morton, 1982, 1983) are convergently very similar to *Dianadema* and *Brechites*, respectively, in forming adventitious tubes. However, the shell valves of gastrochaenids do not unite with the tubes. Also, there is no anterior pedal slit nor are there tubules giving access to interstitial waters. Morton (1984a, 2002a) speculated on the process of tube formation in *Brechites vaginiferus* as, earlier, had Gray (1858b) and Smith (1978). These authors agree that the adventitious tube is secreted but once and that posterior extension is possible either as the animal grows or has to extend itself either to keep pace with an accreting habitat or to effect repair. Because the whole body internal to the tube is covered in thick periostracum, Morton (1984a, 2002a) believed erroneously that the tube of *B. vaginiferus* was created by a secretion produced from glands in the apex of the siphons pouring down the outside of the periostracum-covered adult, between it and the burrow, to form a structure that matched the configuration and surface structure of the burrow wall. Subsequently, Morton (2002b, 2003) showed that the tubes of *Humphreyia strangei* and *Dianadema multangularis* could not be secreted in this way, since both are cemented epibenthically with no burrow template. Formation probably results from the mantle epithelium secreting sequentially either periostracum or adventitious tube, in a manner similar to that described by Savazzi (2000) for the ligament of *Bryopa*.

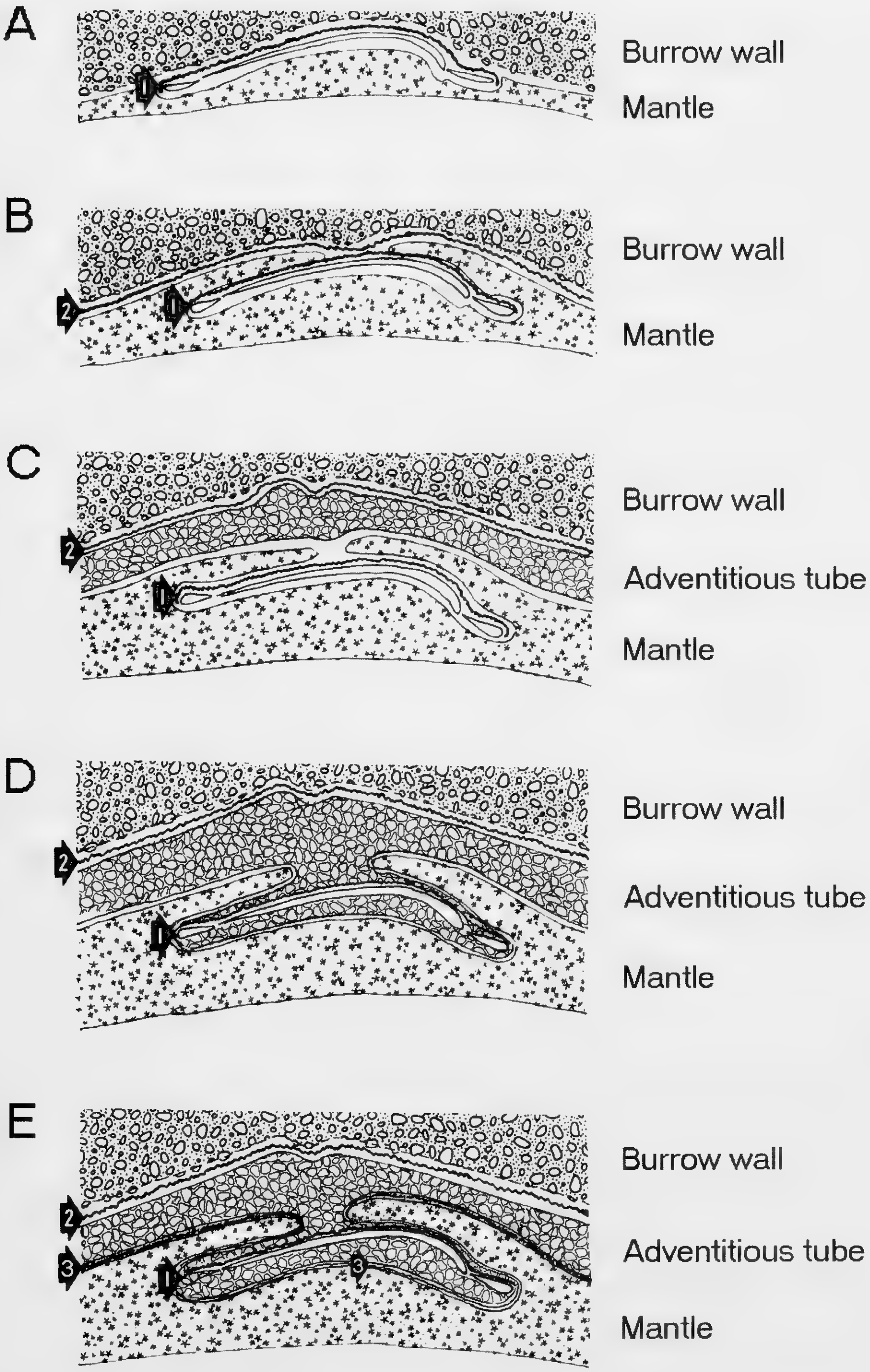

FIG. 15. *Foegia novaezelandiae*. Generalized illustrations of longitudinal sections through the shell, saddle and adventitous tube showing the postulated method of construction (for abbreviations see pp. 38–39).

In *Foegia novaezelandiae* the process of tube formation is more complicated than that of other clavagelloids and is illustrated in Figure 15A–E. Initially, the tube is secreted the same way as in *Brechites vaginiferus* (Morton, 1984a, 2002a), in that the juvenile shell is covered by periostracum: (Fig. 15A, arrow 1). The animal expands hydrodynamically enlarging its burrow to full adult size, and a second layer of periostracum is then secreted by the mantle and covers the whole body. The anterior and posterior pallial crests secrete this too over the tiny shell valves (Fig. 15B, arrow 2). Secretion of periostracum 2 having halted, the adventitious tube is then produced by the mantle (Fig. 15C). Extra secretions of the tube by the pallial crests produce the bulbous protuberances above the true shell valves largely hiding them. Internally too, further secretions by the dorsal mantle unite shell valves, saddle and tube, creating the situation whereby the former are effectively incorporated into the total structure of the adventitious tube (Fig. 15D). Finally (Fig. 15E, arrow 3), a further layer of periostracum is produced by the mantle so that the whole animal, within its tube, is now covered in periostracum which is thin and transparent dorsally (small arrow 3), and thick and wrinkled all over the rest of the mantle (large arrow 3).

The secretion of the adventitious tube of *Foegia novaezelandiae* is thus highly complex involving the mantle in a sequence of secretions of different properties to produce: (i) shell and saddle (covered by periostracum), (ii) a second layer of periostracum, (iii) the main component of the adventitious tube and, finally, (iv) a third layer of periostracum. This results in the peculiar situation wherein the animal is encased within periostracum, within a tube, within periostracum and within a burrow.

The hydrodynamic forces within the mantle and siphons of *Foegia novaezelandiae* which pump the animal up to its full size before production of the adventitous tube and subsequently extend the siphons following contraction, must, as postulated for *Brechites vaginiferus* (Morton, 2002a), in the absence of any adductor muscles, be created by contractions of the pedal disc. In *F. novaezelandiae*, the pedal disc must also create the hydrodynamic forces in the haemocoels of the mantle and siphons, acting agonistically with the circular, longitudinal and transverse muscles within the latter, to effect siphonal extension. The paired supra-branchial osphradia of *F. novaezelandiae* are of interest in this respect. Bivalve osphradia are usually simple structures and generally believed to monitor water flow through the ctenidia (Kraemer, 1981). However, in the case of *F. novaezelandiae*, perhaps they monitor the complex hydrodynamic forces in the mantle cavity and assist in their synchronisation.

Foegia novaezelandiae is also of interest in another respect. The thick anterior covering of periostracum, especially around the pedal disc, is thrown into complex folds not seen in other tube-dwelling clavagelloids, for example, *Brechites vaginiferus* (Morton, 1984a: fig. 12). It also possesses an external covering of an agglomeration of organic material and anucleate “cells”. Sand grains and other inorganic detritus covering the siphonal apices exposed to light are not present in the pedal disc agglomeration in the dark. The “cells” are bacteria: might they be sulphide oxidizing? *Foegia novaezelandiae* is unusual in that it occupies hypoxic mud. Is it possible that it has within the base of its tube and into which interstitial water is pumped, a collection of symbiotic bacteria that help to detoxify the sulphide in the incoming water? Might such bacteria also provide it with a supplementary source of nutrition in the form of reduced carbon and amino acids fixed and produced by them, respectively? This may reduce dependence on short-term inputs of organic matter from the tropical, nutrient deficient waters above (Rochford, 1980). This study cannot answer these questions until more intact specimens are available for study.

Reid (1990) surveyed the occurrence of chemoautotrophic sulphide oxidizing bacteria in the Bivalvia and showed that they occur within the ctenidial filaments in specialized bacteriocytes and are characteristic of hydrothermal vent species, for example, *Calyptogena* and *Bathymodiolus*, shallow water representatives of the Lucinoidea (Taylor & Glover, 2000) and Solemyoidea, many of which inhabit sulphur-rich sediments (Dando et al., 1986). *Foegia novaezelandiae* does not have intracellular, ctenidial bacteria, but the record of free-living bacteria with characteristics of sulphide-oxidizing ones on the pedal disc periostracum is of interest and deserves further study.

It is now known that the adventitious tubes of clavagelloids fulfil a number of functions. These are:

(i) Creating the rigid external skeleton against which the pedal disc can pump interstitial water into and out of the mantle cavity to generate the hydrodynamic pressures necessary in the pallial haemocoels to extend the siphons following retraction.
(ii) The same pumping action may supply the animal with interstitial bacteria and dissolved organic material and mineral salts, which probably act as sources of nutrients accessory to the material collected by suspension feeding from the tropical, nutrient poor overlying water (Rochford, 1980).
(iii) Aeration of the interstitial water may be achieved by pumping mantle cavity water obtained from the sea above via the siphons into the burrow heading.
(iv) Possible detoxification of interstitial water, by burrow aeration.
(v) Possible detoxification of hydrogen sulphide in the incoming interstitial water by (loosely symbiotic?) chemoautotrophic bacteria and the supply of reduced carbon and amino acids to the host.

Our understanding of the adaptive radiation of the Clavagelloidea increases with each new species studied. It stems from initial, but separate, adaptations in the Cretaceous (Clavagellidae: *Clavagella* and *Dianadema*) and Oligocene (Penicillidae: *Brechites* and *Foegia*) to life within a tube but how such adaptations arose and from what ancestor(s) are unknown (Harper et al., 2000).

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NEW SPECIES OF THE GENUS *KELLIA* (BIVALVIA: KELLIIDAE) FROM THE COMMANDER ISLANDS, WITH NOTES ON *KELLIA COMANDORICA* SCARLATO, 1981

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ABSTRACT

A new species, *Kellia kussakini*, is described from the Commander Islands. This species has a small (to 4.8 mm), translucent, pear-shaped, very inflated, almost globular shell (shell length, height, and width almost equal), with a slightly polished, yellowish-gray periostracum and posteriorly placed beaks. It was found in the subtidal zone (depth 5–20 m) of Bering and Medny islands, on a rocky platform, with population density to 1,190 specimens/m^2. Scarlato (1981) described *Kellia comandorica* Scarlato, 1981, from the Commander Islands after study of a small amount of material (10 specimens). Later, Coan et al. (2000) synonymized *K. comandorica* with *K. suborbicularis* (Montagu, 1803). A study of extensive material (146 specimens) has shown that *K. comandorica* is a separate species having characters that distinguish it from other species of *Kellia*. An expanded description of *K. comandorica* is given.

Key words: *Kellia*, Kelliidae, Bivalvia, Commander Islands, morphology, distribution.

INTRODUCTION

The bivalve mollusk fauna of the Commander Islands shelf has been poorly studied. The most complete species list of bivalve mollusks of the Commander Islands was published after examination of the extensive material collected by two joint expeditions of IMB-PRIFO (the sealer “Krylatka”, 1972; RV “Rakitnoye”, 1973) to these islands, as well as an analysis of previous investigations (Kamenev, 1995). However, there still were a number species requiring additional investigation and more accurate identification. Subsequently, a few papers devoted to the study of these species were published (Kamenev, 1996, 2002; Kamenev & Nadtochy, 2000). Further examination of bivalve mollusks collected in the shelf zone of the Commander Islands revealed one new species of the genus *Kellia* which was erroneously identified as *Kellia suborbicularis* (Montagu, 1803) (Kamenev, 1995). In addition, another species of this genus, *Kellia comandorica* Scarlato, 1981, described by Scarlato (1981) based on a small amount of material, is abundant in the intertidal and subtidal zones of the Commander Islands. Scarlato (1981) described *K. comandorica* in detail and provided a comparative diagnosis with distinguishing characters of this species, and photos of the holotype. Coan et al. (2000) considered this species as a synonym of *K. suborbicularis.* A study of a large quantity of *K. comandorica*, which is a common mollusk in the Commander Islands, has clearly shown that it is a well-identifiable, separate species of *Kellia*. The goal of this paper is to describe the new species and expand the description of *K. comandorica,* with new data on its morphology, ecology, and geographical distribution.

MATERIAL AND METHODS

In this study I used the material collected by the joint expeditions of IMB-PRIFO in the subtidal zone of the Kuril Islands (the sealer “Krylatka”, September–October 1969) and Commander Islands (the sealer “Krylatka”, July 1972; RV “Rakitnoe”, August–October 1973) and the expedition of IMB in the intertidal zone of the Commander Islands (June–August 1972). The material of the new species and of *K. comandorica* from the subtidal zone of the Commander Islands was fixed and stored in 70% ethanol in IMB. Material of *K.*

comandorica from the Kuril Islands and the intertidal zone of the Commander Islands was fixed in 70% ethanol and stored dry in IMB.

For comparison purposes, collections of *K. suborbicularis* – 88 specimens from the North Atlantic (CAS, NHM, NMW) and more 300 specimens from the northeastern Pacific (CAS, UW); of *Kellia japonica* Pilsbry, 1895 – 2 specimens from Japan (NSMT Mo 73530) and 16 specimens from the Pacific seas of Russia (MIMB); of *Kellia porculus* Pilsbry, 1904 – 1 specimen from Japan (NSMT Mo 73531); and of *Kellia subrotundata* (Dunker, 1882) – 1 specimen from (NSMT Mo 73532) were used. All material of these species was stored dry.

Shell Measurements

Figure 1 shows the shell morphology measurements. Shell length (L), anterior end length (A), height (H), width (W) (not shown) were measured for each valve. The ratios of these parameters to shell length (A/L, H/L, W/L, respectively) were determined. Shell measurements were made using a caliper and an ocular micrometer with an accuracy of 0.1 mm.

The following material was measured:

(1) 85 specimens, 1 right and 5 left valves of *K. comandorica* from Urup Island, Kuril Islands, (MIMB, 15 specimens, 1 right, 5 left valves) and the Commander Islands (MIMB, IMB, 70 specimens).

(2) 97 specimens of the new species from the Commander Islands (IMB).

(3) 44 specimens of *K. suborbicularis* from the North Atlantic: Weymouth, Dorset, Sea area 16, United Kingdom (NMW 1953.183, 24 specimens); Tenby, Pembrokeshire, Sea area 21, United Kingdom (NMW 1953.183, 9 specimens); Guernsey, Channel Is., Sea area 17, United Kingdom (NMW 1953.183, 3 specimens); Plymouth, United Kingdom (NHM 20030382, 2 specimens); Isle of Herm, Guernsey, United Kingdom (NHM 20030383, 2 specimens); England (CAS 165845, 2 specimens); England (CAS 165846, 2 specimens).

(4) 21 specimens of *K. suborbicularis* from the northeastern Pacific: Monterey Bay, California (CAS 161254, 8 specimens); Orcas Island, San Juan Islands, San Juan County, Puget Sound, Washington (CAS 161256, 7 specimens); Alaska (CAS 161255, 6 specimens).

Statistics

Statistical analysis of the material used a package of statistical programs STATISTICA (Borovikov & Borovikov, 1997) and Data Analysis Module of MS Excel 97.

The calculated indices (A/L; H/L; W/L) are less susceptible to change compared with other measured parameters. Therefore, the statistical analysis was performed using only these characteristics. All data was tested with a Kolmogorov test for their fit to a normal distribution. The distribution of some indices was different from the norm. Therefore all analyses were performed on $\log_{10}$ transformations of the original variables. All indices for pairs of different valves of *Kellia* species were compared using the Student (T) parametric test and one-way analysis of variance (ANOVA).

Throughout this study, statistical significance was defined as $P < 0.05$.

Abbreviations

The following abbreviations are used in the paper: CAS – California Academy of Sciences, San Francisco; IMB – Institute of Marine Biology, Russian Academy of Sciences, Vladivostok; MIMB – Museum of the Institute of Marine Biology, Vladivostok; NHM – The Natural History Museum, London; NMW – National Museums & Galleries of Wales, Cardiff; NSMT – National

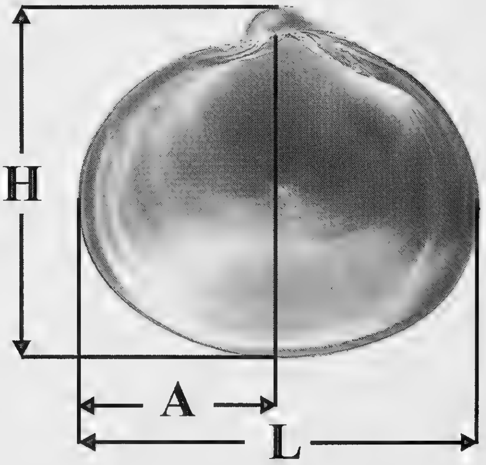


FIG. 1. Placement of shell measurements: L – shell length; H – height; A – anterior end length.

Science Museum, Tokyo; PRIFO – Pacific Research Institute of Fisheries and Oceanography, Vladivostok; UW – University of Washington, Seattle; ZIN – Zoological Institute, Russian Academy of Sciences, St.-Petersburg.

SYSTEMATICS

Family Lasaeidae Gray, 1842
Genus *Kellia* Turton, 1822

Type species: *Mya suborbicularis* Montagu, 1803

Diagnosis

Shell small (< 30 mm), thin, ovate to globular, inflated, inequilateral, equivalve. Surface with growth lines. Periostracum thin, adherent, colorless, gray, green to yellow. Beaks prosogyrate, almost central. Hinge plate narrow. Right valve with one cardinal tooth and posterior lateral tooth; left valve with two cardinal teeth and posterior lateral tooth. Ligament internal, partly lodged in a lanceolate resilifer, situated between cardinal and lateral teeth. Pallial line without pallial sinus.

Kellia comandorica Scarlato, 1981
(Figs. 2–20, Table 1)

Kellia comandorica Scarlato, 1981: 321, pls. 284 (holotype), 285.
Kellia suborbicularis (Montagu, 1803), Coan et al., 2000: 323 (partim).

Type Material and Locality

Holotype (ZIN 9372), Commander Islands, Coll. E. F. Gurjanova, 1930 (Scarlato, 1981).

Material Examined

16 lots (MIMB 2989, 2990, 2992, 2994, 2996–3000, 3047–3050, 3052, 3053, 3055) from the tidal zone of Urup Island, Kuril Islands (15 specimens, 1 right, 5 left valves); 63 lots (MIMB 2993, 3001, 3002, 3052, 3054, IMB) from the intertidal and tidal zones of the Commander Islands (131 specimens). Total of 146 specimens, 1 right, and 5 left valves.

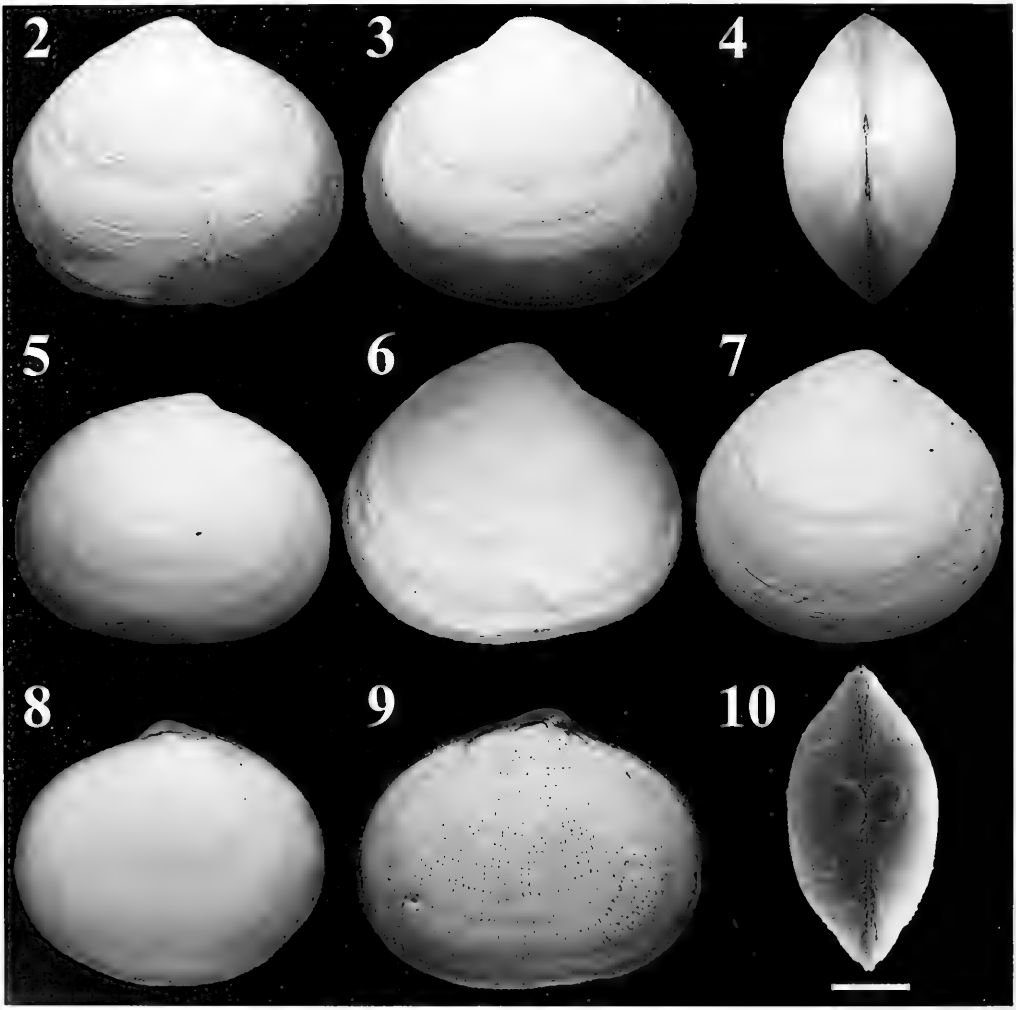
Description (expanded from that of Scarlato,1981)

Exterior: Shell small (to 16.8 mm), ovate-angular, high (H/L = 0.735–0.976), equivalve, inflated (W/L of valve 0.198–0.397), inequilateral, thin, solid. Surface with conspicuous, often rather rough growth lines. Periostracum thin, adherent, non-polished, colorless or gray, extending into inner surface. Beaks small, moderately projecting above dorsal margin, slightly anterior to midline (sometimes central) (A/L = 0.314–0.5), rounded, prosogyrate. Anterior and posterior ends rounded. Anterodorsal margin slightly convex, gently descending ventrally, smoothly transitioning to slightly curved anterior margin. Ventral margin slightly curved. Posterodorsal margin slightly convex, rather steeply descending to rounded posterior margin.

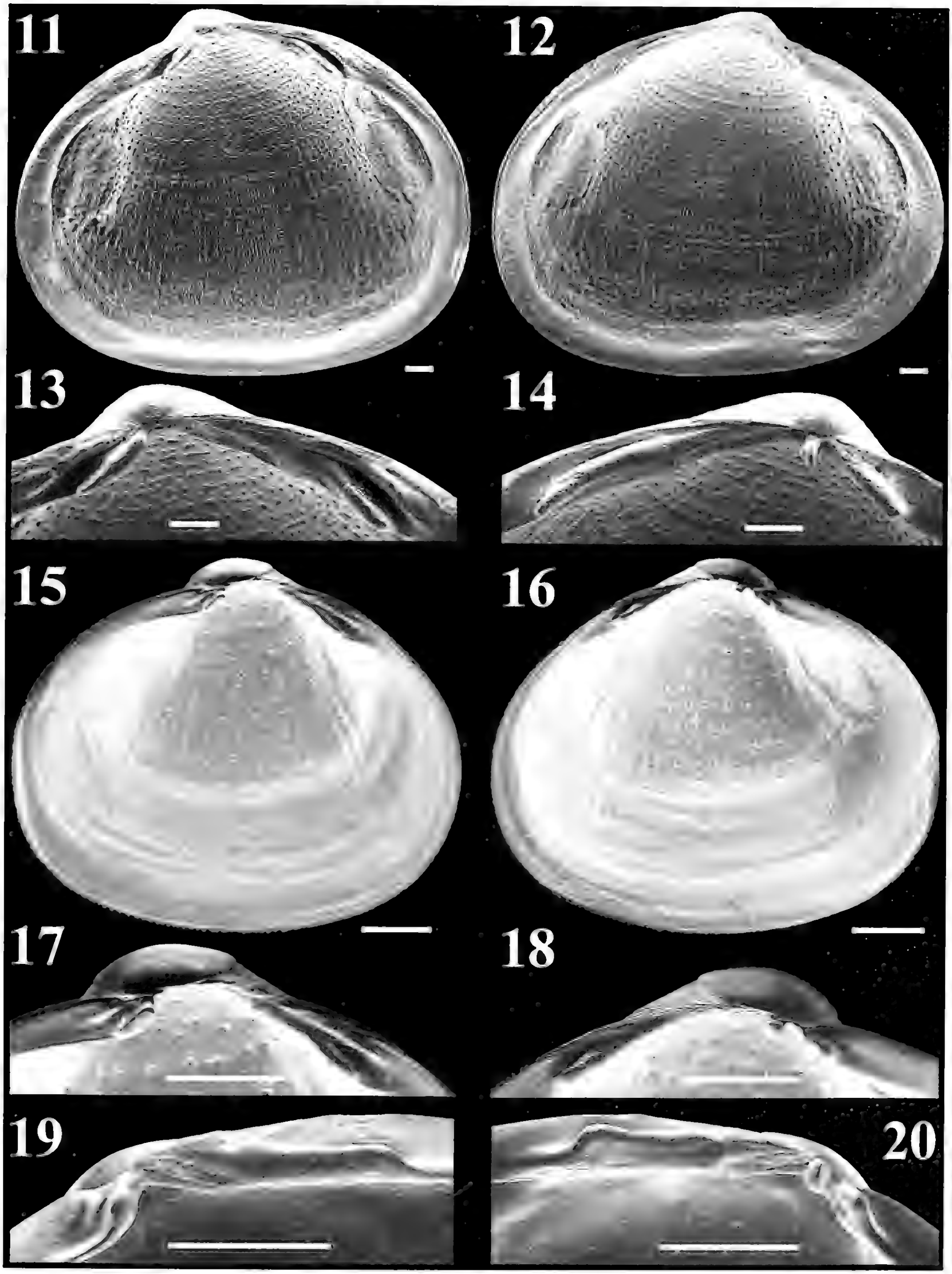
TABLE 1. *Kellia comandorica* Scarlato, 1981. Summary statistics of the shell measurements (mm) and indices: L – shell length; A – anterior end length; H – height; W – width. Numerator indicates the summary statistics for the right valve, denominator – for the left valve.

Statistics	L	A	H	W	A/L	H/L	W/L
Mean	9.31 9.21	4.26 4.21	7.91 7.82	2.47 2.47	0.458 0.458	0.846 0.846	0.264 0.265
SD	0.33 0.32	0.15 0.15	0.29 0.28	0.10 0.10	0.003 0.003	0.005 0.005	0.003 0.003
SE	3.04 2.99	1.41 1.39	2.72 2.69	0.92 0.93	0.027 0.027	0.049 0.048	0.031 0.030
Min	3.4 3.4	1.6 1.6	2.5 2.5	0.9 0.9	0.314 0.314	0.735 0.735	0.198 0.198
Max	16.8 16.8	7.8 7.8	15.2 15.2	5.1 5.2	0.500 0.500	0.976 0.976	0.389 0.397
n	86 90	86 90	86 90	86 90	86 90	86 90	86 90

Interior: Right valve with one cardinal tooth and posterior lateral tooth; left valve with two cardinal teeth and posterior lateral tooth. In right valve, cardinal tooth large, elongate, flattened, with a flat top, anteroventrally directed, situated at edge of inner part of anterodorsal shell margin; posterior lateral tooth large, long, extending along posterodorsal shell margin. In left valve, anterior cardinal tooth large, elongate, flattened, often triangular, anteroventrally directed, situated at edge of inner part of anterodorsal shell margin; posterior cardinal tooth small, rounded, isolated, fingerlike, with rounded top, situated exactly under beak; posterior lateral tooth large, long, extending along posterodorsal shell margin. Internal ligament



FIGS. 2-10. *Kellia comandorica* Scarlato, 1981. 2-4: MIMB (3002), Gladky Cape, Medny Island, Commander Islands, intertidal zone, shell length 16.4 mm. 5: MIMB (2994), Lidina Cape, Urup Island, Kuril Islands, 20 m, shell length 16.0 mm. 6: Poludennaya Bight, Medny Island, Commander Islands, 20 m, shell length 11.8 mm. 7: Poludennaya Bight, Medny Island, Commander Islands, 20 m, shell length 12.2 mm. 8: Peschany Cape, Medny Island, Commander Islands, shell length 13.1 mm. 9: MIMB (2998), Van-der-Linda Cape, Urup Island, Kuril Islands, 10 m, shell length 14.7 mm. 10: Polovina Cape, Bering Island, Commander Islands, 5 m, dorsal view of both valves of a young specimen. Bar = 1 mm.



FIGS. 11–20. *Kellia comandorica* Scarlato, 1981. 11–14: Peschany Cape, Medny Island, Commander Islands, 15 m. 11, 12: Right and left valves of an adult specimen. 13, 14: Hinge of right and left valves. 15–20. Phedoskina Cape, Bering Island, Commander Islands, 5 m. 15, 16: Right and left valves of a young specimen. 17, 18: Hinge of right and left valves. 19, 20: Ventral view of hinge of right and left valves showing resilifer. Bar = 500 μm.

well-developed, large, situated between cardinal and lateral teeth, posteriorly directed, partly lodged in lanceolate resilifer extending obliquely posterior to beaks. Anterior adductor muscle scar large, rounded; posterior muscle scar large, ovate-angular, longer and wider than anterior scar. Pallial line without pallial sinus. Shell interior with conspicuous radial rows of fossae extending to pallial line.

Variability

Shell shape and proportions, as well as width of the valves vary markedly (Table 1, Figs. 5–7). The shell shape varies from ovate-elongate with relatively small shell height to rounded with height almost equal to shell length. The shell is most often slightly angular but sometimes it is regularly ovate without angles. The specimens frequently have a deformed shell because of living in small holes and crevices of boulders and rocky platforms, preventing normal growth. The position of the beaks is also variable. Usually the beaks are anteriorly placed but sometimes they occupy the central position. The sizes and shape of cardinal and lateral teeth in both valves vary little. All investigated specimens, independent of the age, habitat, and geographic area, had conspicuous radial rows of fossae on the inner shell wall.

Distribution and Habitat (Fig. 21)

Kellia comandorica occurs near the Commander Islands and Urup Island (Kuril Islands). Near Bering Island and Medny Island (Commander Islands), *K. comandorica* is a common species of the bottom fauna. It was recorded from the intertidal zone to 20 m depth, on boulders and rocky platforms, at a bottom temperature from 4.0 to 10.2°C, with population density to 170 specimens/m^2. Near Urup Island (Kuril Islands) this species was found at depth from 5 to 20 m, on boulders and rocky platforms, with population density to 40 specimens/m^2.

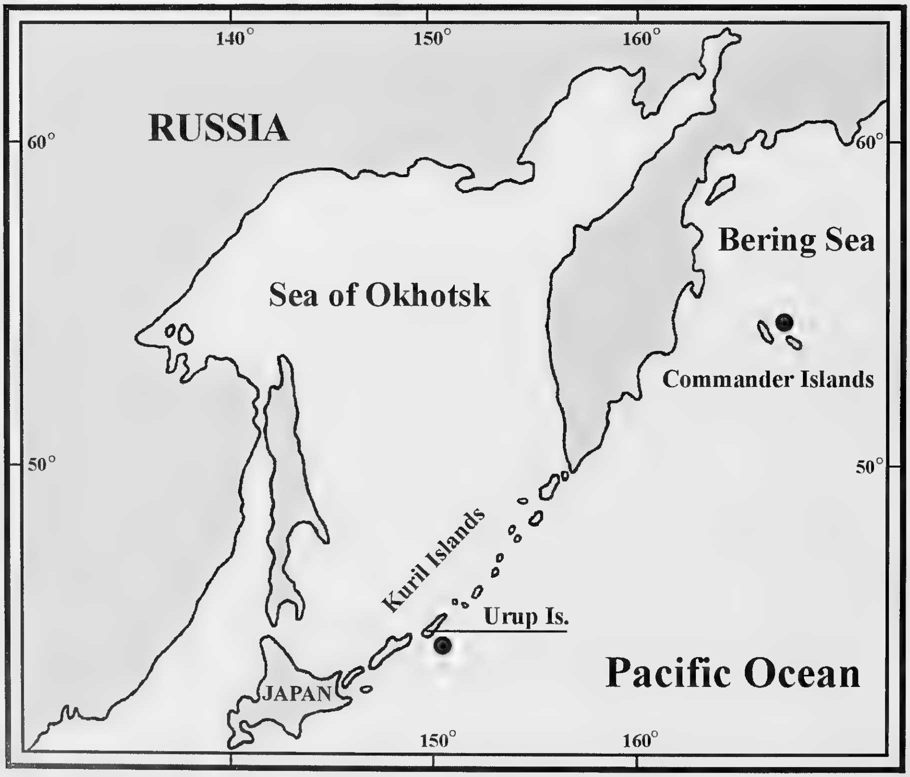
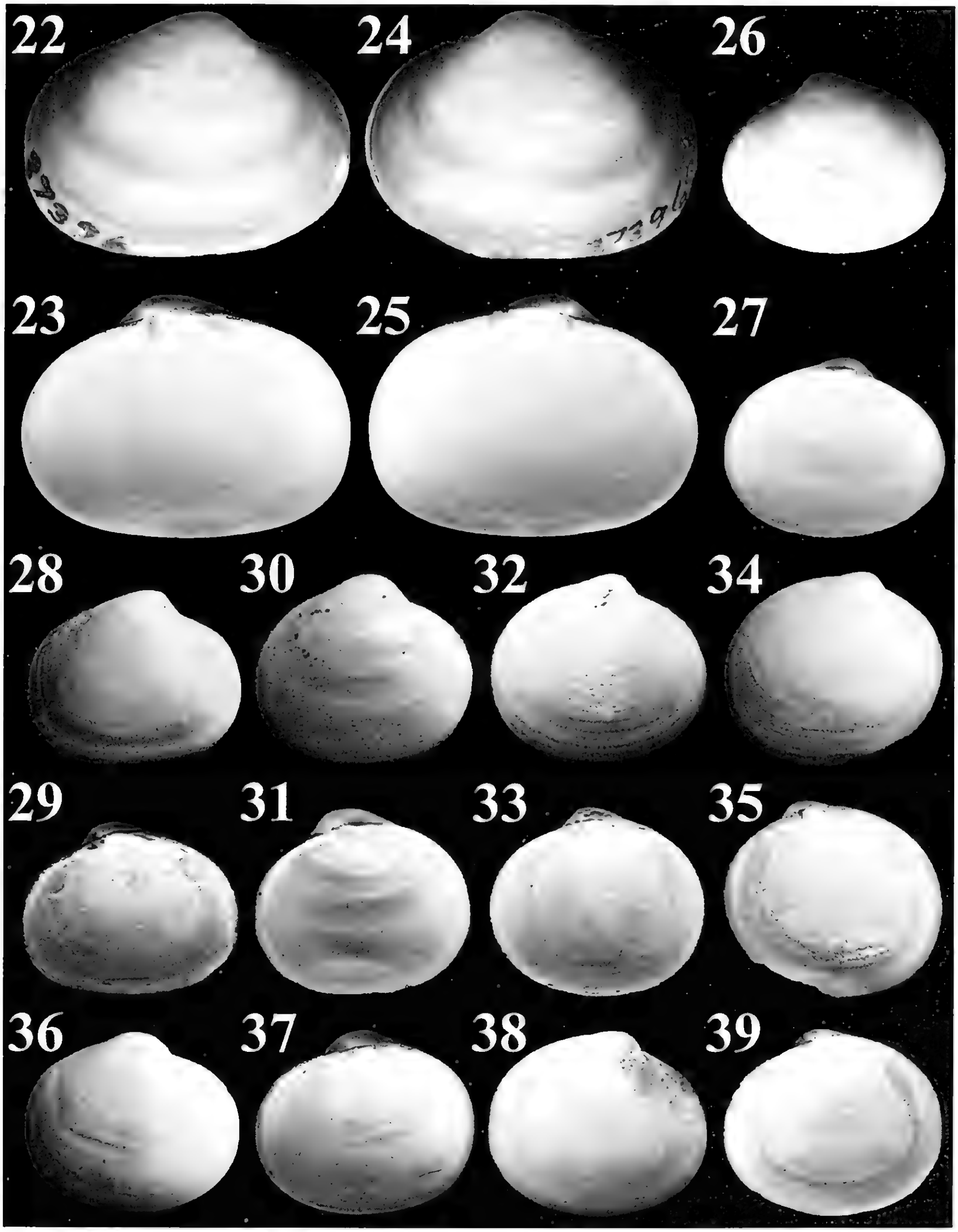


FIG. 21. Distribution of *Kellia comandorica*, Scarlato 1981.



FIGS. 22–39. Shells of *Kellia* species. 22–27. *Kellia suborbicularis* (Montagu, 1803) from the northeastern Pacific. 22–25: CAS (161254), Monterey Bay, California, 18–22 m, shell length 26.1 mm. 26–27: CAS (161255), Alaska, left valve, shell length 13.8 mm. 28-33. *Kellia suborbicularis* (Montagu, 1803) from the North Atlantic. 28–29: NMW (1953.183), Tenby, Pembrokeshire, Sea area 21, United Kingdom, right valve, shell length 11.7 mm. 30–31: NHM (20030382), Plymouth, United Kingdom, right valve, shell length 9.0 mm. 32–33: CAS (165845), England, right valve, shell length 8.9 mm. 34–35: *Kellia japonica* Pilsbry, 1895, NSMT (Mo 73530), Nagashima, Mie Prefecture, Japan, right valve, shell length 11.5 mm. 36–37: *Kellia subrotundata* (Dunker, 1882), NSMT (Mo 73532), Nosappu Cape, Hokkaido, Japan, right valve, shell length 11.4 mm. 38–39: *Kellia porculus* Pilsbry, 1904, NSMT (Mo 73531), Ushimado, Okayamo Prefecture, Seto Inland Sea, Japan, right valve, shell length 8.3 mm.

TABLE 2. Differentiating characters of *Kellia* species. L – shell length; H – height; W – valve width; A – anterior end length.

Characters	*K. suborbicularis* (United Kingdom)	*K. suborbicularis* (NE Pacific)	*K. comandorica*	*K. kussakini*	*K. japonica*	*K. porculus*	*K. subrotundata*
Shell	solid	solid	solid	fragile, translucent	solid	solid	solid
Shell shape (H/L)	ovate-angular (0.857)	ovate-elongate (0.809)	ovate-angular (0.846)	pear-shaped, globular (0.950)	rounded quadrate (0.878)	subspherical (0.880)	ovate-subquadrate (0.842)
Shell max. length, mm	11.7	26.1	16.8	4.8	11.5	13.0	11.4
Valve (W/L)	very inflated (0.304)	inflated (0.260)	inflated (0.264)	very inflated (0.340)	very inflated (0.304)	inflated (0.289)	very inflated (0.330)
Beaks (A/L)	low, slightly anterior to midline (0.443)	low, anterior to midline (0.414)	low, slightly anterior to midline (0.458)	high, slightly posterior to midline (0.517)	low, strongly anterior to midline (0.261)	high, anterior to midline (0.386)	high, swollen, slightly anterior to midline (0.439)
Periostracum	slightly polished, yellowish-gray	polished, yellow or grayish-yellow	non-polished, colorless or gray	slightly polished, yellowish-gray	polished, yellow	polished, yellow or grayish-yellow	polished, yellow
Shell surface	with faint or conspicuous growth lines	with faint growth lines	with conspicuous, rough growth lines	with faint growth lines	with faint growth lines	with faint growth lines	with faint growth lines
Internal shell surface	sometimes with faint radial striae	sometimes with faint radial striae	with conspicuous radial rows of fossae	smooth	sometimes with faint radial striae	sometimes with faint radial striae	sometimes with faint radial striae

Comparisons

Kellia comandorica is easily distinguished from other species of this genus by its shell with radial rows of fossae on the inner wall (Table 2). Moreover, *K. comandorica* differs from *Kellia kussakini* by its larger, lower, and less inflated ovate-angular shell with anteriorly placed beaks.

In shell shape and proportion *K. comandorica* is similar to *K. suborbicularis* from the North Atlantic. However, with the exception of the above-mentioned distinguishing character, in contrast to *K. suborbicularis* from the North Atlantic, this species has a less inflated shell with the non-polished periostracum and less anteriorly placed beaks (Table 1, 3). Mean values and variances of the indices characterizing the position of beaks (A/L) and the relative width (W/L) were significantly different in these species (Table 4, Figs. 28–33).

Unlike *K. comandorica*, the shell of *K. suborbicularis* from the northeastern Pacific is non-angular, rounded-ovate or ovate-elongate with faint growth lines and the polished yellow or grayish-yellow periostracum, interiorly smooth, sometimes with the faint radial striae especially noticeable along the ventral shell margin (Tables 1, 2, 4, 5, Figs. 22–27).

In contrast to *K. japonica*, *K. porculus* and *K. subrotundata*, *K. comandorica* has a less inflated shell with a non-polished gray periostracum, conspicuous growth lines, and less anteriorly placed beaks (Table 2, Figs. 34–39).

Remarks

In the northwestern Pacific, the Russian and Japanese malacologists recognize another species *K. japonica* (Scarlato, 1981; Kafanov, 1991; Okutani, 2000), which Coan et al. (2000) also considered a synonym of *K. suborbicularis*. However, the very wide geographic distribution of *K. suborbicularis* may suggest that it is a composite that includes several species (Scarlato, 1981). The placement of *K. japonica* in synonymy with *K. suborbicularis* further extends the range of *K. suborbicularis.*

The study of different-age individuals (from 0.3 mm to 11.7 mm) of *K. suborbicularis* from the North Atlantic showed that the shell shape varies from ovate-elongate to globular (Figs. 28–33). However, the proportion of specimens with the ovate-elongate shell was small. On the whole, in comparison with *K. suborbicularis* from the northeastern Pacific, individuals of this species from the North Atlantic have a relatively small (< 12 mm), markedly more rounded, higher, and more inflated shell with less anteriorly placed beaks and a slightly polished yellowish-gray periostracum (Tables 3, 5). Mean values and variances of the indices characterizing the position of beaks (A/L), the relative height (H/L) and width (W/L) in *K. suborbicularis* from the North Atlantic were significantly different from the mean values and variances of the same indices of this species from the northeastern Pacific (Table 4).

TABLE 3. *Kellia suborbicularis* (Montagu, 1803) from the North Atlantic (NMW 1953.183; NHM 20030382, 20030383; CAS 165845, 165846). Summary statistics of the shell measurements (mm) and indices: L – shell length; A – anterior end length; H – height; W – width. Numerator indicates the summary statistics for the right valve, denominator – for the left valve.

Statistics	L	A	H	W	A/L	H/L	W/L
Mean	$\frac{6.91}{6.92}$	$\frac{3.02}{3.02}$	$\frac{5.92}{5.92}$	$\frac{2.12}{2.13}$	$\frac{0.443}{0.442}$	$\frac{0.857}{0.857}$	$\frac{0.303}{0.304}$
SD	$\frac{0.32}{0.32}$	$\frac{0.12}{0.12}$	$\frac{0.27}{0.27}$	$\frac{0.11}{0.12}$	$\frac{0.005}{0.005}$	$\frac{0.006}{0.006}$	$\frac{0.005}{0.005}$
SE	$\frac{2.11}{2.11}$	$\frac{0.81}{0.81}$	$\frac{1.80}{1.80}$	$\frac{0.75}{0.77}$	$\frac{0.033}{0.034}$	$\frac{0.037}{0.037}$	$\frac{0.035}{0.036}$
Min	$\frac{2.7}{2.7}$	$\frac{1.2}{1.2}$	$\frac{2.1}{2.1}$	$\frac{0.6}{0.6}$	$\frac{0.346}{0.337}$	$\frac{0.776}{0.776}$	$\frac{0.211}{0.211}$
Max	$\frac{11.7}{11.7}$	$\frac{4.6}{4.6}$	$\frac{9.4}{9.4}$	$\frac{3.8}{3.8}$	$\frac{0.500}{0.500}$	$\frac{0.944}{0.944}$	$\frac{0.367}{0.367}$
n	$\frac{44}{44}$	$\frac{44}{44}$	$\frac{44}{44}$	$\frac{44}{44}$	$\frac{44}{44}$	$\frac{44}{44}$	$\frac{44}{44}$

TABLE 4. Results of comparison by pairs of mean values (Student (T) test) and variances (ANOVA) of indices of the right and left valves of *Kellia comandorica*, *K. kussakini*, and *K. suborbicularis*: L - shell length; A - anterior end length; H - height; W – width; P – probability that index values in *K. comandorica*, *K. kussakini*, and *K. suborbicularis* are drawn from the same population; n – number of valves of compared species, respectively; * – significant difference.

	Right valves					Left valves				
Indices	T	P	F	P	n	T	P	F	P	n
K. comandorica and *K. suborbicularis* (North Atlantic)										
A/L*	-2.60	0.006	7.66	0.006	86/44	-2.73	0.004	8.75	0.004	90/44
H/L	1.45	0.080	1.77	0.187	86/44	1.44	0.008	1.76	0.187	90/44
W/L*	6.24	< 0.001	42.69	< 0.001	86/44	6.23	< 0.001	43.38	< 0.001	90/44
K. comandorica and *K. suborbicularis* (Northeastern Pacific)										
A/L*	8.23	< 0.001	48.43	< 0.001	86/21	8.43	< 0.001	51.50	< 0.001	90/21
H/L*	3.78	< 0.001	10.62	0.002	86/21	3.87	< 0.001	11.24	0.001	90/21
W/L	0.83	0.205	0.47	0.492	86/21	0.87	0.196	0.49	0.486	90/21
K. kussakini and *K. comandorica*										
A/L*	13.46	< 0.001	178.21	<0.001	86/97	13.59	< 0.001	179.79	< 0.001	86/97
H/L*	11.02	< 0.001	125.47	<0.001	86/97	11.25	< 0.001	128.38	< 0.001	86/97
W/L*	15.99	< 0.001	252.99	<0.001	86/97	16.04	< 0.001	253.16	< 0.001	86/97
K. kussakini and *K. suborbicularis* (North Atlantic)										
A/L*	-12.39	< 0.001	160.41	< 0.001	97/44	-12.26	< 0.001	159.50	< 0.001	97/44
H/L*	-8.88	< 0.001	76.69	< 0.001	97/44	-8.85	< 0.001	79.36	< 0.001	97/44
W/L*	-5.79	< 0.001	35.06	< 0.001	97/44	-5.65	< 0.001	33.44	< 0.001	97/44
K. kussakini and *K. suborbicularis* (Northeastern Pacific)										
A/L*	18.60	< 0.001	205.68	< 0.001	97/21	18.60	< 0.001	205.68	< 0.001	97/21
H/L*	11.88	< 0.001	147.89	< 0.001	97/21	11.89	< 0.001	148.39	< 0.001	97/21
W/L*	13.55	< 0.001	111.36	< 0.001	97/21	13.80	< 0.001	109.01	< 0.001	97/21
K. suborbicularis (North Atlantic) and *K. suborbicularis* (Northeastern Pacific)										
A/L*	4.34	< 0.001	13.74	< 0.001	44/21	4.24	< 0.001	12.95	< 0.001	44/21
H/L*	4.82	< 0.001	23.61	< 0.001	44/21	4.84	< 0.001	23.76	< 0.001	44/21
W/L*	6.09	< 0.001	27.30	< 0.001	44/21	6.16	< 0.001	27.03	< 0.001	44/21

Most specimens of *K. suborbicularis* from the northeastern Pacific had a ovate-elongate, markedly less inflated shell, reaching more than 26 mm in length, with more anteriorly placed beaks and yellow, strongly polished periostracum (Figs. 22–27, Table 5). The specimens with an analogous shell shape (more 20 mm in length) were also recorded off the Kuril Islands (materials from the expedition with the R/V “Akademik Oparin”, 1 July – 4 August 2003). All these morphological characteristics are observed in *Kellia laperousii* (Deshayes, 1839) (Oldroyd, 1925; Scarlato, 1981), which Coan et al. (2000) also considered to be a synonym of *K. suborbicularis*. They stated that no consistent difference from the North Atlantic *K. suborbicularis* can be found when similar-sized specimens are compared. However, a detailed study of this question is needed. Taking into account the results of comparison of specimens of *K. suborbicularis* from the North Atlantic and the northeastern Pacific, I think that most likely a separate species *K. laperousii* occurs in the North Pacific.

The species of the genus *Kellia* – *K. japonica*, *K. porculus* and *K. subrotundata* – living off the coast of Japan (Okutani, 2000), are most similar to *K. suborbicularis* in shape and shell proportions (Tables 2, 3, Figs. 28–39). In addition, the species from Japan are also very similar to each other. Some differences between these species exist in the degree of inflation of the shell, the position and form of the beaks, and the color of the periostracum (Table 2). However, the differ-

TABLE 5. *Kellia suborbicularis* (Montagu, 1803) from the northeastern Pacific (CAS 1612564, 161255, 161256). Summary statistics of the shell measurements (mm) and indices: L – shell length; A – anterior end length; H – height; W – width. Numerator indicates the summary statistics for the right valve, denominator – for the left valve.

Statistics	L	A	H	W	A/L	H/L	W/L
Mean	15.56	6.40	12.55	4.06	0.414	0.809	0.259
	15.56	6.40	12.55	4.08	0.414	0.809	0.260
SD	0.97	0.37	0.75	0.30	0.004	0.008	0.005
	0.97	0.37	0.75	0.30	0.004	0.008	0.005
SE	4.47	1.70	3.44	1.36	0.020	0.038	0.023
	4.47	1.70	3.44	1.37	0.020	0.038	0.021
Min	9.4	4.2	7.3	2.0	0.380	0.743	0.213
	9.4	4.2	7.3	2.0	0.380	0.743	0.213
Max	26.1	10.4	19.4	8.2	0.463	0.873	0.314
	26.1	10.4	19.4	8.2	0.463	0.873	0.314
n	21	21	21	21	21	21	21
	21	21	21	21	21	21	21

ence in shell proportions can be attributed to the individual variability of one species. Because only a very limited material on *Kellia* species from Japan was at my disposal, no final conclusion can be made. It is not improbable that after a detailed study of more extensive material, these species prove to be a synonym of one species different from *K. suborbicularis* or *K. laperousii*.

Kellia kussakini **Kamenev, new species**

Figs. 40–53, Table 6

Type Material and Locality

Holotype (MIMB 7770), Phedoskina Cape, Bering Island, Commander Islands, Pacific Ocean, 5 m, rocky platform, bottom water temperature of 10.0°C, Coll. V. I. Lukin, 23-IX-1973 (RV "Rakitnoye"); paratypes (96) (MIMB 7771) from holotype locality.

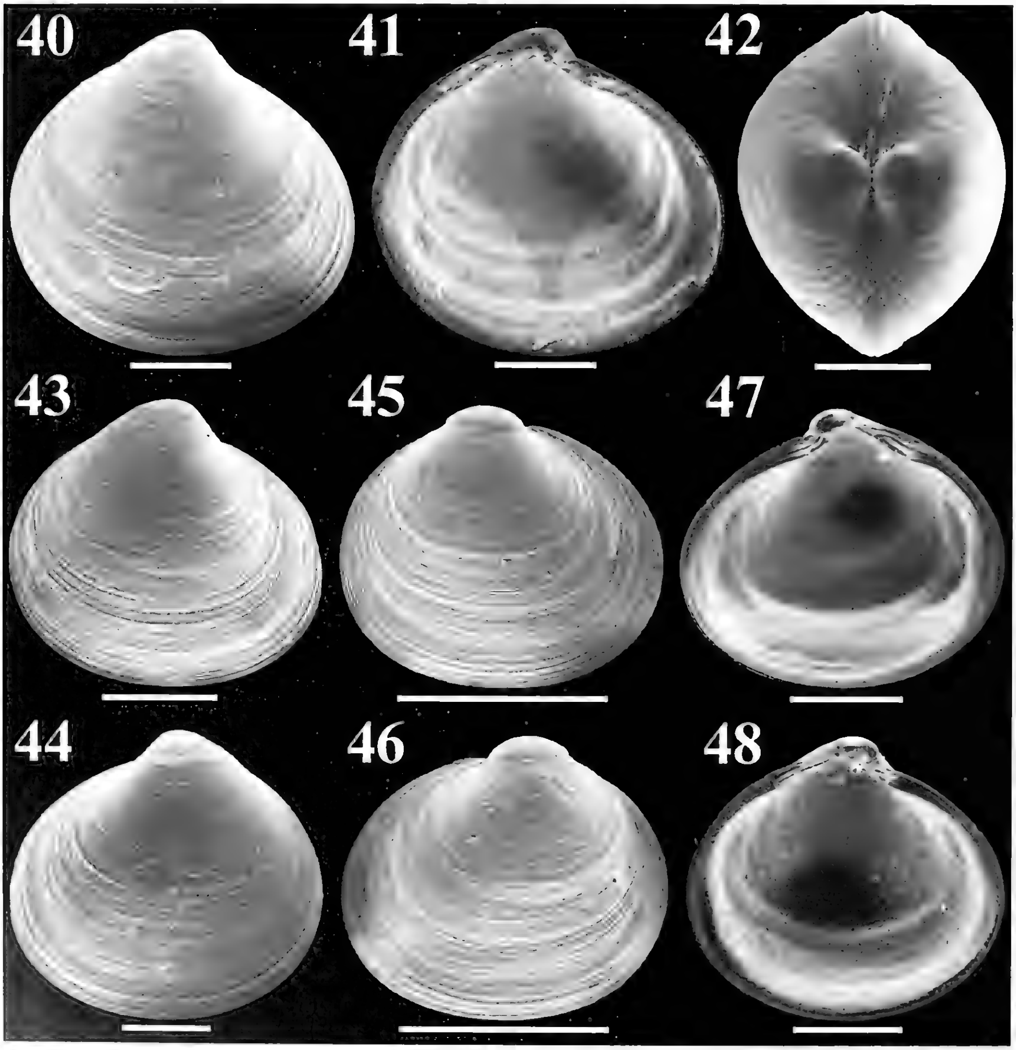
Other Material Examined

38 specimens with slightly damaged shells from type locality; 1 specimen from Najushka Bight, Bering Island, Commander Islands, Pacific Ocean, 20 m, rocky platform, bottom water temperature of 9.8°C, Coll. G. T. Belokonev, 24-IX-1973 (RV "Rakitnoye"); 1 specimen from Nerpichy Cape, Bering Island, Commander Islands, Pacific Ocean, 10 m, rocky platform, bottom water temperature of 7.4°C, Coll. V. I. Lukin, 21-VII-1972 (the sealer "Krylatka"); 2 specimens from Peschany Cape, Medny Island, Commander Island, Bering Sea, 10 m, boulders, bottom water temperature of 5.0°C, Coll. V. P. Kashenko, 10-VII-1972 (the sealer "Krylatka"); 5 specimens from Poludennaya Bight, Medny Island, Commander Island, Pacific Ocean, 15 m, rocky platform, bottom water temperature of 4.2°C, Coll. V. I. Lukin, 17-VII-1972 (the sealer "Krylatka"); 1 right valve from Vodopadsky Cape, Medny Island, Commander Islands, Pacific Ocean, 20 m, rocky platform, bottom water temperature of 7.6°C, Coll. G. T. Belokonev, 11-IX-1973 (RV "Rakitnoye"). Total of 47 specimens and 1 right valve.

Description

Exterior: Shell very small (to 4.8 mm), pear-shaped, with slightly narrowing anterior end, almost globular, very high (H/L = 0.833–1.036, shell height almost equal to or sometimes greater than length), equivalve, very inflated (W/L of valve = 0.278–0.429, shell width almost equal to length), inequilateral, thin, fragile, translucent. Surface with faint growth lines. Periostracum thin, adherent, slightly polished, yellowish-gray, extending into inner surface. Beaks small, high, strongly projecting above dorsal margin, slightly posterior, sometimes central or slightly anterior (A/L = 0.371–0.579), rounded, prosogyrate. Anterior end slightly narrowed, rounded, lower than posterior shell end. Posterior end rounded. Anterodorsal margin slightly convex, rather steeply descending ventrally, smoothly transitioning to strongly curved anterior margin. Ventral margin strongly curved. Posterodorsal margin slightly convex, steeply descending ventrally, smoothly transitioning to curved posterior margin.

Interior: Right valve with one cardinal tooth and posterior lateral tooth; left valve with two cardinal teeth and posterior lateral tooth. In right valve, cardinal tooth large, elongate, flattened, with rounded or flat top, anteroventrally directed, situated at edge of inner part of anterodorsal shell margin; posterior lateral tooth large, long, extending along posterodorsal shell margin. In left valve, anterior cardinal tooth larger, than posterior, elongate, flattened, with rounded top, anteroventrally directed, situated at edge of inner part of anterodorsal shell margin; posterior cardinal tooth smaller, rounded, isolated, fingerlike, with rounded top, situated exactly under beak; posterior lateral tooth large, long, ex-



FIGS. 40–48. *Kellia kussakini* Kamenev, new species. 40, 41: Holotype (MIMB 7770), Phedoskina Cape, Bering Island, Commander Islands, Pacific Ocean, 5 m. 42–48: Paratypes (MIMB 7771) from holotype locality. 42: Dorsal view of both valves. 43, 44: Right and left valves of an adult specimen. 45, 46: Right and left valves of a young specimen. 47, 48: Right and left valves without ligament. Bar = 1 mm.

tending along posterodorsal shell margin. Internal ligament well developed, large, situated between cardinal and lateral teeth, posteriorly directed, partly lodged in lanceolate resilifer extending obliquely posterior to beaks. Anterior adductor muscle scar large, rounded; posterior muscle scar large, ovate-angular, longer and wider than anterior scar. Pallial line without pallial sinus. Shell interior smooth, without radial rows of fossae or striae.

Variability

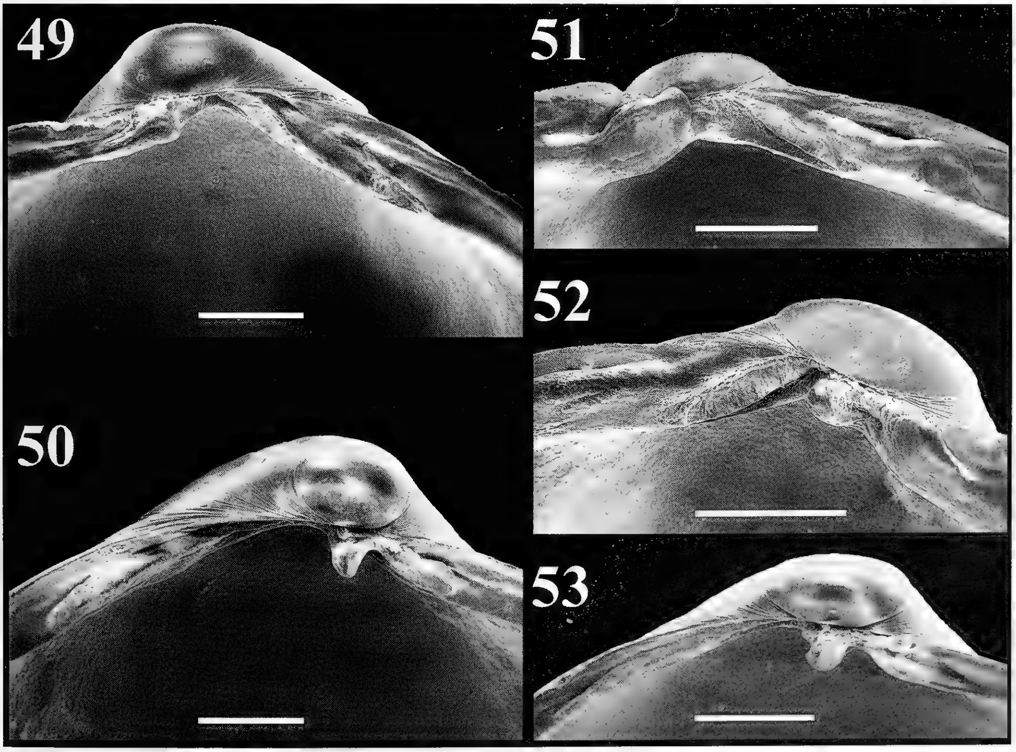
Shell shape and proportions change little with age. In young specimens (< 2.5 mm), the shell is less high, less inflated, and beaks are more posteriorly placed. In adults, shell height and width, the position of beaks vary slightly (Table 6, Figs. 43–46). As a whole, shell remains pear-shaped, with more narrow anterior end, and almost globular because of almost absolute equality of the length, height, and width. The beaks are mostly posteriorly placed (the beaks of 8 out of 97 measured specimens are anteriorly placed). The sizes and shape of cardinal and lateral teeth in both valves vary little. A few specimens had three cardinal teeth in the left valve (Fig. 53).

Distribution and Habitat (Fig. 54)

This species was recorded near Bering and Medny islands, Commander Islands, at a depth from 5 to 20 m, on boulders and rocky platforms, at a bottom water temperature from 4.2°C to 10.0°C, with population density to 1,190 specimens/m^2 (type locality).

Comparisons

This species is easily distinguished from other species of this genus by its small, almost globular, very high, and inflated shell with posteriorly placed high beaks (Table 2). Mean values and variances of the indices characterizing the position of beaks (A/L), the rela-



FIGS. 49–53. *Kellia kussakini* Kamenev, new species, paratypes (MIMB 7771) from holotype locality. 49, 50: Hinge of right and left valves. 51, 52: Ventral view of hinge of right and left valves showing resilifer. 53: Hinge of left valves with three cardinal teeth. Bar = 300μm.

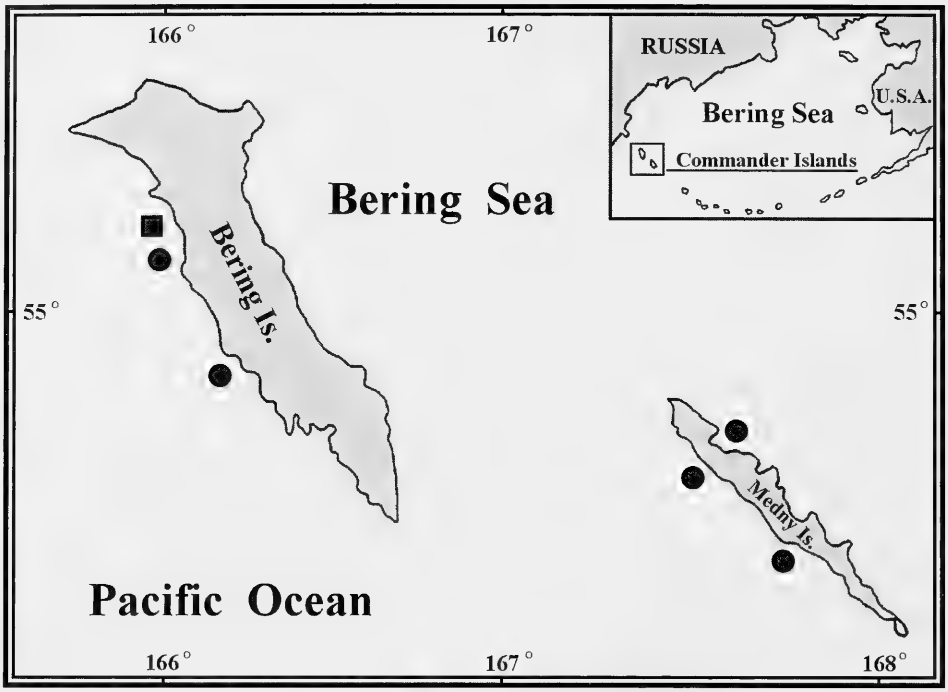


FIG. 54. Distribution of *Kellia kussakini* (■ – type locality).

TABLE 6. *Kellia kussakini* Kamenev, new species. Shell measurements (mm), indices of holotype (MIMB 7770), and summary statistics of holotype and paratypes (MIMB 7771) characters: L – shell length; A – anterior end length; H – height; W – width. Numerator indicates shell measurements, indices, and summary statistics for the right valve, denominator – for the left valve.

Statistics	L	A	H	W	A/L	H/L	W/L
				Holotype			
	4.0 4.0	2.1 2.1	3.8 3.8	1.4 1.4	0.525 0.525	0.950 0.950	0.350 0.350
				Holotype and paratypes			
Mean	2.95 2.95	1.52 1.52	2.71 2.71	1.01 1.01	0.517 0.517	0.917 0.917	0.340 0.340
D	0.06 0.06	0.03 0.03	0.06 0.06	0.03 0.03	0.003 0.003	0.004 0.004	0.003 0.003
SE	0.60 0.60	0.29 0.29	0.59 0.59	0.27 0.27	0.027 0.027	0.037 0.037	0.034 0.034
Min	1.4 1.4	0.8 0.8	1.2 1.2	0.4 0.4	0.444 0.444	0.833 0.833	0.278 0.278
Max	4.8 4.8	2.6 2.6	4.6 4.6	1.8 1.8	0.579 0.579	1.036 1.036	0.429 0.429
n	97 97	97 97	97 97	97 97	97 97	97 97	97 97

tive height (H/L) and width (W/L) in *K. kussakini* were significantly different from the mean values and variances of the same indices of *K. comandorica* and *K. suborbicularis* (Table 4). Besides, unlike *K. comandorica*, it has a smooth interior shell wall without the radial rows of fossae.

In shell shape, *K. kussakini* is close to *K. porculus* (Figs. 38, 39), living off the coast of Japan, from which it is distinguished in having a more high, very inflated, fragile and translucent shell with posteriorly placed beaks and a slightly polished, yellowish-gray periostracum (Table 2).

Etymology

The specific name honors Oleg G. Kussakin, Academician of the Russian Academy of Sciences, a famous Russian researcher of the marine fauna of the intertidal zone of Russian Pacific seas and world isopod fauna, who devoted all his life to the study of the northwestern Pacific fauna.

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REVISION OF THE REPRODUCTIVE MORPHOLOGY OF THREE *LEPTAXIS* SPECIES (GASTROPODA, PULMONATA, HYGROMIIDAE) AND ITS IMPLICATION ON DART EVOLUTION

Joris M. Koene[1] & Igor V. Muratov[2]

ABSTRACT

Many species of land snails have one or more sharp, calcareous "love darts" that are used to stab the partner during mating. These darts are produced and stored in specialized organs called stylophores. Because their number and position varies among species, stylophores are often used for identification and classification, especially in the family Hygromiidae. Having several stylophores, and thus several darts, is presumably the ancestral state from which species with one stylophore evolved. Species with small accessory sacs or rudimentary stylophores located above the functional stylophore are therefore thought to represent intermediate forms between species with double and single stylophores. We investigated the stylophores, darts, and associated reproductive organs of three species of the hygromiid genus *Leptaxis* – *L. erubescens*, *L. nivosa* and *L. undata*. In all the specimens of the investigated species, a small sac located just above the stylophore was found to be present. We conclude that this previously overlooked organ represents a rudiment of a stylophore, leading us to conclude that *Leptaxis* should be considered as an intermediate form in the evolution towards a single stylophore in the Hygromiidae.

Keywords: love dart, dart sac, stylophore, snail, stylommatophora, Helicoidea, rudiment.

INTRODUCTION

In the reproductive system of many hermaphroditic land snail species, one or more sharp, calcareous structures are present. When these are produced in a specialized organ, the stylophore (also referred to as dart sac), they are called darts. In many species, these "love darts" are stabbed through the partner's skin during mating (Adamo & Chase, 1990; Reyes Tur et al., 2000). In *Helix aspersa* (Müller, 1774) – often called *Cornu aspersum*, *Cryptomphalus aspersus*, or *Cantareus aspersus* – this "dart shooting" results in the transfer of an allohormone that inhibits sperm digestion and thereby increases sperm storage and fertilization success (Koene & Ter Maat 2001; Koene & Chase, 1998a; Rogers & Chase, 2001, 2002; Landolfa et al., 2001; Landolfa, 2002).

Recently, a comparative study demonstrated that the evolution of darts may be driven by sexual conflict (Koene & Schulenburg, submitted), thus explaining the diversity in number and shape of darts. For example, *Trichia* has two conical darts without blades (Schileyko, 1978a); *Leptaxis* and *Hygromia* each have one dart with two (differently arranged) blades (respectively: Spence, 1911; Giusti & Manganelli, 1987); *Helix* has a dart with four blades (Hasse et al., 2002); and *Monachoides* has one dart with seven blades (Koene & Schulenburg, submitted). Some species, such as *Cepaea nemoralis* and *C. hortensis*, which are otherwise remarkably similar, can most easily be distinguished by the shape of their darts (Kerney et al., 1983). Despite the large diversity in shapes, darts are rarely used for taxonomic purposes. Conversely, stylophores are traditionally used for identification and classification of land snails within the superfamily Helicoidea (Nordsieck, 1987; Schileyko, 1989). Species with one stylophore are thought to have evolved from ancestral species bearing several stylophores (Schileyko, 1989). When more than one stylophore is present, different arrangements are possible. Several stylophores can be arranged around the vaginal duct (e.g., *Humboldtiana*: Thompson & Brewer, 2000). Two pairs of stylophores can be present on opposing sites of the vaginal

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duct (e.g., *Trichia*: Schileyko, 1978a). Alternatively, only one pair of stylophores can be present (*Hygromia*: Giusti & Manganelli, 1987). In these latter two cases, within each stylophore pair, the stylophore that is furthest away from the genital opening normally does not contain a dart, but see Taniushkin et al. (1999) for a possible case of atavistic development of darts in the upper stylophores of *Xeropicta krynickii* (Krynicki, 1833).

There are also species with morphologies that clearly represent intermediate stages between the above-mentioned forms. In such cases, a stylophore has become reduced in size and no longer produces a dart; such a rudimentary organ is then often referred to as an accessory sac (Nordsieck, 1993), internal dart sac (Giusti & Manganelli, 1987), or upper stylophore (Schileyko, 1989). Because these terms all describe the same organ, probably at different stages of reduction, we have chosen to use the term upper stylophore throughout the rest of this paper. Obviously, these intermediates provide important information about the course of evolution of the stylophore(s). Because rudimentary organs can be greatly reduced in size, they have sometimes been overlooked in previous studies. This is the case for the genus *Leptaxis*, which is why we redescribe the morphology of the stylophores, darts and associated reproductive organs of three species of this genus.

MATERIAL AND METHODS

Species of the genus *Leptaxis* inhabit Macaronesia, which includes 32 islands grouped in five major archipelagos: Azores, Canaries, Cape Verde, Madeira, and Selvagens

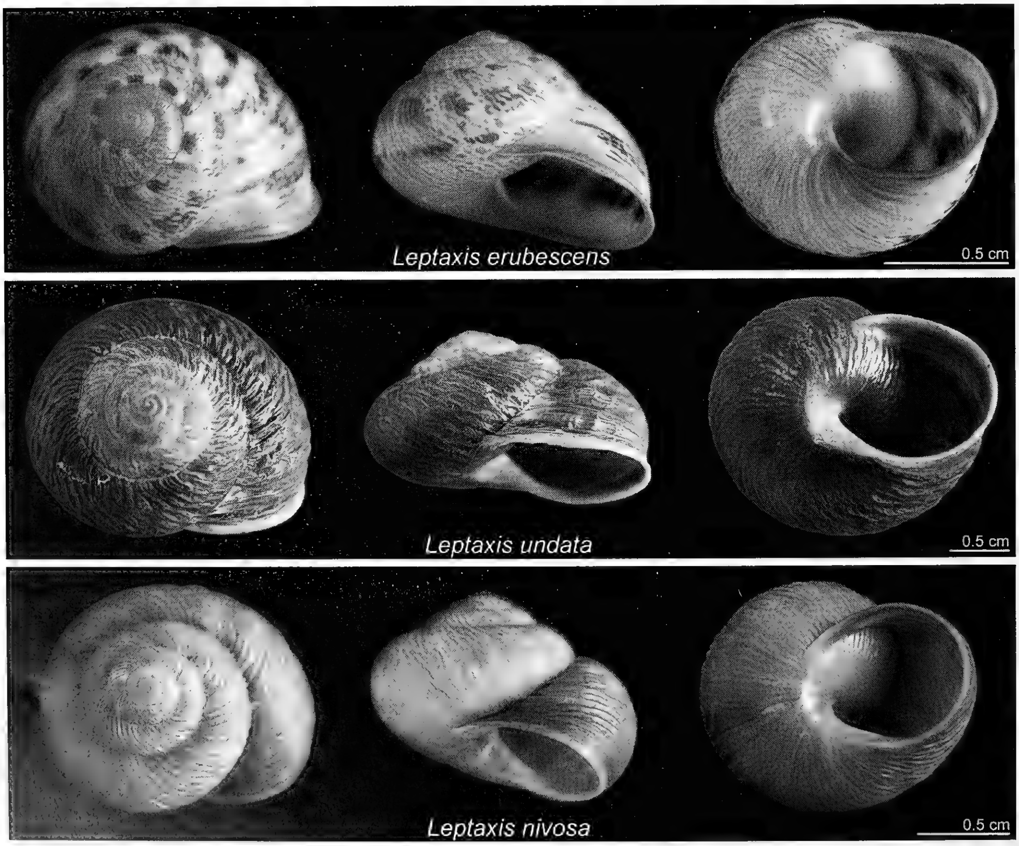

FIG. 1. Shells of the investigated *Leptaxis* species.

(Mitchell-Thomé, 1976). We have focused on the reproductive morphology of species endemic to the Madeiran archipelago. Among these, *Leptaxis erubescens* (Lowe, 1831) is the only species of this genus that occurs on all the different island groups – Madeira, Porto Santo, and The Desertas – of this volcanic archipelago (Cook, 1996). The other *Leptaxis* species are confined to one of the island groups (Cook, 1996). Of these species we investigated, *L. undata* (Lowe, 1831) from Madeira and *L. nivosa* (Sowerby, 1824) from Porto Santo. Figure 1 shows the shells of the investigated species.

Dry and alcohol preserved specimens of *L. erubescens* (N = 2) were obtained from the malacological collection of the Academy of Natural Sciences of Philadelphia (ANSP 128459 A9427H). Several specimens (frozen at –80°C) of this species (N = 4), as well as of *L. undata* (N = 4) and *L. nivosa* (N = 5), were generously made available to us by P. Van Riel (Royal Belgian Institute of Natural Sciences, Brussels).

The specimens of each species, which were all adult, were dissected to remove the reproductive tract. Subsequently, the reproductive organs were drawn using a camera lucida. To

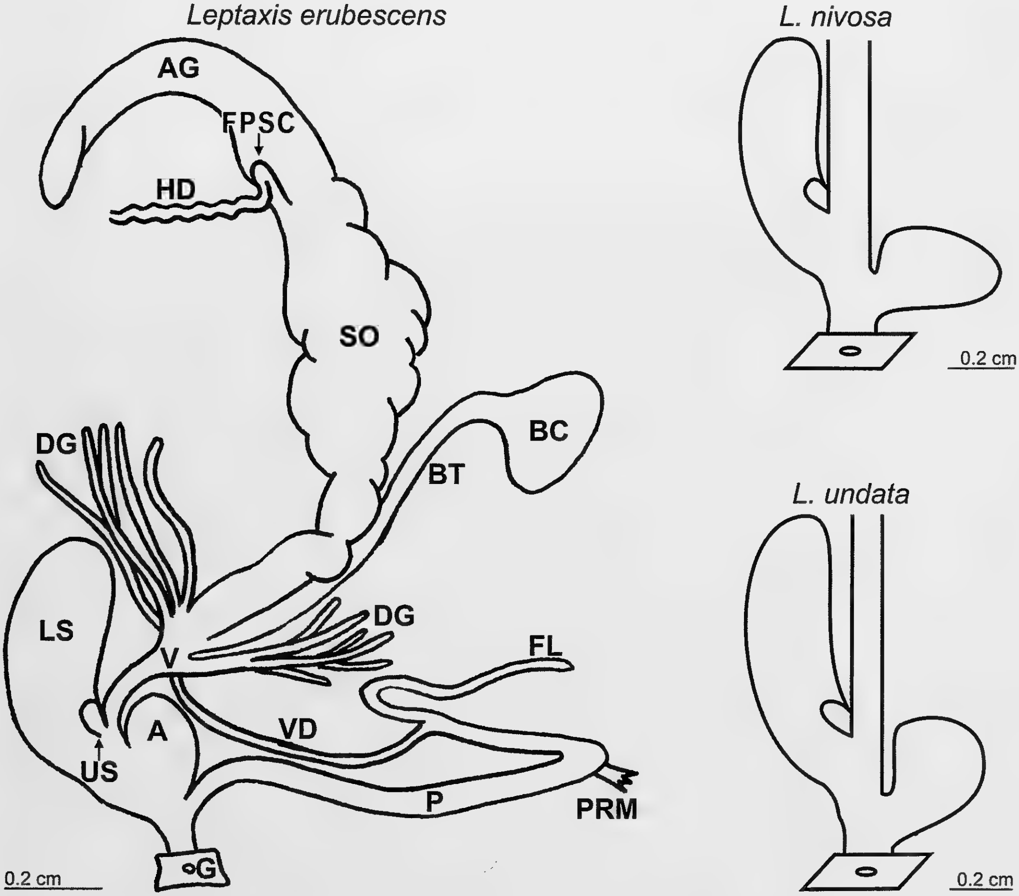

FIG. 2. Comparison of the position and relative size of the upper and lower stylophores of *Leptaxis erubescens*, *L. undata* , and *L. nivosa*. The reproductive system of *L. erubescens* is shown to depict the other reproductive structures that are mentioned in the text. Abbreviations: A, appendage; AG, albumen gland; BC, bursa copulatrix; BT, bursa tract; DG, digitiform gland; FL, flagellum; FPSC, fertilization pouch-spermathecal complex; G, genital pore; HD, hermaphroditic duct; LS, lower stylophore; P, penis; PRM, penis retractor muscle, SO, spermoviduct; US, upper stylophore; V, vaginal duct; VD, vas deferens.

avoid damage of the darts, the stylophores were carefully cut out of the reproductive tracts and placed overnight in 1N NaOH, which dissolved all the tissue and mucus but left the dart intact. For cross-sections darts were carefully broken in two. The intact and broken darts were consecutively prepared for electron microscopy by placing them on small aluminium plates with an electrically conducting adhesive (Leit-Tab, Plano). Subsequently, they were coated with gold using a Metalloplan (Leitz). The darts were then placed under a scanning electron microscope (S-530 SEM, Hitachi) and photos were taken.

RESULTS

In all the mature specimens of each species, one large stylophore, containing one dart, was present. This stylophore was positioned in such a way that it curved slightly around the vaginal duct. Besides this stylophore, we also found a small sac situated between the larger stylophore and the vaginal duct in all species. The position of this organ suggests that we are dealing with the rudiment of an upper stylophore. Additionally, a flattened, non-hollow appendage at the base of the vagina is present. Figure 2 gives an overview of the morphology of the investigated *Leptaxis* species showing the positions and relative sizes of the stylophores, the small sac (i.e., upper stylophore) and the appendage. The two mucus glands of each of the species are situated above the stylophore around the vaginal duct. Each of these digitiform glands has several branches that join at the base. These glands, as well as the rest of the reproductive system, are only depicted for *L. erubescens*.

The darts of all three species have a round base and a broad corona by which they are attached to a tubercle in the stylophore (Fig. 3).

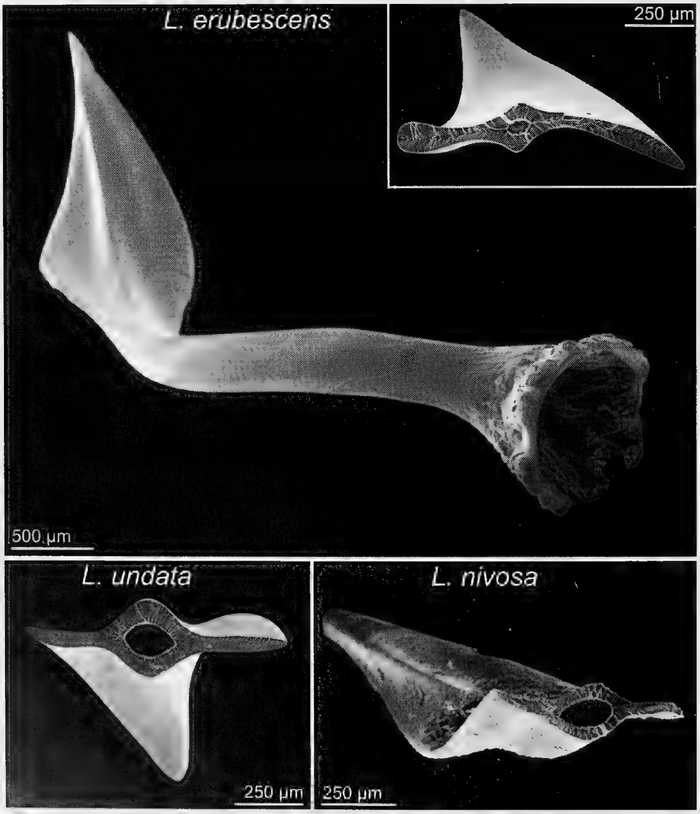

FIG. 3. Electron microscopic pictures of the darts of *Leptaxis erubescens*, *L. undata*, and *L. nivosa*.

Approximately halfway towards the tip of the dart the curved shaft broadens and flattens out, thus forming two large blades (Fig. 3). The dart is curved and lightly contorted, which is illustrated by the electron microscopic picture of the side view of a dart of *L. erubescens* (Fig. 3), also reflecting the shape of the stylophore.

DISCUSSION

It has long been thought, based on morphological data, that the genus *Leptaxis* fully conforms to the European Hygromiidae with one stylophore (Mandahl-Barth, 1943; Backhuys, 1975; Schileyko, 1989). Interestingly, Pilsbry (1894: 292–293) stated after having investigated several *Leptaxis* species: "I had expected to find in *Leptaxis* some archaic characters preserved; for its geographic position and the shell-peculiarities argue for the group an ancient origin; but the evidence shows that however remote in the past the type was derived from the continental fauna, the main anatomical features of modern European Helices were then well established". Our finding of the small organ just above the stylophore in the investigated species of *Leptaxis* suggests that Pilsbry was correct in expecting some ancient characters.

The position of the previously overlooked organ is consistent with the position of the upper stylophore in the genus *Trichia* (Schileyko, 1978a) and the internal or accessory dart sac in the genus *Hygromia* (Giusti & Manganelli, 1987; Nordsieck, 1987). Therefore, we conclude that the investigated species of the *Leptaxis* genus possess a rudiment of an upper stylophore. This rudiment has probably been overlooked for so long because the small organ is well hidden in connective tissue between the vaginal duct and the much larger functional stylophore that contains the contorted dart. Nevertheless, the presence of the upper stylophore in *Leptaxis* has important implications for the phylogenetic position of this genus within the Hygromiidae. Much of the molluscan phylogeny is heavily based on traits of the reproductive morphology and, especially within the Hygromiidae, the presence and number of (reduced) stylophores play an important role in the classification within the family (Nordsieck, 1987, 1993; Schileyko, 1989).

Several observations can be made with respect to the reproductive morphology of the family Hygromiidae. There are clear morphological differences between the phylogenetically older subfamily Trichiinae and the younger subfamily Hygromiinae. All Trichiinae have two pairs of stylophores, that is, two upper and two lower stylophores (e.g., *Trichia*: Schileyko, 1978a). Most of the differences in the stylophore morphology between genera of Trichiinae are relatively small, while important morphological changes are found within the Hygromiinae. In this subfamily, one pair of stylophores has been lost, consequently many species have one upper and one lower stylophore (e.g., *Hygromia*: Giusti & Manganelli, 1987). Additionally, a further reduction of the upper stylophore and an enlargement of the lower stylophore occurred (e.g., *Leptaxis*: this paper; *Lindholmomneme*: Schileyko, 1978b), culminating with total loss of the upper stylophore (e.g., *Monachoides*: Schileyko, 1978b, 1989).

Simultaneously with this evolution towards a single stylophore, the dart seems to become more elaborate. Perpendicular blades on the dart occur in several genera of Hygromiinae, resulting in different dart shapes, and increasing the dart's surface area. Presumably, this allows the dart to transfer larger amounts of the product from the mucus glands (Fedoseeva, 1994; Adamo & Chase, 1996; Koene & Schulenburg, submitted). However, it is still unclear whether the hygromiid dart is used in a similar way as the helicid dart (Koene & Chase, 1998a, b; Rogers & Chase, 2001; Landolfa et al., 2001) to transfer an allohormone (Koene & Ter Maat, 2001, 2002). Hence, behavioural data are required to determine how the *Leptaxis* dart is used. Observations of the mating behaviour of *Leptaxis* may also shed light on the function of the appendage at the base of the genital system (see also Mandahl-Barth, 1943).

To conclude, we found the rudiment of an upper stylophore in three species of *Leptaxis*, which has previously gone unnoticed (Mandahl-Barth, 1943; Backhuys, 1975, Schileyko, 1989). The presence of this small organ is of importance because it indicates that *Leptaxis* links Hygromiinae with two (upper and lower) stylophores (e.g., *Lindholmomneme*) and Hygromiinae with single stylophores (e.g., *Monachoides*). Therefore, our findings lead us to conclude that this genus is an intermediate form in the evolution towards a single stylophore.

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PRELIMINARY PHYLOGENETIC STUDY OF BRADYBAENIDAE (GASTROPODA: STYLOMMATOPHORA: HELICOIDEA)

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ABSTRACT

Morphological variation in the terminal genitalia of genera of Bradybaeninae is compared and discussed. This is the first attempt to study the anatomy of the endemic Chinese bradybaenids *Cathaica* (*Pliocathaica*), *Pseudiberus* (*Platypetasus*), and *Metodontia*. A preliminary phylogenetic analysis of bradybaenids was performed based on the character matrix from the present study. The focus was primarily on the terminal genitalia. *Helix* (Helicidae) and *Camaena* (Camaenidae) were used as outgroups. The results suggest that several previous taxonomic arrangements for the subdivision of this family, based on the analyses using shell features and/or superficial anatomy of genital system, are unsuitable. The cladistic analysis suggests that the use of the subfamily Helicostylinae, *sensu lato*, might not be suitable for use as the sister group of the known Bradybaeninae.

Two new endemic genera from western China are described based on the comparison of the terminal genitalia: ***Aegistohadra*** n. gen. and ***Eueuhadra*** n. gen. They are monophyletic and are readily distinguished from other bradybaenids by a synapomorphy, the presence of penial caecum. *Nanina delavayana* Heude, 1885, is designated as the type species of *Aegistohadra*. The type species of ***Eueuhadra*** is a new species, ***E. gonggashanensis***.

Key words: Stylommatophora, Helicoidea, Bradybaenidae, China, terminal genitalia, phylogeny, phylogenetic analysis, new taxa.

INTRODUCTION

The Bradybaenidae (= Bradybaenidae + Helicostylidae, *sensu* Schileyko 1991) are a large group of terrestrial snails widely distributed in eastern Asia, with one species in Europe. Historically, more than 150 authors (Richardson, 1983; Wu, unpublished catalogue) have published on Chinese bradybaenids. However, most work on the classification of higher taxa of China was based on shell, not anatomical characters (Pilsbry, 1888–1894; Möllendorff, 1899; Dautzenberg, 1914–1915; Bavay & Dautzenberg, 1900, 1915; Blume, 1925; Ping & Yen, 1932; Yen, 1939; Zilch, 1940; almost all previous work). Therefore, knowledge on the bradybaenid systematics has remained unsatisfactory.

The monograph by Wiegmann (1900), in which species from 12 genera and subgenera are described, was the first study dealing specifically with the anatomy of bradybaenid genitalia. More recently, some malacologists have made comparative studies of the genital morphology, mainly based on their native bradybaenid taxa (Schileyko, 1978; Azuma, 1982; literature of Japanese workers, cited by Nordsieck, 2002; Lee & Kwon, 1993, 1994; Wu, 2001; Wu & Guo, 2003). Many authors have focused on the general structures, such as the size of dart sac, the presence/absence of a flagellum, and the number of mucous glands. Schileyko (1978) gave a much more precise, detailed description of the terminal genitalia of Russian bradybaenids that includes the above traditionally described character and internal dissections of the penis and dart apparatus. More recently, Nordsieck (1987) stated that the bradybaenid groups are characterized by apomorphies of the genital organs.

However, similar work covering most endemic Chinese bradybaenid taxa, which is essential for understanding the general anatomy of bradybaenids and construction of a sound taxonomic framework, has been lacking.

The present work compares the structure of the terminal genitalia of some genera of the

Bradybaenidae based on dissection of their type species or non-type congeners. Two new bradybaenid genera are proposed based on anatomical and shell characters. A preliminary phylogenetic analysis is performed based on the data obtained from these dissection results. This phylogeny is compared to the three bradybaenid subdivision plans comprehensively reviewed recently by Nordsieck (2002), widely used thus far in China (e.g., Yen, 1939; Zilch, 1960), Russia (e.g., Schileyko, 1978), and Japan (e.g., Kuroda & Habe, 1949; Minato, 1988).

MATERIALS AND METHODS

This study is based on specimens from the collections of the Zoological Museum, Institute of Zoology, Chinese Academy of Sciences (IZCAS), and from those belonging to Forschungsinstitut und Naturmuseum Senckenberg (SMF). Many genera are represented by the non-type congeners rather than by the type species, because of the paucity of alcohol-preserved specimens in museums and the absence of specimens from type localities.

All examined specimens (except specimens of IZCAS00067, which were first fixed in formalin before being placed in 70% ethanol) are preserved in 70% ethanol. For preparing the dissections, a tiny hole was carefully drilled into the shell apex to assist removal of the soft parts of the snail using water pressure. All the illustrations were drawn using a stereo microscope and camera lucida. Shell and genital measurements were taken with 0.01 mm and 0.1 mm accuracy respectively for the new taxa described. Whorl number was counted as described by Kerney & Cameron (1979) and was taken with 1/8 whorl accuracy. Both color and length of soft parts in the descriptions refer to those observed and measured after alcohol preservation. Type specimens of the new species are deposited in IZCAS, Beijing.

Taxa studied are listed in Appendix I along with locality data and museum accession numbers. Descriptions of new taxa are given in Appendix II.

Abbreviations

The abbreviations used in the text and in the illustrations are explained as: ADC – channel connecting accessory sac and dart sac; AG – albumen gland; App – vaginal empty appendicula; AS – accessory sac (= inner stylophore in Giusti et al., 1992); ASC – accessory sac chamber; At – atrium; BC – bursa copulatrix; BCD – bursa copulatrix duct; C23 – chamber produced by V2 and V3 in dart sac; DS – dart sac (= outer stylophore in Giusti et al., 1992); Dt – love dart; DtC – chamber containing the dart = dart sac chamber; DVM – membranous sac surrounding dart sac and/or distal region of vagina near atrium (= basal genital sheath in Cuezzo, 1998). When preparing the genitalia for observation, the structures were carefully preserved for future examination.

Ep – epiphallus, the region between the penis and the insertion of the vas deferens. The delimitation is esily recognized when the ephiphallic papilla (= verge in Cuezzo, 1998: 102) is present. When the epiphallic papilla is lacking, the continuous ridge structure can help to distinguish the epiphallic region from that of penis (Cuezzo, 1998). It is notable that the concept used by Cuezzo (1998) differs from that used by Giusti et al. (1992), who defined the epiphallus as "from end of vas deferens to point of attachment of penial retractor". The term epiphallus of Cuezzo (1998) is used here, because the point of attachment of penial retractor varies among different bradybaenid groups, and in most cases it is not level with the ephiphallic papilla.

EpP – epiphallic papilla (= "penial" verge in Schileyko, 1991); MAC – mucous gland-accessory sac channel; MG – mucous gland (= dart gland in Nordsieck, 2002); OD – oviduct; Ov – ovotestis; P – penis; according to the epiphallus concept used by Cuezzo (1998), the term penis used in this study refers to the region between the epiphallic papilla and the atrium, or when the epiphallic papilla is absent, it refers to the region close to the atrium and internally possesses the similar and continuous pilaster/ridge structure.

PLs – polylayered structure in dart sac and/or accessory sac, produced by wavy and spongy connective tissue. PLs is not separate, but connected tightly with neighboring tissue, and if present, is visible when the dart apparatus is dissected sagittally. This structure occurs as occupying most part of dart sac (e.g., in Fig. 14C) or a small and limited region (e.g., in Fig. 11B) in the dart apparatus; PR – penial retractor muscle; PS – penial sheath; PP – penial pilaster(s)/ridge(s); SPC – simple penial caecum; T – talon; UV – free oviduct; Va – vagina; VD – vas deferens; V1 – a valvule opposite the opening of mucous glands, in sag-

TABLE 1. Data set containing 28 characters (characters 0–27) and 26 taxa used in the phylogenetic analysis.

	0	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	27
Camaena Albers, 1850	0	0	0	0	0	1	1	2	0	0	1	2	0	2	2	2	2	2	3	3	2	2	2	2	2	2	2	0
Helix Linnaeus, 1758	0	0	0	1	0	1	1	2	0	0	1	1	2	1	1	0	0	0	0	2	0	0	2	0	0	0	0	0
Mastigeulota Pilsbry, 1895	0	0	0	1	0	0	0	0	0	1	0	1	2	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Metodontia Möllendorff, 1886	0	0	0	1	0	0	0	0	0	0	0	1	2	1	0	1	0	0	0	2	0	0	0	0	0	0	0	0
Fruticicola Held, 1838	1	2	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	2	1	0	0	0	1	0	0	0
Acusta Martens, 1860	0	0	0	1	2	1	1	2	0	0	0	0	0	1	1	1	1	1	1	2	1	0	0	0	0	1	0	0
Bradybaena Beck, 1837	1	1	2	1	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	2	0	0	0	0	0	0	0	0
Karaftohelix Pilsbry, 1927	1	2	1	1	1	1	1	2	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0
Cathaica Möllendorff, 1884	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Pliocathaica Andreae, 1900	0	0	0	1	0	1	1	2	0	0	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0
Aegista Albers, 1850	0	0	0	1	0	1	1	2	0	0	1	1	3	1	1	1	0	0	0	2	0	0	0	0	0	0	0	0
Plectotropis Martens, 1860	0	0	0	1	0	1	1	2	0	0	1	1	3	1	1	0	0	0	0	2	0	0	0	0	0	0	0	0
Pseudaspasita Möllendorff, 1901	0	0	0	1	0	1	1	2	0	0	1	1	1	1	1	1	0	0	0	2	0	0	0	0	0	0	0	0
Platypetasus Pilsbry, 1895	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Stilpnodiscus spa	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Stilpnodiscus spb	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Laeocathaica Möllendorff, 1899	0	0	0	1	2	1	1	2	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
Pseudobuliminus Gredler, 1886	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	2	0	0	0	0	0	0	0	0
Trishoplita Jacobi, 1898	0	0	0	1	0	1	1	2	0	0	1	0	0	0	1	1	1	1	2	0	0	0	0	0	0	0	0	0
Euhadra Pilsbry, 1890	0	0	0	1	0	1	1	2	0	0	1	0	0	0	1	1	1	1	2	0	0	0	0	0	0	0	0	0
Nesiohelix Kuroda & Emura, 1943	0	0	0	0	0	1	1	2	0	0	1	0	0	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0
Aegistohadra, n. gen.	0	0	0	0	0	1	1	2	1	0	1	0	0	1	1	1	1	0	0	2	0	0	0	0	0	0	1	0
Eueuhadra, n. gen.	0	0	0	0	0	1	1	2	1	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0
Calocochlea Hartmann, 1842	1	1	2	0	0	1	2	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0
Pfeifferia Gray, 1853	1	1	2	0	0	1	2	1	0	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	1
Trichobradybaena Wu, 2003	1	1	2	1	0	0	0	0	0	1	0	0	0	1	0	1	1	0	0	2	0	0	0	0	0	0	0	0

ittal plane of dart sac (as in Fig. 6D); V2 – a valvule opposite V1 and closest to atrium, together with V1 forming a muscular tube containing dart(s) (as in Fig. 6D); V3 – a valvule between V2 and V4, in sagittal plane of dart sac (as in Fig. 6D); V4 – most inner/proximal valvule in DC, together with V1 forming a chamber containing love dart(s) (as in Fig. 6D). Terms V1–V4 are employed, for convenience only, to show the sagittal plane of dart sac.

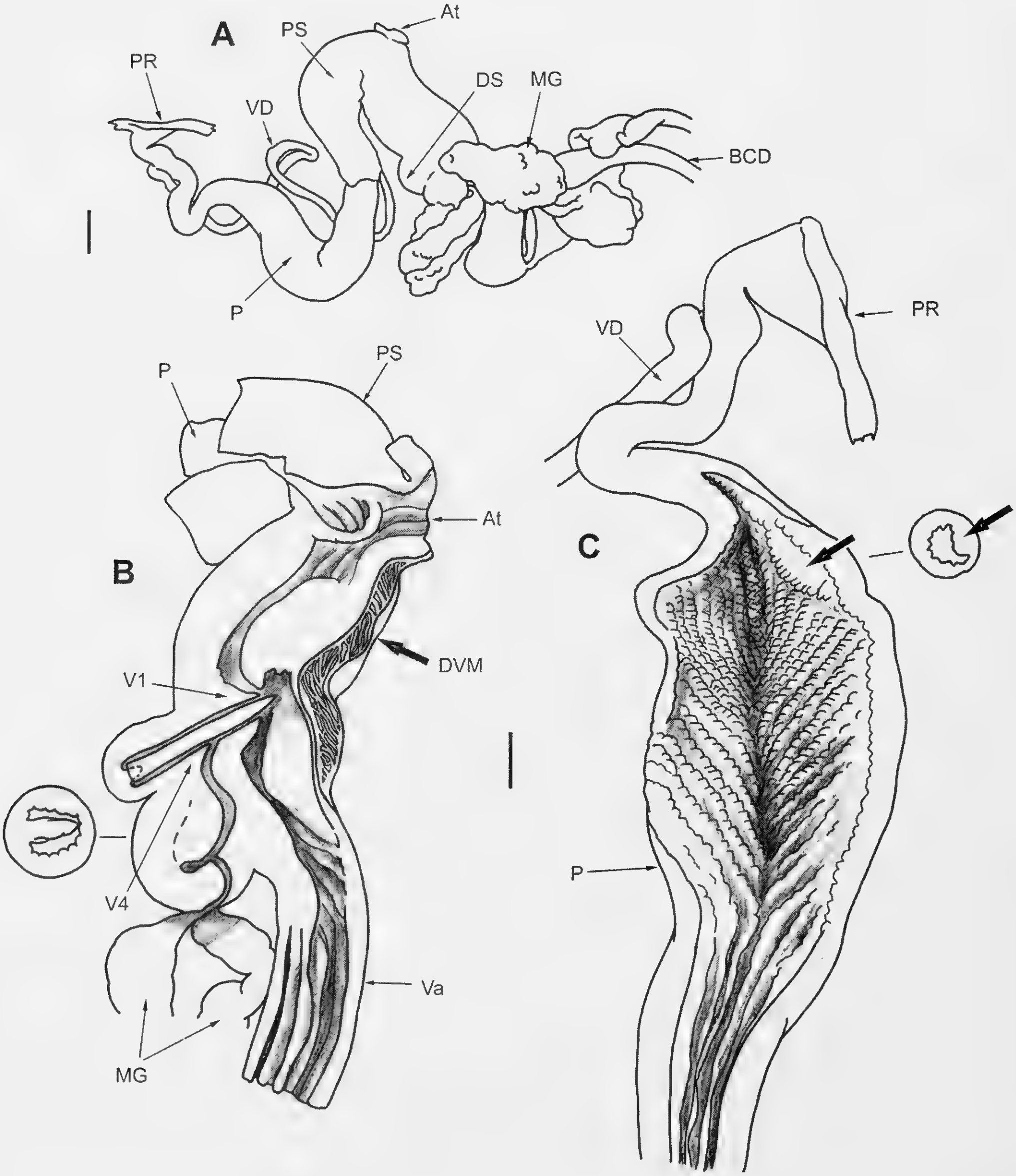

FIG. 1. *Fruticicola fruticum* (O. F. Müller, 1774), IZCAS01009-2. A, general view of genitalia; B, dart sac and part of vagina, sagittal section, with cross-section of accessory sac. Structured DVM indicated by a thick solid arrow; C, penis, opened, with cross-section, showing a fold formed by the penial pilasters. A & B showing the elongated vagina section between dart sac and atrium. Bars equal 1 mm.

Each view of the three dimensional portrayal represents only one part of the boundary of the chamber near it.

Cladistic Analysis

Cladistic analyses were performed using the computer program Hennig86 Version 1.5 (Farris, 1988) and program Winclada Version 1.00.08 (Nixon, 2002). The analysis of the character distribution on the cladograms was carried out using the program Winclada.

All the 28 characters used, observed from terminal genitalia except Character 27 from mantle, are based on a selection made after my study of the representatives for terminal groups. Of the characaters (0–27), seven binary characters and the remaining multistate characters were coded as non-additive. To avoid artificial judgement, character polarity is obtained as one of the results of the analysis rather than as an apriori assumption (Nixon & Carpenter, 1993). Therefore, all characters involved are treated as undirected and unordered. No missing character state occurred in the examined terminals (Table 1). Considering that fused coding involves a loss of phylogenetic information (Lee & Bryant, 1999), the inapplicable characters (e.g., coding of character 1 was separated from that fused with character 0) were separately coded when the character-variable is inapplicable in some taxa.

Selection of the Ingroup and Outgroup Taxa

Besides including two newly proposed genera, the ingroup bradybaenid taxa considered were those included in the subfamily Bradybaeninae by Richardson (1983), except *Armandiella* Ancey, *Tricheulota* Pilsbry, *Plecteulota* Möllendorff, *Neseulota* Ehrmann, *Archaeoxesta* Kobelt, *Coccoglypta* Pilsbry, *Coneulota* Pfeffer, *Dolicheulota* Pilsbry, and *Ponsadenia* Schileyko, because alcohol-pre-

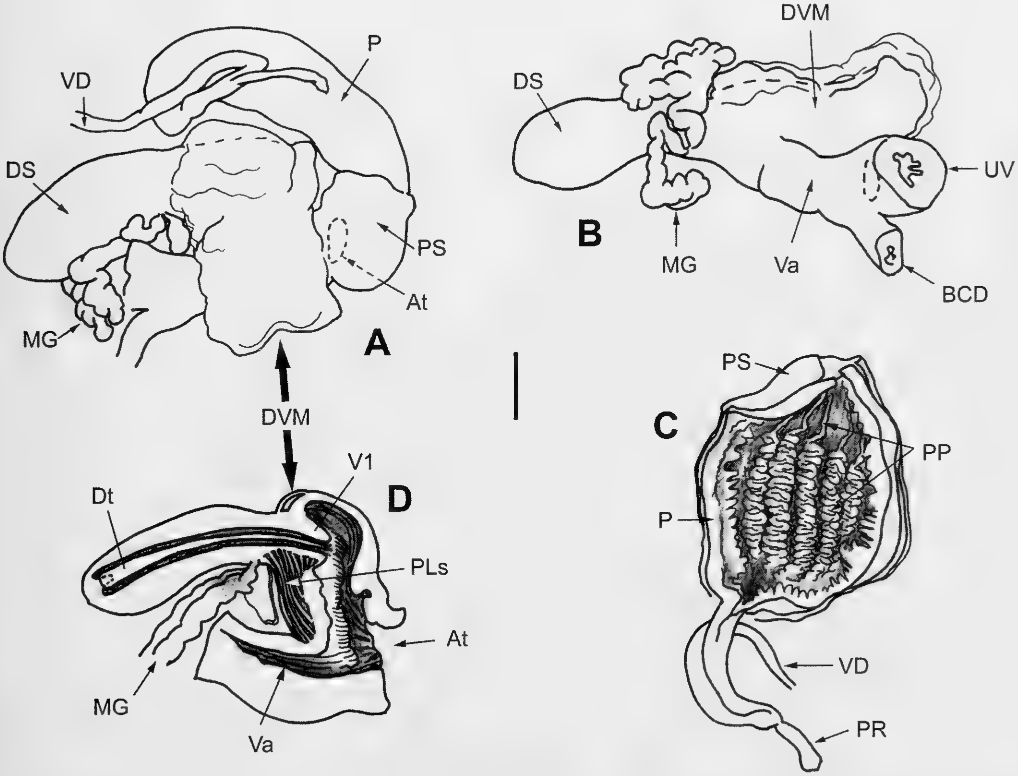

FIG. 2. *Bradybaena similaris* (Rang, 1831), IZCAS01072-1. A, lateral view of dart apparatus and penial complex; B, basal view of dart apparatus; C, penis, opened; D, dart sac, sagittal section. DVM indicated by thick solid arrows in A & D. Bar equals 1 mm.

served material was unavailable. *Semibuliminus* Möllendorff was excluded because it was recently grouped into *Metodontia* (Wu, in review). *Halolimnohelix* Germain, *Haplohelix* Pilsbry, *Urguessella* Preston, and *Vicarihelix* Pilsbry listed in Richardson's bradybaenid catalog (1983; also in Thiele, 1931) were excluded because they are, on the basis of anatomy, non-bradybaenid helicoids (Nordsieck, 1986, 1987; Schileyko, 1991).

Results of previous cladistic analyses for Helicoidea were used as the departure point for outgroup selection. According to the cladogram based on a molecular database (Wade et al., 2001: fig. 3c), the Camaenidae–Helicidae–Polygridae group forms the sister group of Bradybaenidae. In another anatomy-based cladistic analysis of Xanthonychidae (= Helminthoglypidae; Cuezzo, 1998), the sister relationship of the Bradybaenidae and Xanthonychidae–Helicidae groups are supported by four synapomorphies. Therefore, in this study, the Helicidae and Camaenidae were chosen as outgroups.

All the 23 genera and subgenera were treated as separated terminal taxa. The type species was available for only 11 ingroup and one outgroup genera. These are: *Acusta*,

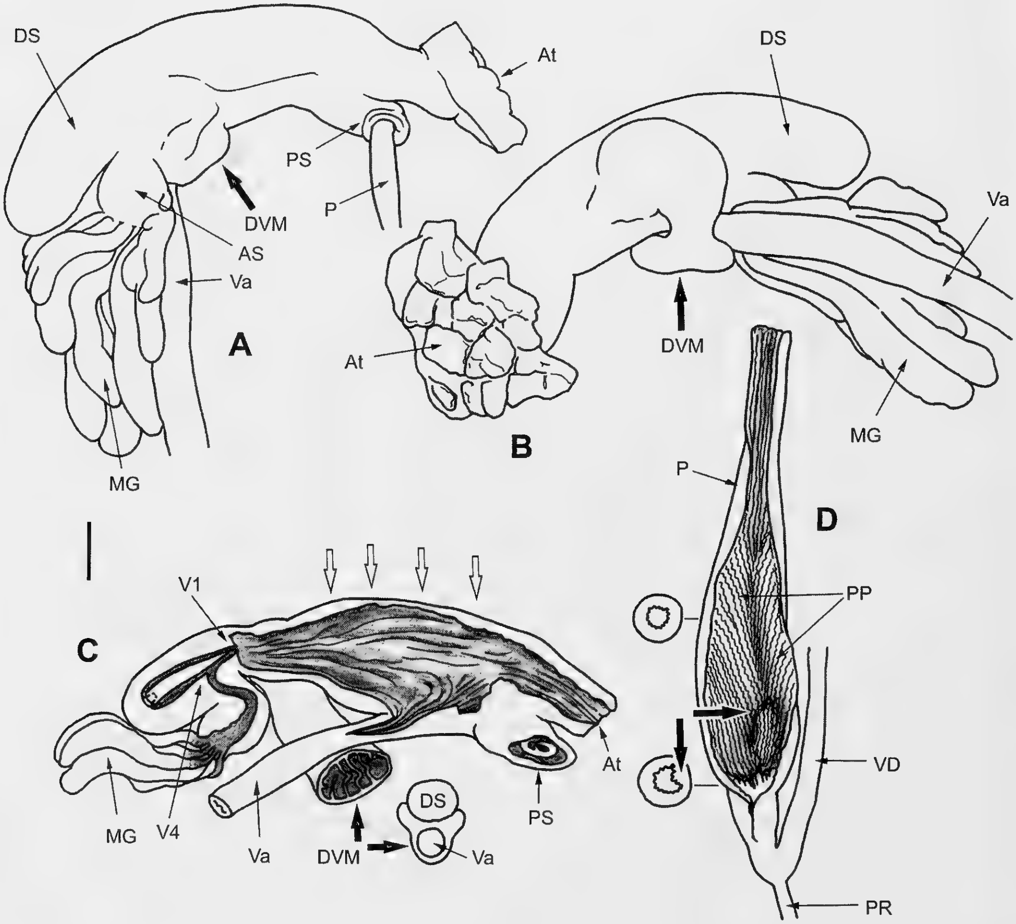

FIG. 3. *Karaftohelix weyrichii* (Schrenck, 1867), IZCAS01080-2. A, B, lateral views of dart sac, DVM indicated by thick solid arrows; C, dart sac, sagittal section, with cross-section showing DVM, DVM indicated by thick solid arrows, neck-structure indicated by thick hollow arrows; D, penis, opened, with cross-sections, fold formed by the penial pilasters indicated by thick solid arrows. Bar equals 1 mm.

Bradybaena, *Cathaica*, *Fruticicola*, *Mastigeulota*, *Pseudaspasita*, *Nesiohelix*, *Aegistohadra* n. gen., *Eueuhadra* n. gen., *Trichobradybaena*, *Pfeifferia*, and *Helix*. Otherwise, only those species commonly accepted in a group were used as the representatives for their generic group.

RESULTS

Character Descriptions

Character 0: Presence of the membranate sac surrounding the dart sac and/or the distal region of the vagina near to the atrium (DVM).
(0) absent; (1) present (Figs. 1B, 2A, 2D, 9A, indicated by thick solid arrows).
Remarks: The dart sac is inserted on the vagina. In very few cases, the dart sac is basally wrapped by a layer of membrane, which sometimes appears to be sac-like (Fig. 3A–C, indicated by thick solid arrows) near the atrium, completely or partially.

Character 1: The DVM inernally simple or structured:
(0) not applicable because DVM absent; (1) DVM present, internally simple (Figs. 2A, 2D, 9A, indicated by thick solid arrows); (2) DVM present, internally structured, with numerous cells (Figs. 1B, 3C, indicated by thick solid arrows).

Character 2: The proximal dart sac and/or the distal region of the vagina are/is wholy encircled by the DVM or not:
(0) not applicable because DVM absent; (1) DVM present, proximal dart sac partially encircled by DVM (Figs. 1B, 3B, C, indicated by thick solid arrows); (2) DVM present, proximal dart sac wholly wrapped by DVM (Fig. 2A, indicated by thick solid arrows).

Character 3: Presence of the penial sheath:
(0) absent; (1) present.
Remarks: In *Nesiohelix swinhoei*, *Aegistohadra* n. gen., *Eueuhadra* n. gen., *Pfeifferia micans*, and *Calocochlea coccomelos*, the penial sheath is lacking (Figs. 5D, 6A, C, 7A, B, 8A, B, 9A, D). In the other genera, the penial sheath is always present (e.g., Azuma, 1982). In the outgroup *Helix pomatia*, the penial sheath is present and developed, wrapping the whole penis and the basal part of penial retractor (Fig. 10D, E, indicated by thick solid arrows). In bradybaenid genera, the penial sheath, if present, cannot be morphologically distinguished from that of *Helix*.

Character 4: Differentiation status of the penial pilasters:
(0) penial pilasters not differentiated; (1) penial pilasters differentiated near epiphallus; (2) penial pilasters differentiated near atrium.
Remarks: Differentiated penial pilasters are those thickened, deep, and/or morphologically distinguishable from the neighboring zig-zag ones of moderate thickness. In most species examined, the penial pilasters are somewhat thickened near the epiphallus, becoming thinner near the atrium (e.g., Figs. 2C, 11C, 12C, 13C, 14E, 15D). It is characteristic that the pilasters on the penial inner wall differentiate towards the atrium or to-

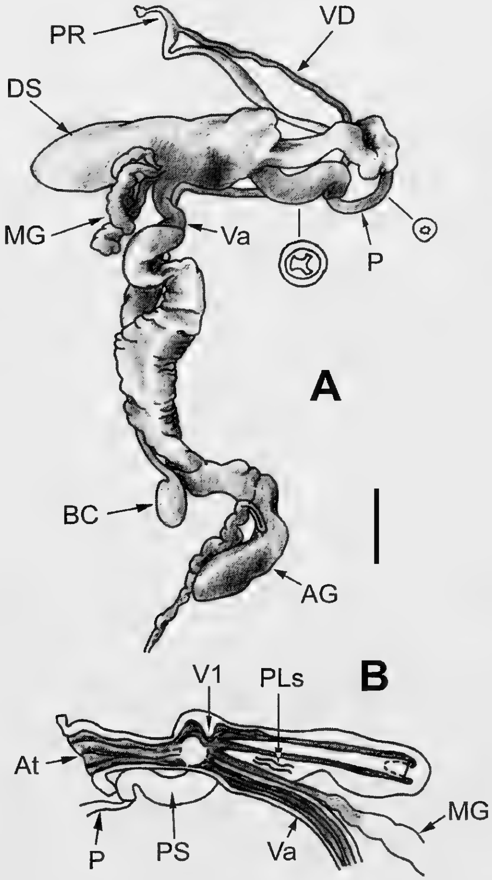

FIG. 4. *Metodontia yantaiensis* (Crosse & Debeaux, 1863), IZCAS00131-1. A, general view of genitalia, with cross-sections of penial sheath and penis; B, dart sac, sagittal section. Bar equals 1 mm.

wards the epiphallus. In *Fruticicola fruticum* and *Karaftohelix weyrichii*, the penial pilasters differentiate near the epiphallus and form an asymmetrically projecting fold (Figs. 1C, 3D), which is similar to the asymmetrical epiphallic papilla of *Nesiohelix swinhoei* (Fig. 5E), and assumed to serve as the epiphallic papilla. In *Stilpnodiscus moellendorffi* (Fig. 16B), *S. yeni*, *S. entochilus*, and *Laeocathaica* (*Laeocathaica*) *subsimilis* (Fig. 17B), the penial pilasters become thickened and differentiated near the atrium. Especially

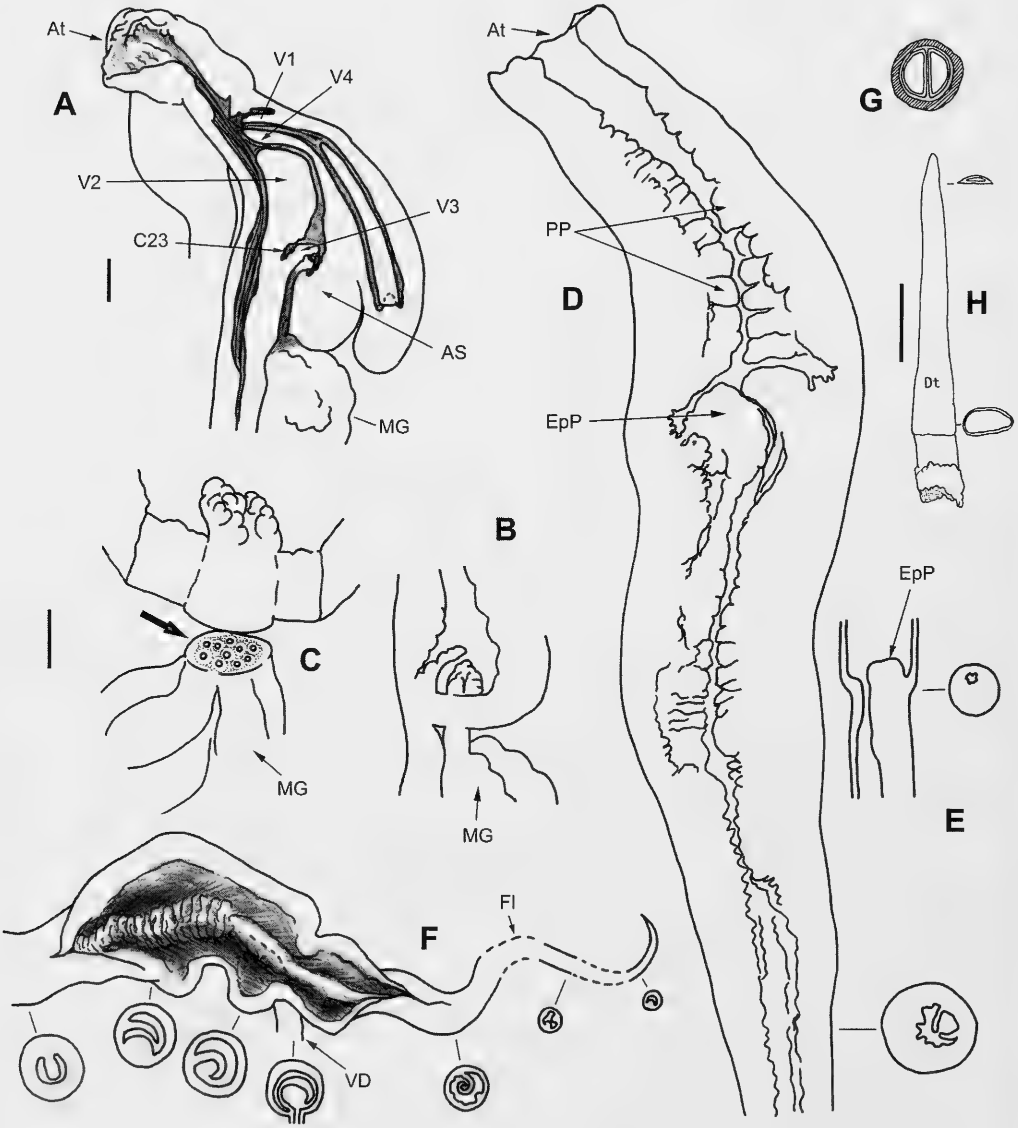

FIG. 5. *Nesiohelix swinhoei* (L. Pfeiffer, 1865), IZCAS00055-2. A, dart sac, sagittal section; B, sagittal section of accessory sac; C, cross section of mucous glands insertion on accessory sac, mucous tube entrance indicated by a thick solid arrow; D, penis and epiphallus, sagittal section, with cross-section of epiphallus; E, sagittal section of penis-epiphallus region, diagrammatic, with cross-section; F, epiphallus and flagellum, opened, with cross-sections; G, cross-section of dart sac, showing two pieces of dart; H, a piece of dart, with cross-sections. Bars equal 1 mm.

in *Stilpnodiscus*, such differentiated pilasters are high and valvule-shaped.

Character 5: Presence of the epiphallic papilla: (0) epiphallic papilla absent (e.g., Fig. 11C); (1) present (e.g., Fig. 12C).

Character 6: Symmetry of the epiphallic papilla (EpP): (0) not applicable because epiphallic papilla absent; (1) epiphallic papilla present and symmetric (e.g., Figs. 12C, 13F); (2)

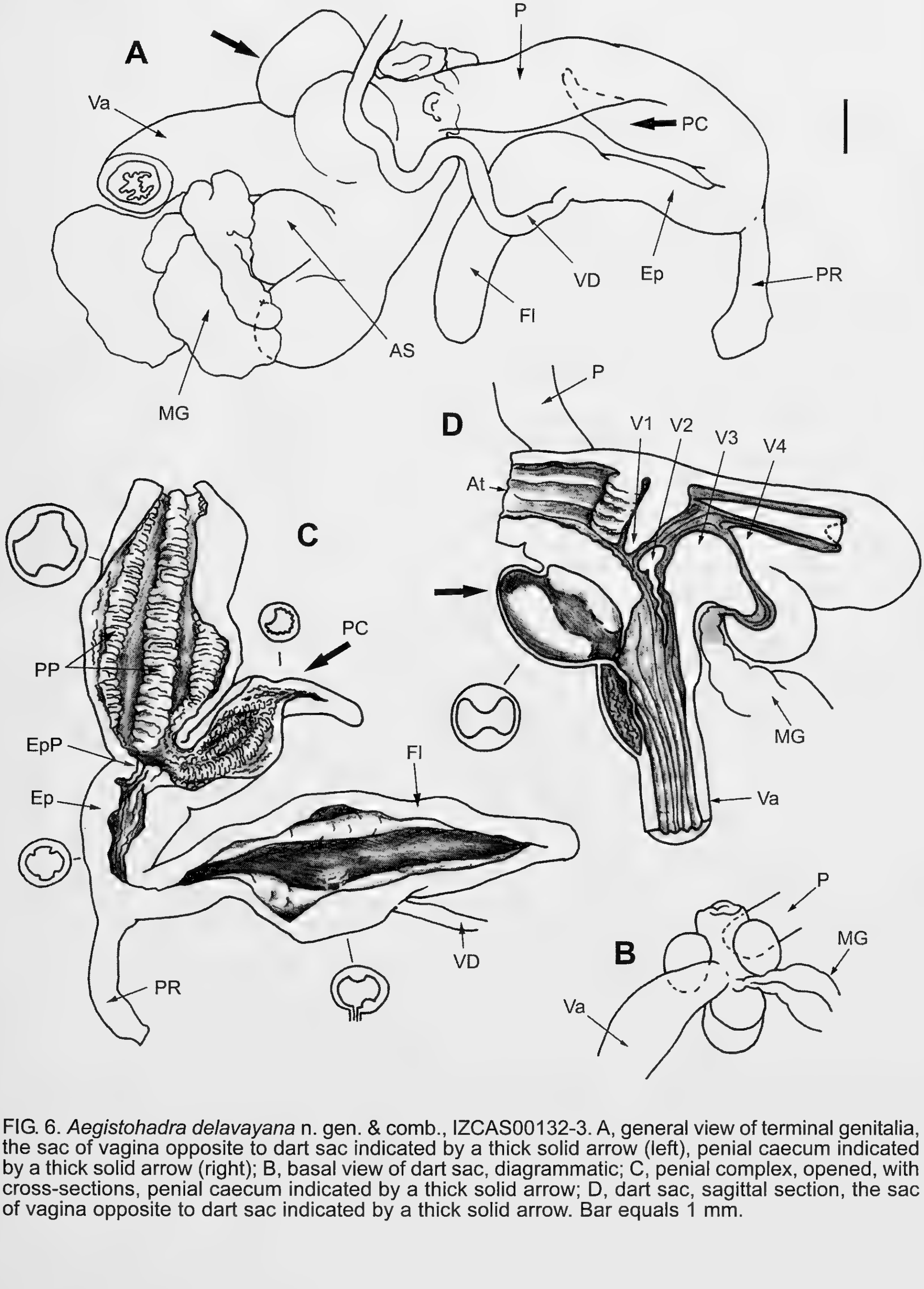

FIG. 6. *Aegistohadra delavayana* n. gen. & comb., IZCAS00132-3. A, general view of terminal genitalia, the sac of vagina opposite to dart sac indicated by a thick solid arrow (left), penial caecum indicated by a thick solid arrow (right); B, basal view of dart sac, diagrammatic; C, penial complex, opened, with cross-sections, penial caecum indicated by a thick solid arrow; D, dart sac, sagittal section, the sac of vagina opposite to dart sac indicated by a thick solid arrow. Bar equals 1 mm.

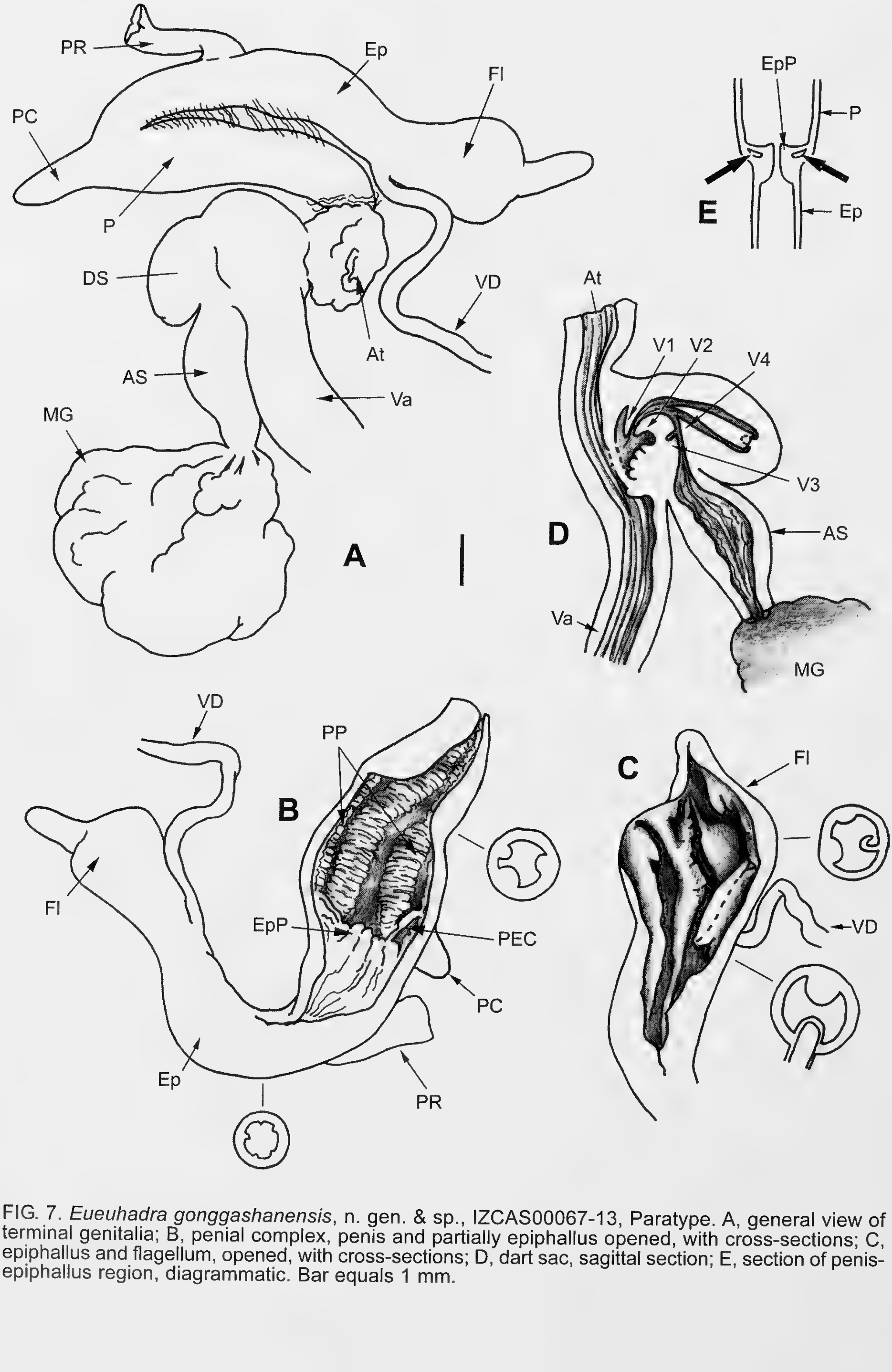

FIG. 7. *Eueuhadra gonggashanensis*, n. gen. & sp., IZCAS00067-13, Paratype. A, general view of terminal genitalia; B, penial complex, penis and partially epiphallus opened, with cross-sections; C, epiphallus and flagellum, opened, with cross-sections; D, dart sac, sagittal section; E, section of penis-epiphallus region, diagrammatic. Bar equals 1 mm.

epiphallic papilla present and asymmetric (Figs. 5E, 8D, 9D).

Remarks: In *Nesiohelix swinhoei*, *Aegistohadra* n. gen., *Eueuhadra* n. gen., *Pfeifferia micans*, *Calocochlea coccomelos*, *Cathaica* (*Pliocathaica*) *gansuica*, *Aegista* (*Aegista*) *accrescens*, *Aegista* (*Plectotropis*) *gerlachi*, *Laeocathaica* (*Laeocathaica*) *subsimilis*, *Acusta ravida*, *Trishoplita dacostae*, and *Euhadra herklotsi* (Figs. 5D, 6C, 7B, 8D, 9D, 12C, 13F, 14E, 17B, 18D, 19D, 20C), a more or less protruding epiphallic papilla is present. In the remaining bradybaenid genera the epiphallic papilla is depressed or missing.

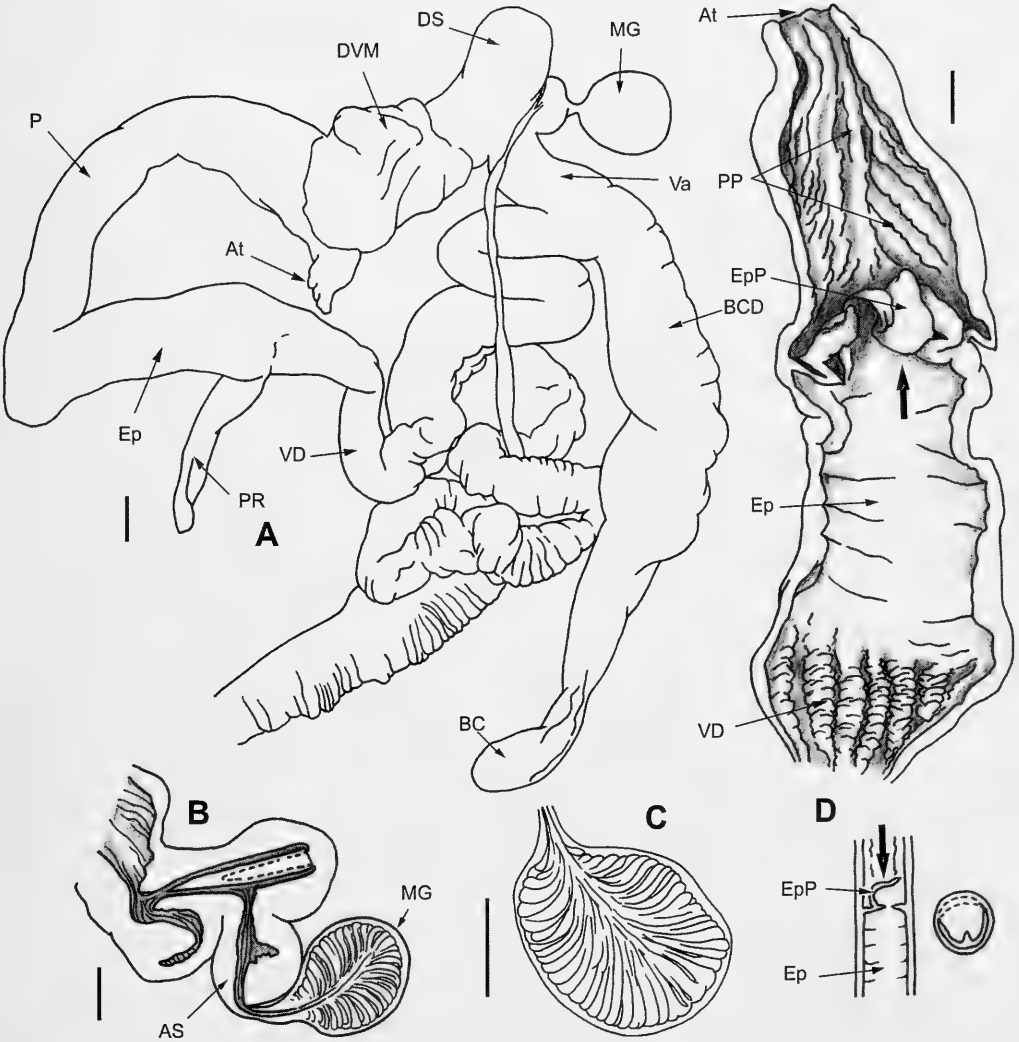

FIG. 8. *Calocochlea coccomelos* (Sowerby, 1840), SMF 323619. A, general view of genitalia; B, dart sac, sagittal section; C, mucous glands, sagittal section; D, above: Penis-epiphallus region, opened; below: cross-section of penis-epiphallus transition, diagrammatic; valve-shaped epiphallic papilla indicated by thick solid arrows. Bars equal 1 mm.

Character 7: The epiphallic papilla valve-shaped or papilla-shaped:
(0) not applicable because epiphallic papilla absent; (1) epiphallic papilla present, valve-shaped (Figs. 8D & 9D, indicated by thick solid arrows); (2) epiphallic papilla present, papilla-shaped (e.g., Figs. 5D, 10D).

Character 8: Presence of the penial caecum:
(0) absent; (1) present (e.g., Figs. 6A, 6C, indicated by thick solid arrows).

Remarks: This structure can be easily distinguished from the following simple penial caecum (SPC) by the PC pilasters, which are differentiated from those of the caecum. In the simple penial caecum (SPC), which characterizes the genera *Trichobradybaena* and *Mastigeulota*, the penial pilasters forming the inner wall of caecum are just the extended parts from its outer/entering pilasters.

Character 9: The simple penial caecum:
(0) absent; (1) present (Figs. 11B, 23A, indicated by thick solid arrows).

Character 10: Presence of the flagellum:
(0) absent; (1) present.

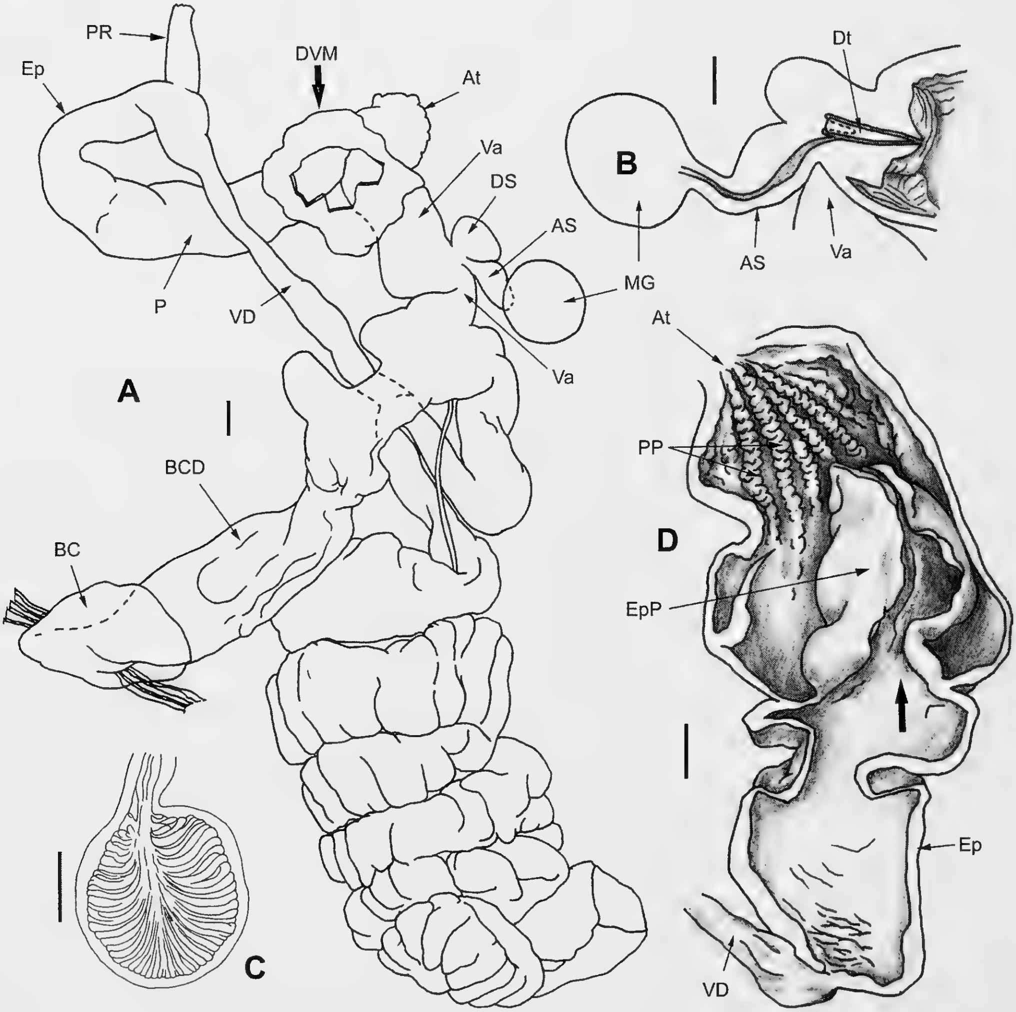

FIG. 9. *Pfeifferia micans* Pfeiffer, 1845, SMF 323620. A, general view of genitalia; B, dart sac, sagittal section except mucous glands; C, mucous glands, sagittal section; D, penis-epiphallus region, opened, valve-shaped epiphallic papilla indicated by a thick solid arrow. Bars equal 1 mm.

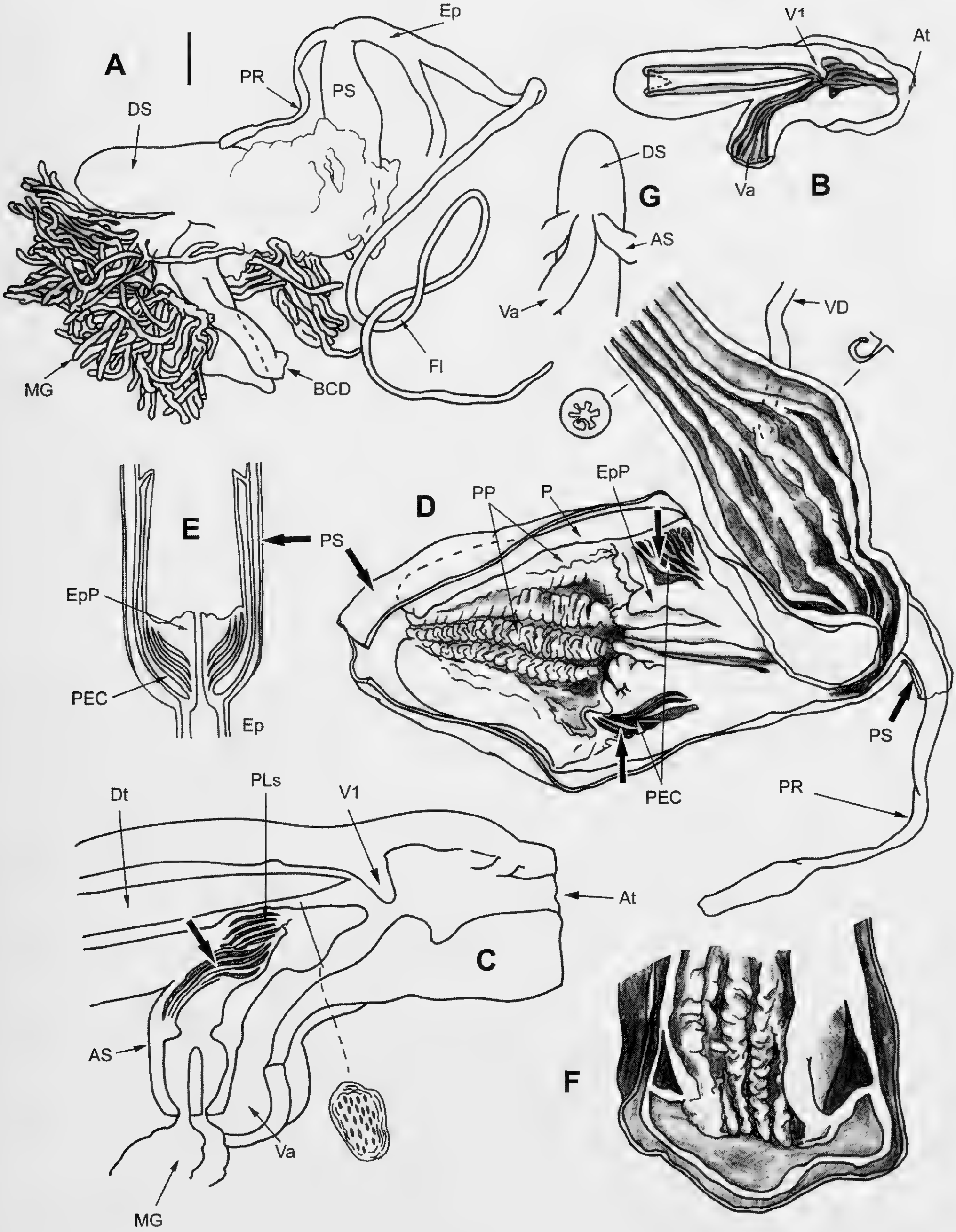

FIG. 10. *Helix pomatia* (Linné, 1758), IZCAS00188-1. A, general view of terminal genitalia, bar equals 2 mm; B, dart sac, sagittal section with mucous glands removed; C, section of partial dart sac, with cross-section; D, penial complex, opened, with cross-sections, middle two thick solid arrows indicating penis-epiphallus chambers; E, section of penis-epiphallus region, diagrammatic, penial sheath indicated by a thick solid arrow; F, distal penis near atrium opening, opened; G, basal view of dart sac, diagrammatic.

Remarks: The flagellum and the vas deferens insertion structure are almost the same in the species examined. Flagellum, if present, with inner ridges simple or somewhat complexly arranged. Insertion of vas deferens on flagellum inwardly forms a more or less distinct C-shaped (in cross-section) fold towards the tip of flagellum (Figs. 5F, 7C, 10D, 13D, 14F, 19E, 20A). The only exception is *Aegistohadra delavayana*, n. comb., in which a depressed pilaster instead of the distinct C-shaped fold is present (Fig. 6C). These structures are the same in bradybaenid genera and in *Helix pomatia*. Therefore, if present, the flagellum of the various groups examined might be considered homologous.

Character 11: Presence of the polylayered structure (PLs) in accessory sac:

(0) PLs absent (e.g., Figs. 1B, 5A, 8B); (1) PLs present (e.g., Figs. 2D, 10C, 11B, 13C, 14C, 22D); (2) not applicable because dart sac absent.

Remarks: In *Metodontia yantaiensis*, the accessory sac has some wavy and spongy connective tissue (polylayered structure, PLs) (Fig. 4B). In *Pseudaspasita binodata*, such structure seems to be weakly developed (Fig. 21C). This kind of structure can be easily distinguished from the folds/pilasters on the inner wall of the accessory sac (Fig. 16E) by the compactness and parallelism in the arrangement of its filaments/layers. In *Bradybaena similaris* and *Cathaica* (*Cathaica*) *fasciola*, the structure is much developed and situated between insertion of mucous glands and vagina (Figs. 2D, 22D). In *Aegista* (*Aegista*) it is highly developed and uppermost, and it wraps the dart chamber (DtC) (Figs. 13C, 14C). In *Aegista* (*Plectotropis*), PLs occupies the whole accessory sac that is externally visible and the region between dart sac and the vagina. Interestingly, in *Helix pomatia*, the polylayered structure is also present, at the pit formed by both dart the sac and each of the accessory sacs/trunk of basal mucous stalks (Fig. 10C). The observed PLs of the taxa studied are provisionally assumed to

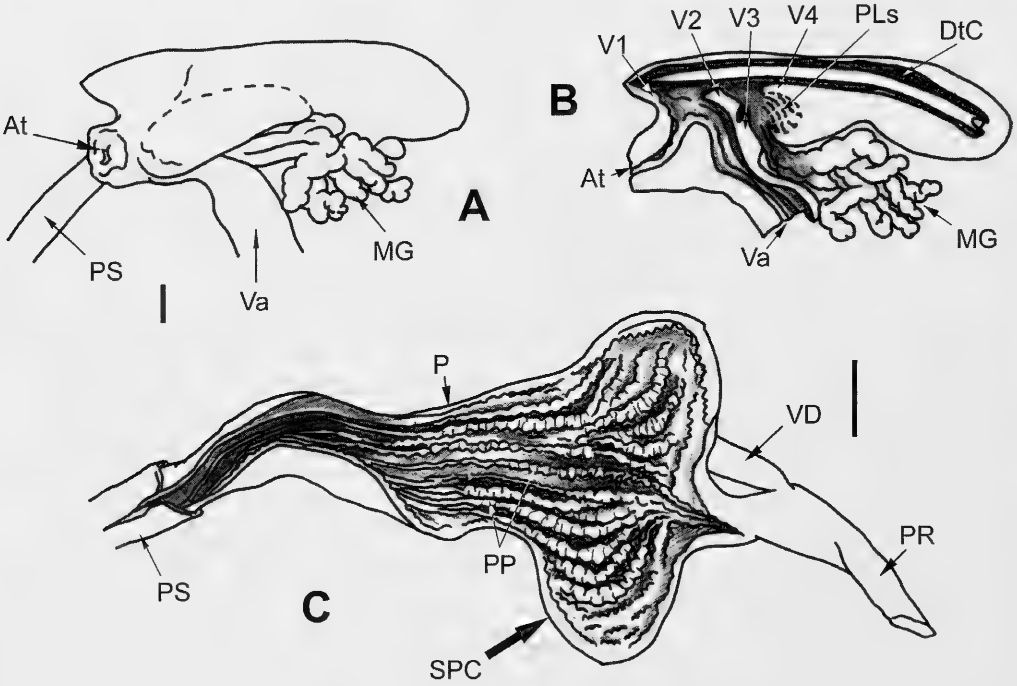

FIG. 11. *Mastigeulota kiangsinensis* (E. Martens, 1875), IZCAS00003-1. A, lateral view of dart apparatus; B, dart sac, sagittal section; C, penis, opened, simple penial caecum (SPC) indicated by a thick solid arrow. Bars equal 1 mm.

be homologous in origin, because they occur only in the specific region in dart apparatus, and assumed to be related to dart shooting or pumping the mucus out during copulation.

Character 12: Distribution of polylayered structure (PLs) in accessory sac:

(0) not applicable because PLs absent; (1) distributed between mucous glands insertion and vagina (region I) (e.g., Fig. 22D); (2) PLs present, distributed between mucous glands insertion and dart caecum (DtC; region II) (e.g., Figs. 4B, 10C, 11B); (3) PLs present at region I & II (e.g., Fig. 14C).

Character 13: The common entrance of mucous glands:

(0) mucous glands without common entrance (e.g., Figs. 19B, 20D); (1) with common en-

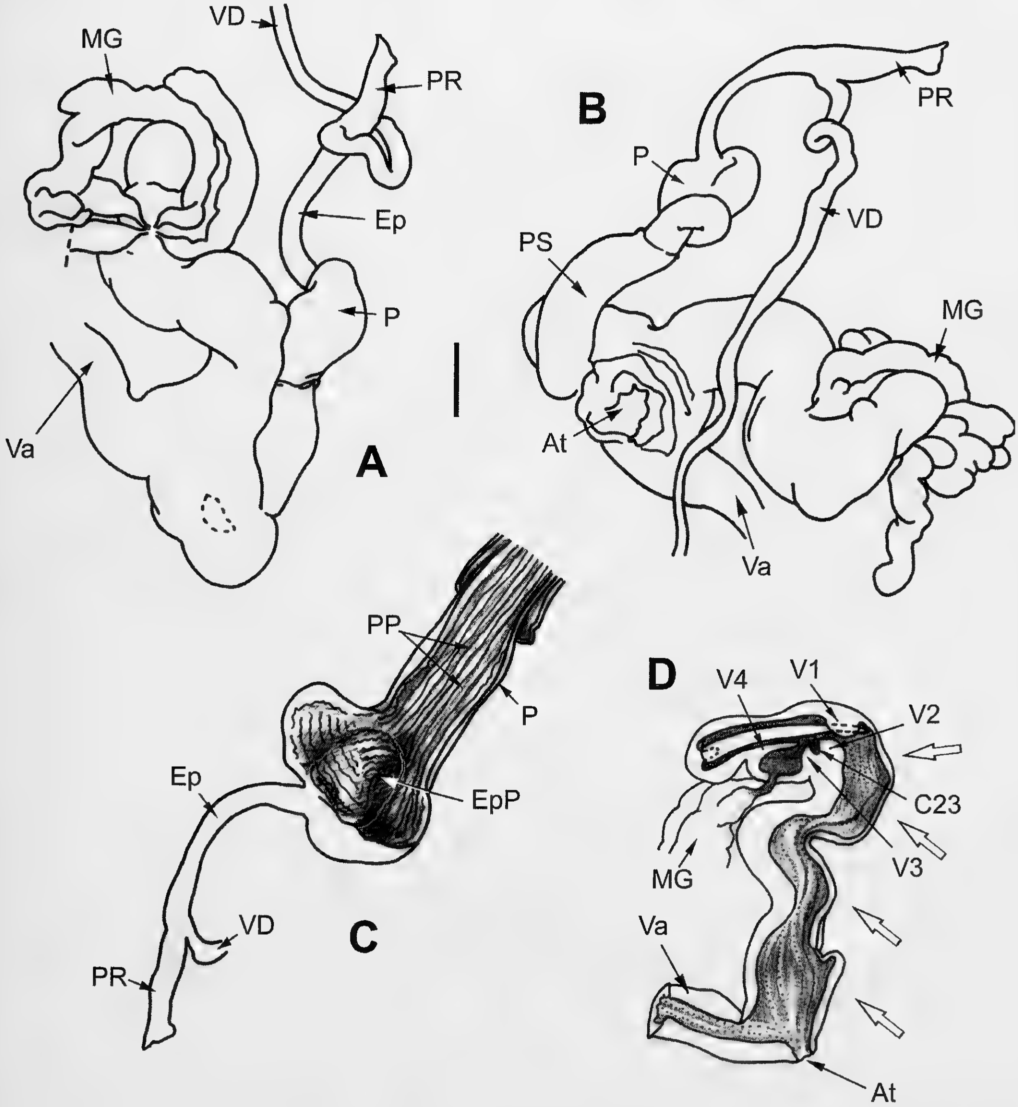

FIG. 12. *Cathaica* (*Pliocathaica*) *gansuica* (Möllendorff, 1899), IZCAS00210-1. A, basal view of dart sac and penial complex; B, lateral view of dart sac and penial complex; C, penis, opened; D, dart sac, sagittal section, neck-structure region of dart sac indicated by four thick hollow arrows. Bar equals 1 mm.

trance; (2) not applicable because dart sac absent.

Remarks: There are two ways by which the mucous glands are inserted on the accessory sac, which can only be observed when the accessory sac is cut open sagittally. Usually, the mucous glands open into the accessory sac through a common duct (Figs. 1B, 2D, 4B, 6D, 7D, 11B, 12D, 13C, 14C, 15C, 16C, 17C, 18B, 21C, 22D, 23E, 24B). Another situation was found in *Karaftohelix weyrichii*, *Trishoplita dacostae*, *Euhadra herklotsi*, and *Nesiohelix swinhoei* (Figs. 3C, 5C, 19B, 20D), with two to numerous separate tubes rather than a common tube opening into the accessory sac.

Character 14: The distinguishability of the accessory sac from outside of the dart sac: (0) indistinct from outside of the dart sac; (1) distinct from outside of the dart sac; (2) not applicable because dart sac absent.

Remarks: The accessory sac cannot always be distinguished externally by an apparent external boundary from the dart sac (e.g., Fig.

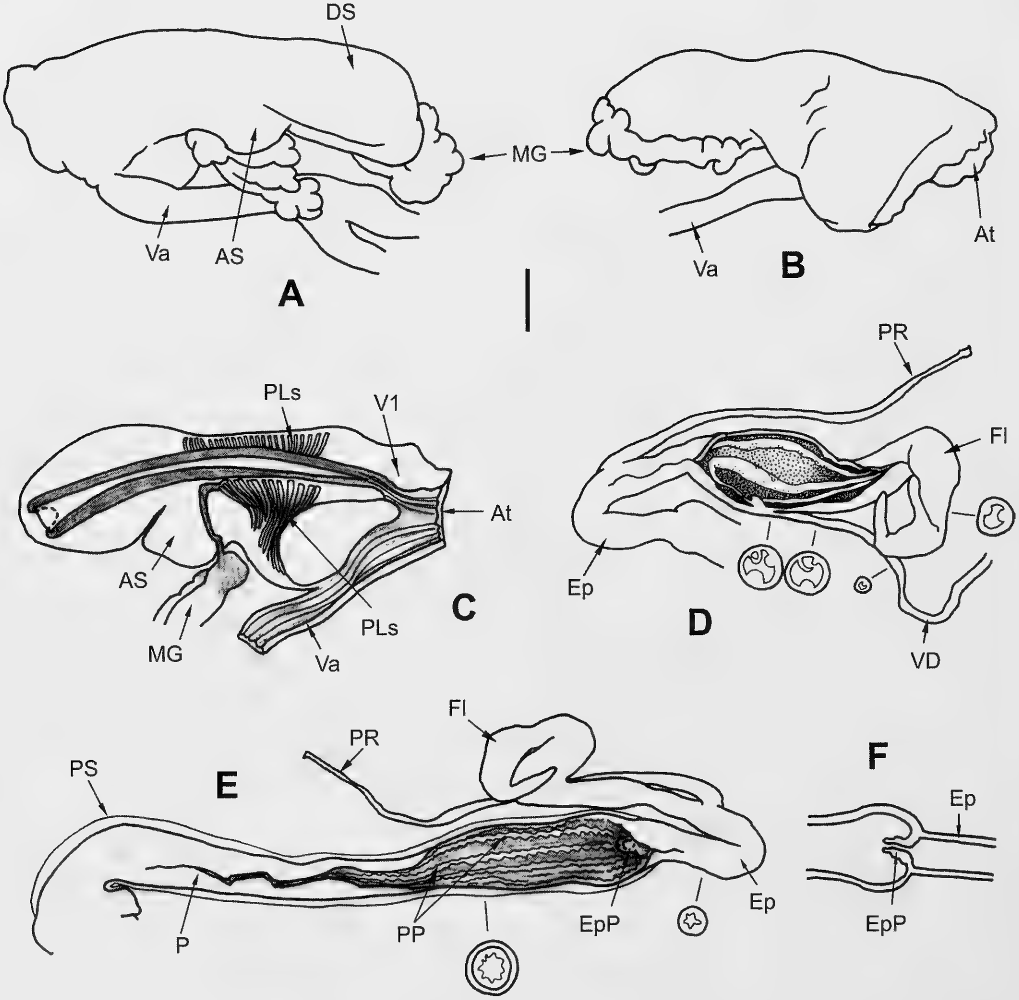

FIG. 13. *Aegista* (*Aegista*) *accrescens* (Heude, 1882), IZCAS00027-4. A, B, lateral views of dart sac; C, dart sac, sagittal section; D, flagellum, opened, with cross-sections; E, penial complex, penis opened, with cross-sections; F, section of penis-epiphallus region, diagrammatic. Bar equals 1 mm.

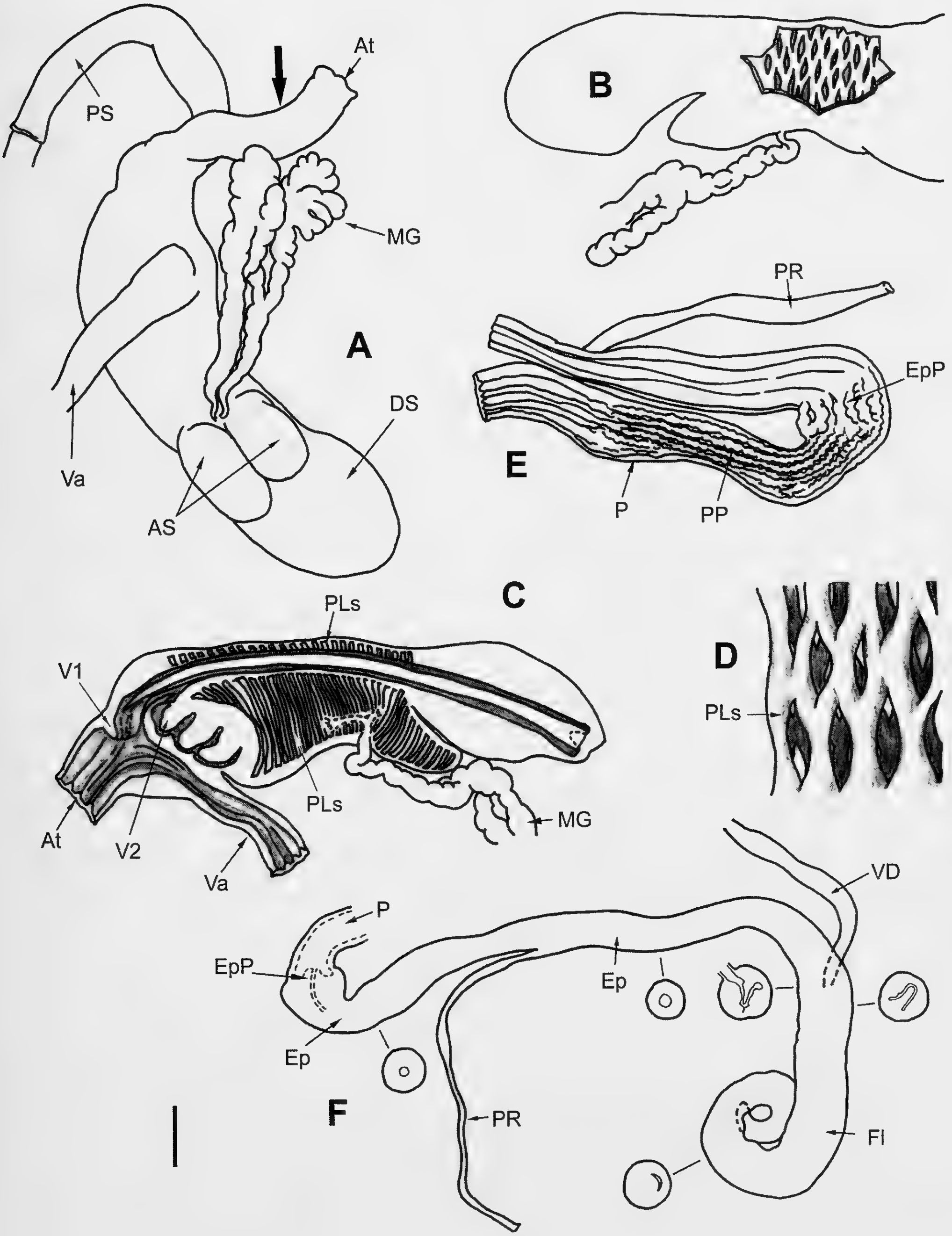

FIG. 14. *Aegista* (*Plectotropis*) *gerlachi* (E. Martens, 1881), IZCAS00044-2. A, basal view of dart sac; B, lateral view of dart sac, outer tissue partially removed to show the polylayered structure inside dart sac; C, dart sac, sagittal section; D, polylayered structure in accessory sac, magnified; E, penis and epiphallus, opened; F, penial complex, with cross-sections. Bar equals 1 mm.

2B). Various genera show different patterns of the accessory sac, which has little relationship with its size from external view. The accessory sac is situated usually on the bottom of dart sac, except in *Acusta*, where it is situated near the top of dart sac (Fig. 18B). The structurally simplest accessory sac is an empty sac, only with a few depressed folds (= pilasters) on its inner wall (e.g., Figs. 1B, 7D & 16C).

Character 15: The accessory sac is bipartite (e.g., Figs. 14A, 22C) or undivided (e.g., Figs. 5A, 7A):

(0) accessory sac divided into two parts; (1) accessory sac undivided; (2) not applicable because dart sac absent.

Character 16: Presence of V1–V4 in the dart apparatus (= V2 is present):

(0) V1–V4 indistinct (= V2 is indistinct/absent) (e.g., Figs. 8B, 9B); (1) V1–V4 distinct (= V2 is distinct) (e.g., Figs. 7D, 23E); (2) not applicable because dart sac absent.

Remarks: Inside the dart sac, several valvules (V1–V4) form a tube that contains one love dart (or two in *Nesiohelix*) serving as mating-related organ (e.g., Figs. 7D, 23E). According to this study, the position and the number of the valvules are intraspecifically stable but vary among the genera studied. The term valvule is used here for the first time in land snail anatomy. It is a small valve-like structure that describes the nature of the chamber boundry (dart sac, accessory sac chanmber), visible in sagittal section. However, the position of VI–V4 can easily be determind even when V2 is absent, because: (1) V1 and V4 always form the opening of a muscular tube containing the love dart(s); (2) the space between V4 and V3 is usually the opening of the accessory sac (the only exception is in *Acusta*, in which the accessory sac is situated on the top of dart sac); (3) the space between V3 and V2 is C23, which varies from presence as a pronounced chamber to totally absence. Such absence means V2 is lacking morphologically. For this reason, the complexity of the development

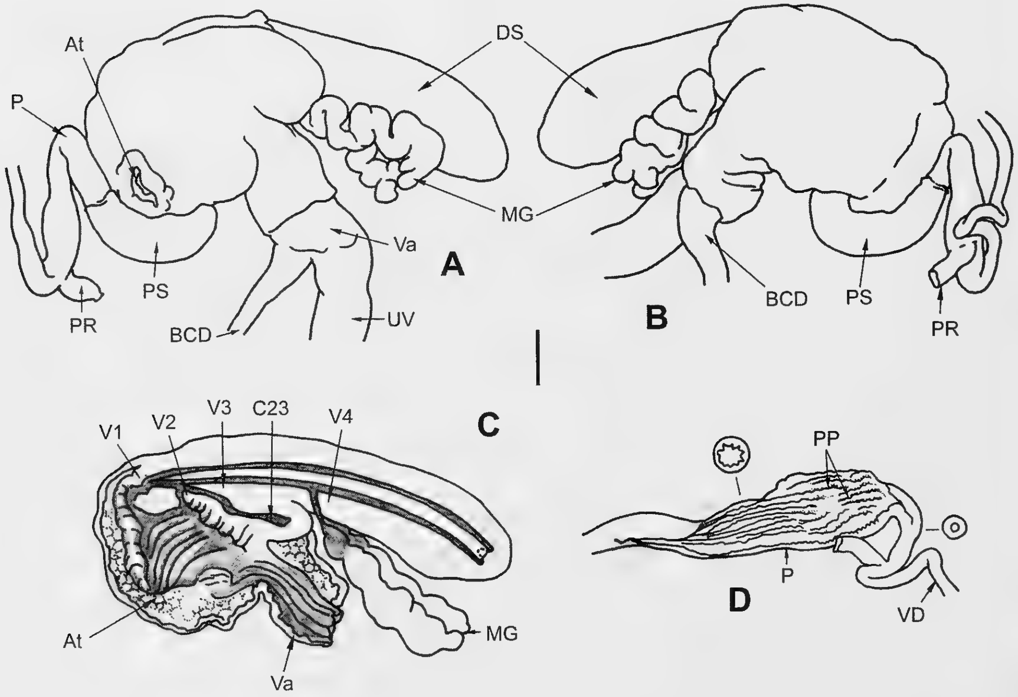

FIG. 15. *Pseudobuliminus* (*Pseudobuliminus*) *piligerus* (Möllendorff, 1899), IZCAS00085-21. A, B lateral views of terminal genitalia; C, dart sac, sagittal section; D, penial complex, penis opened, with cross-sections. Bar equals 1 mm.

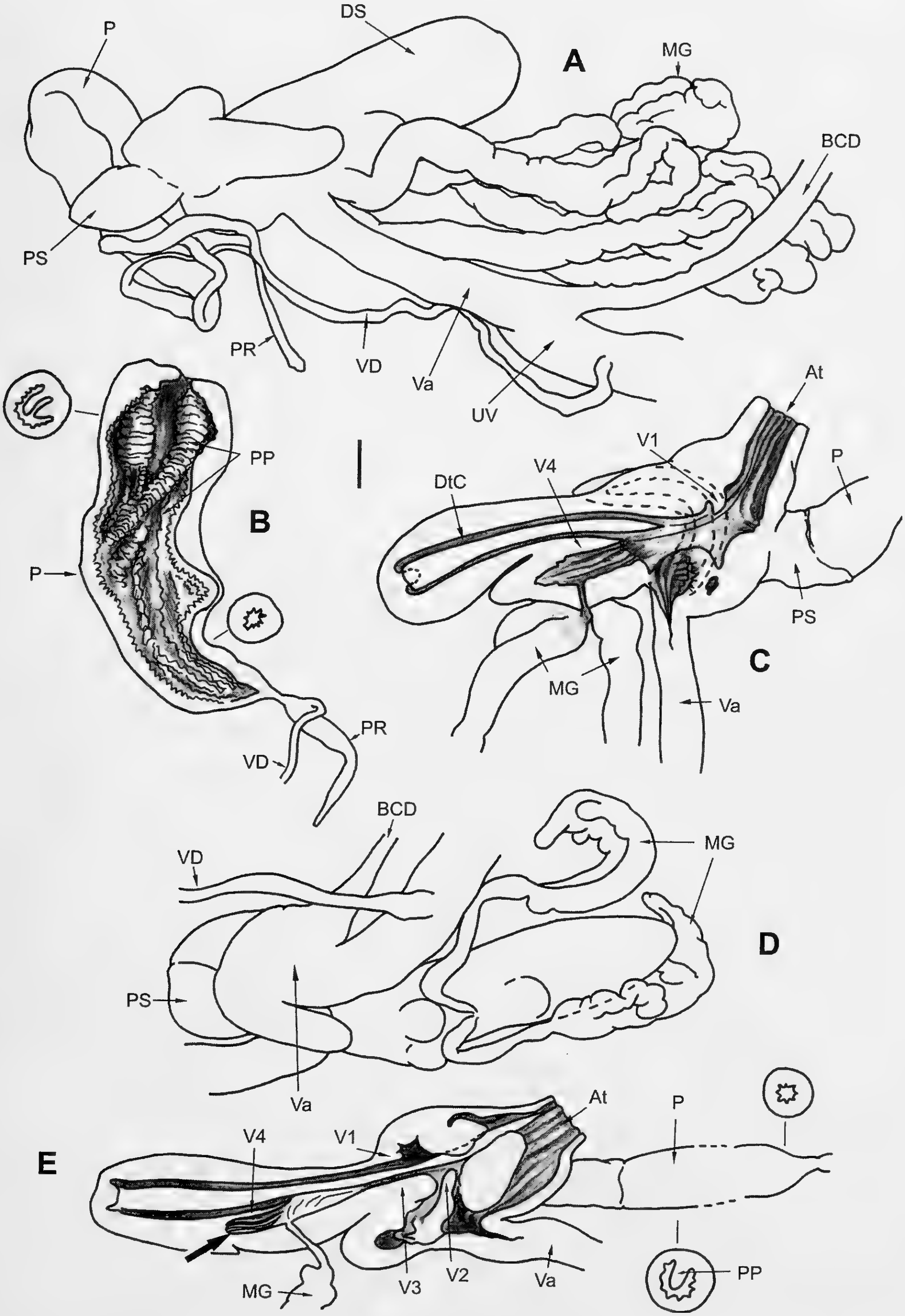

FIG. 16. *Stilpnodiscus*. A, B, C *Stilpnodiscus moellendorffi* Wu, 2001, IZCAS00081-4, Paratype. A, lateral view of terminal genitalia; B, penis, opened, with cross-sections; C, dart sac, sagittal section; D, E *Stilpnodiscus entochilus* Möllendorff, 1899, IZCAS00076-2. D, basal view of dart sac; E, dart sac, sagittal section, in detail, with cross-sections of penis. Bar equals 1 mm.

of the dart sac inner structure is considered, described, and employed for the first time as an important and necesssary character for the dart sac in the Bradybaenidae.

Character 17: Presence of a papilla within accessory sac formed by the mucous glands insertion:

(0) without papilla; (1) with a papilla; (2) not applicable because dart sac absent.

Remarks: A papilla with a tiny pore or several tiny pores for the entrance of mucous from mucous glands into the accessory sac is sometimes present. If the mucous gland ducts merge into one common tube, the papilla also has one pore, as in *Acusta ravida* (Fig. 18B, G). When the mucous glands enter the accessory sac separately, two papillae are present, as in *Trishoplita dacostae* (Fig. 19B, indicated by two lower thick solid arrows) or a somewhat complex structure with numerous pores as in *Nesiohelix swinhoei* and *Euhadra herklotsi* (Figs. 5C, 20D). In most genera, such a structure is absent (other Figs.).

Character 18: Presence of the structure derived from mucous glands entering papilla leading to DtC:

(0) not applicable because mucous glands entrance papilla absent; (1) mucous glands entrance papilla present, its derived part does not lead to DtC; (2) mucous glands entrance papilla present, its derived part leads to DtC (Figs. 19B, 20D, respectively indicated by a upper thick solid arrow).

Character 19: Number of branches of mucous glands:

(0) numerous mucous branches; (1) one spherical mucous gland (Figs. 8, 9); (2) two branches of mucous glands; (3) not applicable because dart sac absent.

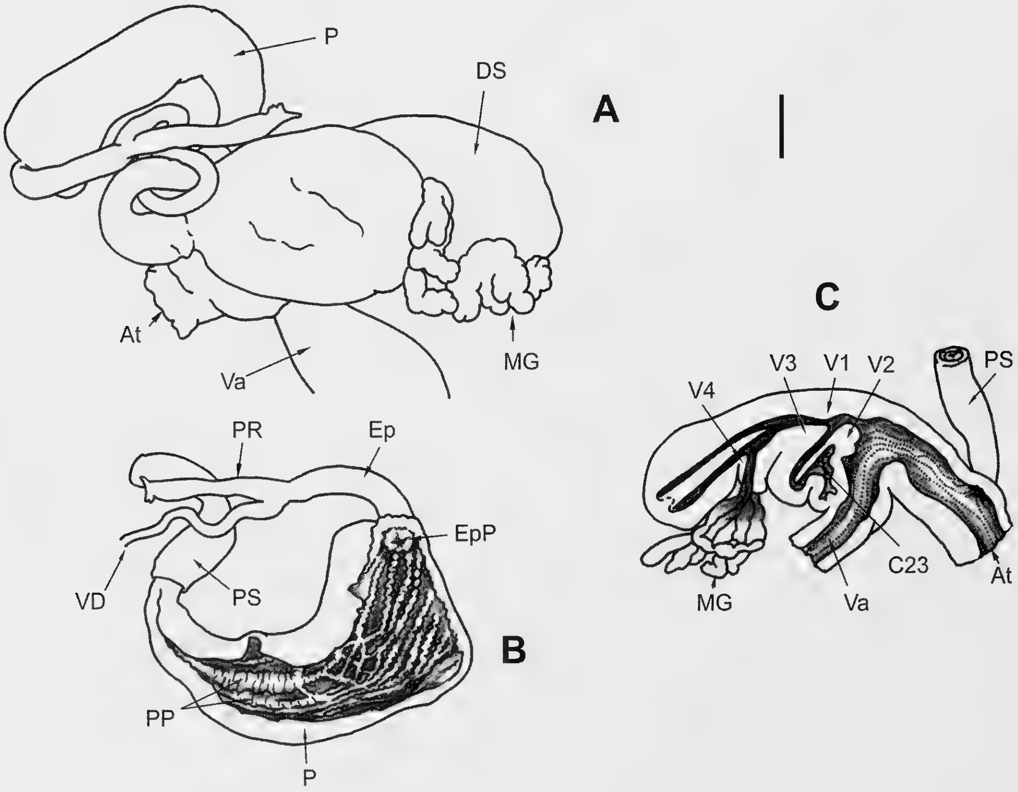

FIG. 17. *Laeocathaica* (*Laeocathaica*) *filippina* (Heude, 1882), IZCAS00006. A, B IZCAS00006-5. A, lateral view of terminal genitalia; B, penial complex, penis opened; C, IZCAS00006-6, dart sac, sagittal section. Bar equals 1 mm.

Character 20: The length of vaginal region between dart sac and atrium:
(0) region short; (1) region pronouncedly elongated (e.g., Figs. 9A, 18B); (3) not applicable because dart sac absent.

Character 21: Proximal part of dart sac elongated, forming a neck-structure.
(0) neck-structure absent; (1) neck-structure present (Figs. 3A, 12D); (2) not applicable because dart sac absent.

Character 22: Presence of penis-epiphallus chamber(s):
(0) absent; (1) a simple chamber present (Fig. 7B, E); (2) more chambers present (Fig. 10D, E).

Remarks: The penis-epiphallus chamber occurs in the wall of penis-epiphallus junction. Dissection shows that there are three cases of differentiation. (1) It is solid (i.e., without any chamber within) between the epiphallic papilla and its wall. (2) There is only a simple chamber between the epiphallic papilla and its wall. (3) As seen in *Helix pomatia* (Helicidae) (Fig. 10D, E), more than one chamber is developed in this area, and some of them extend into the penial wall. All

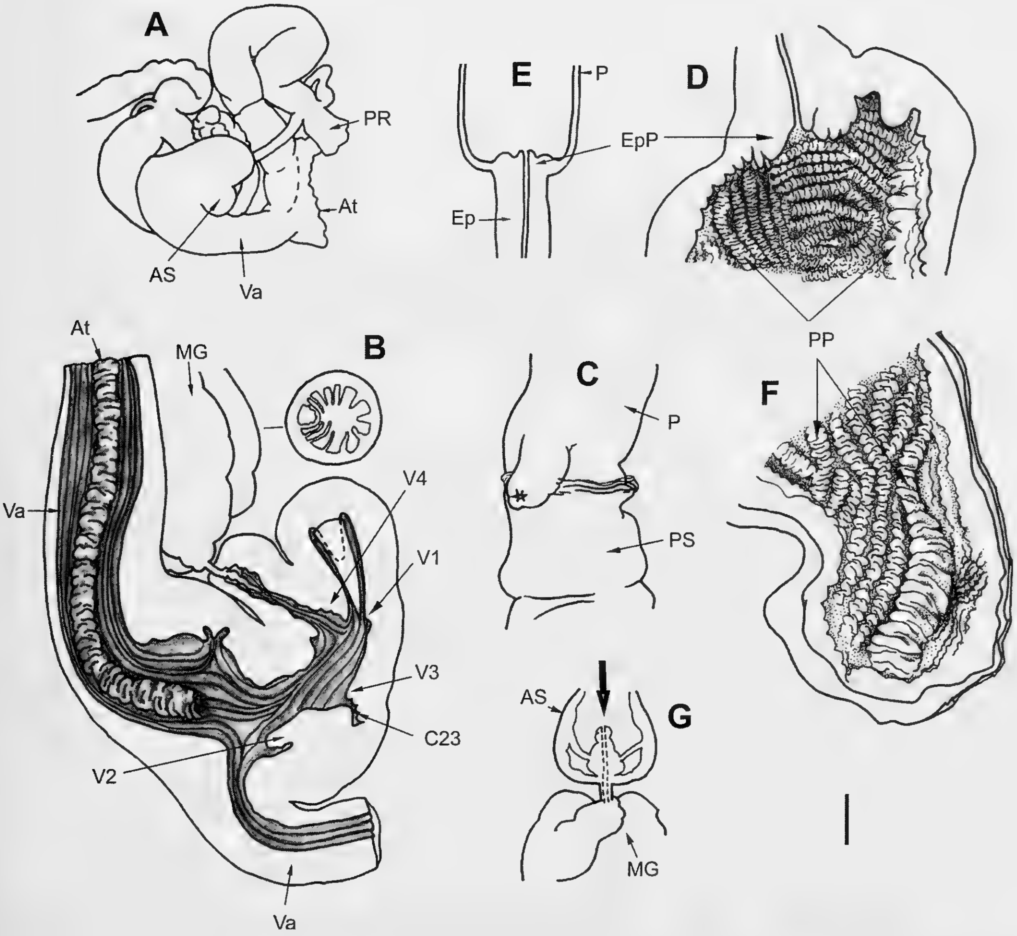

FIG. 18. *Acusta ravida* (Benson, 1842), IZCAS00944-2. A, general view of genitalia; B, dart sac and part of vagina, sagittal section, with cross-section of vagina; C, region near penial sheath; D, proximal region of penis, opened, showing epiphallic papilla; E, section of penis-epiphallus region, diagrammatic; F, distal region of penis, opened; G, section of accessory sac, papilla of entrance for mucous tubes indicated by a thick solid arrow, diagrammatic. Bar equals 1 mm.

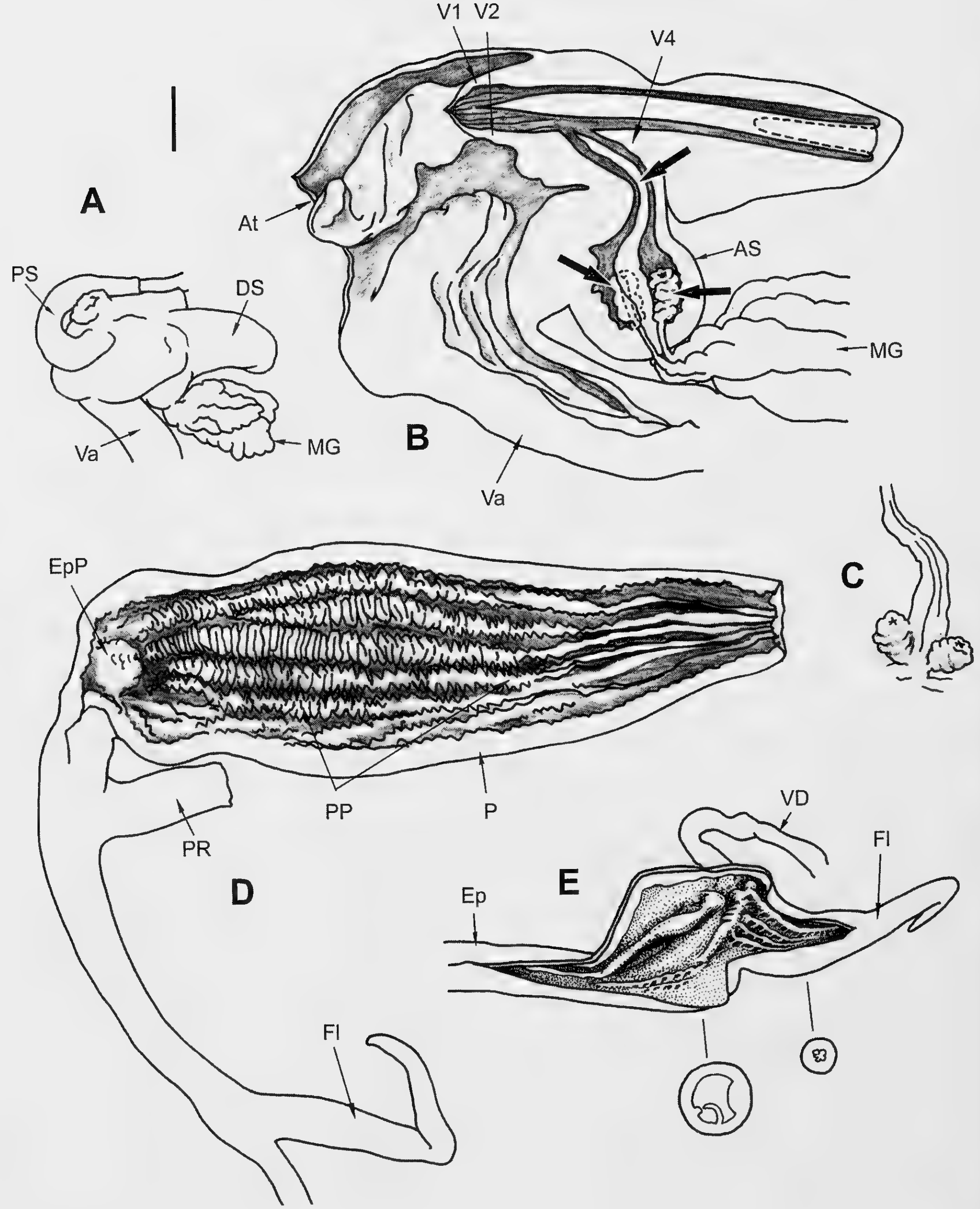

FIG. 19. *Trishoplita dacostae* Gude, 1900. IZCAS00174-2. A, lateral view of dart apparatus; B, dart sac, sagittal section, upper thick solid arrow indicating the structure derived from the mucous glands entering papilla leading to dart chamber, two lower thick solid arrows indicating the mucous glands entering papilla; C, the mucous glands entering papillae and the derived structure; D, penial complex, with penis opened; E, epiphallus and flagellum, opened, with cross-sections. Bar equals 1 mm.

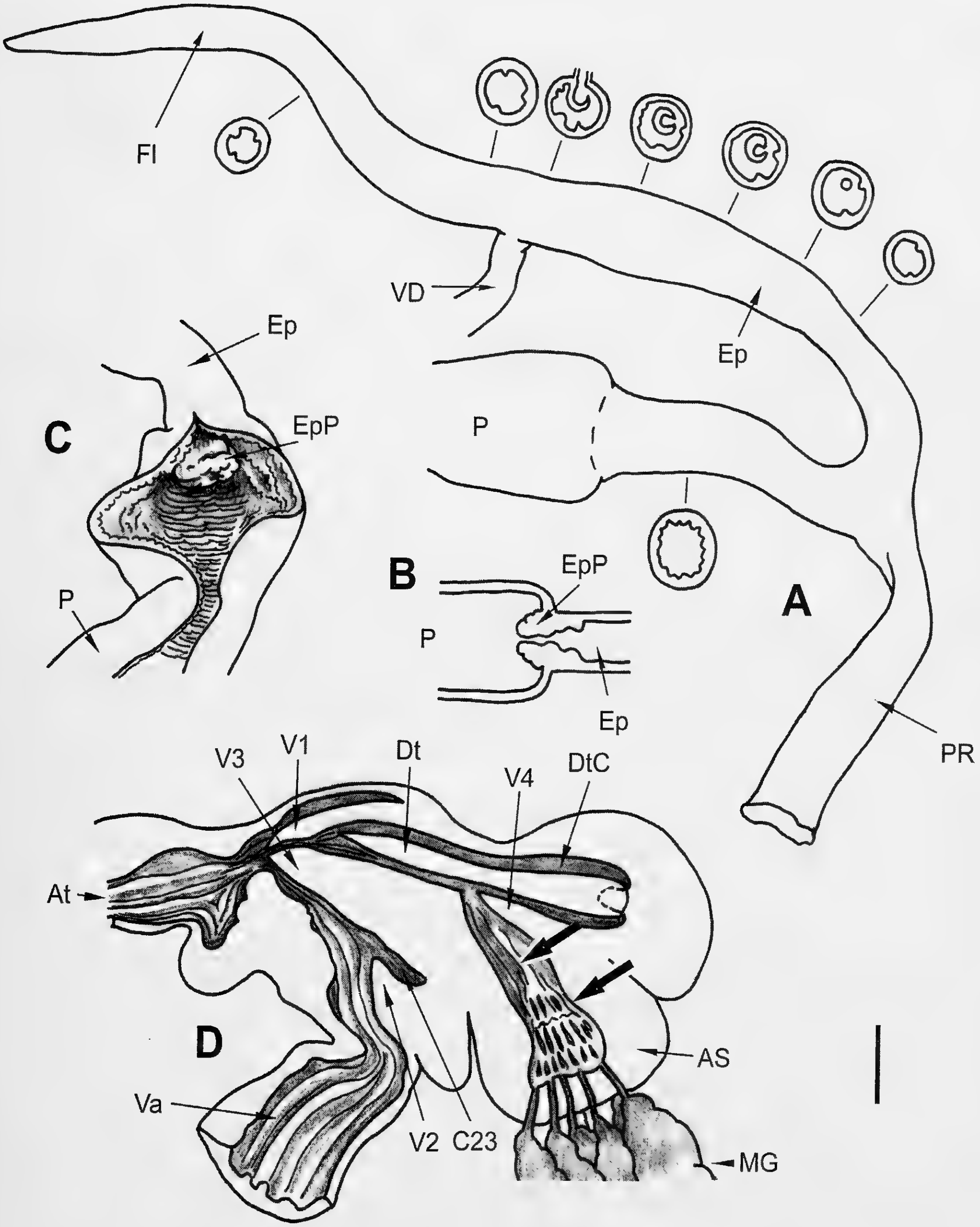

FIG. 20. *Euhadra herklotsi* (E. Martens, 1861), IZCAS01076-1. A, epiphallus and flagellum, with cross-sections; B, section of penis-epiphallus region, diagrammatic; C, penis-epiphallus region, penis opened; D, dart sac, sagittal section, upper thick solid arrow indicating the structure derived from the mucous glands entering papilla leading to dart chamber, lower thick solid arrow indicating the structure of mucous glands entering papilla. Bar equals 1 mm.

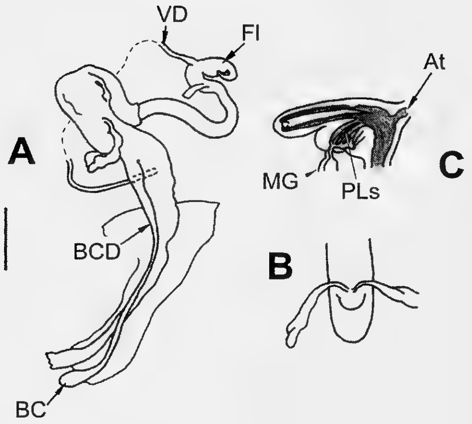

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FIG. 21. *Pseudaspasita binodata* (Möllendorff, 1886), IZCAS01075-2. A, general view of terminal genitalia; B, basal view of dart sac, diagrammatic; C, dart sac, sagittal section. Bar equals 1 mm.

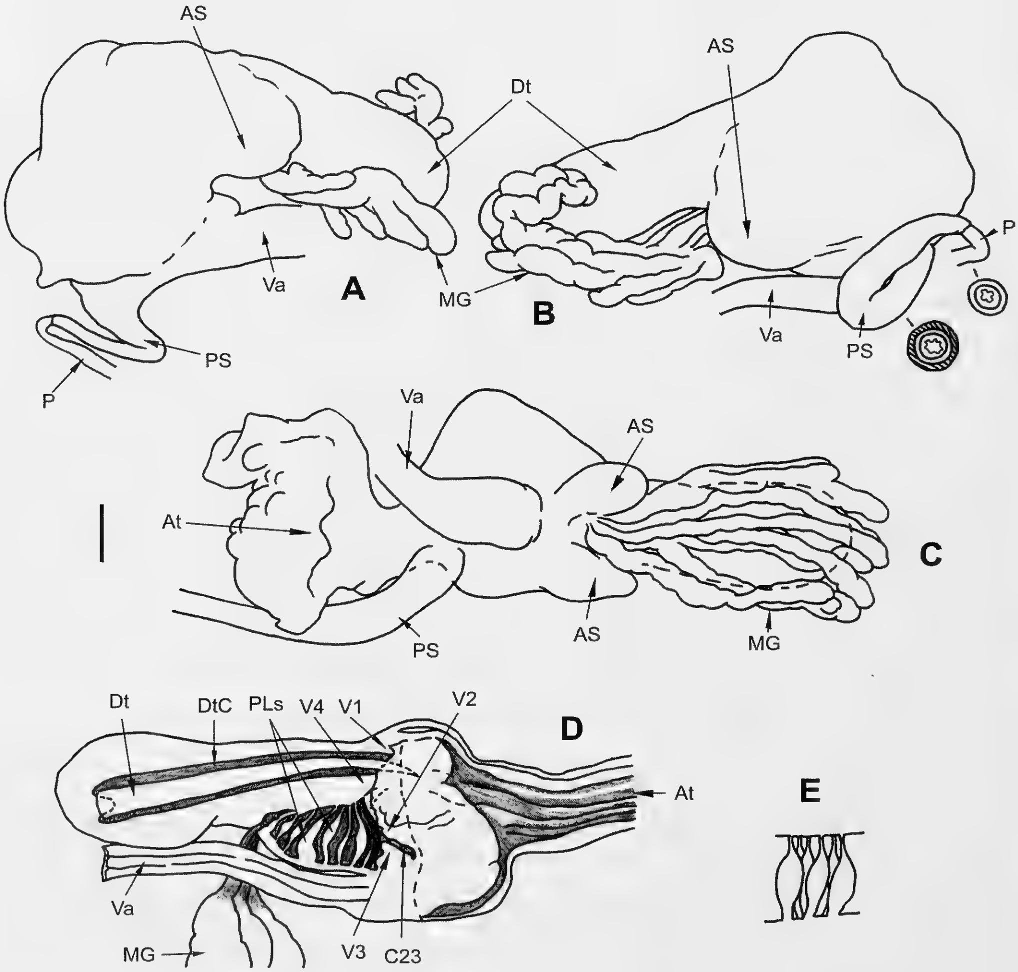

FIG. 22. *Cathaica* (*Cathaica*) *fasciola* (Draparnaud, 1801), IZCAS01074-6. A, lateral view of dart sac; B, lateral view of dart sac, with cross-sections of penial sheath and penis; C, basal view of terminal genitalia; D, dart sac, sagittal section; E, polylayered structure in accessory sac. Bar equals 1 mm.

bradybaenid genera examined, except *Eueuhadra*, n. gen., fall into the first case.

Character 23: Number of darts per dart sac: (0) dart sac containing 1 dart; (1) dart sac containing 2 darts (Fig. 5G, H); (2) not applicable because dart sac absent.

Remarks: In *Nesiohelix swinhoei* (type species of the genus *Nesiohelix*; Richardson, 1983, the type species mistakenly given as *Nesiohelix caspari*; see original introduction of genus by Kuroda & Emura, 1943), the dart sac contains two darts, each of which is wrapped by a muscular tube. These two muscular tubes are attached closely but distinctly divided. In this study, the two darts are the same length rather than "one larger, the other smaller" (Kuroda & Emura, 1943: text-fig. 1), semi-circled in cross-sections, and blunt apically. In some other congeneric species of *Nesiohelix*, such as *N. samarangae* (Kuroda & Miyanaga, 1942) and *N. moreletiana* (Heude, 1882), the dart sac contains two darts (Habe, 1945, not figured), which is confirmed in this study and is an important synapomorphy characterizing *Nesiohelix*.

Character 24: Internal pilaster of accessory sac differentiated or not:
(0) not differentiated; (1) differentiated (Fig. 1B); (2) not applicable because dart sac absent.

Character 25: Position where the accessory sac is inserted on dart sac:
(0) accessory sac inserted on the bottom of dart sac; (1) accessory sac on the upper side of dart sac (Fig. 18B); (2) not applicable because dart sac absent.

Remarks: The accessory sac is usually situated on the bottom of dart sac, except in *Acusta*, where it is situated at/near the top of dart sac (Fig. 18B, compared to its normal position, e.g., that shown in Fig. 9A). The abnormal position of accessory sac can be observed in all anatomically known

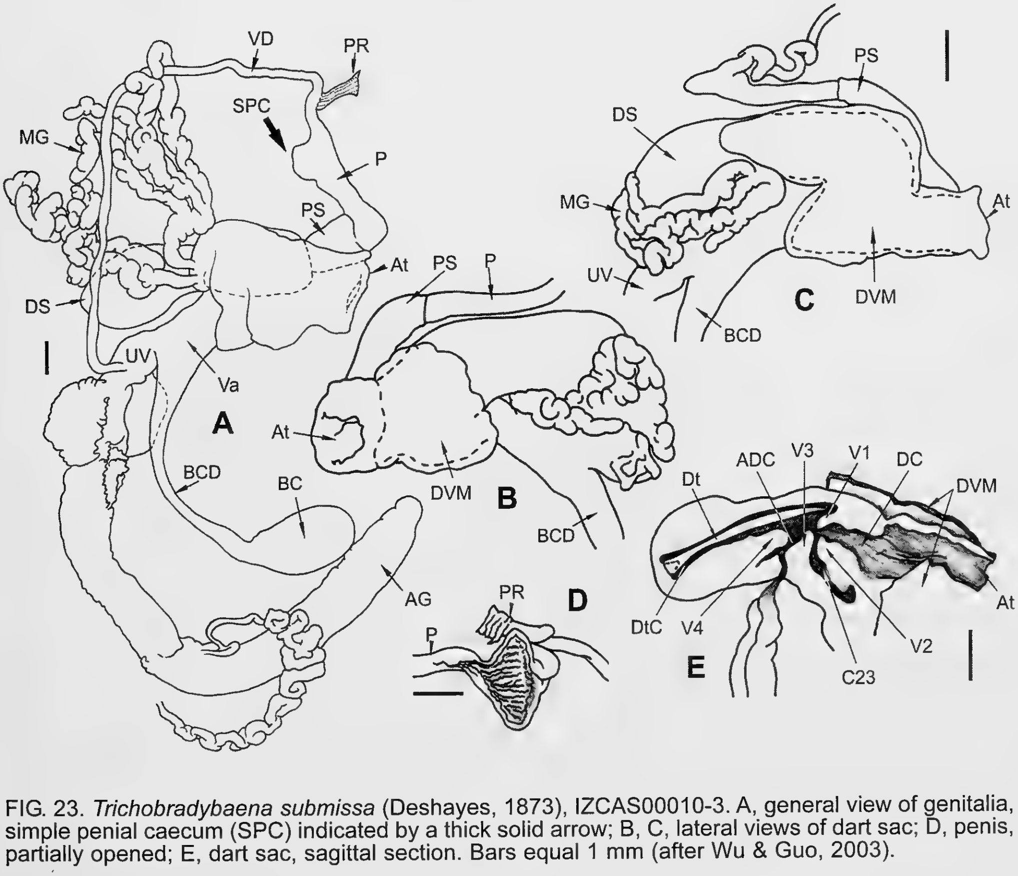

FIG. 23. *Trichobradybaena submissa* (Deshayes, 1873), IZCAS00010-3. A, general view of genitalia, simple penial caecum (SPC) indicated by a thick solid arrow; B, C, lateral views of dart sac; D, penis, partially opened; E, dart sac, sagittal section. Bars equal 1 mm (after Wu & Guo, 2003).

Acusta species and is preliminarily considered as the inverse of accessory sac in position (Wu, unpublished paper on *Acusta*).

Character 26: Presence of sacs inserted on vagina oppsite to dart sac:
(0) absent; (1) present (Fig. 6A, D, indicated by thick solid arrows); (2) not applicable because dart sac absent.

Character 27: Relation of the mantle to the shell.
(0) shell is not partially enclosed by mantle; (1) the mantle partially enclosing shell (observed in *Pfeifferia micans*, SMF323620).

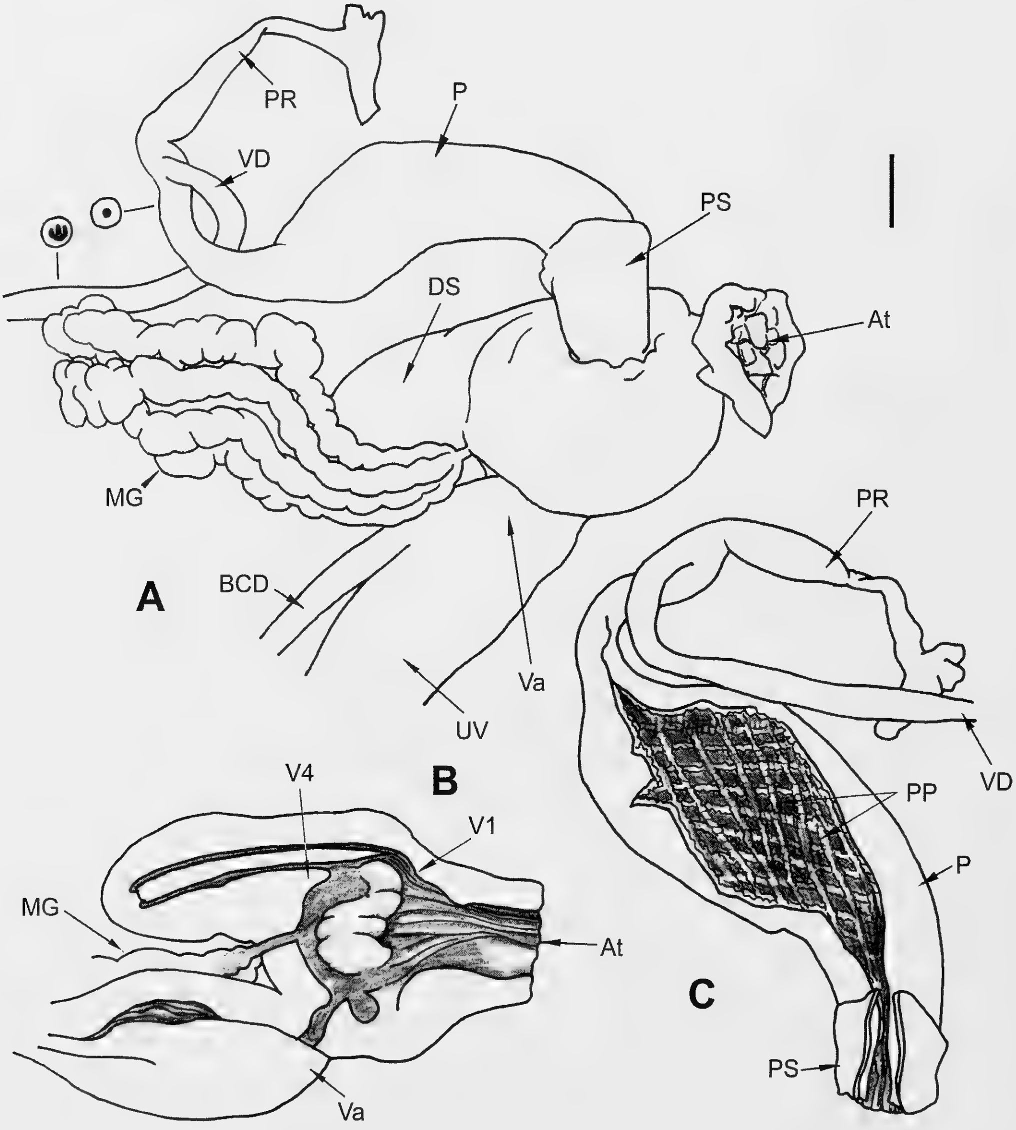

FIG. 24. *Pseudiberus* (*Platypetasus*) *chentingensis* Yen, 1935, IZCAS00163. A, lateral view of terminal genitalia, with cross-sections of epiphallus and vas deferens; B, dart sac, sagittal section; C, penial complex, with penis opened. Bar equals 1 mm.

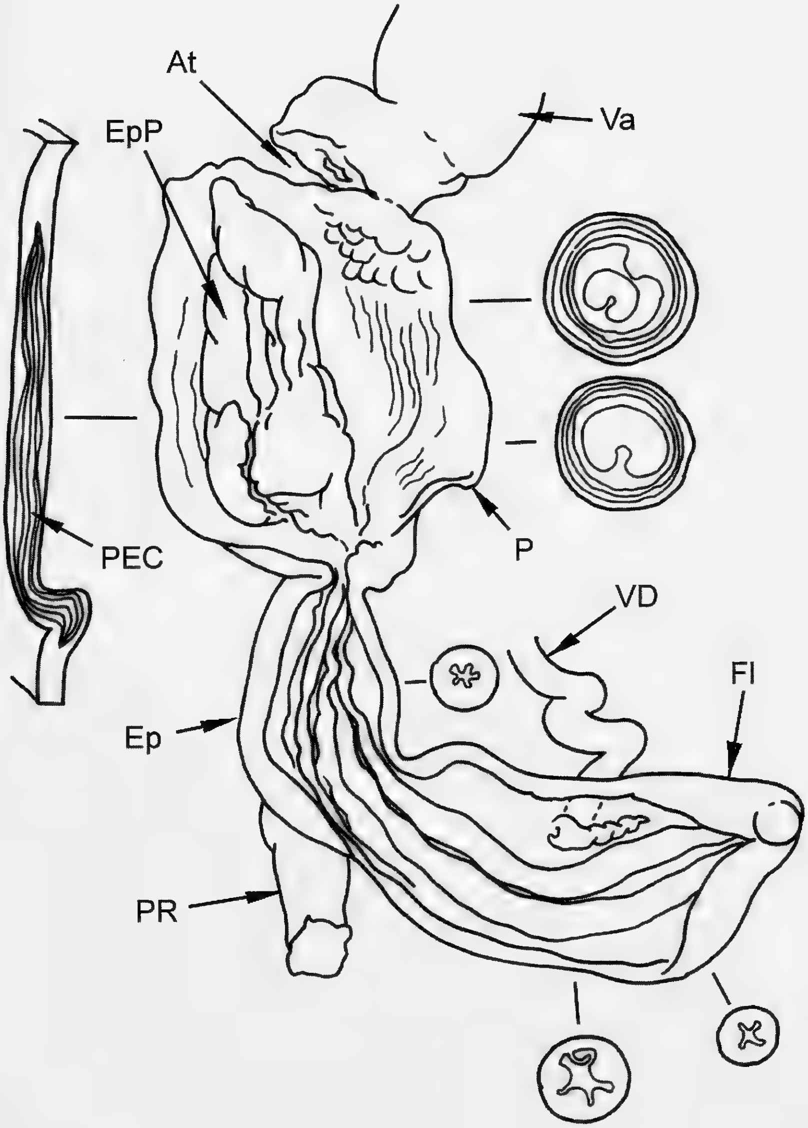

FIG. 25. *Camaena platyodon* (L. Pfeiffer, 1846), IZCAS00833. Male section of terminal gentalia, left, showing saggital section of penial wall; right, showing cross-sections of penis, epiphallus and flagellum.

Cladistic Analysis

The data matrix (Table 1) was submitted to HENNIG86 and Winclada. All the observed apomorphies were included among the characters because they are useful for the characterization of certain terminals, although they are not informative for the construction of the phylogenies. The removal of apomorphies in the analysis will decrease the steps in constructing a cladogram, but will not influence its reliability. Two types of analyses were performed. In the first type of analysis, all characters were weighted equally. Data sets were calculated with an exact algorithm (implicit enumeration). Another type of analysis used the successive weighting function provided by the Hennig86 program, which is considered by Carpenter (1988) to be the best method for weighting characters and choosing among equally parsimonious cladograms. The first analysis produced 11 equally parsimonious trees (EPTs) with length of 96, consistency index (CI) 0.54, and retention index (RI) 0.67. Extended branch swapping was then applied to the initial tree using the branch-breaking (bb*) command, producing 3,502 bb trees. A strict consensus tree (SCT) (Fig. 26) was then summarized from these 3,502 trees with Winclada in order to find the most unambiguous monophylies.

In the second analysis, after two iterations of successive approximations weighting and branch-breaking, 87 trees were retained, each with length 274, CI = 0.73, RI = 0.87. The cladograms obtained by the first and the second type of analyses were then introduced to Winclada for rerooting and mapping the distribution of characters. Based on the trees resulting from the second type of analysis, the rooted SCT was produced using Winclada (Fig. 27).

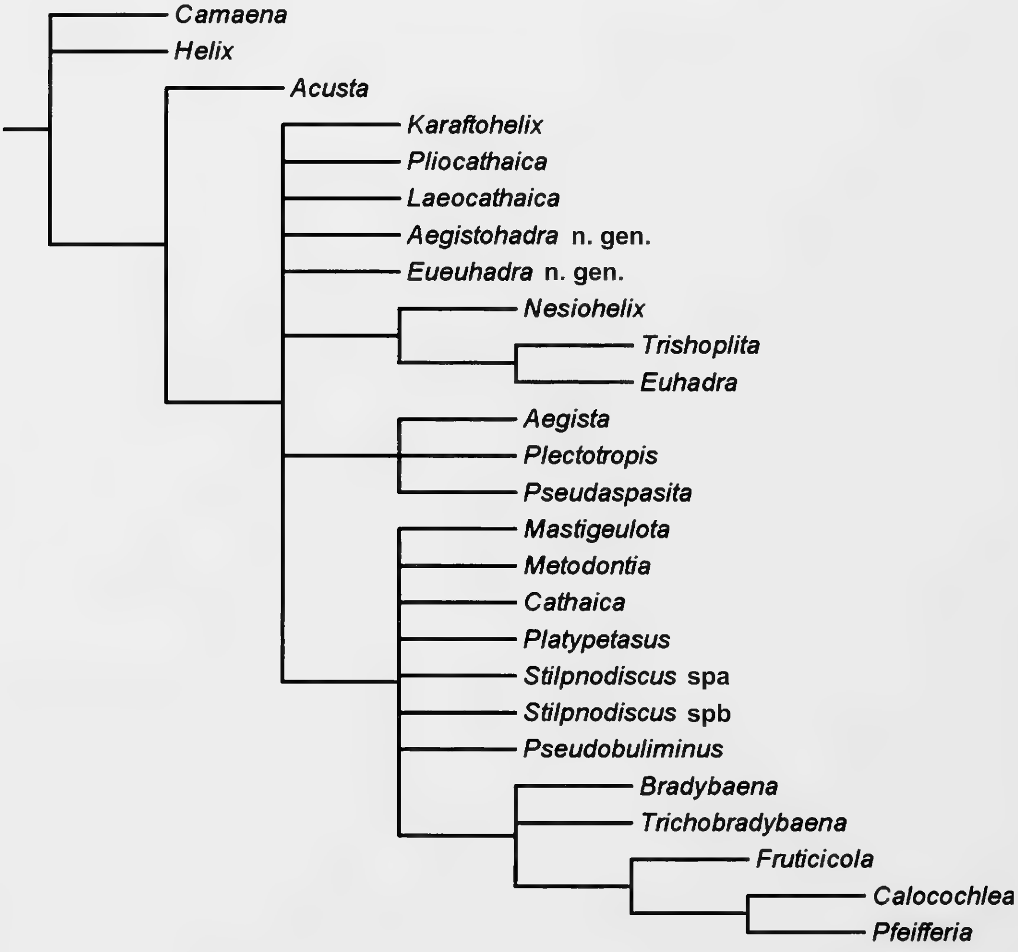

FIG. 26. Rooted SCT resulted from 3,502 EPTs (L = 96, CI = 54, RI = 67) based on equally weighted characters.

In the 3,502 EPTs constructed based on the equally weighted characters, 51 trees were found to be exactly equal respectively, in topology, to those obtained by philosophy of successive approximations weighting. In other words, 51 out of 87 trees based on weighted characters had the exact topology with the cladograms from the first analysis. When the rooted SCT (Fig. 27) was summarized from the 87 trees from the second analysis, only

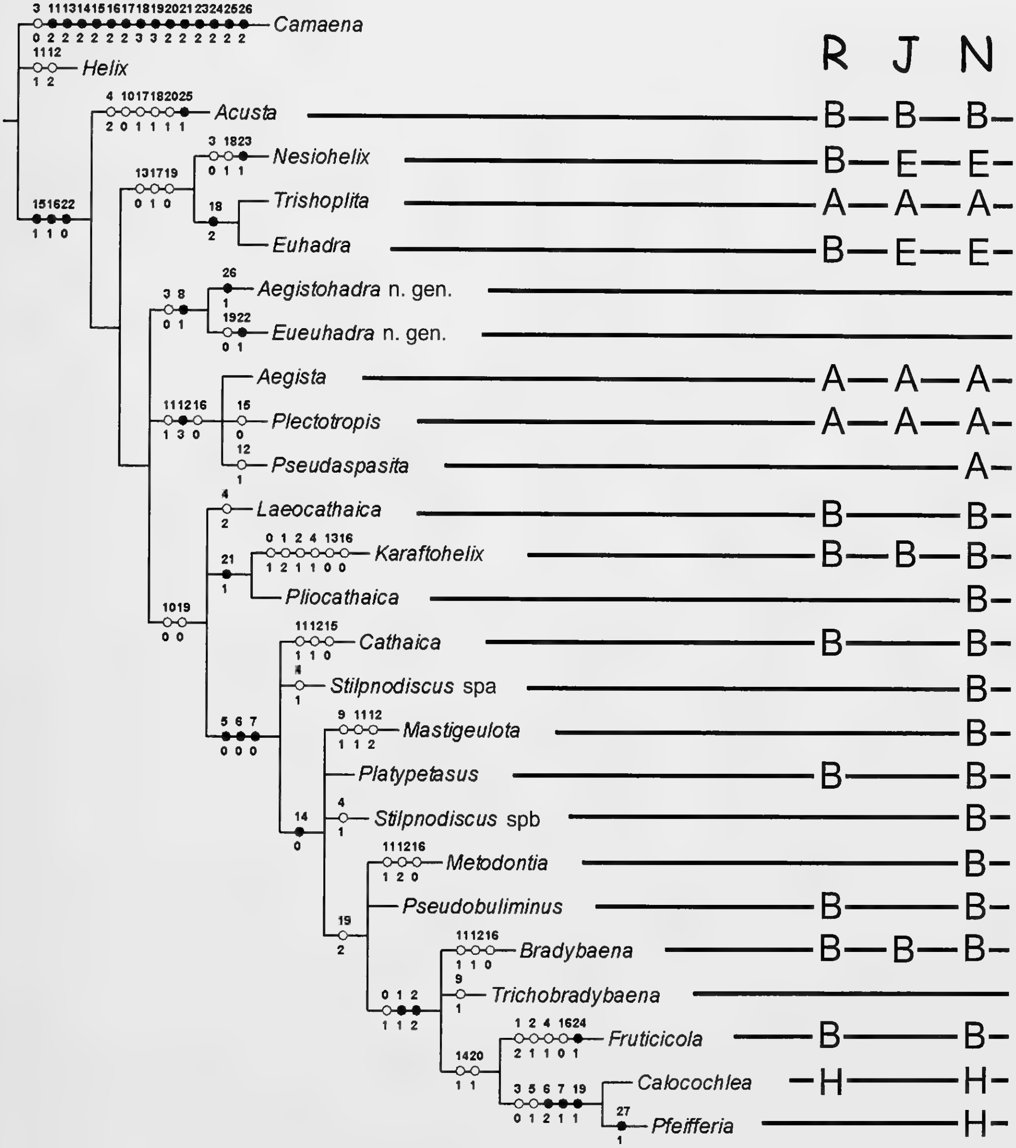

FIG. 27. Left: Rooted SCT resulted from 87 EPTs (L = 274, CI = 73, RI = 87) based on weighted characters, showing the distribution of character states. Solid circle – nonhomoplasious change; empty circle – homoplasious change. Right: Showing suprageneric classification by different authors: A – Aegistinae/Aegistini, B – Bradybaeninae/Bradybaenini, E – Euhadrinae/Euhadrini; H – Helicostylidae/Helicostylinae; R – Russian authors, J – Japanese authors, N – Nordsieck (Nordsieck, 2002).

one node collapsed, so this rooted SCT was thought to be informative and proper for being used both to interpret the present bradybaenid phylogeny and to indicate the reliability of the monophyletic groups.

As shown in the rooted SCT obtained by using the second type of analysis (Fig. 27), the ingroup was well defined by three nonhomoplasious synapomorphies characters 15(1), 16(1), and 22(0) (Fig. 27). Eight clearly distinguished monophylies supported by nonhomoplasious synapomorphy/synapomorphies are as follows:

(a) The clade (*Trishoplita*, *Euhadra*), was supported by character state 18(2). The monophyly of this clade was also confirmed by the SCT;

(b) The clade composed of *Aegistohadra* and *Eueuhadra*, supported by character state 8(1);

(c) The monophyly (*Aegista*, *Plectotropis*, *Pseudaspasita*), supported by character state 12(3). The monophyly of this clade was also confirmed by the SCT;

(d) The clade composed of *Karaftohelix* and *Pliocathaica*, supported by synapomorphic character state 21(1);

(e) The clade composed of *Cathaica*, *Stilpnodiscus*, *Mastigeulota*, *Platypetasus*, *Metodontia*, *Pseudobuliminus*, *Bradybaena*, *Trichobradybaena*, *Fruticicola*, *Calocochlea*, and *Pfeifferia*, supported by synapomorphic character states 5(0), 6(0) and 7(0);

(f) The clade embedded in (e), *Mastigeulota*, *Platypetasus*, *Stilpnodiscus* spb, *Metodontia*, *Pseudobuliminus*, *Bradybaena*, *Trichobradybaena*, *Fruticicola*, *Calocochlea*, and *Pfeifferia*, supported by synapomorphic character state 14(0). The monophyly of this clade was also confirmed by the SCT;

(g) The clade composed by *Bradybaena*, *Trichobradybaena*, *Fruticicola*, *Calocochlea*, and *Pfeifferia*, supported by synapomorphic character states 1(1) and 2(2). The monophyly of this clade was also confirmed by the SCT;

(h) The clade *Calocochlea* and *Pfeifferia*, supported by synapomorphic character states 6(2), 7(1), and 19(1). The monophyly of this clade was also confirmed by the SCT.

Based on the characters extracted from terminal genitalia, only part of the examined bradybaenid genera could be characterized by their autapomorphies. The terminal taxa *Trishoplita*, *Euhadra*, *Aegista*, *Pliocathaica*, *Calocochlea*, *Pseudobuliminus*, and *Platypetasus* had the opposite situation, that is, considering the anatomy of terminal genitalia, they were not characterized by derived characters. As indicated in Figure 27, they seemed to be defined by the "loss of character state(s)" rather than autapomorphies that could be directly observed.

DISCUSSION

The proposed phylogeny of bradybaenid genera has almost no similarity with the previous systems reviewed by Nordsieck (2002). Previously, knowledge of bradybaenid systematics came from the shell and very few genital features, and resulted from methodologically subjective analyses. The present cladograms, with too many branches, are not strongly supported, indicating that this is a preliminary result, providing a testable hypothesis of realtionships among bradybaenid genera. The hypothesis reflected by the cladogram in Figure 27 is preferred, because it represents the best testable systematic hypothesis explaining the present data set.

While the hypothesis presented is limited and requires the addition of data from many unstudied taxa, focus on some monophyletic branches with relatively strong support shows convincing results. The monophyletic clade of *Calocochlea* and *Pfeifferia*, representatives of the Helicostylinae Ihering, 1909, is well nested in the ingroup, suggesting that Helicostylinae are a bradybaenid group rather than a separate family (Helicostylidae *sensu* Schileyko, 1991). In the definition of the family Helicostylidae *sensu* Schileyko (Schileyko, 1991: 221), "the flagellum is variously developed but is always present" is a dubious character, because the present work shows that both *Pfeifferia micans* (type species of *Pfeifferia*) and *Calocochlea coccomelos* have no flagellum (Figs. 8, 9).

The present phylogeny, by artificially excluding helicostyline groups, is more or less compatible with the tripartite plan of bradybaenid genera, that is, tripartitite classification of (1) modified Aegistini (= subfamily Aegistinae *sensu* Kuroda & Habe, 1949, listed as a tribe by Nordsieck, 2002; partial Aegistinae *sensu* Schileyko, 1991), (2) Euhadrini (= Euhadrinae Minato, 1988, listed as a tribe by Nordsieck, 2002: including both *Nesiohelix* and *Euhadra*), and (3) Bradybaenini (= Bradybaeninae *sensu* Kuroda & Habe, 1949, listed as a tribe by Nordsieck, 2002) (Fig. 27). The Aegistini was distinguished from Bradybaenini by the presence of the flagellum. The present phylogenetic hypothesis suggests the flagellum has been at least convergently lost in Bradybaenidae twice (Fig. 27). Accordingly, this character should not be employed as the proper character defining Aegistinae as used in the original designation (Kuroda & Habe, 1949). The present hypothesis shows the reliability for the monophyly of (*Trishoplita*, *Euhadra*), which are distributed in both Aegistini (including genus *Tishoplita*: Kuroda & Habe, 1949; Minato, 1988; Schileyko, 1991; Nordsieck, 2002) and Euhadrini. Therefore, Aegistini should be condisered a paraphyletic group as indicated by the evidence that *Trishoplita* is embedded in the clade of Euhadrini.

As clearly indicated by the all ETPs (3,502 ETPs, not figured) from the first analysis and cladogramed based on the weighted characters (in all 87 ETPs, not figured), *Acusta* occurred most basally in the cladograms. Also indicated by the rooted SCTs (Figs. 26, 27), *Acusta*, which was placed in the Bradybaenini (= Bradybaeninae *sensu* Russian and Japanese authors), was confirmed as the sister group to all the remaining bradybaenids examinated. Thus, the Bradybaeninae is a paraphyletic group, and *Acusta* should not be placed in Bradybaenini (*sensu* Nordsieck, 2002). In summary, the result obtained demonstrates the Bradybaenini (*sensu* Nordsieck, 2002) is not monophyletic.

Cathaica was divided into several subgenera by Andreae (1911) based on shell characters. This study examined two of them, *Cathaica* (*s. str.*) and *Cathaica* (*Pliocathaica*). The results here show that *Cathaica* (*s. str.*) has a much closer relationship to the terminals in Clade (e), than to *Pliocathaica*, which is closest to *Karaftohelix* (Fig. 27). Accordingly, subgroups of *Cathaica* may be polyphyletic.

Some characters used by other authors are thought to be unreliable after careful dissections and thus are omitted from the present study. The widening of the basal bursa copulatrix duct, which was used by Schileyko (1991) as a diagnostic character of Bradybaenidae *sensu* Schileyko, is not included in the present data set, because this part varies in thickness according to physiological state, for example in *Aegista accresens* (Heude, 1882), as observed by the author. Some characters once used to describe the genitalia are ambiguous and thus should be avoid being used. For example, the development status of the accessory sac, which is an autapomorphy in the diagnostic definition for Helicostylidae (*sensu* Schileyko, 1991) as "an accessory sac is weakly developed or lacking", seems not to be so definite and consequently is less informative or misleading. In the Bradybaeninae (*sensu* Nordsieck, 2002), the accessory sac shows a variety of development states, such as size range, differentiation of the internal pilasters, and occurrence of the mucous glands entering papilla. Therefore, the accessory sac comprises a series of characters instead of a character with several character states. In Helicostylinae (= Helicostylidae *sensu* Schileyko, 1991), the genera *Calocochlea* and *Pfeifferia* (Figs. 8B, 9B) have an accessory sac with similar structure as those seen in the bradybaenine, for example, in *Trichobradybaena* (Fig. 23E) and in *Pliocathaica* (Fig. 12D). This suggests some characters, such as seen in the non-homoplasious characters (both synapomorphies and autapomorphies) in this study, should be given special attention as to whether they are shared by or transformed into certain states in any other bradybaenid genus not covered in this work. Careful consideration of this problem will enhance the reliability of the phylogeny obtained.

Cuezzo (1998) points out that there are three different problems seen in the published literature of the Xanthonychidae (= Helminthoglyptidae). I see the same problems in the current the study of the Bradybaenidae. Virtually in all the published literature, the systematics of Bradybaenidae is established on "arbitrary narrative character transformations". Any effort to make a predictive classification of the Bradybaenidae (or any other group), as Nordsieck (2002) suggests, should be based on testable hypotheses, and after as many species as possible are examined. The present work does not aim to provide a definitive classification of the Bradybaenidae, as many genera and and many other important characters, for example, anatomical (besides terminal genitalia), molecular, and chromosomal, are not included in the data set. However, it does suggest that the phylogeny of the Bradybaenidae is complex and considerable further work on the systematics for this group is needed.

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APPENDIX I: Taxa studied

Acusta ravida (Benson, 1842), type species of the genus: IZCAS00944, Jiangning County, Jiangsu Province, coll. unknown. Four adult specimens (two dissected) and two young specimens.

Aegista (*Aegista*) *accrescens* (Heude, 1882): IZCAS00027, Xiushan County (28.4°N, 108.9°E), Sichuan Province, 1986-VII-21, coll. De-Niu Chen & Jia-Xiang Gao. Six adult specimens (three dissected).

Aegista (*Plectotropis*) *gerlachi* (E. Martens, 1881): IZCAS00044, Guangdong Province, other collection data unknown. Nine adult (two dissected) and three young specimens.

Bradybaena similaris (Rang, 1831) (not A. Férussac 1821; see Nordsieck, 2002), type species of the genus: IZCAS01072, Fuzhou, Fujian Province, 1975-X-16, coll. unknown. Forty adult (two dissected) and 17 young specimens.

Cathaica (*Cathaica*) *fasciola* (Draparnaud, 1801), type species of the genus: IZCAS01074, Pi County, Xuzhou, Jiangsu Province, 2000-V-2, coll. Qi-Lian Qin. Numerous specimens (three dissected).

Cathaica (*Pliocathaica*) *gansuica* (Möllendorff, 1899): IZCAS00210, Dachuanxiang, Zhouqu County, Gansu Province, 1200 m alt., 1998-V-9, coll. De-niu Chen & Guo-Qing Zhang. 166 specimens (two dissected).

Fruticicola fruticum (O. F. Müller, 1774), type species of the genus: IZCAS01009, limestone quarry near Klodzko, Wapniarka Mt., Lower Silesia, Poland, 1999-VI-26, coll. Min Wu & Andrzej Wiktor. Seven adult specimens (two dissected) and one young specimen.

Karaftohelix weyrichii (Schrenck, 1867): IZCAS01080, near Yushno-Sakhalinsk City, Sakhalin Island, Russia, 2001-VII-29, coll. Larisa A. Prozorova. One adult (dissected) and four young specimens.

Mastigeulota kiangsinensis (E. Martens, 1875), type species of the genus: IZCAS00003, Huangnipo, Badong County (31.0°N, 110.3°E), Hubei Province, coll. De-Niu Chen, 1984-VI-29. Six adult (two dissected) and one young specimen.

Metodontia yantaiensis (Crosse & Debeaux, 1863): IZCAS00131, Quyang County, Hubei Province, coll. Min Wu. Fifteen adult specimens (two dissected) and 19 young specimens.

Pseudaspasita binodata (Möllendorff, 1886), type species of the genus: IZCAS01075, Beiquan Park, Beipei, Chongqin, 1964-V-12. Twenty-seven adults (two dissected) and 12 young specimens.

Pseudiberus (*Platypetasus*) *chentingensis* Yen, 1935: IZCAS00163, Jiaozuo, Henan Province, 1999-VII-22, coll. Guang-Wen Chen. Six adults (two dissected) and 17 young specimens.

Stilpnodiscus moellendorffi Wu, 2001: IZCAS00081, type specimens, Shanggou, Shawanxiang, Dangchang County, Gansu Province, 1998-VI-6, coll. De-Niu Chen & Guo-Qing Zhang.

Stilpnodiscus entochilus Möllendorff, 1899: IZCAS00076, Guoyuanxiang, Nanping County (now Jiuzhaigou County) (33.2°N, 104.2°E), Sichuan Province, 1000 m alt., coll. De-Niu Chen & Guo-Qing Zhang, 1998-V-18. 25 adult (four dissected) and 17 young specimens.

Laeocathaica (*Laeocathaica*) *subsimilis* (Deshayes, 1873): IZCAS00006, Xingjianxiang, Nanchong (30.8°N, 106.1°E), Sichuan Province, coll. unknown, 1964-V-20. Eleven adult specimens (four dissected).

Pseudobuliminus (*Pseudobuliminus*) *piligerus* (Möllendorff, 1899): IZCAS00085, Anchanghexiang, Wen County (33.0°N, 104.6°E), Gansu Province, 1200 alt., coll. De-Niu Chen & Guo-Qing Zhang, 1998-V-19. 287 specimens (three dissected).

Trishoplita dacostae Gude, 1900: IZCAS00174, Kobayashi Hiyazaki, Japan, coll. unknown, 1998-X. Six adult (three dissected) and six young specimens.

Euhadra herklotsi (E. Martens, 1861): IZCAS01076, Ishigakijima, 1931-VII, coll. Shikanu (?). Two adult specimens (one dissected).

Nesiohelix swinhoei (L. Pfeiffer, 1865), type species of the genus (in Richardson, 1983, the type species mistakenly given as *Nesiohelix caspari*; Kuroda & Emura, 1943): IZCAS00055, Yilan County (24.7°N, 121.7°E), Taiwan Province, coll. unknown, 1896-X. Two adult specimens dissected.

Aegistohadra delavayana (Heude 1885) n. gen. and comb.: IZCAS00132, Zhibenshan Mt., Baoshan (26.3°N, 104.4°E), Yunnan Province, coll. De-Niu Chen, 1981-VI-23. Four adult specimens (two dissected) and three young specimens. Paratypes, IZCAS-type-2902-1 and IZCAS-type-2902-2, Fa Kouan Tchen, coll. Unknown.

Aegistohadra seraphinica (Heude, 1889): paratypes, IZCAS-type-3071-1 and IZCAS-type-3071-2, Si-lin, Guangxi, coll. Unknown.

Eueuhadra gonggashanensis, n. gen. & sp., type species of the genus: IZCAS00067, west slope of Gonggashan Mt., Kangding County (30.0°N, 101.9°E), Sichuan Province; coll. De-Niu Chen & Jia-Xiang Gao, 1982-IX-9. Fifteen adult (four dissected) and seven young specimens; IZCAS01061, border of Jiuzaigou County and Songpan County (33°02’14.4"N, 103°42’32.1"E), Sichuan Province, coll. Min Wu. One adult specimen dissected.

Trichobradybaena submissa (Deshayes, 1873), type species of the genus: IZCAS00010, Hanzhong, Shaanxi Province, 1992-IV-15, coll. De-Niu Chen. Numerous specimens (three dissected).

Helix pomatia (Linné, 1758) (Helicidae), type species of the genus: IZCAS00188, limestone quarry near Klodzko, Wapniarka Mt., Lower Silesia, Poland, 1999-VI-26, coll. Min Wu & Andrzej Wiktor. One adult specimen dissected.

Calocochlea coccomelos (Sowerby, 1840): SMF323619, Philippines: Sibuyan, ex Moellendorff. One specimen dissected.

Pfeifferia micans Pfeiffer, 1845, type species of the genus: SMF323620, Philippinen: Cagayan, Pamplona, O. v. Moellendorff. One adult specimen dissected.

Camaena platyodon (L. Pfeiffer, 1846) (Camaenidae): IZCAS00833, Hainan, other collection data lacking. Eleven adult (three dissected) and one young specimens.

APPENDIX II: New taxa

Aegistohadra, n. gen.

Type species: *Nanina delavayana* Heude, 1885: 102, pl. xxvi, fig. 8.

Aegistohadra delavayana (Heude, 1885), n. gen. & comb.

(Figs. 6, 28–31; Table 2)

Material

Four adults (IZCAS00132-1–4) of which two are full grown but broken and three young shells were examined, Zhibenshan Mt., Baoshan (26.3°N, 104.4°E) (“Yunlong County” in original label is a printing error), Yunnan Province; coll. De-Niu Chen, 1981-VI-23.

TABLE 2. Conchological measurements and counts of specimens IZCAS00132, *Aegistohadra delavayana* n. gen. & comb.

	Shell height	Shell width	No. whorls	No. protoconch whorls	Apertural length	Apertural width	Umbilicus diameter	Height/ width	Umbilicus diameter/ shell width
IZCAS00132-1	16.39	29.10	$4^{7}/_{8}$	$1^{3}/_{8}$	12.81	12.87	4.73	0.56	0.16
IZCAS00132-2	20.98	-	$5^{3}/_{8}$	$1^{3}/_{8}$	15.41	15.96	-	-	-
IZCAS00132-3	20.13	32.14	$5^{3}/_{8}$	$1^{3}/_{8}$	-	-	6.37	0.63	0.20
IZCAS00132-4	21.27	-	$5^{1}/_{4}$	$1^{3}/_{8}$	17.03	16.58	6.32	-	-

Two paratype specimens of *Nanina delavayana* H., IZCAS-type-2902-1 and IZCAS-type-2902-2 (Fig. 32), Fa Kouan Tchen, coll. unknown. Two paratype specimens of *Helix seraphinica* Heude, 1889 (Fig. 33).

Etymology

The genus name is derived from the names of two bradybaenid genera *Aegista* and *Euhadra.*

Diagnosis

Female part of genitalia with sac-shaped structure on vagina opposite to dart sac.

Short Description

Shell strongly depressed, sinistral, thick and solid. Umbilicus broad. Protoconch with radial wrinkles. Penial sheath absent; penis with a penial caecum near penial retractor; epiphallus with a flagellum; penis-epiphallus chamber absent; accessory sac undivided; in dart apparatus polylayered structure absent; V1-V4 in the dart apparatus present; two sacs inserted on vagina opposite to dart sac.

Full Description

Shell sinistral, thin but solid. Apex distinct. Whorls convex. Suture strongly impressed. Umbilicus narrow to moderately wide. Columella oblique; columellar lip dilated, slightly covering umbilicus. Adult shell and young shell with smooth surface, spiral furrows irregularly and sparsely present, ribs absent; growth lines not accompanied by irregular thickenings, background microscopic ripples absent. Protoconch with radial wrinkles. Immature shells unkeeled and unangulated. Body whorl large, unkeeled, weakly descending in front, with convex bottom. Aperture rounded, oblique. Lip toothless, equally expanded, thin within. Peristome reflexed equally. Parietal callus indistinct. Shell dull, opaque; yellowish brown with two brown bands, one above and one beneath periphery, the lower sometimes not as distinct as the upper. Bottom of body whorl yellowish brown (Figs. 29, 30).

Animal uniformly gray. Jaw arcuate with 7–8 ribs dentating the concave margin, ribs contiguous, wide. In a paratype (IZCAS00132-2), radula with 169 rows of teeth, each with one

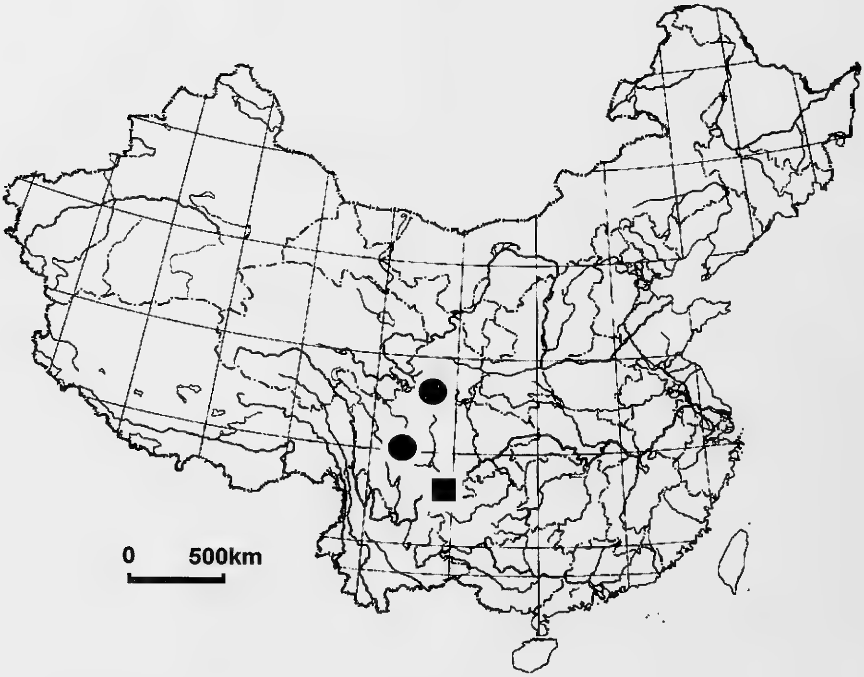

FIG. 28. Distribution map. Square: *Aegistohadra delavayana* n. gen. & comb.; dots: *Eueuhadra gonggashanensis* n. gen. & sp.

central tooth and 53 lateral teeth at each side; central tooth and lateral teeth L_1–L_{19} unicuspid; L_{20}–L_{53} each with an endocone and an ectocone (Fig. 31E).

Genitalia: Penial sheath absent (Figs. 6A, 31A), except for some basal connective tissue present near atrium covering penis. Penis short, slender, with a finger-shaped penial caecum near penial retractor (Figs. 6A, 6C, 31A, 31B). Retractor simple, thin or thick, short or in moderate length. Epiphallus thick, short, with more or less protruding symmetrical epiphallic papilla (Figs. 6C, 31C). Penis-epiphallus chamber absent. Flagellum roundly blunt at end, with fairly smooth surface, thick, short (Figs. 6A, 6C, 31A, 31B); innerly folds not forming a C-shaped open tube towards flagellum or epiphallus (Figs. 6C). Pore of penial papilla located near the pore leading to penial caecum, mainly built by two pilasters derived from four thicker ones longitudinally arranged along penial inner wall (Figs. 6C, 31C). Dart sac developed, with an accessory sac below. Accessory sac large in size, slightly elongated (Figs. 6A, 6D, 31A). Dart sac containing one dart. Dart about 7.0 mm in length, almost straight, slightly expanding basally; cross section of dart throughout rounded or ovate at lower part, upper 1/4 with 2 opposite sharp ridges. (Fig. 31F). Inside dart sac, ADC sharing same entrance with DtC; V1–V4 present, V2 merged into a pilaster towards vagina; V1, V3 and V4 forming DtC; C23 present, but opened to vagina (Fig. 6D). Two sacs on vagina opposite dart apparatus, one with two highly ridged pilasters, and another just beneath the first one and with connective tissue inside, of unknown function (Figs. 6A, B & D); DVM absent. Mucous glands with two lobules, each as long as dart sac, stalks distinct, separated from dart sac and tied tightly to the trunk of vagina, inserting near base of dart sac (Fig. 31A). Lobules simply branched, distally sac-shaped. Bursa copulatrix slightly elongated,

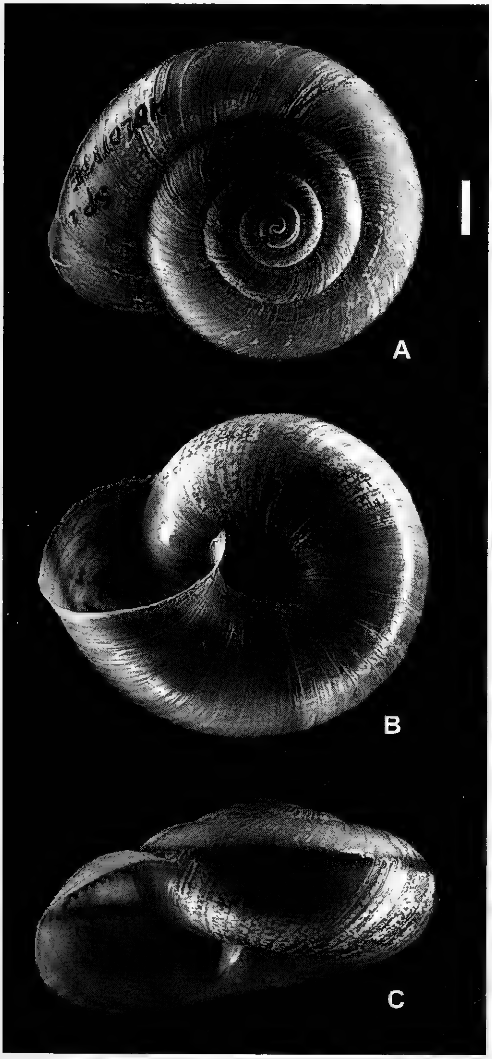

FIG. 29. *Aegistohadra delavayana* n. gen. & comb., shell near mature, IZCAS00132-1. A, apical view; B, basal view; C, apertural view. Bar equals 5 mm.

FIG. 30. *Aegistohadra delavayana* (Heude, 1885), n. gen. & comb., shell, IZCAS00132-3. A broken but adult shell, showing aperture structure. Bar equals 5 mm.

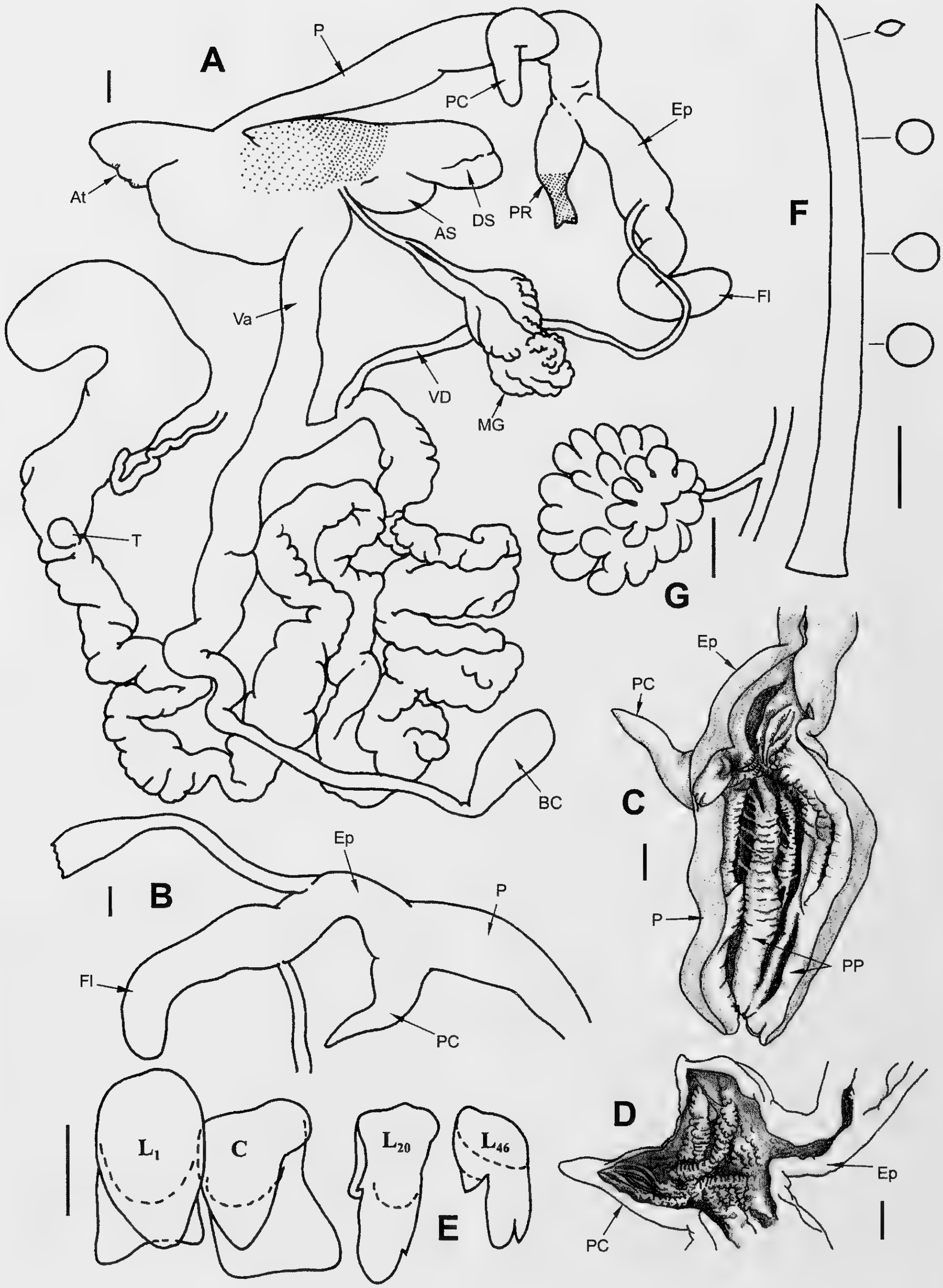

FIG. 31. *Aegistohadra delavayana* (Heude, 1885), n. gen. & comb., IZCAS00132-2. A, general view of genitalia; B, penial complex; C, penis and epiphallus, opened; D, penial caecum (PC), opened; E, teeth of radula, bar equals 25 μm; F, dart, with cross-sections; G, a leaf of ovotestis. A–D, F, G, bars equal 1 mm.

well differentiated from its duct (Fig. 31A). Bursa copulatrix duct moderately long, inserting low on vagina (Fig. 31A). Ovotestis palm-shaped, with single stalk (Fig. 31G). Holotype: dart sac 10.0 mm in length, 2.5 mm in width, ratio of width to length 0.3; mucous duct length 9.3 mm; vagina length 13.8 mm; bursa copulatrix duct 18.0 mm long, basal width 1.3 mm; transverse diameter (maj.) of bursa copulatrix 1.8 mm, sagittal diameter (maj.) of bursa copulatrix 3.5 mm; vas deferens length 16.3 mm; penis length 12.0 mm; flagellum length 5.8 mm; epiphallus 3.8 mm in length; penial retractor 3.8 mm long (Fig. 31G).

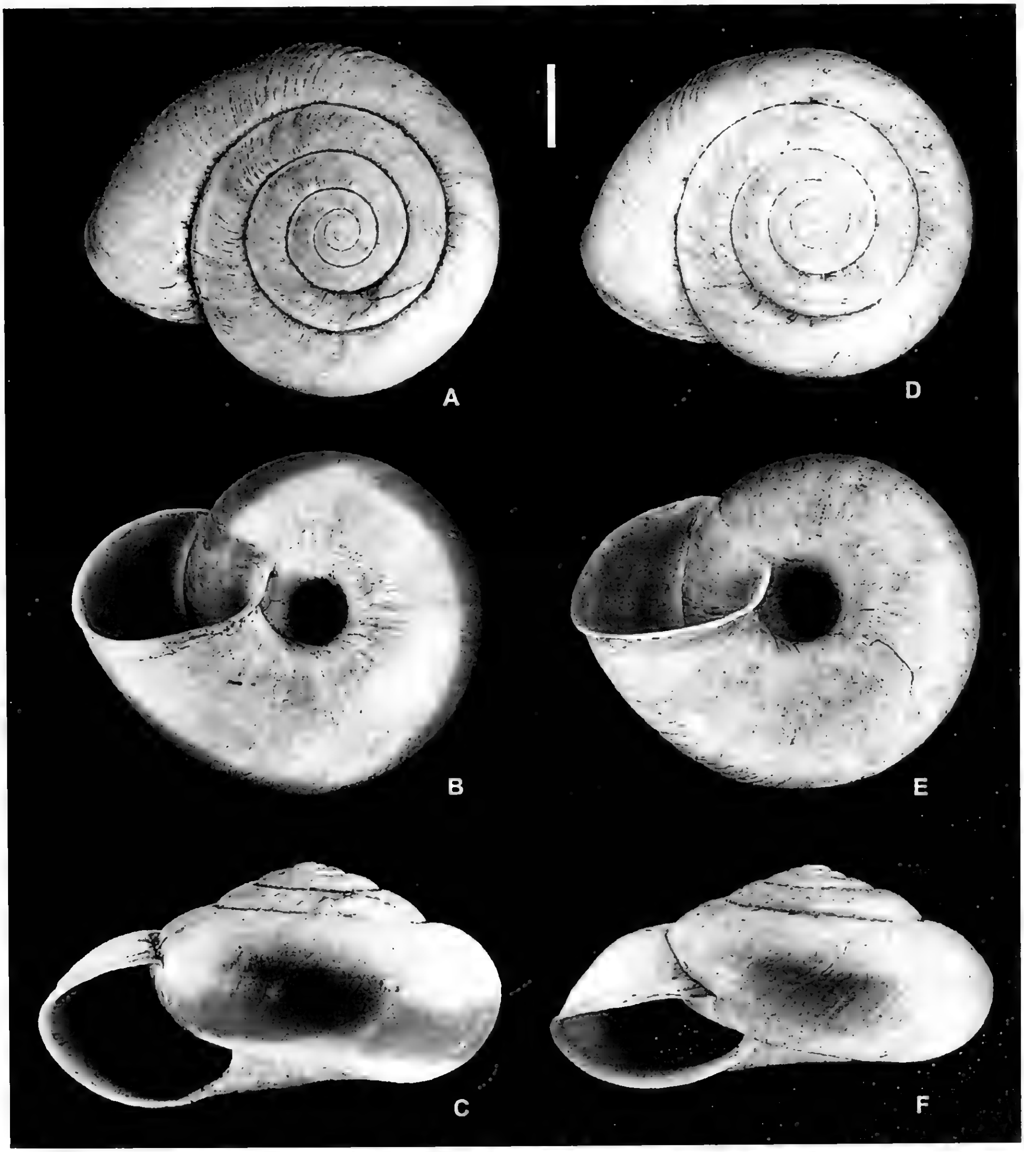

FIG. 32. *Aegistohadra delavayana* (Heude, 1885), n. gen. & comb., shell, paratypes, A–C, IZCAS-type-2902-1; D–F, IZCAS-type-2902-2. Bar equals 10 mm.

Range

Southwestern China (Fig. 28).

Remarks

This species can be distinguished from all known bradybaenid species in that the female part of the genitalia has a sac-shaped structure on the vagina opposite to the dart sac. It also differs from all bradybaenids, except *Eueuhadra gonggashanensis*, n. gen. & sp., in having a pronounced penial caecum.

Based on shell features, although distinctly larger (diam. maj.: 55 mm; min.: 48 mm; alt.: 30 mm), it is possible that *Helix seraphinica* Heude, 1889, from Silin (as "Xilin" in today's spelling, Guangxi Province) should be placed in *Aegistohadra* because of their similar shell shape (Fig. 33), as suggested by H. Nordsieck

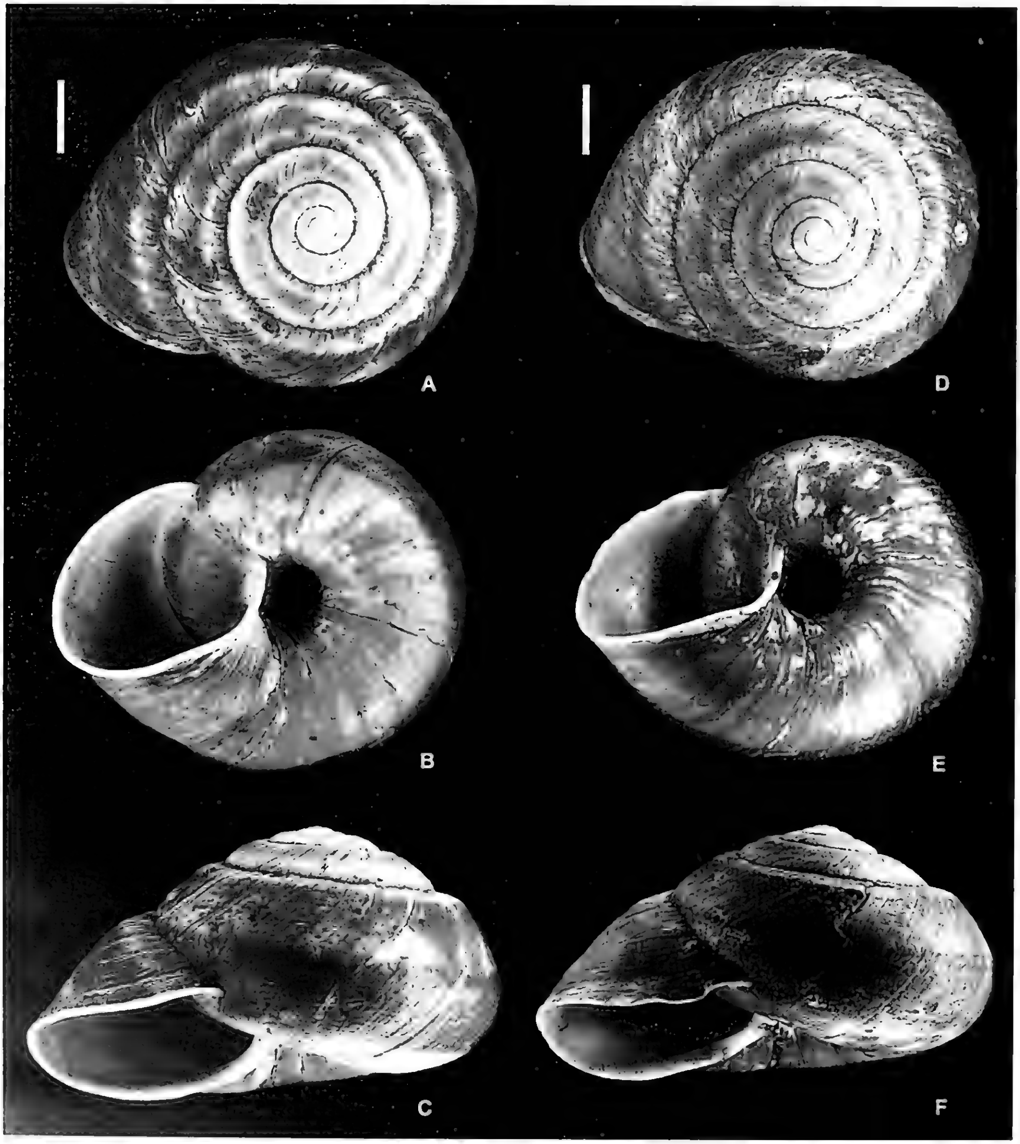

FIG. 33. *Helix seraphinica* Heude, 1889, shell, paratypes, A–C, IZCAS-type-3071-1; D–F, IZCAS-type-3071-2. Bars equal 5 mm.

(pers. comm.). However, *Helix seraphinica* we cannot be certain until its anatomy is known, considering the great morphological diversity shown in helicoid shells.

Eueuhadra n. gen.
Type species: ***Eueuhadra gonggashanensis***, n. sp.

Eueuhadra gonggashanensis, n. sp.
(Figs. 7, 28, 34–39; Table 3)

Material

Holotype (IZCAS00067-1), West slope of Gonggashan Mt., Kangding County (30.0°N, 101.9°E), Sichuan Province; coll. De-Niu Chen & Jia-Xiang Gao, 1982-IX-9. Paratypes 14 (IZCAS00067-2–15), the same data as holotype; seven young specimens (IZCAS00067-16–22) were also examined; paratype 1 (IZCAS01061), border of Jiuzaigou County and Songpan County (33°02'14.4"N, 103°42'32.1"E), Sichuan Province; 3311 m a. s. l.; coll. Min Wu, 2001-X-4.

Etymology

The genus name comes from "eu-" (real) and the bradybaenid genus *Euhadra.* The species is named after the holotype locality: Gonggashan Mountains.

Diagnosis

A simple penis-epiphallus chamber present; dart sac with multiple mucous branches.

Short Description

Shell depressed, dextral, thin but solid. Umbilicus very narrow and more or less covered by columellar margin of the peristome. Protoconch shell granulose.

Penial sheath absent; penis distally with an outstanding tube-shaped penial caecum; epiphallus with a flagellum; a simple penis-epiphallus chamber present; dart sac with a distinct and relatively large accessory sac on the end on which a bundle of mucous glands is inserted per one common duct; accessory sac undivided; in dart apparatus, polylayered structure absent, V1–V4 present.

Range

W China.

Full Description

Shell dextral, depressed, thin but solid. Apex distinct. Whorls convex. Suture impressed. Umbilicus very narrow and more or less covered by columellar margin of peristome. Columella very oblique. Spiral furrows absent, without ribs, growth lines not accompanied by irregular thickenings, microscopic ripples absent. Protoconch finely granulose, granulation regularly arranged. Teleoconch finely and unevenly granulose on upper spire. Immature shells bluntly angulated. Whorls increasing rapidly; body whorl fairly large, unkeeled,

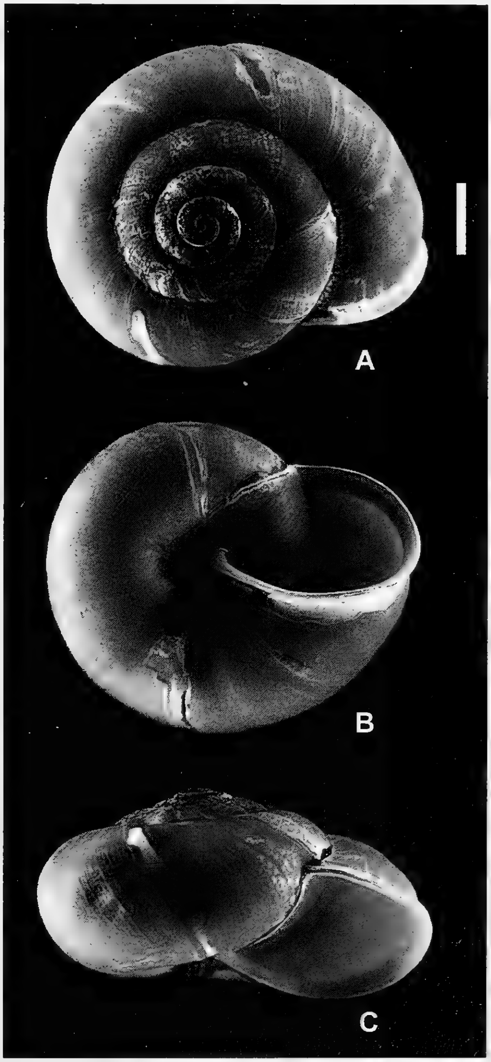

FIG. 34. *Eueuhadra gonggashanensis,* n. gen. & sp., shell, IZCAS00067-1, Holotype, A, apical view; B, basal view; C, apertural view. Bar equals 5 mm.

TABLE 3. Conchological measurements and counts of holotype and paratypes of *Eueuhadra gonggashanensis*, n. gen. & n. sp.

	Shell height	Shell width	No. whorls	No. protoconch whorls	Apertural length	Apertural width	Umbilicus diameter	Height/ width	Umbilicus diameter/ shell width
					Holotype				
IZCAS00067-1	14.64	24.53	5	$1^{3}/_{4}$	12.46	11.57	1.03	0.60	0.04
					Paratypes				
IZCAS00067-2	13.10	23.14	$4^{7}/_{8}$	$1^{7}/_{8}$	11.67	11.06	0.98	0.57	0.04
IZCAS00067-3	11.91	22.90	$4^{3}/_{4}$	$1^{7}/_{8}$	11.69	10.52	1.26	0.52	0.06
IZCAS00067-4	14.08	24.96	$4^{7}/_{8}$	$1^{7}/_{8}$	13.07	11.01	1.56	0.56	0.06
IZCAS00067-5	12.87	23.28	$4^{7}/_{8}$	$1^{7}/_{8}$	11.64	10.80	0.72	0.55	0.03
IZCAS00067-6	12.13	22.20	$4^{3}/_{4}$	$1^{7}/_{8}$	11.17	9.80	0.94	0.55	0.04
IZCAS00067-7	12.34	23.49	$4^{3}/_{4}$	$1^{7}/_{8}$	11.66	10.80	1.20	0.53	0.05
IZCAS00067-8	14.58	26.21	$4^{7}/_{8}$	$1^{3}/_{4}$	13.43	11.63	1.29	0.56	0.05
IZCAS00067-9	12.39	22.82	$4^{7}/_{8}$	2	11.84	11.27	1.40	0.54	0.06
IZCAS00067-10	12.24	22.65	$4^{3}/_{4}$	$1^{7}/_{8}$	11.44	10.67	0.82	0.54	0.04
IZCAS00067-11	11.49	20.48	$4^{3}/_{4}$	2	10.15	9.63	0.93	0.56	0.04
IZCAS00067-12	13.75	23.67	$4^{7}/_{8}$	2	12.11	11.10	1.15	0.58	0.05
IZCAS00067-13	12.45	22.78	5	2	11.44	10.18	0.84	0.55	0.04
IZCAS00067-14	11.79	21.96	$4^{3}/_{4}$	$1^{7}/_{8}$	10.85	10.10	0.94	0.54	0.04
IZCAS01061	11.05	18.66	$3^{7}/_{8}$	$1^{1}/_{4}$	9.01	9.79	0.59	0.59	0.03

slightly descended in front, with convex base. Aperture rather broadly lunate, more or less oblique. Lip toothless, uniformly thickened within, forming a ring-like thickening. Peristome thin, uniformly reflexed. Parietal callus distinct. Periostracum uniformly in greenish brown, bandless. Bottom of body whorl with same or lighter colour (Figs. 34, 35 & 39; Table 3).

Animal with numerous brown spots on the anterior half. Jaw arcuate with 10–12 ribs dentating the concave margin, ribs wide and almost contiguous. Radula of holotype with 133 rows of teeth, each with one central tooth and 44 lateral teeth on both sides; central tooth with 1 tiny cusp at each side; lateral teeth L_1–L_{17} each with an ectocone; L_{18}–L_{31} each with a tiny endocone and an ectocone; main cones and ectocones of L_{32}–L_{44} bicuspid respectively, two cusps of ectocone roundly blunt (Fig. 36D).

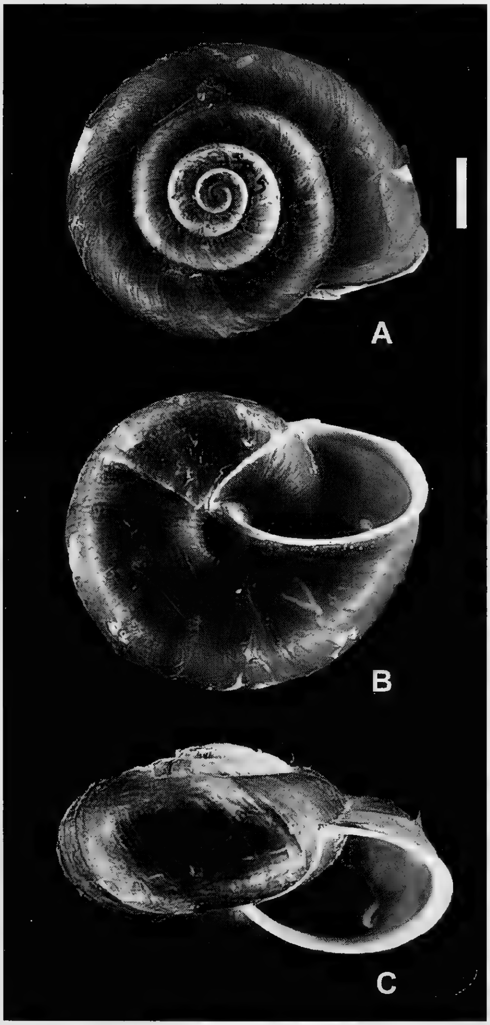

FIG. 35. *Eueuhadra gonggashanensis,* n. gen. & sp., shell, IZCAS00067-5, Paratype, a shell with periostracum on. A, apical view; B, basal view; C, apertural view. Bar equals 5 mm.

Genitalia: Penial sheath absent (Figs. 7A, 36A, 37A). Penis of moderate length, swollen, with a tube-like penial caecum (PC) near penial retractor. Penial retractor short. Epiphallus thick, short. Epiphallic papilla depressed, symmetrical. Penis internally with three thick penial pilasters and two thinner ones among them (Figs. 36B, 37C). Near to the pore leading to penial caecum, a papilla, built partially by above-mentioned pilasters present (Fig. 7B). Flagellum thick, short, smooth, abruptly tapering and forming a vermiform appendix (Fig. 36A). Penis-epiphallus chamber present, small, simple (Fig. 7E). Vas deferens inserted on flagellum, with inner folds forming a C-shaped open tube towards flagellum (Fig. 7C). Dart sac containing one dart. Dart approximately 2 mm, medially rounded, apically trapezoid in cross section (Fig. 37E, only seen from the spirit material of IZCAS01061; in all dissected specimens of IZCAS00067, the darts are completely eroded, because of having been first fixed in formalin before being preserved in alcohol). Mucous glands longer than dart sac, inserted at the end of accessory sac; with 11–13 (in two specimens of IZCAS00067) mucous lobules radially arranged, stalk of lobule indistinct; each lobule simply branched and consisting of slightly expanded vesicles, not expanded distally (Fig. 36A). Accessory sac developed, innerly simple except for some narrow pilasters; a bundle of mucous glands inserting on the end of AS, from a common entering tube, its inner entrance without papilla (Fig. 7D); ADC share the same entrance with DtC; V1–V4 present; V1, V2 and V4 forming DtC; C23 present and tiny, with entrance leading to ADC (Figure 7D). DVM absent. Polylayered structure (PLs) absent. Bursa copulatrix ovate, not well differentiated from bursa copulatrix duct (Fig. 36A). Bursa copulatrix duct of moderate length, wide, inserting high on vagina (Figs. 36A, 37A). Ovotestis palm-shaped, distinctly branched and two stalks closely arranged and having a common duct; in holotype, ovotestis embed-

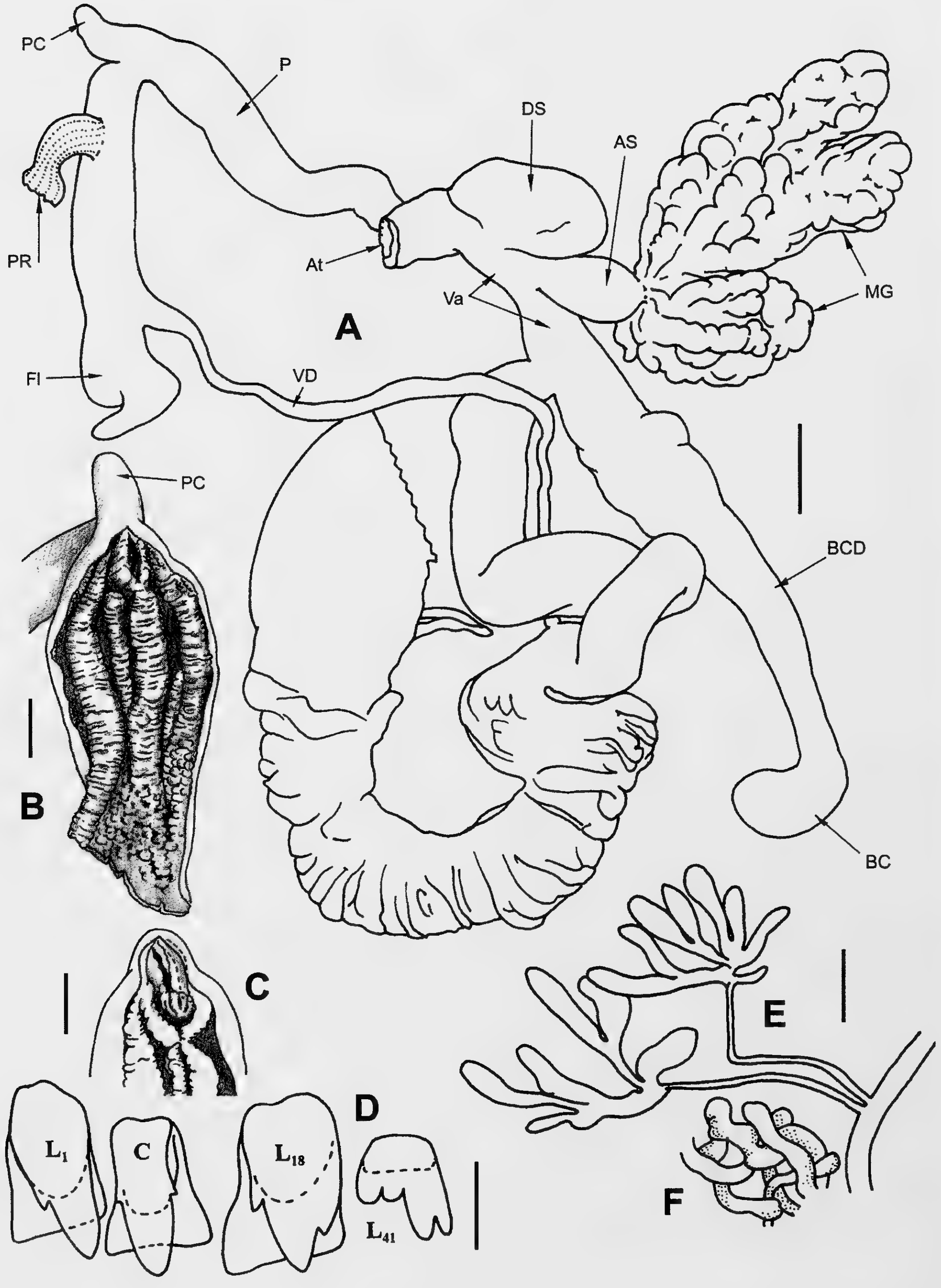

FIG. 36. *Eueuhadra gonggashanensis,* n. gen. & sp., IZCAS00067-1, Holotype, A, general view of genitalia, bar equals 2 mm; B, penis, opened; C, penial caecum, opened; D, teeth of radula, bar equals 25 μm; E, a leaf of ovotestis, bar equals 0.5 mm; F, ovotestis matrix, magnified. B, C, bars equal 1 mm.

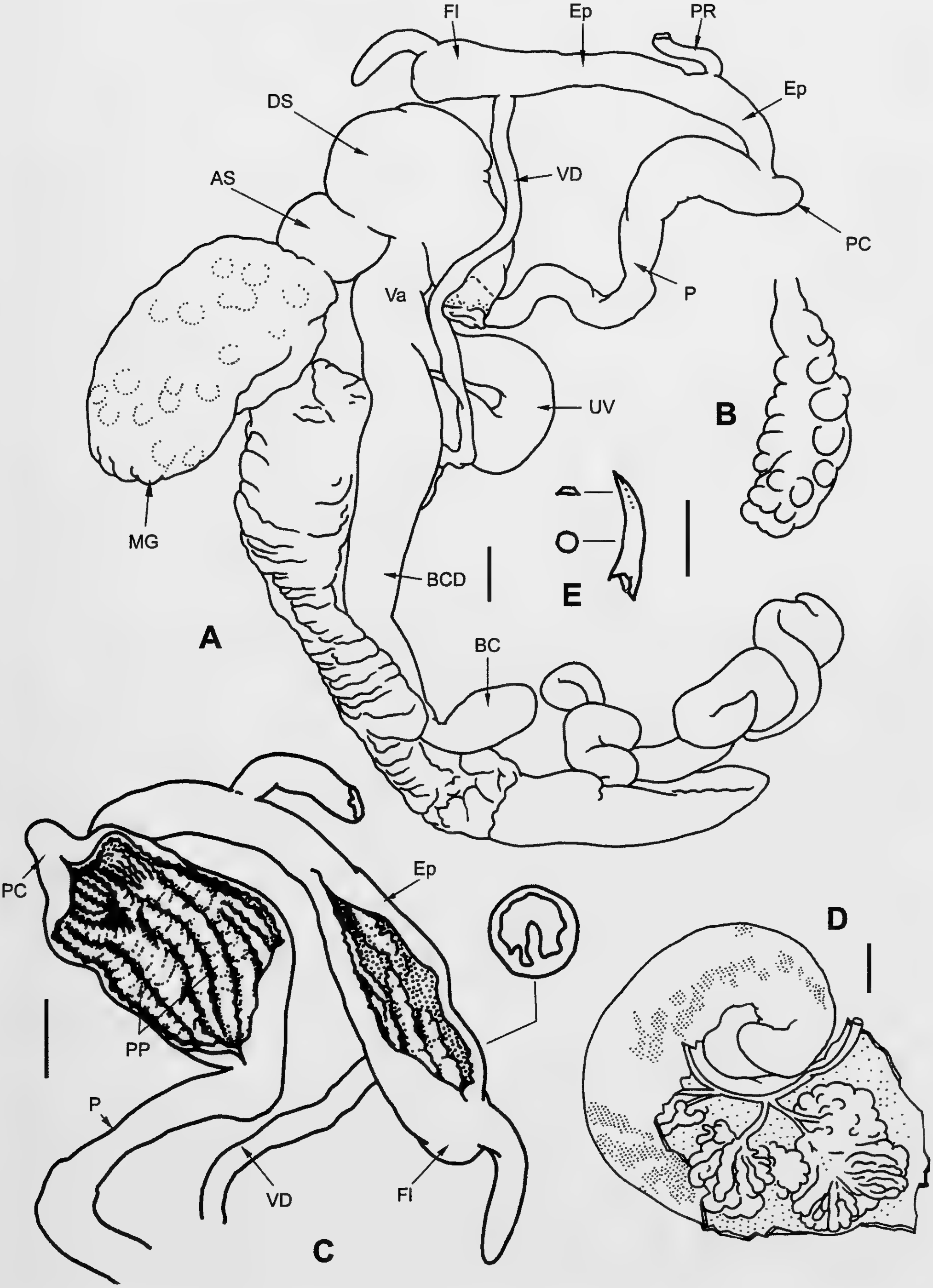

FIG. 37. *Eueuhadra gonggashanensis,* n. gen. & sp., genitalia, IZCAS01061, paratype, A, general view of genitalia; B, a branch of mucous glands; C, penis, penial caecum (PC), and flagellum, opened; D, ovotestis; E, dart with cross sections. Bars equal 1 mm.

ded in matrix composed of disordered fibers (Fig. 36F; in the other examined specimens the matrix normal); stalks fairly long (Figs. 36E, 37D). Holotype: dart sac 3.3 mm in length, 1.8 mm in width, ratio of width to length 0.5; mucous duct length 7.3 mm; vagina length 4.6 mm; free oviduct 12.2 mm; bursa copulatrix duct length 10.3 mm, bursa copulatrix duct basal width 1.5 mm; transverse diameter (maj.) of bursa copulatrix 1.5 mm, sagittal diameter (maj.) 2.2 mm; vas deferens length 13.7 mm; penis length 7.0 mm; epiphallus 6.4 mm; flagellum length 3.0 mm; PR length 2.2 mm.

Range

Western Sichuan, the species was known only from two localities where type and holotype material were collected (Fig. 28).

Remarks

This species differs from all known bradybaenids by having a simple penis-epiphallus chamber. The sisterhood of this species and *Aegistohadra delavayana* (Heude, 1885), n. gen. & comb., is suggested by their common derived character the penial caecum.

Ecology

This species (IZCAS01061) inhabits high mountains (Fig. 38B), in very low density. The environment is extremely wet, inside a dark fir forest, where the stones and fallen trunks are covered by a thick layer of lichen and moss which sometimes reaches the thickness of approximately 50 cm (Fig. 38C, D). The specimen (IZCAS01061), the only collection after careful search of about 500 m^2 in the forest was found inactive under moss. The population in Jiuzaigou seems to be isolated from another known population in the Gonggashan Mountains. Based on 30-days field work covering the area from Dujiangyan to Jiuzaigou along Minjiang River, it has been confirmed that these two populations are fairly sepa-

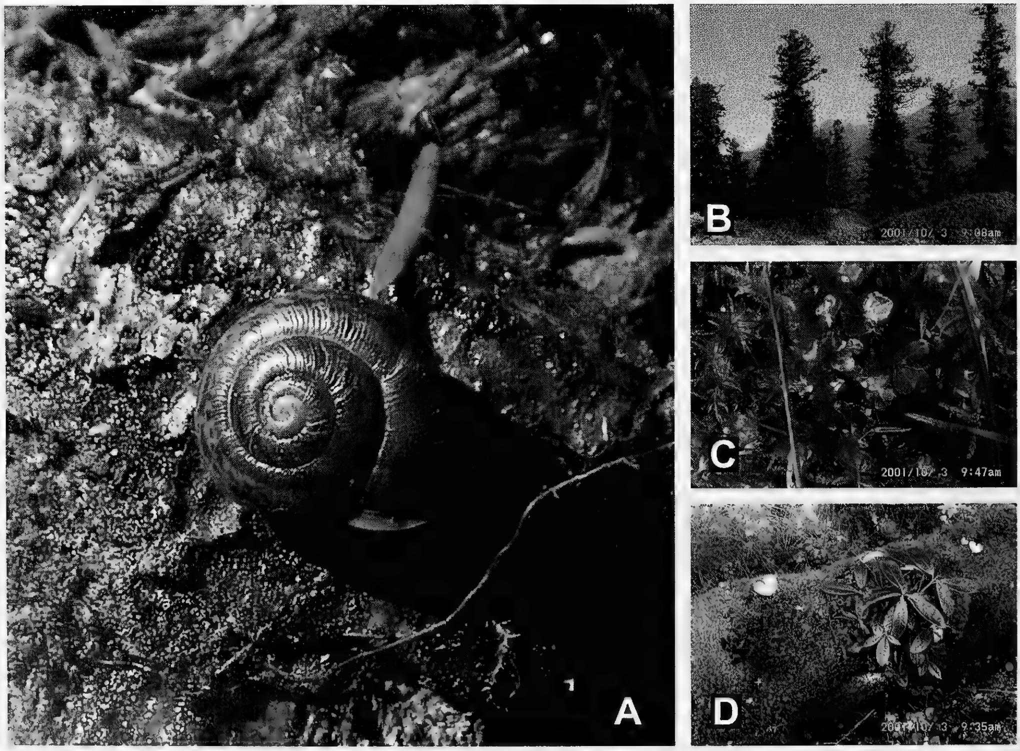

FIG. 38. Habitat of *Eueuhadra gonggashanensis,* n. gen. & sp. A, Paratype, IZCAS01061, in its habitat; B–D, natural environment conditions of locality for Paratype IZCAS01061.

rated. In the same area, no helicoid snails were found and only the non-helicoid snail *Deroceras (Deroceras) altaicum* (Simroth, 1886) (Wiktor et al., 2000), which is widely distributed in the whole vally of Minjiang River and its neighboring mountains. It is also interesting that no conchologically similar species was recorded in this region before (e.g., Pilsbry, 1934).

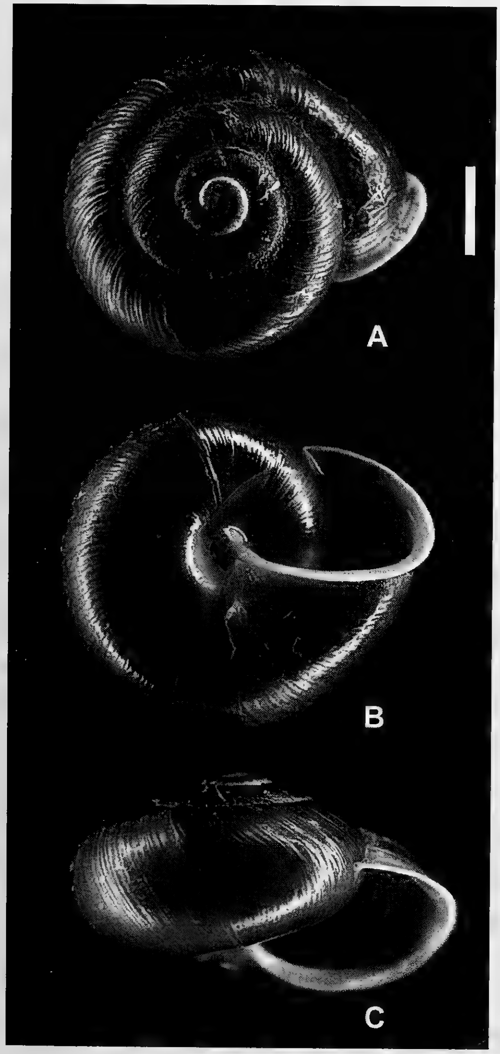

FIG. 39. *Eueuhadra gonggashanensis,* n. gen. & sp., shell, IZCAS01061, paratype, A, apical view; B, basal view; C, apertural view. Bar equals 5 mm.

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TOWARD COMPREHENSIVENESS: INCREASED MOLECULAR SAMPLING WITHIN CYPRAEIDAE AND ITS PHYLOGENETIC IMPLICATIONS

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ABSTRACT

This paper introduces 73 additional taxa to the existing mitochondrial molecular database of 202 taxa for the Cypraeidae and addresses the systematic implications of their inclusion. Five outgroup members from the Ovulidae are also added. Sequence data are included from all previously missing extant named genera (*Propustularia*, *Barycypraea* and *Schilderia*), completing the overall "generic-level" framework for living cowries. Newly added taxa include 47 recognized species, 25 subspecies, and six undescribed taxa. Phylogenetic results generally are consistent with previous arrangements, with few minor adjustments. The most significant findings are that: (1) currently recognized *Nesiocypraea* is broken into two disparate clades, a deeply rooting *Nesiocypraea sensu stricto* group and the more derived *Austrasiatica* (Lorenz, 1989). (2) Two newly included *Barycypraea* taxa are sister to *Zoila*, reaffirming the validity of the subfamilial clade Bernayinae. (3) The inclusion of a significant number of added Erroneini taxa (N = 24) creates a phylogenetic challenge because of poor support and recovered relationships inconsistent at first glance with traditionally recognized affinities. In order to maintain nomenclatural consistency, *Erronea* is maintained at a generic level, whereas *Adusta* is dropped to subgeneric status within *Erronea*. Greater than 90% of currently recognized species are included, and 93% of these are supported by molecular criteria. Moreover, more than 70% of the tested, recognized subspecies are distinct. The phylogeny provides one of the most comprehensive, species-level frameworks to date for testing diversification theories in the marine tropics.

Key words: Cypraeidae, molecular systematics, taxon sampling, *Cypraea*.

INTRODUCTION

Cowries (Gastropoda: Cypraeidae) are taxonomically one of the best known of all molluscan groups, and have been used frequently to examine speciation and biogeographic patterns in the marine tropics (Schilder, 1965, 1969; Foin, 1976; Kay, 1984, 1990; Meyer, 2003). A wealth of taxonomic (Schilder & Schilder, 1938, 1971; Schilder, 1939; Lorenz & Hubert, 1993; Groves, 1994; Lorenz, 2002), anatomical (Troschel, 1863; Vayssière, 1923, 1927; Riese, 1931; Risbec, 1937; Schilder, 1936; Kay, 1957, 1960, 1963, 1985, 1996; Bradner & Kay, 1996; Lorenz, 2000), biogeographic (Schilder, 1965, 1969; Foin, 1976; Burgess, 1985; Liltved, 1989; Lorenz & Hubert, 1993; Lorenz, 2002) and fossil data (Schilder & Schilder, 1971; Kay, 1990, 1996; Groves, 1994) is available for the group; however, what has been lacking is a well-resolved, comprehensive species-level phylogeny. These phylogenetic hypotheses of relationship establish sister pairs at the appropriate taxonomic level and provide the framework to test diversification theories. Meyer (2003) introduced molecular data for 234 taxa in Cypraeidae and generated phylogenetic hypotheses for most major clades as well as sister-group relationships for most species. Systematics for Cypraeidae were reviewed in light of the results and diversification patterns within the tropics were addressed. The study presented herein significantly increases the comprehensiveness of taxon sampling in the group by introducing 73 Cypraeidae and five Ovulidae taxa to the existing molecular dataset and discusses their systematic implications. In addition to broader taxonomic sampling, this paper presents the results of broader geographic sampling. The appendix lists 147 localities added across the various taxa. Five outgroup taxa from six localities are included, and 67 recognized cypraeid species or subspecies are added from 75 localities. The remaining 66 localities were added to supposedly known taxa, but revealed six previously unrecognized taxa, some of which may correspond to names currently in synonymy upon review of type localities.

MATERIALS AND METHODS

Recognition Criteria: ESU versus OTU

The ultimate goal of this project is to construct a comprehensive phylogeny of cypraeid gastropods at the appropriate level for diversification studies. As such, the operational taxonomic unit (OTU) chosen for phylogenetic analyses generally represents an evolutionarily significant unit (ESU) that must fulfill some minimal criteria established through genetic scrutiny. First, mtDNA haplotypes of sampled individuals must represent a monophyletic clade; yet this alone is not sufficient, because any phylogeny has a plethora of monophyletic groups, because a clade requires only two individuals. Thus, auxiliary criteria are required to delineate significant units. Within cowries, these additional criteria are (1) geographic distinction or allopatry, (2) significant genetic distance from the sister group such that pairwise distance comparisons yield a bimodal distribution, and/or (3) taxonomic recognition by previous workers. An OTU is included in analyses only if at least two of these three criteria are met. Most OTUs fulfill all three criteria and are considered evolutionarily significant units (ESUs) (*sensu* Moritz, 1994). These criteria are erected in order to delineate independent evolutionary trajectories, but do not guarantee that the units are reproductively isolated. In a few instances, two of the three criteria (genetic separation and taxonomic recognition) are not supported by the third (exclusive geographic signatures). While the genetic differences (monophyly) between populations indicate some independent period of evolutionary history between geographic regions, it appears that, on occasion, haplotypes from outlying regions can mix back into the sister gene pool. The few cases where all three criteria are not fulfilled always occur on the periphery of regions (e.g., Marquesas, Hawaii) and show asymmetrical, "downstream", dispersal events (Fig. 1). As circumscribed, all ESUs discussed indicate independent evolutionary histories, but alternative criteria, such as either nuclear markers or breeding experiments, are needed to verify reproductive isolation.

Molecular Methods

Most methods follow protocols detailed in Meyer (2003) for all aspects of preservation, extraction, amplification, and sequencing. Tissue samples were acquired from a variety of

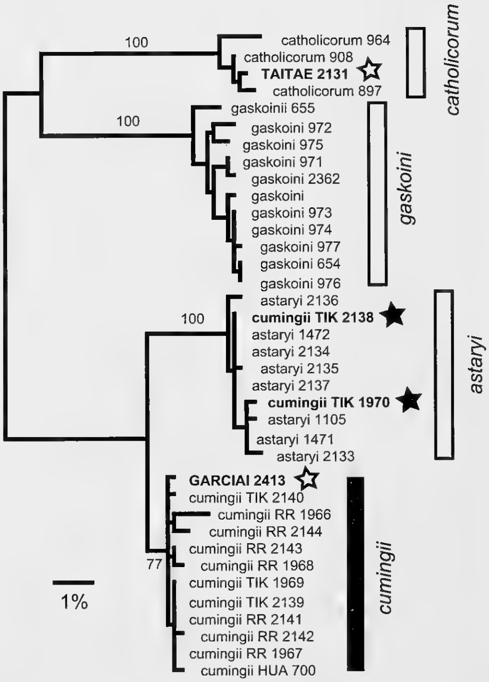

FIG. 1. ESU vs. OTU criteria. Phylogram showing the relationships among members of the Pacific *Cribrarula* subclade, with bootstrap values for major groups. Four distinct clades are evident, and the names presented on the right: *Cribrarula catholicorum*, *C. gaskoini*, *C. astaryi*, and *C. cumingii*. Note that single individuals of two newly included taxa, *C. taitae* and *C. garciai* (white stars), nest within two of the major clades and show little variation (a single mutation). These two new taxa are introduced as OTUs, because of their distinct morphology and geography (American Samoa and Easter Island, respectively), but are currently not considered ESUs by molecular criteria. All individuals from the Marquesas are *C. astaryi*; however, two individuals of *C. cumingii* possess haplotypes belonging to the *C. astaryi* clade as well (dark stars). While the two haplotype clusters are distinct, the pattern indicates uni-directional exchange of larvae downstream from the Marquesas (*C. astaryi*). Molecular criteria recognize these two clades as ESUs with historically limited exchange. (TIK = Tikehau, RR = Rangiroa, HUA = Huahine, all *C. astaryi* from Marquesas, all *C. gaskoini* from Hawaii, and all *C. catholicorum* from Solomon Islands)

sources and locations (listed in the acknowledgements and appendix). Most samples were preserved in 95% ethanol. DNA extraction was performed using DNAzol (Chomczynski et al., 1997) using one-half volumes and following the manufacturer's protocol (Molecular Research Center, Inc.) with the exception that the digestion step was increased by an additional 24 or 48 h. PCR was performed as described in Meyer (2003). COI primers were as follow (from Folmer et al., 1994): LCO-1490 (5'–3') GGT CAA CAA ATC ATA AAG ATA TTG G, and HCO-2198 (5'–3') TAA ACT TCA GGG TGA CCA AAA ATC A. For problematic taxa, these primers were degenerated as follows: dgLCO-1490 (5'–3') GGT CAA CAA ATC ATA AAG AYA TYG G, and dgHCO-2198 (5'–3') TAA ACT TCA GGG TGA CCA AAR AAY CA. Two internal primers were designed for small amplifications of degraded DNA: InCypLCO (5'–3') CGT YTA AAT AAT ATA AGY TTY TG, and InCypHCO (5'–3') CGT ATA TTA ATA ATT GTT GTA AT. Palumbi's (1996) 16Sar and 16Sbr primers were used for 16S: 16Sar (5'–3') CGC CTG TTT ATC AAA AAC AT, and 16Sbr (5'–3') CCG GTC TGA ACT CAG ATC ACG T. Two internal primers were designed for small amplifications of degraded DNA: In16Sar (5'–3') GGG CTA GTA TGA ATG GTT TGA, and In16Sbr (5'–3') ATG CTG TTA TCC CTA TGG TAA CT. The polymerase chain reaction was carried out in 50 µl volumes, using 1 µl of template. Each reaction included 5 µl 10X PCR buffer, 5 µl dNTPs (10mM stock), 2 µl of each primer (10µM stock), 3 µl $MgCl_2$ solution (25 mM stock), 0.2 µl Taq (5 Units/µl stock) and 31.8 µl ddH_2O. Reactions were run for 35-40 cycles with the following parameters: an initial one min denaturation at 95°C; then cycled at 95°C for 40 sec (denaturation), 40°C to 44°C (COI) or 50°C to 54°C (16S) for 40 sec (annealing), and 72°C for 60 sec (extension). Successfully amplified products were cleaned for cycle sequencing using Wizard© PCR Preps (Promega). Sequencing also followed Meyer (2003) with all new sequences generated using ABI chemistry and sequencers. Sequences were generated from the resulting electrophenograms using Sequencher (Gene Codes).

All primer sequences, aligned COI and 16S sequences and Nexus files are available at the archived data web pages of the Florida Museum of Natural History Malacology Department (http://www.flmnh.ufl.edu/malacology/archdata/Meyer2004), and new sequences are deposited in Genbank under accession numbers AY534351 through AY534503.

Phylogenetic Analyses

The 297 operational taxonomic units (OTUs) presented in this paper were selected from an extensive database comprised of over 2,000 sequenced individuals. In general, taxa are included if they exhibit distinctive geographic and/or genetic signatures. In most instances, new OTUs are recognized in the literature as either species (N = 47) or subspecies (N = 25). This paper introduces six previously unrecognized taxa.

The increasing size of this dataset presents computational and heuristic challenges for phylogenetic analyses. Two weighted transversion bias parsimony searches (3:1 and 5:1) were performed on the complete dataset using PAUP* (Swofford, 1998). At first, 250 random-addition replicate searches were performed, but with a tree limit of ten imposed to minimize search time on suboptimal islands. After 250 replicates, the most parsimonious topologies were used as starting trees for exhaustive searches without tree limits. This strategy was employed for both weighted analyses, and the most parsimonious topologies were pooled and evaluated using likelihood criteria. ModelTest v. 3.06 (Posada & Crandall, 1998) was used to select the most appropriate model for likelihood parameters. The most likely weighted parsimonious trees were then compared using consensus methods.

A two-tiered, compartmentalized strategy was adopted that followed Meyer (2003) for levels of topological support. The strict consensus topology derived from the most likely overall analyses was divided into four subequal components called basal, mid1, mid2, and derived. Because the basal, mid1 and mid2 cohorts are necessarily paraphyletic groups that include the common ancestor and some, but not all, of its descendants, representative derived clades were included in the paraphyletic analyses. In this way multiple derived member clades overlapped between more basal and derived analyses, and the overall topology could be "scaffolded" together by linking clades shared in both basal and derived compartments.

Within each of the four subanalyses, parsimony searches were performed using a 5:1 transversion bias. Both bootstrap (Felsenstein, 1985) analyses (1,000 replicates) and decay (Bremer, 1994) analyses (TreeRot v2; Sorenson, 1999) were performed to establish levels of support. Results from Bayesian methods (Mr. Bayes v3.04b) are not reported in this paper, but were generated for the four subgroups and compared to the combined parsimony/likelihood methods utilized in PAUP*. Overwhelmingly, they were consistent with the results presented here, but on few occasions differed in hypotheses of relationship. The scaffolded parsimony global topologies were compared to the scaffolded Bayesian topology using likelihood criteria in PAUP*. The combined topology derived from the compartmentalized Bayesian subsets was less likely than the overall topologies found using the combined parsimony/likelihood criteria. It appears that Bayesian results depended on taxon sampling and outgroup inclusion. While this finding may be of interest to the general systematic community, it is not a point specifically addressed in this paper.

RESULTS

The final culled dataset contained 297 OTUs and 1,107 characters, 493 base pairs from 16S and 614 bases from COI. For 16S, alignment followed those presented in Meyer (2003) based on secondary structure. Weighted parsimony searches resulted in 512 equally most parsimonious trees (MPTs) for 3:1 Ti:Tv and 480 trees for 5:1 searches. Derived portions of the comprehensive topology were consistent. Thus, all named clades (subfamilies, tribes and genera) presented in Figure 2 are found in all topologies, except one mentioned below. However, the topologies recovered from alternate weightings differed in five deeper regions, all of which are poorly supported regardless of methodology. First, 5:1 topologies placed the clade consisting of *Propustularia/Nesiocypraea/Ipsa* basal as sister to all other cowries. In 3:1 topologies this clade moves up one node and is sister to Erosariinae. Second, the pustulose clade consisting of *Nucleolaria/Cryptocypraea/Staphylaea* is monophyletic in 5:1 trees, while in 3:1 topologies these genera are a basal paraphyletic grade leading to the clade including *Monetaria/Perisserosa/Erosaria*. Third, in 5:1 topologies *Perisserosa* is sister to *Erosaria*, whereas in 3:1 trees, *Perisserosa* is sister to *Monetaria*. Fourth, the arrangement of major groups along the backbone from Umbiliini to Cypraeovulinae conflicts. Results from 5:1 searches are shown in Figure 2, whereas in 3:1 topologies, *Notocypraea* and *Cypraeovula* (Cypraeovulinae) are a basal sister grade leading to more derived member groups. Finally, the basal arrangement within Erroneini is different. In 3:1 topologies *Purpuradusta* is more basal, while in 5:1 trees, *Erronea* is more basal.

When alternative topologies were evaluated using ModelTest, the GTR+I+G model was selected as the best-fit model. When both the 3:1 MPTs and 5:1 MPTs were evaluated using the selected likelihood criteria [lset base = (0.315128 0.136452 0.111915), Nst = 6, Rmat = (0.99559 41.36057 1.0461 1.68935 22.78834), rates = gamma, shape = 0.562423, Pinvar = 0.48426], the 5:1 subset was significantly more likely (ANOVA: $p < 0.001$, average –ln likelihood = 49513.8). Therefore, results from the 5:1 searches are presented herein.

The overall relationships among major subgroups recovered in the 5:1 MPTs are more consistent with both morphological and fossil evidence in addition to being more likely based on molecular data. In particular, a monophyletic pustulose clade is more parsimonious for conchological and anatomical features, because it is more likely that a bumpy shell was derived a single time, rather than being derived either twice independently, or derived once then lost. Also, the basal, paraphyletic status of *Notocypraea* and *Cypraeovula* within the 3:1 topologies is inconsistent with the fossil record for both groups relative to more derived members of the 3:1 MPTs (i.e., *Umbilia*, *Barycypraea*, and *Zoila*), which appear earlier in the record and root more deeply in the 5:1 topologies. Also, the sister-group relationship of the two genera is more consistent with paleobiogeography (the breakup of Gondwanaland) and recognized affinities based on both conchological and developmental criteria. The other major discrepancies between the 3:1 and 5:1 MPTs (most basal cowries, *Perisserosa* affinities, and position of *Purpuradusta*) are more ambiguous based on alternate criteria (morphological or paleontological).

Suprageneric Relationships (Fig. 2)

Overall, suprageneric results were consistent with previous systematic findings (Meyer, 2003), with two exceptions. First, *Ipsa* falls outside Erosariinae and is no longer sister to Erosariini, but instead is allied with newly included *Propustularia* and *Nesiocypraea sensu stricto*. New sequence data from *Nesiocypraea teramachii neocaledonica* did not result in an affinity with other recognized "*Nesiocypraea*" species (*N. hirasei*, *N. sakurai* and *N. langfordi*). Instead, *Nesiocypraea teramachii* roots more deeply in the phylogeny as a distant sister to *Ipsa childreni*, within a clade that includes both *Ipsa* and *Propustularia*. Thus, the inclusion of

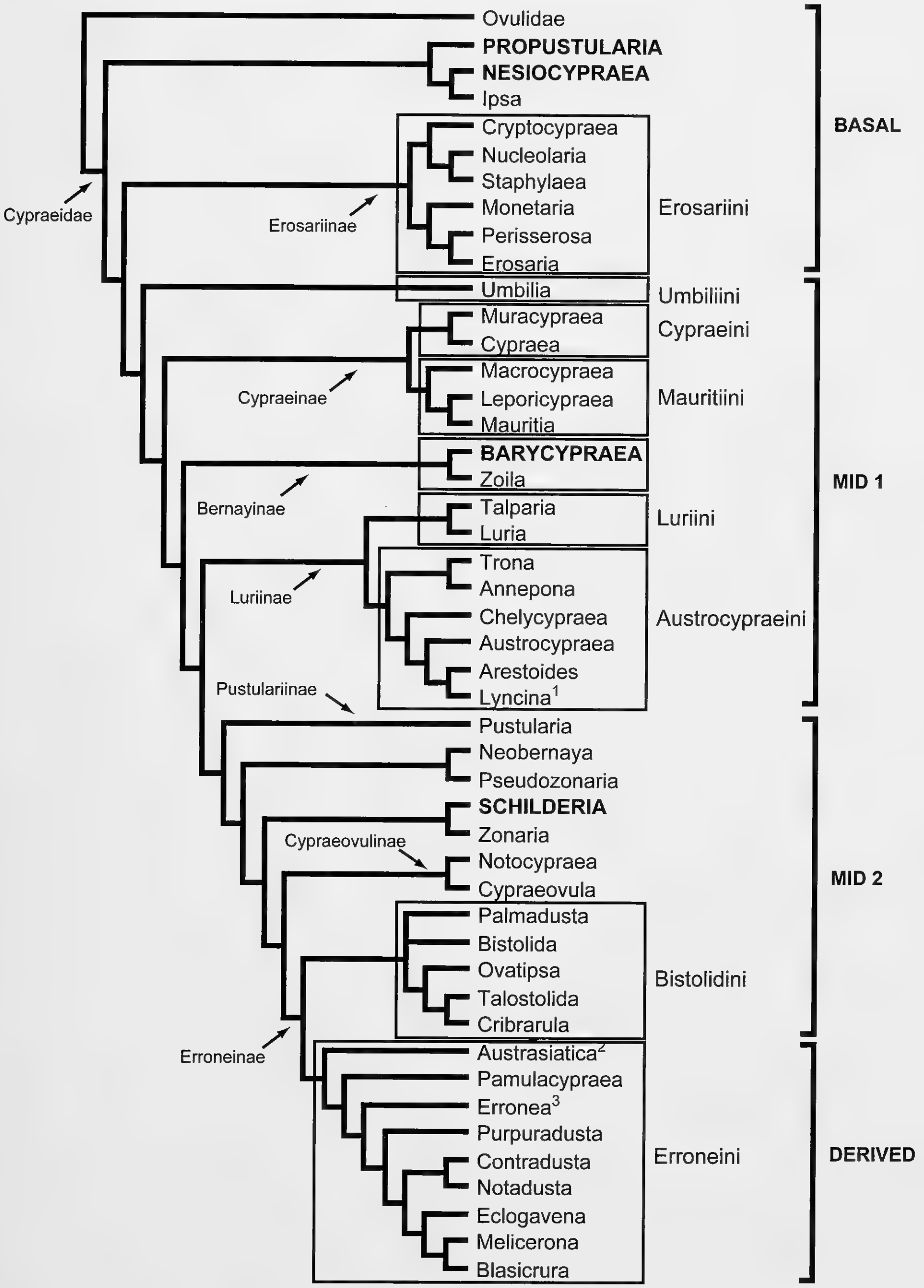

FIG. 2. Strict suprageneric consensus topology of 480 most parsimonious trees derived from a 5:1 Ti:Tv weighted search strategy of all 297 OTUs. Subfamilies are indicated with arrows and tribes are listed to the right. The four compartments for further subanalyses are bracketed to the right. The four newly added genera are capitalized and bolded. [1]*Lyncina* includes the subclades *Callistocypraea*, *Miolyncina* and *Lyncina* as reported in Meyer (2003). [2]*Austrasiatica* replaces the prior use of *Nesiocypraea* for the same clade. [3]*Erronea* now includes *Adusta*, formerly recognized as the sister taxon.

two new ancient lineages (*Propustularia* and *Nesiocypraea*) affects the relative position of *Ipsa*. Moreover, the finding that *Nesiocypraea teramachii* is not related to other previously recognized *Nesiocypraea*, compels me to recognize the clade *Austrasiatica* proposed by Lorenz (1989) at the generic level for the group including *Austrasiatica hirasei*, *A. sakurai*, and *A. langfordi*. There are some conchological and anatomical features that support this separation. The left posterior terminal ridge in *Nesiocypraea* is more produced and separate from the body of the shell, whereas in *Austrasiatica*, the ridge is continuous with the body. Lorenz (pers. comm.) also states that (1) *Nesiocypraea* lacks a distinct embryonic banding, having instead only a darker middorsal zone, (2) *Nesiocypraea* have a proportionally larger spire, and (3) the darker pattern of the shell is absent in juvenile *Austrasiatica,* only gained after the deflection of the labral margin; whereas, the darker pattern can be part of juvenile *Nesiocypraea* shells. Additionally, the rachidian tooth of *Nesiocypraea* lacks the prominent paired basal denticles present in the three *Austrasiatica* taxa, and the tooth shape is less elongated and squared, whereas the rachidian in *Austrasiatica* narrows toward the cusps (Bradner & Kay, 1996). The fact that *Austrasiatica* was erected to differentiate the three species (albeit incorrectly aligned with *Schilderia*) is also an indication that the two lineages possess independent histories. The deep position of *Propustularia* within the cowrie phylogeny is not surprising because it is one of the oldest of extant taxa, extending back to the Lower Eocene (Kay, 1996).

The second suprageneric difference concerns the relative position of *Zoila* in the overall phylogeny and is caused by the inclusion of sequence data for two taxa from the ancient lineage *Barycypraea*. These new data indicate that *Barycypraea teulerei* and *Barycypraea fultoni* are sister taxa, and they are sister to *Zoila*. This *Barycypraea*/*Zoila* clade is recognized as the extant members of the subfamily Bernayinae, a group that includes many extinct fossil members and extends back into the Mesozoic (Kay, 1996). These new data change the relative position of *Zoila* to Cypraeinae (Meyer, 2003); however, the topology in this region of the phylogeny is poorly supported.

The final suprageneric addition to the molecular database is the inclusion of sequence data from *Schilderia achatidea*, the single, living representative from an older, more diverse genus of European affinities. Previously, the paraphyletic arrangement of the genera *Pseudozonaria* and *Zonaria* was a surprising result (Meyer, 2003). These new data for *Schilderia* place the genus as sister to *Zonaria* to the exclusion of *Pseudozonaria* (and *Neobernaya*), and phylogenetic results maintain their independent, paraphyletic status. These finding are more consistent with geographic affinities than recognized taxonomic affinities (*Pseudozonaria* is often considered a subgenus of *Zonaria*), as both *Neobernaya* and *Pseudozonaria* are currently restricted to the eastern Pacific whereas *Schilderia* and *Zonaria* are restricted to the western Atlantic.

Basal Compartment (Fig. 3)

Five Ovulidae taxa are added in these analyses: *Pseudocypraea exquisita*, *Volva volva*, *Primovula concinna*, *Dentiovula takeoi*, and *Prosimnia semperi*. Within Ovulidae, only a few major clades are well supported and may be the results of poor taxon sampling. First, the clade Eocypraeinae appears well supported and includes *Pedicularia*, *Jenneria* and *Pseudocypraea*. Eocypraeinae is sister to a strongly supported clade (Ovulinae) that includes the remaining Ovulidae. Within the Ovulinae, two subgroups are well supported and represent the major clades Volvini and Ovulini. Of the added Ovulidae, *Volva* falls into Volvini, but *Prosimnia* unexpectedly falls into Ovulini as do *Primovula* and *Dentiovula*. These results are generally consistent with Cate's (1974) arrangement of higher-level relationships within the Ovulidae. *Cyphoma gibbosum* falls basal to these two sisters in the strict consensus topology; however, its position is poorly supported, and it is expected to move within the Volvini with the inclusion of more taxa. Monophyly of Ovulidae is not addressed herein and would require the inclusion of more distant representatives from Lamellaridae, Triviidae and Eratoidae.

The Cypraeidae basal group includes the genera *Propustularia*, *Nesiocypraea*, *Ipsa*, *Cryptocypraea*, *Nucleolaria*, *Staphylaea*, *Monetaria*, *Perisserosa*, and *Erosaria*. *Propustularia*, *Nesiocypraea*, and *Ipsa* form a clade that roots deeply within the phylogeny and is sister to all other cowries. Each of the three genera is represented by only a single taxon, and only *Nesiocypraea* contains additional recognized species missing from the dataset (*Nesiocypraea midwayensis, N. lisetae* and *N. aenigma*). While sharing a most recent common ancestor, the three genera are highly divergent from each other, representing significant periods of independent history. Two

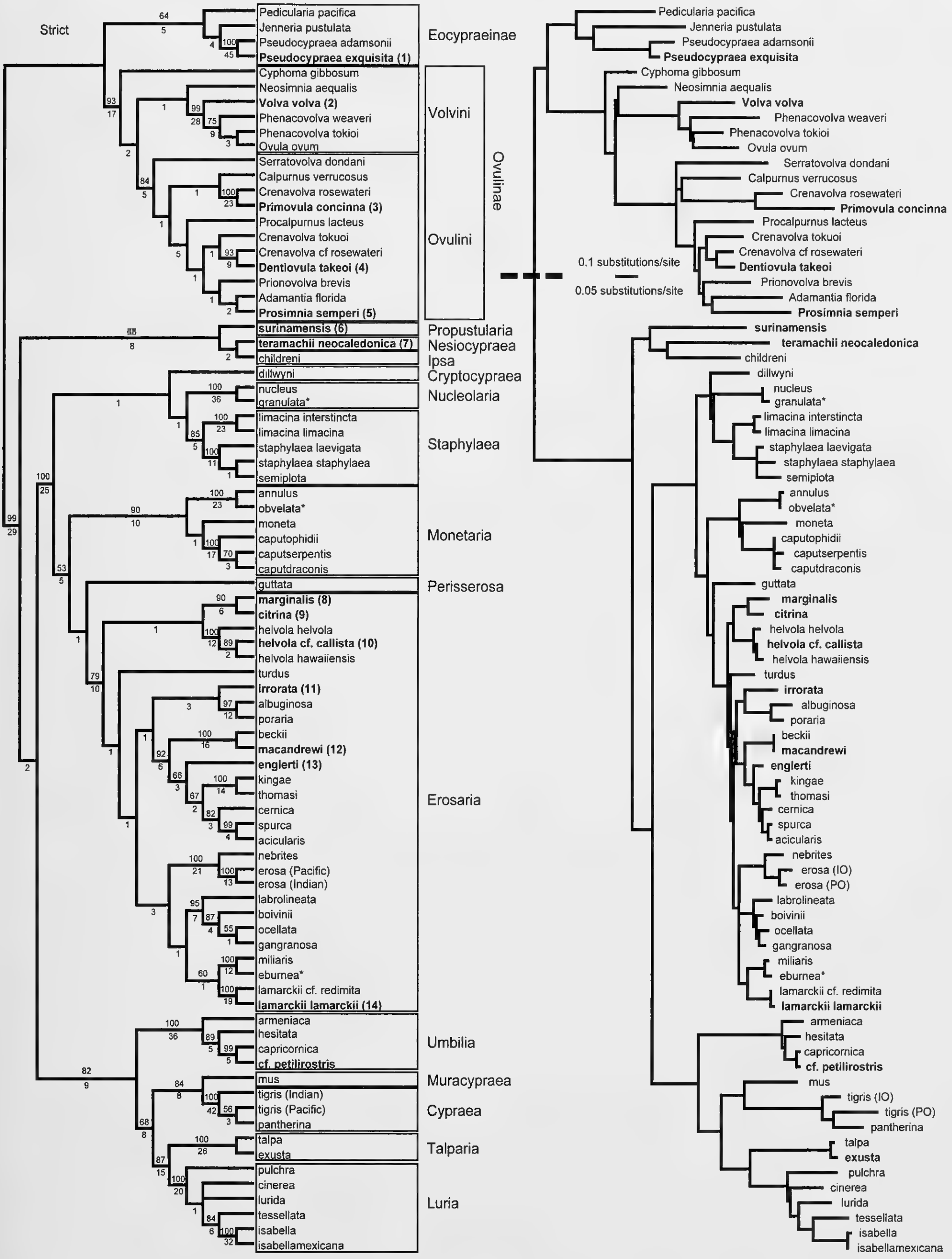

FIG. 3. Basal Compartment cladogram and phylogram. Bootstrap values are presented above branches in the cladogram and rescaled decay values below. Bolded taxa are new additions to the data set. Their identity number shown in parentheses follows the listing in the Appendix. Generic or suprageneric groupings are indicated to the right of the cladogram. OTUs with an asterisk (*) are not ESUs based on molecular criteria. Phylogram to the right is based on likelihood distances using a GTR+I+G model of sequence evolution. Note that the scaling for branch lengths changes between Ovulidae and Cypraeidae.

are known exclusively from the Indo-Pacific (*Nesiocypraea* and *Ipsa*) and one (*Propustularia*) from the western Atlantic, but has a fossil record from North America, the Caribbean, and Europe (Kay, 1996). The splits among these ancient groups are among the earliest of all extant species and may have occurred in the Mesozoic. While reasonably supported as a clade, this basal group is not strongly supported as the most basal sister, and in other analyses (3:1) moves up to become sister of the remaining basal taxa (Erosariinae).

The final six genera from the basal compartment form the strongly supported clade Erosariinae and is the sister group to all remaining extant species. Membership and relationships within the Erosariinae are consistent with previous findings (Meyer, 2003). Five taxa from *Erosaria* are added: *Erosaria marginalis*, *E. citrina*, *E. helvola* cf. *callista*, *E. macandrewi*, and *E. englerti*. Ten independent lineages are strongly supported (bootstraps > 90/decays > 6) within *Erosaria*, but interrelationships among them are not (< 50/< 4). *Erosaria marginalis* and *E. citrina*, both from the western Indian Ocean, are strongly supported as sister taxa. This clade is poorly supported as sister to the *E. helvola* complex. Within *Erosaria helvola*, three ESUs are identifiable: *E. helvola hawaiiensis* from Hawaii, *E. helvola* cf. *callista* from the Marquesas, and *E. helvola helvola* from the remainder of the IndoPacific. The newly included ESU, *E. helvola* cf. *callista*, may need a new name, because the type locality of *E. helvola callista* is Tahiti (Shaw, 1909), not the Marquesas. These five taxa are sister to the remaining *Erosaria*; however, the basal position is poorly supported. *Erosaria turdus* is a monotypic, deeply divergent lineage. Newly added *Erosaria irrorata*, a species restricted to the oceanic islands of the Pacific, is poorly supported as sister to a strongly supported clade (97/12) including *E. albuginosa* and *E. poraria*. These three taxa are sister to a well-supported lineage (92/6) of eight taxa that I tentatively recognize as *Paulonaria* at the subgeneric level. New sequence data from *Erosaria macandrewi*, a Red Sea taxon, closely ally that species with *E. beckii*. These two species are sister to the remaining *Paulonaria* taxa. The final additional taxon within *Paulonaria* is *Erosaria englerti*, a species endemic to Easter Island and Sala y Gomez. *Erosaria englerti* shares a more recent common ancestor with the remaining five *Paulonaria* taxa. All other relationships within *Erosaria* are the same as those presented in Meyer (2003) and are indicated in Figure 3. Newly added haplotypes from *E. lamarckii lamarckii* populations of the western Indian Ocean exhibit a recent divergence from the previously recorded *E. lamarckii* cf. *redimita* of the Andaman Sea. One final finding from additional *Erosaria* sequence data is that haplotypes from *Erosaria miliaris* and *E. eburnea* individuals interfinger, indicating that either the divergence between these two taxa is very recent and lineage sorting has not occurred, or that these two taxa represent a cline across the western Pacific from a colored dorsum in the west to white shells in the east.

Mid1 Compartment (Fig. 4)

The second paraphyletic compartment contains mostly large-shelled taxa from the following tribes: Umbiliini, Cypraeini, Mauritiini, Luriini, Austrocypraeini, and the genus *Pustularia*. All six clades are well supported (> 70/> 5) except for Austrocypraeini. As in Meyer (2003), interrelationships among these major suprageneric clades are resolved in the consensus, but poorly supported. Austrocypraeini and Luriini are sisters and recognized as the subfamily Luriinae. *Barycypraea* and *Zoila* are sisters and recognized as the subfamily Bernayinae. Cypraeini and Mauritiini are sisters and recognized as the subfamily Cypraeinae. In the current topology, *Pustularia* and all remaining cowries share a more recent common ancestor. This large clade is sister to Luriinae, which in turn is sister to Bernayinae, and this inclusive clade is sister to Cypraeinae. As in Meyer (2003), Umbiliini is sister to all remaining mid1, mid2 and derived taxa.

Within the mid1 compartment, 13 taxa are added to the sequence database. The first addition falls within the genus *Umbilia* and is tentatively recognized as *Umbilia* cf. *petilirostris*. A single divergent sequence was generated from tissue samples collected from the deep waters in the Capricorn Channel off Queensland, Australia. Seven sequenced individuals were completely identical, while an eighth sample from a subadult shell was significantly divergent. This single sample may represent the newly described *Umbilia petilirostris* Darragh, 2002; however, authors disagree on its taxonomic status (Wilson & Clarkson, in press). Until more comprehensive sampling is done in the region, I present the divergent sequence as a different ESU, which does not preclude it from being lumped within *U. capricornica* at a later date with more exhaustive sampling. The relationships within *Umbilia* remain as in previous analyses (Meyer, 2003).

The second taxon added to mid1 is *Leporicypraea mappa aliwalensis* from Natal, South

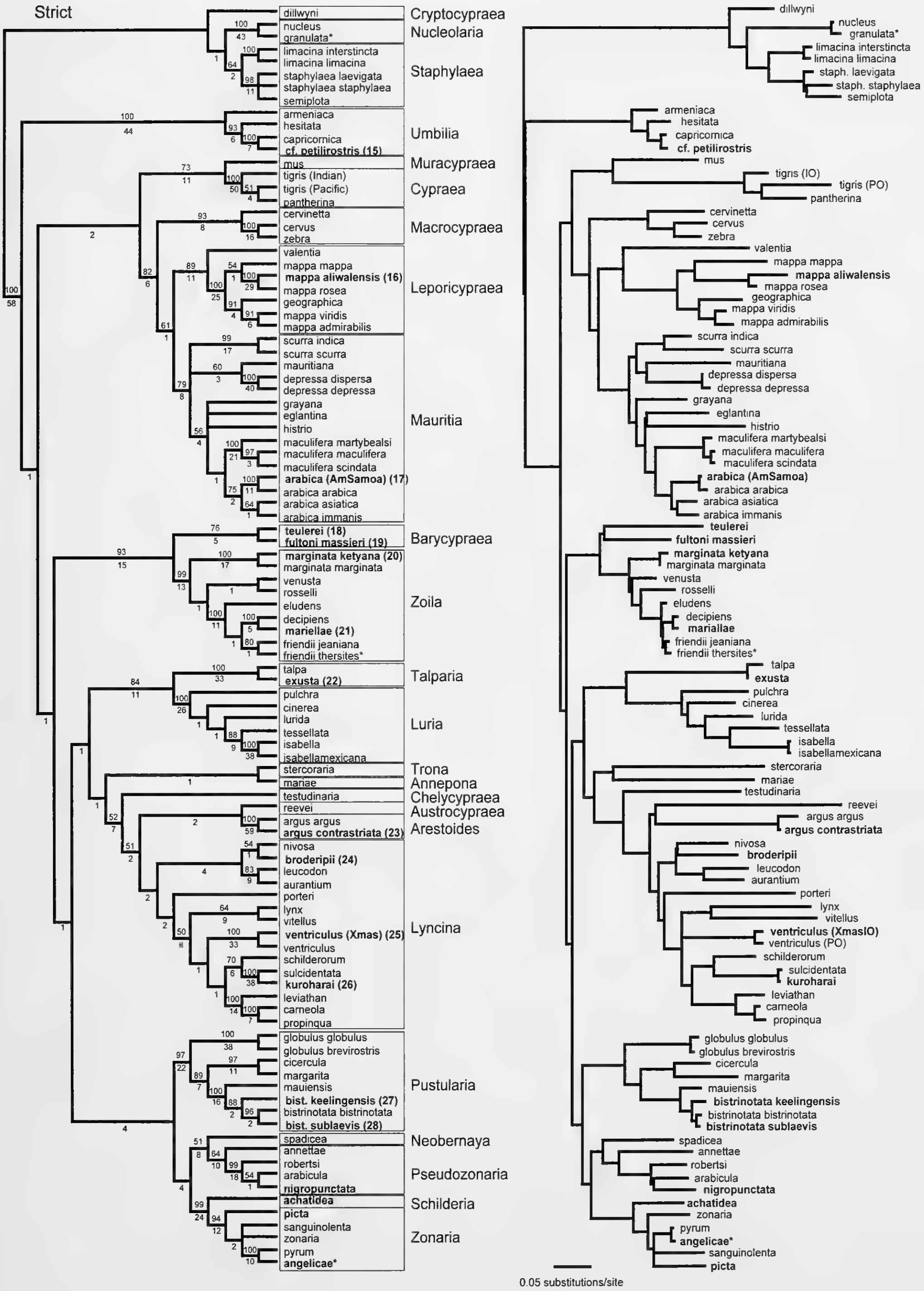

FIG. 4. Mid 1 Compartment cladogram and phylogram. All other information as in Fig. 3.

Africa, and falls as sister to *Leporicypraea mappa rosea*. Lorenz (2002) has recently revised the taxonomy of the *mappa* group in light of molecular findings. Importantly, the names I associated previously with ESUs have changed, and those changes are reflected in the Appendix and also discussed herein. The taxon I previously recognized as *Leporicypraea mappa viridis* from SE Polynesia is now recognized as *Leporicypraea admirabilis*. The taxon I previously recognized as *Leporicypraea mappa panerythra* from the non-continental portions of the western Pacific is now recognized as *Leporicypraea mappa viridis*. The other taxon names remain the same. Sequences of *L. mappa* "*rewa*" from Pacific localities (Fiji, Vanuatu, Palau, and South China Sea) interfinger with haplotypes of *L. mappa geographica* individuals from Indian Ocean localities (NW Australia, Phuket, Seychelles, and Zanzibar). Therefore, I recognize only a single taxon, *L. mappa geographica,* for this clade. Because of its conchological distinctiveness and sympatry with conspecifics, Lorenz (2002) elevated *L. mappa geographica* to specific status with Indian and Pacific subspecies. Based on the genetic difference between *mappa*-complex conspecifics and geographic overlap, specific status is certainly acceptable. However, the remaining *L. mappa* subspecies are paraphyletic. The phylogeny Lorenz (2002: 27) presents is correct and reflects this arrangement. Certainly, other recognized cowrie species are derived from paraphyletic parent species (e.g., *Eclogavena coxeni* and others; see Meyer, 2003: table 4, and cases herein), and *L. geographica* would have to be added to this list. These results suggest a third species sister to *L. geographica* should be recognized that would include both *L. mappa viridis* and *L. mappa admirabilis*. *L. mappa geographica* individuals have been found sympatrically with both *L. mappa mappa* and *L. mappa viridis* individuals in the Pacific Ocean. However, as yet, *L. mappa mappa* and *L. mappa viridis* haplotypes have not been found together.

One new undescribed taxon is added to *Mauritia*. Haplotypes of *M. arabica* individuals from American Samoa cluster independently from haplotypes of *M. arabica* individuals from other Pacific localities. Shells from Samoan individuals tend to be smaller, more heavily margined and more circular than individuals from other Pacific localities. Results from increased sampling in both *M. depressa depressa* (N = 10) and *M. depressa dispersa* (N = 10) maintain their independent, reciprocally monophyletic status, albeit recently diverged. As in previous findings, the interrelationships among major lineages in *Mauritia* are poorly supported. Consensus methods and poor support result in two polytomies (Fig. 4). Further genetic data will be needed to address this region of the phylogeny as all extant taxa have been sampled.

New sequence data from *Barycypraea teulerei* and *B. fultoni* place them as sister taxa and align them with the genus *Zoila* to form the group Bernayinae. Sequence data presented for *Barycypraea fultoni* are of *B. fultoni amorimi* from Mozambique. The Australian *Zoila marginata* complex is split into two ESUs as increased sampling indicates fixed molecular differences between populations separated by the Southwest Cape region between capes Naturaliste and Leeuwin. Further sampling directly within this region may uncover intermediate haplotypes that would link the two ESUs and suggest a cline instead of two independent lineages. Such a finding is the case in the *Zoila friendii* complex. However, as none have been discovered yet, I present the data as two tentative ESUs: *Zoila marginata marginata* to the south and *Z. marginata ketyana* to the west. Other described *Z. marginata* taxa (Lorenz, 2001; 2002) within each ESU interfinger, and do not fulfill molecular criteria for recognition. Sequence data from *Zoila mariellae* are the final addition to the Bernayinae clade. While the exact provenance of the animal sequenced is unknown, it is likely from the northwestern shelf of Australia. Molecular results place *Z. mariellae* as a distinct sister to *Z. decipiens*, also from the northwestern shelf, as expected.

Following along the phylogeny, the clade Luriinae comes next. *Talparia* and *Luria* are strongly supported as the clade Luriini. A small fragment from 16S was amplified from a degraded *Talparia exusta* specimen, and as expected, the taxon is sister to the more widespread *Talparia talpa*. Surprisingly, sequence divergence between the two species appears to be relative small, indicating a more recent divergence than expected. Better-preserved material from *T. exusta* is needed before these relative results can be confidently assessed. The inclusion of four new taxa to the Austrocypraeini (*Arestoides argus contrastriata*, *Lyncina broderipii*, *L. ventriculus* from the Indian Ocean, and *L. kuroharai*) does not help in resolving interrelationships among member taxa. *Arestoides argus* is broken into a Pacific clade, *A. argus argus*, and a western Indian Ocean clade, *A. argus contrastriata*, based on additional sequence data from the Indian Ocean. *Lyncina broderipii* appears as sister to *L. nivosa* within the *Callistocypraea* clade, as predicted in Meyer (2003). A single sampled individual of *L. ventriculus* from Christmas Island in the Indian Ocean falls significantly outside the haplotype cluster of individuals (N = 6) from various regions of the Pacific basin. *Lyncina ventriculus* is an oceanic taxon, and because of the geographic gap between sites across continental Southeast Asia, I choose to present the Christmas Island form as new, undescribed, distinct ESU. Further sampling of individuals from Christmas Island may change this interpretation, but they are currently lacking. A single sample of *Lyncina kuroharai* was sequenced and the results place it closely related to *L. sulcidentata*, an endemic Hawaiian taxon. The shallow split between these two taxa indicates a relatively recent common ancestor. Faunal ties have been documented in other cowrie species between Hawaii and Japan, most notably in *Luria isabella*, and the close affinities between *L. kuroharai* and *L. sulcidentata* represent another example of this biogeographic link.

The final two ESUs added within the mid1 compartment are members of the genus *Pustularia*, and more specifically are recognized subspecies of *Pustularia bistrinotata*. A single *P. bistrinotata keelingensis* individual was sequenced, is distinct, and appears as sister to the remaining *P. bistrinotata* complex. Furthermore, *P. bistrinotata sublaevis* individuals (N = 5) from southeast Polynesia (Tuamotu and Societies) cluster together, forming a third ESU within *P. bistrinotata*.

Mid2 Compartment (Fig. 5)

The third phylogenetic compartment, mid2, contains members from the genera *Neobernaya*, *Pseudozonaria*, *Schilderia*, *Zonaria*, the subfamily Cypraeovulinae, and the tribe Bistolidini of the subfamily Erroneinae. Interrelationships among member clades are consistent with previous findings (Meyer, 2003). *Neobernaya* and *Pseudozonaria* are sisters, and that clade is sister to the remaining cowries. The inclusion of sequence data from the genus *Schilderia* (*S. achatidea*), place the group as sister to *Zonaria*, and together this clade shares a more recent ancestor with the remaining taxa. The subfamily Cypraeovulinae includes both the South African *Cypraeovula* and South Australian *Notocypraea* and is sister to the western IndoPacific Erroneinae, which is composed of two tribes: Bistolidini and Erroneini.

Within the mid2 compartment, 25 taxa are added to the existing sequence database; at least one ESU is added within each genus except the monotypic *Neobernaya*. *Pseudozonaria nigropunctata*, a Galapagos endemic, falls into the eastern Pacific clade as a divergent sister to *P. arabicula*, although not strongly supported. The position of *Schilderia achatidea* has been mentioned previously as sister to *Zonaria*, now found exclusively in the eastern Atlantic. Two taxa are added from *Zonaria*. *Zonaria picta* from the Cape Verde Islands falls near the base of *Zonaria*, and its relationship with other Zonarid taxa is ambiguous, resulting in a polytomy at the base of the group. Alternative phylogenetic reconstructions at the base of the group show small internodes, indicative of a short radiative burst, with little divergence since. New sequence data from *Pseudozonaria angelicae* are extremely similar to haplotypes from *P. pyrum* (both *P. pyrum angolensis* and *P. pyrum senegalensis*). I include *P. angelicae* as a taxon in the phylogeny, but prefer to consider it at most a subspecies until further sequence data are available within the *P. pyrum* complex, as I have reservations concerning divergences along the mostly continuous West African/Mediterranean coastline.

Sequence data from six additional taxa are included within Cypraeovulinae, two from *Notocypraea* and four from *Cypraeovula*. In *Notocypraea*, I tentatively recognize two ESUs within *Notocypraea angustata*, with a phylogenetic break somewhere between Port Lincoln and Port Macdonnel, South Australia. Two divergent haplotype clusters exist without intermediate states. Again, further data may change this interpretation, but at present I chose to represent these as different ESUs indicating distinct evolutionary trajectories. Sequence data from a single specimen of *Notocypraea hartsmithi*, a rare species from southeastern Australia, indicate that the species is sister to all remaining *Notocypraea* taxa. Within *Cypraeovula*, four taxa are added, but their inclusion does not change previous interpretations that the group is composed of predominately four divergent lineages with minor differences within each. New sequence data from both *Cypraeovula fuscorubra* and *C. fuscodentata* closely align these taxa with *C. capensis*. New sequence data from *C. mikeharti* and *C. algoensis* closely align those taxa with *C. edentula* and *C. alfredensis*. Noting the shallow divergences among recognized species in Figure 5, I am doubtful that many of the described subspecies within *Cypraeovula* (summarized in Lorenz, 2002) will fulfill my molecular criteria for ESU status. As some species are differentiated currently by only a

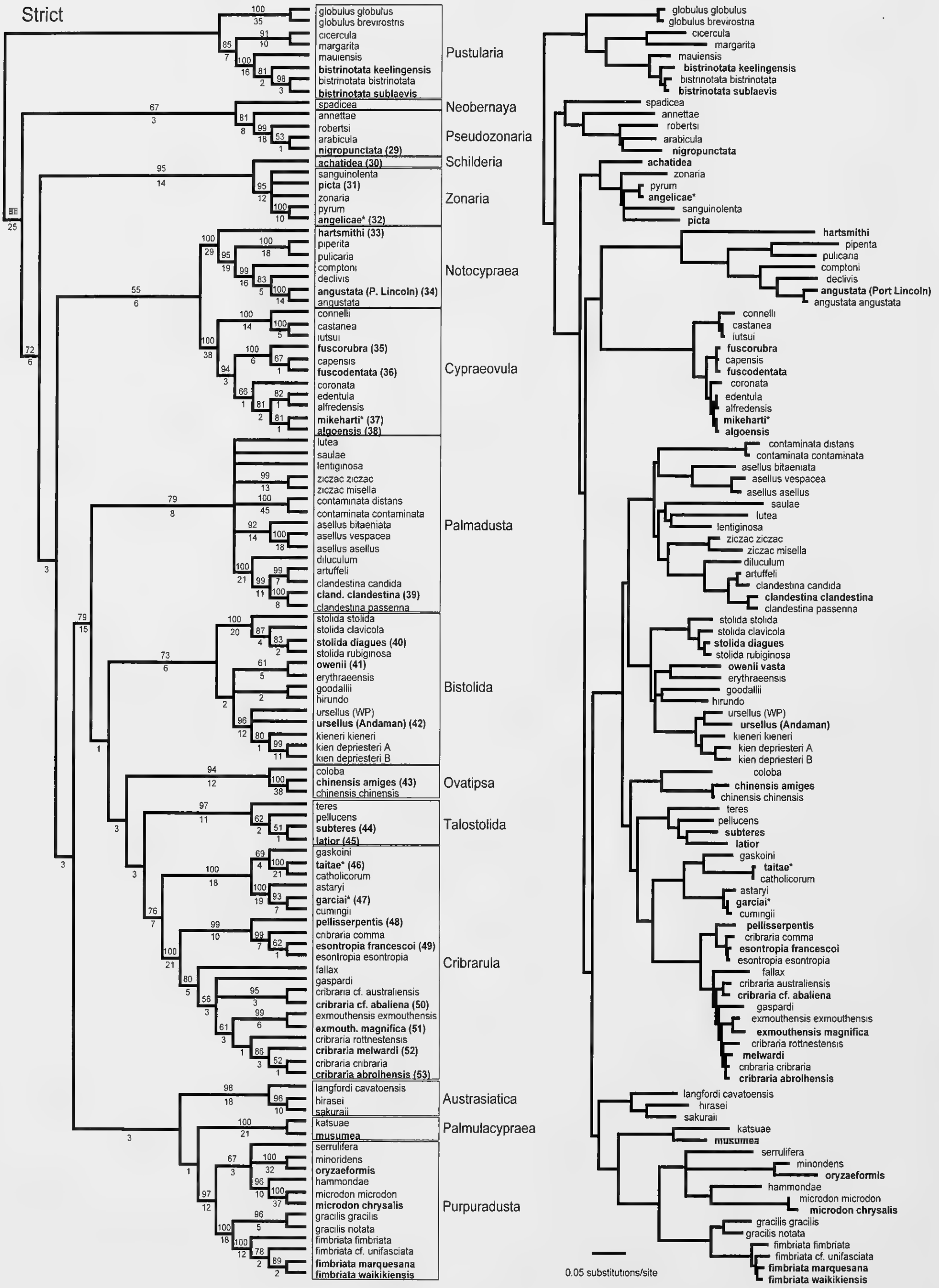

FIG. 5. Mid 2 Compartment cladogram and phylogram. All other information as in Fig. 3.

single mutation (e.g., *Cypraeovula mikeharti/ C. algoensis* or *C. castanea/C. iutsui*), there simply is not enough room for differences to have accumulated between taxa. This is not to say that described entities are not independent. Indeed, because *Cypraeovula* taxa are direct developers with limited dispersal and gene flow, regional differences are expected on small geographic scales, much like the South Australian endemic clades *Umbilia*, *Zoila*, and *Notocypraea*. However, based on the genetic similarity among sampled member *Cypraeovula*, much of this variation has to be very recently derived. This pattern is borne out in the South Australian direct developers that have been more extensively sampled.

The tribe Bistolidini within Erroneinae is composed of members from five genera: *Palmadusta*, *Bistolida*, *Ovatipsa*, *Talostolida* and *Cribrarula*. As in Meyer (2003), the basal root of Bistolidini is poorly resolved. Overall analyses place either *Palmadusta* as sister to the other four genera or *Palmadusta* and *Bistolida* as a clade, sister to the remaining three. Compartmentalized analyses place *Palmadusta* at the base, although poorly supported. The addition of 15 ESUs did not help in resolving this issue. Only one taxon is added to the *Palmadusta* clade, but it alters the subspecific designations previously ascribed (Meyer, 2003). New haplotypes from Andaman Sea *P. clandestina* individuals form a distinct monophyletic clade. This new ESU is sister to the western Indian Ocean *P. clandestina passerina*, and the two of them are sister to the Pacific *P. clandestina* clade and the Japanese endemic *P. artuffeli*. Based on a review of *P. clandestina* subspecies and type localities, the Pacific clade that I had formerly (Meyer, 2003) recognized as *P. clandestina clandestina* should be *P. clandestina candida*, and the new *P. clandestina* clade from the Andaman Sea now bears the name *P. clandestina clandestina*. I also reviewed the subspecies and type localities for the three *P. asellus* ESUs previously unnamed (Meyer, 2003). Based on increased sampling and conchological comparisons, I tentatively ascribe the following subspecific designations for the three clades: *P. asellus asellus* for the western Indian Ocean clade, *P. asellus vespacea* for the Seychelles to western Pacific clade, and *P. asellus bitaeniata* for the Melanesian and Pacific clade (Fig. 5, Appendix). Unfortunately, the addition of *P. clandestina clandestina* does not help in resolving the basal nodes of *Palmadusta*. As shown in Figure 5, the base of *Palmadusta* is poorly resolved and sister group assignments are ambiguous. A few lineages remain strongly supported (*P. asellus*, *P. clandestina/diluculum*, *P. ziczac* and *P. contaminata*), but confident hypotheses of other interrelationships require further data.

Three taxa are added to *Bistolida*: *B. stolida diagues*, *B. owenii* and an undescribed, distinct eastern Indian Ocean clade of *B. ursellus*. Individuals of *B. stolida diagues* from the Seychelles fall as sister to *B. stolida rubiginosa*. *Bistolida owenii*, a western Indian Ocean taxon, is sister to the Red Sea endemic *B. erythraeensis*. A new *Bistolida ursellus* sequence from the Andaman Sea is poorly supported as sister to the remaining *B. ursellus* taxon from the Pacific basin. Its placement is equally parsimonious as either sister to *B. ursellus* (Pacific) or forming a *B. ursellus* grade leading to the *B. kieneri* lineage. The topology of the two *B. ursellus* taxa as sisters is more likely and consistent with morphology.

One taxon is added to *Ovatipsa* and two taxa to *Talostolida*. Within *Ovatipsa*, the subspecies *O. chinensis amiges* from the Pacific basin and Western Australia is distinct from *O. chinensis chinensis* from the Philippines westward through the Indian Ocean to the east coast of Africa. Various other *O. chinensis* subspecies have been described within the Indian Ocean (e.g., Lorenz & Hubert, 1993), and preliminary data indicate that these Indian Ocean subspecies may represent very recent divergences within what I am currently recognizing as *O. chinensis chinensis*. However, until more individuals are sampled, I maintain them all under the taxon *Ovatipsa chinensis chinensis*. Within *Talostolida*, two taxa are added that appear as sisters to each other: *T. subteres* from southeastern Polynesia and *T. latior* from Hawaii. These two taxa are sister to *Talostolida pellucens*. All four taxa currently included within *Talostolida* are deeply divergent independent ESUs. A single haplotype of *Talostolida teres "alveolus"* (*sensu* Lorenz, 2002) is completely identical to haplotypes of *T. teres teres* individuals from both the Society Islands and the Tuamotu. Moreover, *T. teres* individuals from SE Polynesia have been described by Lorenz (2002) as a distinct subspecies *T. teres "janae"*; however sampled individuals of *T. teres* from SE Polynesia interfinger with individuals sampled from the Western Pacific (Papua New Guinea and Guam). Therefore, the data do not support *T. teres* "*janae*" as a valid taxon, based on my criteria. All Marquesan individuals sequenced possess *T. pellucens* haplotypes, whereas all *T. teres*-like individuals from the remainder of SE Polynesia possess *T. teres* haplotypes.

The *Cribrarula* clade includes eight additional taxa, making it the most diverse genus within Bistolidini. Two taxa, *Cribrarula taitae* from American Samoa and *C. garciai* from Easter Island, are added to the deeply divergent Pacific subclade. Both taxa are recently divergent members from their respective sister taxon. *Cribrarula taitae* appears as a closely related sister to *C. catholicorum*, and *C. garciai* is closely related to *C. cumingii*. Only a single individual from each of the two taxa was included in these analyses, and the results would be better addressed with multiple samples. Two members are added to the Western Indian Ocean subclade: *Cribrarula pellisserpentis* and *C. esontropia francescoi*, both from Madagascar. *Cribrarula esontropia francescoi* is a closely related sister to *C. esontropia esontropia*, which includes *C. esontropia cribellum* (Meyer, 2003). *Cribrarula pellisserpentis* is a deeply divergent member within the western Indian Ocean subclade and is sister to the other three ESUs. Four taxa are added to the remaining *Cribrarula* member clade. A single individual of *C. cribraria* from Masirah, Oman, appears significantly divergent from population samples of the previously unnamed *C. cribraria* ESU from the Andaman Sea. Conchologically, this individual approximates the western Indian Ocean taxon *C. cribraria abaliena* and is tentatively recognized as such. A single individual of *C. cribraria australiensis* from Western Australia falls within the Andaman *C. cribraria* cluster; therefore, I tentatively adopt the name *C. cribraria* cf. "*australiensis*" for a taxon that extends from the Andaman Sea southward to Western Australia. More exhaustive sampling is required to confirm these geographic patterns. A single individual of *C. exmouthensis magnifica* from Broome is significantly different from samples of *C. exmouthensis exmouthensis* from the Exmouth Gulf region, therefore validating the status of that taxon. Additional samples of *C. cribraria rottnestensis* (N = 3) further validate the taxon's uniqueness. Eight individuals of *C. melwardi* from northeastern Australia all share a common ancestor and are reciprocally monophyletic with respect to the remaining *C. cribraria* individuals. Moreover, a single *C. cribraria cribraria* individual from the same reef (Lamont Reef in the Bunker Group) clusters as expected with other Pacific *C. cribraria cribraria* individuals. The final taxon included is *C. cribraria abrolhensis* (N = 3), and haplotypes are shallowly divergent but reciprocally monophyletic with respect to samples of *C. cribraria cribraria* (N = 30) from predominately western Pacific localities (Appendix). More thorough analyses and discussion of this fascinating, species-rich group is in preparation (Meyer et al., in prep.).

Derived Compartment (Fig. 6)

The final compartment analyzed is the derived monophyletic clade recognized as the tribe Erroneini. This clade includes the following nine genera: *Austrasiatica*, *Palmulacypraea*, *Erronea*, *Purpuradusta*, *Contradusta*, *Notadusta*, *Eclogavena*, *Melicerona* and *Blasicrura*. Many (25) taxa are added within the tribe, and phylogenetic analyses result in some surprising affinities. For the most part, major genera are well supported, but their interrelationships are not. Three taxa currently ascribed to *Austrasiatica* were included in previous analyses (Meyer, 2003); however, they were considered as representatives of the genus *Nesiocypraea*. As discussed earlier, the finding that *Nesiocypraea teramachii* is distantly related raises the subgenus *Austrasiatica* to generic status for the clade that includes *Austrasiatica langfordi*, *A. hirasei* and *A. sakurai*. As in Meyer (2003), *Austrasiatica* is sister to all other Erroneini taxa, followed by *Pamulacypraea* as sister to the remainder. As predicted in Meyer (2003), the newly added *Pamulacypraea musumea* falls as sister to *P. katsuae*. Even with the addition of 24 taxa (a 67% increase), the topology among the rest of the major Erroneini lineages is ambiguous. Six added "*Erronea*" species form a basal grade leading to the *Adusta*/*Erronea* split previously recognized in Meyer (2003). I take a conservative approach and redefine *Erronea* to include all these taxa and subsume *Adusta* to a well-supported subclade within the group, as the new data demonstrate that *Adusta* and *Erronea* (including the more recent additions) are not equivalent (sisters). If *Adusta* were to be maintained at equivalent generic status, *Erronea* would represent a paraphyletic group. *Purpuradusta*, *Eclogavena*, *Melicerona* and *Blasicrura* are all well-supported monophyletic lineages. As in Meyer (2003), *Notadusta* is well supported only if restricted to members of the *Notadusta punctata* complex. However, because *Notadusta martini* is often considered a member of *Notadusta*, I include it within *Notadusta* here, although poorly supported. In a similarly conservative manner, I include two of the added taxa within *Contradusta*, although again poorly supported. Support for relationships among these seven genera is poor and is likely because of the short internode length between divergent lineages.

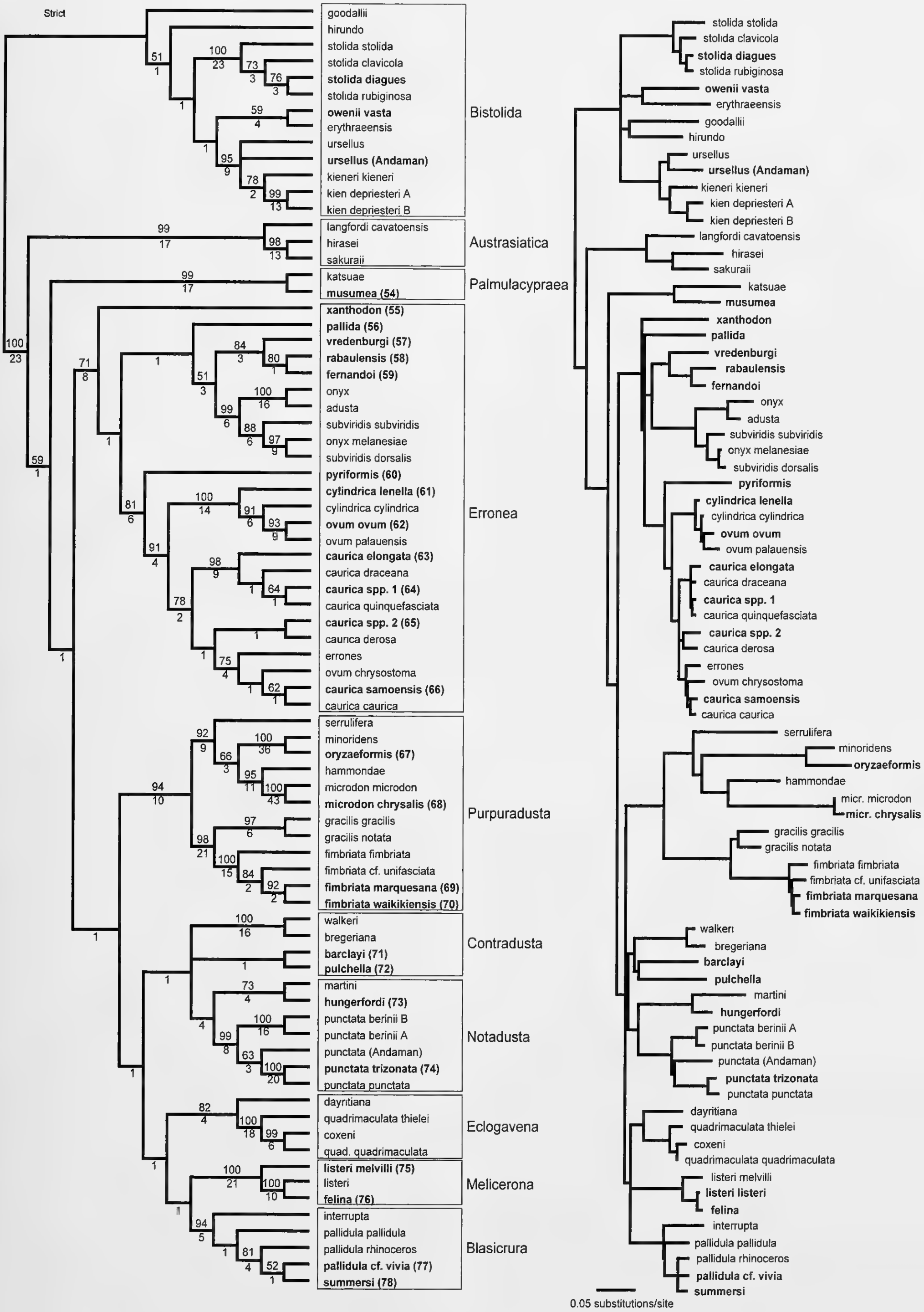

FIG. 6. Derived Compartment cladogram and phylogram. All other information as in Fig. 3.

Twelve additional taxa are added to *Erronea*. Six of the additions are traditionally recognized as distinct species, four have been recognized as subspecies, and two are newly discovered, but may have names associated with them that have been placed into synonymy. Of the new species, three form a relatively well-supported clade: *Erronea rabaulensis* shares a more recent common ancestor with *E. fernandoi* (80/1), and those two are sister to *E. vredenburgi* (84/3). The three additional *Erronea* species all nest deeply within the clade, and their relationships are not well supported. *Erronea pallida* appears as sister to the clade of the previously described three species and *Adusta*. *Erronea pyriformis* is relatively well supported (81/6) as the sister to the clade previously recognized as *Erronea* (Meyer, 2003). Finally, *Erronea xanthodon* falls at the base of *Erronea* and is sister to all other *Erronea* taxa. Within the crown *Erronea* subclade, six taxa are added that are all traditionally recognized at the subspecific level. Individuals of *Erronea cylindrica lenella* (N = 8, all from New Caledonia) form a monophyletic group strongly supported (91/6) as sister to the clade including the remaining E. *cylindrica* individuals plus two subspecies of *E. ovum*. These results imply that *E. cylindrica* at the specific level is a paraphyletic taxon. Newly added individuals of *Erronea ovum ovum* from both Singapore and the Philippines (N = 15) form a monophyletic group sister to *E. ovum palauensis* (N = 7). The four remaining, newly added taxa are all members of the *Erronea caurica* complex. First, individuals (N = 7) of the newly described *E. caurica samoensis* appear as a distinct lineage sister to individuals (N = 15) from the remainder of the Pacific and Western Australia (*E. caurica caurica*). Four geographically structured haplotype clades are found exclusively in the Western Indian Ocean. *Erronea caurica dracaena* is currently restricted to the Seychelles based on sampling. Newly added individuals from East Africa and Madagascar form a haplotype clade that I recognize as *Erronea caurica elongata*. Individuals of *E. caurica quinquefasciata* from the Red Sea, East Africa and Oman form the third monophyletic group. Finally, newly sequenced individuals from Masirah (N = 7) form a private haplotype clade (*E. caurica* ssp. #1) sister to *E. caurica quinquefasciata*. The final, newly added taxon (*E. caurica* ssp. #2) within the *E. caurica* complex is a clade (N = 18) that includes individuals primarily from India, but with a few individuals from Masirah, Oman. This haplotype clade is sister to the clade recognized previously as *E. caurica cf. derosa* from the Andaman Sea (Meyer, 2003). The *Erronea caurica* complex and the associated *E. cylindrica*, *E. ovum* and *E. errones* species will be more thoroughly addressed in another paper (Meyer, in prep.) as the group exhibits remarkable geographic structuring, polyphyly of recognized species (*E. ovum*), and evidence of introgression based on nuclear markers.

Purpuradusta is well supported and contains four newly added taxa that fall in expected relationships. The southeastern Polynesian endemic species *Purpuradusta oryzaeformis* is distinct and sister to *P. minoridens* that ranges throughout the remainder of the western IndoPacific. A single specimen of *P. microdon* from East Africa falls outside the haplotype clade of other sampled individuals from the Pacific basin (N = 5). This East African population is recognized as *Purpuradusta microdon chrysalis*. Two peripheral populations of *Purpuradusta fimbriata* in the Pacific Basin are introduced. First, Hawaiian populations of *P. fimbriata* are distinct (N = 7) and were previously recognized as *P. fimbriata waikikiensis*; thus this name is resurrected as a valid entity. Second, individuals from the Marquesas are also distinct genetically, consistent with the subspecies designation of Lorenz (2002), *P. fimbriata marquesana* (N = 14). Both of these Pacific *P. fimbriata* subclades share a more recent history with the widespread Pacific subspecies *P. fimbriata unifasciata*, as expected.

Two newly added species, *"Erronea" barclayi* and *"Erronea" pulchella*, come out as sister species in phylogenetic analyses. Moreover, these two taxa appear as sister to *Contradusta* in the most likely topology. Because of these results, and the poorly supported nature of their relationships, I tentatively place the two taxa in the genus *Contradusta*, with the caveat that they may be removed with future data. These results are somewhat surprising, particularly because *"Contradusta" pulchella* is thought to be closely related to *Erronea pyriformis* because of the darkly stained columellar dentition and overall conchological similarities. The sister relationship between *Contradusta pulchella* and *C. barclayi* is more acceptable as their divergence is deep, and the phylogenetic affiliations of *C. barclayi* were more difficult to predict based on morphological criteria. Another surprising result is the sister relationship between *Notadusta martini* and *"Erronea" hungerfordi*. Given these phylogenetic results, I tentatively place *"Erronea" hungerfordi* within *Notadusta*, but with little confidence, although it is reasonably supported (73/4), and suspect that it may be removed with more samples and sequence data. Within the remaining *Notadusta* complex, individuals of *N. punctata trizonata* (N = 9) form a monophyletic group sister to the Pacific *N. punctata punctata* clade. Finally, in regards to *Notadusta*, *"Notadusta" rabaulensis* was mentioned previously as a member of *Erronea* and *"Notadusta" musumea* as *Palmulacypraea*, further reducing the membership of *Notadusta* (Meyer, 2003).

The final four additions to the dataset fall into *Melicerona* and *Blasicrura*. First, two taxa are added to *Melicerona*. Samples of *Melicerona listeri melvilli* (N = 5) from Queensland, Australia, form a monophyletic group sister to the remaining *Melicerona* taxa. (Two rostrate and melanistic individuals interfinger among the other three haplotypes indicating that the teratology is likely driven by phenotypic responses to environmental conditions rather than having a genetic basis.) Samples of *Melicerona felina* from both Oman and East Africa form a monophyletic group, and because the haplotypes from the two regions interfinger, there is no evidence for a distinction between the subspecies *M. felina felina* and *M. felina fabula*. Within *Blasicrura*, two taxa are added, based on the sequencing results. First, samples of *Blasicrura summersi*, a Fijian and Tonga endemic, appear as a recently divergent sister to the also newly included *B. pallidula* cf. *vivia* from American Samoa. This clade is sister to the Melanesian subspecies *Blasicrura pallidula rhinoceros*, as expected based on geography. This resulting topology indicates that the *Blasicrura pallidula* complex is paraphyletic.

DISCUSSION

The ultimate goal of this project is to construct a comprehensive phylogeny of cypraeid gastropods at the appropriate level for diversification studies. From a molecular perspective, all ESUs presented are effectively equal units of diversity, whether they are currently recognized as species, subspecies or some other level. There are some noted exceptions as OTUs were used on occasion that represented unsorted or clinal variation within an ESU (e.g., *Erosaria miliaris/eburnea*). However, on a general scale, each taxon shown in the phylogenies (Figs. 3–6) represents an independent evolutionary trajectory.

Because so much taxonomic information is available for cowries, it is informative to see how molecular criteria compare with recognized taxonomic entities. The most recent compilation of the cowries is that of Lorenz (2002), and I will use his checklist (pp. 250–291) as a benchmark for comparisons. Lorenz recognizes 232 species, of which I have sequenced 210 (> 90%), and they are presented herein. The missing species are as follows: *Nesiocypraea aenigma*, *N. lisetae*, *N. midwayensis*, *Austrasiatica alexhuberti*, *Erosaria ostergaardi*, *Zoila perlae*, *Lyncina camelopardis*, *L. joycae*, *Pustularia chiapponii*, *Cypraeovula colligata*, *C. cruickshanki*, *C. immelmani*, *Palmadusta androyensis*, *P. johnsonorum*, *Austrasiatica deforgesi*, *Palmulacypraea boucheti*, *P. omii*, *Eclogavena luchuana*, *Erronea* (?) *angioyorum*, and *E. nymphae*. Sequences from samples of both *Purpuradusta barbieri* and "*Talostolida*" *rashleighana* have been obtained, but were too late for inclusion in these analyses. All missing species are rare, with small ranges located generally at the periphery of their putative sister species based on conchological and anatomical characters. Of the 210 sequenced species, phylogenetic comparisons and molecular criteria support all but 15 (93%) as ESUs. The 15 recognized species not supported by my criteria are discussed below. For *Nucleolaria granulata*, *Monetaria obvelata*, *Erosaria eburnea*, *Zoila orientalis*, *Z. thersites*, *Luria controversa*, *L. gilvella*, *Notocypraea occidentalis*, and *Palmadusta humphreysii*, multiple individuals were sequenced and the haplotypes interfingered within their closest relative. For the next six species that I do not support, only a single individual was sequenced, thus they may indeed represent a very young independent trajectory. However, when compared to the genetic diversity within their closest relative, the genetic difference is unremarkable, and in some instances, only a single mutation different from putative conspecifics: *Zonaria angelicae*, *Z. petitiana*, *Cypraeovula mikeharti*, *Bistolida brevidentata*, *Cribrarula garciai*, and *C. taitae*.

While genetic data are overall broadly consistent with taxa recognized at the specific level, the results are even more remarkable when compared among taxa recognized at subspecific levels. Lorenz recognizes 260 taxa at the subspecific level. Of those 260 subspecies, I have sequenced at least two individuals from 160 in order to assess their validity. Molecular criteria support 113 (> 70%) of these taxa as legitimate ESUs. Moreover, sequence results indicate an additional 20 distinct ESUs not recognized as subspecies by Lorenz (but sometimes mentioned as important varieties or forms). A full listing of sampled taxa and their current ESU status as indicated by the prior criteria can be found at the Cowrie Genetic Database Project Website (http://www.flmnh.ufl.edu/cowries). The website includes other information, such as localities sampled, numbers of individuals for each taxon, and photographs of the specimens sequenced.

Overwhelming molecular support for traditionally recognized taxa, both at specific and subspecific levels, is extremely encouraging. First, from a taxonomic standpoint, these molecular results corroborate the excellent work done by centuries of malacological researchers, at both professional and amateur levels. Similar molecular surveys of other diverse groups will provide valuable comparisons in order to assess taxonomic congruence (e.g., Jackson & Cheetham, 1990) and address concordant diversification patterns. Second, from a molecular perspective, sequence data provide a suitable, objective, relative metric for circumscribing appropriate evolutionary units. Assuming rate constancy in the molecules (COI only, in prep.), molecular divergences can constrain the tempo of diversification and assess the distinctiveness of purported taxa. A growing body of molecular data across the diversity of life undoubtedly will provide insight to some of our most fundamental evolutionary questions.

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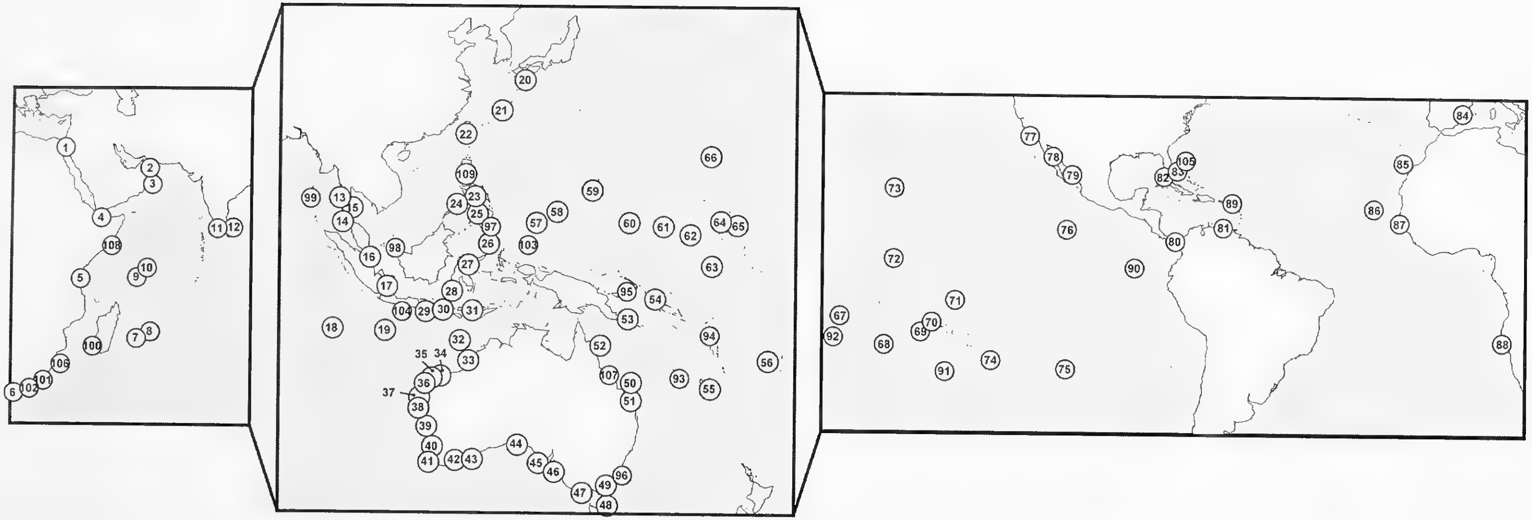

1 - Elat - Red Sea
2 - Muscat
3 - Masirah
4 - Djibouti
5 - Dar es Salaam, Zanzibar
6 - Hout Bay to Cape St. Francis
7 - Reunion
8 - Mauritius
9 - Mahe, Seychelles
10 - Praslin, LaDigue
11 - Tuticorin, India
12 - Sri Lanka
13 - Mergui archipelago
14 - Phuket
15 - Koh Samui, Koh Tao
16 - Singapore
17 - N. Java
18 - Cocos Keeling
19 - Christmas Island
20 - Japan
21 - Okinawa
22 - Taiwan
23 - Cebu, Olango Island
24 - Coron, Palawan
25 - Bohol, Balicasag
26 - Manado
27 - Tomini
28 - Spermonde
29 - Bali
30 - Lombok
31 - Timor
32 - NW Shelf (Cassini, Seringapatam, Cartier)
33 - Broome
34 - Onslow
35 - Exmouth
36 - Coral Bay
37 - Quobba
38 - Dirk Hartog, Sharks Bay
39 - Horrocks, Jurien
40 - Perth, Rottnest, Mandurah
41 - SW Cape
42 - Albany
43 - Esperance
44 - Ceduna, Great Australian Bight
45 - Port Lincoln
46 - Kangaroo Island
47 - Port Macdonnell
48 - Tasmania
49 - Lakes Entrance
50 - Capricorn Channel
51 - Moreton Bay
52 - Lizard Island, GBR
53 - Louisades, PNG
54 - Solomon Islands
55 - New Caledonia
56 - Fiji
57 - Palau
58 - Yap
59 - Guam
60 - Chuuk
61 - Pohnpei
62 - Kosrae
63 - Nauru
64 - Kwajelein
65 - Majuro
66 - Wake
67 - American Samoa
68 - Rarotonga
69 - Society Islands
70 - Tuamotu
71 - Marquesas
72 - Kiritimati
73 - Hawaii
74 - Pitcairn
75 - Easter Island
76 - Clipperton Island
77 - California
78 - Baja, Sea of Cortez
79 - Puerto Vallarta
80 - Panama
81 - Colombia
82 - Florida Keys
83 - Florida
84 - Mediterranean
85 - Canary Islands
86 - Cape Verde Islands
87 - Senegal
88 - Angola
89 - Martinique
90 - Galapagos
91 - Rapa
92 - Tonga
93 - Chesterfields
94 - Vanuatu
95 - Rabaul
96 - New South Wales
97 - Balut
98 - South China Sea
99 - Andaman Is.
100 - Tulear
101 - Natal
102 - Cape St. Francis to East London
103 - Helen Reef
104 - S. Java
105 - Bahamas
106 - Mozambique
107 - Dingo Beach
108 - Somalia
109 - Luzon Is.

FIG. 7. Sampled localities indicated for listed taxa in Appendix (column 3).

APPENDIX 1: Sampled Taxa and Supplementary Data

New taxa and sequence data are numbered and bolded. Additional, newly sampled localities for taxa previously reported are also bolded. Crossouts are names previously used in Meyer (2003) that are corrected herein because of taxonomic revisions. *for the legend see Fig. 7.

OTUs	Authors	Sampled localities*	Accession #	
			16S	COI
		OUTGROUPS		
Jenneria pustulata	Lightfoot, 1786	79	AY161402	AY161635
Pseudocypraea adamsonii	Sowerby I, 1832	5	AY161403	AY161636
1. *Pseudocypraea exquisita*	**Petuch, 1979**	**23**	**AY534351**	**AY534428**
Pedicularia pacifica	Pease, 1865	57, **59**	AY161384	AY161617
Crenavolva tokuoi	Azuma, 1989	25	AY161390	AY161623
Prionovolva brevis	Sowerby I, 1828	23	AY161391	AY161624
Serratovolva dondani	Cate, 1964	23	AY161392	AY161625
Phenacovolva tokioi	Cate, 1973	26	AY161393	AY161626
Crenavolva cf rosewateri	Cate, 1973	25	AY161394	AY161627
2. *Volva volva*	**Linnaeus, 1758**	**22**	**AY534352**	**AY534429**
Phenacovolva weaveri	Cate, 1973	25	AY161395	AY161628
3. *Primovula concinna*	**Adams & Reeve, 1848**	**57**	**AY534353**	**AY534430**
4. *Dentiovula takeoi*	**Cate & Azuma, 1973**	**3**	**AY534354**	**AY534431**
5. *Prosimnia semperi*	**Weinkauff, 1881**	**57**	**AY534355**	**AY534432**
Adamantia florida	Kuroda, 1958	25	AY161396	AY161629
Calpurnus verrucosus	Linnaeus, 1758	30	AY161397	AY161630
Calpurnus lacteus	Lamarck, 1810	59	AY161398	AY161631
Ovula ovum	Linnaeus, 1758	28	AY161399	AY161632
Cyphoma gibbosum	Linnaeus, 1758	83	AY161400	AY161633
Simnia aequalis	Sowerby I, 1832	78	AY161401	AY161634

(continues)

(continued)

OTUs	Authors	Sampled localities*	Accession # 16S	Accession # COI
		INGROUPS		
6. Propustularia surinamensis	**Perry, 1811**	**89**	**AY534356**	**AY534433**
7. Nesiocypraea teramachii neocaledonica	**Lorenz, 2002**	**93**	**AY534357**	**AY534434**
Ipsa childreni	Gray, 1825	59, 64	AY161404	AY161637
Cryptocypraea dillwyni	Schilder, 1922	59	AY161411	AY161644
Nucleolaria nucleus	Linnaeus, 1758	5, 53, 64, 69	AY161417	AY161650
Nucleolaria granulata	Pease, 1862	73	AY161418	AY161651
Staphylaea limacina interstincta	Wood, 1828	5, 9	AY161412	AY161645
Staphylaea limacina limacina	Lamarck, 1810	23, 30, 51	AY161413	AY161646
Staphylaea staphylaea laevigata	Dautzenberg, 1932	5, 8	AY161414	AY161647
Staphylaea staphylaea staphylaea	Linnaeus, 1758	20, 51, 52, 53, 59	AY161415	AY161648
Staphylaea semiplota	Mighels, 1845	73	AY161416	AY161649
Monetaria annulus	Linnaeus, 1758	3, 5, 8, 10, 30, 52, 68	AY161405	AY161638
Monetaria obvelata	Lamarck, 1810	68, 69, 70	AY161406	AY161639
Monetaria moneta	Linnaeus, 1758	5, 8, 30, 71, **59**	AY161407	AY161640
Monetaria caputserpentis caputophidii	Schilder, 1927	73	AY161409	AY161642
Monetaria caputserpentis caputserpentis	Linnaeus, 1758	5, 19, 59, 66, 71, **91**	AY161408	AY161641
Monetaria caputdraconis	Melvill, 1888	75	AY161410	AY161643
Perisserosa guttata	Gmelin, 1791	25	AY161419	AY161652
8. Erosaria marginalis	**Dillwyn, 1827**	**5, 108**	**AY534358**	**AY534435**
9. Erosaria citrina	**Gray, 1825**	**100, 101**	**AY534359**	**AY534436**
Erosaria helvola helvola	Linnaeus, 1758	5, 10, 30, 53, 59, 69, 70	AY161429	AY161662
Erosaria helvola hawaiiensis	Melvill, 1888	73	AY161430	AY161663
10. Erosaria helvola cf. callista	**Shaw, 1909**	**71**	**AY534360**	**AY534437**
Erosaria turdus	Lamarck, 1810	1, 2	AY161420	AY161653
11. Erosaria irrorata	**Gray, 1828**	**69, 70**	**AY534361**	**AY534438**
Erosaria albuginosa	Gray, 1825	79	AY161427	AY161660
Erosaria poraria	Linnaeus, 1758	19, 59, 69	AY161428	AY161661
Erosaria beckii	Gaskoin, 1836	59, **23, 31**	AY161425	AY161658
12. Erosaria macandrewi	**Sowerby II, 1870**	**1**	**AY534362**	**AY534439**
13. Erosaria englerti	**Summers & Burgess, 1965**	**75**	**AY534363**	**AY534440**

(continues)

(continued)

OTUs	Authors	Sampled localities*	Accession # 16S	Accession # COI
Erosaria kingae	Rehder & Wilson, 1975	74	AY161424	AY161657
Erosaria thomasi	Crosse, 1865	71	AY161426	AY161659
Erosaria cernica	Sowerby II, 1870	38, **73**	AY161423	AY161656
Erosaria spurca	Linnaeus, 1758	84, 85, 86	AY161421	AY161654
Erosaria acicularis	Gmelin, 1791	83	AY161422	AY161655
Erosaria labrolineata	Gaskoin, 1849	52, **25**	AY161433	AY161666
Erosaria boivinii	Kiener, 1843	20, 23	AY161434	AY161667
Erosaria ocellata	Linnaeus, 1758	2, 12	AY161431	AY161664
Erosaria gangranosa	Dillwyn, 1817	14	AY161432	AY161665
Erosaria lamarckii cf redimita	Melvill, 1888	14	AY161437	AY161670
14. Erosaria lamarckii lamarckii	**Gray, 1825**	**5**	**AY534364**	**AY534441**
Erosaria miliaris	Gmelin, 1791	15, 33	AY161435	AY161668
Erosaria eburnea	Barnes, 1824	54, **55**	AY161436	AY161669
Errosaria nebrites	Melvill, 1888	1, 2	AY161438	AY161671
Erosaria erosa (Indian)	Linnaeus, 1758	5, 8, 10, 14	AY161440	AY161673
Erosaria erosa (Pacific) *cf. chlorizans*	Melvill, 1888	19, 30, 59, 69	AY161439	AY161672
Umbilia armeniaca	Verco, 1912	43, 44, 45	AY161493	AY161726
Umbilia hesitata	Iredale, 1916	48, 49	AY161492	AY161725
Umbilia capricornica	Lorenz, 1989	50	AY161494	AY161727
15. Umbilia cf. petilirostris	**Darragh, 2002**	**50**	**AY534365**	**AY534442**
Macrocypraea cervinetta	Kiener, 1843	79	AY161485	AY161718
Macrocypraea cervus	Linnaeus, 1771	83, **82**	AY161486	AY161719
Macrocypraea zebra	Linnaeus, 1758	82, **83**	AY161487	AY161720
Leporicypraea valentia	Perry, 1811	25	AY161484	AY161717
Leporicypraea mappa rosea	Gray, 1824	8	AY161480	AY161713
16. Leporicypraea mappa aliwalensis	**Lorenz, 2002**	**101**	**AY534366**	**AY534443**
Leporicypraea mappa mappa	Linnaeus, 1758	22, 23, **98**	AY161481	AY161714
Leporicypraea geographica	Schilder & Schilder, 1933	5, 10, 14, 32, **54, 56, 57, 98**	AY161482	AY161715
Leporicypraea mappa ~~panerythra~~ ***viridis***	~~Melvill, 1888~~; Kenyon, 1902	55, 57, 59, 64	AY161479	AY161712
Leporicypraea mappa ~~viridis~~ ***admirabilis***	~~Kenyon, 1902~~; Lorenz, 2002	71	AY161483	AY161716
Mauritia scurra indica	Gmelin, 1791	30, 59, 71	AY161477	AY161710
Mauritia scurra scurra	Gmelin, 1791	5, 10	AY161478	AY161711

(continues)

(continued)

OTUs	Authors	Sampled localities*	Accession #	
			16S	COI
Mauritia mauritiana	Linnaeus, 1758	5, 19, 52, 70	AY161474	AY161707
Mauritia depressa dispersa	Schilder & Schilder, 1939	10, 19	AY161475	AY161708
Mauritia depressa depressa	Gray, 1824	59, 64, 69	AY161476	AY161709
Mauritia grayana	Schilder, 1930	2, 3	AY161467	AY161700
Mauritia eglantina	Dulcos, 1833	32, 52, 59, 64	AY161469	AY161702
Mauritia histrio	Gmelin, 1791	5, 9, 19	AY161470	AY161703
Mauritia arabica arabica	Linnaeus, 1758	19, 21, 22, 23, 25, 29, 30, 32, 33, 52, 55, 56, 59, 61, 63, 64	AY161465	AY161698
***17. Mauritia arabica arabica* (Am. Samoa)**		**67**	**AY534367**	**AY534444**
Mauritia arabica asiatica	Schilder & Schilder, 1939	2, 11, 13, 15, 19, 23, 29, 30	AY161466	AY161699
Mauritia arabica immanis		5, 7, 8	AY161468	AY161701
Mauritia maculifera (Marquesas) ***martybealsi***	**Lorenz, 2002**	71	AY161472	AY161705
Mauritia maculifera (N. Pacific) *maculifera*	Schilder, 1932	59, 66, 73	AY161471	AY161704
Mauritia maculifera (Polynesia) ***scindata***	**Lorenz, 2002**	69, 70	AY161473	AY161706
18. Barycypraea teulerei	**Cazenavette, 1846**	**3**	**AY534368**	**AY534445**
19. Barycypraea fultoni	**Sowerby III, 1903**	**106**	**AY534369**	**AY534446**
Zoila marginata marginata	Gaskoin, 1849	43, 44, 45, 46	AY161495	AY161728
20. Zoila marginata ketyana	**Raybaudi, 1978**	38, 39, 40	**AY534370**	**AY534447**
Zoila rosselli	Cotton, 1948	37, 38, 39, 40, 41, 42, 43	AY161497	AY161730
Zoila venusta	Sowerby II, 1846	39, 40, 41, 43	AY161496	AY161729
Zoila eludens	Raybaudi, 1991	35	AY161499	AY161732
Zoila decipiens	Smith, 1880	33, 34	AY161498	AY161731
21. Zoila mariellae	**Raybaudi, 1983**	**32 (?)**	**AY534371**	**AY534448**
Zoila thersites	Gaskoin, 1849	45, 46	AY161503	AY161736
Zoila jeaniana sherlyae	Raybaudi, 1990	37	AY161500	AY161733
Zoila jeaniana jeaniana	Cate, 1968	36	AY161501	AY161734
Zoila friendii friendii	Gray, 1831	39, 40, 41, 42, 43	AY161502	AY161735
Muracypraea mus	Linnaeus, 1758	81	AY161491	AY161724
Cypraea tigris (Indian)	Linnaeus, 1758	3, 5, 8, 9, 10, 14	AY161489	AY161722
Cypraea tigris (Pacific)		15, 18, 19, 23, 30, 32, 33, 52, 56, 57, 59, 60, 61, 62, 63, 64, 69, 70, 73	AY161488	AY161721
Cypraea pantherina	Lightfoot, 1786	1	AY161490	AY161723

(continues)

(continued)

OTUs	Authors	Sampled localities*	Accession # 16S	COI
Talparia talpa	Linnaeus, 1758	5, 30, 64	AY161464	AY161697
22. Talparia exusta	**Sowerby I, 1832**	**4**	**AY534372**	**AY534449**
Luria lurida	Linnaeus, 1758	84, 86, 87	AY161462	AY161695
Luria cinerea	Gmelin, 1791	83, **82, 105**	AY161461	AY161694
Luria pulchra	Gray, 1824	2	AY161463	AY161696
Luria tessellata	Swainson, 1822	73	AY161460	AY161693
Luria isabella	Linnaeus, 1758	5, 8, 9, 20, 30, 65, 69, 73, **98**	AY161458	AY161691
Luria isabellamexicana	Stearns, 1893	76, 79	AY161459	AY161692
Annepona mariae	Schilder, 1927	59, 64, 70	AY161443	AY161676
Trona stercoraria	Linnaeus, 1758	87	AY161441	AY161674
Chelycypraea testudinaria	Linnaeus, 1758	5, 59, 64	AY161442	AY161675
Lyncina (Austrocypraea) reevei	Sowerby I, 1832	41, 45	AY161444	AY161677
Lyncina (cf. Miolyncina) porteri	Cate, 1966	97	AY161448	AY161681
Lyncina (Arestoides) argus argus	Linnaeus, 1758	30, 59	AY161445	AY161678
23. Lynicna (Arestoides) argus contrastriata	**Perry, 1811**	**10**	**AY534373**	**AY534450**
24. Lyncina (Callistocypraea) broderipii	**Sowerby I, 1832**	**101**	**AY534374**	**AY534451**
Lyncina (Callistocypraea) nivosa	Broderip, 1827	13, 14	AY161446	AY161679
Lyncina (Callistocypraea) leucodon	Broderip, 1827	23, **57**	AY161447	AY161680
Lyncina (Callistocypraea) aurantium	Gmelin, 1791	59, **54**	AY161449	AY161682
Lyncina ventriculus	Lamarck, 1810	59, 69, 70	AY161452	AY161685
25. Lyncina ventriculus (Xmas IO)		**19**	**AY534375**	**AY534452**
Lyncina sulcidentata	Gray, 1824	73	AY161450	AY161683
26. Lyncina kuroharai	**Kuroda & Habe, 1961**	**20**	**AY534376**	**AY534453**
Lyncina schilderorum	Iredale, 1939	69, 70, 73	AY161451	AY161684
Lyncina lynx	Linnaeus, 1758	9, 30, 69, **5**	AY161456	AY161689
Lyncina vitellus	Linnaeus, 1758	5, 8, 30	AY161457	AY161690
Lyncina leviathan	Schilder & Schilder, 1937	5, 20, 55, 59, 69, 73	AY161453	AY161686
Lyncina carneola	Linnaeus, 1758	1, 9, 13, 20, 30, 52, 53, 55, 59, 69	AY161454	AY161687
Lyncina propinqua	Garrett, 1879	69, 71	AY161455	AY161688
Pustularia globulus globulus	Linnaeus, 1758	59	AY161507	AY161740
Pustularia globulus brevirostris	Schilder & Schilder, 1938	5, 10	AY161508	AY161741

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OTUs	Authors	Sampled localities*	Accession # 16S	 COI
Pustularia bistrinotata bistrinotata	Schilder & Schilder, 1937	27, 59, 64	AY161504	AY161737
27. Pustularia bistrinotata keelingensis	**Schilder & Schilder, 1940**	**98**	**AY534377**	**AY534454**
28. Pustularia bistrinotata sublaevis	**Schilder & Schilder, 1938**	**69, 70**	**AY534378**	**AY534455**
Pustularia mauiensis	Burgess, 1967	73	AY161505	AY161738
Pustularia cicercula	Linnaeus, 1758	5, 14, 59, 64, 69	AY161506	AY161739
Pustularia margarita	Dillwyn, 1817	59	AY161509	AY161742
Neobernaya spadicea	Swainson, 1823	77	AY161517	AY161750
Pseudozonaria annettae	Dall, 1909	78	AY161518	AY161751
Pseudozonaria arabicula	Lamarck, 1810	79	AY161519	AY161752
29. Pseudozonaria nigropunctata	**Gray, 1828**	**90**	**AY534379**	**AY534456**
Pseudozonaria robertsi	Hildalgo, 1906	80	AY161520	AY161753
30. Schilderia achatidea	**Sowerby I, 1837**	**84**	**AY534380**	**AY534457**
Zonaria sanguinolenta	Gmelin, 1791	87	AY161512	AY161745
31. Zonaria picta	**Gray, 1824**	**86**	**AY534381**	**AY534458**
Zonaria zonaria	Gmelin, 1791	87	AY161513	AY161746
Zonaria pyrum senegalensis	Schilder, 1928	87	AY161510	AY161743
Zonaria pyrum angolensis	Odhner, 1923	88	AY161511	AY161744
32. Zonaria pyrum angelicae	**Clover, 1974**	**87**	**AY534382**	**AY534459**
33. Notocypraea hartsmithi	**Schilder, 1967**	**96**	**AY534383**	**AY534460**
Notocypraea piperita	Gray, 1847	41, 43, 45, 48	AY161524	AY161757
Notocypraea pulicaria	Reeve, 1846	41	AY161525	AY161758
Notocypraea comptoni	Gray, 1847	43, 45, 47, 48, 49	AY161521	AY161754
Notocypraea angustata	Gmelin, 1791	47, 48	AY161522	AY161755
***34. Notocypraea angustata* (Port Lincoln)**		**45**	**AY534384**	**AY534461**
Notocypraea declivis	Sowerby II, 1870	47, 48	AY161523	AY161756
Cypraeovula connelli	Liltved, 1983	102	AY161527	AY161760
Cypraeovula castanea	Higgins, 1868	6	AY161526	AY161759
Cypraeovula iutsui	Shikama, 1974	102	AY161528	AY161761
Cypraeovula capensis	Gray, 1828	102	AY161530	AY161763
35. Cypraeovula fuscorubra	**Shaw, 1909**	**6**	**AY534385**	**AY534462**
36. Cypraeovula fuscodentata	**Gray, 1825**	**6**	**AY534386**	**AY534463**
Cypraeovula coronata	Schilder, 1930	102	AY161529	AY161762

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OTUs	Authors	Sampled localities*	Accession #	
			16S	COI
37. **Cypraeovula mikeharti**	**Lorenz, 1985**	**6**	**AY534387**	**AY534464**
38. **Cypraeovula** algoensis	**Gray, 1825**	**6**	**AY534388**	**AY534465**
Cypraeovula edentula	Gray, 1825	102	AY161531	AY161764
Cypraeovula alfredensis	Schilder & Schilder, 1929	102	AY161532	AY161765
Palmadusta contaminata distans	Schilder & Schilder, 1938	5	AY161555	AY161789
Palmadusta contaminata contaminata	Sowerby I, 1832	25, 32, 71	AY161556	AY161790
Palmadusta asellus cf. *bitaeniata*	Geret, 1903	30, 63	AY161543	AY161777
Palmadusta asellus cf. *asellus*	Linnaeus, 1758	5	AY161545	AY161779
Palmadusta asellus cf. *vespacea*	Melvill, 1905	10, 23, 25	AY161544	AY161778
Palmadusta saulae	Gaskoin, 1843	13, 20	AY161554	AY161788
Palmadusta lentiginosa	Gray, 1825	3, 11	AY161557	AY161791
Palmadusta humphreysii	Gray, 1825	55, **51**	AY161550	AY161784
Palmadusta lutea	Gmelin, 1791	23, 64	AY161549	AY161783
Palmadusta ziczac ziczac	Linnaeus, 1758	25, 54	AY161552	AY161786
Palmadusta ziczac misella	Perry, 1811	5	AY161553	AY161787
Palmadusta diluculum	Reeve, 1845	5, 10	AY161558	AY161792
Palmadusta clandestina passerina	Melvill, 1888	3, 5, 10, **8**	AY161548	AY161782
39. **Palmadusta** clandestina **cf.** *clandestina* **(Andaman)**	Linnaeus, 1758	**14**	**AY534389**	**AY534466**
Palmadusta artuffeli	Jousseaume, 1876	20	AY161546	AY161780
Palmadusta clandestina ~~clandestina~~ cf. *candida*	Pease, 1865	23, 30, 33, 38, 53, 55, 59, 64, **28**	AY161547	AY161781
Bistolida stolida stolida	Linnaeus, 1758	24, 32, 55, 59, **23, 51, 64**	AY161536	AY161770
Bistolida stolida clavicola	Melvill, 1888	5	AY161534	AY161768
40. **Bistolida** stolida diag**u**es	**Melvill, 1888**	**10**	**AY534390**	**AY534467**
Bistolida stolida rubiginosa	Gmelin, 1791	30	AY161535	AY161769
Bistolida erythraeensis	Sowerby I, 1837	4	AY161533	AY161767
41. **Bistolida** o**w**enii	**Sowerby I, 1837**	**100**	**AY534391**	**AY534468**
Bistolida goodallii	Sowerby I, 1832	69, 72	AY161537	AY161771
Bistolida hirundo	Linnaeus, 1758	14, 15, 52, 53, 55, 59, **12**	AY161539	AY161773
Bistolida ursellus	Gmelin, 1791	25, 59	AY161541	AY161775
42. **Bistolida** **ursellus** **(Andaman)**		**14**	**AY534392**	**AY534469**

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OTUs	Authors	Sampled localities*	Accession # 16S	Accession # COI
Bistolida kieneri kieneri	Hidalgo, 1906	5, 8, 9	AY161542	AY161776
Bistolida kieneri depriesteri A	Schilder, 1933	29, 52	AY161540	AY161774
Bistolida kieneri depriesteri B		19, 28, 29	AY161538	AY161772
Ovatipsa chinensis ***chinensis***	Gmelin, 1791	5, **25, 29**	AY161559	AY161793
43. Ovatipsa chinensis amiges	**Melvill & Standen, 1904**	38, 53, 59, 73, **23**	**AY534393**	**AY534470**
Ovatipsa coloba	Melvill, 1888	14, **3**	AY161560	AY161794
Talostolida teres	Gmelin, 1791	53, 59, 69, **98**	AY161561	AY161795
Talostolida pellucens	Melvill, 1888	5, 14, 19, 30, 38, 59, 64, 73, 76, 80, **71**	AY161562	AY161796
44. Talostolida subteres	**Weinkauff, 1881**	**70**	**AY534394**	**AY534471**
45. Talostolida latior	**Melvill, 1888**	**73**	**AY534395**	**AY534472**
Cribrarula gaskoini	Reeve, 1846	73	AY161572	AY161806
Cribrarula catholicorum	Schilder & Schilder, 1938	54	AY161575	AY161809
46. Cribrarula taitae	**Burgess, 1993**	**67**	**AY534396**	**AY534473**
Cribrarula cumingii	Sowerby I, 1832	69, 70	AY161573	AY161807
47. Cribrarula garciai	**Lorenz & Raines, 2001**	**75**		**AY534474**
Cribrarula astaryi	Schilder, 1971	71	AY161574	AY161808
Cribrarula cribraria comma	Perry, 1811	5	AY161565	AY161799
48. Cribrarula pellisserpentis	**Lorenz, 1999**	**100**	**AY534397**	**AY534475**
49. Cribrarula esontropia francescoi	**Lorenz, 2002**	**100**	**AY534398**	**AY534476**
Cribrarula cribellum	Gaskoin, 1849	7	AY161563	AY161797
Cribrarula esontropia	Duclos, 1833	7	AY161564	AY161798
Cribrarula fallax	Smith, 1881	41	AY161569	AY161803
Cribrarula cribraria (Andaman) ***australiensis***	**Lorenz, 2002**	14, **38**	AY161567	AY161801
50. Cribrarula cribraria cf. abaliena	**Lorenz, 1989**	**3**	**AY534399**	**AY534477**
Cribrarula gaspardi	Biraghi, &, Nicolay, 1993	64	AY161570	AY161804
Cribrarula ~~cribraria~~ exmouthensis	Melvill, 1888	35	AY161571	AY161805
51. Cribrarula exmouthensis magnifica	**Lorenz, 2002**	**33**	**AY534400**	**AY534478**
Cribrarula cribraria cribraria	Linnaeus, 1758	15, 24, 38, 52, 53, 55, 59, **23, 50, 98**	AY161566	AY161800
52. Cribrarula cribraria melwardi	**Iredale, 1930**	**50**	**AY534401**	**AY534479**
Cribrarula cribraria rottnestensis	Raybaudi, 1987	40	AY161568	AY161802
53. Cribrarula cribraria abrolhensis	**Lorenz, 2002**	**38**	**AY534402**	**AY534480**
~~Nesiocypraea~~ ***Austrasiatica*** *langfordi*	Kuroda, 1938	93	AY161516	AY161749

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OTUs	Authors	Sampled localities*	Accession # 16S	Accession # COI
~~*Nesiocypraea*~~ ***Austrasiatica*** *hirasei*	Roberts, 1913	25	AY161514	AY161747
~~*Nesiocypraea*~~ ***Austrasiatica*** *sakurai*	Habe, 1970	25	AY161515	AY161748
Palmulacypraea katsuae	Kuroda, 1960	25	AY161584	AY161818
54. Palmulacypraea musumea	**Kuroda & Habe, 1961**	**55**	**AY534403**	**AY534481**
55. Erronea xanthodon	**Sowerby I, 1832**	**51**	**AY534404**	**AY534482**
56. Erronea pallida	**Gray, 1824**	**16**	**AY534405**	**AY534483**
57. Erronea vredenburgi	**Schilder, 1927**	**104**	**AY534406**	**AY534484**
58. Erronea rabaulensis	**Schilder, 1964**	**95**	**AY534407**	**AY534485**
59. Erronea fernandoi	**Cate, 1969**	**109**	**AY534408**	
Erronea (Adusta) onyx	Linnaeus, 1758	3, 14, 20, 57, **11**	AY161608	AY161842
Erronea (Adusta) adusta	Lamarck, 1810	5, **9**	AY161610	AY161844
Erronea (Adusta) subviridis subviridis	Reeve, 1835	55, **51**	AY161612	AY161846
Erronea (Adusta) onyx melanesiae	Schilder, 1937	54	AY161609	AY161843
Erronea (Adusta) subviridis dorsalis	Schilder & Schilder, 1938	33, **38**	AY161611	AY161845
60. Erronea pyriformis	**Gray, 1824**	**107**	**AY534409**	**AY534486**
Erronea cylindrica ***cylindrica***	Born, 1778	16, 24, 30, 33, 59	AY161607	AY161841
61. Erronea cylindrica lenella	**Iredale, 1939**	**55**	**AY534410**	**AY534487**
62. Erronea ovum ovum	**Gmelin, 1791**	**16, 23**	**AY534411**	**AY534488**
Erronea ovum palauensis	Schilder & Schilder, 1938	57	AY161601	AY161835
Erronea errones	Linnaeus, 1758	11, 14, 16, 30, 52, 55, 57, 58, **33, 53, 56**	AY161606	AY161840
Erronea ovum chrysostoma	Schilder, 1927	53, 54	AY161600	AY161834
Erronea caurica caurica	Linnaeus, 1758	23, 30, 33, 38, 52, 53, 55, 64	AY161602	AY161836
Erronea caurica cf. derosa	Gmelin, 1791	14, **11**	AY161603	AY161837
Erronea caurica dracaena	Born, 1778	9, 10	AY161604	AY161838
Erronea caurica quinquefasciata	Roding, 1798	1, 3, 5	AY161605	AY161839
63. Erronea caurica elongata	**Perry, 1811**	**5**	**AY534412**	**AY534489**
64. Erronea caurica spp. 1		**3**	**AY534413**	**AY534490**
65. Erronea caurica spp. 2		**3, 11**	**AY534414**	**AY534491**
66. Erronea caurica samoensis	**Lorenz, 2002**	**55, 67**	**AY534415**	**AY534492**
Purpuradusta serrulifera	Schilder & Schilder, 1938	69, 71	AY161578	AY161812
Purpuradusta minoridens	Melvill, 1901	14, 32, **31, 98**	AY161577	AY161811
67. Purpuradusta oryzaeformis	**Lorenz & Sterba, 1999**	**69, 70**	**AY534416**	**AY534493**

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OTUs	Authors	Sampled localities*	Accession # 16S	Accession # COI
Purpuradusta microdon ***microdon***	Gray, 1828	52, 59, **56**	AY161576	AY161810
68. Purpuradusta microdon chrysalis	**Kiener, 1843**	**5**	**AY534417**	**AY534494**
Purpuradusta hammondae	Iredale, 1939	23, 38, **98**	AY161579	AY161813
Purpuradusta gracilis notata	Gill, 1858	3, 5	AY161581	AY161815
Purpuradusta gracilis gracilis	Gaskoin, 1849	14, 15, 20, 28, 33, 59, **11, 51**	AY161580	AY161814
Purpuradusta fimbriata fimbriata	Gmelin, 1791	5, 9, 14	AY161582	AY161816
Purpuradusta fimbriata unifasciata	Mighels, 1845	30, 31, 59, 64, 69, **18, 19, 23, 61, 70**	AY161583	AY161817
69. Purpuradusta fimbriata marquesana	**Lorenz, 2002**	**71**	**AY534418**	**AY534495**
70. Purpuradusta fimbriata waikikiensis	**Schilder, 1933**	**73**	**AY534419**	**AY534496**
Contradusta walkeri	Sowerby I, 1832	14, 23, 38, **98**	AY161598	AY161832
Contradusta bregeriana	Crosse, 1868	54, **92**	AY161599	AY161833
71. Contradusta? barclayi	**Reeve, 1857**	**106**	**AY534420**	**AY534497**
72. Contradusta? pulchella	**Swainson, 1829**	**22**	**AY534421**	**AY534498**
73. Notadusta? hungerfordi	**Sowerby III, 1888**	**22**	**AY534422**	
Notadusta martini	Schepman, 1907	64	AY161590	AY161824
Notadusta punctata punctata	Linnaeus, 1771	23, 52, 53, 55, 59, 64	AY161589	AY161823
74. Notadusta punctata trizonata	**Sowerby II, 1870**	**69, 70**	**AY534423**	**AY534499**
Notadusta punctata (Andaman)		14	AY161588	AY161822
Notadusta punctata berinii A	Dautzenberg, 1906	5	AY161587	AY161821
Notadusta punctata berinii B		10	AY161586	AY161820
Melicerona listeri	Gray, 1824	19, 30, **12**	AY161585	AY161819
75. Melicerona listeri melvilli	**Hidalgo, 1906**	**50**	**AY534424**	**AY534500**
76. Melicerona felina	**Gmelin, 1791**	**3, 5**	**AY534425**	**AY534501**
Eclogavena dayritiana	Cate, 1963	24	AY161596	AY161830
Eclogavena quadrimaculata thielei	Schilder & Schilder, 1938	33	AY161591	AY161825
Eclogavena quadrimaculata quadrimaculata	Gray, 1824	16, 24, 27, 32, 52, 57	AY161592	AY161826
Eclogavena coxeni	Cox, 1873	54	AY161597	AY161831
Blasicrura pallidula pallidula	Gaskoin, 1849	15, 17	AY161594	AY161828
Blasicrura pallidula rhinoceros	Souverbie, 1865	32, 52, 54	AY161593	AY161827
77. Blasicrura pallidula cf. vivia	**Steadman & Cotton, 1943**	**67**	**AY534426**	**AY534502**
Blasicrura interrupta	Gray, 1824	14, 30, **12**	AY161595	AY161829
78. Blasicrura summersi	**Schilder, 1958**	**92**	**AY534427**	**AY534503**

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NEW SPECIES OF THE GENUS *ABRINA* (BIVALVIA: SEMELIDAE) FROM THE COMMANDER AND KURIL ISLANDS

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ABSTRACT

A new species, *Abrina scarlatoi*, is described from the Commander and Kuril islands. This species has a small (to 11.2 mm), ovate-trigonal, high, almost equilateral shell with a non-polished, gray or light brown periostracum and conspicuous growth lines. The external ligament is attached to a short, wide nymph. The internal ligament is lodged in an ovate-elongate resilifer, which extends obliquely posterior to the beaks. *Abrina scarlatoi* was found in shelf zones of the Commander Islands (depth 3–100 m) and Kuril Islands (intertidal zone to 120 m), on rocky platforms and boulders, covered by a thick layer of lime red algae, brown algae, and sponges, with a population density up to 30 specimens/m^2. The taxonomic status of *Abrina magna* Scarlato, 1965, and *A. hainanensis* Scarlato, 1965, is also discussed.

Key words: *Abrina*, Semelidae, Bivalvia, Commander and Kuril islands.

INTRODUCTION

Previously, four species of the genus *Abrina* – *A. cuneipyga* Scarlato, 1981; *A. sachalinica* Scarlato, 1981; *A. shiashkotanika* Scarlato, 1981; and *A. tatarica* Scarlato, 1981 – have been listed in Russian fauna (Scarlato, 1981). However, examination has shown that they are species of *Macoma* Leach, 1819 (Tellinidae) (Kamenev & Nadtochy, 1999).

Study of the bivalve fauna of the Commander Islands shelf revealed an unknown species tentatively assigned to the genus *Abrina* Habe, 1952 (Kamenev, 1995; Bujanovsky, 1997). Detailed examination of the material from the Commander Islands and additional specimens from the Kurils has led me to regard it as a new species of *Abrina*.

MATERIAL AND METHODS

In this study, I have used the material collected by the IMB intertidal expedition to the Kuril Islands (June–July, 1967), joint IMB-PRIFO expeditions to the Commander Islands (8–28 July 1972, sealer "Krylatka"; 30 August–6 October 1973, R/V "Rakytnoe") and the Kuril Islands (July–November 1987, R/V "Tikhookeansky"), and joint IMB - PIBOC expedition to Sakhalin Island and the Kuril Islands (1 July–4 August 2003, R/V "Akademik Oparin").

For comparison purposes, collections of the following taxa were used: *Abrina lunella* (Gould, 1861) (NSMT); *A. kinoshitai* (Kuroda & Habe, 1958) (NSMT, NSMI); *A. declivis* (Sowerby, 1868) (SBMNH); *A. magna* Scarlato, 1965, and *A. hainanensis* Scarlato, 1965 (both ZIN), and different species of other genera of the Semelidae (UW, CAS, USNM). *Abrina declivis* was stored in 70% ethanol. All other materials were stored dry.

Shell Measurements

Figure 1 shows the position of the shell morphology measurements. Shell length (L), height (H), width of each valve (W) not shown, anterior end length (A), maximal distance from posterior shell margin to top of pallial sinus (L1), and minimal distance from top pallial sinus (L2) to anterior adductor muscle scar (L2) were measured for each valve. The ratios of these parameters to shell length (H/L, W/L, A/L, L1/L, L2/L, respectively) were determined. Shell measurements were made using an ocular micrometer with an accuracy of 0.1 mm. I made measurements of 34 specimens of the new species.

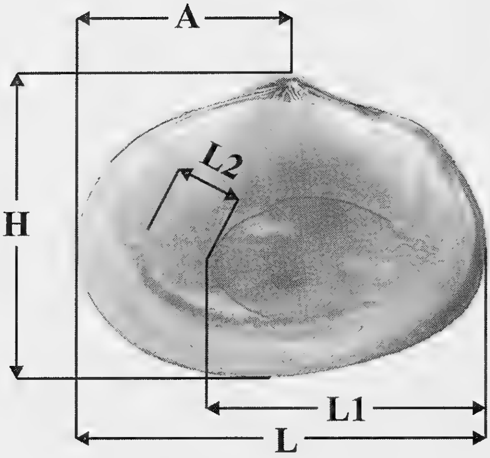


FIG. 1. Placement of shell measurements: L - shell length; H - height; A - anterior end length; L1 - maximal distance from posterior shell margin to top of pallial sinus; L2 - minimal distance from top of pallial sinus to anterior adductor muscle scar.

Abbreviations

The following abbreviations are used in the paper: CAS – California Academy of Sciences, San Francisco; IMB – Institute of Marine Biology, Russian Academy of Sciences, Vladivostok; MIMB – Museum of the Institute of Marine Biology, Vladivostok; NHMI – Natural History Museum and Institute, Chiba; NSMT – National Science Museum, Tokyo; PIBOC – Pacific Institute of Bioorganic Chemistry, Russian Academy of Sciences, Vladivostok; PRIFO – Pacific Research Institute of Fisheries and Oceanography, Vladivostok; SBMNH – Santa Barbara Museum of Natural History, Santa Barbara; USNM – United States National Museum of Natural History, Smithsonian Institute, Washington, D.C.; UW – University of Washington, Seattle; ZIN – Zoological Institute, Russian Academy of Sciences, St. Petersburg.

SYSTEMATICS

Family Semelidae Stoliczka, 1870
Genus *Abrina* Habe, 1952
Type species: *Abra kanamarui* Kuroda, 1951;
= *Macoma lunella* Gould, 1861

Diagnosis

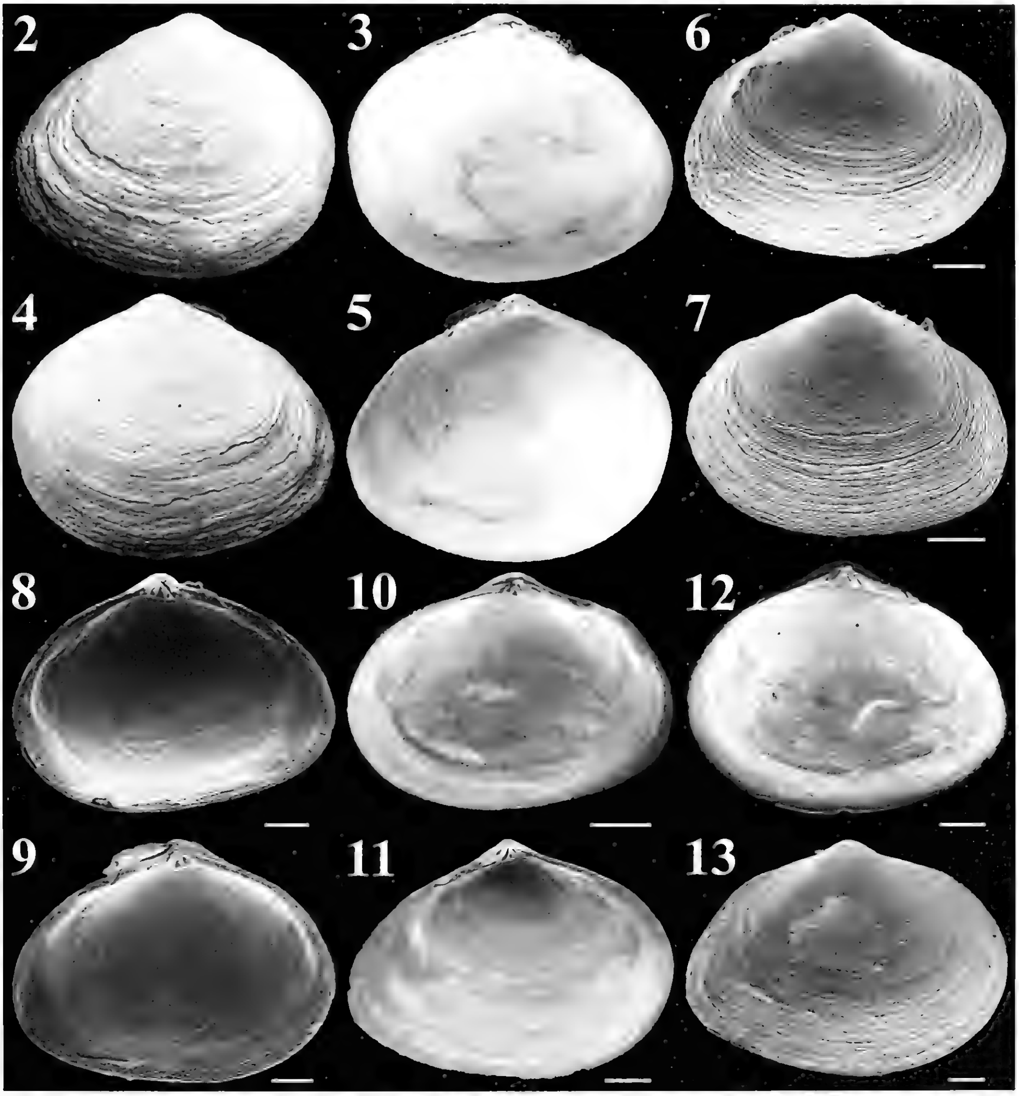
Shell small (< 20 mm), thin to medium in thickness, moderately inflated, subtrigonal, ovate-trigonal or ovate, white, equivalve or with right valve sometimes more inflated, equilateral to longer anteriorly. Posterior end attenuate, with radial ridge along posterodorsal margin, sometimes flexed to right. Periostracum thin, adherent or dehiscent, silky to dull, colorless, tan, gray, light brown. Surface with faint or conspicuous growth lines. Beaks orthogyrate, central or posterior. Hinge weak, two cardinal teeth in each valve; lateral teeth absent. Ligament opisthodetic, parivincular, both external and internal; external seated on a nymph not projecting above dorsal margin; internal lodged in oblique resilifer posterior to cardinal teeth. Pallial sinus long, sometimes slightly different length and form in each valve, partly confluent with pallial line.

Abrina scarlatoi Kamenev, new species

Figs. 2–19, Table 1

Type Material and Locality

Holotype (MIMB 9529), Polovina Bight, Bering Island, Commander Islands, Bering Sea, 3 m, rocky platform, bottom water temperature of 8.0°C, Coll. V. N. Romanov, 26-VII-1972 (sealer "Krylatka"); paratypes (30): paratypes (2) (MIMB 9530) from the holotype locality; paratypes (5) (MIMB 9531), Tonky Cape, Bering Island, Commander Islands, Bering Sea, 10 m, rocky platform, bottom water temperature of 9.1°C, Coll. S. D. Vavilin, 13-IX-1973 (R/V "Rakitnoye"); paratype (MIMB 9532), Kamni Bobrovye – Kitolovnaya Bed, Medny Island, Commander Islands, Bering Sea (54°58.0'N, 167°21.5'E), 100 m, rocky platform, Coll. V. I. Lukin, 18-IX-1973 (R/V "Rakitnoye"); paratypes (2) (MIMB 9533), Cherny Cape, Medny Island, Commander Islands, Bering Sea, 15 m, rocky platform, bottom water temperature of 9.4°C, Coll. V. I. Lukin, 17-IX-1973 (R/V "Rakitnoye"); paratypes (2) (MIMB 9534), Palata Cape, Medny Island, Commander Islands, Pacific Ocean, 20 m, rocky platform, bottom water temperature of 5.0°C, Coll. V. I. Lukin, 16-VII-1972 (sealer "Krylatka"); paratype (MIMB 9535), Sivuchy Kamen, Medny Island, Bering Sea, 10 m, boulders, bottom water temperature of 8.6°C, Coll. V. I. Lukin, 2-X-1973 (R/V "Rakytnoe"); paratypes (3) (MIMB 9536), Tonky Cape, Bering Island, Commander Islands, Bering Sea, 20 m, rocky platform, bottom water temperature of 9.0°C, Coll. G. T. Belokonev, 13-IX-1973 (R/V "Rakytnoye"); paratypes (2) (MIMB 9537), Vodopadskogo Cape, Medny Island, Commander Islands, Pacific Ocean



FIGS. 2–13. *Abrina scarlatoi* Kamenev, new species. FIGS. 2–5: Holotype (MIMB 9529), Polovina Bight, Bering Island, Commander Islands, Bering Sea, 3 m, shell length 9.8 mm. FIGS. 6, 7: Paratype (MIMB 9538), Phedoskina Cape, Bering Island, Commander Islands, Pacific Ocean, 5 m, right and left valves of a young specimen. FIGS. 8, 9: Paratype (MIMB 9531), Tonky Cape, Bering Island, Commander Islands, Bering Sea, 10 m, right and left valves with ligament. FIG. 10: Paratype (MIMB 9530), from holotype locality, right valve without ligament. FIG. 11: Paratype (MIMB 9534), Palata Cape, Medny Island, Commander Islands, Pacific Ocean, 20 m, left valve without ligament. FIG. 12: Paratype (MIMB 9533), Cherny Cape, 15 m, Medny Island, Commander Islands, Bering Sea, right valve without ligament. FIG. 13: MIMB 9549, Nadezda Strait (Rashua Island - Matua Island), Kuril Islands, 48°00'N, 153°15'E, 50 m. Bar = 1 mm.

(54°38.6'N, 167°43.5'E), 40 m, rocky platform, Coll. V. I. Lukin, 3-X-1973 (R/V "Rakytnoe"); paratypes (3) (MIMB 9538), Phedoskina Cape, Bering Island, Commander Islands, Pacific Ocean, 5–15 m, rocky platform, bottom water temperature of 9.8–10.0°C, Coll. V. I. Lukin, 23-IX-1973 (R/V "Rakytnoe"); paratypes (3) (MIMB 9539), Peregrebnogo Cape, Bering Island, Commander Islands, Bering Sea, 15–20 m, rocky platform, bottom water temperature of 10.0°C, Coll. B.I. Sirenko, 5-IX-1973 (R/V "Rakytnoe"); paratype (MIMB 9540), Bujan Bight, Bering Island, Commander Islands, Bering Sea, 5 m, rocky platform, bottom water temperature of 7.6°C, Coll. V. I. Lukin, 28-VII-1972 (sealer "Krylatka"); paratype (MIMB 9541), Poloviny Bay, Bering Island, Commander Islands, Bering Sea, 10 m, rocky platform, bottom water temperature of 9.8°C, Coll. V. I. Lukin, 27-IX-1973 (R/V "Rakytnoe"); paratypes (4) (MIMB 9542) Ushishir Islands, Kuril Islands (42°30.2'N, 152°51.0'E), 87–120 m, boulders covered by Spongia, Coll. G. M. Kamenev, 19-VII-2003 (R/V "Akademik Oparin").

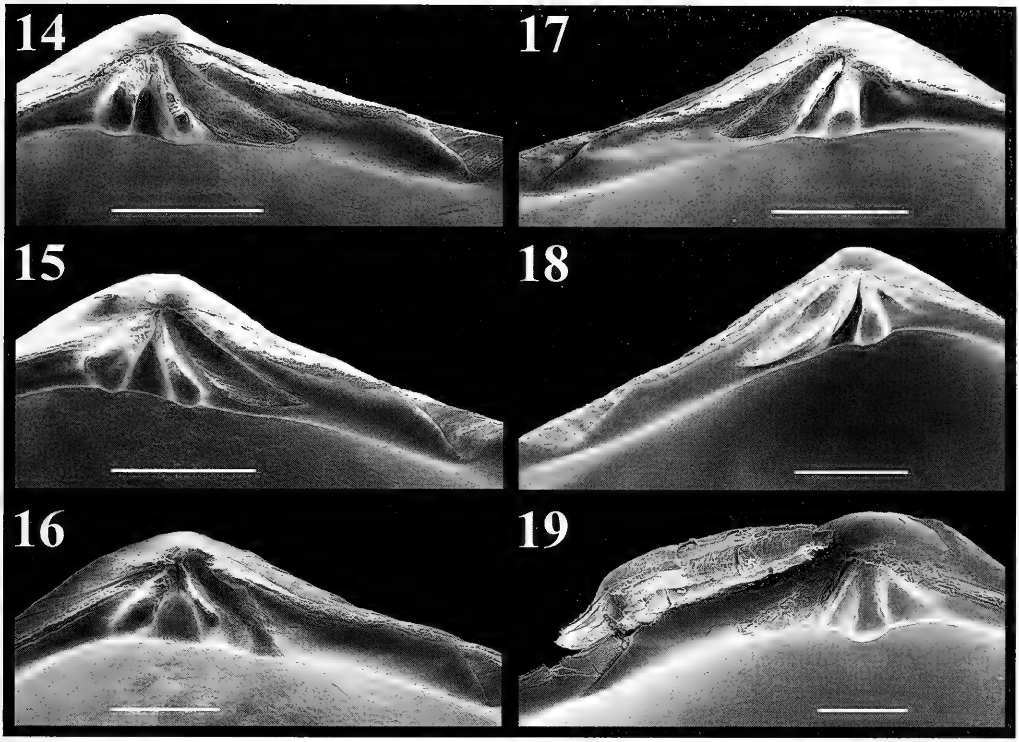
Other Material Examined

One slightly damaged specimen (MIMB 9543), Korabelnaya Bight, Medny Island, Commander Islands, Bering Sea, 5 m, rocky platform, bottom water temperature of 6.8°C, Coll. V. I. Lukin, 14-VII-1972 (sealer "Krylatka"); one slightly damaged specimen (MIMB 9544), Kamny Bobrovye, Medny Island, Commander Island, Bering Sea, 5 m, bottom water temperature of 5.6°C, Coll. V. I. Lukin, 13-VII-1972 (sealer "Krylatka"); one left valve (MIMB 9545), Palata Cape, Medny Island, Commander Islands, Pacific Ocean, 15 m, rocky platform, bottom water temperature of 5.2°C, Coll. V. I. Lukin, 16-VII-1972 (sealer "Krylatka"); one left valve (MIMB 9546), Phedoskina Cape, Bering Island, Commander Islands, 20 m, rocky platform, bottom water temperature of 9.9°C, Coll. V. I. Lukin, 23-IX-1973 (R/V "Rakitnoye"); one slightly damaged specimen (MIMB 9547), Utesnaya Bight, Second Kuril Strait, Paramushir Island, Kuril Islands, intertidal zone, boulders with brown algae of the genera *Fucus* and *Alaria*, Coll. M. B. Ivanova, 7-VII-1967; one specimen (MIMB 9548), Burevestnik Village, Iturup Island, Kuril Islands, Sea of Okhotsk, intertidal zone, boulders with brown algae of the genus *Alaria*, Coll. O. G. Kusakin, 24-VII-1967; one specimen (MIMB 9549), Nadezda Strait (Rashua Island - Matua Island), Kuril Islands (48°00'N, 153°15'E), 50 m, rocky platform, Coll. V. I. Lukin, 19-VIII-1987 (R/V "Tikhookeansky"). Total of 5 specimens and 2 left valves.

Description

Exterior: Shell small (to 11.2 mm), ovate-trigonal, high (H/L = 0.740–0.827), equivalve, moderately inflated (W/L = 0.181–0.235), almost equilateral (slightly longer anteriorly, sometimes equilateral or longer posteriorly), thin, solid, white under periostracum. Surface with conspicuous growth lines. Periostracum non-polished, gray, sometimes light brown, dehiscent, easily peeled off near beaks, extending into inner surface, thrown into small wrinkles, more conspicuous at shell margins. Beaks orthogyrate, small, slightly rounded, moderately projecting above dorsal margin, slightly posterior or anterior to midline, sometimes central (A/L = 0.474–0.583). Anterior end rounded. Posterior end narrow, obliquely subtruncate, with faint radial ridge from beaks to ventral limit of posterior end. Anterodorsal margin slightly convex, gently descending ventrally, smoothly transiting to rounded anterior end. Ventral margin slightly curved. Posterodorsal margin short, straight, gently descending ventrally, forming noticeable angle at transition to posterior margin. Posterior margin straight, rather steeply descending ventrally, forming rounded angle at transition to ventral margin. External ligament short (1/2 posterodorsal margin length), attached to short, wide nymph not projecting above dorsal margin.

Interior: Hinge plate wide, sometimes projecting into shell cavity in area of cardinal teeth. Hinge weak, with two cardinal teeth in each valve. In left valve, anterior tooth wide, long, reaching edge of hinge plate; posterior tooth very narrow, lamellate, shorter, not reaching edge of hinge plate, almost parallel to anterior tooth. In right valve, anterior and posterior teeth almost same length and width (anterior tooth slightly shorter and wider). Internal ligament well developed, reaching edge of hinge plate, lodged in ovate-trigonal or ovate-elongate resilifer, which extends obliquely posterior to beaks. Anterior adductor muscle scar large, ovate, vertically extended; posterior adductor scar large, rounded, shorter and wider than anterior scar. Pallial sinus distinct, moderate, reaching past midline (L1/L = 0.603–0.698), broad, rounded anteriorly, of



FIGS. 14–19. The hinge of the different age specimens of *Abrina scarlatoi* Kamenev, new species. FIGS. 14–16. Hinge of right valve. FIG. 14: Paratype (MIMB 9538), Phedoskina Cape, Bering Island, Commander Islands, Pacific Ocean, 10 m, shell length 6.2 mm. FIG. 15: Paratype (MIMB 9536), Tonky Cape, Medny Island, Commander Islands, Bering Sea, 20 m, shell length 6.8 mm. FIG. 16: Paratype (MIMB 9533), Cherny Cape, Medny Island, Commander Islands, Bering Sea, shell length 7.6 mm. FIGS. 17–19. Hinge of left valve. FIG. 17: Paratype (MIMB 9530), from holotype locality, shell length 6.2 mm. FIG. 18: Paratype (MIMB 9534), Palata Cape, Medny Island, Commander Islands, Pacific Ocean, 20 m, shell length 7.5 mm. FIG. 19: Paratype (MIMB 9531), Tonky Cape, Bering Island, Commander Islands, Bering Sea, 10 m, shell length 8.5 mm. Bar = 500 μm.

same shape and size in both valves (L1/L and L2/L of left valve 0.655 and 0.184; L1/L and L2/L of right valve 0.654 and 0.187), substantially detached, confluent with pallial line for more than 1/2 of its length. Shell interior often with faint radial striae.

Variability

Shell shape and proportions change with age. In young specimens (< 4 mm), in contrast to adults, the shell is more elongate and angular; the posterodorsal margin at the transition to the posterior margin forms a distinct angle; the posterior margin more steeply descends ventrally, forming a pointed acute angle at the transition to ventral margin; the ventral margin is almost straight; the beaks are placed more posteriorly (A/L = 0.54–0.583). The periostracum of young specimens has very fine, short, discontinuous radial lines in the area of the beaks. In young and adult specimens, the relative length, shape, and degree of confluence of the pallial sinus with the pallial line vary slightly. Sometimes, the length and shape of pallial sinus of right and left valves are slightly different (Table 1).

Distribution and Habitat (Fig. 20)

Commander Islands: Bering Island and Medny Island; Kuril Islands: Paramushir Island; Nadezda Strait (Rashua Island - Matua Island) (48°00'N, 153°15'E); Ushishir Islands (42°30.2'N, 152°51.0'E); Iturup Island.

Near the Commander Islands, this species was found at depths from 3 m (Polovina Bight, Bering Island) to 100 m (Kamni Bobrovye - Kitolovnaya Bed, Medny Island, 54°58'N, 167°21'5E) on a rocky platform and boulders covered by a thick layer of lime red algae, with a population density up to 30 specimens/m^2; near the Kuril Islands – from the intertidal zone (Paramushir Island, Iturup Island) to 120 m (Ushishir Islands) on boulders covered by brown algae of the genera *Fucus* and *Alaria* or sponges.

Comparisons

In contrast to other species of *Abrina*, *A. scarlatoi* has the shell with rough, conspicuous growth lines, gray, a non-polished, dehiscent periostracum, wide hinge plate, and a short, wide nymph (Table 2). Moreover, *A. scarlatoi* differs from *A. lunella* (Figs. 21–28) in its smaller, higher shell with less posteriorly placed beaks and in having the hinge with non-bifid cardinal teeth and a very narrow, lamellate posterior cardinal tooth in the left valve (Gould, 1861; Kuroda, 1951; Habe, 1952, 1977, 1981; Kuroda et al., 1971; Ito et al., 1986; Kamenev & Nadtochy, 1999; Okutani, 2000); from *A. kinoshitai*, in a smaller, higher, more inflated, ovate-trigonal shell without a flexure of the posterior end, with less posteriorly placed beaks, a shorter pallial sinus of the same shape and size in both valves, and in having the hinge with non-bifid cardinal teeth and a very narrow, lamellate posterior cardinal tooth in the left valve (Ito, 1967, 1989; Kuroda et al., 1971; Habe, 1977; Tsuchida & Kurozumi, 1995; Kamenev & Nadtochy, 1999); from *A. declivis*, in the more elongate shell with a much less attenuate posterior end and in having the hinge with non-bifid cardinal teeth and a very narrow, lamellate posterior cardinal tooth in the left valve (Scott, 1994); from *A. sibogai* (Prashad, 1932), *A. inanis* (Prashad, 1932), and *A. weberi* (Prashad, 1932), in the shell with less posteriorly placed beaks and lacking lunule and a escutcheon (Prashard, 1932).

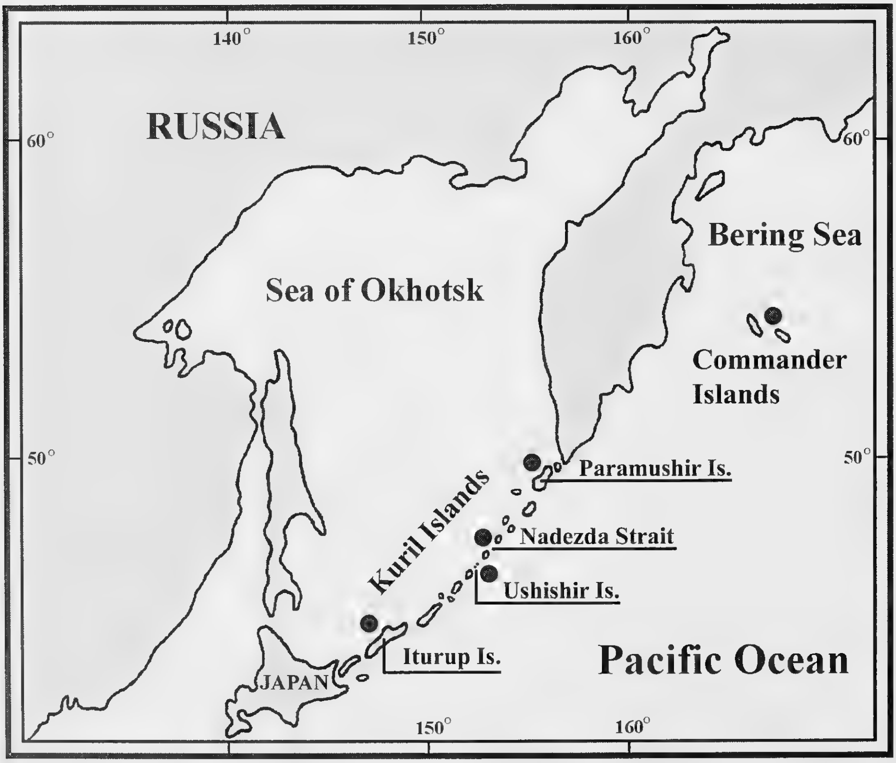


FIG. 20. Distribution of *Abrina scarlatoi*.

TABLE 1. *Abrina scarlatoi* Kamenev, new species. Shell measurements (mm), indices and summary statistics of all characteristics: L - shell length; H - height; W - width; A - anterior end length; L1 - maximal distance from the posterior shell margin to the top of pallial sinus; L2 - minimal distance from the top of pallial sinus to the anterior adductor muscle scar. Numerator indicates shell measurements and indices for the left valve, denominator - for the right valve.

Depository	L	H	W	A	L1	L2	H/L	W/L	A/L	L1/L	L2/L
Holotype MIMB 9529	9.8	8.1	2.2	4.7	6.4	2.1	0.827	0.224	0.480	0.653	0.214
	9.8	8.1	2.2	4.7	6.4	2.1	0.827	0.224	0.480	0.653	0.214
Paratype MIMB 9530	7.6	6.0	1.6	3.9	5.0	1.4	0.789	0.211	0.513	0.658	0.184
	7.6	6.0	1.6	3.9	5.0	1.4	0.789	0.211	0.513	0.658	0.184
Paratype MIMB 9530	6.2	4.7	1.2	3.4	4.1	1.2	0.758	0.194	0.548	0.661	0.194
	6.2	4.7	1.2	3.4	4.1	1.2	0.758	0.194	0.548	0.661	0.194
Paratype MIMB 9531	8.5	6.6	1.9	4.3	5.7	1.7	0.776	0.224	0.506	0.671	0.200
	8.5	6.6	1.9	4.3	5.7	1.7	0.776	0.224	0.506	0.671	0.200
Paratype MIMB 9531	8.0	6.4	1.8	4.0	5.3	1.6	0.800	0.225	0.500	0.663	0.200
	8.0	6.4	1.8	4.0	5.3	1.6	0.800	0.225	0.500	0.663	0.200
Paratype MIMB 9531	7.6	6.0	1.7	3.9	5.1	1.3	0.789	0.224	0.513	0.671	0.171
	7.6	6.0	1.7	3.9	5.1	1.3	0.789	0.224	0.513	0.671	0.171
Paratype MIMB 9531	6.8	5.4	1.6	3.4	4.7	1.0	0.794	0.235	0.5	0.691	0.147
	6.8	5.4	1.6	3.4	4.5	1.2	0.794	0.235	0.5	0.662	0.176
Paratype MIMB 9531	5.6	4.3	1.1	3.0	3.6	0.9	0.768	0.196	0.536	0.643	0.161
	5.6	4.3	1.1	3.0	3.6	0.9	0.768	0.196	0.536	0.643	0.161
Paratype MIMB 9532	7.7	5.7	1.4	3.9	4.8	1.6	0.740	0.182	0.506	0.623	0.208
	7.7	5.7	1.4	3.9	5.0	1.5	0.740	0.182	0.506	0.649	0.195
Paratype MIMB 9533	7.6	6.1	1.6	3.6	5.1	1.2	0.803	0.211	0.474	0.671	0.158
	7.6	6.1	1.6	3.6	5.0	1.2	0.803	0.211	0.474	0.658	0.158
Paratype MIMB 9533	6.6	5.0	1.4	3.2	4.4	1.2	0.758	0.212	0.485	0.667	0.182
	6.6	5.0	1.4	3.2	4.3	1.3	0.758	0.212	0.485	0.652	0.197
Paratype MIMB 9534	7.5	5.9	1.5	3.9	5.2	1.5	0.787	0.200	0.520	0.693	0.200
	7.5	5.9	1.5	3.9	5.0	1.7	0.787	0.200	0.520	0.667	0.227
Paratype MIMB 9534	5.4	4.0	1.1	2.7	3.5	1.0	0.741	0.204	0.500	0.648	0.185
	5.4	4.0	1.1	2.7	3.5	1.0	0.741	0.204	0.500	0.648	0.185
Paratype MIMB 9535	7.3	5.5	1.6	3.7	4.7	1.3	0.753	0.219	0.507	0.644	0.178
	7.3	5.5	1.6	3.5	4.5	1.4	0.753	0.219	0.479	0.616	0.192
Paratype MIMB 9536	7.2	5.6	1.4	3.6	4.9	1.5	0.778	0.194	0.500	0.681	0.208
	7.2	5.6	1.4	3.6	4.8	1.5	0.778	0.194	0.500	0.667	0.208
Paratype MIMB 9536	6.8	5.1	1.4	3.6	4.3	1.6	0.750	0.206	0.529	0.632	0.235
	6.8	5.1	1.4	3.6	4.4	1.4	0.750	0.206	0.529	0.647	0.206
Paratype MIMB 9536	4.5	3.5	0.9	2.4	3.0	0.9	0.778	0.200	0.533	0.667	0.200
	4.5	3.5	0.9	2.4	3.0	0.9	0.778	0.200	0.533	0.667	0.200
Paratype MIMB 9537	7.2	5.4	1.4	3.5	4.6	1.5	0.750	0.194	0.486	0.639	0.208
	7.2	5.4	1.4	3.5	4.6	1.5	0.750	0.194	0.486	0.639	0.208
Paratype MIMB 9537	5.9	4.5	1.2	3.0	3.7	1.2	0.763	0.203	0.508	0.627	0.203
	5.9	4.5	1.2	3.0	3.7	1.2	0.763	0.203	0.508	0.627	0.203
Paratype MIMB 9538	3.7	2.8	0.7	2.0	2.3	0.7	0.757	0.189	0.541	0.627	0.189
	3.7	2.8	0.7	2.0	2.3	0.7	0.757	0.189	0.541	0.622	0.189
Paratype MIMB 9538	6.5	4.9	1.4	3.3	4.2	1.2	0.754	0.215	0.508	0.646	0.185
	6.5	4.9	1.4	3.3	4.2	1.2	0.754	0.215	0.508	0.646	0.185
Paratype MIMB 9538	6.2	4.8	1.3	3.1	3.8	1.3	0.774	0.210	0.500	0.613	0.210
	6.2	4.8	1.3	3.1	3.9	1.3	0.774	0.210	0.500	0.629	0.210
Paratype MIMB 9539	5.7	4.4	1.2	3.0	3.6	0.8	0.772	0.211	0.526	0.632	0.140
	5.7	4.4	1.2	3.0	3.8	0.8	0.772	0.211	0.526	0.667	0.140
Paratype MIMB 9539	3.7	2.8	0.7	2.0	2.4	0.6	0.757	0.189	0.541	0.649	0.162
	3.7	2.8	0.7	2.0	2.4	0.6	0.757	0.189	0.541	0.649	0.162
Paratype MIMB 9539	2.4	1.9	0.5	1.4	1.6	0.4	0.792	0.208	0.583	0.667	0.167
	2.4	1.9	0.5	1.4	1.6	0.4	0.792	0.208	0.583	0.667	0.167
Paratype MIMB9540	5.3	4.3	1.1	2.8	3.7	0.8	0.811	0.208	0.528	0.698	0.151
	5.3	4.3	1.1	2.8	3.6	0.9	0.811	0.208	0.528	0.679	0.170

(*continues*)

(*continued*)

Depository	L	H	W	A	L1	L2	H/L	W/L	A/L	L1/L	L2/L
Paratype MIMB 9541	3.9	3.1	0.8	2.2	2.5	0.6	0.795	0.205	0.564	0.641	0.154
	3.9	3.1	0.8	2.2	2.5	0.6	0.795	0.205	0.564	0.641	0.154
Paratype MIMB 9542	11.2	9.0	2.4	5.5	7.2	1.7	0.782	0.214	0.491	0.643	0.152
	11.2	9.0	2.4	5.5	7.2	1.8	0.782	0.214	0.491	0.643	0.160
Paratype MIMB 9542	10.5	8.5	2.3	5.3	7.0	2.2	0.804	0.219	0.505	0.667	0.210
	10.5	8.5	2.3	5.3	7.0	2.2	0.804	0.219	0.505	0.667	0.210
Paratype MIMB 9542	11.2	9.1	2.4	5.1	7.8	1.7	0.813	0.214	0.455	0.696	0.152
	11.2	9.1	2.4	5.1	7.8	1.8	0.813	0.214	0.455	0.696	0.161
Paratype MIMB 9542	4.1	3.3	1.0	2.2	2.7	0.8	0.791	0.244	0.537	0.659	0.195
	4.1	3.3	1.0	2.2	2.7	0.8	0.791	0.244	0.537	0.659	0.195
MIMB 9547	6.0	4.8	1.3	3.3	4.0	1.1	0.800	0.217	0.550	0.667	0.183
	6.0	4.8	1.3	3.3	4.0	1.1	0.800	0.217	0.550	0.667	0.183
MIMB 9548	7.8	6.1	1.6	4.0	4.7	1.3	0.782	0.205	0.513	0.603	0.167
	7.8	6.1	1.6	4.0	4.7	1.3	0.782	0.205	0.513	0.603	0.167
MIMB 9549	9.4	7.1	1.7	4.7	6.3	1.9	0.755	0.181	0.500	0.670	0.202
	9.4	7.1	1.7	4.7	6.3	2.0	0.755	0.181	0.500	0.670	0.213

Statistics	L	H	W	A	L1	L2	H/L	W/L	A/L	L1/L	L2/L
Mean	6.81	5.31	1.42	3.46	4.47	1.26	0.778	0.208	0.514	0.655	0.184
	6.81	5.31	1.42	3.45	4.46	1.28	0.778	0.208	0.514	0.654	0.187
SD	2.10	1.72	0.48	0.96	1.43	0.43	0.023	0.014	0.026	0.024	0.024
	2.10	1.72	0.48	0.96	1.42	0.44	0.021	0.014	0.027	0.019	0.021
SE	0.36	0.30	0.08	0.16	0.24	0.07	0.004	0.002	0.005	0.003	0.004
	0.36	0.30	0.08	0.16	0.24	0.07	0.004	0.002	0.005	0.003	0.004
Min	2.4	1.9	0.5	1.4	1.6	0.4	0.740	0.181	0.455	0.603	0.140
	2.4	1.9	0.5	1.4	1.6	0.4	0.740	0.181	0.455	0.603	0.140
Max	11.2	9.1	2.4	5.5	7.8	2.2	0.827	0.244	0.583	0.698	0.235
	11.2	9.1	2.4	5.5	7.8	2.2	0.827	0.244	0.583	0.696	0.227
N	34	34	34	34	34	34	34	34	34	34	34
	34	34	34	34	34	34	34	34	34	34	34

Etymology

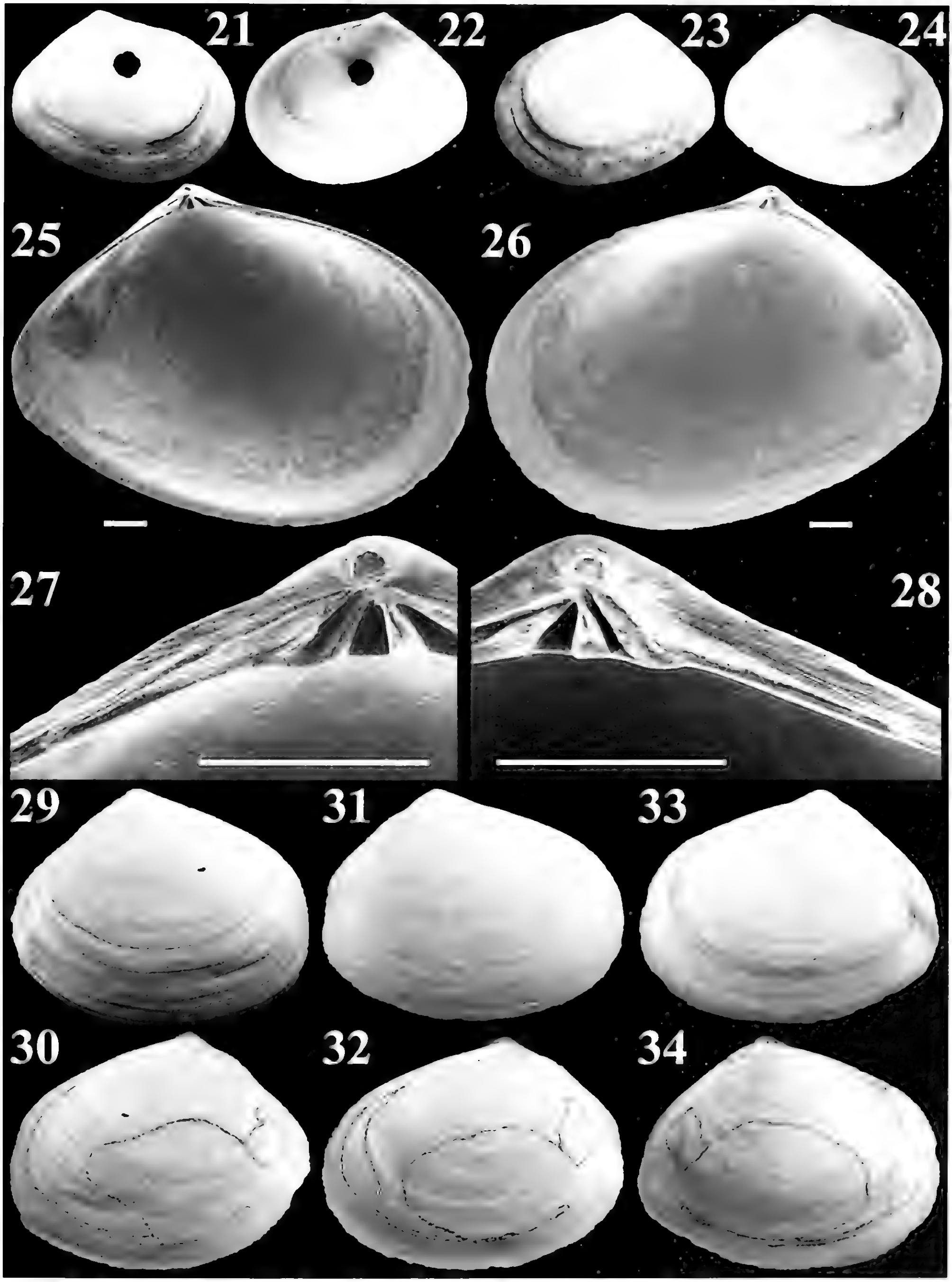
The specific name honors Orest A. Scarlato, Academician of the Russian Academy of Sciences, a famous Russian researcher of the marine bivalve fauna of Russia.

Remarks

The genus *Abrina* also includes species *A. magna* Scarlato, 1965, and *A. hainanensis* Scarlato, 1965, described by Scarlato (1965) from Hainan Island, South China Sea, China. All the material of *A. magna* (4 specimens and 103 shells) was collected from assemblages of empty shells on sandy beaches of Hainan Island and northern Vietnam. The material of *A. hainanensis* (the holotype and 10 additional specimens) is much smaller, but with the exception of the holotype, was also sampled from assemblages of empty shells on sandy shores Hainan Island and the Gulf of Thailand (Bangkok). The holotype was collected in the intertidal zone of Hainan Island in the estuary of river, on silty sand among the mangroves.

Having studied all materials relating to these species in the ZIN collection, I think that Scarlato (1965) erroneously assigned these species to *Abrina*. The hinge plate in these species is very wide, projects into the shell cavity in the area of resilifer. The hinge is weak, with two cardinal teeth in the right valve and two cardinal teeth in the left valve of *A. hainanensis*, and one cardinal tooth in the left valve of *A. magna* (Figs. 29–34). External and internal ligaments are very large. The external ligament is deeply sunken, almost internal, separated from the resilium by a slight ridge. The resilium is lodged in a large, trigonal resilifer behind the cardinal teeth. Lateral teeth are absent.

Thus, the hinge of both species is identical to the hinge of the genus *Psammotreta* (Tellinidae) (Keen, 1969), except that the left valve of *A. magna* bears one cardinal tooth instead of two. To all appearances, the posterior cardinal tooth on the left valve of *A. magna* is partly or com-



FIGS. 21–34. Shells of *Abrina* species. FIGS. 21–28. *Abrina lunella* (Gould, 1861), NSMT (Mo 73503), Shiroko, Suzuka-shi, Mie Prefecture, Japan. FIGS. 21–24: Shell length 12.8 mm. FIGS. 25, 26: Shell length 10.2 mm. FIGS. 27, 28: Hinge of left and right valves. Bar = 1 mm. FIGS. 29–34. *Abrina magna* Scarlato, 1965. FIGS. 29, 30: ZIN (17), Tonkin Bay, North Vietnam, South China Sea, right valve, length 63.0 mm. FIGS. 31–34. ZIN (20), North Vietnam, South China Sea. FIGS. 31, 32: Right valve, length 49.6 mm. FIGS. 33, 34: Left valve, length 45.5 mm.

TABLE 2. Differentiating characters of *Abrina* spp. L - shell length; H - height; W - valve width; A - anterior end length.

Characters	*A. lunella*	*A. kinoshitai*	*A. scarlatoi*	*A. declivis*	*A. sibogai*	*A. inanis*	*A. weberi*
Shell shape (H/L)	ovate-trigonal, high (0.737)	ovate-elongate, low (0.625)	ovate-trigonal, high (0.778)	subtrigonal	ovate-elongate, high (0.836)	ovate-trigonal, low (0.450)	ovate-trigonal, high (0.714)
Shell max. length, mm	16.3	14.8	11.2	10.0	13.4	20.0	14
Valve (W/L)	moderately inflated (0.226)	moderately inflated (0.160)	moderately inflated (0.208)	inflated	moderately inflated (0.198)	moderately inflated (0.06)	inflated (0.243)
Beaks (A/L)	high, posterior to midline (0.624)	low, posterior to midline (0.643)	low, almost central (0.514)	high, almost central	low, posterior to midline	high, posterior to midline	high, posterior to midline
Periostracum	polished, colorless	polished, colorless or grayish	non-polished, gray or light brown	polished to dull, light brown	polished, whitish	polished, whitish	polished
Shell surface	with faint growth lines	with faint growth lines	with conspicuous, rough growth lines	with faint growth lines	with faint growth lines	with faint growth lines	with faint growth lines
Lunule and escutcheon	absent	absent	absent	absent	present	present	present
Nymph	long, narrow	long, narrow	short, wide	long, narrow	long, narrow	long, narrow	long, narrow
Hinge plate	narrow	narrow	wide	narrow	narrow	narrow	narrow

pletely reduced with age. Unlike *A. hainanensis*, all valves of *A. magna* were very large, 42 to 73 mm long (valves of *A. hainanensis* are 9.5 to 22.3 mm in length). Moreover, since all material on this species was collected in assemblages of empty shells, almost on all left and right valves the cardinal teeth were partly or completely destroyed, and the ligament and periostracum were lacking. Therefore, it is not inconceivable that the thin and weak posterior cardinal tooth was broken in all left valves.

Examination of the descriptions and figures of members of the genus *Psammotreta* (Keen, 1969, 1971; Habe, 1977; Lamprell & Whitehead, 1992; Okutani, 2000) shows that *A. magna* is most likely a synonym of *Psammotreta (Tellinimactra) edentula* (Spengler, 1798), inhabiting the intertidal and upper subtidal zones of Japan, South China, North Vietnam and Australia. *Abrina magna* is identical to *P. (T.) edentula* in hinge structure and morphology of the external and internal ligaments. Moreover, it has similar shape, proportions and size of the shell, a very deep pallial sinus in both valves, and scars of the anterior and posterior adductors differing in shape and size (Figs. 29–34). It is possible that the material of *A. hainanensis* comprises young specimens of *P. (T.) edentula*. However, it is not unlikely that *A. hainanensis* is a separate species of the same subgenus. A more thorough study of specimens of different species of *Psammotreta* is needed to make a correct identification of *A. magna* and *A. hainanensis*.

DISCUSSION

Scarlato (1981) described new species of *Abrina* on the basis of a study of young specimens of *Macoma* (Kamenev & Nadtochy, 1999). The main morphological characteristic on the basis of which these species were previously included in *Abrina*, was the presence of an internal ligament in an oblique resilifer posterior to the cardinal teeth. The genera *Abrina* and *Macoma* are similar in most morphological characteristics. The main distinguishing characteristic of *Abrina* is the presence of a well-developed internal ligament in the resilifer, a narrow groove posterior to the cardinal teeth. In *Macoma*, an internal ligament is absent. However, studies of the common northwestern Pacific *Macoma* species – *M. loveni* (Jensen, 1905), *M. calcarea* (Gmelin, 1791), *M. balthica* (Linne, 1758), *M. crassula* (Deshayes, 1855), *M. lama* Bartsch, 1921, *M. incongrua* (Martens, 1865) – show the presence of an internal ligament in young specimens (Kamenev & Nadtochy, 1999). Thus, a well-developed internal ligament lodged in oblique resilifer in representatives of the genus *Macoma* is a juvenile characteristic that is preserved in *Abrina* during its entire life.

Morphological similarity of the genera *Abrina* and *Macoma*, and the presence of an internal ligament in young specimens of species of *Macoma*, at first leads one to suggest that the present species is a juvenile of species of *Macoma*. In *Macoma*, a well-developed resilium is found only in individuals up to 5–6 mm in shell length, whereas in specimens with a shell length more than 10 mm, it is lacking (Kamenev & Nadtochy, 1999). A study of *A. scarlatoi* of different ages showed that both young and adult specimens of this species have a well-developed resilium, lodged in the oblique resilifer posterior to the cardinal teeth. The shape of the resilifer changes with age, but its position and relative size remain unchanged. Furthermore, *A. scarlatoi* differs from most species of *Macoma* (Scarlato, 1981; Coan et al., 2000) in the lack of a flexure to the right of the posterior shell margin and by having pallial sinuses of similar shape and size in both valves. Therefore, I think that the species described herein belongs to the genus *Abrina*, not to *Macoma*.

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SHELL STRUCTURES OF SELECTED GASTROPODS FROM HYDROTHERMAL VENTS AND SEEPS

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ABSTRACT

Shell structures of 24 gastropod species from hydrothermal vents and seeps are electron microscopically investigated, and the ecological and phylogenetic implications of their shell structures are discussed. The presence of prismatic complex crossed lamellar, and regularly foliated structure in the Neolepetopsidae provides further evidence for their position as sister group of the Acmaeidae. The Lepetodriloidea are considered to be derived from, or to have a common ancestor with the Fissurellidae based on their complex crossed lamellar structure and on the presence of shell pores. The earlier hypothesis that Peltospiridae derived from Neomphalidae by reduction of complex crossed lamellar structure cannot be supported; both groups show the same array of shell structures. It is shown that shell pores are a frequent feature in Neomphalidae and Peltospiridae. Dissolution of the inner shell walls is documented for *Bathynerita naticoides*. The trend that small and thin-shelled gastropod groups tend to reduce their shell structure to intersected crossed platy, can also be observed in the vent/seep gastropods. Generally, their shell structures appear to reflect those of the phylogenetic group to which they belong, rather than being influenced by the peculiarities of the extreme environment they inhabit.

Keywords: Gastropoda, shell structure, deep-sea, hydrothermal vent, cold seep, phylogeny.

INTRODUCTION

Chemosynthetic ecosystems in the deep-sea harbor highly endemic faunas (Tunnicliffe et al., 1996). The gastropods that live there are no exception to this: 95–98% of the species and 70% of the genera are endemic to vents and seeps, and five families are found exclusively here (Warén & Bouchet, 2001). Origin and phylogenetic relationships of many of the endemic taxa are still debated.

Shell structures have only been described for three out of the about 125 gastropods species known from chemosynthetic ecosystems: *Neomphalus fretterae* (Batten, 1984), *Melanodrymia aurantiaca* (Hickman, 1984), and *Lepetodrilus elevatus* (Hunt, 1993). The scope of the present study is to provide an overview over the shell structures of the gastropod families present at chemosynthetic ecosystems, and to discuss their ecological and phylogenetic implications. Additionally, these data can help to clarify the identity of fossil vent and seep gastropods.

MATERIALS AND METHODS

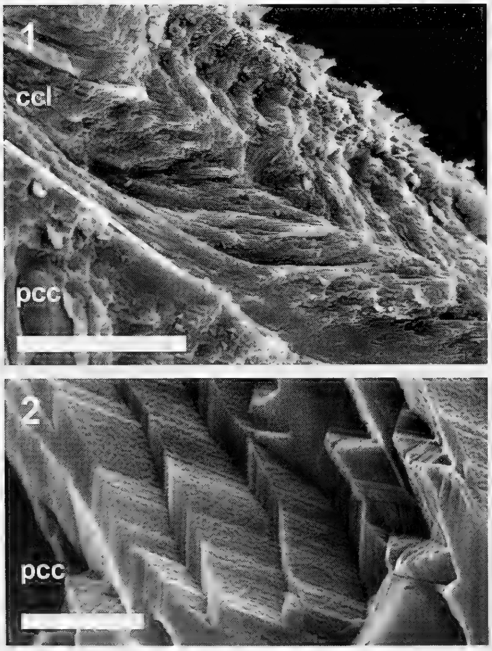
The majority of the material used here is from the study of Warén & Bouchet (2001), and was provided by the Muséum National d' Histoire Naturelle in Paris (MNHN). Three additional species were provided by the Natural History Museum of Los Angeles County (LACM).

All investigated specimens had the size of adult specimens as reported in the literature. The shell structure of protoconchs and ontogenetic changes in shell structures were not the subject of this study. Shell mineralogy was not studied, and is only inferred from the known mineralogy in related groups or is noted in cases when the structures have an unequivocal mineralogy. To observe the shell structures, pieces of shell were broken off the apertural region to obtain fresh fracture zones. The material was then mounted on stubs, coated with gold, and observed with several scanning electron microscopes in Paris and Hamburg.

The different types of shell structures were determined following the scheme of Carter & Clark (1985) and Hedegaard (1990, 1997). All figures in this study are oriented in a way that the outer side of the shell is up. The shell structures present in each species are listed from the outer side of the shell towards the inside. The taxonomic framework is that of Warén & Bouchet (2001).

Abbrevations in Figures

ccl	complex crossed lamellar
hom	homogenous
ica	intersected crossed acicular
icp	intersected crossed platy
nac	nacre
pcc	prismatic complex crossed lamellar
per	organic periostracum
rfo	regularly foliated
rsp	regular spherulitic prismatic
scl	simple crossed lamellar
spr	simple prismatic



FIGS. 1, 2. *Neolepetopsis* cf. *gordensis*. FIG. 1: Upper side of shell with the outer complex crossed lamellar layer and the prismatic complex crossed lamellar layer below (bar = 100 μm). FIG. 2: Detail of the prismatic complex crossed lamellar layer (bar = 10 μm).

RESULTS

Subclass Patellogastropoda
Family Neolepetopsidae

The prismatic complex crossed lamellar and regularly foliated structures are always composed entirely of calcite (Hedegaard, 1990).

Neolepetopsis cf. *gordensis* McLean, 1990
- complex crossed lamellar (Fig. 1)
- prismatic complex crossed lamellar (Figs. 1, 2)

Mid-America Trench, Jalisco Block, 18°22'N–104°23'W; seep in 3,000–3,300 m (MNHN).

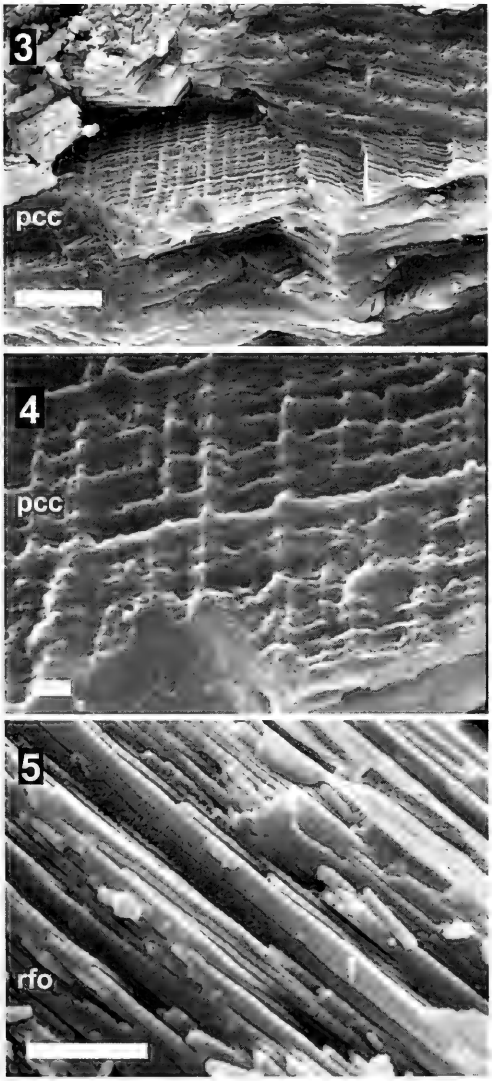
Eulepetopsis vitrea McLean, 1990
- prismatic complex crossed lamellar (Figs. 3, 4)
- regularly foliated (Fig. 5)
- simple prismatic

East Pacific Rise, NE of l'Ille de Paques, site Rehu, 17°24'S–113°12'W; vent in 2,578 m (MNHN).

The prismatic complex crossed lamellar layer in this species has a very similar appearance as the "outer calcitic crossed lamellar" layer of *Patella crenata* described by Bandel & Geldmacher (1996). These authors compared their terminology only to those of Bøggild (1930) and MacClintock (1967), but not to those of the more recent works of Lindberg (1986, 1988) and Hedegaard (1990). However, due to their similarity the "outer calcitic crossed lamellar" layer of *Patella crenata* is here considered the same structure as prismatic complex crossed lamellar.

Paralepetopsis ferrugivora Warén & Bouchet, 2001
- prismatic complex crossed lamellar (Figs. 6, 7)

Mid-Atlantic Ridge, Lucky Strike; vent in about 1,650 m (MNHN). This specimen lacked any further details on its label, the depth is derived from the description of the Lucky Strike vent field (Van Dover et al., 1996). Hedegaard (1990) noted that the prisms of the prismatic complex crossed lamellar structure are always convex towards the outer side of the shell. This is also observed in the three neolepetopsids investigated here. Hedegaard (1990) also pointed out that these prisms show ribbed surfaces, which he interpreted as the edges of the second order lamellae. This is also observed here, and these ribs have quite different appearances: in *Neolepetopsis* cf. *gordensis* they are fine tubercles (Fig. 2), in *Paralepetopsis ferrugivora* they are coarse and irregular (Fig. 7), and in *Eulepetopsis vitrea* they form a distinct grid-like pattern with tuberculate intersections (Fig. 4).



FIGS. 3–5. *Eulepetopsis vitrea*. FIG. 3: Outer prismatic complex crossed lamellar layer (bar = 10 µm). FIG. 4: Close-up on the grid-like, ribbed surface of the prisms (bar = 1 µm). FIG. 5: Regularly foliated layer (bar = 10 µm).

Subclass Cocculiniformia
Family Pyropeltidae

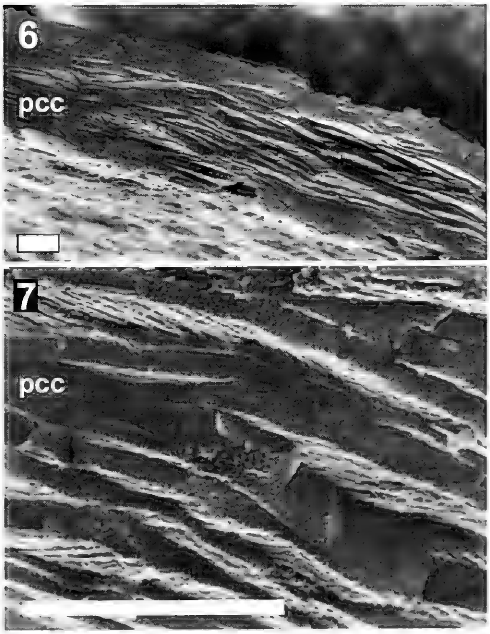
Pyropelta musaica McLean & Haszprunar, 1987
- simple prismatic (Figs. 8, 9)
- simple crossed lamellar (Figs. 8, 9)
- simple prismatic (Fig. 8)

California, Santa Catalina Basin, between San Clemente and Santa Santa Catalina, 33°12'N, 118°30'W; whale bone from 1,240 m; (LACM 146909).

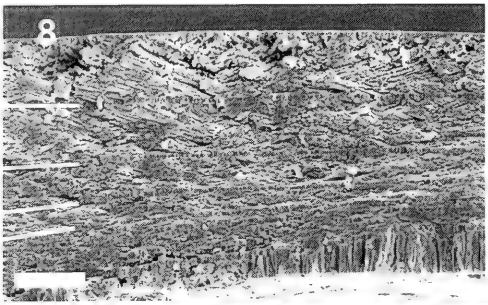
The shell consists of at least five alternating layers of simple crossed lamellar and simple prismatic structure, with the simple crossed lamellar layer becoming progressively thicker towards the outer side of the shell. The microcrystals of the simple crossed lamellar layers are not very densely packed.

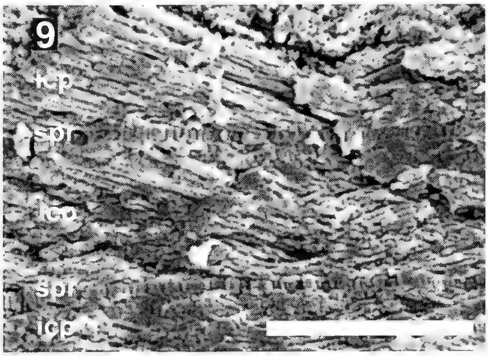
Subclass Vetigastropoda
Family uncertain

Sahlingia xandaros Warén & Bouchet, 2001
- simple prismatic (Fig. 10)
- intersected crossed acicular or platy (Fig. 10)
- homogenous (Fig. 10)



FIGS. 6, 7. *Paralepetopsis ferrugivora*. FIG. 6: Overview showing that the entire shell is composed of prismatic complex crossed lamellar structure (bar = 10 µm). FIG. 7: Close-up on the prisms, showing their ribbed surface (bar = 10 µm).





FIGS. 8, 9. *Pyropelta musaica*. FIG. 8: Cross-section showing five layers with simple crossed lamellar structure, with four thin layers with simple prismatic structure between them, marked by thin white bars (bar = 10 µm). FIG. 9: Close-up on three simple crossed lamellar layers (bar = 10 µm).

Alaska, Aleutian Trench, Kodiak Seep, 56°55.65'N, 149°32.90'W (LACM 1999-45); seep in 4,430 m.

The crossed layer has a granular appearance making it difficult to distinguish between intersected crossed acicular or platy structure.

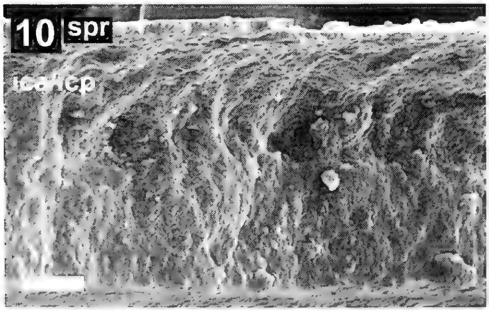
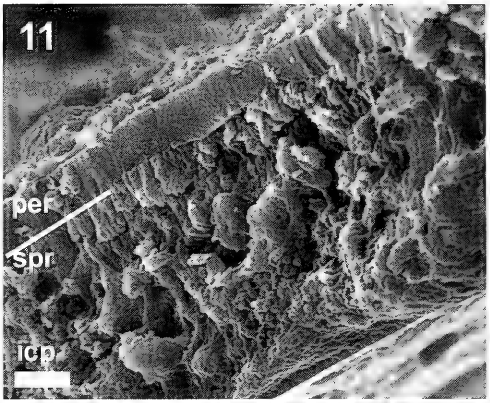
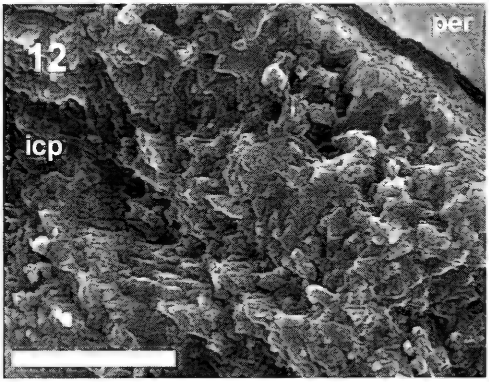


FIG. 10. *Sahlingia xandaros*, showing the thin outer layer of simple prismatic structure, the remaining shell is composed of intersected crossed acicular or platy structure (bar = 10 µm).





FIGS. 11, 12. *Protolira valvatoides*. FIG. 11: Organic periostracum, simple prismatic, and intersected crossed platy structure (bar = 10 µm). FIG. 12: Outer side of shell with organic periostracum and the intersected crossed platy layer (bar = 10 µm).

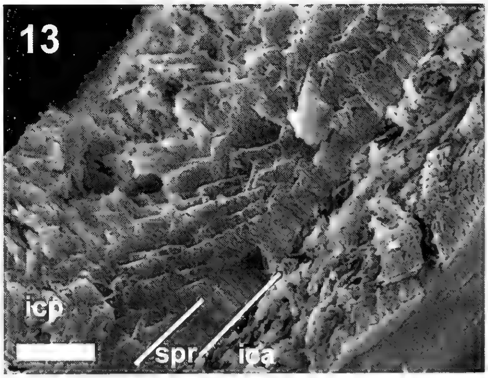


FIG. 13. *Bruceiella athlia*, showing the intersected crossed platy and simple prismatic layers, and the intersected crossed acicular layer below (bar = 10 µm).

Family Skeneidae

Protolira valvatoides Warén & Bouchet, 1993
- simple prismatic (Fig. 11)
- intersected crossed platy (Figs. 11, 12)
- simple prismatic (Fig. 11)

Mid-Atlantic Ridge, Lucky Strike, site Pagodas, 54°18.32'N–32°16.51W; vent in 1,685 m (MNHN).
Many of the microcrystals have a granular appearance, and show cavities between each other.

Bruceiella athlia Warén & Bouchet, 1993
- intersected crossed platy (Fig. 13)
- simple prismatic (Fig. 13)
- intersected crossed acicular (Fig. 13)

Aleutian Trench, site Shumagin, 54°18.06'N–157°12.11'W; seep in 2,524 m (MNHN).
Many of the microcrystals have a granular appearance, and show cavities between each other.

Family Sutilizonidae

Sutilizona theca McLean, 1989
- simple prismatic (Fig. 14)
- intersected crossed platy (Fig. 14)

East Pacific Rise, 11°46'N, 103°47'W; vent in 2,715 m (Paratype LACM 2355).

Family Lepetodrilidae

Hunt (1992) used powder diffraction to show that the shell of *Lepetodrilus elevatus* is composed entirely of aragonite. It is therefore assumed that the shells of the lepetodrilids investigated here are also composed of aragonite.

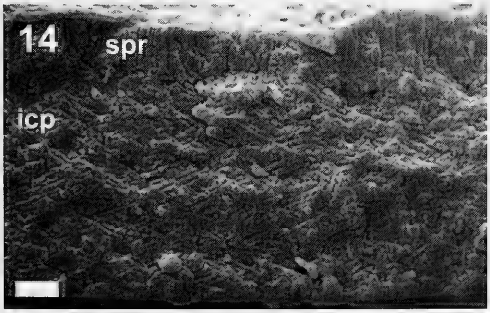


FIG. 14. *Sutilizona theca*, showing the thin outer layer of simple prismatic structure, the remaining shell is composed of intersected crossed platy structure (bar = 3 µm).

Lepetodrilus pustulosus McLean, 1988
- simple prismatic (Fig. 15)
- complex crossed lamellar (Figs. 15, 16)

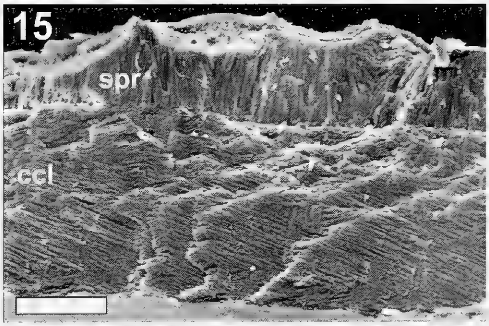
East Pacific Rise, sites Parigo, Genesis, Elsa, 12°48.52'N–103°56.48'W; vent in 4,808 m (MNHN).
There are occasionally fine pores perpendicular to the shell's surface, with an average diameter of 1 µm (Fig. 16).

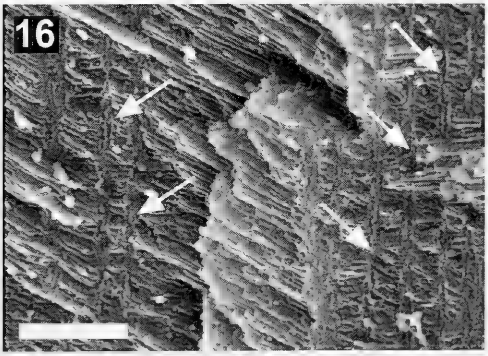
Pseudorimula midatlantica McLean, 1992
- homogenous
- complex crossed lamellar

Mid-Atlantic Ridge, Snake Pit, site Elan, 23°23'N–44°56'W; vent in 3,520 m (MNHN).
There are occasionally fine pores perpendicular to the shell's surface, with an average diameter of 1–2 µm.

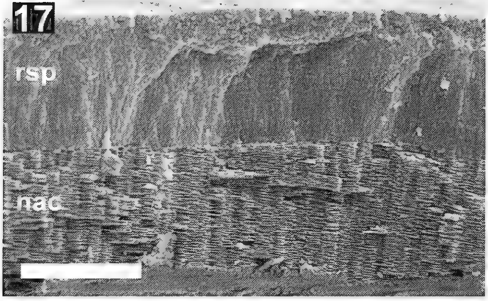
Family Trochidae

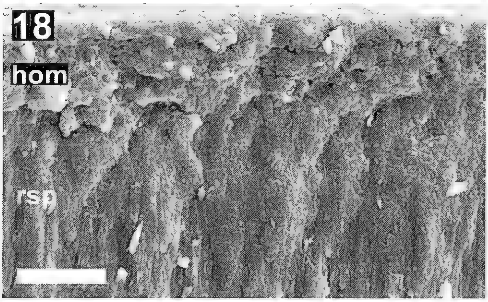
Bathymargarites symplector Warén & Bouchet, 1989





FIGS. 15, 16. *Lepetodrilus pustulosus*. FIG. 15: Cross section showing the outer simple prismatic layer, and the inner complex crossed lamellar layer (bar = 100 µm). FIG. 16: Close-up on the crossed lamellar layer, arrows indicate the fine, vertical pores (bar = 10 µm).





FIGS. 17, 18. *Bathymargarites symplector*. FIG. 17: Overview showing the regular spherulitic prismatic upper layer, and the nacreous inner layer (bar = 50 µm). FIG. 18: Close-up on the outer side of the shell showing the thin homogenous layer and the upper part of the regular simple prismatic layer (bar = 10 µm).

- homogenous (Fig. 18)
- regular spherulitic prismatic (Figs. 17, 18)
- columnar nacre (Fig. 17)

East Pacific Rise 13°N; the label in the box indicates "same as Warén & Bouchet, 1993: 11–13, figs. 10A–E, 11A–B"; it is thus likely to be from a vent in 2,616–2,635 m (MNHN).

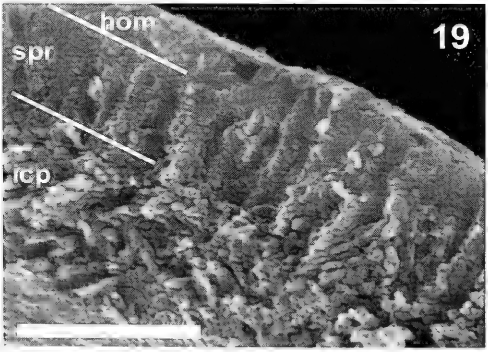


FIG. 19. *Retiskenea diploura*, the homogenous, simple prismatic, and intersected crossed platy structures merge into each other (bar = 10 µm).

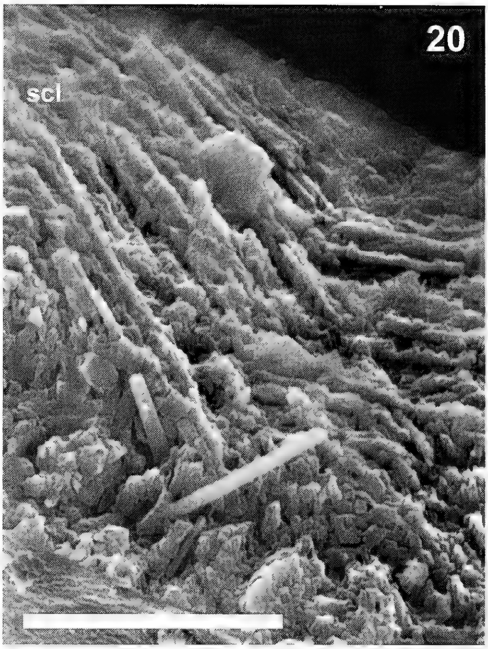


FIG. 20. *Melanodrymia aurantiaca*, view on the simple crossed lamellar structure (bar = 10 µm).

Subclass uncertain
Family Neomphalidae

Retiskenea diploura Warén & Bouchet, 2001
- homogenous (Fig. 19)
- simple prismatic (Fig. 19)
- intersected crossed platy (Fig. 19)
- simple prismatic

Aleutian Trench, site Shumargin, 54°18.17'N–157°11.82'W; seep in 4,808 m (Paratype, MNHN).

The microcrystals of the crossed platy layer are not very densely packed and have a granular appearance.

Melanodrymia aurantiaca Hickman, 1984
- simple prismatic (Fig. 20)
- simple crossed lamellar (Fig. 20)
- simple prismatic (Fig. 20)

East Pacific Rise, sites Parigo, Pogosud, Genesis, 12°48.52'N–103°56.48'W; vent in 2,630 m (MNHN).

Hickman (1984) reported a thick layer with complex prismatic structure in this species. Hedegaard (1990) pointed out that Mac Clintock's (1967) "complex prismatic" structure is identical with the "simple crossed lamellar" structure of Carter & Clark (1985). Thus, the superficial differences between

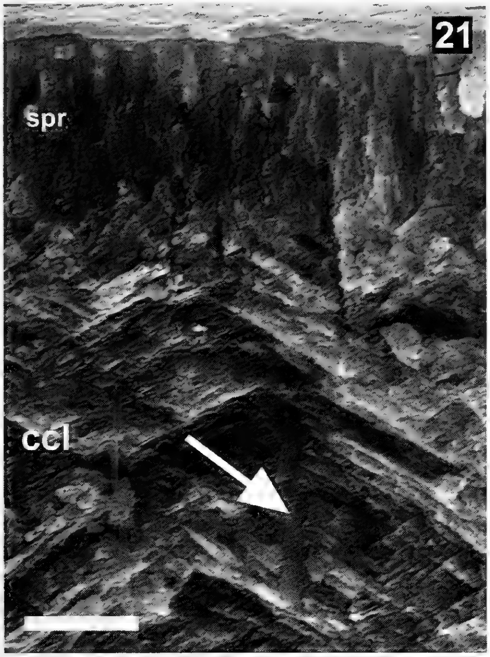


FIG. 21. *Cyathermia naticoides*, upper part of a cross-section with simple prismatic and complex crossed lamellar structure, arrow indicates a shell pore (bar = 10 µm).

Hickman's (1984) and my descriptions of the shell structures of *Melanodrymia aurantiaca* is likely to be only a difference in terminology.

Cyathermia naticoides Warén & Bouchet, 1989
- simple prismatic (Fig. 21)
- complex cross lamellar (Fig. 21)

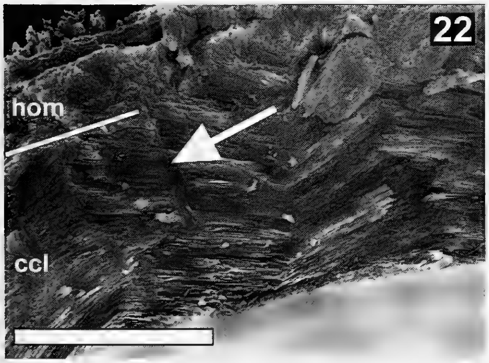


FIG. 22. *Pachydermia laevis*, homogenous and complex crossed lamellar structure, arrow indicates a shell pore (bar = 100 µm).

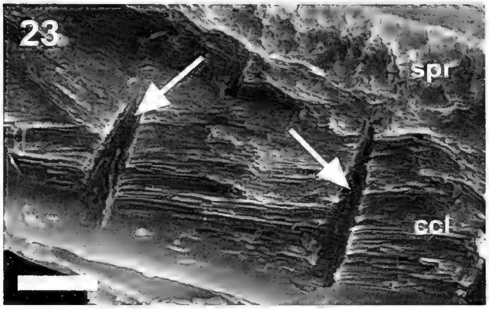


FIG. 23. *Peltospira smaragdina* has an outer layer with simple prismatic structure, and an inner layer with complex crossed lamellar structure, arrows indicate the broad shell pores (bar = 10 µm).

East Pacific Rise, sites Julie, Genesis, Parigo, 12°48.96'N–103°46.62'W; vent in 2,630 m (MNHN).

Pachydermia laevis Warén & Bouchet, 1989
- homogenous (Fig. 22)
- complex crossed lamellar (Fig. 22)

East Pacific Rise, site Genesis, 12°48.56'N–103°46.58'W; vent in 2,630 m (MNHN).
There are occasionally fine pores perpendicular to the shell's surface with an average diameter of 3 µm (Fig. 22).

Planorbidella planispira (Warén & Bouchet, 1989)
- homogenous
- complex crossed lamellar
- simple prismatic

East Pacific Rise, site Elsa, 12°48.09'N–103°46.34'W; vent in 2,630 m (MNHN).

Family Peltospiridae

Peltospira smaragdina Warén & Bouchet, 2001
- simple prismatic (Fig. 23)
- complex cross lamellar (Fig. 23)

Mid-Atlantic Ridge, Lucky Strike, site Sintra, 37°17.50'N–32°16.47'W; vent in 1,622 m (MNHN).
There are occasionally fine pores perpendicular to the shell's surface, with an average diameter of 4 µm (Fig. 23).

Ctenopelta porifera Warén & Bouchet, 1993
- homogenous, with traces of unidentified shell structures (Figs. 24, 25)
- simple prismatic (Fig. 25)

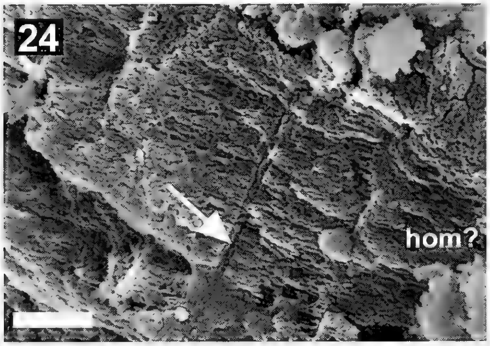
East Pacific Rise, sites Totem, Genesis, Elsa, 12°48.71'N–103°56.53'W; vent in 2,630 m (MNHN).

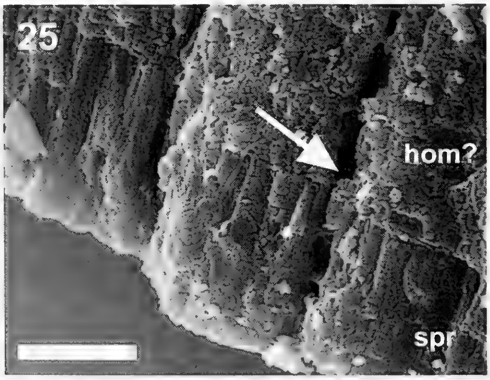
The shell is perforated by fine pores with an average diameter of 4 µm (Figs. 24, 25); these pores have not been observed in the internal septum.

Lirapex costellata Warén & Bouchet, 2001
- simple prismatic
- complex crossed lamellar
- homogenous
- simple prismatic

Mid-Atlantic Ridge, Lucky Strike, site Tour Eiffel, 37°17.32 N–32°16.51'W; vent in 1,685 m (MNHN).

Hedegaard (1990) presented shell structure data for three species he considered peltospirids. Among these, *Hyalogyrina glabra* has subsequently been assigned to the heterobranch family Hyalogyrinidae (Warén & Bouchet, 2001). The other two – *Xyloskenea costulifera* and *Bathyxylophila excelsa* – were placed in the Skeneidae (Marshall, 1988), and no subsequent work has been done on them. However, the Skeneidae are a heterogenous group of small-shelled trochoids, and the assignment of *Xyloskenea costulifera* and *Bathyxylophila excelsa* to either the Skeneidae or the Peltospiridae is still uncertain (Marshall, pers. comm., 2003).



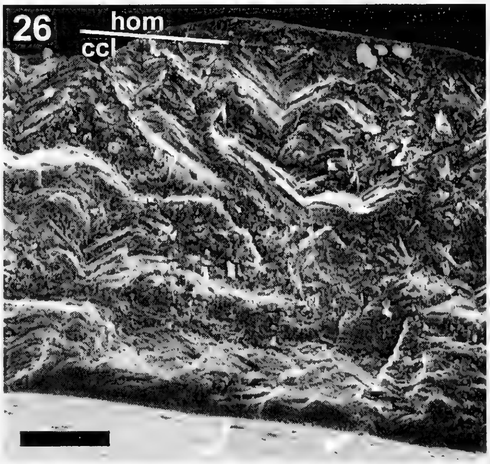


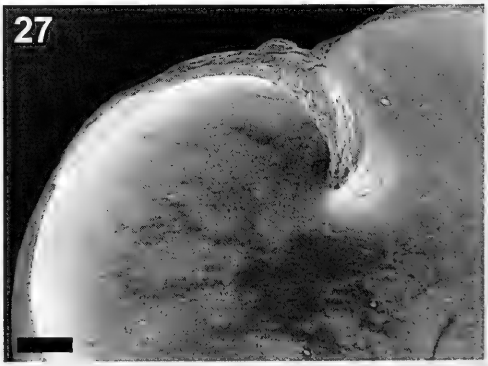
FIGS. 24, 25. *Ctenopelta porifera*. FIG. 24: Outer layer with homogenous, and remnants of an unidentified structure, arrow indicates a shell pore (bar = 10 µm). FIG. 25: Lower side of shell with homogenous?, and simple prismatic structure, arrow indicates a shell pore (bar = 10 µm).

Subclass Neritimorpha
Family Neritidae

Bathynerita naticoidea Clarke, 1989
- homogenous (Fig. 26)
- simple cross lamellar (Fig. 26)
- simple prismatic

Louisiana Slope, Bush Hill Seep, 27°46.91'N–91°30.34'W; seep in 540–580 m (MNHN).





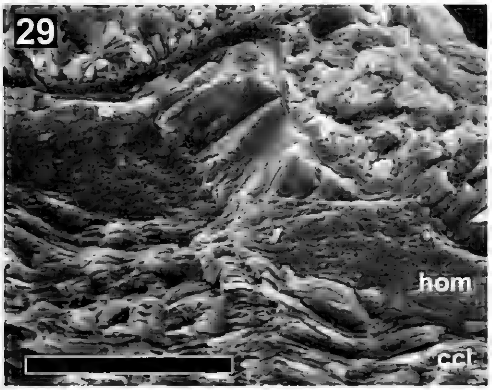
FIGS. 26, 27. *Bathynerita naticoidea*. FIG. 26: Mainly complex crossed lamellar structure, and thin, homogenous outer layer (bar = 100 µm). FIG. 27: View on the shell's interior showing that the inner walls are dissolved (bar = 100 µm).

Hedegaard (1990) found the outer, homogenous layers of the five Neritidae investigated by him to be composed of calcite. It is thus likely that the thin homogenous outer layer of *Bathynerita naticoidea* is also composed of calcite. The inner shell walls of *Bathynerita naticoidea* are dissolved (Fig. 27). Dissolution of the inner shell walls is characteristic for the Neritidae, but has apparently never been documented for *Bathynerita naticoidea*.

Family Phenacolepidae

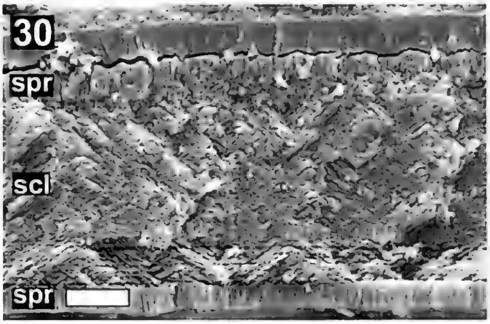
Shinkailepas briandi Warén & Bouchet, 2001
- homogenous (dense) (Fig. 29)
- homogenous (granular) (Fig. 29)
- complex crossed lamellar (Figs. 28, 29)
- intersected crossed platy (Fig. 28)
- simple prismatic

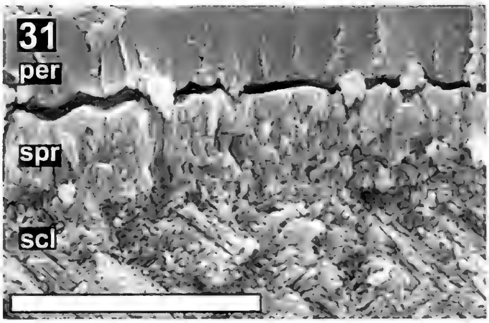
Mid-Atlantic Ridge, Lucky Strike, site Sintra, 37°17.50'N–32°16.47'W; vent in 1,622 m (MNHN).

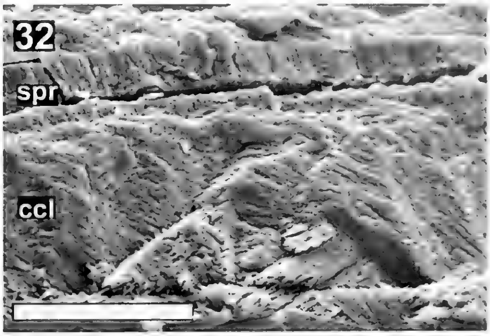


FIGS. 28, 29. *Shinkailepas briandi*. FIG. 28: Inner side of the shell, showing the transition from complex crossed lamellar to intersected crossed platy structure (bar = 10 μm). FIG. 29: Outer side of the shell showing the homogenous outer layer; the homogenous layer is very dense in the rib, and more granular away from the rib (bar = 100 μm).

The homogenous outer layer that builds the ridges on the shell surface is similar to the outer layer described for *Phenacolepas pulchellus* by Hedegaard (1990). Hedegaard (1990) assumed that this layer has calcitic shell mineralogy, which is also likely in the species investigated here.







FIGS. 30–32. *Provanna variabilis*. FIG. 30: Overview showing the inner and outer, simple prismatic layers, and a central layer with complex crossed lamellar structure (bar = 10 μm). FIG. 31: Close-up on the upper side of the shell, showing the slightly detached organic periostracum, and the transition from the outer simple prismatic to the complex crossed lamellar layer (bar = 10 μm). FIG. 32: Inner simple prismatic layer is absent in this part of the shell (bar = 50 μm).

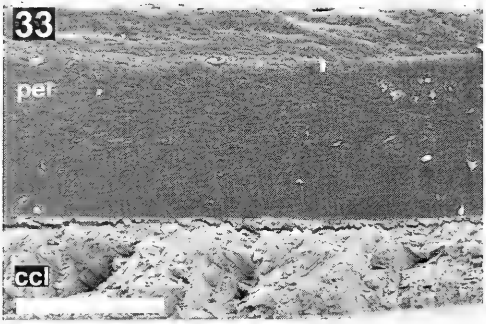


FIG. 33. *Alviniconcha hessleri*, the organic periostracum is about two and a half times thicker than the shell (bar = 100 µm).

Subclass Caenogastropoda
Family Provannidae

Provanna variabilis Warén & Bouchet, 1986
- simple prismatic (Figs. 30–32)
- complex crossed lamellar (Figs. 30–32)
- simple prismatic (Fig. 30)

Juan de Fuca Ridge, 47°57'N–129°04'W; vents in 2,212 m (MNHN).

In the innermost portion of the complex crossed lamellar layer the microcrystals are sometimes only loosely packed, although they are densely packed in the remaining part of the layer (Fig. 30). The inner simple prismatic layer may be present or absent at different parts of the shell (compare Figs. 30 and 32).

Alviniconcha hessleri Okutani & Ohta, 1988
- simple prismatic
- complex crossed lamellar (Fig. 33)
- simple prismatic

Mariana Back Arc Basin, site Alice Springs, 18°12.59'N–144°42.43'E; vent in 3,630–3,655 m (MNHN).

Subclass Heterobranchia
Family Xylodisculidae

Xylodiscula analoga Warén & Bouchet, 2001
- intersected crossed platy (Fig. 34)
- simple prismatic (Fig. 34)

Mid-Atlantic Ridge, Lucky Strike, site Tour

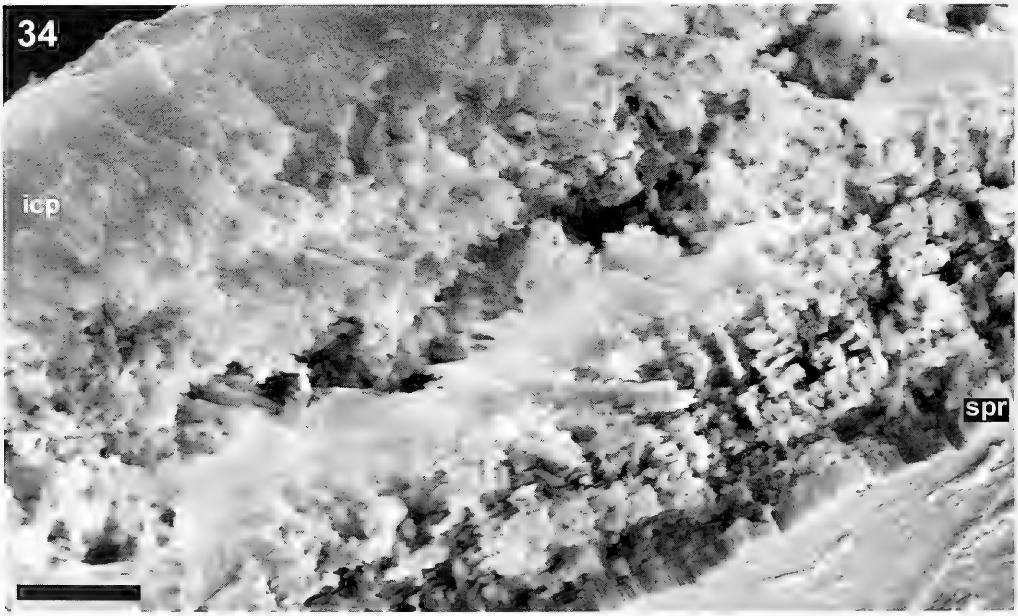


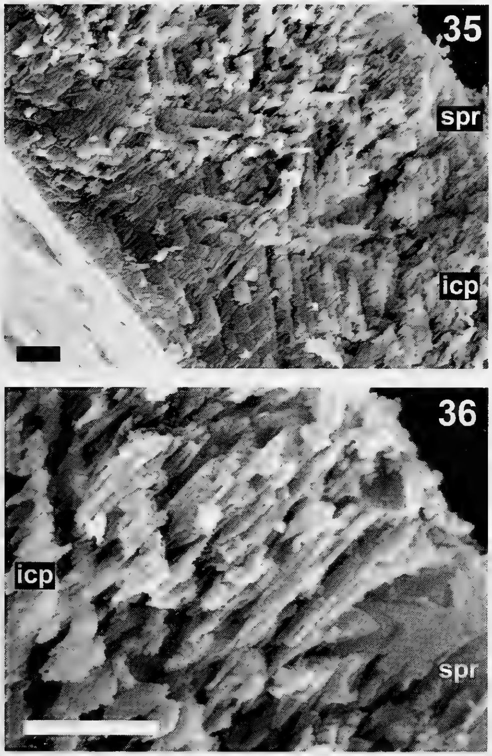
FIG. 34. *Xylodiscula analoga* has mainly intersected crossed platy structure, and a thin layer with simple prismatic structure at the inner side of the shell. The "smeared" area in the center of the picture and the loose packing of microcrystals probably indicate a high content of organic material (bar = 10 µm).

Eiffel, 37°17.32'N–32°16.51'W; vent in 1,685m (MNHN).
The microcrystals are not very densely packed.

Family Hyalogyrinidae

Hyalogyrina umbellifera Warén & Bouchet, 2001
- simple prismatic (Figs. 35, 36)
- intersected crossed platy (Figs. 35, 36)

Aleutian Trench, site Shumagin, 54°18.17'N–157°11.82'W; seep in 4,808 m (Paratype, MNHN).
This composition of shell structure is similar to that described for *Hyalogyrina glabra* (Hedegaard, 1990). The microcrystals are not very densely packed.



FIGS. 35, 36. *Hyalogyrina umbellifera*. FIG. 35: Thin outer layer with simple prismatic structure, and intersected crossed platy structure below (bar = 10 µm). FIG. 36: Close-up on the transition from simple prismatic to intersected crossed platy structure, note the loose packing of the microcrystals (bar = 10 µm).

DISCUSSION

Among the purposes of this study was to investigate whether the peculiarities of the vent/seep environment influence the shell structures of the gastropods groups living there. The microcrystals that build the shell structures are not very densely packed in several species (e.g., in *Retiskenea diploura*, *Hyalogyrina umbellifera*, *Xylodiscula analoga*, and to a lesser extend also in *Pyropelta musaica*, *Protolira valvatoides*, and *Bruceiella athlia*). Such loose packing is rarely observed in gastropods from shallow-marine environments, even in very thin-shelled species (Bandel, pers. comm. 2003; pers. observations). This loose packing is most probably the result of a high organic content in the shell. Loose packing occurs most frequently in small, thin shells with intersected crossed platy structure. This makes it at present impossible to distinguish whether it is related to the extreme vent/seep habitat, or to shell thickness and structure, or both.

An obvious correlation, although not related to the vent/seep habitat, is that between the presence of intersected crossed platy structure and shell thickness. This structure occurs more frequently in small, thin-shelled species than in larger, thicker-shelled ones. Hedegaard (1990) noted that among the Archaeogastropoda, intersected crossed platy structure dominates in species from small-shelled groups. In case of the vent/seep gastropods investigated here, this tendency can not only be observed among archaeogastropods, but also among the Heterobranchia, in the families Hyalogyrinidae and Xylodisculidae.

There are no apparent correlations between shell structures and depth or habitat.

Neolepetopsidae

Anatomical and molecular data indicate a sister group relationship of Neolepetopsidae and Acmaeidae (Lindberg, 1998; Harasewych & McArthur, 2000). The three neolepetopsids investigated here have prismatic complex crossed lamellar shell structure, which Hedegaard (1990) considered as apomorphy of the Acmaeidae. Hedegaard (1990) also pointed out that regularly foliated structure is present only in few acmaeids, and considered the reduction of this structure as an apomorphy of the Acmaeidae *sensu stricto*. Regularly foliated structure is present in *Eulepetopsis vitrea*, but absent in *Neolepetopsis* cf. *gordensis* and *Paralepetopsis ferrugivora*. The position of the Neolepetopsidae as sister group of the Acmaeidae within the Acmaeoidea can thus be supported. However, it should be noted that the patellid *Patella crenata* also has prismatic complex crossed lamellar structure (Bandel & Geldmacher, 1996), raising some doubt whether this shell structure can actually be considered as an apomorphy of the Acmaeidae.

Pyropeltidae

Pyropelta musaica has simple crossed lamellar structure like the three cocculinids investigated by Hedegaard (1990), but a multilayered occurrence of this structure separated by thin layers of a different structure as in *Pyropelta musaica* was not described. Neither does a fossil cocculinid from the Cretaceous show such a pattern (my data). A total of five investigated Cocculiniformia are far too few to propose this alternation of shell structures as an apomorphy of the Pyropeltidae. However, when future research confirms that this pattern does not occur in other cocculiniforms, it could be used for phylogenetic purposes, and also to identify members of the Pyropeltidae in the fossil record.

Sahlingia

Sahlingia xandaros has only simple prismatic and intersected crossed platy structures, which are not very conclusive for phylogenetic purposes.

Skeneidae

The two skeneids have the same shell structures as the three skeneids investigated by Hedegaard (1990).

Lepetodrilidae and Sutilizonidae

The Lepetodrilidae are considered here to be derived from, or to have a common ancestor with the Fissurellidae. The two decisive factors are their complex crossed lamellar structure, and their fine shell pores. Among the slit-bearing Vetigastropoda, the Pleurotomariidae, Haliotidae, and Seguenziidae have a nacreous shells (Bøggild, 1930; Erben & Krampiz, 1972; Bandel, 1979; Hedegaard, 1990; Harasewych, 2002) and are thus less likely to be related. This also pertains to the Palaeozoic slit-bearing Porcellidae, for which nacre is inferred from the presence of nacre in its Mesozoic sister group, the Cirridae (Kiel & Frýda, 2004). The two remaining slit-bearing groups, Fissurellidae and Scissurellidae, have crossed lamellar structure (Batten, 1975; Bandel, 1998), have shell morphologies similar to those of the lepetodrilids, and are anatomically similar (Warén, pers. comm., 2003). Among these, only the fissurellids show shell pores as found in the lepetodrilids. Shell pores evolved independently in several groups of mollusks (Reindl & Haszprunar, 1996), can be present or absent in genera of the same family (e.g., Peltospiridae or Neomphalidae as shown herein), and may even be present or absent in species of the same genus – for example, *Shinkailepas briandi* without pores (herein) and *Shinkailepas myojinensis* with pores (Sasaki et al., 2003). However, shell pores have never been reported in scissurellids but frequently in fissurellids. Thus, the coincidence of similar shell shape, shell structure, and the presence of shell pores in both groups allows me to propose a close phylogenetic relationship between Fissurellidae and Lepetodrilidae.

The sutilizonid *Sutilizona theca* has intersected crossed platy structure, which is neither very conclusive for phylogenetic analysis, nor does it contradict previously suggested relationships (Haszprunar, 1988; Ponder & Lindberg, 1997; Warén & Bouchet, 2001).

Trochidae

Bathymargarites symplector has columnar nacre which is a common shell structure among the Trochidae (Wise, 1970; Erben, 1974; Hedegaard, 1990; Hickman & McLean, 1990). It is, however, the only gastropod with nacreous shell investigated here. Among other trochids from vents and seeps, nacre was reported from *Cataegis meroglypta* (McLean & Quinn, 1987; Warén & Bouchet, 1993), and from species of *Falsimargarita* (Warén & Bouchet, 2001).

Neomphalidae and Peltospiridae

Hedegaard (1990) proposed that the Peltospiridae is derived from the Neomphalidae by reduction of crossed lamellar structure. However, this was based on the incorrect higher taxonomic placement of his species – none of them appears to belong to the Peltospiridae. Two of the three peltospirids investigated here show complex crossed lamellar structure, whereas two of the six Neomphalidae with known shell structure lack complex crossed lamellar structure. These new observations negate derivation of the Peltospiridae from the Neomphalidae, but do provide additional evidence that both families are related, as indicated by anatomical and molecular studies (Israelsson, 1998; McArthur & Tunnicliffe, 1998; Warén & Bouchet, 2001).

Shell pores in the Neomphalidae were first reported from *Neomphalus fretterae*, which has two types of pores, averaging 0.1 µm and 1.0 µm in diameter (Batten, 1984). Four out of the nine species of the Neomphalidae and Peltospiridae investigated here (including *Neomphalus fretterae*) have pores in their shells. In *Peltospira smaragdina*, *Pachydermia laevis*, and *Ctenopelta porifera*, the pores have an average diameter of 1.0–4.0 µm. The latter species has additional macropores 30.0–70.0 µm in diameter (Warén & Bouchet, 1993). The function of such shell pores is still controversial (Reindl & Haszprunar, 1996). Batten (1984) found the highest concentration of pores in *Neomphalus fretterae* around muscle insertion fields, and therefore interpreted them as muscle insertions. In the case of *Ctenopelta porifera*, Warén & Bouchet (1993, 2001) suggested the macropores to be related to chemosymbiosis.

Although the shell structure of the protoconch is not the scope of this study, Batten's (1984) interpretation of the multi-layered protoconch of *Neomphalus fretterae* deserves comment. Batten (1984) speculated that the three shell layers of the protoconch "may indicate that the veliger larval stage may have an extended planktonic mode." Calcification of the protoconch in archaeogastropods, however, takes place at the beginning of their benthic life, after the velum has been discarded (Bandel, 1982), and thus after the free-swimming larval stage. The additional inner layers have thus been built by the benthic juvenile or adult, possibly to strengthen the apical portion of the sub-limpet shell.

Neritidae and Phenacolepidae

Both investigated species, *Bathynerita naticoidea* and *Shinkailepas briandi*, have crossed lamellar structures like their shallow-marine relatives. Likewise, both species have a homogenous outer layer with presumably calcitic mineralogy. In this respect, both species differ from the neritilliid *Pisulina*, in which the thin outer layer has simple prismatic structure (Kano & Kase, 2000). In contrast to the classification of Warén & Bouchet (2001), *Bathynerita* has recently been considered to be more closely related to the Phenacolepidae than to the Neritidae (Hodgson et al., 1998; Kano et al., 2002). Unfortunately, shell structures are too uniform among the two groups to provide further evidence to this hypothesis. The inner shell walls of *Bathynerita naticoidea* are dissolved, a feature that is characteristic for all known neritoids, but had not yet been demonstrated for *Bathynerita*.

Provannidae

The observed shells structures in the two provannids are similar to those of other caenogastropods (Bandel, 1990).

Hyalogyrinidae and Xylodisculidae

Both investigated species have homogenous and intersected crossed platy structure, whereas all other known heterobranchs have crossed lamellar structure (Bandel, 1990). This deviation might result from their small and thin shells, rather than being of phylogenetic importance.

In sum, the shell structures of the vent and seep gastropods appear to reflect those of the phylogenetic group to which they belong, rather than being influenced by the peculiarities of the extreme environment they inhabit.

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CREPIDULA CACHIMILLA (MOLLUSCA: GASTROPODA), A NEW SPECIES FROM PATAGONIA, ARGENTINA

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ABSTRACT

A new species, *Crepidula cachimilla*, is described based on a population from 15 m depth in San Antonio Oeste, Argentina. Shell length ranged from 5.4 to 28.5 mm for males and from 9.6 to 52.2 mm for females. The minimum shell length recorded for a brooding female was 23.5 mm, and the maximum shell length was 49.3 mm. A detailed anatomical description is given, showing as main characters of the species a relative thick columellar muscle, a greater closure of the pallial cavity aperture by a fusion of the mantle border, a very small osphradium, with about 16 broad filaments, endostyle divided by a middle longitudinal furrow, very large salivary glands, duplication of both gastric ducts to the digestive gland, male seminal vesicle very long and with irregular walls, pallial oviduct with a broad vaginal duct and a tall papilla originating both from pallial floor and roof. Brood egg masses of mature females contained from 15 to 65 egg capsules. The triangular-shaped egg capsules measured between 2.2 and 3.4 mm in length and between 2.3 and 3.8 mm in width. Each egg capsule contained between 129 and 563 eggs. The number of eggs per capsule and the egg diameter did not correlate with female shell length. Uncleaved eggs measured between 180 and 200 µm in diameter. They all developed synchronously within the egg capsules. Prehatching veliger shells measured between 260 and 300 µm in length. After hatching at the veliger stage, protoconch length during metamorphosis ranged between 700 and 800 µm. These parameters neither coincide with those reported by Hoagland (1977) for the similar Californian *Crepidula onyx*, nor with the reproductive characters reported by Miloslavich & Penchaszadeh (2001) for *Crepidula aplysioides*, which supposedly occurs in the region.

Key words: *Crepidula cachimilla*, new species, Calyptraeoidea, anatomy, reproduction, southwestern Atlantic, Patagonia, hermaphroditism.

INTRODUCTION

According to Dall (1909: 234), *Crepidula onyx* (G. B. Sowerby I, 1824) occurs along the Pacific coast from North America to Chile. Based on shell and radular morphology, Parodiz (1939) reported this species on the Atlantic coast of Argentina, from San Matías Gulf to Punta Norte, and Aguirre & Farinati (2000) recorded fossils of this species from the Quaternary period in northeastern Argentina. Hoagland (1977) suggested that the Atlantic material studied by Parodiz (1939) should be attributed to *C. aplysioides*. *Crepidula aplysioides* has been defined both anatomically (Simone, 2002) and by reproductive patterns (Miloslavich & Penchaszadeh, 2001). Based on the differences with the studied sample, we conclude that our material from San Antonio Oeste, Argentina, belongs to an undescribed species. In this paper, we describe this new species, which is restricted to an area of Patagonia, southwestern Atlantic.

The study on the calyptraeids has grown considerately in the last few years with the addition of knowledge on the anatomy (e.g., Simone, 2002), molecular biology (e.g., Collin, 2000), and reproductive strategies (e.g., Miloslavich & Penchaszadeh, 2001). From the eastern coast of Americas, knowledge of the informally defined "*Crepidula plana* complex" is of particular importance (Collin, 2000; Simone, submitted; Simone et al., 2000), of which this paper is a part.

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MATERIALS AND METHODS

Three samples were collected in March, May, and August 2001 at 15 m depth at Playa Orengo, San Antonio Oeste (40°53'S, 64°36'W), Argentina, by SCUBA diving. The animals were attached to the bivalves *Atrina seminuda* (d'Orbigny, 1846) and *Aulacomya atra* (Molina, 1782) and to stones. Approximately 370 specimens were collected.

Live individuals were carried to the laboratory, carefully detached from their substratum, measured to the nearest 0.1 mm precision with a digital vernier calliper, and some specimens dissected for anatomical description in vivo.

Shell parameters were measured following Hoagland's (1977) definitions. "D" refers to the length of the shell arc, whereas convexity is the relation between shell arc and shell length; "SL" refers to shell length.

The sexual characteristics of the population were determined by the presence or absence of a penis.

A total number of 47 egg masses was found and fixed in 5% seawater-formalin. Four randomly chosen egg capsules per egg mass were detached, and their length and width were measured under a stereomicroscope. Eggs and embryos contained within these egg capsules were counted and measured, and the presence or absence of cannibalism or nurse eggs was analyzed with a Kruskal-Wallis test.

Settlement size was estimated by measuring the protoconch length under SEM.

Simple linear regression type 2 following natural logarithmic (ln) transformations was carried out to identify the parameters of taxonomic value.

Radular characteristics of six individuals of different sizes were also studied with SEM.

The anatomical study was performed using standard methodology, with non-narcotized specimens fixed in 70% ETOH. Dissections were performed under a stereomicroscope, with the specimens immersed in fixative. All drawings were done with the aid of a camera lucida.

Abbreviations of anatomical structures are as follows: aa, anterior aorta; ab, auricle region beyond ventricle connection; ac, anterior extremity of gill on mantle border; ad, adrectal sinus; af, afferent gill vessel; ag, albumen gland; an, anus; ap, aperture of visceral vas deferens into pallial cavity; au, auricle; bg, buccal ganglion; ce, cerebro-pleural ganglia; cg, capsule gland; cm, columellar muscle; cv, ctenidial vein; dd, duct to digestive gland; dg, digestive gland; di, septum separating haemocoel from visceral mass; dm, dorsal shell muscle; dp, posterior duct to digestive gland; en, endostyle; es, esophagus; ey, eye; fd, foot dorsal surface; ff, female folds of genital papilla; fg, food groove; fl, female papilla; fp, female pore; gd, gonopericardial duct; gf, gastric fold; gi, gill; gp, pedal ganglion; gs, gastric shield; ig, probable ingesting gland; in, intestine; iu, "U"-shaped loop of intestine on pallial roof; ki, kidney; ll, left lateral expansion (flap) of neck; lm, lateral shell muscle; m1–m14, odontophore muscles; mb, mantle border; ml, mantle region restricting pallial cavity; mo, mouth; ne, nephrostome; ng, nephridial gland; nr, nerve ring; od, odontophore; os, osphradium; ov, pallial oviduct; oy, ovary; pb, proboscis; pc, pericardium; pd, penis sperm groove; pe, penis; pp, penis papilla; pr, propodium; py, pallial cavity; rg, repugnatorial gland; rl, right lateral expansion (flap) of neck; rn, radular nucleus; rs, radular sac; rt, rectum; sa, salivary gland duct; sd, pallial sperm groove; se, subesophageal ganglion; sg, salivary gland; si, siphon-like fold; sr, seminal receptacles; ss, style sac; st, stomach; su, supraesophageal glangion; sv, seminal vesicle; sy, statocyst; te, cephalic tentacle; tg, integument; tm, net of transversal muscles of haemocoel; ts, testis, ve, ventricle; vg, vaginal duct; vm, visceral mass; vo, visceral oviduct.

Abbreviations of institutions: AMNH, American Museum of Natural History, New York, New York, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MACN, Museo Argentino de Ciencias Naturales "B. Rivadavia", Buenos Aires, Argentina; MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

RESULTS

Crepidula cachimilla, new species
(Figs. 1–44)

Crepidula onyx Sowerby: Parodiz, 1939: 701, pl. 1, fig. 1; Scarabino, 1977: 185, pl. 3, fig. 5 (*non* G. B. Sowerby I, 1824).

Crepidula aplysioides Reeve: Hoagland, 1977: 369 (Argentinean material only) (*non* Reeve, 1859).

Type Material

Holotype: AMNH 306947. Paratypes: AMNH 306957 to 306961, 14 paratypes (5 dry specimens); AMNH 306948 to 306956, 9 paratypes

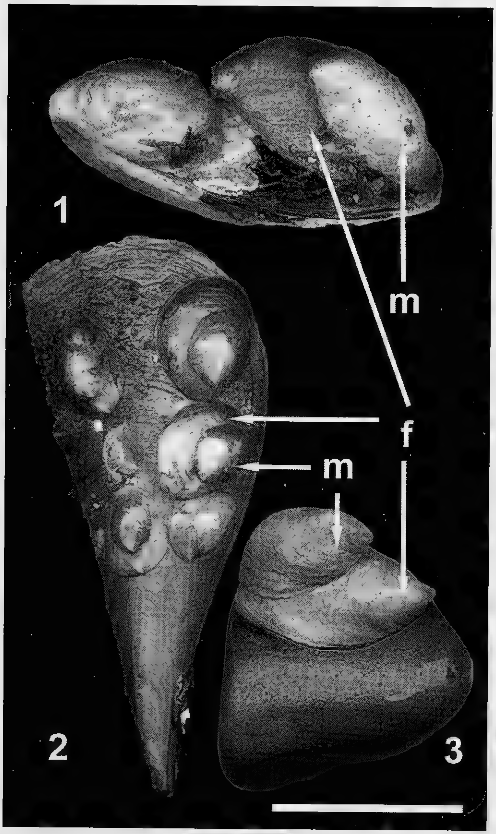
(4 females, 5 males preserved in ethanol); MZSP 41427 (15 paratypes); FMNH (10 paratypes).

Type Locality

Río Negro, San Antonio Oeste, Playa Orengo, Argentina (40°53'S, 64°36'W), 15 m depth, on shells of *Atrina seminuda* and *Aulacomya atra* and on stones (Figs. 1–3).

Etymology

The name of the species alludes to the mapuche word meaning great friend and is dedicated to our colleagues at the Invertebrates I Laboratory of the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires.



FIGS. 1–3. *Crepidula cachimilla* on different substrata. FIG. 1: *Aulacomya atra*. FIG. 2: *Atrina seminuda*. FIG. 3: Rock. Scale bar = 3 cm. f: female; m: male.

Diagnosis

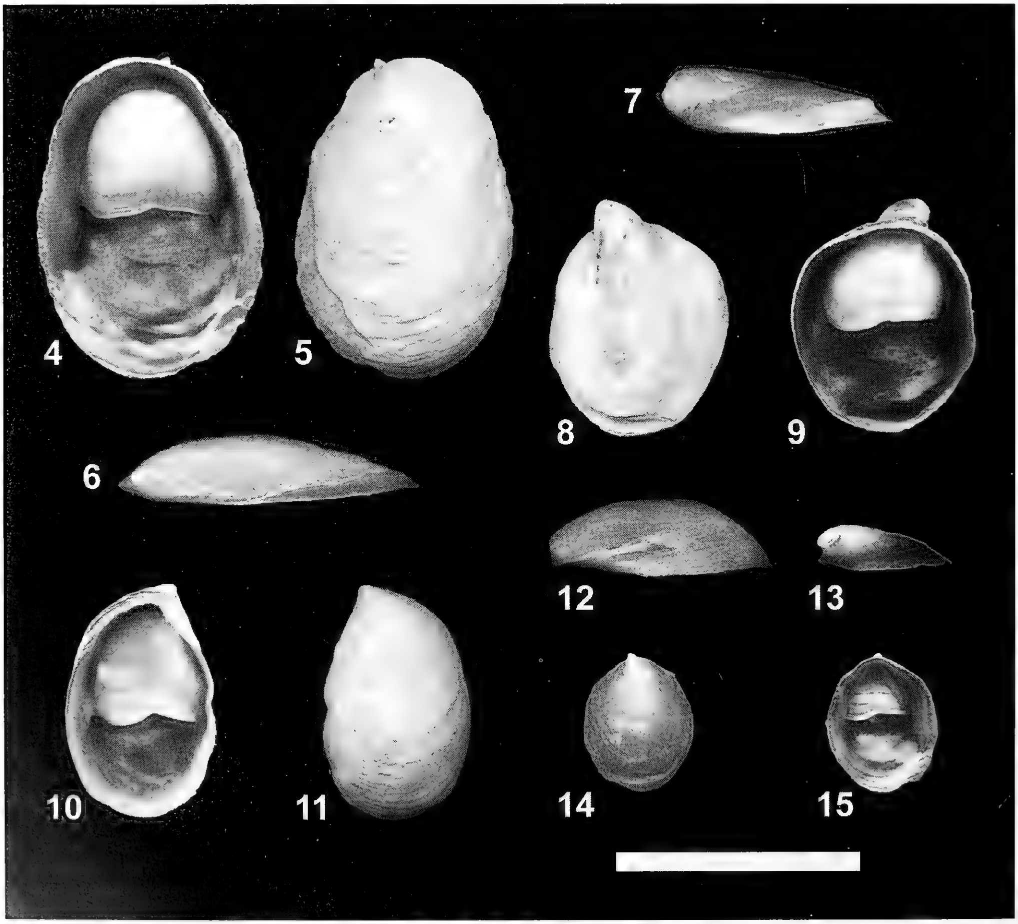
Shell outer surface smooth, lacking periostracum; apex projecting posteriorly, slightly away from posterior shell edge. Columellar muscle somewhat thick. Pallial cavity aperture restricted at right by a closure of mantle edge. Osphradium small, approximatgely 1/8 of mantle aperture length, with about 16–17 broad, closely spaced filaments. Endostyle divided by a middle longitudinal furrow. Hypobranchial gland greatly reduced. Transversal fold of kidney at level of nephrostome. Salivary glands very large, slightly larger than haemocoel. Both gastric ducts to digestive gland duplicated. Male seminal vesicle very large, coiled, wall markedly irregular. Female seminal receptacles reunited in a same region, mostly 4–5; vaginal duct long, broad; genital papilla tall, with a pair of separate longitudinal folds, ending subterminally.

Description

Shell (Figs. 1–15): To 50 mm in length and 38 mm in width; walls with 0.46–0.60 mm thick; slightly to strongly convex (convexity = 1.095–1.350) (Table 1, including other measurements). Growth lines covering entire shell and septum. Color opaque-brown, internally bright-chocolate brown. In males, always opaque-brown externally and bright-brown internally. Few individuals (about 1%) with a white shell. Periostracum totally deciduous. Male specimens with very thin, brittle, flattened shells (Figs. 4–15). Protoconch smooth, with 1.4 whorls; transition to teleoconch not clearly defined. Aperture elliptical or subcircular. Apex solid, generally prominent, turned to right in females, almost central in males, slightly above margin, never reaching margin in males, extending beyond it in females. Flattened septum never convex, ridge central, margin with a clear central notch, covering less than half of ventral surface. Septal edge translucent, sinuous, slight turned towards right. Muscle scars inconspicuous.

Head-Foot (Figs. 16–18): Head differentiated, on long, dorsoventrally flattened neck, about half length of foot. Proboscis short, cylindrical. Tentacles long, stubby, apex somewhat bifid. Eyes dark, small, located on obsolete ommatophores in basal region of lateral margin of tentacles. Neck with pair of lateral, flattened lappets (nuchal lobes); left expansion narrower than right; right expansion bringing low food groove along its dorsal limit with head (Fig. 17: fg). Foot very ample, occupying about 3/4 of shell concavity, dorsoventrally greatly flattened, thin; clear longitudinal inner sinus running in median line; shell septum as dorsal foot limit. Mantle fusing with dorsal surface of foot, protruding beyond its borders. Furrow of pedal glands transverse, in anterior margin of foot; anterior margin of foot covered dorsally by posterior region of neck ventral surface. Columellar muscle somewhat reduced, small, but somewhat thickened, contouring whole anterior border of shell septum, slightly taller at right (Figs. 17, 40: cm). Inner haemocoel cavity narrow, running approximately in center of neck region. Inner space almost filled by great quantity of transverse, very slender muscular fibers; these fibers connecting ventral surface of dorsal haemocoel wall with dorsal surface of its ventral wall, contouring salivary glands and esophagus (Fig. 18: tm). No vestiges of operculum except in very young specimens, being circular, paucispiral, thin, semi-transparent, flexible.

Mantle Organs (Figs. 16, 19–22): Mantle border thick, slightly hollow due to broad collar sinuses (Fig. 21). Mantle border surrounding entire shell ventral margin, free in anterior third, attaching to foot borders in posterior 2/3, situ-



FIGS. 4–15. *Crepidula cachimilla*. FIGS. 4–6: Female holotype, AMNH 306947. FIGS. 7–9: Female paratype 1, AMNH 306949. FIGS. 10–12: Female paratype 2, AMNH 306950. FIGS. 13–15: Male paratype 5, AMNH 306955. Scale bar for FIGS. 4–12 = 4 cm. Scale bar for FIGS. 13–15 = 2 cm.

ated slightly away from foot edge, connecting to it by a thin, semi-transparent portion. Mantle border without appendages, but entirely edged by series of minute repugnatorial glands, immersed in central region of mantle edge (Fig. 21: rg). Mantle border with special arrangement of folds in middle region of pallial cavity aperture, a somewhat narrow fold located from gill anterior end running towards left, decreasing and disappearing abruptly at level of osphradium, its broader region with a broad central furrow, its posterior edge expanding weakly beyond mantle border covering ventrally anterior region of gill, its anterior edge slightly projecting, but not extending beyond mantle edge (Figs. 19, 20, 22).

Dorsal shell muscle well developed (Fig. 16: dm), origin small, in about middle-right region of shell, just anterior to septum, its fibers running anteriorly, spraying like fan, inserting in adjacent anterior region of dorsal surface of pallial cavity. Lateral shell muscle (Figs. 16, 19, 20: lm) small, fan-like, located close to right side of mantle border, in region where pallial cavity penetrates shell septum chamber, with a differentiated muscular branch running towards mantle border, thickness restricting pallial aperture (Fig. 20). Pallial cavity aperture occupying about 2/3 of right-anterior half of shell border (compared to a clock in dorsal view, with head at 12 o'clock, pallial aperture from 11 to 2 o'clock) (Fig. 19); right region of pallial cavity aperture restricted by a broad closure of mantle border, forming a transverse septum (Fig. 20). Pallial cavity deep, broad, triangular, arched, dorsoventrally flattened. Anterior extremity of pallial cavity a little larger than its aperture because of closure in left and right extremities produced by fusion of mantle and foot (Figs. 19, 20: ml). Pallial cavity narrowing gradually towards posterior, penetrating at left of visceral mass; cavity length about 2/3 length of animal (Figs. 16, 19).

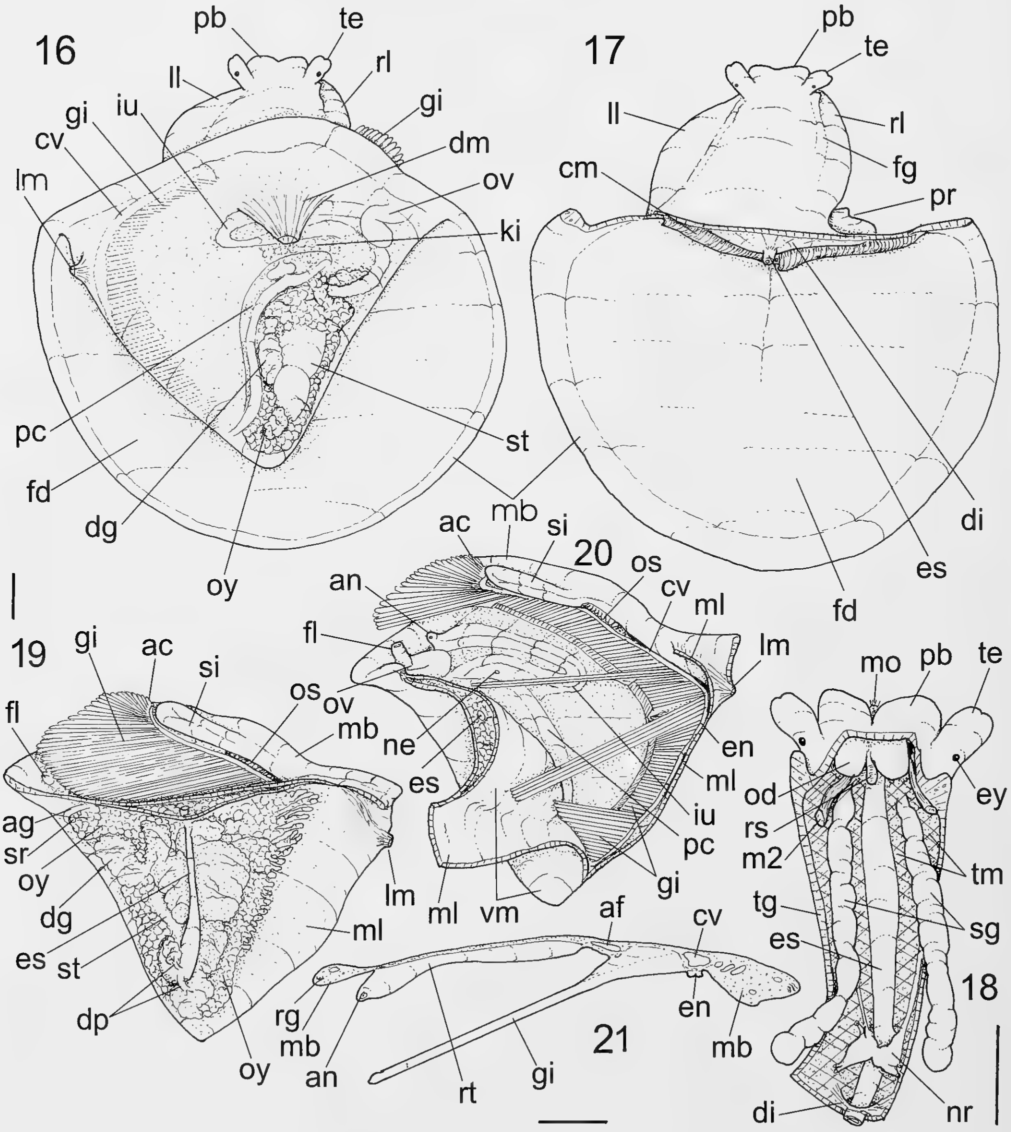
Osphradium small, monopectinate, located between anterior half of gill and mantle border, at some distance from gill anterior end, located about in left region of pallial aperture somewhat perpendicular to longitudinal axis of body (Figs. 19, 20). Osphradium length little more than 1/8 of pallial aperture length, in form of a small fold, attached to mantle, separated from gill structures. Osphradium leaflets cy-

TABLE 1. Measurements in mm of the holotype and paratypes.

Specimen	Total length (L)	Height	Width	D	Septum length	Septum free shell length	Convexity (D/L)
Holotype AMNH 306947 (female)	52.5	8.5	36.4	59.3	24.9	18.35	1.13
Paratype 1 AMNH 306948 (female)	30.9	8.4	21.8	35.4	12.2	16.1	1.14
Paratype 2 AMNH 306949 (female)	42.8	9.2	29.5	47.5	28.8	22.3	1.11
Paratype 3 AMNH 306950 (female)	38.7	7.8	27.4	41.3	11.3	19.1	1.07
Paratype 4 AMNH 306951 (female)	31.9	12.6	19.8	42.1	13.3	15.8	1.34
Paratype 5 AMNH 306952 (male)	20.1	6.4	14.7	23.8	8.8	9.3	1.18
Paratype 6 AMNH 306953 (male)	23.3	5.7	17.7	25.7	10.9	10.3	1.10
Paratype 7 AMNH 306954 (male)	15.3	3.7	11.6	17.2	5.8	8.3	1.12
Paratype 8 AMNH 306955 (male)	12.3	3.9	10.2	14.2	3.9	6.4	1.15
Paratype 9 AMNH 306956 (male)	26.6	8.2	20.2	30.9	12.1	13.3	1.16

lindrical, close from each other, somewhat thick, low, about 16–17 in number (Fig. 22: os) in females. Osphradium ganglion narrow.

Gill very large, its base narrow, edging anterior and left margin of pallial cavity almost the entirety of its length; anterior gill extremity in right-anterior region of pallial cavity aperture, near its right limit, on thick mantle border; gill posterior extremity in posterior end of pallial cavity (Fig. 20). Gill filaments triangular at their base and with very long, almost straight, narrow, stiff rod turned to right (Fig. 21: gi); rods



FIGS. 16–21. *Crepidula cachimilla* female anatomy. FIG. 16: Whole dorsal view, specimen extracted from shell. FIG. 17: Same, head-foot, dorsal view, visceral mass and pallial structures removed. FIG. 18: Head and haemocoel, ventral view, foot and neck "sole" removed. FIG. 19: Pallial cavity and visceral mass extracted, ventral view. FIG. 20: Same, left pallial connection sectioned, ventral portion of visceral mass deflected, most gill filaments artificially sectioned. FIG. 21: pallial cavity roof, transversal section in region tangent to rectum. Scales = 2 mm.

extending about three times longer than their triangular, membranous base; rods beginning in ctenidial vein region, in left margin of cavity roof, and touching food groove of head-foot, in right margin of cavity floor; rod apex rounded, preceded by thicker region. Gill filaments connected to each other by cilia, mainly in their thicker apical region, holding them in a somewhat firm position. Gill filaments longer in central gill region, shorting gradually in both extremities; gill anterior extremity with short filaments, abruptly turning forwards, located on mantle border (Fig. 22). Ctenidial vein narrow, with uniform width along its entire length. Endostyle well developed (Figs. 20, 21, 22: en), yellowish, in form of broad, flat glandular ridge located in middle level of ventral surface of ctenidial vein along its entire length. Endostyle divided longitudinally by a shallow middle furrow. Hypobranchial gland extremely thin, practically absent. About 1/3 of visceral mass encroaching on pallial cavity roof (Fig. 20), occupying about 1/3 of this cavity in posterior-right region; pericardium and kidney located posteriorly; a long intestinal loop, anus and pallial oviduct located anteriorly.

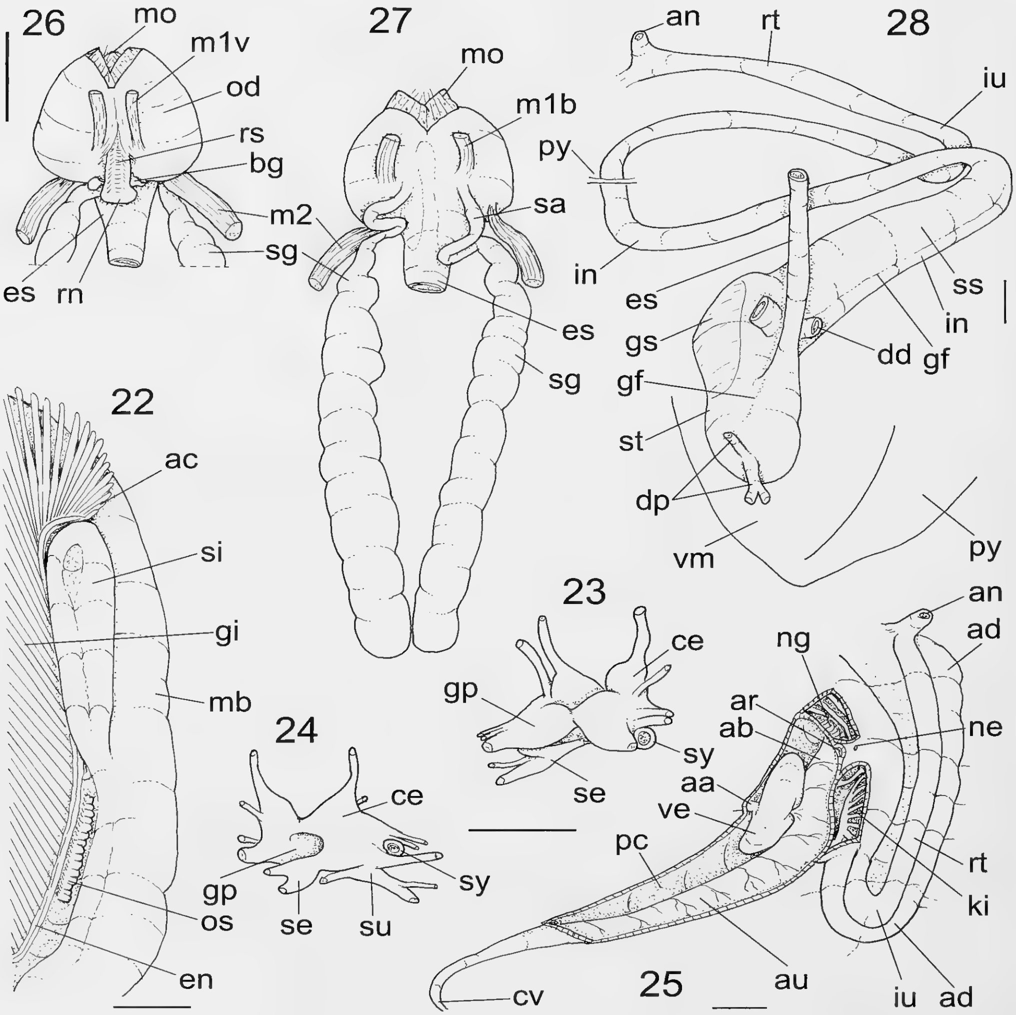
Visceral Mass (Figs. 16, 19, 20): Form of a dorsoventrally flattened cone, housed in shell chamber produced by septum, which separates visceral mass from dorsal surface of foot. Left and anterior region of visceral mass occupied by pallial cavity (Figs. 16, 19, 20). Remaining regions of visceral mass with stomach as central structure, immediately surrounded by greenish-beige digestive gland (except in some ventral and dorsal areas). Gonad surrounding digestive gland, more concentrated anteriorly and at left. Visceral mass encroaching on right-posterior region of pallial cavity roof, possessing another ventral flap as pallial cavity floor (Fig. 20: vm). Anterior extremity of visceral mass ventral flap ending at anterior border of shell septum, covering columellar muscle (Fig. 17).

Circulatory and Excretory Systems (Figs. 20, 25): Pericardium somewhat triangular, broad, oblique to longitudinal axis of animal (Fig. 16: pc). Pericardium left region very narrow, in form of a vein connecting gill with auricle, beginning at posterior extremity of gill in posterior-left end of pallial cavity, running to surround area where visceral mass encroaches into pallial cavity, gradually increasing towards anterior and right (Fig. 25). Remaining pericardium limits: (1) anterior and ventral – pallial cavity; (2) posterior – visceral mass (gonad generally); (3) dorsal – mantle; (4) right – kidney. Auricle thin walled, long, narrow, running all along pericardium length, attached to its anterior and dorsal inner surfaces (Fig. 25), connecting with ventricle approximately in its middle portion; auricle having a broad portion beyond ventricle as blind sac (Fig. 25: ab), bearing orifice to nephridial gland. Ventricle elliptical, very muscular; its connection with auricle located about in middle region of its anterior surface, on opposite side bearing origin of aortas. Anterior aorta broad, running towards opposite side from posterior aorta. Anterior aorta running towards right, surrounding posterior inner pericardium surface, then penetrating head haemocoel.

Kidney occupying about half of area of visceral mass within pallial cavity (Fig. 20). Kidney limits: (1) dorsal – mantle; (2) ventral – pallial cavity; (3) posterior-right – visceral mass (gonad generally); (4) posterior-left – pericardium; (5) anterior – an intestinal loop; (6) lateral-right – intestine and oviduct (when present). Kidney central region hollow, with single anterior lobe (Fig. 25). Kidney lobe slightly uniform, covering dorsal surface, intestinal region passing through kidney chamber, and about 1/4 of inner space of kidney adjacent to intestine. Renal lobe having longitudinal, branching, narrow folds; a larger fold located at left of nephrostome having a series of anterior branches situated somewhat uniformly; another transversal, somewhat tall fold located at level of nephrostome. Nephridial gland in renal limit with pericardium, very small, having a series of triangular, transversal, narrow folds connected with dorsal renal lobe (Fig. 25: ng). Nephrostome a very small slit located in central region of ventral wall (Figs. 20, 25: ne), in anterior region of hollow portion of kidney; no inner glandular folds close to it. Adrectal sinus very broad, edging externally intestine loop exposed in pallial cavity, connected to main kidney chamber but separated by a thin septum (Figs. 20, 25: ad).

Digestive System (Figs. 16, 26–28): Proboscis short, broad (Figs. 16–18: pb). Pair of narrow ventral proboscis retractor muscles very thin, immersed in proboscis wall. Mouth longitudinal, in center of anterior proboscis surface. Buccal mass very large, occupying most of proboscis inner space and short portion of haemocoel posterior to it. Jaw plates in dorsal wall of buccal mass thin, almost vestigial, broader laterally, short longitudinally. Pair of broad, low dorsal folds beginning well posterior to jaws; dorsal chamber between these folds shallow. Odontophore large, occupying most of buccal mass.

Odontophore muscles similar to other species of *Crepidula* (Simone, 2002) (Figs. 26, 27: m1); several very narrow jugal muscles connecting buccal mass with adjacent wall of snout, more concentrated anteriorly around mouth: m1b pair of dorsal protractor muscles narrow, thin, superficial, originating in anterodorsal region of mouth, close to median line, inserting in posterodorsal-lateral region of odontophore; m1v similar to m1b but located in ventral surface; m2 pair of retractor muscles of buccal mass (retractor of pharynx) broad,

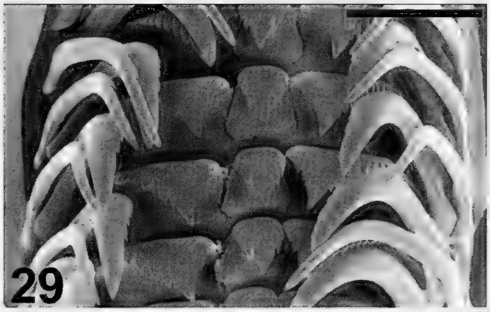


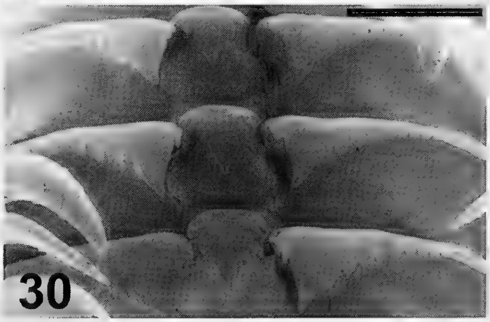
FIGS. 22–28. *Crepidula cachimilla* anatomy. FIG. 22: Anterior portion of pallial cavity, close to mantle border, mantle border slightly deflected for showing anterior gill region. FIG. 23: Central nervous system (nerve ring), ventral view. FIG. 24: Same, dorsal view. FIG. 25: Middle and posterior-right region of pallial roof, ventral view, ventral wall of pericardium and kidney partially removed. FIG. 26: Buccal mass, ventral view. FIG. 27: Same, dorsal view, salivary gland (sg) fully shown. FIG. 28: Middle and distal digestive tubes shown as in situ, ventral view, some adjacent structures also represented. Scales = 1 mm.

originating in lateral-ventral region of haemocoel just posterior to snout (Fig. 18), running towards anterior, inserting in lateral-posterodorsal region of odontophore cartilages; m2a pair of dorsal tensor muscles of radula, continuation of m2 after insertion in cartilages, running towards anterior, inserting in subradular cartilage in middle region of its dorsal inner surface; mt dorsal transversal muscle, or approximator muscle of cartilages, connecting dorsally both posterodorsal-lateral surfaces of cartilages, lying between superficial membrane that covers odontophore and tissue on middle region of radula; m4 pair of median dorsal tensor muscle of radula very large, thick, originating in ventral-middle-posterior region of odontophore cartilages, running towards medial, contouring medial-ventral surface of cartilages, running on their dorsal surface, inserting in subradular cartilage dorsal-posterior-medial extremities; m5 pair of median radular tensor muscle thick, originating in median-posterodorsal region of odontophore cartilages, near side of m2 insertion and m2a origin, covering perpendicularly m4 middle region, running medially, inserting along both sides of radular sac (each m5 branch covering a side of radular sac, medially and dorsally); m6 horizontal muscle very thin, uniting anterior half of odontophore cartilages, inserting on their dorsal margin; m7 pair of ventral tensor muscle of radula thin, narrow, originating inside radular sac ventral surface close to each other, running anteriorly, separating gradually from each other, inserting in radula ventral border; m8 pair of strong muscles originating in posterodorsal-lateral regions of odontophore cartilages near insertion of m2, running attached to dorsal margin of odontophore cartilages, inserting in their anterodorsal region close to horizontal muscle (m6); m9 pair of dorsal-medial tensor muscle of radula broad, thin, originating along dorsal-median surface of radular sac (in its region internal to odontophore), crossing to dorsal surface, inserting in dorsal-ventral border of subradular cartilage; mj jaws and peribuccal muscles somewhat thick, surrounding lateral and dorsal wall of buccal mass, originating around mouth, inserting in middle level of lateral and dorsal wall of odontophore; m11 pair of ventral tensor muscles of radula weakly present; m14 pair broad, thin, originating in posterodorsal region of odontophore, close to m2 and m5 origins, running towards ventral and anterior, inserting in snout inner ventral surface in about middle level of odontophore; tissue covering middle region of radula within odontophore, on its dorsal surface.

Radula short, little more than odontophore length (Figs. 29, 30); rachidian tooth narrow, strongly curved inwards, central cusp large, sharp, secondary cusps 2–4 similar-sized pairs (formula 2-1-2/0-0 to 4-1-4/0-0), weak pair of lateral reinforcements on its borders; lateral tooth broad (about three times broader than rachidian), curved inward, with about 7–10 short, triangular cusps, along edge on marginal side and 1-3 very weak cusps on edge on rachidian side, cusps decreasing laterally, disappearing about in middle region of tooth, with thick, arched border (formula from 1-1-7/0-0 to 3-1-10/0-0); inner marginal tooth long, curved, tall, tip sharply pointed (cusp formula 0-1-5/0-0 to 2-1-7/0-0); outer marginal tooth narrower than inner marginal tooth, thin, and with two small cusps along its inner margin only (cup formula 0-1-2/0-0 to 0-1-3/0-0).

Pair of buccal ganglia large, close to each other near median line (Fig. 26: bg), located between buccal mass and adjacent esopha-

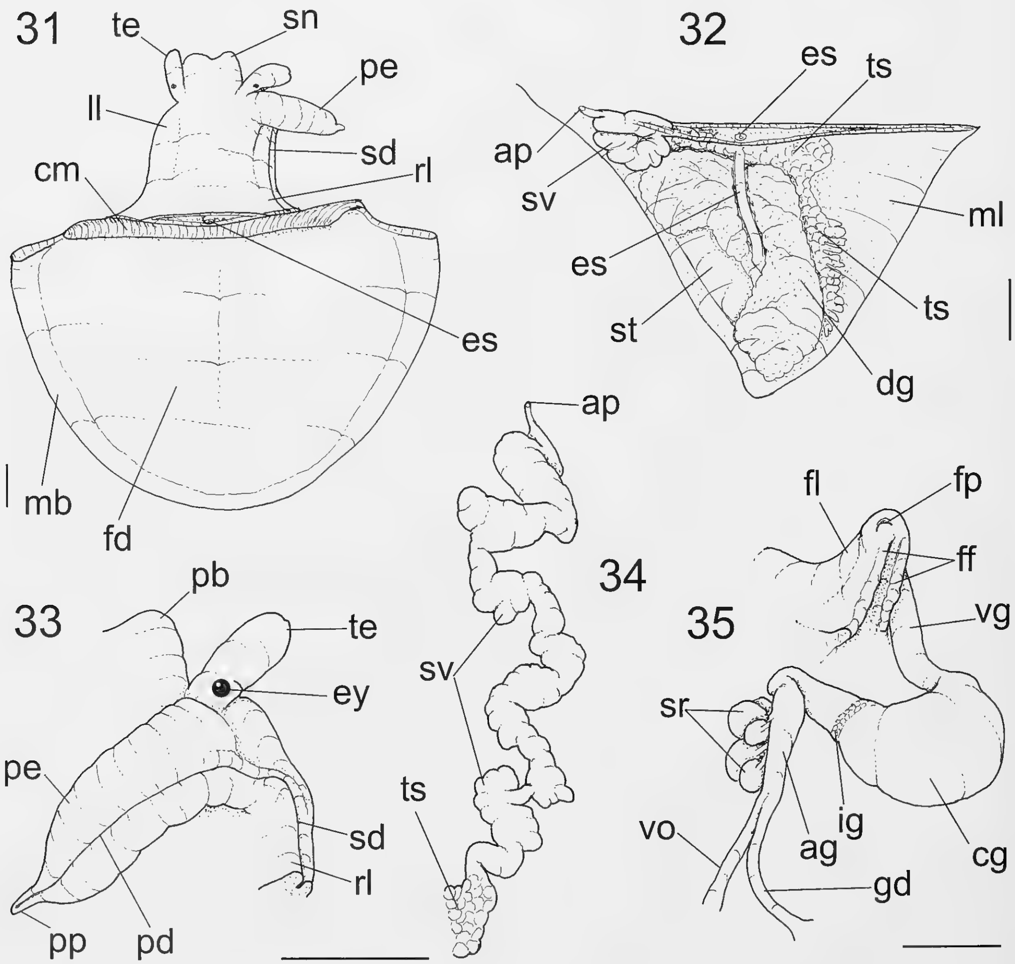




FIGS. 29, 30. Radula of *Crepidula cachimilla*. FIG. 29: General view of the radula. Scale bar = 100 µm. FIG. 30: Detail of the central and lateral tooth. Scale bar = 64 µm.

gus. Salivary glands not passing through nerve ring, longer than haemocoel, fitting inside it, bent (Figs. 18, 27: sg); distal end rounded, of about 1/3 of haemocoel width, running towards anterior possessing approximately same width along its length, narrowing close to buccal mass. Ducts of salivary glands broad, sinuous (Fig. 27: sa), running in dorsal surface of buccal mass, penetrating adjacent buccal mass wall a short distance, apertures small, in anterior region of dorsal folds of buccal mass.

Esophagus (Figs. 18, 28: es) narrow, long; anterior esophagus inner surface with pair of broad folds, running straight posteriorly, becoming gradually slender. Stomach (Fig. 28) somewhat conical, large, occupying about half of visceral mass size; esophagus inserting in left side of its posterior-left region, close to shell apex. Anterior duct to digestive gland located in region of stomach ventral surface preceding style sac, separated into two similar-sized, well-spaced ducts, each running in opposite directions, highly dichotomic. Posterior duct to digestive gland also duplicated (distance between this pair greater than that of anterior ducts), each one running in opposite direc-



FIGS. 31–35. *Crepidula cachimilla* anatomy. FIG. 31: Head-foot, male, dorsal view, pallial structures and visceral mass removed. FIG. 32: Visceral mass and adjacent part of pallial cavity, male, ventral view. FIG. 33: Penis and adjacent structures, dorsal view, penis deflected. FIG. 34: Visceral vas deferens extracted, seminal vesicle (sv) uncoiled. FIG. 35: Pallial oviduct, ventral view as in situ, most integument and pallial cover removed (except close to papilla). Scale bars = 1 mm.

tions, both very narrow, located in ventral region of stomach almost at its posterior end, one of them turned posteriorly.

Stomach gradually narrowing towards anterior and left, arriving close to left-posterior extremity of pallial cavity. Gastric shield occupying about 1/3 of stomach inner surface, located in its right side (Fig. 28: gs). Pair of longitudinal folds separating intestine from style sac running at left (Fig. 28: gf), in region anterior to anterior ducts to digestive glands, abruptly separating one another perpendicularly, in a T-fashion, surrounding entire stomach circumference in this region, forming a low, narrow fold separating style sac from main gastric chamber. A weak constriction marking region between style sac and main gastric chamber, clearer at right. Digestive gland pale brown in color, surrounding stomach except some areas on dorsal and ventral surfaces (Figs. 16, 20, 24). Intestine narrow, sinuous (Fig. 28: in), running on anterior border of visceral mass from left to right, initially in its ventral region, slightly near median line cross to its dorsal region and running up to right-anterior extremity of visceral mass (Fig. 28); running towards left in this region, becoming broader and exposed in pallial cavity, surrounding right and anterior border of kidney, abruptly running towards right in a U-shape, parallel to preceding loop (Figs. 16, 21, 28, 25: iu). Anus small, siphoned, located in right region of pallial cavity close to mantle border (Figs. 21, 28, 25). Final intestine loops filled with several small, elliptical fecal pellets.

Male Genital System (Figs. 31–34): Mature males up to 28 mm in shell length. Testis white, located mostly in anterior region of visceral mass (Fig. 32: ts). Sperm duct differentiable in region of testis just at right of esophagus penetration into visceral mass. Seminal vesicle intensely coiled, locally accumulated in anterior-right region of visceral mass (Fig. 32: sv); if uncoiled, presenting about same length as visceral mass; wall glandular, greatly irregular, varying from broad to very narrow along its length (Fig. 34). Seminal vesicle abruptly narrowing near pallial cavity, having a very narrow aperture located in right-posterior end of this cavity (Figs. 32, 34: ap). Pallial sperm groove starting immediately below this aperture, running as a relatively deep, narrow furrow with elevated edges. Pallial sperm groove running along right neck lobe close to its edge (Fig. 31: sd), slightly dorsal; abruptly curving towards left close to penis base, connecting to its posterior base region (Fig. 33). Penis located behind right cephalic tentacle, curved in same direction, of about 3–4 times its size (Fig. 31). Distal papilla long, about 1/4 of length of remaining penis region, about 1/5 of its width (Fig. 33). Penis groove deep, central, running along ventral surface up to penis papilla tip (Fig. 33).

Female Genital System: Ovary cream yellow, surrounding digestive gland, more concentrated in anterior region of visceral mass (Fig. 19: oy); when mature, oocytes distinguishable by their transparency. Visceral oviduct formed by gradual decrease from right-anterior end of ovary. Gonopericardial duct narrow, relatively short, originating in right-ventral extremity of pericardium, running ventral to visceral glands in area in which visceral mass encroaches toward pallial roof, inserting in posterior extremity of pallial oviduct, joined with insertion of visceral oviduct (Fig. 35: gd). Pallial oviduct narrow, located in right-anterior end of pallial cavity (Figs. 16, 20: ov). Seminal receptacles (sr) located in right side of last portion of visceral oviduct, four to five in number, with three always significantly larger (Fig. 35: sr); each a small sac; duct very narrow, long; their insertion preceding albumen gland, on right surface. Albumen gland long, narrow, whitish, its walls thick, glandular; located in anterior-right extremity of visceral mass, about half size of capsule gland (Fig. 35: ag). Separating albumen from capsule glands a narrow differentiable, paler colored tissue, most probably an ingesting gland (Fig. 35: ig). Capsule gland a continuation of albumen gland, but situated perpendicular and slightly dorsal to it, broad, spherical (Fig. 35: cg); walls thick glandular, pale brown; inner duct narrow, U-shaped, length about 1/8 of pallial cavity aperture. Vaginal duct (vg) relatively broad, equal in size to albumen gland. Genital pore preceded by tall, long papilla close to mantle border, at right and slightly removed from anus (Fig. 20: fl). Genital papilla with broader base and somewhat conical form; pair of well-spaced low folds running along its posterior-left side; both start gradually in papilla base and terminate at some distance from pore (Fig. 35: ff); posterior fold originating on surface of pallial cavity floor; anterior fold originating from pallial roof. Genital pore a transverse apical slit, perpendicular to papilla folds (Fig. 35: fp).

Reproduction

Animals categorized into four sexual phases: (1) undifferentiated juveniles, (2) males, (3) transitional individuals, and (4) females. These are easily recognizable under a microscope by observation of the external development of the reproductive organs. Juveniles are without visible sexual organs. Males have a well-developed penis. Transitional individuals have a penis in retraction phase and a developing genital papilla. Females lack a penis and have an easily distinguishable papilla.

Undifferentiated juveniles were between 3.7 and 5.1 mm SL (mean: 4.3 SD: 0.4 N: 11). Males were 5.4–28.5 mm SL (mean: 14.1 SD: 0.8 N: 103), always attached to larger individuals. Females were 9.6–52.2 mm SL (mean:

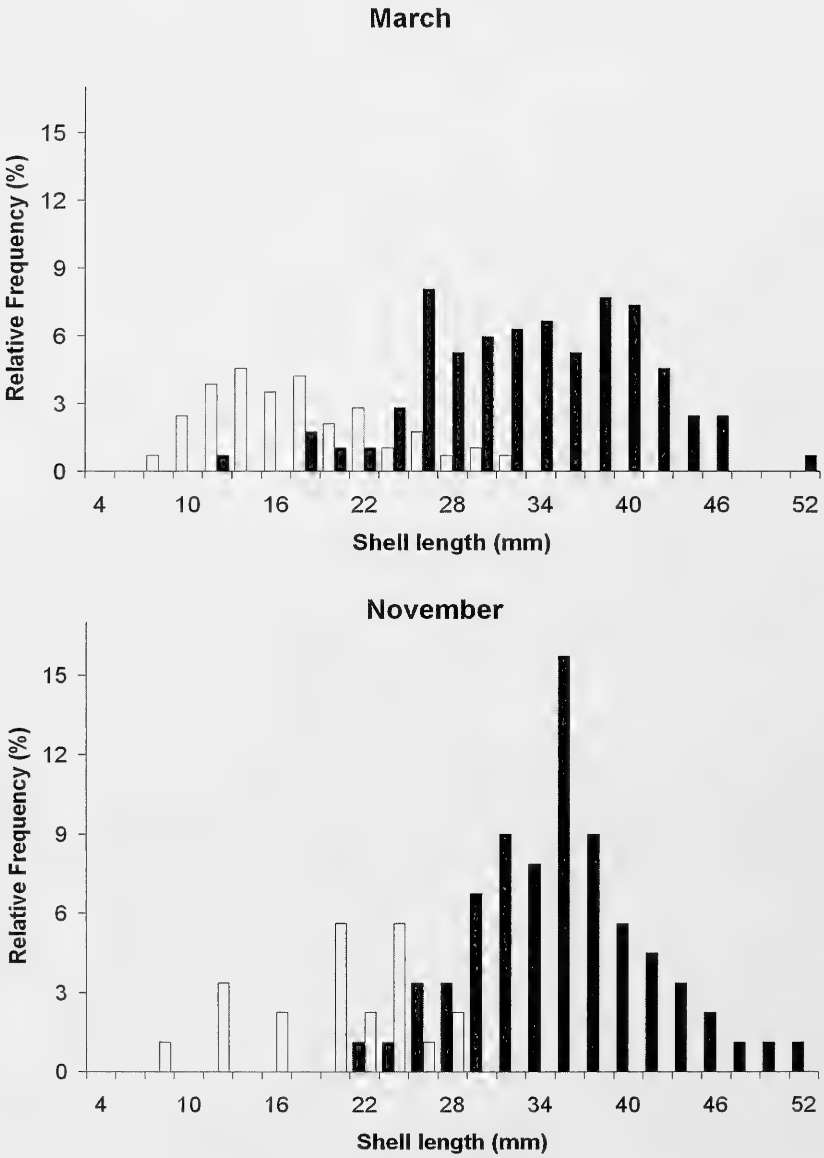


FIG. 36. *Crepidula cachimilla* sex proportion in March (N: 270) and November (N: 286). White: males; black: females.

37.3 SD: 0.9 N: 252), forming stacks of 2–5 individuals. The smallest brooding female was 23.5 mm SL; the largest was 49.5 mm SL.

Peak of female development from August to April (observed in 47 brooding females). Notable period of reproductive rest between March and November. No juveniles were encountered in the field during winter, being reflected in the diminution in the proportion of males in the population and their larger shell length in comparison with the summer (Fig. 36).

Egg masses with 15–65 capsules (Fig. 37) (mean: 35, SD: 14, N: 47). Egg capsules (Fig. 38) 2.2–3.3 mm in length (mean: 2.8, SD: 0.5, N: 148) and 2.3–3.4 mm in width (mean: 2.6, SD: 0.4, N: 148). Each egg capsule containing 129–441 uncleaved eggs (Fig. 39) (mean: 226, SD: 57, N: 148) in a whitish viscous liquid. All eggs developing into veliger larvae (Fig. 40) and hatching. It was not possible to measure hatching time. No nurse eggs or cannibalism was observed. No differences in number of embryos between initial and late brood stages in females of same size found.

Neither ln-transformed mean capsule size (r^2 = 0.01) nor ln-transformed capsule number per mass (r^2 = 0.13) correlated with shell length of brooding females. There was no positive correlation between ln-transformed egg number per capsule and ln-transformed capsule size (r^2 = 0.33) or ln-transformed female size (r^2 = 0.02).

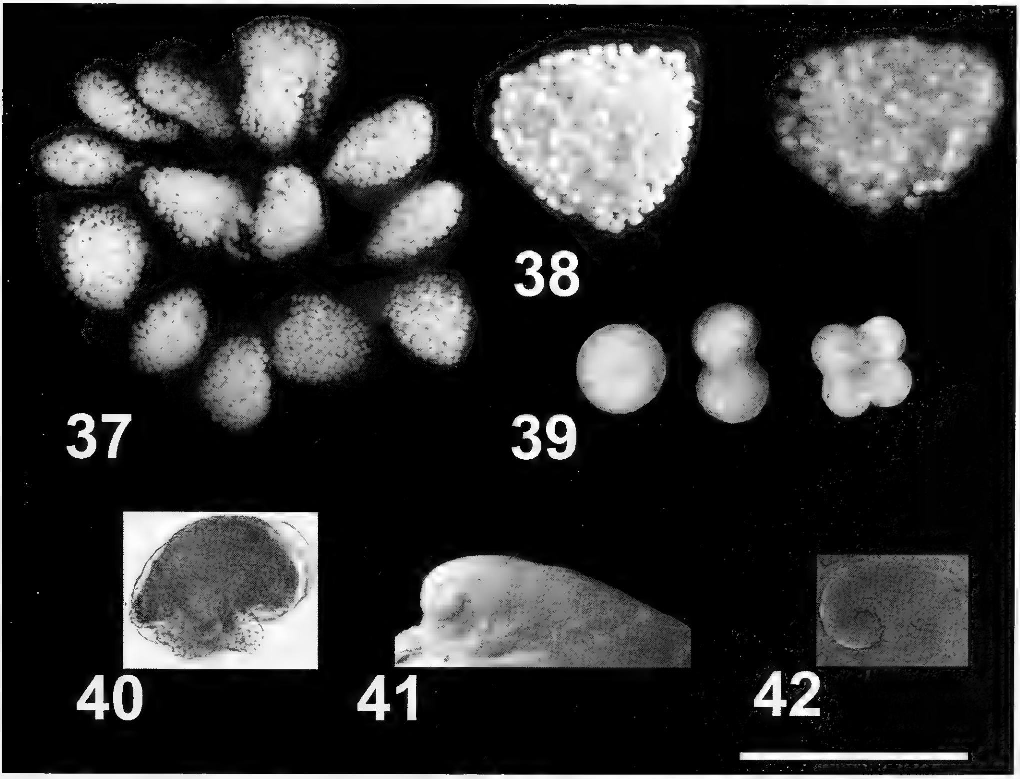
Uncleaved egg diameter 180–200 μm (mean: 191.7; SD: 7.2, N: 20). Protoconch length of juvenile shells (Figs. 41, 42) 700–800 μm (mean: 760 SD: 65 N: 11).

Habitat

Between 10 and 20 m depth, attached to hard substrata.

Distribution

Known only from northeastern Patagonia including the records from Golfo San Matías to Punta Norte of Parodiz (1939).



FIGS. 37–42. *Crepidula cachimilla* egg mass and protoconch. FIG. 37: Egg mass. Scale bar = 7 mm. FIG. 38: First and late stage egg capsule. Scale bar = 3.5 mm. FIG. 39: Eggs in first division stages. Scale bar = 500 μm. FIG. 40: Prehatching stage. Scale bar = 350 μm. FIG. 41: Protoconch on an adult shell. Scale bar = 800μm. FIG. 42: Detail with SEM of protoconch of an adult shell. Scale bar = 1,100 μm.

TABLE 2. Reproductive characteristics for *Crepidula* species from America compared with *C. cachimilla*.

Species	Reference regarding reproduction	Number of capsule per egg mass	Number of eggs per capsule	Uncleaved egg diameter (µm)	Nurse eggs
Crepidula onyx G. B. Sowerby I, 1824	Coe, 1942	50–100	100–200	no data	see discussion
C. onyx G. B. Sowerby I, 1824	Hoagland, 1986	19–60 (mean: 49)	100–300 (mean: 220)	160–180 (mean 172)	yes (6/capsule)
C. cachimilla	this study	15–65 (mean: 35 ± 14, N: 47)	129–563 (mean: 281 ± 74, N:148)	180–200 (mean: 191.7 ± 7.2, N: 20)	no
C. aplysioides Reeve, 1859	Miloslavich & Penchaszadeh, 2001	23 ± 5	3–12	300	no
C. coquimbensis Brown, 1996	Brown, 1996	-	62–135	195–263	-
C. dilatata Lamarck, 1811	Gallardo, 1977	22–29	308–1,016	-	yes
C. protea Orbigny, 1841	Hoagland, 1983	26–48	30–120	170	no
C. argentina Simone, Pastorino & Penchaszadeh, 2000	Cledon & Penchaszadeh, 2001	10–46	81–448	144–161	no
C. philippiana Gallardo, 1977	Gallardo, 1977	16–34	145–431	-	yes
C. fecunda Gallardo, 1977	Gallardo, 1977	-	mean 542	204–238	no
Bostrycapulus aculeatus (Gmelin, 1791)	Miloslavich et al., 2003	4–9 (mean: 9 ± 2, N: 51)	12–65 (mean: 38 ± 11, N: 57)	300–630 (mean: 417 ± 43, N: 263)	yes

(*continues*)

(*continued*)

Species	Hatching stage	Male shell length (mm)	Brooding female shell length (mm)	Maximum female shell length (mm)	Septum shape
Crepidula onyx G. B. Sowerby I, 1824	planktotrophic veliger larvae	4–30	-	60	-
C. onyx G. B. Sowerby I, 1824	veliger larvae	-	21–50	50	-
C. cachimilla	veliger larvae 260–300 μm	5.4–28.5	23.5–49	52.2	See shell description and figures
C. aplysioides Reeve, 1859	crawling juvenile 600 μm	-	9.4–18.2	-	-
C. coquimbensis Brown, 1996	crawling juvenile	-	-	-	S-shaped, apex never reaching margin
C. dilatata Lamarck, 1811	crawling juvenile	-	-	-	S-shaped, apex never reaching margin
C. protea Orbigny, 1841	veliger larvae	4.6–8.0	7.3–20	-	-
C. argentina Simone, Pastorino & Penchaszadeh, 2000	veliger larvae 190–230 μm	3.95–8.85	14.5–36	36	-
C. philippiana Gallardo, 1977	crawling	-	-	-	S-shaped, apex never reaching margin
C. fecunda Gallardo, 1977	-	-	-	-	S-shaped, apex never reaching margin
Bostrycapulus aculeatus (Gmelin, 1791)	4–20 crawling (mean: 13 ± 6, N: 5)	-	15–36	-	S-shaped, apex never reaching the margin

DISCUSSION

The shell of *Crepidula cachimilla* is similar to species occurring in the western Atlantic belonging to the "*Crepidula plana* complex" (Collin, 2000; Simone, submitted). Its most distinctive characters are the projecting apex, located somewhat away from the posterior shell base, and the absence of periostracum.

The characters of *Crepidula cachimilla* presented in the Diagnosis, mostly morphological, as well as those summarized in the Table 2, are the main basis differentiating this species. That set of characters easily separates the new species from the remaining South American taxa. From the Atlantic species with known anatomy, *C. cachimilla* has a thicker columellar muscle, a condition found only in other species in early stages of the development, after which the columellar muscle becomes reduced. As stated by Simone (2002), based on comparison of the ontogeny and phylogeny, the lateral and dorsal shell muscles are also derived from the columellar muscle, and are both thick in *C. cachimilla*; however, the respective scars in the shell are inconspicuous. The restriction of the pallial cavity aperture is one of the synapomorphies of the family Calyptraeidae (Simone, 2002); however, in *C. cachimilla* this state is still more developed, as it is greatly restricted on the right side by a broad fusion of the mantle border. The hypobranchial gland is normally reduced in *Crepidula*, being a thin glandular layer surrounding the visceral structures encroached into pallial cavity roof (Simone et al., 2000; Simone, 2002); however, *C. cachimilla* has practically no developed hypobranchial gland, the region where it would occur being thin and transparent. The contrary happens with the salivary glands, which are normally small; in *C. cachimilla*, these glands are longer than the haemocoel, being folded inside this cavity. This state is comparable with that of *Bostrycapulus aculeatus* (Gmelin, 1791) (also known as *Crepidula aculeata*); however, in that species, these glands are still larger (Simone, 2002). Other notable feature of *C. cachimilla* is the duplication of both ducts to digestive gland in the stomach.

Despite the conchological peculiarities of *C. cachimilla*, shell characters alone do not clearly distinguish it from *C. onyx*, which it resembles in shape, color, and size. This similarity led Parodiz (1939) to assume that the studied species was *C. onyx*. Such misidentifications are common in this family, with *C. argentina* (Simone et al., 2000) having been confused with *C. protea* in Argentina.

There are subtle differences in shell shape between *C. cachimilla* and *C. onyx*. *Crepidula cachimilla* tends to have a more pointed apex, and the shell also seems to be less convex, but these features can be strongly affected by the substratum.

Anatomical differences between *C. cachimilla* and *C. onyx* are not yet known, because there has not been a detailed anatomical study of the latter. However, the radular morphology of *C. onyx* (Hoagland, 1977) is markedly different from that of the studied species, in which the central tooth has 2–4 cusps (formula 2-1-2/0-0 to 4-1-4/0-0); the lateral tooth 7–10 cusps, (formula 7-1-0/0-0 to 10-1-0/0-0); and the inner marginal tooth has 1–3 cusps (1-1-0/0-0 to 3-1-0/0-0). In addition, the uncleaved eggs of the Argentinean material are larger than those of the Californian *C. onyx* population described by Hoagland (1986). The main difference between the species is the occurrence of six "malformed", or nurse eggs per sac (Hoagland, 1986) and the fact that "frequently fully half the entire number of embryos disintegrate within the capsules and are used as food by the survivors" (Coe, 1942). Although we are unable to assess the frequency of this phenomenon in California, such malformed eggs or disintegrating embryos were absent in the studied Argentinean material.

Aguirre & Farinati (2000) reported the presence of *C. onyx* among other *Crepidula* species from Quaternary sediments in Argentina. Because of the shell of the species described here is very similar to that of *C. onyx*, it is reasonable to assume that these fossil records belong to the species described here. The occurrence of these fossils proves that this is not an exotic species recently introduced to the area. Additional differences between the reproductive parameters reported by Hoagland (1986) and Coe (1942) for *C. onyx* and *C. cachimilla* are: the larger egg diameters and the complete lack of nurse eggs or cannibalism in *C. cachimilla*, and the different radular morphology. On this basis, the material studied by Parodiz (1939) should be assigned to the new species described here instead of being assigned to *C.* aplysioides, as proposed by Hoagland (1977).

Crepidula cachimilla also differs from other species in many reproductive strategy characteristics. *Crepidula aplysioides* Reeve, 1859, is a small (up to 2.0 cm SL; brooding female between 9.4 and 18.2 mm SL) tropical and subtropical species with egg capsules containing fewer eggs than *C. cachimilla* (Hoagland, 1977). Further reproductive characteristics are given by Miloslavich & Penchaszadeh (2001). The number of eggs per capsule separates *C. cachimilla* from *C. coquimbensis* Brown & Olivares, 1996; *C. dilatata* Lamarck, 1822; and *C. protea* Orbigny, 1841 (Table 2). In *C. cachimilla* (Table 2), the egg diameter clearly differs from that of *C. argentina* (Cledón & Penchaszadeh, 2001), *C. philippiana* (Gallardo, 1977, 1996), *C. fecunda* (Gallardo, 1979) and *C. dilatata* (Gallardo, 1977; Chaparro & Paschke, 1990) (Table 2). In *C. cachimilla* (Table 2), eggs per capsule are more numerous, and both males and females are larger than those of *C. protea* (Hoagland, 1983). The larval shell at hatching and the protoconch of juveniles are larger in *C. cachimilla* (Table 2) than in *C. argentina* (Cledón & Penchaszadeh, 2001) (Table 2).

According to our observations on *C. cachimilla*, broods containing a large number of capsules (more than 40) always belong to females larger than 31 mm SL. Because of the number of eggs per capsule does not depend on the female size, we used this parameter as species representative.

A more extensive comparison of the morphology of *C. cachimilla* with other species of the "*Crepidula plana* complex" is being published elsewhere (Simone, submitted), with a phylogenetic analysis of all known species occurring from Florida to Patagonia. *Crepidula cachimilla* is separated from the remaining species by such plesiomorphies as the thickness of the shell muscles (columellar, lateral and dorsal muscles), which are very thin in the other species; the nephridial gland having clearly transverse septa, whereas in the remaining species this gland has irregular longitudinal folds; the larger size of the salivary glands, which are normally reduced; and retention of the ventral tensor muscle of the radula (m11), mostly lost in other species.

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RESEARCH NOTES

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CHROMOSOMES OF THE CHINESE MUSSEL *ANODONTA WOODIANA* (LEA 1834) (BIVALVIA, UNIONIDAE) FROM THE HEATED KONIN LAKES SYSTEM IN POLAND

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ABSTRACT

The chromosome complement of freshwater mussel *Anodonta woodiana* was investigated using Giemsa, Ag-NOR and chromomycin A_3 staining. The diploid chromosome number of this species is 2n = 38, and the arm number (FN) = 76. Nucleolar organizer region (NOR) was found on one chromosome pair, and it was connected to GC-rich chromatin, as visualized by CMA_3 staining.

Key words: *Anodonta woodiana*, chromosomes, freshwater bivalve, karyotype, NOR.

INTRODUCTION

The freshwater bivalve mollusk *Anodonta woodiana* is native to eastern Asia. In recent years, it has been discovered in Europe (Kiss & Pekli, 1988; Beran, 1997) and on several Indonesian islands (Watters, 1997). It has also been collected in the wild in the Dominican Republic and Costa Rica (Watters, 1997).

In the heated Konin Lakes of Poland, *Anodonta woodiana* appeared in the mid-1980s following the introduction of silver carp, *Hypophthalmichthys molitrix* (Val.), from Hungary (Afanasjev et al. 2001; Kraszewski & Zdanowski, 2001). *Anodonta woodiana* was observed as a dominant species in some parts of this system of lakes (Protasov et al., 1994).

Within Unionidae, the chromosome number is known for 26 species, and most of them have 38 (reviewed in Nakamura, 1985; Barsiene, 1994; Thiriot-Quiévreux, 2002). Five species of *Anodonta* have been studied cytogenetically, but only diploid chromosome number (2n = 38) and fundamental arm number (FN = 76) have been established (Nakamura, 1985; Barsiene, 1994).

The present report describes the karyotype and location of nucleolar organizer regions (NORs) of *Anodonta woodiana* from Poland.

MATERIALS AND METHODS

Nineteen specimens of *Anodonta woodiana* from the Konin Lakes in central Poland were studied for chromosome complement.

A 0.4% solution of cobalt chloride was injected *in vivo* (0.05–0.1 ml per specimen, depending on shell length, which ranged from 10 to 17 cm). Cobalt chloride blocks two major steps of cellular respiration. As the result of tissue hypoxia it stimulates cell proliferation (Webb, 1962, cited by Cucchi & Baruffaldi, 1989).

After 60 h, 0.1% colchicine solution was injected to the mussel's foot *in vivo* for 6 h. From 0.5 to 1.0 ml of colchicine solution were used (depending on the mussel's size). Gills were dissected, homogenized in distilled water, and hypotonized for 60 min in distilled water. Cell suspensions were fixed by 3:1 methanol/acetic acid and centrifuged three times at 1,000 rpm. Each slide preparation was made using air-drying technique (Thiriot-Quiévreux & Ayraud, 1982).

For conventional karyotypes, chromosome preparations were stained with 5% Giemsa in distilled water for 20 min. CMA_3 staining was done according to Sola et al. (1992) and Ag-NOR staining as described by Howell & Black (1980).

TABLE 1. Relative lengths (RL) and centromeric indices (CI) of *Anodonta woodiana* chromosomes.

Chromosome pair no.	RL	SD	CI	SD	Classification
1	3.75	± 0.06	46.50	± 4.39	m
2	3.39	± 0.08	49.09	± 0.50	m
3	2.98	± 0.06	43.34	± 2.83	m
4	2.60	± 0.03	43.93	± 3.20	m
5	2.53	± 0.07	43.06	± 2.21	m
6	2.41	± 0.04	45.65	± 0.99	m
7	2.42	± 0.01	45.19	± 5.49	m
8	2.31	± 0.13	45.38	± 1.19	m
9	2.21	± 0.07	43.39	± 2.46	m
10	2.15	± 0.09	43.76	± 1.96	m
11	3.20	± 0.02	35.78	± 2.34	sm
12	2.96	± 0.14	37.26	± 1.45	m-sm
13	2.82	± 0.03	33.47	± 1.07	sm
14	2.60	± 0.08	36.02	± 2.51	sm
15	2.51	± 0.09	29.65	± 4.91	sm
16	2.50	± 0.17	37.31	± 1.19	m-sm
17	2.22	± 0.11	38.11	± 0.68	m-sm
18	2.16	± 0.01	38.27	± 2.27	m-sm
19	2.28	± 0.04	31.96	± 2.01	sm

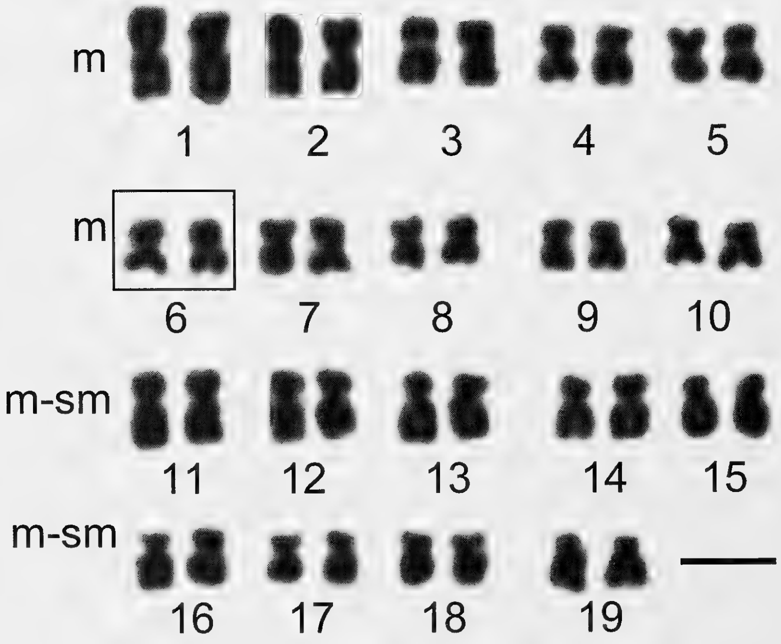


FIG. 1. Karyotype of Chinese mussel (*Anodonta woodiana*). m – metacentric chromosomes, m-sm – meta-submetacentric and sm – submetacentric chromosomes. NOR-bearing chromosome pair is framed. Scale bar equals 5 μm.

Chromosome spreads were analyzed under a Nikon Optiphot 2 fluorescent microscope equipped with UV filters for identification of fluorescent signals and photographed by Coolpix 995 camera.

Ten metaphase plates were karyotyped. Morphometric measurements of chromosomes were made using the freeware computer application MicroMeasure version 3.3 available on the Internet at: http://www.colostate.edu/Depts/Biology/MicroMeasure. The relative length (RL) (100x chromosome length/total haploid length) and the centromeric index (CI) (100x length of the short arm/total chromosome length) were calculated. Chromosomes were classified according to Levan et al. (1964). In case of six animals sequential staining CMA_3/Ag-NOR was done, and at least three metaphase plates from each specimen were analysed. About 50 interphase nuclei were observed from the same six individuals after silver staining.

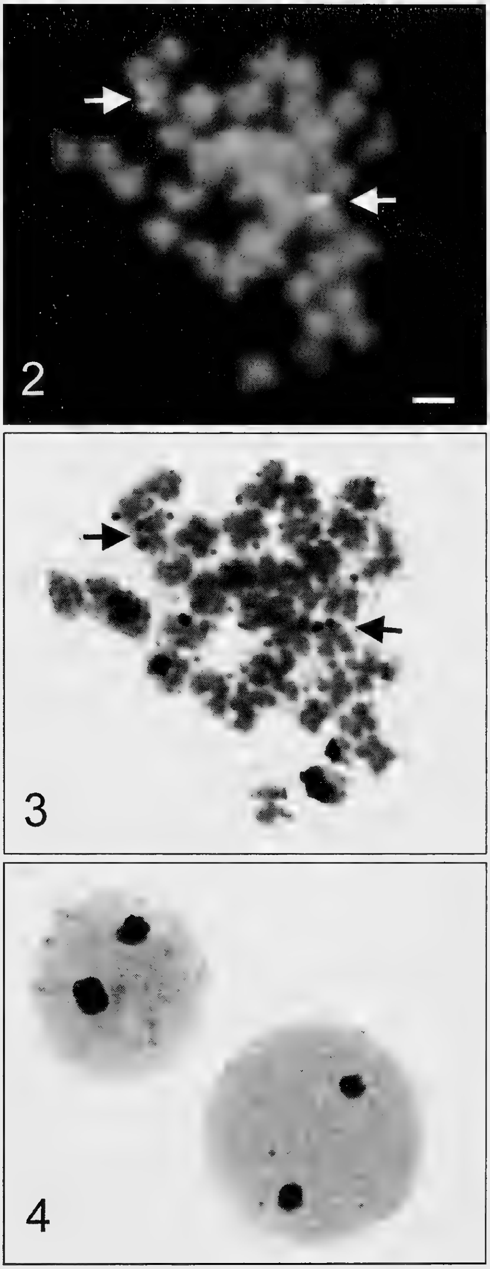
RESULTS

From 19 individuals of *Anodonta woodiana*, 211 Giemsa-stained metaphase plates were analysed, showing that the diploid chromosome number was $2n = 38$ (Fig. 1). Relative length ranged from 3.74 to 2.15 (Table 1), and the karyotype consisted of 10 pairs of metacentric, five pairs of meta-submetacentric, and four pairs of submetacentric chromosomes (FN = 76) (Fig. 1, Table 1).

Staining with fluorochrome CMA_3 revealed bright positive bands at terminal position on the short arm of one chromosome pair of *Anodonta woodiana* (Fig. 2). The same results were obtained using silver staining (Ag-NOR). Sequential CMA_3/Ag-NOR staining procedure of the same metaphases showed that the CMA_3 and silver positive signals appeared at the same chromosome site of metacentric chromosome pair no. 6 (Fig. 3). The number of silver-stained interphase nucleoli in *A. woodiana* cells never exceeded two nucleoli per cell (Fig. 4).

DISCUSSION

The karyotype of the Chinese mussel has been described for the first time in the present paper. The chromosome number of *Anodonta woodiana*, $2n = 38$ (Fig. 1), is coincident with



FIGS. 2–4. *Anodonta woodiana*. FIG. 2: Metaphase chromosomes of after CMA_3-staining. Arrows indicate NOR chromosomes. Scale bar equals 5 µm. FIG. 3: Metaphase chromosomes of after Ag-staining. Arrows indicate NOR chromosomes. FIG. 4: Silver stained interphase nuclei with two active nucleoli.

that reported for other *Anodonta spp.* – *A. anatina*, *A. grandis*, *A. piscinalis*, *A. cygnea*, *A. subcircularis* (Nakamura,1985; Barsiene, 1994). Such a diploid chromosome number is the most frequent one among the bivalve species previously studied. About 47% of species within the class Bivalvia, particularly from Palaeoheterodonta and Heterodonta possess 38 chromosomes (Thiriot-Quiévreux, 1994).

Fundamental chromosome arm number (FN) reported for four Unionidae species equaled 76 (Nakamura, 1985). The same value of FN was observed in *Anodonta woodiana*, because only bi-armed chromosomes (meta- and submetacentrics) were found (Fig. 1; Table 1).

In eukaryotes, the 18S, 5.8S, and 28S ribosomal RNA genes (called major rDNA) are present in high copy number and are clustered as tandem repeats at one or more chromosomal sites, termed nucleolar organizer regions (NORs) (Long & David, 1980). These clusters can be visualized indirectly by staining complex of residual acidic protein associated with the fibril center of the nucleolus (Ag-NORs) (Jordan, 1987) or using chromomycin A_3 (CMA_3) staining, which binds to GC rich chromatin (Amemiya & Gold, 1986). These methods do not detect the regions containing 5S (minor) rDNA, another multicopy ribosomal gene not involved in the formation of the nucleolus (Little & Braaten, 1989).

The single NOR locus in Chinese mussel (Fig. 3) represents one of the NOR patterns observed in bivalves. The number of NOR-bearing chromosome pairs in these mollusks varies from one in *Mya arenaria* (Thiriot-Quiévreux et al., 1998), *Donax trunculus* (Martinez et al., 2002) and *Brachidontes pharaonis* (Vitturi et al., 2000) to three in *Mytilus californianus* (Martinez-Lage et al., 1997; Gonzalez-Tizon et al., 2000) and *M. trossulus* (Martinez-Lage et al., 1997). The chromosomal location of NORs in most species was terminal, as was found in *A. woodiana* (Figs. 2, 3). It has been suggested that a single pair of chromosomal NORs located terminally may represent a plesiomorphic character (Amemiya & Gold, 1990; Thiriot-Quiévreux, 1994).

GC-rich CMA_3 positive heterochromatin connected to NORs is typical of fish and amphibians (Amemiya & Gold, 1986), although it has also been observed in bivalve mollusks (Martinez-Exposito et al., 1997; Martinez-Lage et al., 1994). Staining with fluorochrome CMA_3 has revealed the existence of GC bands on one chromosome pair, at the same location as Ag-NOR in *Anodonta woodiana* (Figs. 2, 3). Other bivalve species show CMA_3 positive bands on two or more chromosome pairs. In mytilids, some CMA_3 bands were present at the NOR sites but also CMA_3-negative NORs were present and CMA_3 bands not connected to NORs were found (Martinez-Lage et al., 1995; Vitturi et al., 2000). The interstitial locations of CMA_3 bands were observed on *Donax trunculus* (Martinez et al., 2002) and *Dreissena polymorpha* chromosomes (Woznicki & Boron, 2003). Apart from the single Ag-NOR site CMA_3 positive signals were found in zebra mussel on almost all chromosomes except pairs 1, 5 and 16 (Woznicki & Boron 2003). The association of NORs with CMA_3-bright bands shows that the use of combined, sequential CMA_3/Ag-NOR staining proved to be practicable and reliable for the detection of ribosomal regions of the bivalve mollusks chromosomes.

Present findings provide an initial step in the cytogenetic characterization of invasive aquatic species, *Anodonta woodiana* and the first case of NORs description in the species from genus *Anodonta*.

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LOCOMOTION IN *HELIX ASPERSA*

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ABSTRACT

The pedal waves in *Helix aspersa* move faster than the foot of the animal. On the other hand, a histological study of the foot could not identify an organized muscular structure expected to be capable of wave construction. Instead, a non-organized tissue with relatively few muscle cells and many collagen fibers mixed with vessels and empty cavities was found.

We could demonstrate that the movement of the waves was uncoupled from the movement of the foot and that the forward displacement of the snail is due to rhythmic fluid accumulation under pressure. This pressure generates a force in backward direction on the substratum, which in turn is used as push off by the animal to move in a forward direction. The snail does not crawl, the waves move independently from the foot sole, and the animal glides smoothly without changing the length or the shape of the foot.

The problem how waves are constructed starting from the available muscular material is not solved. We advance a cautious hypothesis that it happens by a cyclic reversible recruitment of cells at the moving front and a corresponding dropping off at the rear.

Key words: *Helix*, locomotion, haemolymph.

INTRODUCTION

During a study of the changes in the shape of smooth muscle cells when undergoing contraction, our attention was drawn to the foot of the snail as a possible suitable model. Common garden snails were caught, fixed and processed for histological examination. This showed that the foot did not contain one or more large muscles orientated in one direction, but many discrete muscle cells and fibers distributed in an irregular three-dimensional pattern. Moreover, collagen fibers and empty clefts or holes made up the larger part of the space. When watching the characteristic waves on the foot sole, the question arose how an apparently unorganized group of individual muscle cells and fibers could manage to assemble ordered unidirectional waves. Closer examination showed that the waves moved faster than the foot, which led to the conclusion that the movement of the waves was uncoupled from the advancing movement of the foot. A transmission by a fluid interphase, in this case the haemolymph, was considered as a likely possibility and became the aim of this study. Because we do no not know exactly how these waves are structured, the use of the term is purely descriptive. What we see are narrow, dark, transverse stripes separated by wider light segments, which we will call "junctions" for convenience.

MATERIALS AND METHODS

Snails (n = 150) of the species *Helix aspersa* were collected in spring and early summer. They were housed in plastic boxes and fed lettuce. Their average weight was 5.2 g (3.9–7.2 g). After dissection, tissues of 20 animals were fixed in a 4% aqueous solution of formalin. Bouin's, methacarn, and isopropanol fixatives were used when appropriate. Sections of paraffin-embedded material were stained with Sirius red haematoxylin. Additional stains were Masson's trichrome, PAS, PAS with amylase digestion, haematoxylin and eosin, alcian blue at pH 4.2, mucicarmin, Von Kossa's for calcium, Kernechtrot and Fontana's silverstaining for melanin. A contracted foot of 21 mm length and an expanded one of 32 mm length were cut in uninterrupted serial sections.

Speeds of the animals were recorded while gliding on perplex plates over a distance of 50 mm, and for each animal five consecutive displacements were timed. Videotapes were made from animals in different positions, on different substrata and under different angles of illumination. Standard and scanning radiographs of resting and moving animals were taken. Injections of Indian ink droplets in the foot of anaesthetized animals were studied by videotape and after killing by histology in order to establish the exact location in the foot.

Repeated attempts to record electrical activity were unsuccessful.

RESULTS

Histology

The foot contains from the tip to the tail a moderate number of slender discrete smooth muscle cells or fibers embedded in a loose network of many collagen fibers. Fibers lie in longitudinal, circular, and vertical directions without any preferential pattern. They make many short contacts with each other (Fig. 1). Many vacuolated interstitial cells and many empty spaces occupy the interstitium. Thin-walled muscular vessels (arteries) and spaces lined by flattened endothelial type cells, probably representing veins, can be identified. Many empty spaces not lined by cells are distributed throughout and are particularly concentrated at the margins of the foot sole. The existence of a ramified communicating system of channels can be demonstrated convincingly by the injection of Evans blue in the tail of a fixed foot. The dye spreads diffusely in the core of the foot and then moves to the margins where it is easily recognized because of their thinness. If sufficient pressure is applied, the dye fills the head and induces the eversion of the antennae.

Few nerve fibers can be detected by routine stains. We used a Mab against acetylated tubulin (Sigma T 6793, clone 6-11B-1) and DAB as chromogen to demonstrate a nervous network making contact with the smooth muscles. We only found thin ramifications extending to the base of the epithelial cells of the sole that had all the characteristics of sensitive nerve endings. In addition, the sole shows transverse lines regularly spaced at 1.0–1.5 mm intervals in a contracted foot of 25 mm length. Histology reveals that they are condensations of collagen fibers closely apposed to the sole epithelium. We did not find mention of these structures in the literature. Findings on mucus cells are not reported because they are not relevant to this study.

Displacement of the Waves

The snail *Helix aspersa* moves according to a monotaxic anterograde "wave" pattern. The waves move faster than the animal. The junction length is ± 4 mm, the thickness of the wave is 1.0–1.5 mm. The wave is composed of two layers, a cranial one which is lighter and a darker caudal one. Generally 10 to 12 waves can be counted at one point in time. Table 1 shows figures that allow calculation of the ratio of the speed of the waves to the speed of the animal. The waves move 2.3 times faster than the animal. Prior & Gelperin (1974) found in *Limax maximus* a ratio of 2.2. Jones & Trueman (1970) detected in *Patella vulgata* a ratio of 3.5. Bonse (1935) reports ratios between 0.93 and 1.48 in *Helix pomatia*. Unfortunately, these authors did not elaborate on this phenomenon in later studies.

TABLE 1. Speed of animals versus speed of waves.

Speed of animals (n = 90 individuals)	
Distance covered in 30 sec	$\overline{S}$ = 50 mm
Speed per second	1.6 mm
Speed of waves (n = 60 individuals)	
Length of junction	$\overline{S}$ = 4 mm
Number of waves in 30 sec	$\overline{S}$ = 27.5
Distance covered in 30 sec	4 mm x 27.5 = 110 mm
Speed per second	3.7 mm
Ratio speed of waves/speed of animals	2.3

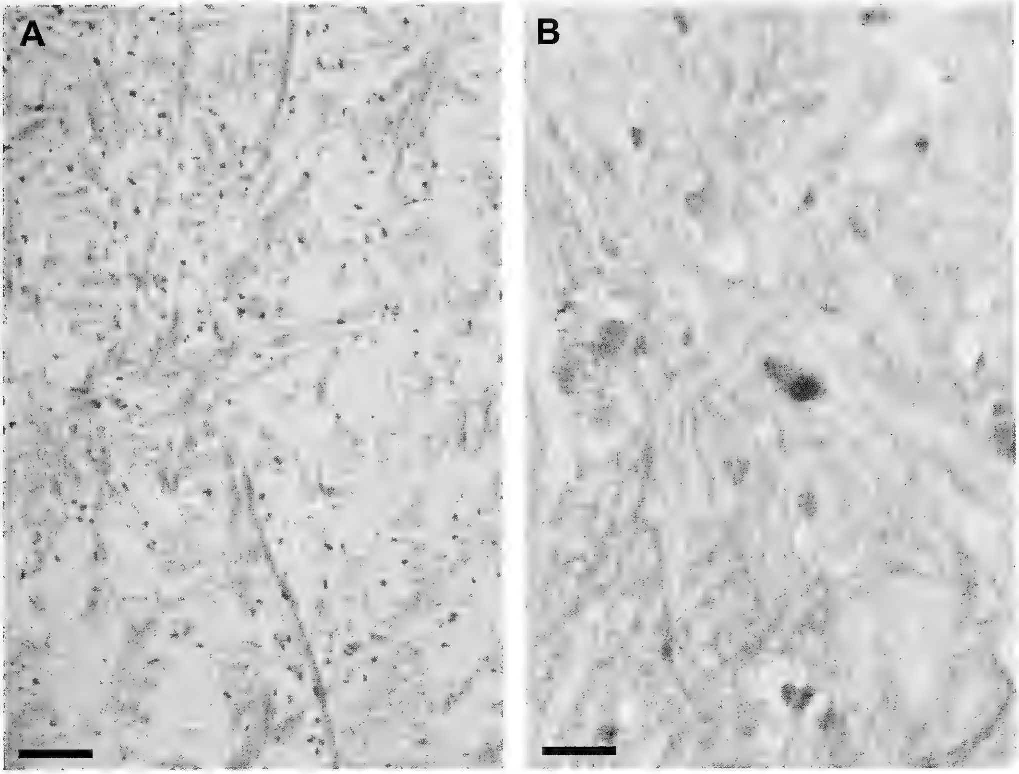

FIG. 1. Section of foot. A. Irregular distribution of muscle fibers in red and collagen fibers in green. Masson's trichrome stain. Scale bar = 200 µm. B. Collagen fibers are red and are closely apposed to the muscle fibers which show many contacts. Sirius Red Hematoxylin. Scale bar = 50 µm.

Because the progression of waves is not matched by a corresponding progression of the foot, the waves cannot act as "toes" on which the snail could lean to move ahead. Hence the problem of how the waves command foot movement must be addressed.

Independent from the waves, other irregular undulations are seen at the very margins of the foot over a width less than 1 mm. They move in a caudal direction at a pace of 1 mm every 1–3

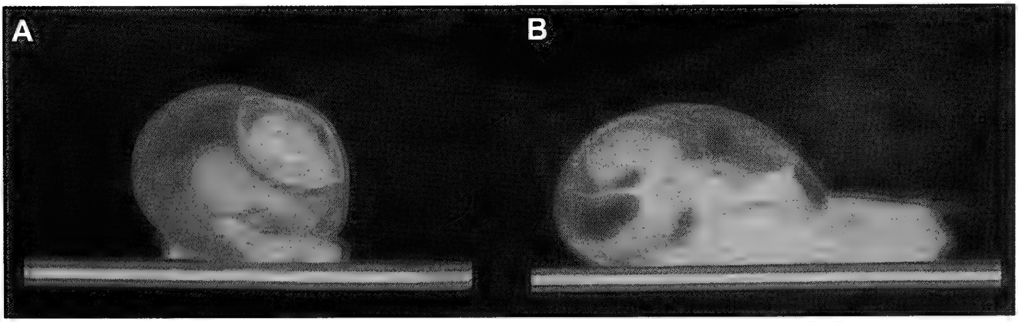

FIG. 2. Scanning radiograph showing the tight apposition of the foot on the substratum. A. Frontal view. B. Lateral view.

TABLE 2. Time to pull different weights over a distance of 50 mm in three snails (A–C) of comparable body weight (body weight is given in parentheses).

	Time in sec		
Weight	A (5.9 g)	B (5.4 g)	C (5.3 g)
9 g	29	35	27
15 g	40	41	42
21 g	90	65	70

sec and reach the tail. They were mentioned by Bonse (1935), and their function is unknown.

Before a wave appears, the tip of the foot is dilated by fluid accumulation. In this dilated portion, the first wave is formed. Successive waves develop in caudal direction, but at the very moment they are formed they start to move in cranial direction. It is clear that this is not comparable to a peristaltic wave system originating in the tail and rushing to the tip. When the animals stops, the waves also stop, the most caudally situated first. There is no jamming at the tail. Accidental amputation of the tail does not stop emergence of waves.

When the moving animal is grasped by the observer and turned upside down waves continue for a few minutes. Visual observation confirmed by videotaping show that the waves do not cause a retraction of the foot surface but that the junctions bulge as they are filled with fluid. It is clear that the junctions by their expansion push on the substratum and that they are the propulsive elements. Bonse (1935) and Lissmann (1945) have demonstrated that the pressure of the foot on the substratum decreased when the wave passed and resumed to normal when the junction moved over the recorder plate.

Waves can persist in feet severed from the body. They can last for 15 min and thereafter continue as irregular slow movements for two hours. These contractions come to an end in the tip of the foot where they first originated: primum movens, ultimum moriens! The marginal undulations were very resistant and could be observed up to six hours after sectioning. In the slug *Limax maximus*. Prior & Gelperin (1974) detected waves after decapitation and demonstrated that the presence of the central nervous system was necessary to initiate them. However, once started, the waves could form independently. The important conclusion of these findings is that waves can develop and function without a pulsating heart.

In our material, the snail does not lift its foot in a detectable amplitude during forward movement. We could substantiate this in three ways. First, by visual observation of the moving animals with an amputated tail. Second, by allowing the snail to glide on black paper and studying the mucus trail. Over distances from 50 cm to 1 m this is a straight ribbon without any irregularities either in the centre or at the margins. Third, by scanning radiography of resting and moving animals, which demonstrates that the foot really sticks over its whole length to the substratum (Fig. 2).

The snail glides on its own slime. The bulging junction exerts a backward pressure parallel to the substratum. This can convincingly be demonstrated by videotaping: when the snail rests on a thin plastic strip and is held by an observer, the marker lines on the strip move backwards. With the same method, it is possible to measure the energy that the snail uses for forward displacement. When we attach to the strip a string with a weight that we let hang over the border of a table, we can measure the time in which the animal can push backwards the plastic strip with its attached weight. Table 2 shows the figures for three snails of comparable weight. It appears that animal A, for instance, can pull a weight of 9 g over a distance of 50 mm in 29 sec, which is the same speed as a free moving animal. When the weight increases, the speed decreases accordingly. Calculating the energy in our first example, we arrive at 0.0015 milliwatt.

The displacement of haemolymph in the foot as demonstrated by the bulging of the junctions is not visible when the foot rests on the substratum, because it is a pressure mechanism and not a crawling mechanism. The pressure generates a force that is parallel to the substratum and directed backwards. These are the conditions for developing shear stress. However, due to the fact that the mass of the substratum is too big to be displaced, the displacement or shear strain, occurs in the opposite direction. This may be an explanation why a backward moving force induces a forward displacement.

Finally, the behavior of injected Indian ink should be reported. Histological examination showed that the droplets were generally present in pre-existing clefts in the core of the foot. Sometimes they accumulated in the numerous spaces close to the epithelium. A linear deposit of a few mm in longitudinal direction is particularly suited for examination. When the arriving wave hits the posterior end of the ink deposit, it is slightly pushed forward and during the passage of the wave slightly stretched. Once the wave has passed, the deposit resumes its original shape and position. The image looks like the wobbling of a leaf on the waves in a pond. During these small changes in the shape and position of the ink deposits special attention was paid to the shape of the foot and to the continuity of the forward movement. Analysis of the videotapes could not disclose any change, leading to the conclusion that the behavior of the ink material is an internal event and is not coupled to the foot sole.

DISCUSSION

Our study demonstrates that in *Helix aspersa* the pedal waves move faster than the foot. The shape of the foot and the continuity of the forward movement do not show any temporal or topographic relationship with the wave movement. The displacement and deformation of Indian ink droplets is not coupled to similar changes in the foot sole. These findings allow the conclusion that the waves act indirectly by the intermediary of the haemolymph. This conclusion is also corroborated by the observation of the filling with fluid of the segments ("junctions") between the waves, resulting in the pressure on the substratum, leading in turn to the forward movement. In addition, the temporal persistence of waves after severing the foot from the body indicates that a pulsating heart is not necessary to maintain waves.

The question of how waves are built up from non-organized muscles is not solved. Authors who describe muscle bundles in different fixed directions are fortunate and use these to explain the locomotion of the foot in snails and slugs. Jones (1975) published an exhaustive report on locomotion in Pulmonata. However, he did not address the problems of our present study. To the best of our knowledge, he is the first author who succeeded in catching moving waves. He described in *Agrolimax reticulatus* the fixation of waves by immersing the moving animals in liquid nitrogen (Jones, 1973). In cryostat sections, he reported a compression of oblique muscles and an almost complete occlusion of the haemocoel. He presented a micrograph showing muscle fibers that are reduced to strings, lying in many directions and occupying a very small fraction of the tissue area. For a morphologist, it is difficult to correlate this tissular arrangement with waves. In *Helix pomatia*, he described the foot as highly muscular. We did not study *Helix pomatia*, but we can confirm that in *Helix aspersa* and in several other snails this is not the case.

In his review on locomotion of molluscs, Trueman (1983) described for *Helix* a model of locomotion based on a crawling mechanism. Crawling is a biphasic activity. A transient stationary point or zone serves as an anchor for the contracting or elongating free moving and uplifting segment of the animal. When waves are present, it is assumed that the wave is the anchor and that the animal advances because of the successive anchoring of the waves. The author refers to the work of Denny (1980), who studied the physicochemical properties of the mucus of *Agrolimax columbianus*. This author proposed a dual reaction of mucus changing from a solid phase in the stationary state to a liquid phase in the moving state, acting like a material ratchet. These properties of the mucus may facilitate the crawling mechanism proposed by Trueman.

Several other students of snail locomotion also propose the crawling mechanism for forward displacement: Trappman (1916), Miller (1974), Gainey (1976), and Moffett (1979).

In a study on the histology of the foot and the locomotion of Gastropoda, Elves (1961) mentioned that in *Discus rotundatus* the musculature of the foot is not well developed, and muscle fibers are of small size and few in number. He devoted a short description to *Helix aspersa* and described in the foot a reticulum of connective tissue fibers and large muscles which run both longitudinally and dorsoventrally. However, in the accompanying diagram, he depicted the muscular component as a few scattered small bundles occupying a small fraction of the total transverse section area. In his discussion, he mentioned that the locomotion may be influenced by an interplay between haemocoel turgor and muscular waves.

An interesting type of forward displacement in terrestrial gastropods was discussed by Pearce (1989). It was termed "loping" (derived from galloping) and differs from the gliding progression. In the loping motion, the gastropod lifts its head from the substratum and thrusts it forward, then replaces it on the substratum, forming a low arch in the sole behind the head through which the rest of the body flows to the new stationary point of contact. The mucus trail left consists of more or less elongated dots, in contrast to the continuous mucus trail during gliding progression. Hence, loping is a perfect example of crawling and a strong argument for the existence of a different "ordinary" (terminology of Pearce) gliding mechanism. Interestingly, the waves of ordinary gliding are present with loping, but there is no interference.

We can only speculate about what happens in *Helix aspersa*. The signal for wave formation starts at the tip of the foot, resulting in the successive appearance of waves in the caudal direction. At the very moment the waves are induced, they start moving in cranial direction back to their initial inductive signal. The waves are not at all sinusoidal peristaltic contractions or pressure waves like in blood vessels. They resemble slice-like condensations of tissue (muscle, collagen, and interstitial cells), which move in an upright position along a horizontal plane parallel to the foot sole. A possible explanation how to visualize the formation of such a structure could be that the slices of condensed tissue while moving acquire cells at the advancing front and release them again at the trailing front. This phenomenon of recruitment is known in the forward movement of cells in culture. Bretcher & Aguado-Velasco (1988) describe how lamellipodia, which are formed by cells when they start moving, recruit plasma membrane material at the expense of the trailing end of the cell. In fact, these cells do not advance by moving but by growing. The concept of recruitment can perhaps explain why waves are bilayered, the frontal directed half being the recruitment front and the rear half being the propulsion machine.

Concerning the muscular structure of the foot an interesting micrograph is published by Bernard (1968). It shows in the foot of the large marine snail *Polinices lewisi* muscle and collagen fibers in a three-dimensional pattern reminiscent of the foot of *Helix aspersa*. Waves were not mentioned, and the foot aspirates and expels ambient water.

Analyses of movie films of waves in *Helix pomatia* have been reported by Bonse (1935) and Lissman (1945) and in *Patella vulgata* by Jones & Trueman (1970). However, these excellent studies do not address the basic question how we can understand the formation of waves or why they move faster than the animals.

ACKNOWLEDGMENTS

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COLORATION IN HELICINIDAE (MOLLUSCA: GASTROPODA: NERITOPSINA)

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ABSTRACT

The coloration of Costa Rican Helicinidae has been studied, with special attention paid to the arboreal species. It is shown that either shell color or mantle pigmentation contribute to the coloration visible in the living animals. Ecological and systematic implications are given. This paper is supplementary to Richling (2004).

Keywords: Helicinidae, Costa Rica, Central America, classification, coloration.

INTRODUCTION

During a recently published revision of the systematics and species differentiation in Costa Rican Helicinidae (Richling, 2004), the role of coloration was studied. As the plates were printed in black and white, I provide here the same plates in color and give additional notes on species in relationship to color patterns. Further details on the species, especially those in Figure 6, material and methods and literature are given in Richling (2004).

RESULTS AND DISCUSSION

Coloration in land snails is mainly determined by the need for camouflage. Thus, it depends strongly on the habitat of the respective species. The Costa Rican species inhabit tropical rain forests and can be split into two groups: arboreal species and ground dwellers crawling in leaf litter. The arboreal species show a variable, bright coloration, as can be found in other arboreal land snails, for example, species of *Liguus* (Orthalicidae), *Amphidromus* (Camaenidae), and *Cepaea* (Helicidae), with yellow and red prevailing. They are seldomly greenish in adaptation to leaves.

All Costa Rican species of the genus *Helicina* exhibit this pattern (Figs. 3, 4, 5A–D), with a greenish color developed in certain specimens of *Helicina funcki* L. Pfeiffer, 1849 (Fig. 3A), and *Helicina escondida* Richling, 2004 (Fig. 4H). The ground dwellers, *Lucidella lirata* (L. Pfeiffer, 1847), *Alcadia hojarasca* (Richling, 2001), and *Alcadia boeckeleri* (Richling, 2001), are uniformly brownish, and in addition exhibit a rough surface, that is, periostracal hairs or ridges on the shell (Figs. 2O–Q, 5F–H). *Pyrgodomus microdinus* (Morelet, 1851) is the only exception in its strong association to surfaces of calcareous rocks. In living individuals, the bright yellow empty shell (Fig. 2R) becomes greenish-grayish because of the underlying dark pigmentation of the mantle. Furthermore, *P. microdinus* glues particles of detritus on its shell, thus perfectly resembling the rock surface (Fig. 5E). The same applies to the Jamaican *Eutrochatella pulchella* (Gray, 1825), in which the active camouflage is functionally replaced by the white-yellowish mottling of the shell (Figs. 6M, P).

When comparing the coloration of living animals with empty shells, it becomes obvious that in the Costa Rican arboreal species, two different ways are utilized to produce the variable and bright coloration. On one hand, the species have a variable shell color combined with rather thick shells and a uniform mantle pigmentation, for example, *Helicina funcki*, which can even be nearly reddish; *H. pitalensis* Wagner, 1910; *H. beatrix* Angas, 1879; *H. talamancensis* (Richling, 2001); and *H. punctisulcata cuericiensis* Richling, 2004 (Figs. 1A–E, L–M, 2A–E). On the other hand, the shells are thin and more or less transparent with exception of the outer lip (Figs. 1F–K, 2F–N), but the mantle is variously mottled and causes the visible coloration, for example, *Helicina tenuis* L. Pfeiffer, 1849; *H. gemma* Preston, 1903; *H. monteverdensis* Richling, 2004; *H. escondida* Richling, 2004; and *H. chiquitica* (Richling, 2001) (Figs. 3D–E, 4C–H, 5A–D). As an artifact in empty shells, the transparency becomes less, for example, compare Figure 2I and Figure 4F. The latter way seems to have evolved in connection with the very limited availability of calcium carbonate in Costa Rica.

It seems that the optimal coloration of small-sized arboreal Helicinidae, about 3–4 mm, is dark. Evidence is given by the very small species *H. chiquitica*, in which most individuals are dark (Fig. 5C), populations of *Helicina monteverdensis* of a reduced average body size (Fig. 4G), and juveniles of *Helicina funcki* (Fig. 3B).

Due to the high adaptability of the coloration, its value for systematics is limited, although the present study shows that in arboreal species the way to achieve the final coloration is typical for each species. For thin-shelled species, the varying and patterned mantle pigmentation is characteristic. When looking at a number of individuals, this pattern shows at certain specificity for different species, but single specimens might show exceptions. In some cases, it is even typical at population level, for example, in *Helicina tenuis* from Cabo Blanco on the Pacific plain (Fig. 3D) and La Selva on the Caribbean plain (Fig. 3E), or in *Helicina monteverdensis* in populations about 5 km from each other (Figs. 4F, G).

The coloration of head and foot seldom shows species specificity: the upper side is usually dark, especially towards the head and tentacles, whereas the lower side is light. Among the Costa Rican species, *Helicina talamancensis* represents the only exception. In all specimens studied, the whole body is whitish except for the sharply separated black tentacles (Fig. 4B).

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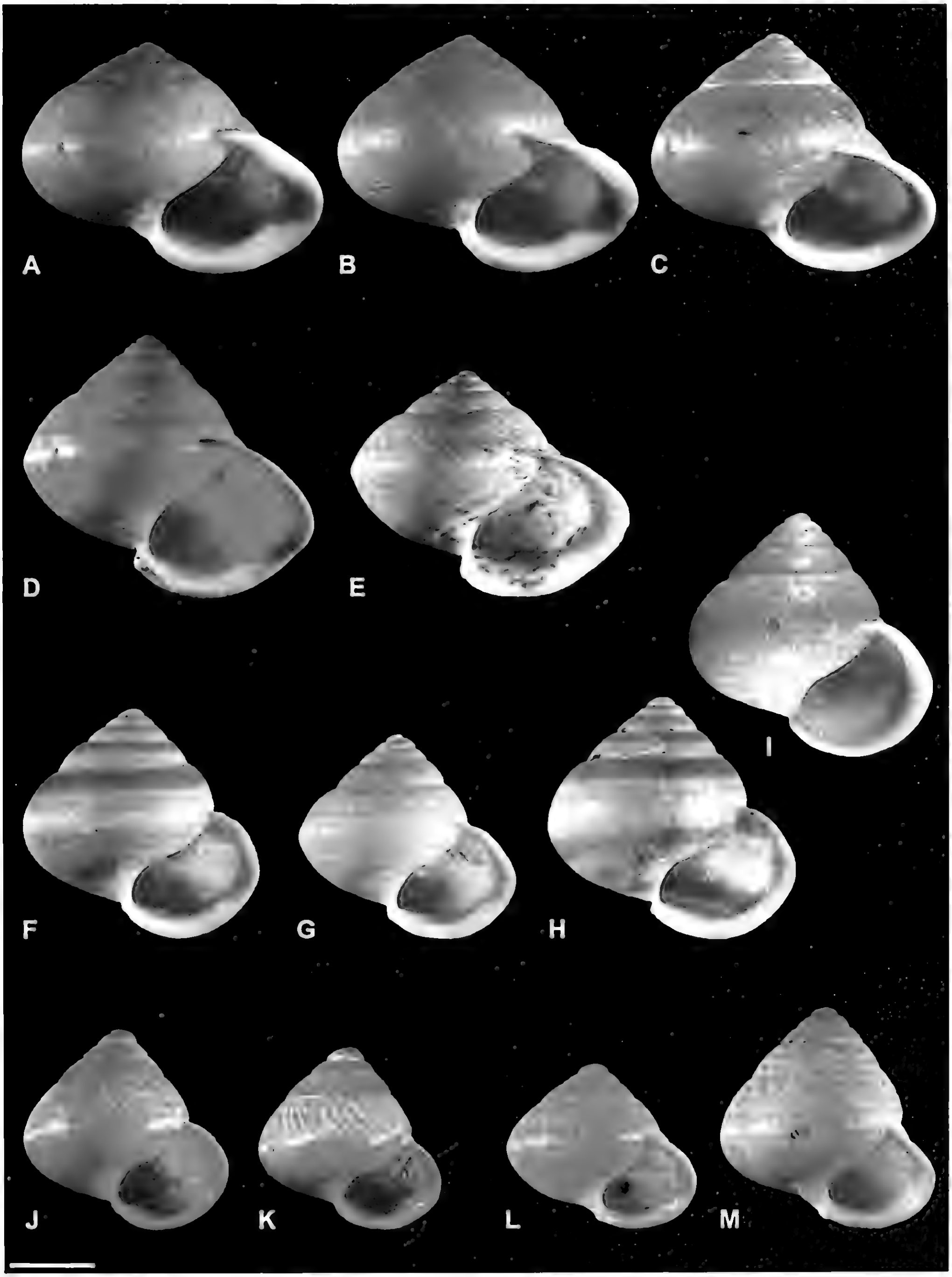

FIG. 1. Shell coloration of Costa Rican species. A–C. *Helicina funcki*. A. Rio Barbilla. B. Manzanillo. C. Santa Elena. D–E. *H. pitalensis*. D. Bajo Bonito. E. Península de Osa. F–I. *H. tenuis*. F–H. Cabo Blanco. I. La Selva. J–K. *H. echandiensis* Richling, 2004, campamento Echandi. L–M. *H. punctisulcata cuericiensis*, Estación Cuerici; scale bars = 4 mm (A–E), 3 mm (F–M).

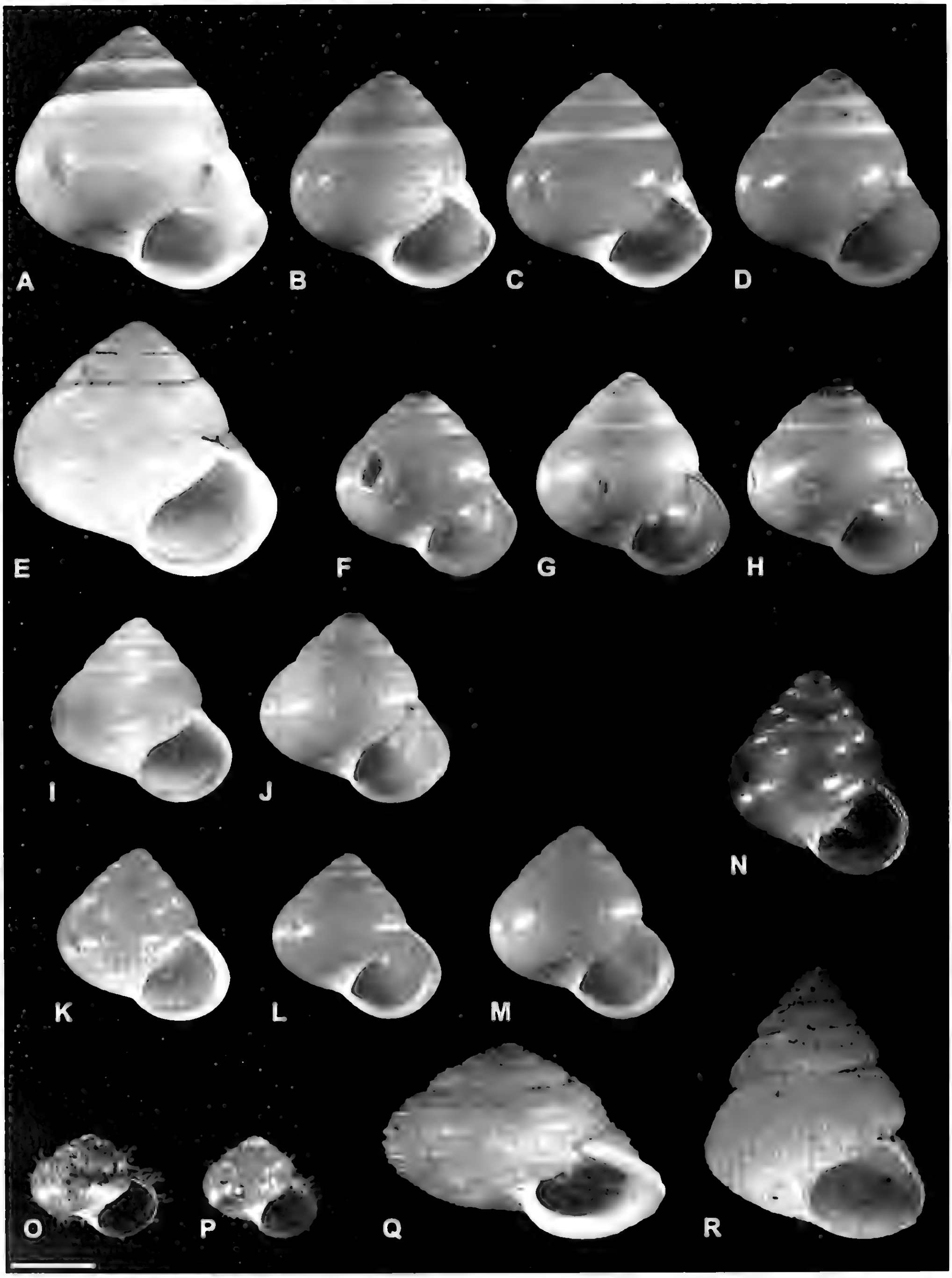

FIG. 2. Shell coloration of Costa Rican species. A. *Helicina beatrix beatrix*, Guayacán. B–C. *H. b. confusa* (Wagner, 1908). B. Uatsi. C. Shiroles. D. *H. b. riopejensis* Richling, 2004, Río Peje. E. *H. talamancensis*, Bajo Bonito. F–H. *H. gemma*. F. Cacao. G. Las Pavas. H. Siquirres. I–J. *H. monteverdensis*, Monteverde. K–M. *H. escondida*, Río Barbilla. N. *H. chiquitica*, Río Barbilla. O. *Alcadia hojarasca*, Mirador Gerardo. P. *A. boeckeleri*, Pitilla. Q. *Lucidella lirata*, Cahuita. R. *Pyrgodomus microdinus*, Fila de Cal; scale bars = 3 mm (A–M), 2 mm (N–P), 1.2 mm (Q–R).

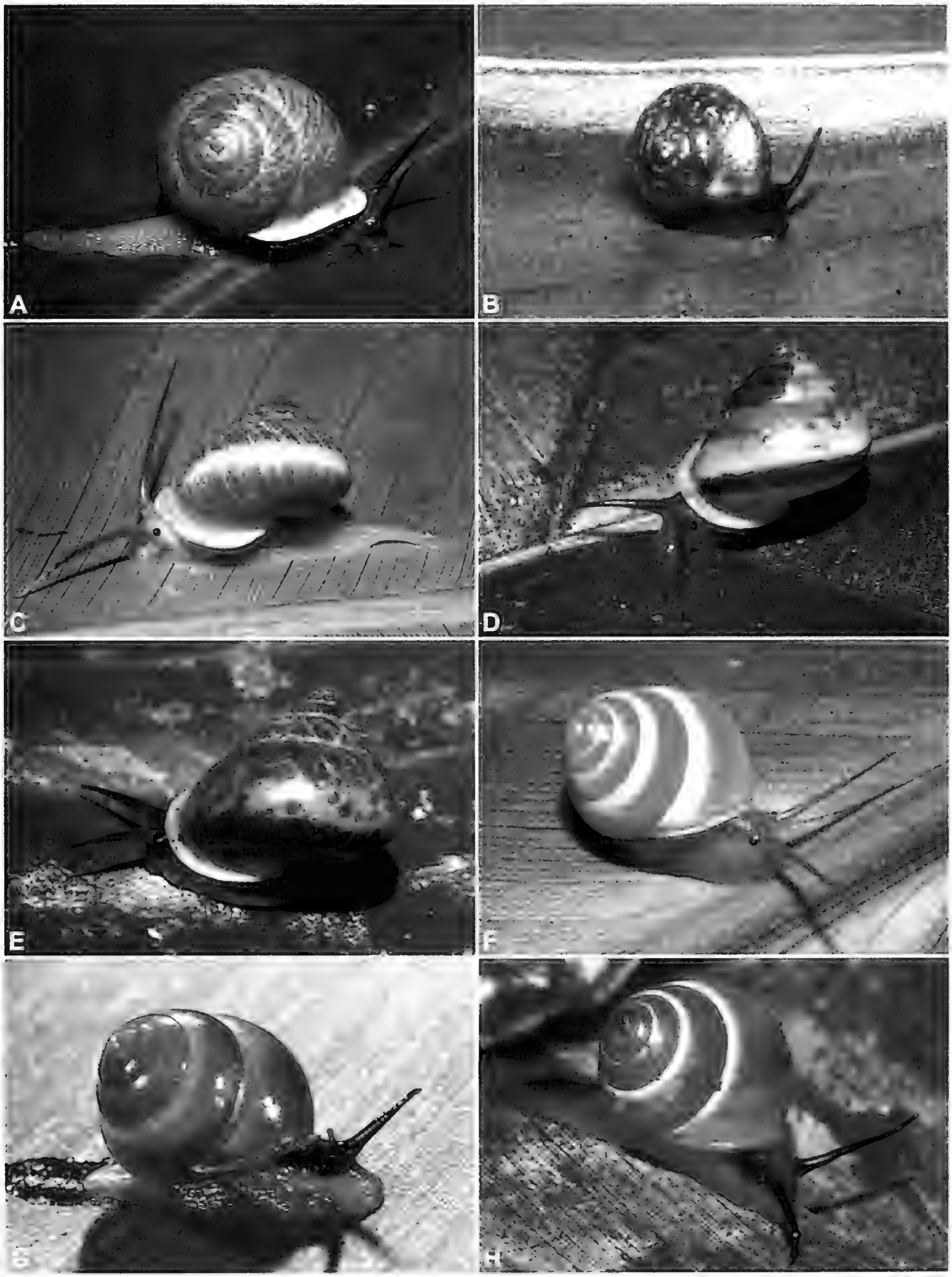

FIG. 3. Living animals of Costa Rican species. A. *Helicina funcki*, Cahuita. B. *H. funcki*, juvenile, Uatsi. C. *H. pitalensis*, Bajo Bonito. D. *H. tenuis*, Cabo Blanco. E. *H. tenuis*, La Selva. F. *H. beatrix confusa*, Uatsi. G. *H. beatrix confusa*, Shiroles (photograph: Vollrath Wiese). H. *H. beatrix riopejensis*, Río Peje.

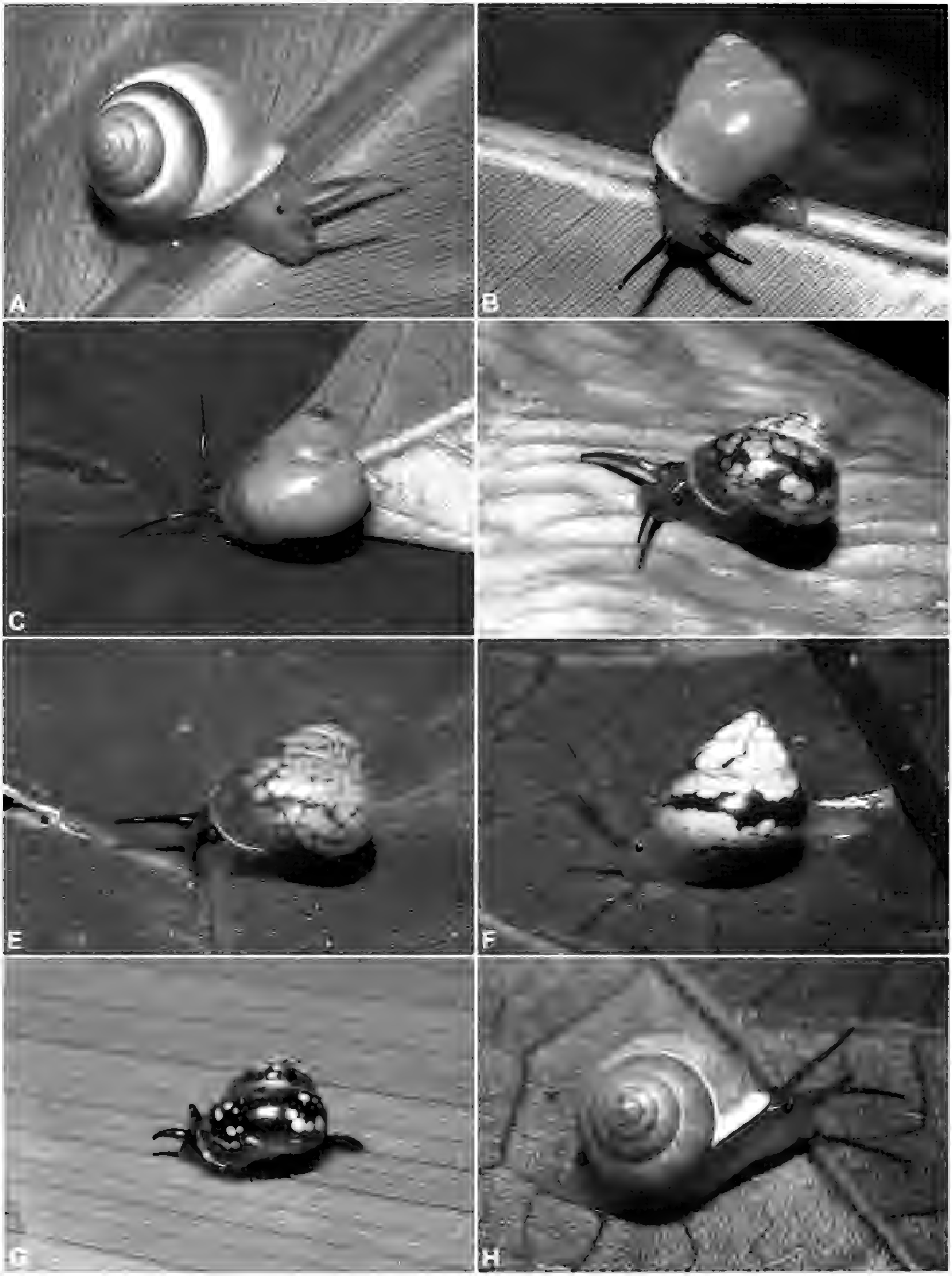

FIG. 4. Living animals of Costa Rican species. A. *Helicina beatrix beatrix*, Guayacán. B. *H. talamancensis*, Bajo Bonito. C. *H. gemma*, Cacao. D. *H. gemma*, Las Pavas. E. *H. gemma*, Siquirres. F. *H. monteverdensis*, Monteverde. G. *H. monteverdensis*, Mirador Gerardo. H. *H. escondida*, Shiroles.

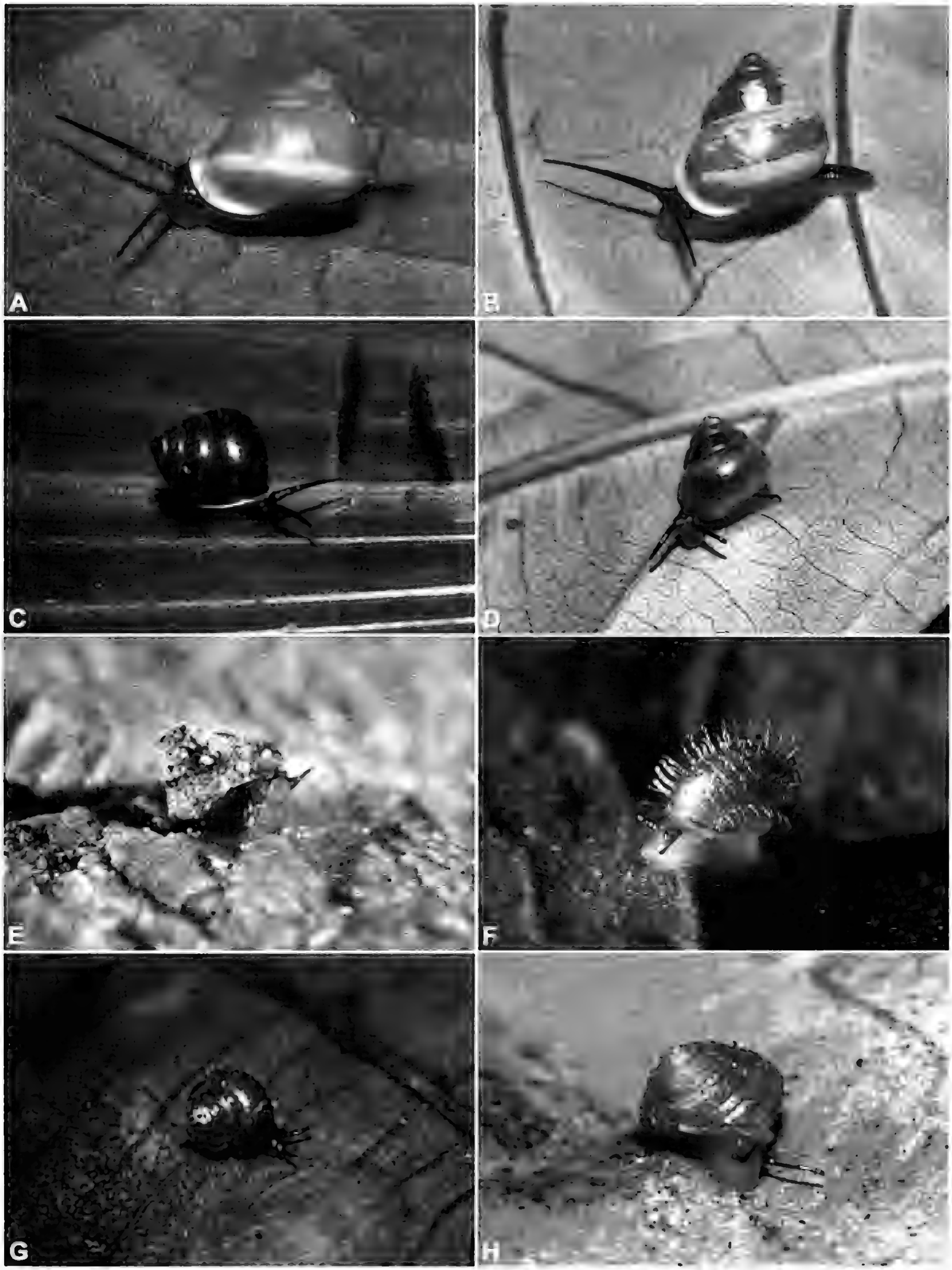

FIG. 5. Living animals of Costa Rican species. A. *Helicina escondida*, Shiroles. B. *H. escondida*, Rio Barbilla. C. *H. chiquitica*, Rio Barbilla. D. *H. chiquitica*, Rio Pacuarito. E. *Pyrgodomus microdinus*, Fila de Cal (photograph: Vollrath Wiese). F. *Alcadia hojarasca*, Mirador Gerardo. G. *A. boeckeleri*, Pitilla. H. *Lucidella lirata*, Cahuita.

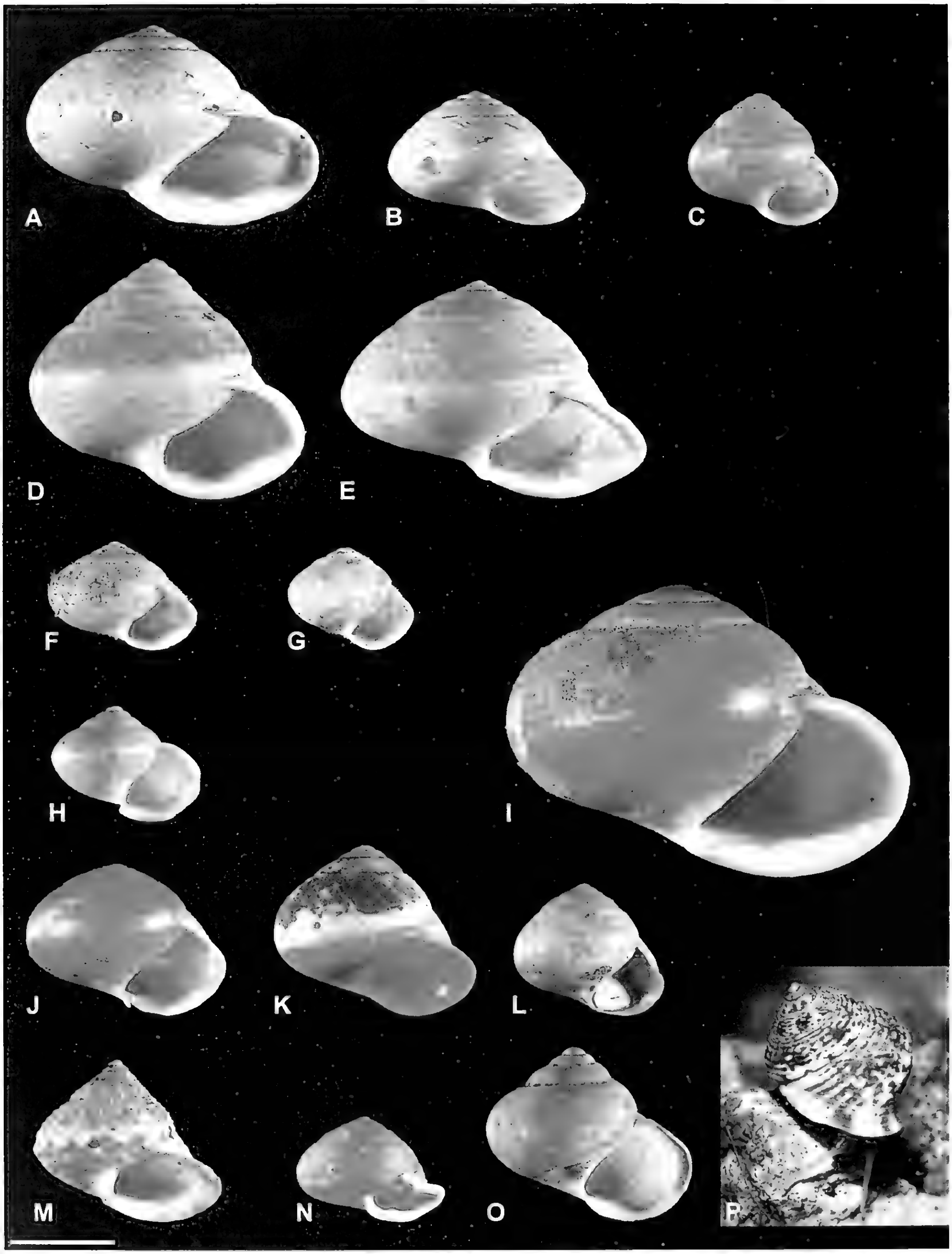

FIG. 6. Shell coloration. A. *Helicina neritella* Lamarck, 1799, Jamaica. B. *H. platychila* (Mühlfeldt, 1816), Dominica. C. *H. orbiculata* (Say, 1818), Florida. D. *H. turbinata* Wiegmann, 1831, Mexico. E. *H. amoena* L. Pfeiffer, 1849, Guatemala. F. *H. dysoni* L. Pfeiffer, 1849, Trinidad & Tobago. G. *H. sericea* Drouet, 1859, Suriname. H. *Angulata brasiliensis* (Gray, 1825), Brazil. I. *Alcadia major* (Gray, 1824), Jamaica. J. *A. hollandi* (C. B. Adams, 1849), Jamaica. K. *A. jamaicensis* (Sowerby, 1841), Jamaica. L. *A. rotunda* (Orbigny, 1841), Cuba. M. *Eutrochatella pulchella*, Jamaica. N. *Lucidella aureola* (Férussac, 1822), Jamaica. O. *Schasicheila alata* (L. Pfeiffer, 1848), Mexico. P. *Eutrochatella pulchella*, Jamaica; scale bar = 5 mm (A–O).

LETTER FROM THE EDITOR

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SPECIES CHECK-LISTS: DEATH OR REVIVAL OF THE NOUVELLE ÉCOLE?

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With more than 100,000 described species, mollusks belong to the second largest phylum after the Arthropoda. Mollusks have attracted a large number of shell collectors, amateur malacologists, field biologists, conservationists, as well as evolutionary biologists, taxonomists and systematists.

As a result, there are huge amounts of malacological publications available for most regions of our planet, and our knowledge of the group is increasing day by day. However, despite the extensive work that has been done, nomenclature and taxonomy of many groups are still in a confused state, and the systematics of numerous taxa is embroiled in controversy. Moreover, the problems increase with the recent advent of new anatomical and molecular methods, where the new types of data are often in conflict with the traditional, that is, shell-based taxonomy.

This confusion affects most taxonomic levels from subspecies to higher taxa and makes it difficult for many non-biologists and even professional biologists to apply or understand the correct name for a taxon. The consequences are not-trivial, as an incorrect determination or classification can be the deciding factor in many diverse scientific and non-scientific activities.

To maintain order in the sometimes chaotic system of publications and taxa, species check-lists are often generated for individual biogeographic regional and/or systematic groups. For the uninitiated, it is difficult to imagine how much work is involved to generate a widely acceptable check-list. Often international groups of scientists have to sort through hundreds or even thousands of primary publications, look at many voucher specimens and work through quantities of field records. They have to carefully consider frequently contradicting information, make educated decisions about the "correct" nomenclature and taxonomy, and ensure compliance with the International Code of Zoological Nomenclature. And finally, these check-lists have to be updated on a regular basis in order to keep pace with the malacological research.

Given the nature of species check-lists there are, however, some critical points I would like to discuss. This could possibly help to further improve the quality of those check-lists and/or to point out some possible pitfalls the users should be made aware of. Although the following points might apply to many species-check lists, I will focus my attention on the two most recent European lists, the "Mollusques continentaux de France: liste de référence annotée et bibliographie" by Falkner et al. (2002), and the "Check-list of the non-marine Molluscan species-group taxa of the states of Northern, Atlantic and Central Europe" (CLECOM I) by Falkner et al. (2001).

(1) Naming Species

Identifying a species, a "good species", has often been a very difficult task, due, in part, to the large variety of species concepts and in part to difficulties in the objective selection and interpretation of the characters used, often resulting in a personal view of what a species is. The famous malacologist W. Kobelt (1881) once wrote [translated from German]: "*I obey a simple, practical rule, no matter how unscientific it may be. I call a good species what I can diagnose without long and careful comparisons and measurements ...*". More than half a century ago, matters changed due to the introduction of the biological species concept (BSC) (Mayr, 1940) and of other, progressively more refined concepts (review by Hull, 1997). Many traditional taxonomists, nevertheless, continue working as in the past. They use an often arbitrary chosen level of morphological difference, frequently calculated "at a glance" to decide what a new "good species" is. However, these good species are actually "morphospecies" (see Giusti & Manganelli, 1992), and it is usually tacitly taken for granted that they correspond to biological species.

Obviously, this practice is extremely subjective. Extremism gave rise to "the lumpers", who require robust differences to segregate taxa, and in doing so, tend to accept very polymorphic species. Others, "the splitters", base their taxonomic decisions on low levels of differentiation. More recently, subjective decisions were brought into clear view when molecular research revealed that both splitters and lumpers are frequently wrong, because the levels of morphological difference are often independent of genetic divergence (organisms with a low level of morphological difference may have high levels of genetic divergence, and vice versa).

A quick glance at many papers shows that the authors continue to use superficial shell morphological/typological procedures. These are sometimes based on simple differences in shell height or diameter, or on the relationship height/diameter, differences that repeatedly have been shown to be unsuitable for species differentiation. A first conclusion is that creating taxa simply on the basis of shell characters (qualitative and quantitative) should always be done with extreme caution (many cases of convergence in shell shape in not related groups are known, convergent evolution is rampant; Davis, 1979), unless there are very compelling reasons (fossils, rare deep sea taxa, taxa of family-level groups notorious for being over-named and for having high intraspecific variation, etc.). The situation may not substantially change even when other characters, anatomical, eco-ethological, are added (anatomical characters are not always highly revealing; peculiar ecology, parasitology or ethology may be the source of certain shell differences).

The situation is rendered more problematic by the so-called "fanatisme du nobis" (Dance, 1970), that is, the introduction of new names to give "eternity" to one's own name. The more new names one introduces, the greater is the possibility one of them survives as that of a "good species" or "good subspecies".

The International Code on Zoological Nomenclature (ICZN) was created to manage, in a legalistic manner, the naming of species. But it has been abused and indirectly supports proliferation of names that cannot be suppressed and therefore must be considered valid and listed in check-lists until a future revision is made. The last edition of the ICZN (1999) called for adequate and rigorous species definitions (see also Hawskworth & Bisby, 1988: 12–13), but since then, the literature shows that this call remains unheaded in many instances.

Recent creation of new species based on dubious characters is the survival/revival of the school called "Nouvelle École", founded by the French malacologist Jules-René Bourguignat in the second half of the 19th century, according to which a species should be determined on arbitrarily chosen characters, which nearly always meant shell characters. If an individual was found to differ from all others by three characters or more, it should be considered to belong to a species new to science (Dance, 1986). This school has been unanimously condemned, but never completely abandoned. As a matter of fact, many taxonomists officially criticize the Nouvelle École, but actually follow a very similar if not identical practice. Continuation of this practice is fueled by the fact that at least some of the species described by the followers of the Nouvelle École subsequently turn out to be "good species" (see above). Moreover, recently the method of the Nouvelle École is spreading again due to the strategy of the "valeur patrimoniale" of local faunas to support conservation programs (Falkner et al., 2001: 6; 2002: 19; Bouchet, 2002: 8–12). According to such strategy, "*It is extremely difficult to convince engineers or politicians of the value and need for protection of a special, even unique, unnamed form, but from the moment that a name can be provided there exists a recognizable unit which can be referred to*" (Falkner et al., 2001: 6). Though these intentions are honorable, taxa of the species group should never be described for "political" reasons! Apart from the fact that that strategy opens doors to irresponsible students and amateurs, it risks to reduce taxonomy to a mere artifice possibly with grim consequences: "*if the philosophy of the Nouvelle École had become widely popular its effect on systematic conchology, as may be imagined, could have been catastrophic*" (Dance, 1986).

While I reject the subjective and unethical practice just described, I am concerned about how one manages the many names given to taxa that have uncertain value. Each taxon correctly (legally) described has value unless the contrary is demonstrated. At the same time, it is a considerable disservice to science and society to inflate check-lists with numerous dubious nominal species/subspecies! I am convinced that these taxa must be evaluated critically and that, when it is eventually decided they must be listed as potentially endangered or as a part of a special ecosystem, their uncertain taxonomic status should be made clear.

(2) The Use of Subspecies

Subspecies are even more difficult to define objectively than species as was well known from the late 19th century (Kobelt, 1881, continued the sentence given above as follows: "... *That which I can distinguish only by precise measurements I call a variety*"). Alas, some malacologists still name subspecies as it was done by Kobelt for varieties (minor variations), just to distinguish a little characterized local form, and as a tool to satisfy their "fanatisme du nobis".

Difficulties in using subspecies come, first of all, from the fact that not all species concepts recognize the subspecies status. One species concept that explicitly does is the BSC. However, although often claimed by malacologists, the BSC, in its true meaning, is rarely applied in malacology, because it places the taxonomy of natural species within the scheme of population genetics. Within the framework of the BSC, the concept of subspecies gradually evolved from a simple "unit of convenience" (Blackwelder, 1967; Dobzhansky et al., 1977; Mayr, 1963, 1982) to became applicable to populations that are kept isolated usually by geographical barriers and that exhibit recognizable phylogenetic partitioning due to the time-dependent accumulation of genetic differences (O'Brien & Mayr, 1991). Therefore, subspecies should presently never be used without an immense amount of rigorous data that clearly demonstrate that the concept can be applied legitimately, that is, allopatric populations that have diverged sufficiently genetically (based on real genetic data) where they would be elevated to full species were it not for the complete sameness of the mate recognition system and the full capacity to produce a F1 and F2 generation if given the opportunity (Davis, 1994).

It is obvious that most check-lists that use subspecies are not based on such rigorous work. To give an example from CLECOM, for Germany there are 36 (!) species and subspecies listed for the minute rissooidean genus *Bythiospeum*. I do not know of any molecular or detailed anatomical study that has looked at variability within and between populations to infer possible genetic breaks in taxa of *Bythiospeum* that, in turn, could be used to deduce reproductive isolation. Therefore, I would consider the splitting of *Bythiospeum* a simple matter of pure subjectivity. In fact, preliminary genetic data produced by one of my collaborators indicate that the number of *Bythiospeum* species in Europe is much lower than hitherto believed and that the genus appears to be paraphyletic, demonstrating the diagnostic inadequacy of the morphological methods used up-to-day.

Unfortunately, CLECOM gives contradicting information as to legitimacy of the subspecies listed. Whereas on page 3 of the introduction to CLECOM I it is said that "... *the CLECOM check-list will contain the nomenclaturally correct names of the species and subspecies that are considered to be valid*", further down on the same page it is written "... *Inclusion of named subspecies in the CLECOM database results inevitably in both well-founded and even spectacular forms being mentioned along with some 'weak' subspecies.*" Moreover, it is said that "*In the exciting faunistic literature of northern, western and central Europe subspecies are widely, if not generally, neglected.*" If so, a check-list that is based on this literature should ignore subspecies as well.

One reason for including subspecies in CLECOM is related to conservation purposes: "*Our only tool to make this diversity apparent to conservation authorities, researchers in applied sciences and others who require recognising its existence is the application of trinominal nomenclature.*" Many conservationists are well aware of the need to protect intraspecific diversity but adopt different strategies. In recent years, several approaches have been deployed using "conservation units" instead of dubious subspecies (e.g., Crandall et al., 2000; Fraser & Bernatchez, 2001).

But surely it is inappropriate to name subspecies as a convenience and in the absence of well-founded data, no matter how honorable the intentions are.

(3) Data Sources

In the introduction to the (sub)generic list of CLECOM I+II by Bank et al. (in: Falkner et al., 2001) it is said that "*The list presented in this paper is based on the study of hundreds of publications ...; only a selection of them could be cited in the reference list.*" I can only imagine how many publications the CLECOM committee must have had studied. But it certainly would be useful to list all those publications as they are the primary data source and as a check-list can only be as good as the publications it is built upon.

Another data source that is often used in check-lists is unpublished information. Philippe Bouchet specifically acknowledged this valuable source in his introduction to the French list of continental molluscs. However, unpublished data are not subject to the scrutiny of the scientific community and its quality and reliability may vary. Therefore, if unpublished data are used in check-lists, they should be clearly marked as such.

Another data source of great value for check-lists is molecular data. The advance of robust population genetics, phylogeographic and phylogenetic studies has lead to numerous re-assignments of species, genera and families. Yet, these data are (still) largely neglected in check-lists. To give an example, the molecular work my group has done in the past ten years on several European taxa of the superfamily Rissooidea largely has been ignored by CLECOM. Instead, the rissooidean systematics of that list is still mainly based on traditional (mostly shell-based) data. It is not that the molecular genetic data have been ignored because they often contradict the findings of members of the CLECOM team. Rather, it is important that CLECOM incorporate new findings based on genetic data much more quickly, even if these findings are inconvenient. One of the declared goals of the CLECOM list is to promote a stable nomenclature of European non-marine molluscs. But this can only be achieved by an objective assessment of all data available.

With regard to promotion of a stable nomenclature (one of the two primary goals of the ICZN), it is important that check-lists are not used to introduce changes in the names of various taxa, species in particular. Apparent novelties in this field must be the subject of careful evaluation by the scientific community before they are proposed as unquestionable to a vast public of non-specialists. Stability of nomenclature is not necessarily achieved by an uncritical application of the law of priority, but through the conservation of the names in use, no matter if they are not the oldest names available, as clearly seen in many findings of the ICZN over the past few decades. The adoption of new systematic hierarchical ordering in check lists (as done by CLECOM) that were neither adopted before nor previously checked by the scientific community is another critical point we should raise. As such new systems are unknown in the scientific literature or in private or public collections, they inevitably are a source of confusion, particularly for non-specialists. Moreover, as experience shows, they are inevitably subject to rapid change when they are subjected to rigorous scientific evaluation.

Check lists should be a catalogue of all the species of a certain group for a given geographical area, not a vehicle for promoting the reconstruction of phylogenetic history or promoting a particular phylogenetic hypothesis.

(4) Need for Further Research

The introduction to CLECOM begins with the headline “The need for a uniform catalogue to promote biodiversity studies”. And indeed, comparing the various activities ongoing at national levels and formulating coherent syntheses that can be used by both scientists and policy-makers is a declared goal of the CLECOM committee.

In order to indicate taxa that need further research, the CLECOM list uses question marks for those taxa. However, it appears as if those question marks are heavily underutilized in CLECOM. To use the *Bythiospeum* example above, none of the 36 dubious species and subspecies listed for Germany carries a question mark. In fact, none of the numerous German taxa of the superfamily Rissooidea (a highly controversial group with many cryptic radiations) is, according to the CLECOM list, in need of further studies. But numerous recent publication using molecular markers have shown that many of these groups are in urgent need of revision.

We do not know the reason the above omissions, but it seems that CLECOM is trying to suggest that almost everything is known about the systematics and taxonomy of the European non-marine mollusks. This certainly will not promote further research and it will not help to protect biodiversity either. In fact, it only discourages biologists from asking meaningful questions and therefore contradicts the declared goals of the same CLECOM.

In conclusion, the above points highlight some of the problems I see with recently published check-lists. Success and acceptance of those lists depend not only on the quality and quantity of the databases, but also on the ability to consolidate conflicting information and ensure a critical assessment of their own work. In order to promote nomenclatural stability, it is also necessary to clearly state the subspecies and species concepts upon which the list is based and the operational criteria used to implement those concepts.

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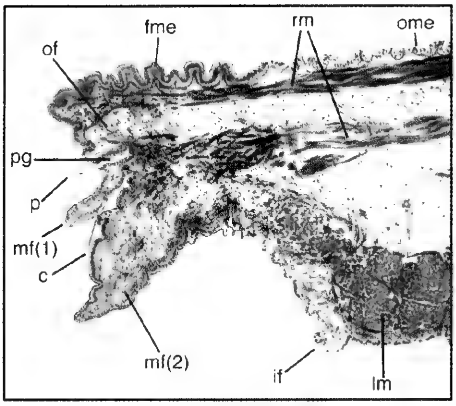

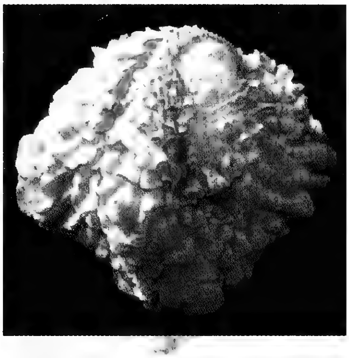

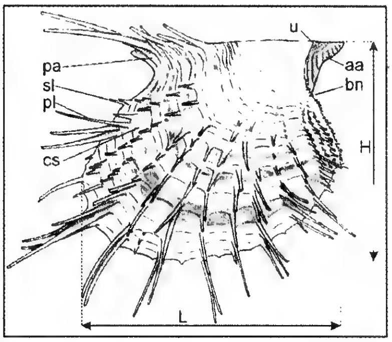

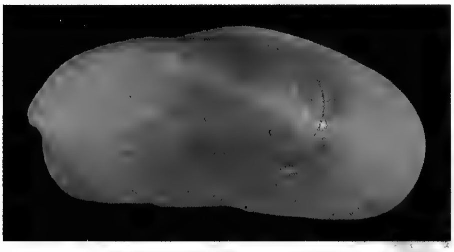

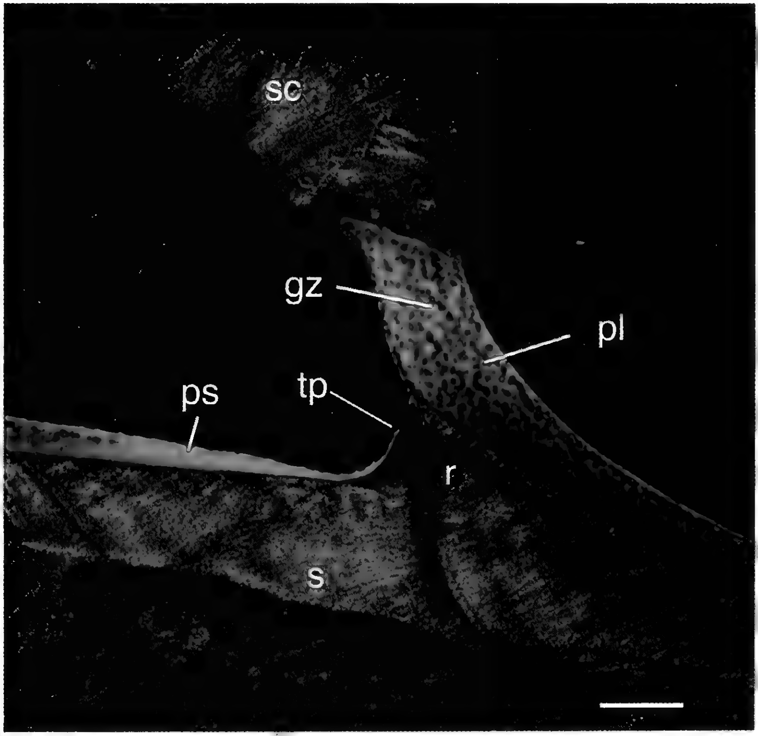

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BIVALVE STUDIES IN THE FLORIDA KEYS

Proceedings of the International Marine Bivalve Workshop
Long Key, Florida, July 2002

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INTERNATIONAL MARINE BIVALVE WORKSHOP 2002: INTRODUCTION AND SUMMARY

Paula M. Mikkelsen[1] & Rüdiger Bieler[2]

In July 2002, a two-week workshop on marine bivalves, with an emphasis on systematics, anatomy, and natural history, was organized to further knowledge of living marine bivalves and to train graduate-level students in this understudied field of modern malacology. With support from and in the spirit of the National Science Foundation's Partnerships in Enhancing Expertise in Taxonomy (PEET) program, students worked one-on-one in teams with expert scientists on selected bivalve species or groups of species. This volume, for the most part comprising papers co-authored by the scientist-student research teams, represents the scientific results of projects initiated at the workshop.

The Florida Keys at the southernmost tip of peninsular Florida, a region emphasized by the organizers' joint research program since 1994, formed a biologically diverse and logistically convenient site for a workshop of this type. As defined by this research venture, the Florida Keys includes the entire island chain and surrounding waters, from Broad Creek at the northern end of Key Largo (including Card and Barnes sounds, but not Biscayne Bay) through and including the Dry Tortugas, plus the approximate southeastern half of Florida Bay (excluding the more brackish areas in the outfall of the Florida Everglades), and offshore areas to the reef line and beyond (with collection and literature records to a maximum depth

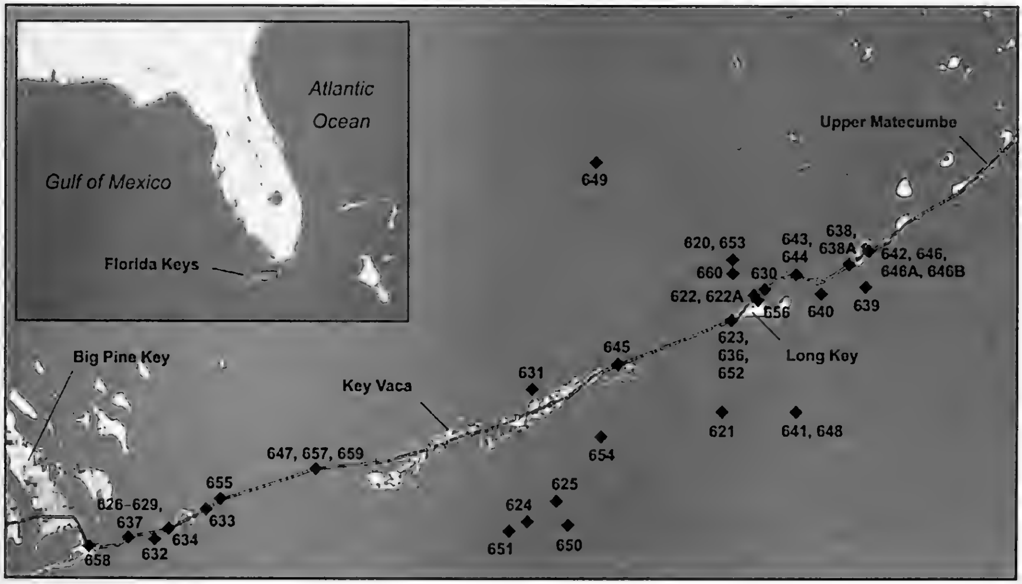

FIG. 1. Field stations (black diamonds) sampled during the International Marine Bivalve Workshop, July 2002. Re-sampled or neighboring stations are here combined; see text for individual station data. Station FK-619 (Lake Surprise), about 48 km northeast, is not shown. West-to-east extent of the displayed area, ranging from Big Pine Key to Upper Matecumbe, is approximately 85 km.

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of 300 m). Included within these limits is the Florida Keys National Marine Sanctuary, the second largest marine sanctuary in the United States, as well as a variety of other jurisdictions protecting various terrestrial and marine sites. The workshop was held at the Keys Marine Laboratory on Long Key, a venue centrally located in the Keys allowing ready access to a large portion of the archipelago including offshore and bayside habitats (Fig. 1). Easily accessible habitats included intertidal rocks, sand and seagrass flats, rock ledges, seawalls, mangroves, mud channels, patch reefs, back reefs, artificial reefs (shipwrecks), and the only living near-shore coral reefs in the continental United States.

Tourism is the leading industry of Florida and the Florida Keys has long been a favorite destination for ocean-oriented vacationing, diving, sport fishing, and shell collecting. In spite of a century of avid shell collecting and molluscan research in the Keys, Levy et al. (1996) noted, "except for a few ecological inventories that include mollusks, there is a lack of comprehensive, ecosystem-wide species inventories in the Florida Keys." Coral reef conservation efforts stress corals, sponges, algae, spiny lobster and fish, and, except for a few members of the "charismatic macrofauna" [e.g., the queen conch, *Strombus gigas* Linnaeus, 1758, and Flamingo Tongue, *Cyphoma gibbosum* (Linnaeus, 1758)], regularly ignore mollusks. This deficiency has been acutely sensed since the establishment of the Florida Keys National Marine Sanctuary (FKNMS) in 1990, created to protect and restore fragile marine habitats from the environmental impact of human use. The FKNMS Draft Management Plan listed only 630 marine species (Lyons & Quinn, 1995), only slightly fewer than a considerably earlier yet little-known, privately published list of 710 species by Lermond (1936). The molluscan species list compiled by the organizers' research program has more than doubled to nearly 1,700 species through original fieldwork, museum collection surveys, and extensive literature research; approximately 400 of these species are bivalves (Mikkelsen & Bieler, 2000; Bieler & Mikkelsen, 2004).

Twelve international specialists in marine bivalve systematics participated by mentoring a student during the workshop. They included scientists with a wide range of specialties, spanning functional morphology, phylogenetics, molecular biology, and faunal diversity research. A list of readily obtained Florida Keys bivalves was provided early in the planning process, allowing each scientist to select and prepare materials to study a taxon in the field. The 12 student participants were selected from 49 applicants in response to notices distributed at meetings and on internet listservers. Research teams were formed by pairing an alphabetical list of scientists with a reverse-alphabetical list of students. Together with the six members of the organizing team, this was a highly international group of 30 individuals representing 17 nations and five continents of origin or residence (Fig. 2). The participants were:

Mr. Kyle Bennett, Rutgers University, New Brunswick, New Jersey, U.S.A.
Dr. Rüdiger Bieler, Field Museum of Natural History, Chicago, Illinois, U.S.A. [organizer]
Mr. Gregorio Bigatti, Universidad de Buenos Aires, Argentina.
Mr. Matthew Campbell, Indiana University, Bloomington, Indiana, U.S.A.
Mr. Anton Chichvarkhin, Rossiiskoi Akademii Nauk, Vladivostok, Russia.
Ms. Louise Crowley, City University of New York and American Museum of Natural History, New York, New York, U.S.A. [organizing team].
Ms. Grete Dinesen, University of Aarhus, Denmark.
Dr. Osmar Domaneschi, Universidade de São Paulo, Brazil.
Ms. Joanne Dougherty, Villanova University, Villanova, Pennsylvania, U.S.A.
Dr. Emily Glover, The Natural History Museum, London, United Kingdom.
Ms. Johanna Järnegren, Norges Teknisk-Naturvitenskapelige Universitet, Trondheim, Norway.
Ms. Isabella Kappner, University of Illinois at Chicago and Field Museum of Natural History, Chicago, Illinois, U.S.A. [organizing team].
Ms. Lisa Kirkendale, Florida Museum of Natural History, Gainesville, Florida, U.S.A.
Ms. Martina Knapp, Universität Wien, Austria.
Dr. José H. Leal, The Bailey-Matthews Shell Museum, Sanibel, Florida, U.S.A.
Ms. Amy Maxmen, Harvard University, Cambridge, Massachusetts, U.S.A.
Dr. Paula M. Mikkelsen, American Museum of Natural History, New York, New York, U.S.A. [organizer].
Dr. Russell Minton, Field Museum of Natural History, Chicago, Illinois, U.S.A. [organizing team].

Ms. Juri A. Miyamae, Swarthmore College, Pennsylvania, and American Museum of Natural History, NSF-REU Summer Intern Program, New York, New York, U.S.A. [organizing team].

Prof. Brian Morton, Swire Institute of Marine Science, University of Hong Kong, China.

Dr. Diarmaid Ó Foighil, Museum of Zoology, University of Michigan, Ann Arbor, Michigan, U.S.A.

Dr. P. Graham Oliver, National Museum of Wales, Cardiff, United Kingdom.

Ms. Melita Peharda, Institut za Oceanografiju i Ribarstvo, Split, Croatia.

Dr. Jay Schneider, George Washington University, Washington, DC, U.S.A.

Ms. Elizabeth K. Shea, Bryn Mawr College, Bryn Mawr, Pennsylvania, U.S.A.

Dr. Luiz Ricardo L. Simone, Museu de Zoologia, Universidade de São Paulo, Brazil.

Dr. Gerhard Steiner, Universität Wien, Austria.

Prof. John Taylor, The Natural History Museum, London, United Kingdom.

Mr. Paul Valentich Scott, Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A.

Dr. Richard Willan, Northern Territory Museum of Arts & Sciences, Darwin, Australia.

The workshop occupied nearly the entire Keys Marine Laboratory facility, including dormitories, wet laboratory for sorting, dry laboratory for microscope work and photography, classroom for presentations and discussion, and small boats for snorkeling trips. Various vehicles facilitated land travel for collecting and other group events; some scuba trips utilized commercial dive boats. Group and team activities included collecting by snorkeling, scuba, shovel-and-sieving (Fig. 3), and cracking dead coral rocks, followed by appropriate laboratory study (Fig. 4) and sharing their findings through discussions and presentations. Each research team included at least one certified scuba diver and this allowed exploration of additional habitats, including an offshore

FIG. 2. Participants of the IMBW gather for a group photograph at Pigeon Key (photograph by L. Simone).

FIG. 3. Shovel-and-sieving typified collecting efforts for shallow-water bivalves in the Florida Keys.

FIG. 4. Following a day's collecting efforts, the laboratory filled with a variety of study activities.

wreck that had become a habitat for several deeper-water bivalve species. In deference to the sanctuary location, no dredging was conducted, and no protected species were collected; workshop activities were intentionally designed around relatively common, shallow-water species. Lectures were presented on most evenings, either by guest speakers or the participants. Each scientist spoke of his/her research or laboratory, and toward the end of the workshop, each student summarized the results of their team investigations.

The IMBW documented 121 species of bivalves from 48 field stations (Fig. 1), including several previously unrecognized taxa and others of poorly known distribution and habitat. Voucher specimens are deposited in the mollusk collections at AMNH, FMNH, and the home institutions of some participants (including Florida Museum of Natural History, Gainesville; Bailey-Matthews Shell Museum, Sanibel Island, Florida; Museum of Zoology, University of Michigan, Ann Arbor; Santa Barbara Museum of Natural History, California; The Natural History Museum, London, United Kingdom; Museu de Zoologia, Universidade de São Paulo, Brazil; and Northern Territory Museum of Arts & Sciences, Darwin, Australia).

WORKSHOP STATIONS

IMBW-FK-619, 14-VII-02, Lake Surprise, Key Largo, MM 107.5, NE end of U.S. Rte. 1 causeway across lake, 25°10.9'N, 80°23.0'W, off mangroves at side of road, by hand on shallow subtidal rocks.

IMBW-FK-620, 16- & 18-VII-02, Old Dan Bank, bayside of Long Key, 24°50.45'N, 80°49.63'W, *Thalassia* seagrass bed with *Halimeda* calcareous algae, *Porites* finger-coral, sponges, hydroids, patches of sand/*Halimeda* shell hash, by hand, 0.3–0.6 m, R/V FLORIDAYS.

IMBW-FK-621, 17-VII-02, "Long Key Artificial Reefs", oceanside of Long Key, 24°44.78'N, 80°50.00'W, sand plain with *Thalassia*/*Syringodeum* seagrass patches, scuba, by hand, 7 m, R/V FLORIDAYS.

IMBW-FK-622, 20-VII-02, directly off Keys Marine Laboratory, bayside of Long Key, 24°49.5'N, 80°48.9'W, seagrass bed with coral rubble, snorkeling, sieving, by hand, 0–1.5 m.

IMBW-FK-622A, 22-VII-02, off Keys Marine Laboratory, bayside of Long Key, 24°49.5'N, 80°48.9'W, about 30 m from shore, thin sand over rock, with *Halodule, Thalassia, Syringodium, Halimeda*, shovel/sieving, 0.5–1 m.

IMBW-FK-623, 20-VII-02, Long Key State Park, oceanside, 24°48.67'N, 80°49.68'W, seagrass bed (predominantly *Thalassia*) on muddy sand, snorkeling, by hand, 0–0.75 m.

IMBW-FK-624, 20-VII-02, Horseshoe Reef, off Fat Deer Key, 24°39.91'N, 80°59.56'W, patch reef with sandy bottom, scuba, 7.3 m, M/V SHUTTERBUG II.

IMBW-FK-625, 20-VII-02, Coffins Patch Sanctuary Preservation Area, off Crawl Key, 24°40.92' N, 80°58.26' W, patch reef with sand patches, gorgonian, pillar coral, scuba, 6.4 m, M/V SHUTTERBUG II.

IMBW-FK-626, 21-VII-02, "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), MM 35, 24°39.3'N, 81°18.2'W, "hole" at center of quarry, rock wall and soft sediment, snorkeling and scuba, to ca. 6.1 m.

IMBW-FK-627, 21-VII-02, "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), MM 35, 24°39.3'N, 81°18.2'W, mangrove area, soft sediment and detritus, hand dredge, < 1 m.

IMBW-FK-628, 21-VII-02, "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), MM 35, 24°39.3'N, 81°18.2'W, *Thalassia* seagrass, shovel/sieve, ca. 1 m.

IMBW-FK-629, 21- & 26-VII-02, "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), MM 35, 24°39.3'N, 81°18.2'W, among rocks along arms of quarry, by hand, snorkeling, to ca. 1 m.

IMBW-FK-630, 22-VII-02, roadside quarry N of Keys Marine Laboratory, Long Key, 24°49.78'N, 80°48.51'W, rock wall and scuzzy algae, hot (36°C) water layer, snorkeling, by hand, > 1 m to horizontal ledge on wall [total depth of quarry not assessed], S = 31 ppt.

IMBW-FK-631, 22-VII-02, Burnt Point, bayside, N point of Long Point Park, 24°45.56' N, 80°59.14' W, rocky bottom, soft coral/sponges, patches of seagrass, snorkeling, 0.6–1.2 m [2.4 m in channel along shore].

IMBW-FK-632, 22-VII-02, Bahia Honda State Park, oceanside, just E of old bridge, 24°39.25'N, 81°16.83'W, seagrass beds with sand blowholes, snorkeling at low tide, 0.6 m.

IMBW-FK-633, 22-VII-02, Missouri Key, 24°40.5'N, 81°14.3'W, coral rubble and seagrass beds, snorkeling and by hand, intertidal zone to 1 m.

IMBW-FK-634, 22-VII-02, Bahia Honda State Park, oceanside, 24°39.69'N, 81°16.11'W, at small roadway bridge over channel W before Sandspur Campground, sandy bottom at low tide, sparse seagrass, by hand, 0–0.1 m.

IMBW-FK-635, 22-VII-02, Veteran's Beach, oceanside, Little Duck Key, 24°40.87'N, 81°13.82'W, *Thalassia/Halodule* seagrass on silty sand, shovel/sieve, low intertidal zone to shallow subtidal.

IMBW-FK-636, 22-VII-02, Long Key State Park, oceanside, 24°48.67'N, 80°49.68'W, sandy beach, seagrass, by hand, snorkeling, intertidal zone.

IMBW-FK-637, 22-VII-02, "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), MM 35, 24°39.3'N, 81°18.2'W, among rocks/rubble along arms of quarry, by hand, intertidal zone.

IMBW-FK-638, 23-VII-02, Anne's Beach, oceanside, Craig Key, MM 72, 24°50.95'N, 80°44.40'W, *Thalassia/Halodule* seagrass, shovel/sieve, by hand, 0.5–1 m.

IMBW-FK-638A, 26-VII-02, Anne's Beach, oceanside, Craig Key, MM 72, 24°50.95'N, 80°44.40'W, *Thalassia/Halodule* seagrass, shovel/sieve, by hand, 0.5–1 m.

IMBW-FK-639, 23-VII-02, Coral Gardens inshore patch reef, oceanside off Lower Matecumbe Key, 24°50.23'N, 80°43.77'W, snorkeling, 3.6–4.6 m, Keys Marine Laboratory boat.

IMBW-FK-640, 23-VII-02, oceanside off Craig Key, 24°49.81'N, 80°45.73'W, nearshore patch reef, hardbottom, snorkeling, 0.1–1.2 m, Keys Marine Laboratory boat.

IMBW-FK-641, 23-VII-02, Tennessee Reef, off Long Key, 24°44.75'N, 80°46.95'W, hard bottom with coral, scuba, 7 m, R/V FLORIDAYS.

IMBW-FK-642, 23-VII-02, "The Billboard" site, oceanside, Lower Matecumbe Key, MM 74.5, 24°51.4'N, 80°43.7'W, thin sand cover on rock platform, small coral, *Thalassia/Halodule* seagrass, *Sargassum,* wading, snorkeling, shovel/sieving, 0.5–1 m.

IMBW-FK-643, 23-VII-02, Fiesta Key causeway, oceanside, 24°50.41'N, 80°46.95'W, at turnoff W of Channel #5 bridge, rocky shore, sand, *Thalassia* seagrass, snorkeling, by hand, 0–3 m.

IMBW-FK-644, 23-VII-02, Fiesta Key causeway, bayside, 24°50.41'N, 80°46.95'W, at turnoff W of Channel #5 bridge, rocky shore, concrete pilings, snorkeling, by hand, 0–3 m.

IMBW-FK-645, 24-VII-02, Grassy Key, oceanside, 24°46.60'N, 80°55.44'W, at turnoff before Tom's Harbor Channel, attached to underside of large, algal-encrusted boulders/rocks along shore, by hand, snorkeling, 1–3 m.

IMBW-FK-646, 25-VII-02, "The Billboard" site, oceanside, Lower Matecumbe Key, MM 74.5, 24°51.4'N, 80°43.7'W, rubble and sand with seagrass, wading, shovel/sieving, 0.5–0.75 m.

IMBW-FK-646A, 24-VII-02, "The Billboard" site, oceanside, Lower Matecumbe Key, MM 74.5, 24°51.4'N, 80°43.7'W, thin sand on rock platform, with *Thalassia, Halodule, Halimeda, Penicillus*, shovel/sieving, 0.5–1 m.

IMBW-FK-646B, 27-VII-02, "The Billboard" site, oceanside, Lower Matecumbe Key, MM 74.5, 24°51.4'N, 80°43.7'W, thin sand on rock platform, with *Thalassia, Halodule, Halimeda, Penicillus,* shovel/sieving, 0.5–1 m.

IMBW-FK-647, 25-VII-02, W side of Pigeon Key, 24°42.2'N, 81°09.3'W, *Thalassia/Halodule/Syringodeum* seagrass on sand/rubble, concrete bridge piers, by hand, snorkeling, shovel/sieving, 0.5–1 m.

IMBW-FK-648, 26-VII-02, Tennessee Reef Light, off Long Key, 24°44.75'N, 80°46.95'W, patch reef, sand, rubble, scuba, 4–7 m, R/V FLORIDAYS.

IMBW-FK-649, 27-VII-02, Sprigger Bank, bayside, just W of Everglades National Park border, 24°54.75'N, 80°56.24'W, *Thalassia/Syringodeum* seagrass, snorkeling, shovel/sieving, 0.1–0.9 m, Keys Marine Laboratory boat.

IMBW-FK-650, 27-VII-02, wreck of "Thunderbolt", approx. 6 nmi S of Marathon, 24°39.68'N, 80°57.82'W, steel wreck with fouling bivalves, alcyonarians and hydroids, orange/red sponge overcoating most specimens, scuba, 34.1 m, M/V SHUTTERBUG II.

IMBW-FK-651, 27-VII-02, "Samantha's patch reef", approx. 5 nmi S of Marathon, 24°39.49'N, 81°00.32'W, coral rock interspersed with sandy channels, scuba, 7.6 m, M/V SHUTTERBUG II.

IMBW-FK-652, 27-VII-02, Long Key State Park, oceanside, 24°48.67'N, 80°49.68'W, seagrass bed (predominantly *Thalassia*) on muddy sand, wading, shovel/sieving, less than 1 m.

IMBW-FK-653, 27-VII-02, Old Dan Bank, bayside of Long Key, 24°50.45'N, 80°49.63'W, *Thalassia* seagrass bed with *Halimeda* calcareous algae, *Porites* finger-coral, sponges, hydroids, patches of sand/

Halimeda shell hash, snorkeling, 0.3–1.5 m, R/V LAST MANGO.

IMBW-FK-654, 28-VII-02, East Turtle Shoal, oceanside off Grassy Key, 24°43.49'N, 80°56.00'W, at Marker "45" in Hawk Channel, silty patch reef, scuba, 7.5 m, R/V FLORIDAYS.

IMBW-FK-655, 28-VII-02, Veteran's Beach, oceanside, Little Duck Key, 24°40.87'N, 81°13.82'W, *Thalassia/Halodule* seagrass on silty sand, shovel/sieve, low intertidal zone to shallow subtidal.

IMBW-FK-656, 28-VII-02, mangrove channel near Goshen House, South Layton Drive, Layton, Long Key, 24°49.40'N, 80°48.77'W, red mangrove roots, snorkeling, 0.6-1.2 m.

IMBW-FK-657, 28-VII-02, Pigeon Key, 24°42.2'N, 81°09.3'W, seagrass, sand, rubble, by hand, wading, 0–0.5 m.

IMBW-FK-658, 26-VII-02, E end of Big Pine Key, Spanish Harbor Channel, 24°38.89'N, 81°19.80'W, pier/pilings, algae-covered rocks, snorkeling, hammer/chisel, 0–2 m.

IMBW-FK-659, 28-VII-02, Pigeon Key, 24°42.2'N, 81°09.3'W, seagrass, scuba, 0.6–1.2 m.

IMBW-FK-660, 28-VII-02, Old Dan Bank, bayside of Long Key, 24°50.08'N, 80°49.63'W, *Thalassia* seagrass bed with *Halimeda* calcareous algae, *Porites* finger-coral, sponges, hydroids, patches of sand/ *Halimeda* shell hash, snorkeling, 0.3–1.5 m, R/V LAST MANGO.

The contributions to this proceedings volume reflect the specialized interests of the participants. The projects were initiated at the 12-day workshop but required substantial follow-up between scientist and student, often communicating and even visiting across continents or oceans. The majority of the studies focused on detailed investigations of the comparative and functional anatomy/morphology of exemplar species in the families Arcidae, Donacidae, Psammobiidae, Pteriidae, and Veneridae. Others took a somewhat broader taxonomic approach and developed regional systematic studies based on morphology and/ or molecules. These resulted in reviews of Florida Keys oysters (Gryphaeidae and Ostreidae), boring bivalves (Gastrochaenidae, Mytilidae, and Petricolidae), and western Atlantic Chamidae. Again other teams, using different experimental setups and analytical approaches, studied predator-prey interactions between naticid gastropods and venerid bivalves, or made fine- and ultrastructural investigations into aspects of periostracal morphology, and oocyte and sperm development in the family Lucinidae. Two additional papers on the entire bivalve fauna of the region, compiled from the organizers' long-term research program, provide a broader look at the diversity of the Florida Keys bivalve fauna.

ACKNOWLEDGMENTS

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SHELL MORPHOMETRY OF WESTERN ATLANTIC AND INDO-WEST PACIFIC *ASAPHIS*; FUNCTIONAL MORPHOLOGY AND ECOLOGICAL ASPECTS OF *A. DEFLORATA* FROM FLORIDA KEYS, U.S.A. (BIVALVIA: PSAMMOBIIDAE)

Osmar Domaneschi[1] & Elizabeth K. Shea[2]

ABSTRACT

The genus *Asaphis* has long been considered monotypic, with *A. deflorata* having a worldwide, tropical distribution. Recent research has provided evidence for a tropical, western Atlantic species, *A. deflorata*, and a tropical Indo-West Pacific species, *A. violascens*. Ecological and other aspects of the biology of these species have been studied extensively but morpho-functional features have been known for the Indo-West Pacific species only, so that separation of them has been based on shell sculpture alone. This paper examines the shell morphometry of western Atlantic and Indo-West Pacific specimens of *Asaphis*, and the functional morphology and ecological aspects of a population of the genus present in the Florida Keys, USA. It is our aim to improve knowledge about the biology of the western Atlantic *Asaphis* and identify new characters that may support either their monotypy or the two valid species hypothesis. In addition to confirming that shell sculpture may be a good character in distinguishing both forms, our ecological and morpho-functional data also concur in validating *A. deflorata* as a distinct species. Growth rates, maturity levels and predominantly upper shore intertidal position of the Keys population are consistent with a previous study of the Bahamas population of *A. deflorata*. In both studied areas, *A. deflorata* constitutes the sole bivalve present in the upper shore; conversely, most specimens of the Indo-West Pacific *A. violascens* occupy an intermediate to subtidal position, and share the intertidal region horizontally and vertically with other species of bivalves. The functional anatomy of *A. deflorata* is very similar to that of *A. violascens*; however, the hind gut provides a useful parameter for separation of both species, as it progressively widens, coils and spirals in the Atlantic form, whereas it has an extraordinary dilation in its proximal end only, in the Indo-West Pacific *A. violascens*.

Key words: functional morphology, shell morphometry, ecology, *Asaphis*, Psammobiidae, Bivalvia.

INTRODUCTION

Bivalves of the genus *Asaphis* Modeer, 1793, are commonly found intertidally in gravelly sand, cobble-covered sediments (Depledge, 1985; Britton, 1985; Berg & Alatalo, 1985) or around mangrove roots (Coomans, 1969; Stanley, 1970; Berg & Alatalo, 1985). Populations attain sufficiently high densities to support sustained collection for human consumption (Fisher, 1978; Berg & Alatalo, 1985; Willan, 1993), and their viability as an aquaculture resource has been investigated (Berg & Alatalo, 1981, 1985). The natural variability in shell color gives the Atlantic *Asaphis* its common name, gaudy asaphis, and a place in shellcraft industry (Abbott, 1974; Berg & Alatalo, 1985).

Prashad (1932) considered the Indo-Pacific specimens of *Asaphis* as belonging to *A. dichotoma* (Anton, 1838), and distinct from those living in the Western Atlantic assigned to *A. deflorata* (Linné, 1758). Abbott (1950) considered both Indo-Pacific and western Atlantic forms to be conspecific, and proposed that the genus is monotypic, with *A. deflorata* having a worldwide, tropical distribution. This hypothesis was codified in Abbott (1974), but more recent research (Willan, 1993) provides evidence for a tropical western Atlantic species, *A. deflorata*, and a tropical Indo-West Pacific species, *A. violascens* (Forsskål, 1775).

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The Indo-Pacific *Asaphis* was generally known as *A. dichotoma* until the early 1970s (Willan, 1993), when Cernohorsky (1972) altered its name, without explanation, to *A. violascens*. Willan (1993) has vindicated such an alteration. In this paper, Willan observed that the separation between *A. deflorata* and *A. violascens* was based on shell sculpture alone. Actually, there have been no comprehensive studies to date on the functional morphology of the Atlantic *Asaphis* that allow comparison with that performed by Purchon (1960) on the stomach, and by Narchi (1980) on the functional anatomy of the Indo-Pacific species. Specimens of *Asaphis* from the Indo-Pacific Ocean (Singapore?), were sent by Purchon to R. Tucker Abbott, Pennsylvania, USA, who identified them as *A. deflorata* (Purchon, 1960).

Ecological and biological data on *Asaphis* spp. have been provided by Stanley (1970), Narchi (1980), Britton (1985), Depledge (1985), Berg & Alatalo (1985), Soemodihardjo & Matsukuma (1989), Willan (1993), and Kurihara et al. (2000, 2001).

This paper examines the shell morphometry of the two *Asaphis* spp. *sensu* Willan (1993), and the functional morphology and ecological aspects of *Asaphis deflorata* from the Florida Keys, USA. It is also the aim of this study to identify characters that may support Abbott's (1950) or Willan's (1993) proposal.

MATERIALS AND METHODS

Survey Site

Asaphis deflorata was collected during the International Marine Bivalve Workshop (IMBW) held in the Florida Keys, USA, 19–30 July 2002 from Station IMBW-FK-629, "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), MM 35, Monroe County, Florida Keys 24°39.3'N, 81°18.2'W. Mikkelsen & Bieler (2004) provide a listing of all stations and a map of the studied area. Collections were made in accordance with permit requirements of the State of Florida, under a Research/Collecting Permit issued by the U. S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service to Drs. Paula Mikkelsen and Rüdiger Bieler (Permit FKNMS 2002-079). Individual Florida Saltwater Fishing Licenses (FSFL) numbers were "M–N1I2Y018675" (OD) and "M–N1A79018604" (EKS).

Field Survey

Sampling was performed at low tide when the clams' intertidal habitat was fully exposed; waters receded ~ 4 m from the high tide mark during the sampling period. Specimens were collected along a 4 m transect, from four 0.25 m^2 quadrats. The first quadrat was placed at the low water mark, and three additional samples were taken at 0.5 m intervals moving toward the high tide mark. The quadrat area was excavated to 10–12 cm, the maximum depth allowed by the local rocky gravel substratum along the transect. All sediments were sieved through two sieves, with mesh openings of 10.0 mm and 0.4 mm, respectively.

Behavior

Behavior of *A. deflorata* was observed in the Keys Marine Laboratory on Long Key, and taking photographs in the field and snorkeling during high tide. Results were compared with those obtained by Stanley (1970) and Berg & Alatalo (1985) observing specimens both in laboratory and in field. Laboratory observations included analyses of the burrowing period (Stanley, 1970) of seven individuals each of 1.0, 1.1, 1.3, 1.8, 2.5, 4.5, and 5.7 cm shell length, lying either on the right or left shell valve on a coarse sand substratum free from natural obstacles as pebbles, shells and rubbles. The ability of the species to surmount sediment deposits through maximum extension of the siphons was evaluated by firmly trapping ten specimens (shell length range: 2.5–5.7 cm) posterior end up among pebbles on the bottom of small aquaria. This procedure simulates the condition in which several specimens were found in nature: wedged and trapped both in crevices and among pebbles within the sediment. A new 1–2 cm-thick layer of coarse sand was added every time the siphons tip reached sediment surface, simulating catastrophic burial by sand as it is known to happen in nature (Stanley, 1970; Berg & Alatalo, 1985). This procedure was repeated till the specimens failed to reach the water column. Extrusion of both siphons from the substratum and the ability of the inhalant to take either suspended or deposited material in were observed in ~ 30 specimens kept buried for eight days in clean, coarse sand in aquaria.

Morphometrics

To evaluate if growth data are taxonomically important in distinguishing the Atlantic *A. deflorata* from Indo-West Pacific *A. violascens*, shell length, height and width of complete shells from ten different localities in the Indo-West Pacific, and deposited at the Delaware Museum of Natural History - DMNH, USA (n = 23; shell length range (slr): 28.5–74 mm), and of our material (n = 32; slr: 20.6–59.2 mm) were measured to 0.1 mm with dial calipers, and recorded in an Excel spreadsheet. Such growth data were modeled using a Model II regression analysis in Systat v. 5.2.1 for Macintosh. To accomplish this, the loss function was changed from the ordinary least squares regression equation to: LOSS = (Y - (B0 + B1*X))^2/ABS (B1), where Y and X are the dependent and independent variables, and B0 and B1 are the two parameters to be estimated.

To evaluate if radial ribs are taxonomically important, ribs were counted in the best-preserved shell valves toward the umbo and at the valve margin of the Atlantic *Asaphis* (n = 10; shell length range: 35–59.2 mm) (our material) and the Indo-West Pacific *Asaphis* (n = 10; slr: 41–56.5 mm) (the Delaware Museum of Natural History - DMNH, USA collection). The degree of branching was recorded as a ratio of margin/umbo ribs, where a larger number indicates more branching.

Principal components and cluster analyses (McCune & Mefford, 1999) were used to assess the degree of similarity or difference between the Atlantic and the Indo-Pacific *Asaphis* spp. Six shell characters were included in the analysis: shell length, height, width, number of ribs at margin, number of ribs at umbo, and the ratio of margin/umbo ribs. T-tests were used to assess significance in character differences.

Museum Collections

Asaphis violascens. Delaware Museum of Natural History, USA: Solomons Island, lots 185776 (1 v., 2 spec.) and 129978 (1 v., 1 spec.); Fiji Islands, lots 185057 (1 spec.), 211943 (2 v.), 205760 (2 spec.) and 166675 (2 spec.); Japan, lots 185777 (2 spec.), 109642 (1 spec.); Western Australia, lot 175710 (3 spec.); Guam Island, lot 174675 (1 spec.); Philippines, lots 152564 (1 v.), 122836 (1 v.), 122499 (1 v.) and 194390 (1 spec.); Ambon Island, lot 168461 (4 spec.); Palau, lot 211968 (1 v., 1 spec.); Northern Australia, lot 181892 (1 spec.); Malaysia, lot 201332 (1 spec.); Singapore, lot 21545 (2 v.); Moorea Island, lot 152461 (1 v.). Instituto de Biociências, Universidade de São Paulo (IBUSP), Brazil: four whole specimens and fourteen single shell valves from Hong Kong, China, not numbered, on which Narchi (1980) based part of his work on *A. violascens*; material qualitatively analyzed for shell features.

The following museum molluscan database were examined in mid-January 2003 to assess the historical and recent distribution of *A. deflorata*: the Academy of Natural Sciences of Philadelphia (ANSP), National Museum of Natural History (USNM), Florida Museum of Natural History (FLMNH), the University of Miami Rosentiel School of Marine and Atmospheric Sciences (RSMAS), and the Florida Marine Research Institute (FMRI).

Specimen identifications in the museum collections were assumed to be correct and were not verified by the authors; however, specimen identifications of the RSMAS collection were verified by P. M. Mikkelsen, to whom we are grateful, those of the DMNH collection by E. K. Shea, and of the Instituto de Biociências, Universidade de São Paulo by O. Domaneschi.

Anatomy

Live specimens (shell length range: 6.9–59.2 mm) were dissected and examined for the presence of developed gonads and eggs or sperm using a compound microscope. Specimens were recorded as immature when no gonad tissue could be located; mature males and females were identified when sperm or eggs were present.

Studies of the anatomical features and drawings were made based on living and relaxed and preserved specimens. Magnesium sulfate and refrigeration were used as relaxing agents. Ciliary currents of feeding and cleansing were observed in live specimens using both colloidal graphite and carmine powder suspensions, carborundum grade F3 and graded sand particles. Complete serial histological sections (4 to 8 µm thick) were taken from a specimen 1.5 cm in shell length fixed in Bouin acetic and stained with Ehrlich's haematoxylin and eosin.

RESULTS

Ecology

At the "The Horseshoe" site, *A. deflorata* is restricted to the intertidal zone, in patches of gravelly coarse sand covered with pebbles and rubble on a coral ground. The beach slope of the sampled area is slightly larger than 10° and waters were calm and receded approximately 4 m from the high tide mark during the studied period.

Live, sparse unburied specimens were found lying by the high tide mark; buried specimens occurred till a maximum depth of 10–12 cm, the latter determined by the rocky, impenetrable substratum underneath. Crevices and restricted spaces among pebbles within the substratum were usually occupied by individuals. Depths of 5 to 15 cm (Berg & Alatalo, 1985) and deeper (Stanley, 1970) have been registered for the species. Our experiments showed the species can extend their siphons as long as 1.5 times the shell length. This allows us to predict that the largest specimens (~ 8 cm in shell length - Stanley, 1970; Berg & Alatalo, 1985) burrow as deep as ~ 20 cm. In pockets of sand crowded with *Asaphis*, larger and smaller specimens were intermingled indifferently, occupying the substratum without horizontal or vertical segregation according to size. Their normal life position was with the posterior end up and the longitudinal axis at an angle of between 10° to 30° from the vertical. This angle increased to 90° in some specimens buried shallowly both in crowded or shallow pockets of sand. This supports Stanley's (1970) statements that life position and burial depth of *A. deflorata* in nature are in part controlled by boundary effects.

Along the transect, each station (quadrat) sampled had a different sediment composition, and a correspondingly different population density and structure (Fig.1). Station 1 was composed of rubbles and pebbles and no living specimen was present (n = 0). Station 2 was composed of pebble-covered, gravelly silt; a few (n = 27) living specimens were present, intermingled among a larger number (not recorded) of buried, recently dead shells retained in their life position. Station 3 was composed of gravelly coarse sand with silt; in spite of being dominated by one extremely large piece of coral rubble, it yielded the largest number of specimens (n = 238). Station 4 was

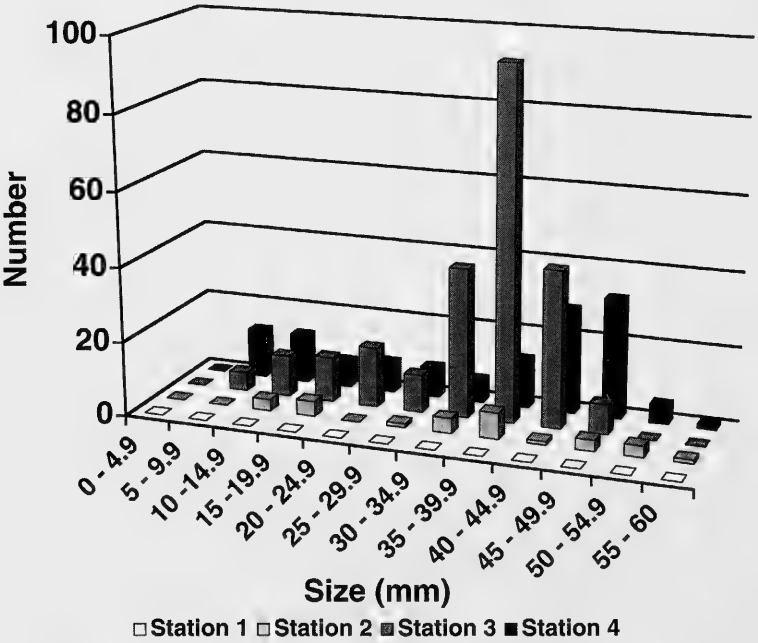

FIG. 1. *Asaphis deflorata*. Size distribution of live specimens collected at Stations (St.) 1–4 in July 2002, from the "The Horseshoe" site population, Florida Keys, USA. Total number of specimens by station: St. 1 (n = 0); St. 2 (n = 27); St. 3 (n = 238); St. 4 (n = 137).

composed of gravelly coarse sand and had a smaller yield (n = 134). Dead shells were scarce in stations 3 and 4. Over 93% of the 399 specimens collected came from stations 3 and 4, the nearest to the high tide mark and regularly exposed during ebb tides.

Morphometrics

Shell length ranged between 6.9–59.2 mm (n = 399). Almost 70% of the specimens collected were 30–50 mm in shell length; approximately 25% of the population was between 5–30 mm, and only 2.5% was > 50 mm. Based on the measurements of living and dead collected specimens, the height and width of *A. deflorata* grow gradually without obvious interruption or change in the growth trajectory over the size range of 6.9–59.2 mm (Fig. 2A). Overall, shell length of *A. deflorata* is 1.54 times the height, and 2.26 times the width.

Parameters of the growth equations that describe *A. violascens* (DMNH collection) fall within the 95% confidence intervals for *A. deflorata*, reflecting the overall similarity in ontogenetic trajectories (Fig. 2B); overall shell ratios are also similar, with the shell length of *A. violascens* 1.44 times the height and 2.22 times the width.

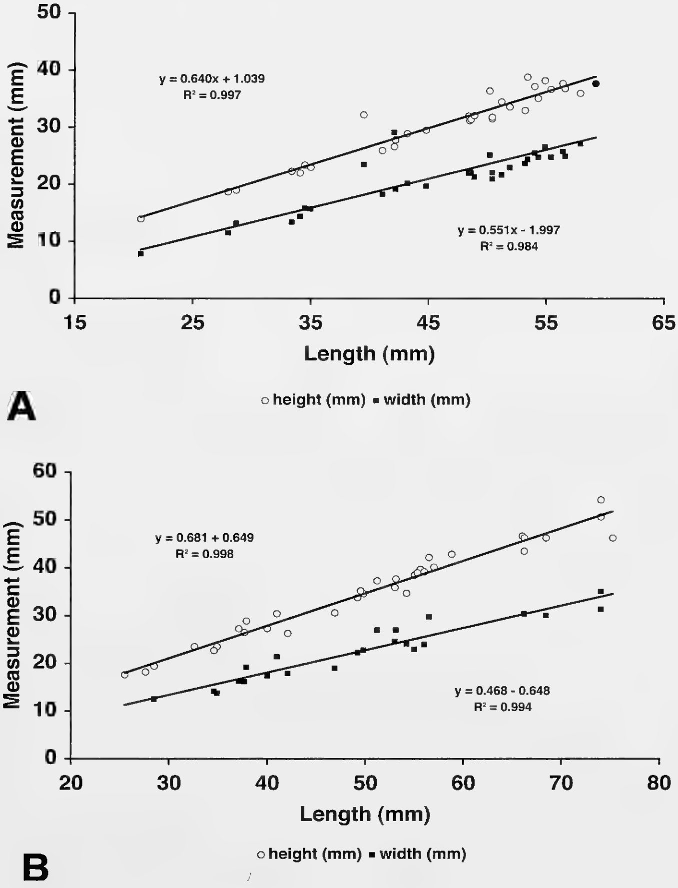

FIG. 2. Model II regression analysis of height and width vs. length for: A, *Asaphis deflorata* from "The Horseshoe" site population, Florida Keys, and B, *A. violascens* at Delaware Museum of Natural History, U.S.A. Although the regression equations are different for each variable, the slope and intercept are within the 95% confidence intervals of each other, and thus the growth trajectories are essentially the same.

TABLE 1. Comparison of observed rib counts (our data - *D & S*) made on well-preserved shells of *Asaphis deflorata* (n = 10; slr: 35–59.2 mm) from the "The Horseshoe" site population, Florida Keys, USA and of *A. violascens* (n = 10; slr: 41–56.5 mm) in the collection at the Delaware Museum of Natural History, USA, and rib counts predicted for both species by Willan (1993 - *W*); n, total number; SD, standard deviation; slr, shell length range; $\bar{x}$, average.

Shell character	*Asaphis deflorata* range ($\bar{x}$ ± SD)	*Asaphis violascens* range ($\bar{x}$ ± SD)
Rib number (*W*)	60–90	40–60
Rib number – at umbo (*D & S*)	48–80 (56.3 ± 10.9)	23–80 (32.3 ± 17.0)
Rib number – at margin (*D & S*)	80–102 (92.8 ± 7.9)	52–100 (68.4 ± 12.9)
Rib branching (*W*)	less frequent	more frequent
Rib branching index (*D & S*)	1.35–2.58 (1.70 ± 0.38)	1.25–2.91 (2.31 ± 0.5)

Rib counts both at the umbo and at margin of *A. deflorata* from the "The Horseshoe" site and of *A. violascens* (DMNH collection) have a wider range than predicted for both species by Willan (1993), and the ranges overlap (Table 1). In spite of this, principal components analysis (PCA) (Fig. 3) shows that two groups are consistently found: one that contains *A. deflorata* specimens with a few *A. violascens* specimens, and one that is solely composed of *A. violascens*. It is also evident that *A. violascens* generally has fewer, more branching, ribs than *A. deflorata*, and these differences are significant at P = 0.05 (t-test: ribs near umbo P = 0.002; ribs at margin P = 0.000; branching ratio P = 0.018). Cluster analysis (Fig. 4) shows that all *A. deflorata* specimens are clustered in a group that shares < 25% of the information with the majority of *A.*

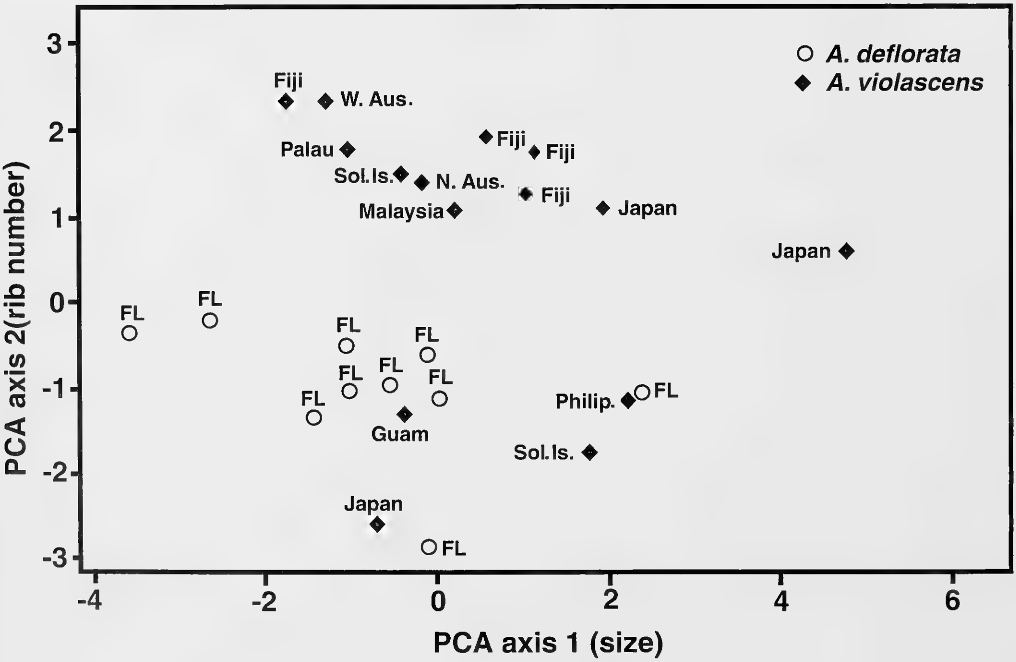

FIG. 3. First two axes of the principal components analysis account for > 85% of the overall variance. Size (length, width and height) increases from left to right along axis 1. Umbo and margin rib counts decrease from bottom to top along axis 2, whereas the branching ratio increases from bottom to top.

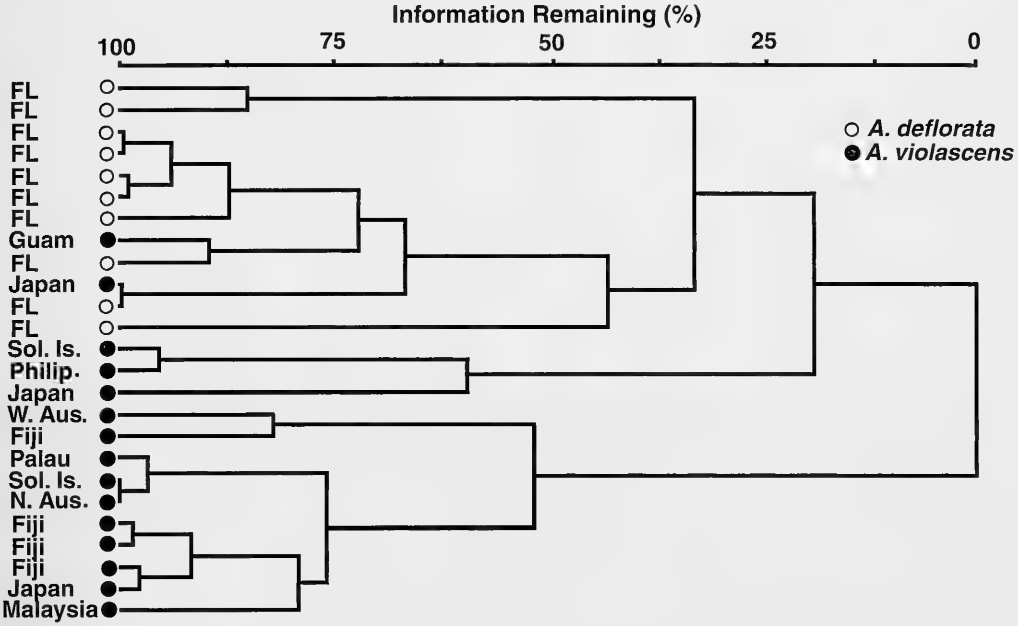

FIG. 4. Cluster diagram (Jaccard distance measure, group average linkage) showing the overall similarities between each specimen in length, height, width, number of ribs at umbo, number of ribs at margin, and branching ratio. Branch points at 0 indicate no relationship between variables; branch points at 100% mean the specimens were virtually identical overall. FL, Florida, USA; Sol. Is., Solomons Island; Philip., Philippines; W. Aus., Western Australia; N. Aus., Northern Australia.

violascens; however, two anomalous specimens of *A. violascens* cluster within the *A. deflorata* branch. Thus, there is no relationship between the two major groups, even though PCA analysis shows that several *A. violascens* group within that of *A. deflorata*. Regardless of these outliers, t-tests show that the number of ribs at the umbo and at margin, and the degree of branching distinguish the species and that size measurements do not. Other useful shell characters in distinguishing *A. deflorata* from *A. violascens* are: the presence of a discernible, rounded posterior radial ridge and posterior slope in the Atlantic *Asaphis* (our material), not discernible (Willan, 1993; IBUSP collection) in the Indo-West Pacific specimens; a smooth inner surface in the Atlantic *Asaphis*, contrasting with the well-marked, ridged inner surface in specimens from Hong Kong (IBUSP collection).

Sexual Maturity

In the sampled population, all specimens < 24 mm in shell length were immature, and all specimens > 32 mm had recognizable eggs or sperm in the gonad tissue. The gonads of most specimens > 24 mm in shell length were identifiable as male or female; just two specimens of 26 mm and 34 mm in shell length were not.

Distribution

Asaphis deflorata has historically been collected along the Atlantic and Gulf coasts of Florida, as far north as Saint Augustine Beach (FLMNH 16923), and as far south as the Dry Tortugas (FLMNH 16919) as well as in the Bahamas. Rios (1994) registered the species for Atol das Rocas, off northeast Brazil. Most of these records have collection dates between 1878 and 1966. None of the collections assessed had specimens of *A. deflorata* collected after 1975, although extant populations exist at other Caribbean sites including the Bahamas (FLMNH 247323), Cuba (ANSP 192408), and Trinidad & Tobago (FLMNH 226465).

Functional Anatomy

Shell: The shell of *A. deflorata* from the "The Horseshoe" site population (Fig. 5), matches the general shell characterization described by Abbott (1974) and Rios (1994) for the species in Atlantic waters of the Caribbean region, Bermuda and off northeast Brazil.

Shell oval-elongate, equivalve, moderately inflated; umbos subcentral anterior. Maximum shell height at the umbonal-ventral axis; maximum width at the level of umbos. Posterior margin truncate; anterior margin broadly rounded; ventral margin straight to slightly convex; shell ends gaping slightly. Shell with rounded posterior ridges and discernible posterior slope marked by stronger radial ribs; posterior ridges more conspicuous at the dorsal half of the shell, running diagonally to and fading as it meets the acute-rounded confluence of both posterior and ventral shell margins. Outer surface sculptured with numerous fine, radial ribs ranging in number from 80–102 (n = 10; shell length range: 35–59.2 mm) at shell margin (Table 1). Few ribs with a weak tendency to fork; radial ribs stronger, wider apart and scaly to slightly nodulose posteriorly. Fine commarginal ridges smoothly crossing the radial elements and

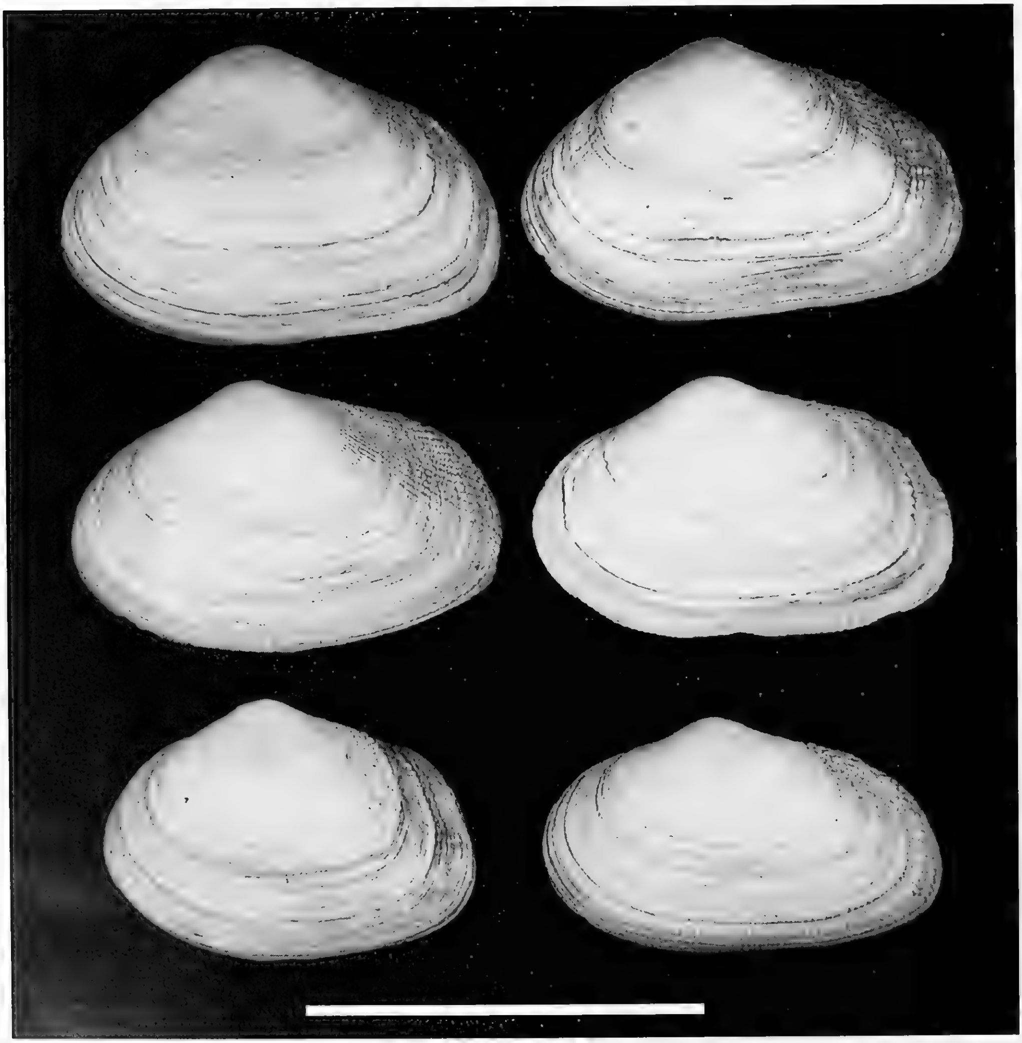

FIG. 5. *Asaphis deflorata*. External view of the left shell valves of specimens from the "The Horseshoe" site population, Florida Keys, USA, showing radial ornamentation and little variation in shell outline. Scale bar = 5 cm.

expanding into scale-like or nodulose processes on the posterior radial ribs. Exterior dull; yellowish to creamish white predominate in the population. Periostracum thin, dehiscent. Interior often glossy, brightly colored; radial ornamentation on the outer surface not interfering on the inner surface, which is smooth throughout. A deep violet blotch often present, spreading over from the nymph through the posterior margin; a similar, smaller, often fading blotch can be present at the level of the anterior adductor muscle scar. Anterior adductor muscle scar elliptical, elongate dorso-ventrally (Fig. 6); posterior one elliptical to rounded; anterior and posterior retractors pedal muscle scars fused dorsally to the corresponding adductor scars. Pallial line recessed deeply from within the smooth shell margin. Cruciform muscle scars faint to invisible. Pallial sinus broad, extending almost to the level with the posterior cardinal tooth; upper limb straight to slightly curved; anterior margin rounded; lower limb detached from pallial line, descending obliquely to coalesce with the latter far from the rear end of the pallial sinus. Extension of the fusion lower limb-pallial line corresponding to one third of the pallial sinus depth; rear end of this extension reaching level with the anterior half of the posterior adductor scar. Striking impression of the fan-shaped siphonal retractor muscle present within the pallial sinus. Hinge plate with two cardinal teeth in each valve (Fig. 7); nymph broad; ligament elongate, thick, tough. Right anterior cardinal tooth conspicuous, emerging from the hinge plate as a knob-like or thick, plate-like projection; right posterior cardinal stronger, elongate, deeply bifid and separated from the anterior tooth by a deep triangular socket. Left anterior cardinal tooth strong, elongated and deeply bifid; left posterior cardinal emerging as a knob-like or thick, plate-like projection.

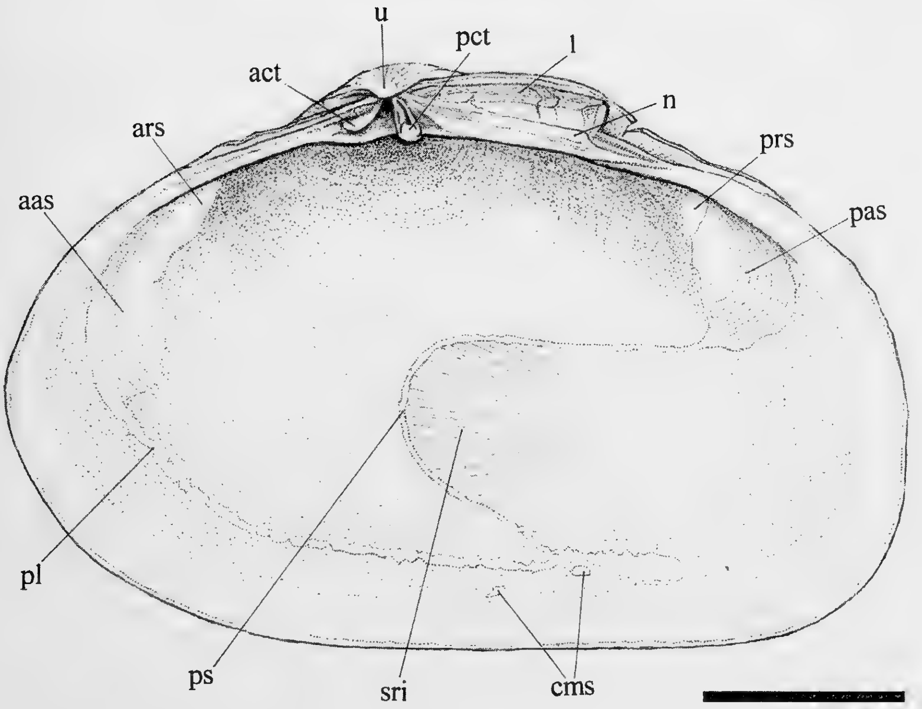

FIG. 6. *Asaphis deflorata*. Internal view of the right shell valve. Abbreviations: aas, anterior adductor muscle scar; act, anterior cardinal tooth; ars, anterior pedal retractor muscle scar; cms, cruciform muscle scars; l, ligament; n, nymph; pas, posterior adductor muscle scar; pct, posterior cardinal tooth; pl, pallial line; prs, posterior pedal retractor muscle scar; ps, pallial sinus; sri, siphonal retractor muscle impression; u, umbo. Scale bar = 1 cm.

Mantle: The mantle lobes are thin and translucent with the usual three folds along their free ventral edges. *Asaphis deflorata* lacks the additional folds that isolate the rejection channel for pseudofaeces (waste canal of Kellogg, 1915), which is present in some Tellinidae and Semelidae (Yonge, 1949), and in species of Mesodesmatidae and Veneridae (Narchi, 1981, 2002). Graham (1934a) and Domaneschi (1992) have given a detailed picture and description of the mantle edges in species of *Gari*. The mantle edges in *A. deflorata* are histologically similar to those described and illustrated in detail by Domaneschi (1992) for *Gari solida* (Gray, 1828).

The outer fold is the least developed; the inner fold is moderately higher and the only to be involved in siphon formation. The middle is a huge, sensory fold, which bears a single row of cylindrical, cup-shaped tentacles and the best supplied with pallial muscles. When the foot and siphons are protracted, the middle folds are extended well beyond the limits of the shell valves, exhibiting an outer surface lined by a thin, translucent periostracum. The periostracal groove lies outside, adjacent and parallel to row of the tentacles. Similar organization has been noted in the other Tellinoidea in the semelid *Ervilia castanea* (Montagu, 1803) by Morton (1990) and in other Psammobiidae – in *Gari solida* by Domaneschi (1992) and in *Heterodonax bimaculatus* (Linné, 1758) by Narchi & Domaneschi (1993).

Each bundle of fibers that comprise the pallial retractor musculature splits into two sets immediately after they originate at the pallial line. Both sets supply mainly the middle fold and respective tentacles, and meet again adjacent to the periostracal groove, as in *Gari tellinella* (Lamarck, 1818) (Graham, 1934b) and *G. solida* (Domaneschi, 1992). A few fibers that supply the outer mantle fold arise from the set running adjacent to the outer mantle epithelium. Muscle fibers that retract the inner mantle fold arise from the inner set underlying the inner mantle epithelium. In addition to these pallial retractors, there are bundles of fibers running transversely across the mantle edge and folds, and bundles of longitudinal fibers restricted to the inner and middle folds, with the bulk of them along the inner face of middle fold. The pallial nerve cord lies embedded in the connective tissue contained by the two sets of pallial retractors. Mucous-gland cells form a well-defined, glandular region along the pedal opening, just dorsal to the base of the inner mantle fold. Mucus-secreting cells are more abundant on both ends of the pedal opening.

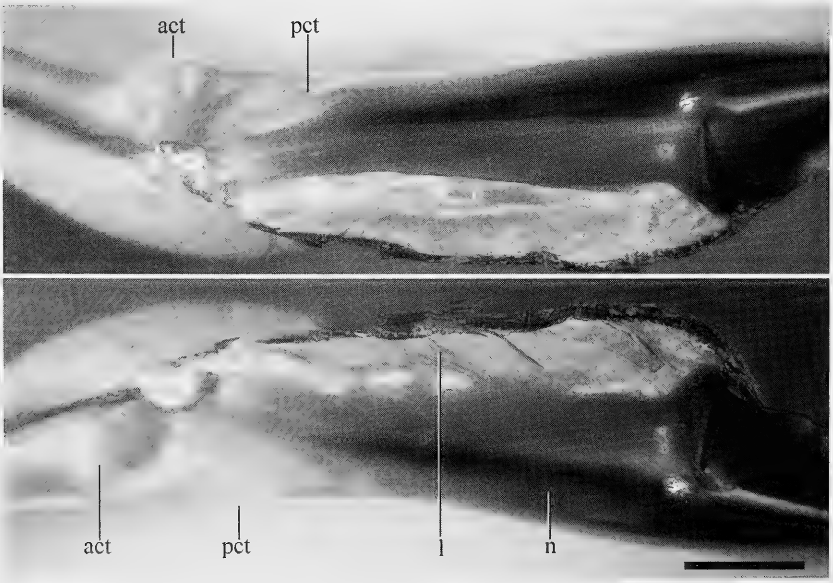

FIG. 7. *Asaphis deflorata*. Hinge plate morphology of the right (bottom) and left (top) shell valves. Abbreviations: act, anterior cardinal tooth; l, ligament; n, nymph; pct, posterior cardinal tooth. Scale bar = 2 mm.

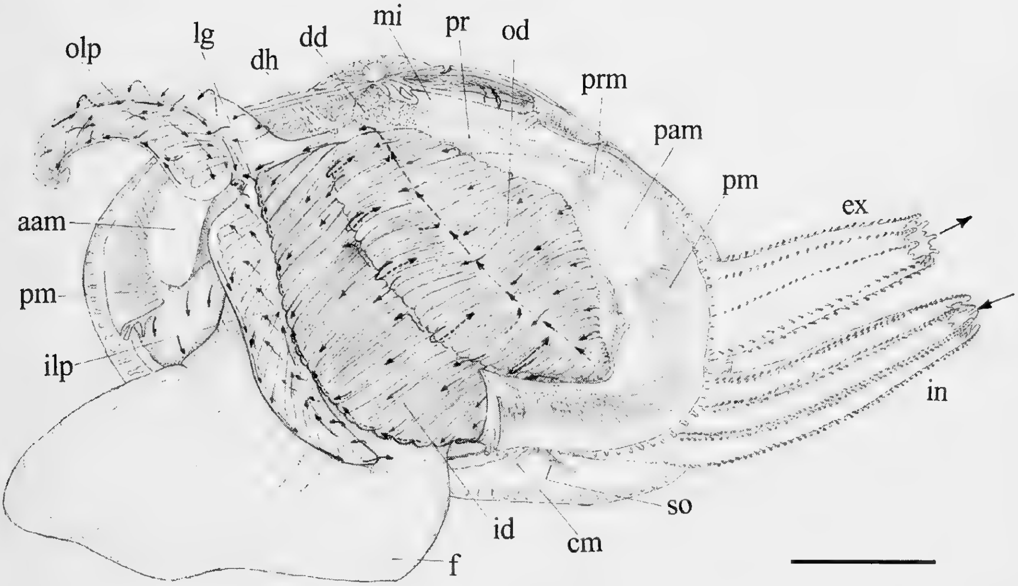

FIG. 8. *Asaphis deflorata*. The animal viewed from the left side after removal of the left shell valve and mantle lobe. The siphons and foot are shown somewhat contracted. Arrows show the direction of the ciliary currents. Abbreviations: aam, anterior adductor muscle; cm, cruciform muscle; dd, digestive diverticula; dh, dorsal hood; ex, exhalant siphon; f, foot; id, inner demibranch; ilp, inner labial palp; in, inhalant siphon; lg, lateral oral groove; mi, mantle isthmus; od, outer demibranch; olp, outer labial palp; pam, posterior adductor muscle; pm, pallial retractor muscles; pr, pericardial region; prm, posterior pedal retractor muscle; so, sense organ. Scale bar = 1 cm.

The cruciform muscle with its specialized sensory organs occurs postero-ventrally, between the base of the inhalant siphon and the pedal gape (Fig. 8). Both structures are diagnostic for the Tellinoidea (Ihering, 1900; Frenkiel, 1979; Morton, 1984, 1990; Morton & Scott, 1990). The sensory organs, which lie at the posterior arms of the cross open directly to the siphonal space at the summit of minute papillae as described by Graham (1934a) and Domaneschi (1992) for *Gari*, and Domaneschi (1995) for *Semele*. The cruciform muscle and its sensory organs have been described by Mouëza & Frenkiel (1974, 1976, 1977), Frenkiel & Mouëza (1977, 1984), Frenkiel (1979), Morton (1990).

Cilia are present all over the inner epithelium of the mantle lobes. They are more concentrated along a well-defined, wide ciliated gutter that lies parallel to the origin of the pallial retractor muscles. Cleansing ciliary currents (Fig. 9) sweep particles forward and downward from the dorsal area adjacent to the posterior adductor muscle to a vigorous C-shaped rejection tract. This rejection tract exactly follows the line of origin of the siphonal retractor muscle. Weak cleansing currents within the limits of the C-shaped tract, and on the dorsal area adjacent to the anterior adductor muscle convey particles downward and backward to the base of the inhalant siphon. Minute, isolated particles coming into contact with inner mantle fold are carried slowly upward to join those coming downward on the mantle surface.

Despite the presence of the ciliated gutter, *A. deflorata* lacks a well-defined, vigorous, rejection current running backward parallel to the mantle edge. Such a vigorous current is present in *A. violascens*, *Heterodonax bimaculatus*, and *Gari solida* (Psammobiidae) (Narchi, 1980; Narchi & Domaneschi, 1993; Domaneschi, 1992, respectively).

Siphons: The siphons, type A of Yonge (1957, 1982), are wide, separate throughout their extent (Fig. 8) and up to 1.5 times the shell length. The inhalant is slightly longer, as in other Psammobiidae (Yonge, 1949; Domaneschi, 1992; Narchi & Domaneschi, 1993). In a week's time in the laboratory, only the inhalant siphon was extruded clear of the sediment surface, but not as far as the 3–5 cm

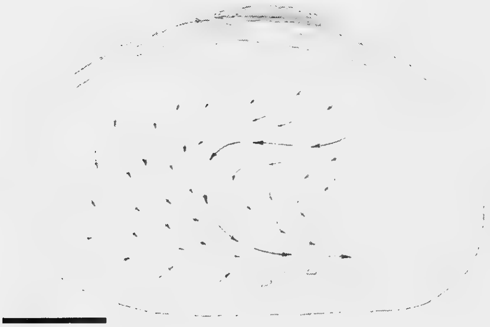

FIG. 9. *Asaphis deflorata*. Ciliary cleansing currents on the inner surface of the right mantle lobe. Scale bar = 1 cm.

as reported by Berg & Alatalo (1985). When extruded and undisturbed, the inhalant was held passively for many hours, with the ring of tentacles either straight or curled inward; retracted, its aperture either flushed with or was kept below the sediment surface. This latter behavior is the rule for the exhalant tip. The inhalant was never seen bending down onto or along the bottom sediment sucking in deposited material as in typical deposit-feeding tellinoideans described by Yonge (1949). Many specimens buried within the sediment in aquaria had the tip of the inhalant siphon completely covered by a 1 cm-thick layer of coarse sand, but maintained an active current flowing through the interstices of the sand grains, as confirmed by pouring carmine powder suspension into the water. Such an ability allows the species to survive buried within either rock-, or cobble-covered gravelly sediment without extruding the siphons into the water column. Berg & Alatalo (1985) stated that they have never observed the tip of the inhalant exposed into the water column in the field.

The inhalant aperture is fringed with twelve simple, finger-like tentacles, six longer alternating regularly with six shorter. From the distal end of each longer tentacles arises a double row of minute, cylindrical, cup-shaped papillae which extend down the length of the siphon. The exhalant aperture is fringed with eight longer tentacles interspersed with eight shorter tentacles. Single rows of minute papillae extend throughout the length of the exhalant siphon, each row associated with longer tentacles.

Brilliant, golden-yellow pigmentation is present in the inner wall of both siphons. Pigments may simply create a speckled pattern, or be grouped into rounded-elongate, regularly arranged spots, or a mixture of both. The larger concentration of pigments in the tips of the siphons gives them a vivid, golden-yellow color, which fades away toward the bases. Narchi (1980) and Domaneschi (1992) also noted a yellow color for the siphons of *A. violascens* and *Gari solida*, respectively. The siphons of *A. deflorata* are sensitive to touch. Although light sensitive, they exhibit a similar response either to high or low luminosity coming from an electronic flash, or a microscope illuminator, respectively.

Labial Palps: The labial palps (Fig. 8) are approximately one half the shell length. When completely expanded, their free distal tips do reach and even surround the posterior border of the visceral mass.

The ventral half of the inner surfaces of the palps are obliquely folded and separated from the dorsal, smooth half by a longitudinal fleshy cord that overhangs slightly the dorsal extremities of the folds. The inner demibranchs of the ctenidia project deeply between the palps, but the ventral tips of their anteriormost filaments are not inserted into a distal oral groove. Thus, the labial palps-ctenidial junction is of Category III (Stasek, 1963).

Exceedingly large palps, provided with different ciliary tracts indicate that *A. deflorata* processes large amounts of particles in the mantle cavity. The palps play an important selective function, even though the wide ctenidia exert a previous selection of the bulk of material entering the mantle cavity as in other suspension feeding tellinoideans. The sorting mechanisms of the palps are shown in Figures 8 and 10.

Particles coming into contact with the smooth outer face of the palps (Fig. 10A) are carried dorsalward (current "a") and then passed to the internal, smooth, dorsal half of the organs. Here, transverse, ventrally directed currents transfer them onto the folded area (Fig. 10B) to be selected.

Transversely directed currents (b), operating obliquely oralward and markedly ventralward across the crests of the folds, to either accept or reject particles, depending upon the size or total volume of particles.

On the aboral face of the folds a current (c) carries isolated particles and small agglomerations of particles dorsally. As they move dorsally, they are influenced by transverse currents "b" and removed anteriorly.

Only minute, isolated particles are caught by cilia on the adoral faces of the folds and are carried dorsalward. Traveling on this current "d", particles reach the dorsal extremity of the folds, where a conspicuous oralward current (e) transports them onto the lateral oral groove, between the palps.

Particles escaping from the action of the previous currents "b", "c", "d", and reaching the floor of the grooves between adjacent folds, are driven ventrally (current "f") onto a rejection current (g) present along the narrow, smooth ventral edges of the palps. Excess material on current "b" also converges onto this current "g".

Currents "c" and "d" function as resorting devices; in combination with current "b", they keep the food material away from rejection tracts, and allow the agglomerations to be disintegrated, resorted, and useful material ingested prior to being discarded as pseudofaeces.

Muscular contractions of the palps increase their sorting efficiency in processing different amounts of particles drawn into the mantle cavity through the inhalant current. By bending laterally, the inner palps touch the visceral mass epithelium where particles are being carried ventrally. Once trapped by currents "a", such particles are passed to the folded surface of the organ and sorted. The outer labial palps do the same, touching the mantle epithelium. Muscular activity is also responsible either for bringing folds closer or forcing them apart, and in keeping them erect or bending them over. Such devices permit total exposure of the ciliary tracts, favoring resorting and ingestion of scarce profitable food, as well as their concealment, which favors rejection when the inhalant flow of water contains excess material.

Foot and Visceral Mass: The foot is a huge, axe-shaped muscular organ that expands far beyond the anteroventral margin of the shell. At the posterior end of its narrow, ventral edge is a distinguishable slit-like opening, related to a shallow depression (duct), both remnant of the byssal complex, as identified by Pelseneer (1911), Graham (1934b), and Domaneschi (1992) for *Gari* spp. No trace of byssus gland was detected within the foot of *A. deflorata*. Pelseneer (1911) and Narchi & Domaneschi (1993) did not find even a byssal groove aperture in *Asaphis violascens* and *Heterodonax bimaculatus*, respectively. Narchi (1980) made no reference to byssal complex in *A. violascens*. Every time it was provided a soft substratum, the foot in all laboratory specimens

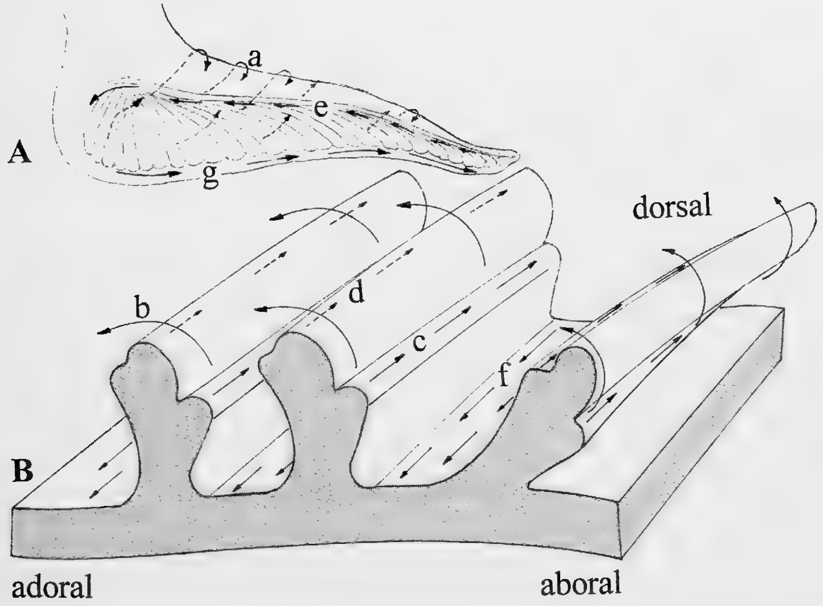

FIG. 10. *Asaphis deflorata*. A, sketch of the left inner labial palp showing the ciliary currents (a), (e) and (g). B, diagrammatic representation of three folds and respective ciliary currents (b), (c), (d) and (f). For lettering (a) through (g), see text on labial palps.

of *A. deflorata* (shell length range: 6.9 to 57 mm) was used exclusively for burrowing, this being slower in larger individuals. Burrowing period (Stanley, 1970) lasted from 2 to 5 hours among individuals < 2.5 cm in shell length (n = 5), and 23 hours and 35 hours in individuals 4.5 and 5.7 cm in shell length, respectively.

The upper, visceral portion of the foot is covered with a low, smooth epithelium. Ciliary currents were detected in all dissected specimens, even though only sparse patches of cilia could be seen in histological sections. Intense cleansing ciliary currents on this visceral portion of the foot sweep and concentrate particles downward over a narrow longitudinal area, juxtaposed with the outer dorsal margins of the inner labial palps and the free edges of the inner demibranchs. Only a weak dorsalward current was observed on a narrow area juxtaposed with the very proximal portion of the inner labial palps. Particles traveling on this current are caught by cilia on the outer, smooth face of the palps and passed to the opposite face of the organs (Fig. 10A).

The most ventral, predominantly muscular portion of the foot is obliquely ridged and lined with a densely ciliated epithelium (cilia 5.7 μm long). Despite being intensively ciliated, no ciliary currents could be detected on this portion of the foot; Domaneschi (1982) stated they are absent in *Gari solida*. Only Pohlo (1972: fig.1) has depicted dorsalward ciliary currents on the most ventral portion of the foot of a psammobiid.

The portion of the foot juxtaposed mainly with the labial palps has a 28 μm-depth, longitudinally striated epithelium. Lack of cilia on this portion was confirmed through histological sections and by observing live specimens.

Ctenidia: The ctenidia are large and occupy most of the mantle cavity when completely expanded (Fig. 8). They are eulamellibranch, plicate and heterorhabidic. The morphology of both demibranchs is much the same, the outer being more shallowly plicate.

The ascending lamellae of both inner demibranchs are attached to the epithelium of the visceral region of the foot by ciliary junctions; behind the foot they connect to each side of a thin, wide triangular membrane the base of which surrounds and attaches to the foot by ciliary junctions. The ascending lamellae of both outer demibranchs connect to the visceral mass epithelium by tissue fusion.

Histological sections prepared from a specimen 1.5 cm in shell length revealed that the deepest plicae (400 μm depth) of the inner demibranch are formed by 35 ordinary filaments. Each filament bears 4.3 μm-long, frontal cilia, these bordered latero-frontally by 17.2 μm-long, latero-frontal cilia. The lateral cilia responsible for the inhalant current of water are roughly 11.5 μm long. Terminal cilia (23 μm long) form a fringe along the lateral walls of the marginal food groove. This is 34.2 μm depth on average and evenly carpeted with 5.7 μm-long cilia.

The frontal surface of a principal filament varies in form throughout its extent; it is ridged near the free ventral margin of both demibranchs, and changes to a broad, shallow gutter toward the ctenidial axis.

The more stretched a particular region of the principal filament is, its frontal gutter is more flattened and broad, the sides of the filament frequently sloping away nearly at the same plane as that of the groove. In strongly contracted plicae, the frontal gutter of the principal filament changes to a narrow, deep central groove. This is flanked by the sides of the filament, which lie at the same plane of that of the frontal surface, as described by Ridewood (1903) for *Gari vespertina* (Gmelin, 1791).

The morphology and respective ciliary mechanisms of the ctenidium (Fig. 11) are of type C (1a) (Atkins, 1937), characteristic of a variety of eulamellibranchs, including the Tellinoidea, as in the Psammobiidae analyzed by Atkins (1937) and Narchi & Domaneschi (1993). Acceptance oralward currents are thus restricted both to the marginal food groove of the inner demibranch and to the ctenidial axis. Frontal ciliary currents on both ordinary and principal filaments of the outer demibranch are exclusively ventralward on the ascending lamella, and round the bend at the free edge, and dorsalward on the descending lamella. Frontal currents are exclusively ventralward on both lamellae of the inner demibranch.

There is a tendency for large particles or masses of particles that reach the free edge of the outer demibranch to be passed straight off onto the inner demibranch. However, an incipient oralward current was also registered along the free ventral margin of the outer demibranch. Particles on this current are carried for short distances anteriorly, then deviate ventralward under the influence of the frontal currents on the inner demibranch.

Another incipient oralward current does exist along and outside the marginal food groove of the inner demibranch. Material traveling on this current usually falls off on the rejections currents of the mantle epithelium.

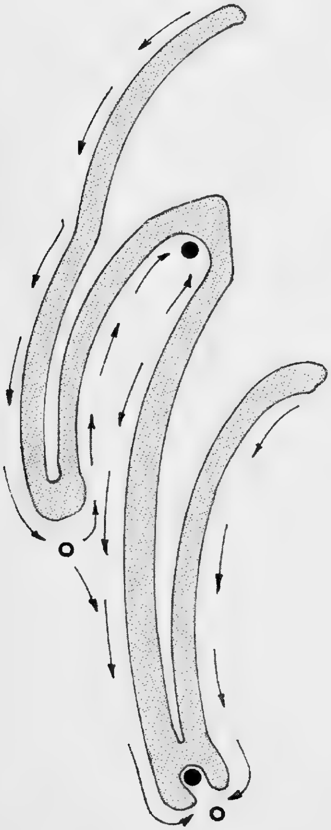

FIG. 11. *Asaphis deflorata*. Diagrammatic transverse section showing the form of the ctenidium and directions of the frontal ciliary currents (arrows). Solid circles, oralward currents; hollow circles, incipient oralward currents.

Adductor Muscles: The anterior adductor muscle (aam) is elliptical and dorsoventrally elongate; the posterior adductor (pam) is subelliptical to rounded and thicker than the anterior (Fig. 12).

Pedal Musculature: The extrinsic pedal musculature (Fig. 12) consists of bilateral pairs of almost equally developed anterior and posterior pedal retractors, one pair of anterior pedal protractor, and one pair of vestigial pedal elevator muscles.

On each side of the roof of the visceral mass, a thin layer of muscle fibers (el) converge dorsally and insert deep on the umbonal cavity, where they leave a single, well-impressed scar, or more than a single scar. Such a muscular layer is functionally not significant compared to the other extrinsic pedal muscles; it corresponds by its insertion on the shell valve to the functional elevator pedal muscle in many other bivalves. In *A. deflorata*, the elevator pedal muscles are atrophied as in other Tellinoidea, for example, *Gari* spp. (Pelseneer, 1911; Bloomer, 1911; Domaneschi, 1992), *Tellina foliacea* (Linné, 1758) (Pelseneer, 1911), *Semele* spp. (Domaneschi, 1982, 1995). Narchi (1980) and Narchi & Domaneschi (1993) did not find pedal elevators muscles in *A. violascens* and *Heterodonax bimaculatus*, respectively.

The anterior and posterior pairs of pedal retractors are equally developed, each attached under the hinge plate internal and contiguous to the adductor, where their edges and respective scars coalesce. The right and the left posterior pedal retractors (prm) pass anteroventrally, converging and meeting in the sagittal plane, almost completely enveloped in the kidneys. Where these muscles meet, their most internal bundle of fibers intersect; the bundles coming from the right pass deeply into the left side of the foot and vice-versa. The most external bundles of each posterior retractor pass directly into the foot. As a whole, the posterior retractors form the innermost muscular layers within the foot.

The anterior pedal retractors (arm) also converge on the sagittal plane, where a few internal bundles of fibers intersect each other and pass deep into the opposite side of the foot. The majority of bundles from each muscle pass directly into the foot, on its corresponding side. Within the foot the anterior retractors form an outer layer in relation to the posterior pedal retractors.

The outermost muscular layer of the foot is composed of fibers coming from a pair of anterior pedal protractor muscles (ppm). Differently from other psammobiids, on each side of *A. deflorata* the anterior protractor is composed of two separate sets (branches) of bundles: one ventral, slender set attaches to the shell juxtaposed to and slightly inserted in the postero-dorsal surface of the anterior adductor; the other set, dorsally placed, gathers the bulk of the fibers. Fibers of the dorsal set insert on the shell valve embracing the ventral half of the origin of the anterior retractor.

From its origin on the shell valve, the slender, ventral set of the protractor muscle passes horizontally into the foot, where the bulk of its fibers go backward, while the remainder twist abruptly, most downward and a few upward, spreading like a fan. Since the bulk of its fibers lies almost to the level with the base of the labial palps, this ventral branch of the protractor may easily be misjudged as related to the palps. However, careful dissections revealed the protractor fibers penetrating exclusively into the visceral region of the foot.

The dorsal set of the protractor has the bulk of its fibers extending almost horizontally and running backward parallel to the longitudinal musculature of the ctenidial axis. Such a juxtaposition makes the identification of both muscles almost impossible. The dorsal set has a large number of its fibers spreading fanwise downward, where they mask those coming from the ventral set. The remaining fibers of the dorsal set spread fanwise dorsally and intermingle with those coming from the vestigial, "elevator" pedal muscle. Narchi (1980) stated that protractor muscles are lacking in *A. violascens*.

Apart from the extrinsic pedal muscles, the visceral mass and the most ventral parts of the foot contain a large number of isolated, transverse bundle of fibers (intrinsic muscles of Bloomer (1911)). The bundles crossing the visceral mass are particularly numerous, thick and long in *A. deflorata*. Such transverse bundles play an important role in moving blood, and moving materials within the organs.

Ctenidial Retractor and Longitudinal, Ctenidial Axis Muscles: The ctenidial retractors (cr) are a pair of thin, but conspicuous muscles, with an origin slightly posterior to the insertion of each vestigial "elevator" pedal muscle on the umbonal cavity. The ctenidial retractor fibers pass downward, meet and intermingle with those muscular fibers running longitudinally throughout the ctenidial axis (cam). The combined action of both, ctenidial retractor and longitudinal, ctenidial axis muscles shortens the ctenidia as a whole and lifts especially the inner demibranchs. Bloomer (1907), Villarroel & Stuardo (1977), and Domaneschi (1982, 1995) described and depict a similar muscle in *Tagelus divisus* (Spengler, 1794), *T. dombeii* (Lamarck, 1818) and *Semele* spp., respectively.

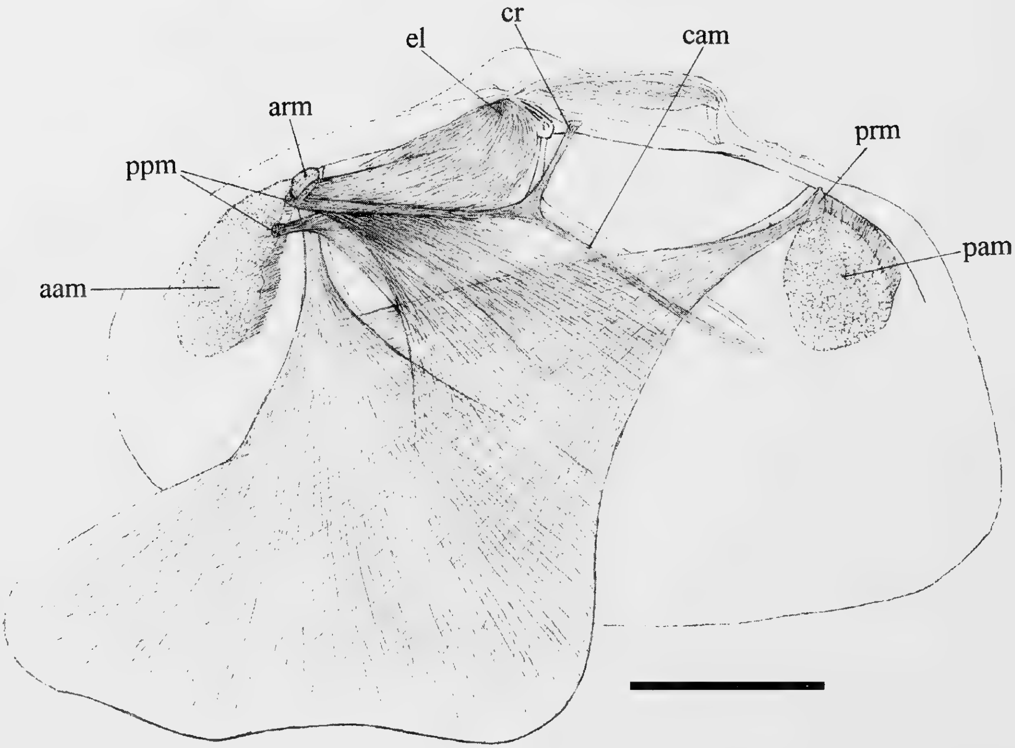

FIG. 12. *Asaphis deflorata*. Musculature, as seen from the left side. Abbreviations: aam, anterior adductor muscle; arm, anterior pedal retractor muscle; cam, longitudinal, ctenidial axis muscle; cr, ctenidial retractor muscle; el, "elevator muscle"; pam, posterior adductor muscle; ppm, ventral and dorsal sets of the pedal protactor muscles; prm, ventral and dorsal sets of the posterior pedal retractor muscle. Scale bar = 1 cm.

Alimentary Canal: The stomach and style sac in *A. deflorata* follow the general psammobiid pattern described by Purchon (1960), Narchi (1980), Domaneschi (1992), and Narchi & Domaneschi (1993), whereas the intestine parallels only that of *A. violascens*, in which the hind gut dilates to store faeces (Purchon, 1960; Narchi, 1980).

The general configuration of the alimentary canal of *A. deflorata* is shown in Figures 13 and 14. The main difference distinguishing it from *A. violascens* lies in the hind gut, as shown in Table 2. The measurements provided below were taken from a transversely sectioned, 1.5 cm-long specimen; dimensions and total numbers of faecal pellets were taken from a 5.2 cm-long specimen.

Essentially the intestine comprises two coiled sections. The first section (mg) lies posterior and adjacent to the distal half of the style sac and is separated from this by gonad follicles, digestive diverticula, and a number of cross strands of muscle fibers. Its external diameter is almost uniform and very reduced (500 µm in average), with a 36 µm-thick wall, the 25 µm-tall columnar epithelium richly provided with 16 µm-long cilia. A feeble layer of circular, muscular fibers is present around the mid gut walls. The cilia cause rotation and relocation of material coming from the stomach and wrap it in a viscous mass. Muscular fibers may be responsible for peristalsis that contributes to compacting, molding and relocating discarded material. This way faecal pellets are completely formed within the mid gut. Faecal pellets are similar in appearance to the contents within the appendix, described below in the stomach section; however, they gather a larger number of inorganic particles that include whitish, hard corpuscles and small quantity of non-identified organic debris and microorganisms. Most sponge spicules and diatom fragments were not affected when the contents of the appendix of the stomach, and faecal pellets were submitted to weak acid solution (HCl); however, the whitish hard fragments dissolved

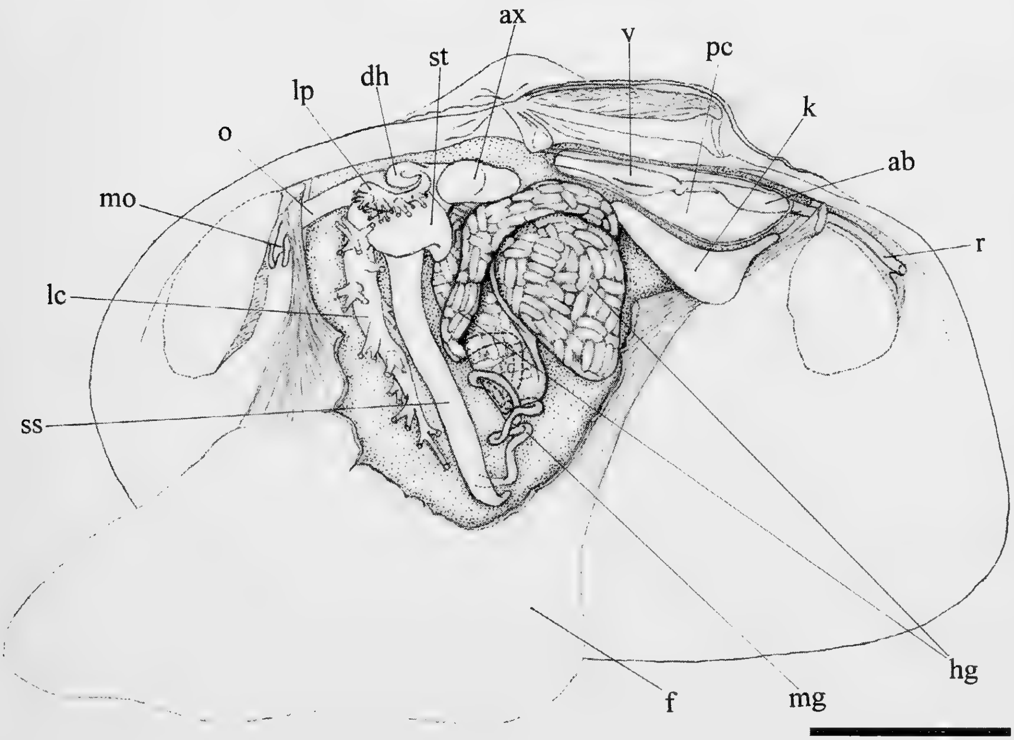

FIG. 13. *Asaphis deflorata*. Configuration of the alimentary canal and part of the excretory and circulatory systems, as seen from the left side. Abbreviations: ab, aortic bulb; ax, appendix; dh, dorsal hood; f, foot; hg, hind gut; k, kidney; lc, left caecum; lp, left pouch; mg, mid gut; mo, mouth; o, esophagus; pc, pericardial cavity; r, rectum; ss, style-sac; st, stomach; v, ventricle. Scale bar = 1 cm.

completely, revealing their calcareous composition.

Midway to the stomach (st), the mid gut portion ends and the intestine dilates to form its second coiled section, the hind gut (hg), dorsally placed. This second section is more extensive, more expanded and more intricately coiled throughout its extension (Fig. 13); its walls comprise a 5.5 µm-thick epithelium surrounded by an either equal or thinner layer of circular, muscular fibers, which allow widening/narrowing of the hind gut diameter. Cilia could not be detected in histological sections of the hind gut. The section walls are so thin and so closely applied together that the examination and tracking of the hind gut course was extremely difficult. Polarized light allowed confirmation of the presence of muscular fibers surrounding the alimentary canal.

The hind gut accumulates small, very regular, rod-shaped faecal pellets. From its proximal end (Fig. 13) the hind gut extends dorsal- and backward to the floor of the pericardial cavity (pc). From here it passes downward to the right side of the animal (Fig. 14), spirals both in a tight and clockwise way, increasing to its maximum width of 6.6 mm, that is, about 14 times wider than the mid gut (Fig. 13). This enormous swelling extends ventrally, where it reduces in diameter and turns abruptly both forward and dorsalward (Fig. 14) passing to the posterior right side of the appendix (ax) of the stomach. Here it returns to a narrow external diameter (~ 250 µm, empty condition; lining epithelium deeply folded), penetrates the pericardium (pc) and terminates in the anal papillae on the posterodorsal face of the posterior adductor muscle. The epithelial cells lining this very rear portion of the intestine are 8–10 µm in height and densely ciliated (cilia 8.3 µm long). Similar to the esophagus, this portion has a deep folded epithelium, surrounded by a thick fibrous-like layer, which includes circular muscular fibers; the muscular layer is thicker around the esophagus.

Approximately 650 faecal pellets, with a most frequent length of 1.5 mm (range: 0.5–2.5 mm) were recovered from a 5.2 cm-long specimen.

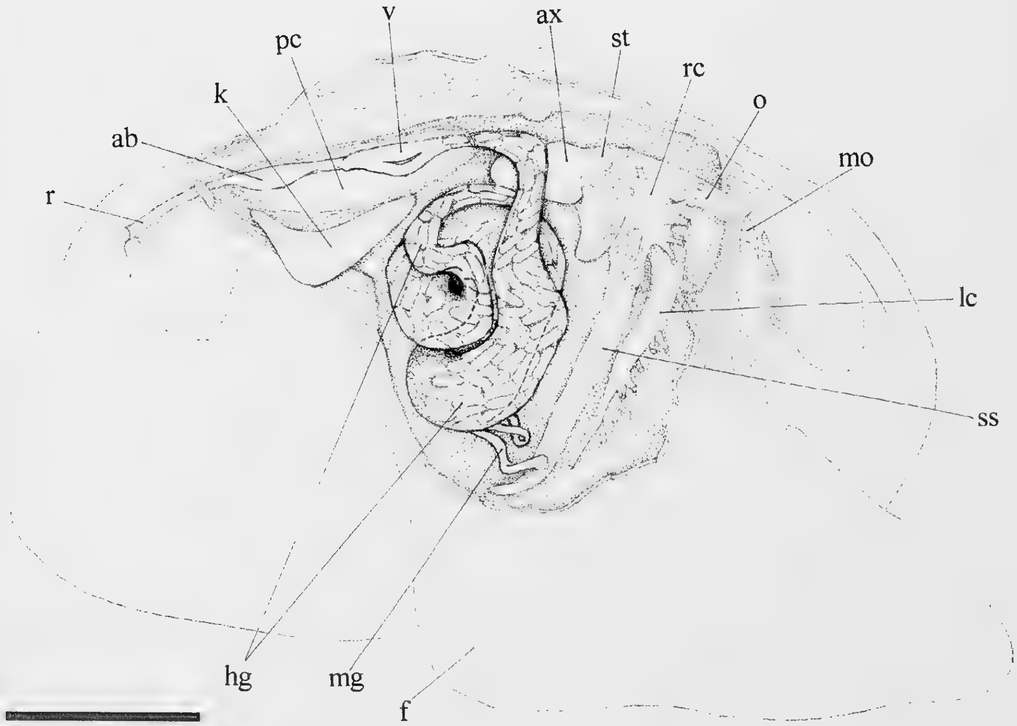

FIG. 14. *Asaphis deflorata*. Configuration of the alimentary canal and part of the excretory and circulatory systems, as seen from the right side. Abbreviations: rc, right caecum. For other lettering, see Fig. 13. Scale bar = 1 cm.

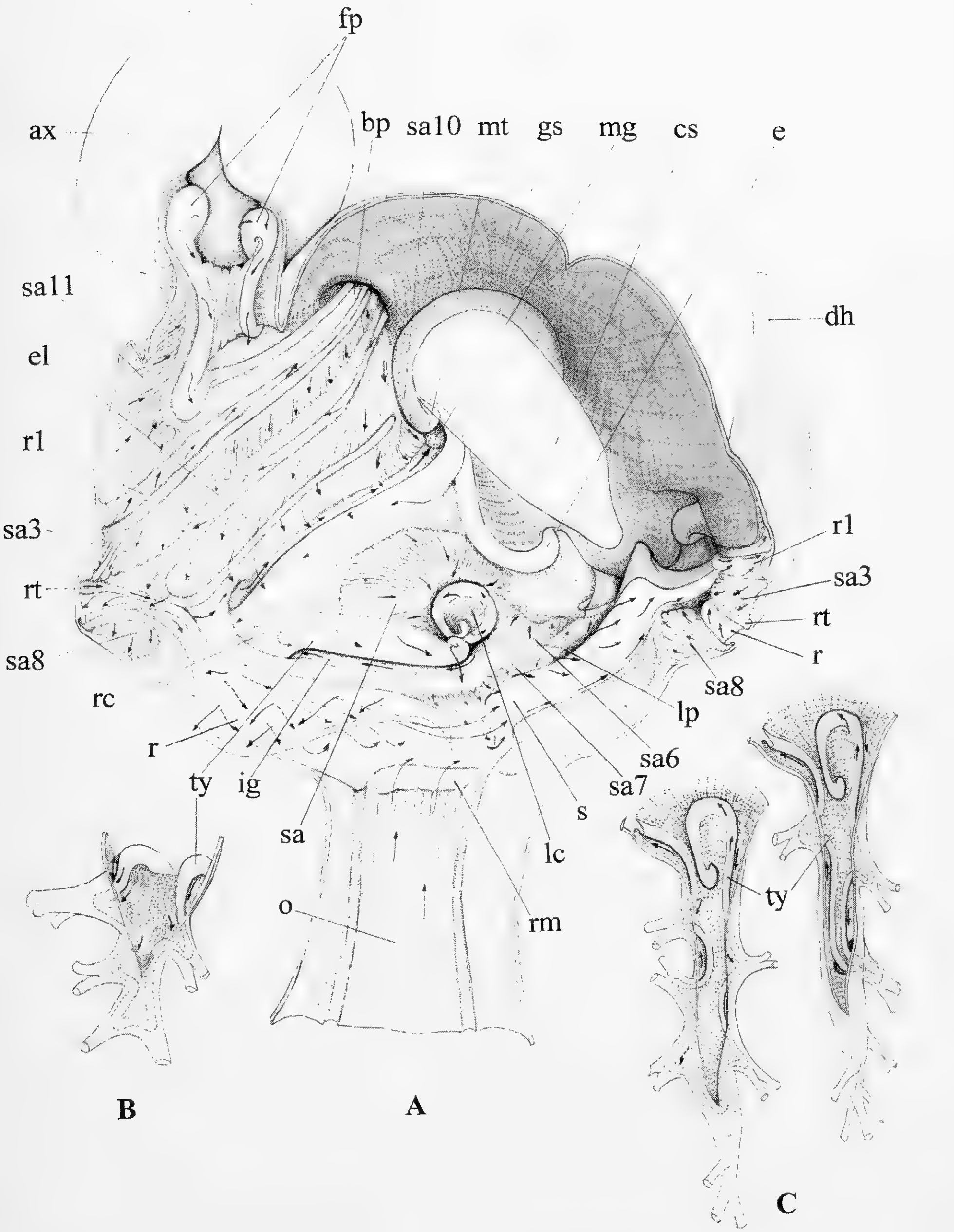

FIG. 15. *Asaphis deflorata*. A. Interior of the stomach after being opened by a longitudinal incision in the dorsal wall. B, C. Internal anatomies of the right and left caeca, respectively. C. anatomical differences found in two different specimens. Abbreviations: ax, appendix; bp, blind pocket; cs, crystalline style; dh, dorsal hood; e, semi-circular elevation on floor of the stomach; el, long forwardly projecting elevation; fp, fleshy pads within the appendix; gs, gastric shield; ig, intestinal groove; lc, left caecum; lp, left pouch; mg, mid gut opening; mt, minor typhlosole; o, esophagus; r, broad fold passing from the anterior floor of the stomach to the interior of the dorsal hood; r1, ridge passing from the posteroventral blind pocket to the interior of the dorsal hood; rc, right caecum; rm, rim to the esophageal orifice; rt, rejection tract; s, swelling on the left anterior wall of the stomach; sa, sa3, sa6, sa7, sa8, sa10, sa11, sorting areas; ty, major typhlosole.

Arranged end to end, all these pellets would perform a beaded, 98 cm-long thread (650 x 1.5 mm).

Stomach: The morphology and functioning of the stomach of *A. deflorata* (Fig. 15) are so similar to those described in details by Purchon (1960) and Narchi (1980) for *A. violascens* that a complete description of the stomach of the former species is here assumed to be unessential. Table 2 shows the main differences between the organs in both species. Apart from those differences, the following aspects of the morphology and functioning of the stomach of *A. deflorata* deserve mention:

- The semi-circular elevation (e) [= shortest branch of the major typhlosole (ty)] borders a shallow, supporting gutter for the rotating crystalline style (cs); the gastric shield (gs) protects this gutter against abrasive materials adhering to the style.
- Entering the right caecum (rc), the longest branch of the major typhlosole sends flares into the openings of five ducts coming from the digestive diverticula; entering the left caecum (lc), it sends flares into the mouth of the largest of such ducts only.
- The left caecum does not receive a constant number of ducts coming from the digestive diverticula in different specimens (Fig. 15C).
- Freshly incised stomachs show that the fold "r" prolongs backward the gutter formed by the floor of the esophagus. The free edges of this fold touch both the crystalline style and the semi-circular branch of the major typhlosole, posteriorly, and a low, broad swelling (s) on the anterior left wall of the stomach. The fold "r" isolates ventrally the entrances of both right and left caeca, the entrance of the left pouch and the transverse section of the intestinal groove, as observed by Purchon (1960) in *A. violascens*. So strategically positioned, the fold "r" favors material entering the esophagus to be caught by the rotating style and mixed with the disintegrating, gelatinous tip of the latter. Thence, material is passed into the dorsal hood (dh),

TABLE 2. Analysis of morphological variation in the alimentary canal of *Asaphis deflorata* [our data] and *A. violascens* [Purchon's (1960 *P*) and Narchi's (1980 *N*) data]; r, fold; sa, sorting area on the inner wall of the stomach.

	A. deflorata	*A. violascens*
Hind gut	widens progressively as it coils and spirals in a tight way throughout its extension; turns to a narrow diameter only within the heart	(*P*) (*N*) extraordinarily ballooned in its proximal end, where mid gut enters dorsally and a narrow, non-coiled hind gut leaves ventrally
Stomach		
"r"	present; passes deep into the dorsal hood	(*P*) (*N*) present; does not enter the dorsal hood
"r1"	present; lying posterior to and throughout the extension of the long sorting area "sa3"	(*P*) described and depicted a similar fold shorter than "sa3"; didn't name it (*N*) just depicted it throughout the extension of "sa3"
"sa7"	present; extending from below the esophagus opening deep into the left pouch	(*P*) (*N*) present; just below the esophagus opening
"sa8"	present; at the stomach roof and anterior wall of the dorsal hood	(*P*) (*N*) neither described nor depicted it
"sa11"	present; a single sorting area	(*P*) (*N*) present; two sorting areas
Appendix	outward ciliary currents present on its fleshy pads	(*P*) (*N*) no outward ciliary currents are present
Left pouch	sorting areas present (sa6, sa7)	Sorting areas present [sa6 (*P*) (*N*)]; two others unnamed (*P*)
Blind pouch	present; a wide cone-shaped depression on the stomach floor	(*P*) (*N*) did not refer to it

following storage of excess material in the appendix (ax). Another important role of the fold "r" is to prevent material entering from the esophagus to be caught earlier by cilia on the intestinal groove.

- The full packed appendix equals the volume of the main cavity of the stomach. A thick, gelatinous mass constitutes the bulk of material often present within this pocket. Lots of amorphous greenish-brown debris and minute, white, mineral corpuscles, many sponge microspicules and broken megascleres, some algae debris, diatoms, a few foraminiferans and unidentified microorganisms and eggs were the most frequent material entangled in a such viscous mass. Outward ciliary currents are present on the two fleshy pads (fp) that protects the appendix entrance and neck respectively. Such currents are not vigorous enough to deal with (remove) the bulk of material and the viscous mass stored in the appendix. Contractions of the appendix walls, as well as of the closest intrinsic, transverse musculature of the visceral portion of the foot probably play an important role in such emptying process. Purchon (1960) stated that the contents of the appendix of *A. violascens* are possibly discharged into the stomach by muscular contraction of its walls.
- The sorting areas sa10 and sa11 are ill-defined and the least conspicuous within the stomach. The same is true for sa7, in its portion below the esophagus only. Only careful analyses of several live and preserved specimens allowed confirmation of their presence in the stomach of *A. deflorata*.

Organs of the Pericardium: The heart lies at the level of the shell ligament (Figs. 13, 14). This organ comprises a ventricle (v) penetrated by the rear end of the hind gut, and a pair of auricles. The posterior aorta dilates just after its emergence from the ventricle to form the aortic bulb (ab), the latter as long as the ventricle (0.1 of the shell length). From the pericardium arise a pair of reno-pericardial apertures which drain primary urine into a pair of kidneys (k) located between the posterior retractor pedal muscles and the floor of the pericardium. The kidneys open into the suprabranchial chamber at the summit of minute papillae, between the ctenidial axis and the line of attachment of the ascending lamella of the inner demibranch to the visceral mass. Close and ventral to the renal apertures are the slit-like gonopores.

DISCUSSION

In considering the Atlantic and the Pacific specimens of *Asaphis* to be conspecific, Abbott (1950) pointed out that, when or if differences can be demonstrated between them, it would be wise perhaps to retain the name *A. deflorata* Linné, 1758, for the western Atlantic specimens and apply *A. violascens* (Forsskål, 1775) to the Pacific ones. Willan (1993) considered that the Atlantic and Pacific *Asaphis* share a common ancestor from which divergence occurred relatively recently. Lacking anatomical studies on the Atlantic specimens has restricted separation between them exclusively on the basis of shell sculpture.

The analysis of *Asaphis* from the "The Horseshoe" site population, West Summerland Key, Florida, USA, has shown that, in addition to shell sculpture, as predicted by Prashad (1932) and Willan (1993), the western Atlantic *Asaphis* also has ecological and morphofunctional characters that distinguish it from its Indo-West Pacific, close relative.

Such a population at the "The Horseshoe" site is restrict to the intertidal region, where it lives buried at moderate depths (0–12 cm) and densely aggregated in gravelly sand, cobble covered environments in the high intertidal zone. The species constitutes the sole bivalve present in the upper shore; no specimen was found subtidally. These characteristics are consistent with previous reports of this Atlantic species (Stanley, 1970; Berg & Alatalo, 1985). In contrast, populations of *A. violascens* in Hong Kong and Indonesia share the intertidal region both horizontally (Narchi, 1980; Britton, 1985; Depledge, 1985) and vertically (Soemodihardjo & Matsukuma, 1989*)* with other bivalve species, and may be found in sandy environments. Most specimens of *A. violascens* occupy an intermediate intertidal, or even subtidal position (Narchi, 1980; Soemodihardjo & Matsukuma, 1989; Willan, 1993) and are found more deeply buried than specimens of other bivalve species, at an average depth of 20 cm (Narchi, 1980; Soemodihardjo & Matsukuma, 1989).

Zonation patterns in intertidal bivalves have been attributed to differences in physiological tolerances to desiccation, salinity and heat stress (Britton, 1985; Depledge, 1985, and citations there). Because *A. deflorata* and *A. violascens* have different horizontal distributions, they likely have different physiological tolerances. The responses of *A. violascens* to temperature, salinity and desiccation have been assessed (Briton, 1985; Depledge, 1985), but similar experiments have not been conducted on *A. deflorata*.

When found in gravelly sand or cobble covered substrata, both *A. deflorata* and *A. violascens* are densely aggregated (Stanley, 1970; Britton, 1985; Berg & Alatalo, 1985; Kurihara et al., 2000, 2001; our data). *Asaphis violascens* collected from sandy beaches, or beaches either with reduced cobble coverage or increasing deposition of sand were drastically lower in density (Soemodihardjo & Matsukuma, 1989; Kurihara et al., 2001). Willan (1993) observed that *A. violascens* is strictly intertidal and inhabits the lower shore where it prefers muddy sand substrata with incorporated gravel or coral rubble; uniform muddy or sandy substrata appear inimical to habitation. Stanley (1970) reported a casual observation of *Asaphis deflorata* in Bermudan sand flats; Berg & Alatalo (1985) could not confirm such behavior for the species population living in the Bahamas beaches. These studies suggest *Asaphis deflorata* is more strongly adapted to a coarse gravelly, cobble-covered sediment than is *A. violascens*.

The presence of live, unburied specimens of *A. deflorata* lying by the high tide mark suggests that the "The Horseshoe" site population faced recent, natural disturbance of the sediment and/or that specimens are able to move out spontaneously. Berg & Alatalo (1985) have never found live individuals lying on the substratum surface in the field and considered this indicative of little natural disturbance in the sediment.

In the laboratory, a few specimens moved in and up within the coarse-sand substratum, this being free from natural obstacles such as pebbles, shells and rocks. Berg & Alatalo (1985) observed that the species can move in and out in disturbed substratum, such as in and around the tag-recapture plots in the field, but have difficulty penetrating the natural, undisturbed, coarse gravel nearby.

The large number of dead shells of *A. deflorata* retained in their life position in station 2, and their scarce presence in stations 3 and 4 (present work) may indicate that mortality in station 2 occurred either from senescence, or possibly from recent, catastrophic modification of the substratum along the low tide water, leading to suffocation or starvation of the trapped animals. Future field investigation on the life cycle of *A. deflorata* inhabiting Florida Keys are necessary to distinguish between these alternatives.

Catastrophic, long-term burial by sand is thought to kill entire local populations of *A. deflorata* (Stanley, 1970). Berg & Alatalo (1985) identified size-independent mortality caused by movements of sand over the habitat of *A. deflorata* in the Bahamas beaches. Long-term burial by a thick layer of sand makes it difficult for clams wedged among pebbles to move to the surface (Berg & Alatalo, 1985).

Although restricted to two days of field work, during a 12-day workshop period, our quantitative data on the "The Horseshoe" site population of *Asaphis* provided reliable results, as they fit well with previous ecological and biological data of Berg & Alatalo (1985) on *A. deflorata* population in the Bahamas. Compared with those data obtained from January 1981 through January 1983 by Berg & Alatalo (1985) on the Bahamas population, our data reveal that both have very similar life history characteristics, including growth rates and spawning times. The population structure in July 2002 of the "The Horseshoe" site is bimodal, as it is in the July population of the Bahamas (Berg & Alatalo, 1985), although the most frequently encountered size is smaller in the former. Size at maturity is similar for both populations, with maturation of the gonads occurring at approximately 24–25 mm in shell length, which corresponds to an age of 2–3 years (Berg & Alatalo, 1985). Gonad conditions at the "The Horseshoe" site in July were consistent with the July data from Berg and Alatalo (1985) and indicate that spawning was imminent.

Statistical analyses show that shell rib number and tendency to fork are good characters in distinguishing *A. deflorata* and *A. violascens*, supporting previous qualitative assessment (Prashad, 1932; Willan, 1993) of these shell characters. However, we found both species have considerably larger rib ranges than predicted, and that these ranges can overlap. Furthermore, the five outlier *A. violascens* specimens that nest within the *A. deflorata* specimens suggest that rib counts and indices may be better regarded as emergent properties of a population, not definitive characters of the individual. Further examination of the effects of environment and geography on rib number are warranted.

Distinguishing characters other than shell sculpture are: the presence of a discernible, rounded posterior radial ridge and posterior slope in the Atlantic *Asaphis* (our material), not discernible (Willan, 1993; IBUSP collection) in the Indo-West Pacific specimens, and a smooth inner surface in the Atlantic *Asaphis*, contrasting with the well-marked, ridged inner surface in specimens from Hong Kong (IBUSP collection). The effects of the environment and geography on these characters also deserve further examination.

Asaphis deflorata is a native species that has been periodically collected in southern Florida and the Florida Keys for over 100 years. *Asaphis deflorata* should be commonly encountered in the Florida Keys because suitable environmental condition occur, including gravelly sand, cobble rich intertidal habitat. The two-week planktonic larval period (Berg & Alatalo, 1985) should provide ample time for dispersal. Dispersal routes are dependent on local current regimes. Overall, current patterns in the Florida Keys move from Florida Bay, through the Keys and then join a southwesterly countercurrent flow (http://oceanexplorer.noaa.gov, accessed 14 January 2003). These patterns suggest that northern populations could serve as a source of larvae to populate more southerly areas.

Prior to the mid 1970s, *A. deflorata* was commonly collected from Key West to Key Biscayne (Miami), and possibly included the Dry Tortugas (FLMNH 16919, collected in 1937). Many pre-1975 collection records suggest Key Biscayne had a robust population of adult *A. deflorata* specimens. Our search did not find any post-1975 records attributed to Key Biscayne. Although the lack of museum records does not prove *Asaphis* is not present in the field, the combination of no records and a single population found after extensive sampling of the molluscan fauna in the Florida Keys (P. Mikkelsen, pers. commun.) suggests the distribution of *A. deflorata* has diminished greatly. Although our data are preliminary, they point to a drastic decline in the distribution of *Asaphis* populations in the Florida Keys. Why the persistent "The Horseshoe" population does not act as a source population requires further investigation. The two-week larval stage of *Asaphis* should provide ample time for distribution to more southerly locations. However, if the spawning season does not coincide with sufficiently strong and appropriately oriented currents, the larvae may never be moved outside the confines of the sheltered "The Horseshoe" site. Because appropriate substrata and quiet waters are found throughout the Keys, this physical barrier is the most likely explanation for the lack of additional southerly populations. Future studies on the distribution of *Asaphis deflorata* should incorporate a systematic examination of the summertime current regime around the "The Horseshoe" site.

The functional morphology of the Atlantic *Asaphis* is very similar to that of the Indo-West Pacific species as described by Narchi (1980). The correct identification of both species based upon the tissues requires the analysis of the alimentary canal. Great similarities support Willan's (1993) opinion that both species share a common ancestor from which morphological and ecological divergence has occurred relatively recently. The most striking anatomical difference lies in the hind gut configuration: progressively widening, and intricately coiled and spiraled throughout its extension in the Atlantic *Asaphis* (our data); extraordinary ballooning of its proximal end only, where the mid gut enters dorsally and a narrow, noncoiled hind gut leaves ventrally, in the Indo-West Pacific specimens (Purchon, 1960; Narchi, 1980).

The long, wide, coiled hind gut of *A. deflorata* and the dilation of that of *A. violascens* are both devices for retention of large amount of faecal pellets. It is difficult to understand how the compacted, randomly positioned faecal pellets are relocated from a wide compartment toward a narrow one, which is even more restricted in its passage through the ventricle. Peristalsis of the hind gut walls and the transverse musculature within the visceral portion of the foot may be the mechanism to achieve relocation of such compacted, rod-shaped faecal pellets. Expansion/contraction of the ventricle, peristalsis, and ciliary action of the very rear sector of the intestine force faecal pellets oriented end-to-end or in small groups to be expelled.

Most specimens of *A. deflorata* examined for alimentary canal morphology had the hind gut packed with faeces, these always fully formed in their origin within the midgut. It is quite probable that faeces storage in *Asaphis* is not correlated with the necessity to consolidate faecal pellets as proposed by Yonge (1949) for deposit-feeding tellinoideans.

Comparing the gross morphology of *Abra profundorum* (Smith, 1885) (Tellinoidea) and that of north Atlantic species of the genus, Allen & Sanders (1966) found a clear correlation between gut length and volume, size of deposit-feeding bivalves and respective palps and ctenidia, and depth they inhabit. A reduction in thickness of the gut walls, an increase of the lumen diameter allowing faecal pellets to be randomly positioned, and the gut taking up an increasingly proportion of the body were correlated with depth by these authors. Allen & Sanders (1966) stated that among the species of *Abra* they compared, "the limit of evolution of the hind gut is reached in *A. profundorum* where many of the adjoining walls of the coiled gut are lost and much of the posterior half of the body above the muscles of the foot becomes a sac containing faeces".

Asaphis deflorata inhabits shallow waters and preferentially the upper shore; nevertheless, this species shares most of the morphological features of the gut referred to by Allen & Sanders (1966) for tellinoideans inhabiting deep waters, except for a loss of walls where the coils and spiral are tightly applied to each other.

Asaphis deflorata has a long intestine, compared with the suspension-feeding psammobiid *Heterodonax bimaculatus* from intertidal, coarse sand (Narchi & Domaneschi, 1993), and only moderately long compared to *Gari solida* from subtidal coarse sand substrata (Domaneschi, 1992). The exceedingly large palps, the presence of simple, digitiform tentacles around the inhalant aperture, but especially the enormous amount of faecal pellets retained within the hind gut suggest that the species deals with and ingests large amounts of material entering via the inhalant siphon. *Asaphis deflorata* shares most of the morpho-functional features considered by Pohlo (1982) to be characteristic of typical suspension feeding tellinoideans: large gills, no waste canal, outer demibranch not upturned, marginal food groove present, animal lying in a vertical position within the sediment and the inhalant siphon does not take deposited material actively. Once extruded into the water column this siphon in *A. deflorata* is kept passively, much the same as in the suspension-feeders tellinoideans studied by Yonge (1949), Pohlo (1972), Domaneschi (1992, 1995). However, its non-straining, curled inward tentacles may allow entrance of large amount of suspended material brought by the rising and falling tides, as well as of dense material lifted from the bottom. Living in the constraint of a cobble-covered sediment, the inhalant aperture more often is flush with, or slightly below the sediment surface. It contributes to the intake of dense, mineral particles, benthonic microorganisms and organic and inorganic debris deposited either outside around the aperture of, or lining the passage of the inhalant siphon through the substratum. Such behavior supports Berg & Alatalo's (1985) statement that *A. deflorata* is a suspension and facultative deposit feeder. Phytoplankton and C_3 plants detritus constitute most of its diet (Berg & Alatalo, 1985).

Like *A. violascens* (Narchi, 1980), *Gari solida* (Domaneschi, 1992), and other Tellinoidea (Pohlo, 1982; Domaneschi, 1995), *A. deflorata* shares a mosaic of morphological features with suspension and specialized deposit-feeding tellinoideans. Such a condition was considered to represent (Pohlo, 1982) an intermediate step in the evolution of the Tellinoidea, the primitive forms represented by early suspension-feeding species, and the most derived, represented by highly specialized, deposit-feeding species.

When present in the beach, *Asaphis deflorata* has been detected to be the only bivalve occupying the upper shore (Stanley, 1970; Berg & Alatalo, 1985; our data). The possession of a huge appendix in the stomach, and of a capacious hind gut allows storage of excess, ingested food and retention of an exceedingly large amount of faecal pellets, respectively. Both features are, probably, adaptations to upper shore life and non-selective feeding habit, as during high tides the species can make the most of the period of submersion, both to get rid of lots of faecal pellets and take into the mantle cavity a large amount of suspended and re-suspended material, processes and ingests it. *Asaphis* feeds only during the period of submergence by high tides and fasts the remainder of the time (Berg & Alatalo, 1985). The huge appendix provides room for the bulk of material entering the stomach and mixed with enzymes liberated by the dissolving head of the style. It also prevents blockage of the main cavity of the stomach, allowing its normal functioning as already proposed by Yonge (1949) for the appendix of other tellinoideans. The capacious hind gut allows retention of a corresponding great volume of material coming from the stomach and being molded into faecal pellets within the mid gut. Faeces have to be eliminated during submergence periods only, when the exhalant current of water takes them far away from the animal; conversely, during low tides the animal is at risk of faeces sedimentation within its own mantle cavity. Purchon (1960) considered the capacious stomach and intestine of *A. violascens* a device for retention of food and faecal material during low tides, as well as for survival when the habitat is covered with sand. Capacious stomach provided with an appendix structurally and functionally similar to the appendix of the tellinoidean bivalves is also shared by the Pholadidae, Xylophaginidae and Teredinidae (Pholadoidea) (Purchon, 1941, 1955), the appendix being exceedingly long and broad to store mainly wood particles in many teredinids (Lopes et al., 2000, and citations there). Purchon (1941, 1955) concluded from that similarities that these structure are homologous and provide reliable evidence of a relationship between these groups. Lopes et al. (2000) discussed the probable implications of the specialization of the appendix, as well as of the digestive system as a whole in the evolution of the xylophagous habit of two species of Teredinidae.

The presence of a thin-walled, huge hind gut suggests that the compacted mass of faecal pellets of *A. deflorata* cannot be promptly and completely eliminated. As retention is not related to the necessity to consolidate faecal pellets, it may be that another purpose is served by such an intriguing hind gut than to store, then eliminate faeces during convenient periods: for example, to allow enough time for the breakdown and consumption of material with a food value present in the faecal pellets; the enzymes required for this process could be the same as those present in the stomach and passed onto the intestine along with discarded material. Similar storage of faeces occurs in some teredinid bivalves (Lopes et al., 2000, and citations there). Long residence of faeces within the anal canal of *Neoteredo reynei* (Bartsch, 1920) was considered by Lopes et al. (2000) as a probable device allowing both enzymatic degradation of material of a food value and absorption to be continued; the presence of epithelial cells richly supplied with microvili, and the highly vascularized anal canal walls of the species giving support to this latter hypothesis.

Allen & Sanders (1966) detected the presence of large numbers of amoebocytes in the gut and surrounding the faecal pellets in *Abra profundorum*, "which would possibly indicate that the pellets provide a surface, upon which bacteria would thrive, attack and convert to a digestible form the carbon compounds indigestible to the mollusc." According to Allen & Sanders (1966), "Newell (1965) has shown that faecal pellets of both *Hydrobia* (gastropod) and *Macoma* (tellinoidean bivalve) are excellent substrates for bacteria", and "that the nitrogenous compounds built up by the growth of the bacteria can be digested by the mollusc".

Neither amoebocytes nor bacteria could be identified within the hind gut of *A. deflorata* through the methodology adopted in histological preparations. This cannot be taken as a definitive result, nor the hypotheses of the presence of amoebocytes and of a possible relationship of the species with symbiotic bacteria can be discarded. Morphological and functional similarities between the gut of this psammobiid and of *A. profundorum* address those hypotheses. Appropriate methodologies were not employed to test the occurrence of such living elements in the gut of *A. deflorata*, as this was not the aim of the present work. The significance of pellet storage and the hypothesis that digestion and absorption of nutrients continue within the hind gut of *A. deflorata* via endogenous enzymes and/or symbiosis remain to be elucidated; it cannot be fully explained until further experimental examination with live specimens has been carried out.

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EXTRAORDINARY FLEXIBLE SHELL SCULPTURE: THE STRUCTURE AND FORMATION OF CALCIFIED PERIOSTRACAL LAMELLAE IN *LUCINA PENSYLVANICA* (BIVALVIA: LUCINIDAE)

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ABSTRACT

The lucinid bivalve *Lucina pensylvanica* possesses an unusual flexible commarginal shell sculpture formed from calcified periostracal lamellae. The lamellae comprise thick, recurved, periostracal extensions with distal calcified scales. The periostracum is also densely embedded with calcareous granules around 2.0–2.5 µm in diameter and a thin (10 µm) layer of prismatic aragonite covers the ventral face of each lamella. Other species of *Lucina* in the western Atlantic possess calcified scales but with different morphologies and the continuous commarginal ridges of the eastern Atlantic *Lucina adansoni* and other African species are similarly constructed and homologous. The periostracal lamellae are a probable apomorphy of the genus *Lucina* and morphology of the calcified structures provides a set of systematic characters of importance in the discrimination of species.

Key words: *Lucina pensylvanica*, periostracum, calcification, shell growth, systematics.

INTRODUCTION

Lucina pensylvanica (Linnaeus, 1758) is one of ten species of chemosymbiotic lucinid bivalves inhabiting intertidal and shallow subtidal habitats in the middle Florida Keys. Remarkably, the shell sculpture consists of closely spaced commarginal lamellae, faced with triangular, calcareous scales that are slightly flexible in live animals. The scales and lamellae become brittle after death and in beach-collected shells the surface is white, relatively smooth with low, thin, commarginal ridges, sometimes with traces of periostracum. Our initial observations suggested that both lamellae and scales were a form of periostracal or extra-periostracal calcification, distinct from the normal shell. Because of the rarity of periostracal calcification in bivalves in general and the probable apomorphy of this character for *Lucina* spp., we decided to investigate the structure and formation of the lamellae in more detail and, if possible, determine the periodicity of their secretion. Additionally, we wanted to compare the form of the periostracal lamellae between *Lucina* species, both to establish the homology of these as well as investigate their possible use as systematic characters. Detailed understanding of lamellar formation may also suggest hypotheses about their possible function.

Periostracal and extraperiostracal calcification is an unusual feature of bivalves but has been described in different forms from a variety of families. Usually in Lucinidae the periostracum is relatively thin (Harper, 1997), although exceptionally the genus *Rasta* has a dense, shaggy periostracum extended into numerous long pipes (Taylor & Glover, 1997). Prominent, sculpture-forming calcified periostracum appears restricted to the genus *Lucina*, of which *L. pensylvanica* is the type species (ICZN, 1977). The morphology of the calcified scales has been used by Gibson-Smith & Gibson-Smith (1982) as a character to divide "*Lucina pensylvanica*" of the western Atlantic into four separate species. Amongst other bivalve families, Veneridae, such as *Lioconcha* and *Callocardia* possess encrustations formed of fine aragonitic needles projecting through the periostracum (Ohno, 1996; Morton 2000); others such as *Granicorium* and *Samarangia* secrete extra-

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periostracal calcareous cements to form a crust of sediment on the shell (Taylor et al., 1999; Braithwaite et al., 2000). Many Anomalodesmata, such as *Laternula* and *Lyonsia*, possess spines formed within the periostracum as do some Gastrochaenidae, such as *Spengleria rostrata* (Spengler) (Carter & Aller, 1975). Amongst the Mytilidae, intraperiostracal aragonitic granules and projecting spikes have been described in *Trichomya* and *Brachidontes* (Carter & Aller, 1975; Bottjer & Carter, 1980; Carter et al., 1990), while intra- and extraperiostracal calcified structures are a feature of various species of Lithophaginae (Carter et al., 1990).

Little is known of biology of *Lucina pensylvanica*. Stanley (1970) demonstrated using x-rays that animals burrowed with the anterior part of the shell lying uppermost in the sediment, an unusual life orientation for Lucinidae. The general anatomy was described by Allen (1958) and Gros et al. (1996) made a detailed description of the gill ultrastructure and chemosymbiotic bacteria. Additionally, Taylor & Glover (2000) illustrated the large bipectinate mantle gills that lie alongside the pallial blood vessel.

Lucina pensylvanica and its close allies are often referred to in the literature under the generic name *Linga*. However, the name should correctly be *Lucina* as *Lucina pensylvanica* was designated the type species of the genus in 1977 (ICZN, 1977).

MATERIALS AND METHODS

Lucina pensylvanica was live collected from a number of oceanside intertidal and shallow water sites in the Florida Keys during the International Marine Bivalve Workshop (IMBW) in 2002 (Mikkelsen & Bieler, 2004, fig. 1 – map). Live animals were abundant only at Station IMBW-FK-642, mile marker 74.5 (24°51.4’N, 80°43.7’W) on Lower Matecumbe Key. Here they occurred in low intertidal to shallow, subtidal pockets of medium to coarse sand, located on a wide, coral-rock platform. The area was vegetated with patches of *Thalassia* and *Halodule*, as well as growths of *Penicillus* and *Halimeda*. Despite similar collecting effort, *Lucina pensylvanica* was much less common at other sites, such as Anne’s Beach, Upper Matecumbe Key (Station IMBW-FK-638) from *Thalassia*-covered sand and Pigeon Key (Station IMBW-FK-657) in a tidal stream with *Thalassia* and *Syringodium*. No live animals were found at any bayside stations. Animals were collected by extensive digging and hand sieving. Voucher specimens held in BMNH, London.

Live animals were fixed in 75% ethanol, 5% seawater formalin or Bouin’s fluid. Tissue samples were also fixed in 2.5% solution of glutaraldehyde in phosphate buffer. Sections of mantle were stained with Mallory’s triple. For optical microscopy of the shell, geological thin sections were made from fresh specimens embedded in resin. Pieces of the same embedded shell were also examined by scanning electron microscopy (SEM) after cutting, polishing and etching in EDTA.

Shell sections were also examined by confocal microscopy using a Leica SP NT in reflected light mode. Simultaneous images were collected at several different wavelengths, and a reference image was obtained with the transmitted light detector. We also carried out an initial test for autofluorescence using a wavelength (lambda) scan. The section was scanned at a single focal plane with each laser in turn. The detector was programmed to step through 25 pre-determined 10 nm-wide detection windows at wavelengths from 495–750 nm that produced an intensity profile for each emission wavelength. This optimised laser detector position and line. The best results were obtained with the 488 nm Argon laser and this was used for all subsequent imaging. No autofluorescence was detected from within the shell matrix, so the first detector window was set at 486–507 nm. This wavelength gave a direct reflection image of the sample and was false coloured in green. Strong autofluorescence from the periostracum was detected at around 550 nm, so the second detector window was set at 537–568 nm and the images coloured red. A stack of 30 images was collected at ~0.4 μm intervals. Each frame was scanned three times and run through a frame-averaging filter to reduce background noise. For single images, the z-axis (depth) data from the entire stack was combined and the brightest pixel from each point computed and displayed (maximum projection image).

Growth Periodicity

Twenty valves from live collected animals were used to study growth periodicity. We embedded these in MET20 resin (Struers Ltd), sectioned them transversely from the umbo to the ventral edge. They were then ground, polished and etched for 20 min in 0.01M HCl and acetate peel replicas prepared following Richardson (2001). Distances between successive periostracal lamellae were measured to the nearest 0.05 mm on 11 shells. Distinctive major lines in the outer and middle shell layers and in the umbonal region (Fig. 22) were correlated with the formation of closely spaced or uncalcified periostracal lamellae. Three separate observers used these major growth marks in both umbo and valve to estimate the age in years of the animal (Richardson, 1993). The major growth increments were treated as annual lines by comparison with a similar study of *Codakia orbicularis* from the Bahamas (Berg & Alatalo, 1984).

RESULTS

Shell Microstructure

The shell consists of three aragonitic layers. The outermost layer is composed of a prismatic layer of irregular acicular crystals, their long axes inclined towards the shell margin (irregular spherulitic structure of Carter & Clark, 1985). This is followed by a middle layer of finely lamellate, crossed-lamellar structure and, within the pallial myostracum comprising irregular prisms, there is an inner layer formed of complex crossed-lamellar structure, intercalated with thin prismatic sheets. This sequence of shell layers resembles most other Lucinidae (Taylor et al., 1973).

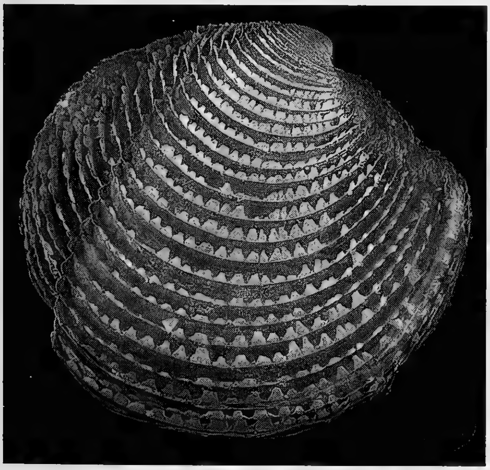


FIG. 1. *Lucina pensylvanica* exterior of right valve showing commarginal periostracal lamellae with projecting calcareous scales. Shell height = 22.8 mm. Station IMBW-FK-642, Mile Marker 74.5, 24°51.4'N, 80°43.7'W, on Lower Matecumbe Key.

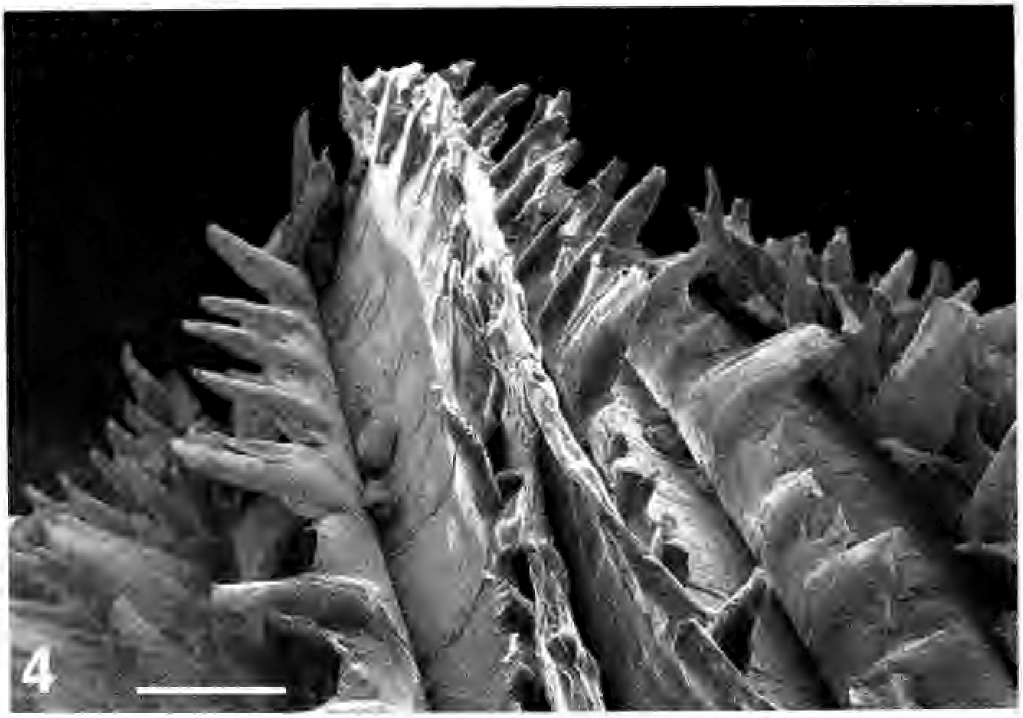
Calcified Periostracal Lamellae

Periostracal lamellae (hereafter referred to as lamellae) consist of an extended periostracum sheet faced with prominent calcified scales (Fig. 1). The lamellae recurve dorsally and are regularly spaced at intervals of 400–1500 μm, extending about 1,000 μm from the shell surface. Interspaces between the lamellae are relatively smooth (Figs. 2, 3) and in live collected specimens are packed with sediment grains (Figs. 8, 9). The discrete, closely-spaced calcareous scales (Fig. 8) are around 600–1,000 μm in height and seemingly embedded into the periostracum. In shape, the scales are triangular to lanceolate, broad at the base (varying between 500–950 μm) and taper distally. When newly formed, they are usually pointed at the tips (Fig. 4) but become truncated with wear. Scale shape varies around the shell; those on the posterior dorsal area are usually broader, more closely spaced and less recurved. Over most of the shell surface, lamellae recurve dorsally but when first formed they extend straight out from the shell margins, with the scales embedded in the sheet of periostracum (Fig. 4). Subsequently, lamellae become progressively recurved away from the commissure (Fig. 4), and the periostracum erodes away from the scales (Figs. 5, 6).

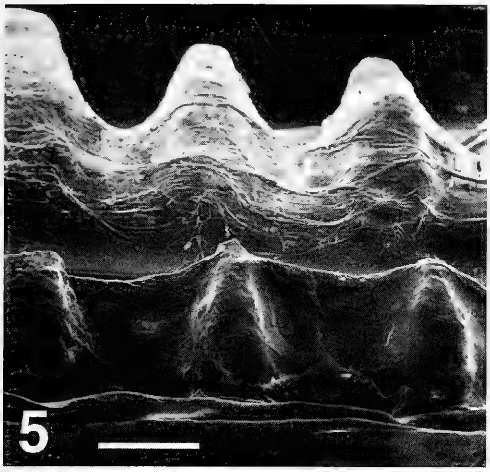
On juvenile shells, the scales are differently shaped (Fig. 7) being lower and quadrate with narrower spaces between, so that they form an almost continuous ridge. The quadrate scales change to a triangular shape at a shell height of around 4.5–5.0 mm.

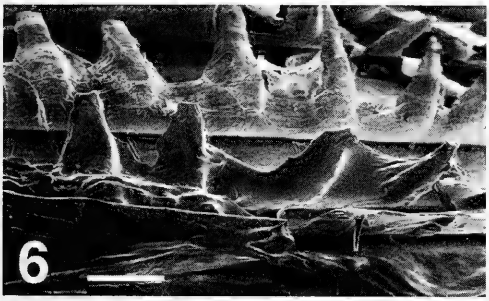
Sections

Optical, scanning and confocal microscopy shows that each lamella is composed of a periostracal extension in which the calcareous scales occupy the distal ventral face (Figs. 8–11). Each lamella projects from a thin ridge in the true shell (Figs. 8–10). Within a lamella the periostracum is about 55 μm thick and continuous with that of the outer shell surface. Between successive lamellae the periostracum gradually increases in thickness from around 1–2 μm at the termination of one extension to about 50 μm at the base of the succeeding extension (Fig. 12). Higher magnification of the calcareous scales reveals a



FIGS. 2–4. *Lucina pensylvanica*. FIG. 2: Surface view of successive commarginal lamellae with scales. Scale bar = 500 µm; FIG. 3: Periostracal lamellae on posterior of shell with pointed scales with smooth periostracal surface between lamellae. Scale bar = 500 µm; FIG. 4: Site of formation of periostracal lamellae at valve margins showing lamellae lying parallel with shell margin but becoming recurved dorsally away from the edge. Scale bar = 500 µm.





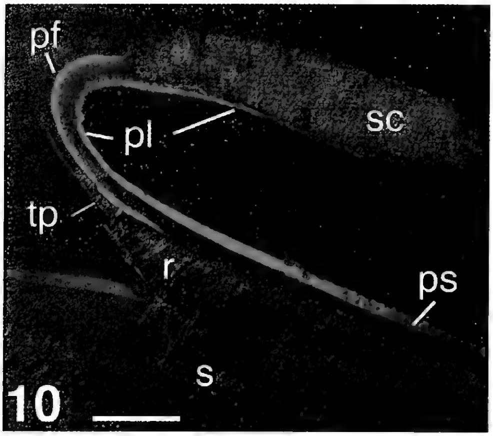
FIGS. 5, 6. *Lucina pensylvanica*. FIG. 5: Ventral view of forming lamella at shell margin showing row of scales embedded in periostracum stretched between them, but in the preceding row this has disappeared. Scale bar = 250 µm; FIG. 6: View of posterior shell margin with pointed scales joined by a membrane of periostracum. Scale bar = 250 µm.

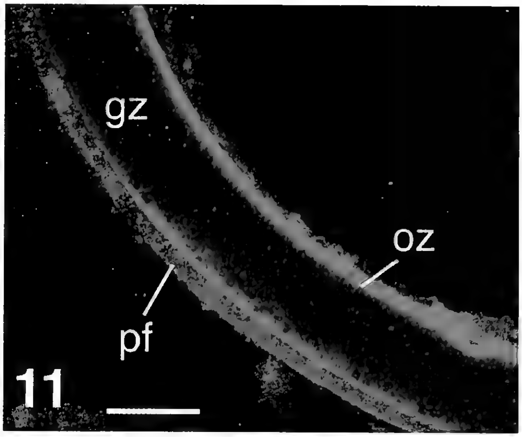
FIG. 7. *Lucina pensylvanica*, juvenile shell (shell height 3.5 mm) with lamellae formed of closely spaced, quadrate scales. Scale bar = 200 µm.

FIGS. 8, 9. *Lucina pensylvanica*. FIG. 8: Transverse section of shell showing two lamellae. Note ridges in shell and sediment trapped behind lamellae. Scale bar = 250 µm; FIG. 9: Transverse section of a single lamella. Scale bar = 250 µm.

thin (1.5–2.0 µm) initial periostracal sheet followed by a layer of aragonitic spherulitic microstructure (Fig. 14). Each scale is about 220 µm thick tapering distally. Within the spherulitic layer of the scale, interpenetrant bundles of long, thin crystals radiate from nucleation sites on the inner periostracal surface. Fine growth lines indicate that the scales are secreted incrementally. Another calcified layer (10–15 µm thick), of short, prismatic aragonite crystals embedded in periostracum, forms the ventral face of each completed lamella (Figs. 11, 13, 18).

Sections of the basal periostracal part of the lamella show that it is densely embedded with tiny calcareous granules about 2–2.5 µm in diameter consisting of aggregations of crystalline aragonite (Figs. 13, 16, 19). Granules are absent in the outermost of part of the periostracum but at about 10 µm from the edge of the lamella increase in abundance (Fig. 12).





FIGS. 10, 11. *Lucina pensylvanica*. FIG. 10: Confocal image of transverse section through a periostracal lamella. Periostracum red; calcified structures green. Scale bar = 100 µm. Abbreviations: pf, calcified prismatic front of lamella; pl, periostracum of lamella; ps, periostracum above shell; r, ridge in outer shell layer; s, shell; sc, scale; FIG. 11: Confocal image of the proximal region of a periostracal lamella, showing detail of the periostracum and the calcified front of the lamella. Scale bar = 50 µm. Abbreviations: as for Fig. 10; gz, granule zone; oz, outer granule-free periostracal zone.

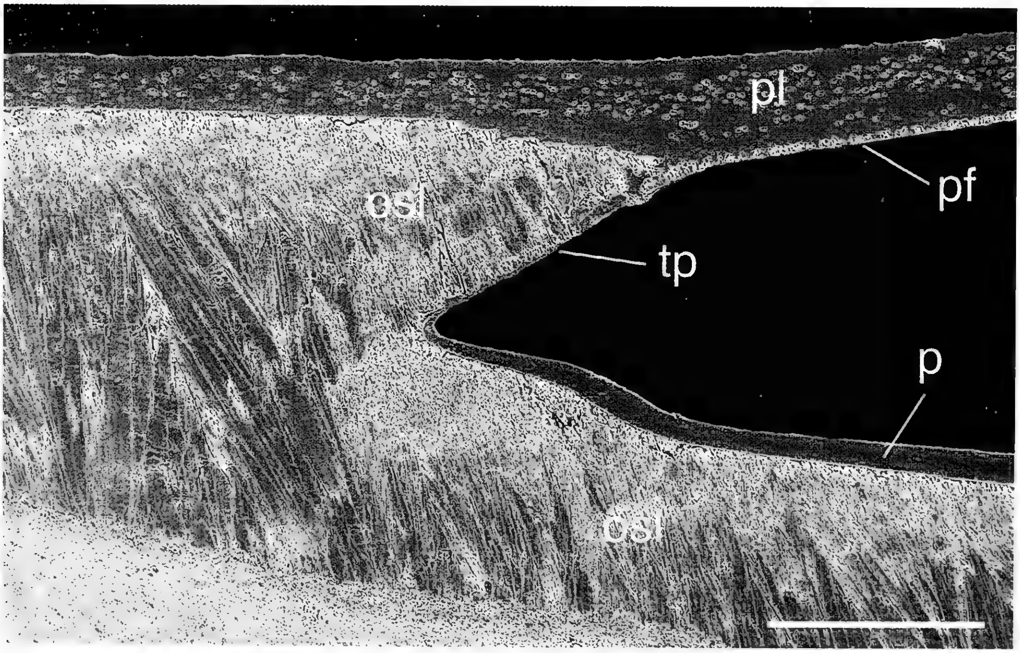
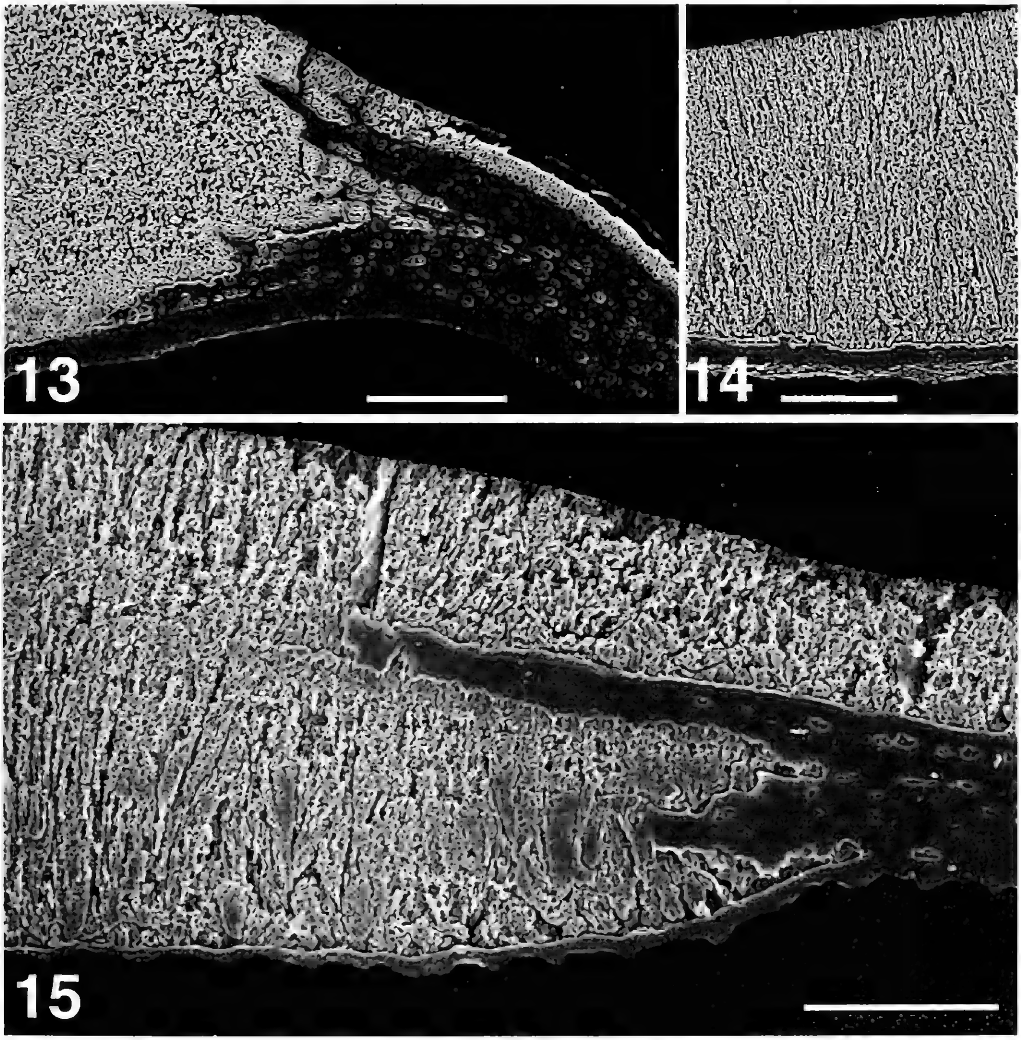


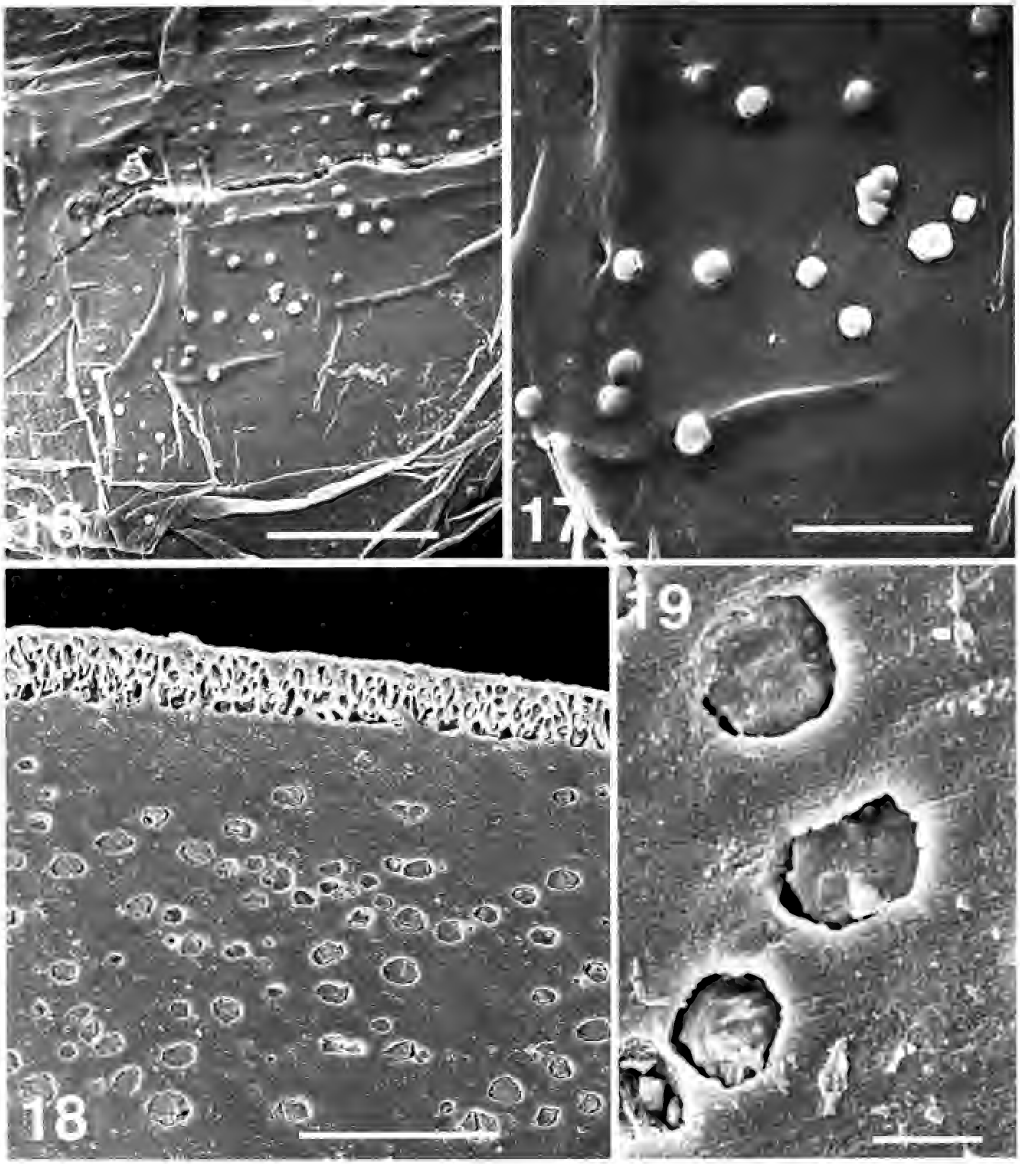
FIG. 12. *Lucina pensylvanica*, SEM image of transverse section through base of a lamella showing shell ridge and thinned periostracum that thickens towards the succeeding lamella. Scale bar = 100 µm. Abbreviations: osl, outer shell layer; p, periostracum; pf, prismatic front of lamella; pl, periostracum of lamella; tp, thin periostracum.

These granules are also present in the normal periostracum secreted above the outer shell layer and gradually increase in frequency between successive lamellae.

Sections of the junction between the calcareous scales and the periostracal lamella show that lines representing growth increments interdigitate from periostracum into the calcified scales and also that the granules increase in density and fuse at the transitional boundary (Figs. 13, 15). The calcified scales are thus secreted contemporaneously with the periostracal layers of the lamella and not laid down subsequent to it. Images clearly show a covering of periostracum eroding from the scale surfaces. We conclude from these observations that both the granules and scales are forms of periostracal calcification.



FIGS. 13-15. *Lucina pensylvanica*. FIG. 13: SEM image of a transverse section through junction between calcareous scale and proximal part of the lamella showing interdigitation of calcareous layer with periostracum and granules. Scale bar = 50 µm; FIG. 14: Section through a calcareous scale showing spherulitic crystal growth arising from thin periostracum layer below. Scale bar = 70 µm; FIG. 15: Section through junction of calcareous scale and periostracum showing continuity of growth increments from the calcified portion into the periostracum. Scale bar = 50 µm. Abbreviations: gz, granule zone of periostracum; p, periostracum; sp, spherulitic crystal growth.



FIGS. 16–19. *Lucina pensylvanica*. FIG. 16: Surface of a forming periostracal lamella at shell margin showing aragonitic granules embedded in surface. Scale bar = 50 µm; FIG.17: Higher magnification image of granules showing crystalline form. Scale bar = 15 µm; FIG.18: Section of periostracal lamella showing discrete aragonitic granules in periostracum and the fringe of prismatic aragonite crystals along the front of the lamella. Scale bar = 20 µm; FIG. 19: Detail of discrete granules embedded in periostracum. Scale bar = 2 µm.

Mantle Edge

The mantle edge of *L. pensylvanica* is thick and divided into several folds (Fig. 20). The large outer fold (of) is thrown into deep corrugations indicating the potential for considerable extension. Epithelial cells at the margin are tall, with nuclei located towards the midpoint, but decrease in height dorsally to the short, cuboidal cells of the general outer

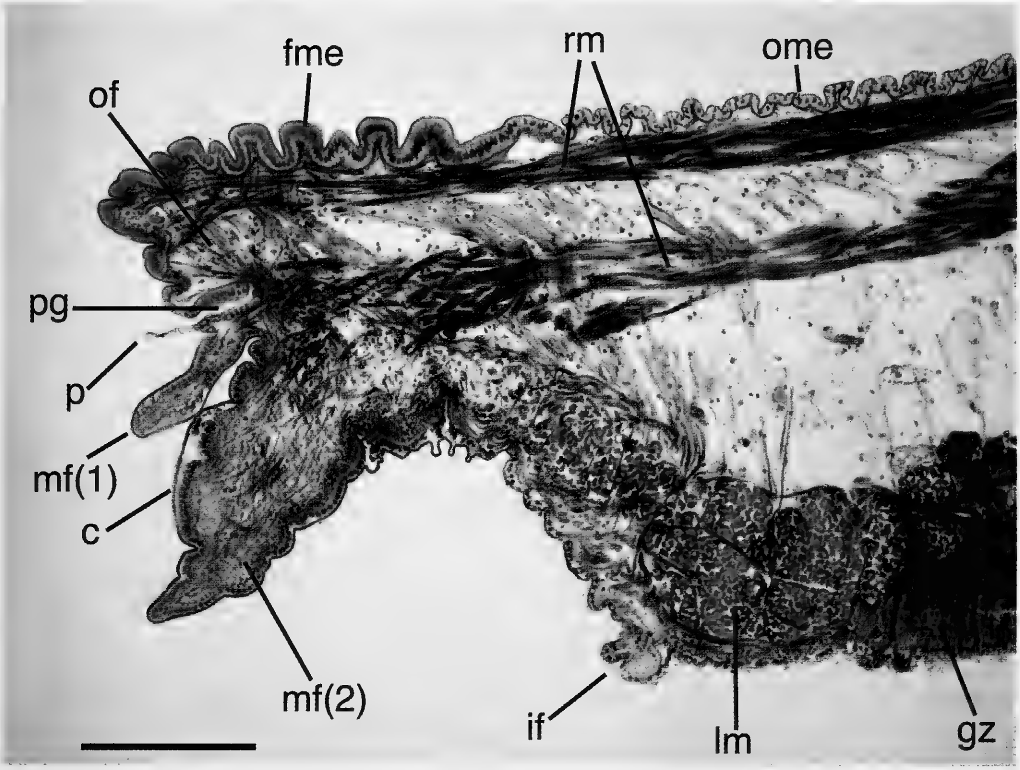


FIG. 20. *Lucina pensylvanica*. Transverse section of anterior mantle edge. Mallory's triple stain. Scale bar = 250 µm. Abbreviations: c, cuticle; fme, corrugated mantle epithelium of outer fold; gz, glandular zone; if, inner mantle fold; lm, longitudinal pallial muscles; mf(1) & mf(2), lobes of middle mantle fold; of, outer mantle fold; ome, outer mantle epithelium; p, periostracum; pg, periostracal groove; rm, radial pallial muscles.

mantle surface. The outer fold is separated from the middle fold by a deep periostracal groove, with the forming periostracum lying against the outer surface of the middle fold. The middle fold is divided into two distinct lobes with the outermost of these (mf 1) forming a short, slender lobe whilst the other (mf 2) is broad and longer. The inner fold (if) is a small, low ridge. Cells of the middle lobes are shorter than those of the outer fold and possess basal nuclei. The epithelium of the middle folds is overlain by a thin cuticle (ct) that extends almost to the inner fold. The mantle surface within the inner fold is ciliated.

Two well-defined bundles of radial muscles extend into the outer and middle folds respectively and a thick bundle of longitudinal pallial muscles (lm) is located near the inner fold (seen in transverse section in Fig. 20). The inner part of the mantle within the inner fold is highly glandular with subepithelial gland cells opening to the inner mantle surface. Two types of gland cell are present; one type, staining blue, is located superficially while the other dark green type lie more deeply.

Periodicity of Lamellae

The lamellae appear regularly spaced but measurements taken from acetate peels of shell sections show that the increments are variable in width and furthermore change with age. Figure 21 demonstrates that for eight live-collected shells widths between successive lamellae increase steadily from around 200–450 µm to a maximum (up to 1,800 µm) at around 25–30 mm shell height. Thereafter, interlamellar spacing becomes much narrower but more variable. Observations of the outer surfaces of larger, dead-collected shells show

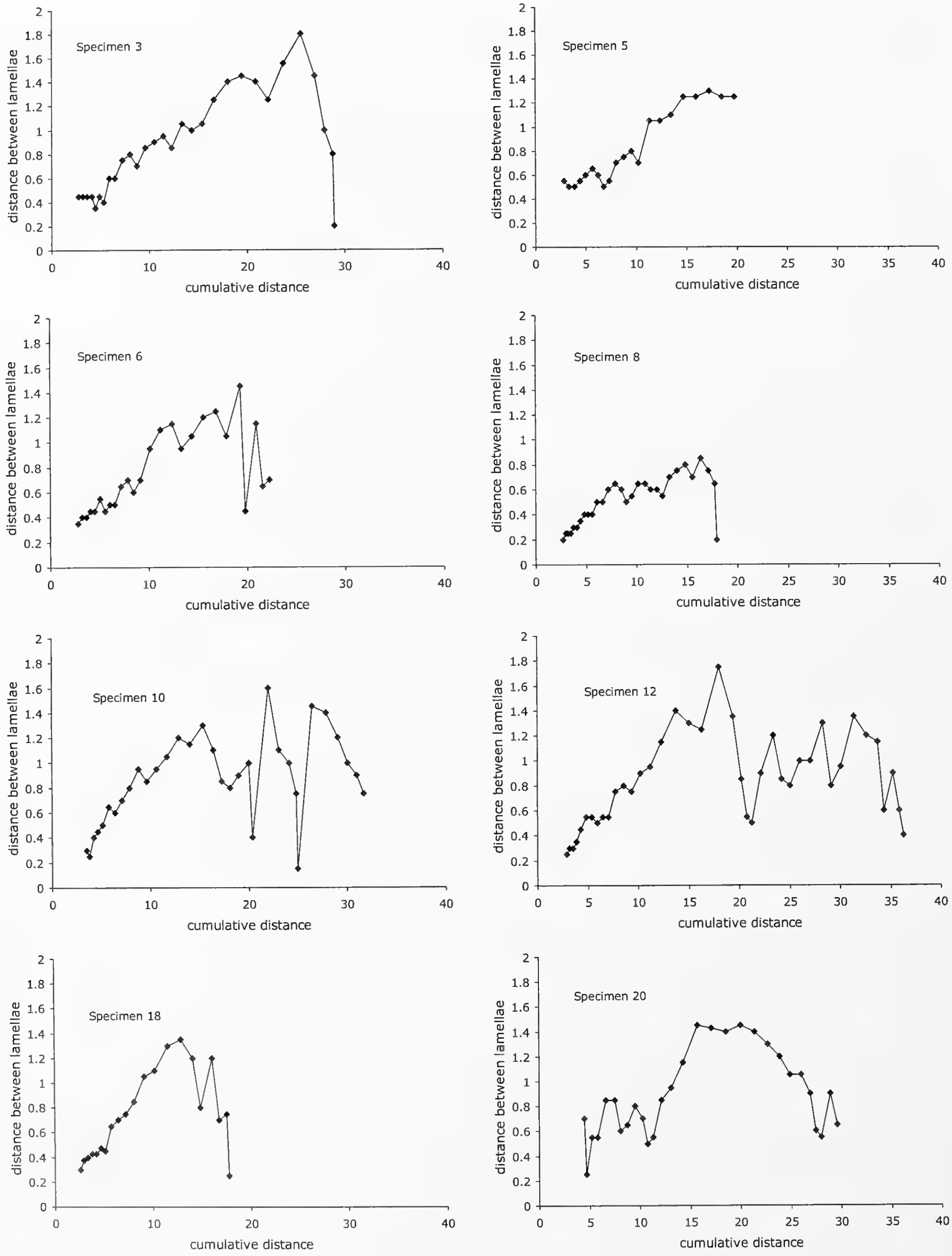


FIG. 21. *Lucina pensylvanica*, interval between successive lamellae plotted against cumulative length around shell circumference for eight individual *Lucina pensylvanica*. Measurements made from acetate peels of transverse sections.

FIG. 22. *Lucina pensylvanica,* acetate peel of transverse section of shell showing major growth line extending through outer and middle shell layers. Scale bar = 500 µm.

that this change in the interlamellar interval is visible on all individuals at shell heights of around 22–27 mm. In older individuals the interval between major growth halts is narrower with fewer lamellae (Fig. 21: specimen 12). Frequently, major growth halts are marked by the secretion of a sequence of several uncalcified periostracal extensions (Figs. 22, 23). Our interpretation of this growth pattern is that shell accretes rapidly and uninterrupted to a

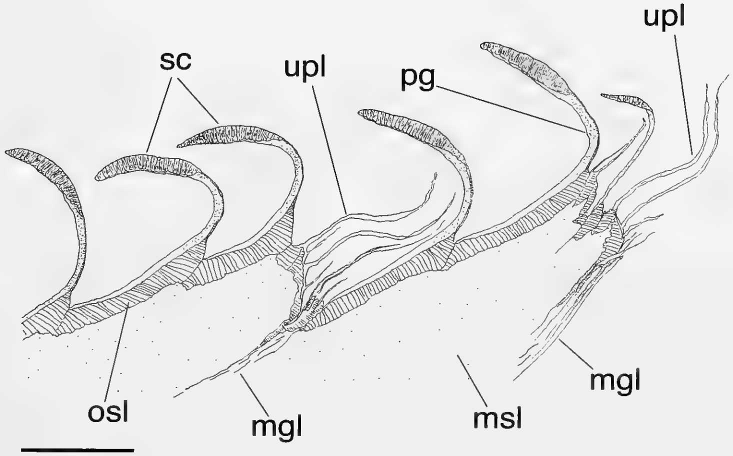


FIG. 23. *Lucina pensylvanica*, semidiagrammatic summary drawing (based on camera lucida image) of transverse section through shell showing successive lamellae and two growth halts where only uncalcified periostracal sheets were secreted. Scale bar = 1.0 mm. Abbreviations: cf, calcified front of lamella; msl, middle shell layer; osl, outer shell layer; ps, periostracum above shell; pl, periostracum of lamella; r, ridge in outer shell layer; sc, scales; upl, uncalcified periostracal lamellae.

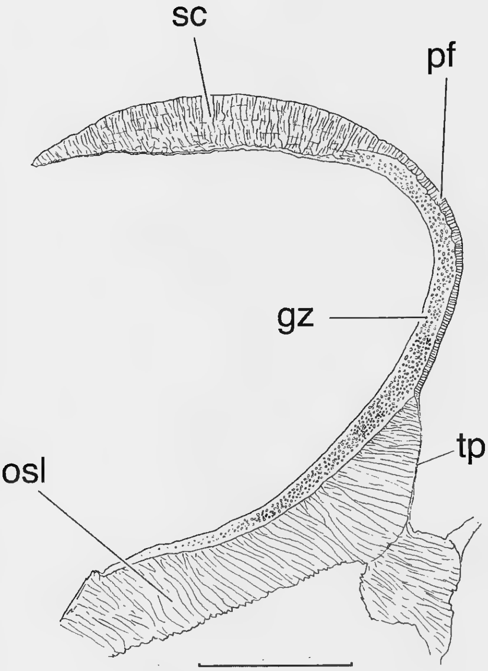


FIG. 24. *Lucina* pensylvanica, semidiagrammatic transverse section through a single periostracal lamella. Scale bar = 500 µm. Abbreviations: gz, granule zone; osl, outer shell layer; pf, thin prismatic ventral fringe to lamella; tp, thin periostracum.

size of around 25 mm. Thereafter, growth rates decline and become more variable. Study of gonads from our small sample indicates that sexual maturity occurs in these bivalves at shell heights of around 20–25 mm (Bigatti et al., 2004). The major change in shell growth pattern may thus coincide with time of first spawning.

A study of growth in *Codakia orbicularis* (Linnaeus, 1758) from the Bahamas showed that prominent growth rings in the shell were annual (Berg & Alatalo, 1984). Following this, the major growth halt lines seen in shell sections (Figs. 22, 23) in our sample could be tentatively interpreted as annual marks and used to estimate the ages of the animals. Table 1 indicates that 20 sectioned shells show between 0–4 major lines and the interpretation is that the animals vary between one and four years old. Proper age estimation should be done using marked and calibrated shells but this was impossible in the time available for the study.

Sequence of Secretory Events

The structure of the commarginal lamellae is summarized diagrammatically in Figures 23–24. Each commarginal lamella represents an extension of the mantle beyond the normal shell profile. Although the lamellae in *L. pensylvanica* are recurved dorsally, observations at the site of secretion show that the lamellae initially project more or less straight from the valve margin and curve dorsally later (Fig. 4). Thus, the mantle is not extended and reflected dorsally as it would be if secreting commarginal lamellae formed from normal shell layers as seen in other bivalves such as the venerid *Placamen calophyllum* (Philippi, 1836) (Checa, 2002).

Initially, the mantle secretes a thin, periostracal sheet, followed by calcification of the distal portion with spherulitic aragonite crystals. Calcification of the distal edge of the lamella is localised, presumably to groups of cells, so that individual scales are formed. At the same time the proximal part of the lamella is laid down as periostracum, embedded with crystalline granules. Finally, the mantle withdraws from the extended position, leaving a thin layer of prismatic crystals along the ventral face of the lamella. The withdrawal of the mantle is marked by a low, commarginal ridge in the shell profile (Figs. 12, 24). Following termination of a lamella, the periostracum is very thin but gradually thickens and becomes densely embedded with granules prior to the next lamellar extension (Fig. 24). Periodically, there are major growth breaks where only extended uncalcified periostracal sheets are formed (Fig. 23).

Comparison with *Lucina adansoni* and Other Species

An interesting comparison may be made with another species, *Lucina adansoni* (Orbigny, 1839) from West Africa. This has a thick, subspherical shell, sculptured, with closely spaced, broad commarginal lamellae about 300 µm in width (Figs. 25, 26). These are often eroded, detached or absent in dead-collected shells or museum specimens. Each lamella is divided into sections (up to 500 µm long) by narrow sutures aligned between successive lamellae. Interspaces between lamellae are often packed with sediment. Thin sections show that the lamellae are similarly constructed to those of *Lucina pensylvanica* (Figs. 27, 28) but instead of discrete scales, the calcified units are fused laterally to form a continuous ridge

TABLE 1. Shell size, age, sex, reproductive condition, position of growth lines and number of observed lamellae in *Lucina pensylvanica*.

ID	L	H	W	Sex	Reproductive state	N major growth lines	Age estimate	N observed lamellae (selected specimens)	FK-station	Location
1	27.9	27.5	15.7	F	Spawned	2	3		642	Lower Matecumbe Key
2	17.7	17.5	8.7	F	Maturing	0	1–2		642	Lower Matecumbe Key
3	27	25.7	13.7	F	Mat./spawning	1	2–3	30	642	Lower Matecumbe Key
4	28.2	28.1	17.6	F	Mature	3	3		642	Lower Matecumbe Key
5	17.9	17.6	9.4	F	Spawning	0	1+	21	642	Lower Matecumbe Key
6	20.5	20.6	11.5	F	Spawned	3	2	26	642	Lower Matecumbe Key
7	42.6	42	27	F	Mature full	2	4		642	Lower Matecumbe Key
8	21.6	20.4	10.9	F	Spawned	1	1–2	30	642	Lower Matecumbe Key
9	27.8	27.8	17.2	M	Mature	4	4–5	30	642	Lower Matecumbe Key
10	27.6	26.8	16.8	M	Mature full	3	3–4	33	642	Lower Matecumbe Key
11	35.4	36	21.9	?		3	4		647	Pigeon Key
12	32.7	32.4	20.8	F	Spawned	2	3	40	647	Pigeon Key
13	28.5	29.2	17.7	F	Spawned	2	2–3		647	Pigeon Key
14	31.5	30.7	19.2	F	Spawning	0	2		638	Lower Matecumbe Key
15	15.9	15.4	8.9	M	Mature	2	2	22	642	Lower Matecumbe Key
16	12.8	12.7	7.1	I		0	1+	16	642	Lower Matecumbe Key
17	16.2	15.3	8.5	M	Almost mature	0	1–2		642	Lower Matecumbe Key
18	16.1	15.7	8.8	F	Maturing	1	1+	21	642	Lower Matecumbe Key
19	13.8	13.2	6.8	F	Maturing	1	2		642	Lower Matecumbe Key
20	26.6	25.4	15.9	F	Mature	2	3	29	642	Lower Matecumbe Key

that is triangular in cross section (Fig. 27). The lamellae are tilted towards the ventral shell margin rather than recurved dorsally as in *L. pensylvanica*. Each lamella is composed of a thick periostracal extension that terminates distally in the calcified unit. This is more heavily calcified than the scales of *L. pensylvanica* but similarly constructed of spherulitic crystal growth. The periostracal extensions are shorter than *L. pensylvanica* but similarly embedded

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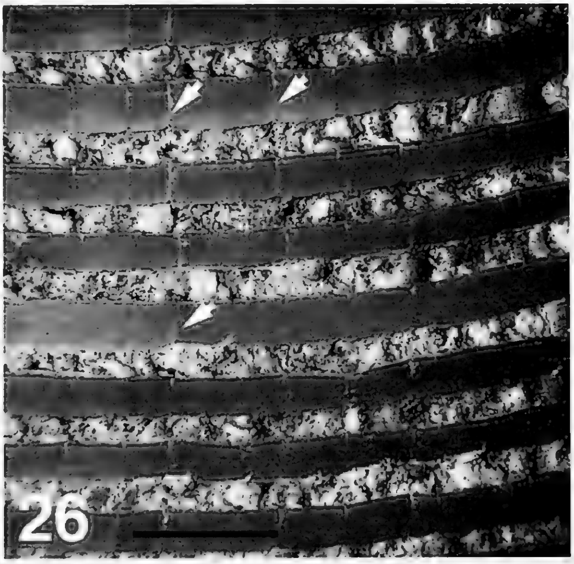

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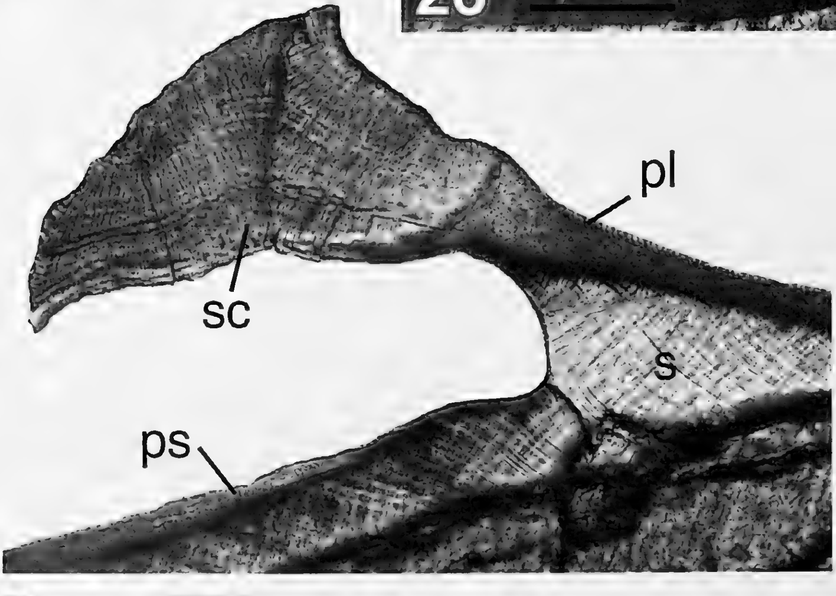

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FIGS. 25–27. *Lucina adansoni*. FIG. 25: Right valve (Leiden RMNH 12179). Cape Verde Islands, SE of Boa Vista 15°59'N, 22°44'W, depth 36 m. Shell height = 32.5 mm; FIG. 26: Detail of commarginal lamellae. Arrows mark suture lines between sections along lamellae. Note sediment grains packed into interspaces between lamellae. Scale bar = 1.0 mm; FIG. 27: Transverse section of a commarginal lamella. Scale bar = 500 µm. Abbreviations: pl, periostracal lamella; ps, periostracum above shell; s, shell; sc, calcareous scale.

with calcareous granules about 2 μm in diameter (Fig. 28). Also, the periostracum gradually increases in thickness between successive lamellae and then thins dramatically at their termination (Fig. 28). Beneath each lamella the outer shell layer forms a steep-faced lip (Fig. 28) about 200 μm high. In worn shells this is the only shell sculpture remaining after the lamellae have become detached.

Calcified periostracal commarginal lamellae similar to those of *L. adansoni* have been observed (BMNH collections) in the southern African species *Lucina carnosa* Dunker, 1858, and *L. roscoeorum* (Kilburn, 1974). The lamellae in the latter species are described (Kilburn, 1974: 340–341, figs, 4, 5) as being "...apically imbricate, rendering their crests somewhat tabulate (i.e. in cross section each would resemble an inverted "L")..." and "... the crests of the lamellae are regularly but superficially incised transversely...".

DISCUSSION AND CONCLUSIONS

We have demonstrated that the structurally complex commarginal shell sculpture of *Lucina pensylvanica* is a form of periostracal calcification, a rather unusual feature amongst bivalves. The calcareous granules within the periostracum were briefly mentioned by Bottjer & Carter (1980), but no details were given. We are not aware of any similar structures in any other lucinid. Most Lucinidae lack prominent commarginal shell sculpture but two species of *Lamellolucina*, namely *L. dentifera* (Jonas, 1846) from the Red Sea and *L. gemma* (Reeve, 1850) from the Philippines possess thin, elevated lamellae with spinose edges (Taylor & Glover, 2002: fig. 6) reminiscent of the lamellae in *L. pensylvanica*. However, the lamellae and spines of *Lamellolucina* are entirely calcareous and comprise extensions of the outer shell layer rather than periostracal

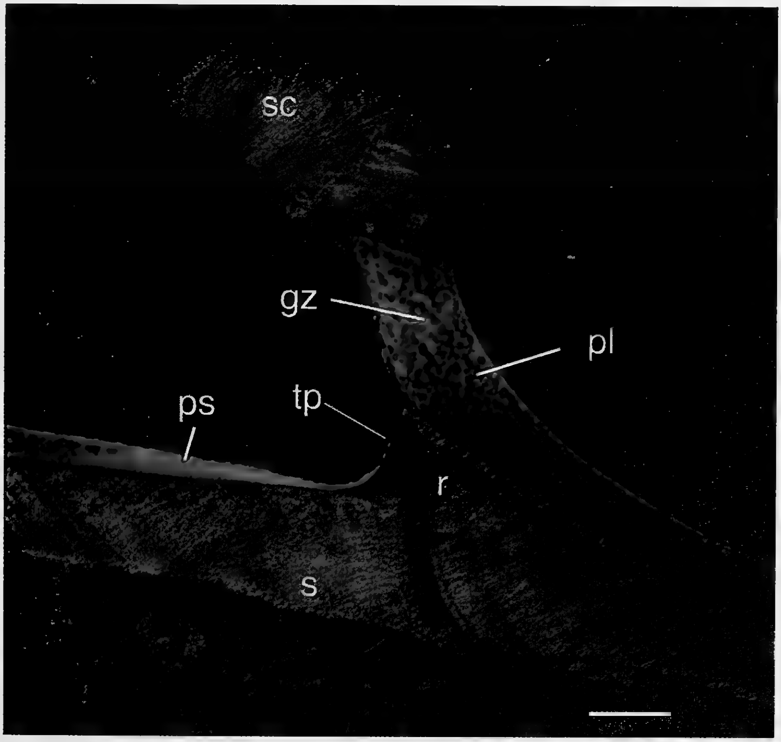

FIG. 28. *Lucina adansoni*, confocal image of transverse section of a commarginal lamella. Periostracum red, calcareous components green. Scale bar = 100 μm. Abbreviations: gz, granule zone of periostracum; pl, periostracal lamella; ps, periostracum above shell; r, ridge in outer shell at base of lamella; s, shell; sc, calcareous scale; tp, thin periostracum.

structures. Similarly, *Lucinisca* species from the western Atlantic and eastern Pacific possess spinose commarginal lamellae, but again these are formed from the outer shell layer rather than periostracum.

A diversity of instances of periostracal calcification has been described from a wide range of different bivalve families (Carter & Aller, 1975; Bottjer & Carter, 1980; Carter et al., 1990; Ohno, 1996; Morton, 2000), but none is comparable with *L. pensylvanica*. Analogous calcareous granules embedded in periostracum have been illustrated for the mytilids *Brachidontes granulatus* (Bottjer & Carter, 1980: fig. 3) and *Trichomya hirsuta* (Carter & Aller, 1975: fig. 1c). Little attention has been paid to this calcification either functionally or as a set of systematic characters and in many cases it is routinely cleaned off specimens.

Function of the Lamellae

Although we have no experimental evidence, we suggest by analogy with sculpture on other bivalves that there might be at least three possible functions of the commarginal lamellae. These include acting as a sculptural aid to burrowing, maintaining stability in the sediment and as a possible deterrent to predators. Unusually amongst bivalves, the commarginal lamellae of *L. pensylvanica* are flexible in life and this property may have added but unknown functional significance.

As demonstrated by Stanley (1970), some lucinids, including *Lucina pensylvanica*, burrow into the sediment vertically with the hinge axis parallel to the sediment surface and rock from side to side to gain purchase into the sand. Unusually for lucinids, *L. pensylvanica* rotates posteriorly after penetrating the sediment to lie with the anterior part of the shell uppermost. The recurved, flexible lamellae and scales might aid this process but we have no experimental evidence similar to that available for the divaricate-ribbed *Divaricella quadrisulcata* (Orbigny, 1846) (Stanley, 1970). However, the external lamellae of *L. pensylvanica* are easily removed to enable a comparison of burrowing performance to be made with and without the structures.

In shallow burrowing bivalves, the ridges and spines on the shell surface have been shown to reduce the effects of scour and may prevent dislodgement from the sediment (Bottjer & Carter, 1980; Stanley, 1981). We have no experimental observations but in *Lucina pensylvanica* and *L. adansoni* the lamellae are extremely effective in trapping sediment close to the shell surface (Figs. 8, 26) and in most live-collected specimens the interlamellar spaces are full of sediment. Compared to other lucinids of similar size from the Florida Keys, *Lucina pensylvanica* is the most shallowly burrowed, living in medium to coarse, mobile sands rather than the thicker *Thalassia*-bound sediments favoured by *Codakia orbicularis* and *Anodontia alba*.

A further possible function of the lamellae might be to deter predation. Strong commarginal lamellae on the venerid *Placamen calophylum* have been shown to deter shell drilling predatory gastropods (Ansell & Morton, 1985). Any test of this suggestion would need experimental analysis.

The function of the discrete aragonitic granules embedded in the periostracum and periostracal extensions of *L. pensylvanica* and *L. adansoni* is unclear, but they may provide additional stiffness to the largely proteinaceous part of the lamellae that supports the more heavily calcified distal scales or ridge. Furthermore, the thin calcified layer along the ventral face of the lamellae may also provide stiffness but, additionally, the differential mechanical properties on either face of the lamella may cause the lamellae to curve dorsally.

Systematic Implications of Commarginal Lamellae in *Lucina*

Although *Lucina pensylvanica* is thought to be widely distributed around the Western Atlantic and Caribbean area, from North Carolina to Brazil (Britton, 1970; Abbott, 1974; Bretsky, 1976), it is much more likely that a complex of several species exists. J. Gibson Smith & W. Gibson Smith (1982) used the morphology of the calcareous scales to divide the "*L. pensylvanica*" of the western Atlantic, naming three new species on the basis of differences in the form of the scales. These they distinguished from *L. pensylvanica*, assuming its type locality to be Florida. All the species are similar in general shell morphology but differ in the form of the calcified periostracal lamellae. We have examined the types of the Gibson-Smith species and also the syntypes of *Lucina pensylvanica* (Linnaeus, 1758), but unfortunately the latter material is heavily worn without any trace of lamellae.

Firstly, *Lucina belizana* J Gibson-Smith & W Gibson-Smith, 1982 (Holotype: BMNH 1980103) from Belize is characterised by fine, close lamellae with delicately pointed, lightly calcified spines. Secondly, *Lucina roquesana* J Gibson-Smith & W Gibson-Smith, 1982 (Holotype and paratype: BMNH 1980105/1–2) from Venezuela has calcified periostracal lamellae, but these bear broad closely spaced, blunt-ended scales that are arranged in a radial rows in successive lamellae. *Lucina podagrina caymanana* J Gibson-Smith & W Gibson-Smith, 1982 (Holotype: BMNH 1980104/1) from the Cayman Islands is similar to *L. roquesana*, but the periostracum is pale brown and the shell less globose (*Lucina podagrina podagrina* Dall, 1903, is a Pliocene fossil species.). J. Gibson Smith & W. Gibson Smith (1982) have undoubtedly highlighted the existence of a species complex within the former "*Lucina pensylvanica*", but in our opinion the taxonomy is even more complicated. For example, another species from the western Atlantic, *Lucina aurantia* Deshayes, 1830, which is usually synonymised with *L. pensylvanica* (Abbott, 1974; Britton, 1971; Bretsky, 1976), has many distinctive shell characters including size and shape, dentition and colour. Some unworn shells have remnants of fine, pointed scales. We are confident that this is yet another unregarded species. Another likely distinct species from the Bahamas has been confused with *L. pensylvanica* but it can readily distinguished by extremely fine pointed scales (specimens from Blue Hole Cay, off Andros Is., collected by P. Mikkelsen and G. Hendler). A thorough systematic revision of the "*Lucina pensylvanica*" complex in the western Atlantic using live-collected animals with morphological and molecular analysis is needed.

On the other side of the Atlantic, *Lucina adansoni*, *L. carnosa*, and *L. rosceorum* seem to form another possibly related clade, linked by the possession of calcified periostracal lamellae that form continuous ridges. As we have demonstrated, these ridges differ in morphology but are similarly constructed and thus homologous with the lamellae of the western Atlantic "*L. pensylvanica*" group. The relationships of the two clades need clarification.

It should be emphasized that in museum specimens the periostracal calcified structures so diagnostic of these *Lucina* species are usually damaged or in the case of beach collected shells, completely worn way. In dried shells, the periostracal lamellae become brittle and are easily damaged without special curatorial care. We recommend wet preservation as the most satisfactory method of preserving these structures.

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PREDATOR-PREY INTERACTIONS BETWEEN *CHIONE ELEVATA* (BIVALVIA: CHIONINAE) AND *NATICARIUS CANRENA* (GASTROPODA: NATICIDAE) IN THE FLORIDA KEYS, U.S.A.

Brian Morton[1] & Martina Knapp[2]

ABSTRACT

Field samples of *Chione elevata* (Veneridae) were collected from two sites (10 x 25 x 25 cm quadrats) on the Atlantic coast of the Florida Keys at Long Key State Park, Long Key, and Anne's Beach, Lower Matecumbe Key. Shells were divided into living, empty (non-drilled) and drilled categories and measured along their greatest lengths. The shells of other bivalve species were also so separated. Generally, the *C. elevata* samples from the four sites were similar to each other, except with regard to the numbers of drill holes, that is, with a significantly higher level of predation at Long Key.

The shells of nine species of bivalves, but especially *Chione elevata,* were drilled in an approximately stereotypical manner, that is, equally on both valves, usually postero-dorsally. Most drillings were successful, and the predator is believed to be *Naticarius canrena* – this being the only naticid shown experimentally to be capable of drilling *C. elevata* in the postero-dorsal location.

Chione elevata possesses an array of potential anti-predator shell defences, notably elevated shell lamellae, similar to those of *Placamen calophyllum* in the Indo-West Pacific. *Placamen calophyllum* is immune from naticid attack except by species of *Polinices*, which drill it at the valve margin. *Naticarius canrena* attacks *C. elevata* by drilling between the shell lamella, at the interspaces, postero-dorsally. In this the thickest region of the bivalve shell, the few incomplete drill holes suggest that *N. canrena* is highly successful. There were very few marginal drill holes. Mid-ventrally, *C. elevata* possesses large, paired pallial glands, and it is possible that this is an anti-predator device inhibiting marginal drilling. *Naticarius canrena*, therefore, has to drill this commonest of all intertidal bivalves postero-dorsally but does so by attacking its prey selectively, that is, smaller individuals attacking smaller bivalves so that drill hole size is always narrower than interlamellar distance.

Key words: Predator-prey interactions, *Naticarius*, *Chione*, Florida Keys, drill hole position, shell defenses.

INTRODUCTION

That many naticid gastropods drill holes in bivalve and some gastropod shells to access the tissues inside is well documented (Taylor, 1998) and has led to the concept of an "arms race" between predator and prey as the former strives to overcome the defences of the latter and the bivalve seeks to improve its ability to defend itself against the gastropod (Vermeij, 1978, 1980). Species of *Austroginella* (Marginellidae) drill holes in their prey (Ponder & Taylor, 1992), and it has been shown recently that juvenile *Nassarius festivus* (Nassariidae) can also drill the shells of conspecifics (Morton & Chan, 1997). There are, however, two major groups of intertidal drilling predatory gastropods: representatives of the Muricidae, generally, on rocky shores and species of Naticidae on soft ones. On Malaysian shores, *Anadara granosa* is drilled by both *Natica maculosa* (Naticidae) and *Thais carinifera* (Muricidae) (Broom, 1981). Muricids drill vertically straight holes in shells of their prey, naticids countersunk ones, and both attack in a stereotypical way to gain access. Thus, Arua (1989) was able to show for an Eocene molluscan community from Nigeria that the most common prey of naticids was the epifaunal, strongly ornamented bivalve

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Tivelina newtoni, whereas the principal prey of muricids was the epifaunal, but also strongly ornamented gastropod *Bonellitia amekiensis*. Today, on a southwestern Australian rocky shore, the muricid *Lepsiella flindersi* attacks the mussel *Xenostrobus pulex* in a stereotypical manner on the posterodorsal side of left and right valves equally (Morton, 1999). Similarly, in a southwestern Australian marsh, *Lepsiella vinosa* attacks another mussel, *X. inconstans*, also in a stereotypical manner posteriorly (Morton, 2004). In the Azores, *Thais haemastoma* drills the intertidal mussel *Trichomusculus semigranatus* only at the posterior margin (Morton, 1995). On Hong Kong shores, *Morula musiva* attacks an array of shallow-water bivalves by drilling at specific locations on each of their shells (Harper & Morton, 1997).

Similar observations have been made upon naticids. In Malaysia, Berry (1982) showed that *Natica maculosa* drills the trochid gastropod *Umbonium vestiarium*. In Europe, Ansell (1982a, b) demonstrated that the bivalves *Venus striatula* and *Tellina tenuis* are drilled by *Polinices alderi*, whereas on the coast of Massachusetts, Edwards & Huebner, (1977) showed that *Mya arenaria* is drilled by *P. duplicatus*.

Virtually all species of bivalves are vulnerable to either muricid or naticid attack and there has been much research conducted on the predator/prey relationship between them. This is because both are readily identifiable in the fossil record (Kitchell et al., 1981), drilled shells are obvious in modern field-collected bivalve assemblages, and the stereotypical feeding behaviour of the predator makes both it and its prey eminently suitable experimental animals. For example, shell height/length parameters can be correlated readily with tissue weights. Thus, Taylor (1970), examined the feeding habits of predatory boring gastropods in a Tertiary mollusc assemblage, and Negus (1975) was able to analyse the drill holes made by *Natica catena* in a collection of *Donax vittatus* shells. Morton (1990a) showed that in the Azores, the commonest shallow subtidal bivalve, *Ervilia castanea*, was drilled by *Polinices alderi* in a stereotypical, posterior, position. Ansell & Morton (1987) demonstrated that various species of Indo-West Pacific naticids attacked different species of bivalve prey in a different sequence according to intra-specific size, inter- and intra-specific shell thicknesses and at different locations on the shells. In an elegant series of laboratory studies, Ansell (1982a, b, c) examined the energetic relationship between *P. alderi* (and *P. catena*) and its bivalve prey.

With respect to the Florida Keys, Roopnarine & Beussink (1999) suggested that during a Pliocene-Pleistocene extinction, *Chione erosa* Dall, 1903, was replaced by *C. cancellata* Linnaeus, 1767. When this occurred, there was an increase in the size of *Chione* selected by naticid predators, and *C. cancellata* responded to this by significantly increasing relative shell thickness. Mikkelsen & Bieler (2000) identified three species of *Chione* from the Florida Keys, with *C. cancellata* being the most widespread. The paper on western Atlantic *Chione* by Roopnarine & Vermeij (2000), however, suggests that *C. cancellata* is a Caribbean species, whereas the Floridian species is *C. elevata* (Say, 1822). There is, thus, a large literature on what was considered, in Florida and north to North Carolina, to be *C. cancellata*, but which actually refers to *C. elevata*.

Species of *Chione* (Chioninae) are characterized by elevated concentric lamellae on the shell valves. These are produced periodically and may represent a defense against drilling predators. For example, Atlantic species of *Chione* (Roopnarine & Vermeij, 2000) are very similar to Indo-West Pacific species of *Bassina* and *Placamen* (Matsukuma & Yoosukh, 1988), and it has been shown for *P. calophyllum* (Philippi, 1836) that its shell lamellae protect it from side-drilling naticid predators (Ansell & Morton, 1985; Morton, 1985). *Polinices tumidus* could, however, attack it by edge drilling. Moreover, when the lamellae of *P. calophyllum* were removed, side-drilling predators could attack it with impunity. This may not be the case in species of Atlantic *Chione*, however, as Roopnarine & Beussink (1999, fig. 1) illustrate a shell of Pliocene *C. erosa* with a drill hole located between adjacent lamellae.

During a ten-day period of study in the Florida Keys, one of the most commonly encountered species of bivalves was *Chione elevata*. In field samples, moreover, many *C. elevata* shells were found to have been drilled by a naticid predator. It was decided, therefore, to undertake a study of this bivalve, its drill holes and try to identify the predator that made them. The overall question that we attempted to answer, however, was: like *Placamen calophyllum*, do the shell lamellae of *C. elevata* protect it from naticid predation (Morton, 1985)? If not, why not?

MATERIALS AND METHODS

For a short period from 20–29 July 2002, a research visit was paid to the Florida Keys. It was determined to research the anatomy of *Chione elevata,* undertake an analysis of drill holes in the shells of field-collected samples of bivalves and attempt to determine which predator made them.

Anatomy

Living individuals of *Chione elevata* were dissected. A single specimen was also fixed in 5% formalin, decalcified and, following routine histological procedures, sectioned transversely at 6 µm, and alternate slides stained in Ehrlich's haematoxylin and eosin and Masson's trichrome.

Field Studies

On the southeastern coast of the keys, that is, the Atlantic side, two shores were chosen for study after reconnaissance of sites on both sides and when very few *Chione elevata* were collected from the Gulf of Mexico side. The two chosen shores were Long Key State Park on Long Key and Anne's Beach on Lower Matecumbe Key, that is, station numbers IMBW-FK-623 and IMBW-FK-638, respectively (Mikkelsen & Bieler, 2004: fig.1). At each of two sampling locations at these two sites, ten 25 x 25 cm quadrats were laid haphazardly on the sandy shore covering the full range of tidal heights. A total of, thus, 40 quadrats was examined by excavating their contents to a depth of ~ 10 cm and sieving them through a one millimeter mesh sieve. All living and empty bivalve shells (plus any naticid shells) were sorted from the samples. These were analyzed in the following manner.

Shells and living individuals of *Chione elevata* were measured along their greatest lengths; in the case of empty valves, only right ones were measured. Empty valves were examined for drill holes. Where these were encountered, the following records were made: (i) which valve; (ii) the location of each drill hole was plotted on a master illustration of the valves; (iii) the outer diameter of the drill hole; and (iv) the distance between adjacent lamellae at the drilling location.

All other bivalve shells with drill holes were identified to species and the locations of them on the left and right valves similarly plotted on master illustrations. Although several other species of naticids are known to inhabit the shallow waters of the Florida Keys (Lyons & Quinn, 1995; Bieler & Mikkelsen, pers. comm.), the only shells ever collected were those of *Naticarius canrena* (Linnaeus, 1758). Similarly, but one living individual of this species was collected from any habitat during the ten-day period of study. Voucher specimens of *Chione elevata* (108 preserved individuals) and *N. canrena* (16 shells) have been deposited in the collections of the Natural History Museum, London (Reg. No's: 20030605 and 20030609, respectively).

Statistical Analyses

The dataset comprising the numbers of living, empty and drilled shell valves of *Chione elevata* among the four locations was tested for normality and homogeneity of variances using the Shapiro-Wilk test and Levene statistic, respectively, both at the 0.05 level of significance before ANOVA. One-way ANOVA's were performed on the dataset to test the null hypothesis that there were no significant differences in these variables among locations. Where differences were detected, Student's Newman-Keuls (SNK) tests were carried out to identify where the differences lay. For the drilled shells, the relationships between shell length and (i) lamella distance and (ii) drill hole diameter were evaluated by regressions.

RESULTS

Anatomy

Shell: The shell of *Chione elevata* is illustrated from various perspectives in Figure 1. In general terms, the shell is approximately equivalve and equilateral, and thus isomyarian, but slightly pointed posteriorly. There is a fine radial sculpture, and each valve is strongly commarginally lamellate (Fig. 1A). In anterior view (Fig. 1B), there is a small anterior lunule (as defined by Carter, 1967) each valve here interlocking by means of marginal denticles. In dorsal view (Fig. 1C), the posterior escutcheon (also as defined by Carter, 1967) is much longer than the lunule and in the case of the former but not the latter, the dorsal edge of the left valve overlaps that of the right. This is also illustrated in posterior view (Fig. 1D). Finally, the shell valve margins

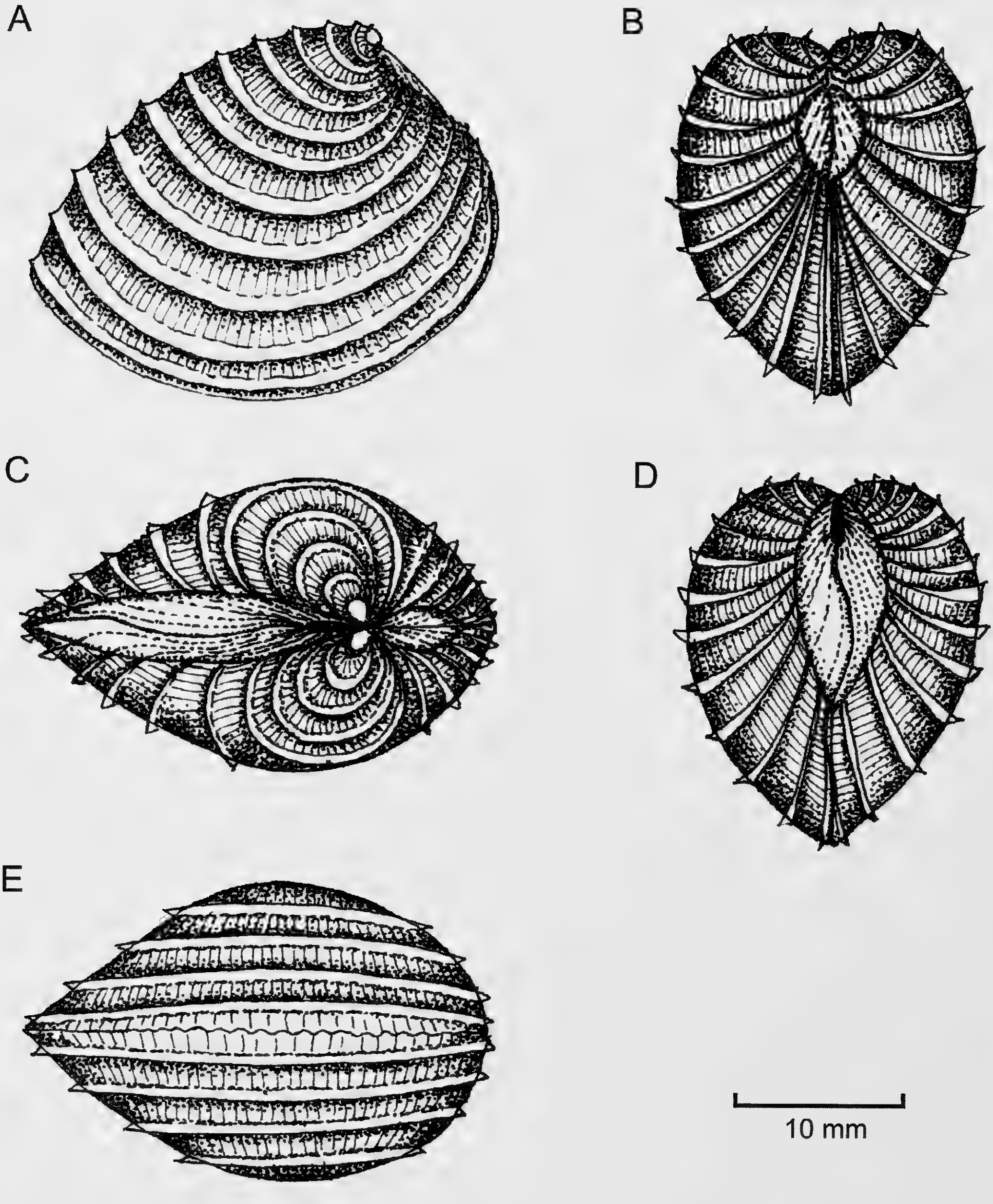

FIG. 1. *Chione elevata*. The shell as seen from: A, the right side; B, anteriorly; C, dorsally; D, posteriorly and E, ventrally.

are interlocked ventrally by the expanding radial ribs (Fig. 1E). The shell valves of *C. elevata* are thus very difficult to separate.

Siphons and Mantle Cavity: A living individual of *Chione elevata* is illustrated in Figure 2 from the right side. The shell is, as described, radially striate and commarginally lamellate. Rays of light purple pattern the generally white-cream outer surface. Anteriorly, there is a large digging foot. Posteriorly, there is a pair of separated siphons. The exhalant

FIG. 2. *Chione elevata*. An individual seen from the right side with siphons and foot extended.

siphon is conical and a ring of short, thin tentacles sub-apically surrounds its aperture. The inhalant siphon is much larger in diameter, but shorter and is fringed apically by a circlet of long siphonal tentacles and papillae. Mid-ventrally, the mantle possesses a line of papillae and pallial fusions, where they occur, are of the inner folds only, that is, type A (Yonge, 1982).

Jones (1979) provided additional details on the gross anatomy of *Chione elevata* (as *C. cancellata*) and other chionine species.

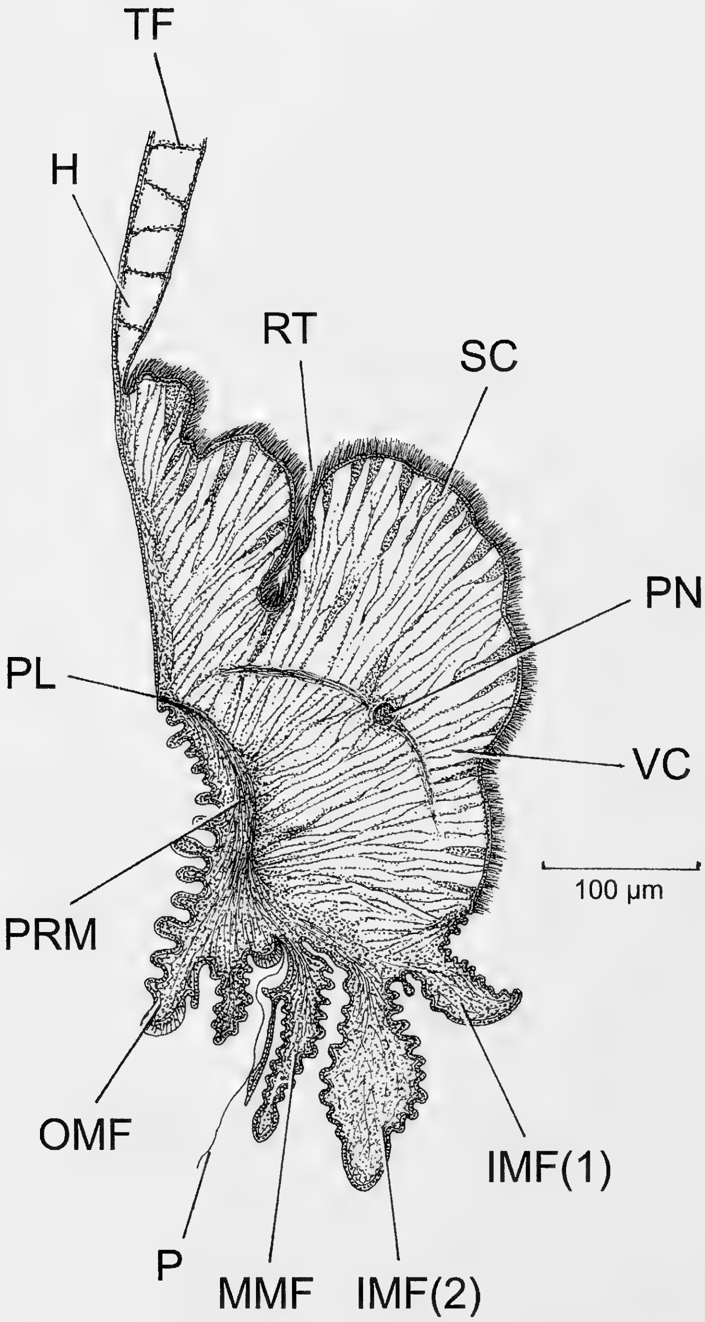

FIG. 3. *Chione elevata*. A transverse section through the left mantle lobe at the margin. H, haemocoel; IMF[1], inner component of the inner mantle fold; IMF[2], outer component of the inner mantle fold; MMF, middle mantle fold; OMF, outer mantle fold; P, periostracum; PL, pallial line; PRM, pallial retractor muscle; PN, pallial nerve; RT, rejection tract; SC, secretory cell; TF, transverse fibres; VC, vacuolated cell.

Mantle Margin: In transverse section, the general surface of the mantle comprises epithelia, cross-connected by transverse fibers (Fig. 3, TF) and enclosing a capacious haemocoel (H). Jones (1979, fig. 21) provided a simple illustration of a transverse section through the mantle margin of *Chione elevata* (as *C. cancellata*). Here, that of *C. elevata* is shown to be very large and complex. It comprises the usual three folds (Yonge, 1982). The outer fold (OMF) is large, and its inner surface secretes a very thin periostracum (P) against the template of the outer surface of the middle mantle fold (MMF). The template is a long thin sheet of tissue arising from the major element of the middle fold. The inner fold is divided into two components, a smaller inner (IMF[1]) and a larger outer (IMF[2]) that also gives rise to the mantle papillae which fringe the mantle margin especially ventrally.

The greatest component of the mantle margin of *Chione elevata* is a large gland comprising elongate vacuolated cells (VC) that lie beneath the inner epithelium and stain a light red in Masson's trichrome: apically, such cells are actively secretory (SC). The gland does not therefore appear to be secreting mucus to bind up pseudofaeces: it is too large for such a purpose and the habitat of coarse coral sand would not necessitate such rejectory capabilities, but otherwise its function is unknown. The illustrations of the sectioned ventral mantle margins of *C. elevata* (as *C. cancellata*) and *C. undatella* (Sowerby, 1835) by Jones (1979, figs. 21, 24) do not identify whether such a gland is present although they appear swollen as described herein.

Field Studies

Overall, 2.3 (± 2.4) living, 13.7 (± 9.6) empty shells and 4.5 (± 4.40) drilled right valves of *Chione elevata* were encountered per quadrat (Table 1). The numbers of living, empty and drilled valves differed among locations, however (Table 2A, $p < 0.05$).

Results of a Student-Newman-Keuls test (Table 3) showed that the two Anne's Beach samples were similar to Long Key State Park A, but also that the two Long Key State Park locations were similar to Anne's Beach A in terms of living *Chione elevata*. Similar results were obtained for the empty shells, that is, the two Anne's Beach sites were similar, as were the two Long Key State Park locations but these were also similar to Anne's Beach B. Only with regard to the drilled valves was a clear intersite difference obtained, that is, the two Long Key State Park locations were similar (6.0 and 8.8 drilled valves·quadrat^{-1}), as were the Anne's Beach ones (1.4 and 1.7 drilled valves·quadrat^{-1}) (Table 1), but also that the two pairs of locations were different from each other (Table 3). That is, there appears to

TABLE 1. Results of the statistical analysis of the *Chione elevata* shell dataset (living, empty and drilled) obtained from the four stations in the Florida Keys (10 x 25 cm x 25 cm quadrats).

Shell Type	Location	Mean	Standard Deviation
Living	Long Key State Park Site A	2.7	1.70
	Long Key State Park Site B	3.4	2.76
	Anne's Beach Site A	2.5	2.99
	Anne's Beach Site B	0.6	0.70
	Average	2.3	2.39
Empty	Long Key State Park Site A	8.9	8.21
	Long Key State Park Site B	9.9	8.14
	Anne's Beach Site A	21.4	8.62
	Anne's Beach Site B	14.7	9.04
	Average	13.7	9.59
Drilled	Long Key State Park Site A	1.4	1.07
	Long Key State Park Site B	1.7	1.77
	Anne's Beach Site A	6.0	2.98
	Anne's Beach Site B	8.8	5.31
	Average	4.5	4.40

TABLE 2. Results of a one-way ANOVA on the *Chione elevata* shell dataset (living, empty and drilled) obtained from the four stations in the Florida Keys.

Shell Type	Comparison	df	Mean Square	F	Significance ($p = 0.05$)
Living	Between groups	3	14.33	2.88	0.049
	Within groups	36	4.98		
	Total	39			
Empty	Between groups	3	325.89	4.50	0.009
	Within groups	36	72.45		
	Total	39			
Drilled	Between groups	3	127.29	12.32	0.000
	Within groups	36	10.34		
	Total	39			

be a higher level of drilling predation, possibly by *Naticarius canrena*, at the Long Key State Park than at the Anne's Beach locations.

Location of Drill Holes: In addition to *Chione elevata*, the field-collected bivalve shells with naticid drill holes comprised nine species. Outlines of the shells of these species are illustrated in Figure 4. Also illustrated are the positions of the drill holes on both the left (∘) and right (•) valves.

The two lucinids, *Ctena orbiculata* (Montagu, 1808) and *Lucinisca nassula* (Conrad, 1846), were both drilled close to the ventral shell margin. All seven other bivalves, that is, the glycymerid *Tucetona pectinata* (Gmelin, 1791), the carditid *Pleuromeris tridentata* (Say, 1832), the cardiid *Laevicardium mortoni* (Conrad, 1830), the venerid *Pitar simpsoni* (Dall, 1895), and three tellinids – *Tellina mera* Say, 1834, *T. iris* Say, 1822, and *T. similis* J. Sowerby, 1806, were all side drilled in most cases close to the umbones and, again mostly, posterior to them.

Figure 5 illustrates diagrammatically the empty right (A) and left (B) valves of *Chione elevata* with the positions of the total numbers of drill holes on them identified. It is obvious that there is, first, an approximately equal distribution of drill holes (and attempts) between the two valves, that is, right 99, left 98. Second, most of the drill holes were, again, approximately equally, in terms of the two valves, distributed around the postero-dorsal region of the shell with a few scattered over the rest of the surface. A third important point is that there are very few failed drill holes, that is, two in the right and four in the left valves. Fourth, only a very few of the drill holes were over the shell lamellae, that is, two on the right and four on the left valves and, in the latter case, these were also at the marginal lamellae.

Shell Measurements: Figure 6A shows the relationship between shell length and the distance between adjacent lamellae demarcating a drill hole site on the shell of *Chione elevata*. The relationship is linear, suggesting that the predator is, for a prey of a particular size, choosing a site appropriate for drilling. That is, smaller predators (making smaller drill holes) chose positions on the *C. elevata* shells where there are smaller interlamellar distances in these younger, smaller bivalve prey. Conversely, larger predators (making larger drill holes) chose positions on shells where there are larger interlamellar distances, that is, older, larger bivalve prey. This conclusion is substantiated in Figure 6B, where it is further shown that drill hole diameter is correlated positively with shell length in *C. elevata*. That is, smaller predators, making smaller drill holes, attack smaller individuals of *C. elevata*.

In summary, therefore, it would appear from this analysis of naticid-drilled shells that

TABLE 3. Student-Newman-Keuls test grouping of the four Florida Keys locations (1 = Long Key State Park Site A, 2 = Long Key State Park Site B, 3 = Anne's Beach Site A, 4 = Anne's Beach Site B) into subsets in terms of the mean number of living, empty and drilled shells of *Chione elevata* in an ascending order.

Shell Type	Subsets
Living	4 = 3 = 1 < 3 = 1 = 2
Empty	1 = 2 = 4 < 4 = 3
Drilled	1 = 2 < 3 = 4

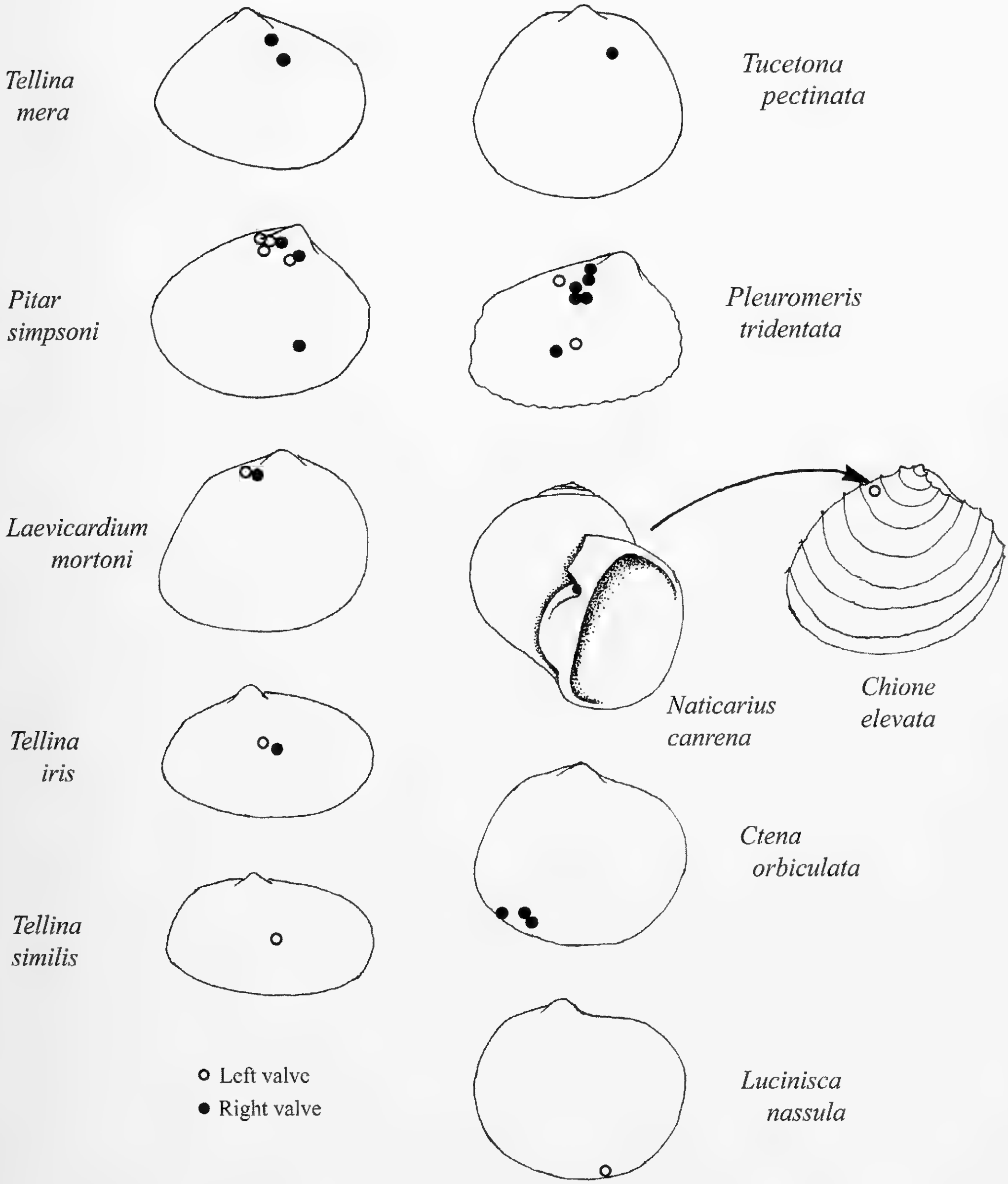

FIG. 4. The positions of drill holes on the left and right valves of empty shells of nine other species of bivalves collected with the *Chione elevata* field samples. Also shown is a ventral view of *Naticarius canrena* and the drill hole one individual of this predator made in the shell of an aquarium-held *Chione elevata*.

Chione elevata (and probably other resident bivalves) is attacked in a stereotypical manner at the posterodorsal margin, and at interlamellar spaces. There were virtually no examples of either marginal or lamellar drilling; that is, the predator avoids the structurally very similar margins and lamellar edges, unlike the situation of *Placamen calophyllum* in the Indo-West Pacific (Ansell & Morton, 1985).

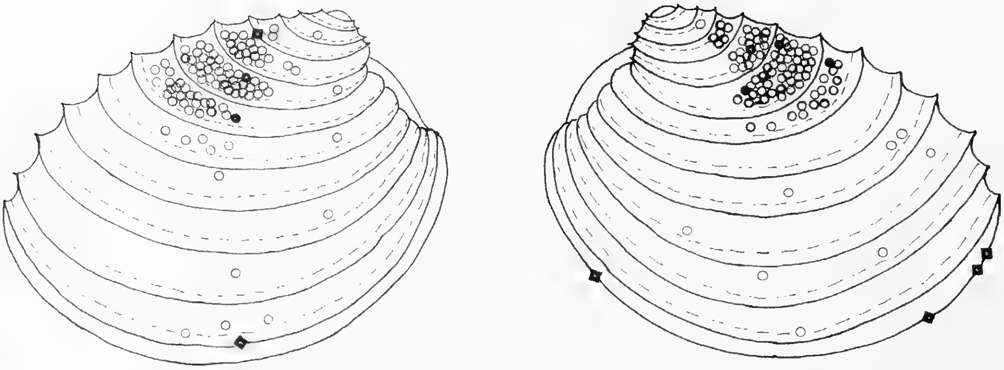

FIG. 5. *Chione elevata*. The composite pattern of drill holes in the field-collected left and right valves of empty shells (○ non-lamella borehole, • attempted borehole, ◆ lamella borehole).

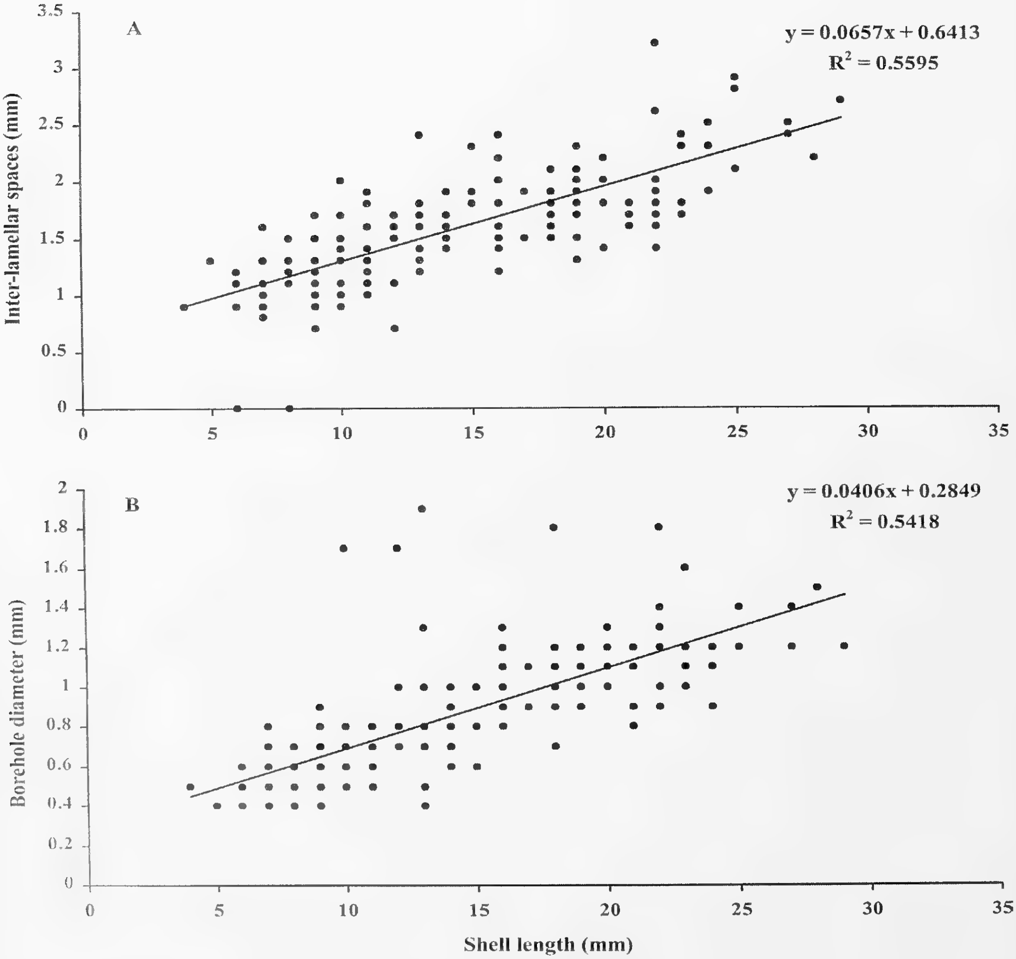

FIG. 6. *Chione elevata*. The relationships between shell length and A, the distance between two lamellae at the position of an interlamellar drill hole and B, the outer diameter of the drill hole.

Laboratory Studies

Although 16 empty shells of *Naticarius canrena* were collected from the 40 quadrats, only one living individual was obtained. This was placed in an aquarium with small individuals of *Chione elevata* and one drill hole was made, on the right valve postero-dorsally (Fig. 4, *C. elevata* shell), that is, in the position typical of the locations of the field collected bivalves of this species (Fig. 5). No other naticid species (not even shells) was ever collected alive. It thus seems possible, at least, that *N. canrena* made the drill holes on all the field-collected bivalves, but especially *C. elevata*, collected during the course of this study.

DISCUSSION

Chione elevata has a shell that, superficially, would appear to offer much protection. Protective characteristics include a tightly fitting margin, with ventrally interlocking ribs, similar interlocking marginal denticles at the anterodorsal lunule, a marginally overlapping escutcheon and internally large, strong cardinal teeth (Jones, 1979). Closed *C. elevata* are extremely difficult to open, even by the authors! Each adductor muscle also has a large slow component for sustained adduction, and the pallial line is deeply inset within the shell margin. With the commarginal lamellae on the outside of a solid, thick shell, *C. elevata* would, superficially, appear to be impregnable. Such characters are also possessed by the Indo-West Pacific *Placamen calophyllum* and are very effective in protecting it from naticid predators (Ansell & Morton, 1985, 1987).

Lamellar protection is not afforded to *Chione elevata*, however, and the only predator identified as being capable of attacking and drilling this species at the study sites on the Florida Keys is *Naticarius canrena* and it does this at the interlamellar spaces. This is the opposite of the situation described for the Indo-West Pacific *Placamen calophyllum*, which is virtually immune from attack by side-drilling naticids because of the shell lamellae but is vulnerable to the edge-drilling *Polinices tumidus*, as described by Ansell & Morton (1985). It is strange therefore that the lamellae of the Atlantic *C. elevata* do not confer any protection from *N. canrena* and further strange that there were very few identified attempts to drill the bivalve at the valve margins, especially ventrally. The ventral mantle margin has a huge gland discharging onto the inner but widely open surfaces of the mantle: does the secretion from this constitute a further defensive adaptation? In the absence of any knowledge about the composition of the secretion from this gland, it is impossible to hypothesize further, but it does not stain for simple mucus.

As noted above, it is thought possible that the major predator of *Chione elevata* on the Atlantic side of the Florida Keys is *Naticarius canrena*. In this study, one such aquarium-held predator did attack the bivalve successfully in the position identified for the great majority of the field-collected empty and drilled valves, that is, postero-dorsally. It is not known for certain, however, if this species made the drill holes at the marginal lamellae. However, since very few drillings represented failed attempts, it is clear that if *N. canrena* is the predator, it has apparently successfully overcome the seemingly impenetrable defenses of *C. elevata* by attacking it at the posterodorsal interlamellar spaces. Younger predators also attack younger prey as with juvenile *Polinices duplicatus* feeding on *Gemma gemma,* that is, drill hole diameter is related directly to predator size (Wiltse, 1980). This has also been demonstrated for *Polinices lewisii* feeding on the littleneck clam, *Protothaca staminea* by Peitso et al. (1994). A thick shell characteristically protects bivalves from drilling predators, for example, *Corbula crassa* in Hong Kong (Morton, 1990b), although Borzone (1988) showed that a species of *Polinices*, as demonstrated here for *N. canrena*, selectively drilled its prey, *Venus antiqua*, in the thickest region of the shell, that is, umbonally. Although no measurements were taken of *C. elevata* shell thickness at the drill hole sites, the posterodorsal region is the thickest, and *N. canrena* has therefore clearly overcome the bivalve's defenses by selective drilling according to relative prey size and shell location characteristics.

The most interesting question derived from this study, however, is: how is it that Indo-Pacific species of *Bassina* and *Placamen* have evolved strong shell lamellae that protect them from side-drilling species of *Natica* but have been overcome by edge-boring species of *Polinices* (Morton, 1985; Ansell & Morton, 1985, 1987), whereas the same shell defences of *Chione* offer no protection from side-drilling *Naticarius* in the western Atlantic?

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OYSTERS OF THE CONCH REPUBLIC (FLORIDA KEYS): A MOLECULAR PHYLOGENETIC STUDY OF *PARAHYOTISSA MCGINTYI*, *TESKEYOSTREA WEBERI* AND *OSTREOLA EQUESTRIS*

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ABSTRACT

We investigated the evolutionary relationships of three species of Florida Keys oysters, *Parahyotissa mcgintyi*, *Teskeyostrea weberi*, and *Ostreola equestris*, using nuclear and mitochondrial (mt) phylogenetic trees. Both 28S (nuclear) and 16S (mt) ribosomal gene trees consistently recovered a paraphyletic *Parahyotissa* in which *P. mcgintyi*, the type species, was robustly sister to a tip clade containing *P. numisma* and *Hyotissa hyotis*. This topology implies that there is no phylogenetic basis for *Parahyotissa* Harry, 1985, and we therefore recommend that all hyotissinid taxa be returned to the genus *Hyotissa* Stenzel, 1971. Phylogenetic placement of *T. weberi* within brooding oyster mt 16S gene trees conclusively demonstrated that it is a distinct ostreinid lineage, lacking any obvious candidate sister species, and falsified the hypothesis that it is a free-living ecomorph of the sponge commensal *Cryptostrea permollis*. Population-level mt COI sequence analysis of American *Ostreola equestris* and New Zealand *Ostrea aupouria* revealed that these two globally disjunct ostreinids, though remarkably close relatives, are reciprocally monophyletic sister taxa. Unlike a large fraction of the Floridian nearshore marine biota, *O. equestris* shows no evidence of a vicariant phylogenetic break distinguishing Gulf of Mexico and Atlantic populations. Our results imply that its present day Gulf/Atlantic distribution has been achieved by range extension from source Atlantic populations followed by a demographic growth pulse in the new Florida Keys/Gulf of Mexico habitats. *Ostreola equestris* individuals display an impressive range of shell morphs and coloration, some externally resembling *T. weberi*, and we present a plate of genotyped individuals that document this diversity.

Key words: Ostreidae, Gryphaeidae, systematics, biogeography, Florida, molecular phylogeny.

INTRODUCTION

The Florida Keys archipelago extends 362 km SW from the tip of peninsular Florida, separating Florida Bay from the Straits of Florida. This subtropical island chain represents the exposed surface layer of a much larger carbonate platform and has a rich bivalve fauna, estimated at approximately 325 species (Mikkelsen & Bieler, 2000). The strategic goal of the International Marine Bivalve Workshop, held at the Keys Marine Laboratory (Long Key) from 19–30 July 2002, was to expand our knowledge of targeted segments of this fauna. We elected to study the local oyster taxa, or at least that fraction accessible by wading, snorkeling and SCUBA diving during our limited sampling window.

Although oysters are among the most studied marine invertebrate taxa, their taxonomy and systematics is still fraught with uncertainty due to their xenomorphic post-larval growth patterns (Ranson, 1951; Quayle, 1988; Yamaguchi, 1994), relative dearth of tractable anatomical characters, and extensive anthropogenic global transfer (Dinamani, 1971; Edwards, 1976; Buroker et al., 1979; Chew, 1990; Carlton & Mann, 1996). Harry's (1985) ambitious taxonomic revision, based largely on morphology, represents the most recent comprehensive reclassification of living oysters. Subsequently, a number of de-

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tailed paleontological studies (Malchus, 1990; Malchus & Aberhan, 1998; Dhondt et al., 1999), together with a steady trickle of molecular phylogenetic analyses (Reeb & Avise, 1990; Littlewood 1994; Banks et al., 1993, 1994; Anderson & Adlard, 1994; Hare & Avise, 1998; Boudry et al., 1998; Ó Foighil et al., 1998; Jozefowicz & Ó Foighil, 1998; Ó Foighil & Taylor, 2000; Campbell, 2000; Steiner & Hammer, 2000; Lam & Morton, 2001; Giribet & Wheeler, 2002; Lapegue et al., 2002), have significantly refined our understanding of many aspects of ostreoidean evolution and systematics.

The ostreoidean fauna of the Florida Keys is atypical in that the ecologically dominant cupped oysters of the adjacent Caribbean and Atlantic seaboards are almost completely absent. Although isolated records occur in the Keys (Mikkelsen & Bieler, 2000), we did not encounter specimens of either the temperate *Crassostrea virginica* (Gmelin, 1791), or the tropical *C. rhizophorae* (Guilding, 1828) (Ostreidae, Crassostreinae). *Crassostrea virginica* populations are critically dependent on estuarine conditions, absent from the Keys, where salinity variation acts to reduce biotic competition and parasitism (Galtsoff, 1964; Ford & Tripp, 1996; Shumway, 1996).

Our sampling efforts yielded three distinct oyster groupings. By far the most common were small flat oysters (Ostreidae, Ostreinae), displaying an impressively diverse and overlapping range of shell morphology and coloration. Based on shell phenotype, many of these were readily identifiable as either *Ostreola equestris* (Say, 1834) or *Teskyostrea weberi* (Olsson, 1951); however, quite a few individuals were difficult to place with confidence. During dives, we encountered specimens of the gorgonian-associated *Dendostrea frons* (Linné, 1758) (Ostreidae, Lophinae) and the equally distinctive *Parahyotissa mcgintyi* Harry, 1985 (Gryphaeidae, Pycnodonteinae). We focused our efforts on the gryphaeid and flat oysters as they require the most systematic attention. In particular, we addressed the following four questions.

Systematic Placement of *Parahyotissa mcgintyi* Harry, 1985

Harry (1985) reorganized the gryphaeid (pycnodonteinid) tribe Hyotissini into the monotypic Indo-Pacific genus *Hyotissa* and a new genus *Parahyotissa* (containing three subgenera and four species) which includes the tropical Atlantic type species *P.* (*Parahyotissa*) *mcgintyi*, and the Indo-West-Pacific *P.* (*Numismoida*) *numisma* (Lamarck, 1819). He distinguished among the two hyotisssinid genera mainly by the relative degree of opening of the left promyal passage: open but reduced in *Hyotissa*, closed in *Parahyotissa*. We aimed to test the phylogenetic robustness of this generic reorganization by constructing nuclear and mitochondrial ribosomal gene trees incorporating these three taxa together with a neopycnodontinid gryphaeid, *Neopycnodonte cochlear* (Poli, 1795), that is sister to the Hyotissini (Ó Foighil & Taylor, 2000).

Phylogenetic Status of *Teskyostrea weberi*

Olsson (1951) considered *Ostrea weberi* to be the most distinctive regional species of oyster, and designated Key West as its type locatity. Harry (1985) supported its taxonomic distinctiveness, placing it in a monotypic new genus, *Teskeyostrea*. Alternatively, Abbott (1974) regarded *T. weberi* as a free-living ecophenotype, and junior synonym, of the sponge commensal *Cryptostrea permollis* (G. B. Sowerby II, 1871), and this taxonomic interpretation has been largely followed in the subsequent literature (Carriker & Gaffney, 1996). *Cryptostrea permollis* is recorded from the northeastern Gulf of Mexico and off North Carolina (Harry, 1985), and we did not encounter it in the Florida Keys. There are multiple records of *C. permollis* in the Florida Keys (Mikkelsen & Bieler, 2000); however, these refer to free-living, *T. weberi* (R. Bieler, pers. comm.). Jozefowicz & Ó Foighil (1998) incorporated, for comparative purposes, Keys specimens they identified as *T. weberi* in their molecular study of Southern Hemisphere flat oysters. However, they were unaware that the range of shell ecomorphs produced by another Keys ostreinid, *Ostreola equestris*, overlaps with that of *T. weberi*. Subsequent unpublished work by one of the authors (P. Baker) showed conclusively that the "*T. weberi*" specimens sequenced by Jozefowicz & Ó Foighil (1998) were actually *O. equestris*. The phylogenetic placement of *T. weberi* therefore still remains to be established. We revisited this issue by generating mitochondrial genotypes – large ribosomal subunit (16S) – from authentic *T. weberi* and incorporating them, together with *C. permollis* and *O. equestris* genotypes, into a phylogenetic analysis of brooding oysters.

Biogeographic Relationships of *Ostreola equestris* and *Ostrea aupouria* (Dinamani & Beu, 1981)

Jozefowicz & Ó Foighil (1998) uncovered a number of unexpectedly close phylogenetic relationships among geographically disjunct ostreinid taxa. Their Keys *Ostreola equestris* samples (misidentified as *Teskeyostrea weberi*, see above) differed from specimens of the New Zealand *O. aupouria* by as little as a single transversion in their mt 16S large subunit ribosomal gene fragments. We aimed to revisit this surprising biogeographic pairing by utilizing Cytochrome Oxidase I (COI), a faster-evolving mt gene fragment more useful in resolving oyster tip taxa (Ó Foighil et al., 1998), and by incorporating samples of *O. equestris* spanning the well-defined Gulf/Atlantic marine biogeographic break in southeastern Florida (Avise, 1992, 2000; Cunningham & Collins, 1994). In the absence of post-separation gene flow, the process of lineage sorting is expected to sequentially lead newly formed daughter populations from initial polyphyly, to paraphyly, and ultimately to reciprocal monophyly (Avise, 2000). We were interested in establishing whether these disjunct New Zealand/American populations were reciprocally monophyletic, or if one was a recent founder of the other. Another objective was to determine how the *aupouria/equestris* genetic disjunction scaled relative to the anticipated Gulf/Atlantic break in *O. equestris*. Two hypothetical topologies, each containing an *O. equestris* Gulf/Atlantic disjunction, are presented as exemplars in Figure 1. There are of course many other topological possibilities.

Shell Phenotype Variation in *Ostreola equestris*

Ostreola equestris is commonly known as the "crested" oyster and, as its informal name implies, it is described as having a shell with raised crenulated margins (Abbott, 1974). We encountered this morph in intertidal Keys habitat; however, subtidal individuals, genotyped in this study for mt markers, were usually cemented to the substratum along their entire left valves, yielding a very thin, contour-hugging, morph that exhibited a wide variety of coloration and sculptural texture, some of which closely approximated the *Teskeyostrea weberi* phenotype (Olsson, 1951; Harry, 1985). Employing genotyped individuals only, we aimed to give a photographic summary of the impressive range of shell phenotypes displayed by our samples of this species.

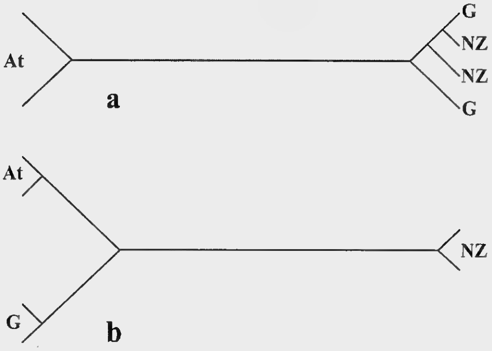

FIG. 1. Two exemplary unrooted mitochondrial tree topologies predicted by distinct hypotheses of historical relationships among geographically disjunct sister populations of New Zealand (*Ostrea aupouria*) and American (*Ostreola equestris*) ostreinids. Both hypotheses assume *a priori* that *O. equestris* has undergone cladogenesis into distinct Atlantic (At) and Gulf (G) lineages, a well-documented pattern among coastal Floridian marine taxa (Avise, 1992, 2000; Cunningham & Collins, 1994). There are of course many other hypothetical topologies that could be entertained. a, *O. aupouria* (NZ) represents a recent founder population of Gulf *O. equestris* (G) and genotypes of the former are predicted to nest within a Gulf tip clade; b, *O. aupouria* (NZ) has experienced a distinct evolutionary history that predates the origin of the Gulf/Atlantic disjunction in *O. equestris* and all three groupings are predicted to be reciprocally monophyletic with the stem branch leading to *O. aupouria* (NZ) being the most pronounced.

MATERIALS AND METHODS

A summary of sampling locations and of voucher specimen information is outlined in Table 1, and specific sampling details for Floridian taxa are given in the following paragraphs. For specimens collected in the Florida Keys, all collections were made via snorkeling in depths from 1–5 m, except collections from IMBW-FK-650 where SCUBA was used to sample specimens from roughly 30 m. These specimens were preserved in 95% denatured alcohol and then transferred to 95% non-denatured alcohol upon return to the Department of Malacology at the Florida Museum of Natural History. Specimens collected elsewhere were sampled from shore and preserved in ≥ 70% ethanol.

TABLE 1. Species identification and sampling locality data, together with voucher specimen information. UMMZ and FLMNH numbers respectively refer to the voucher specimen catalog numbers of the Mollusk Division, University of Michigan Museum of Zoology, and the Department of Malacology, Florida Museum of Natural History. See Mikkelsen & Bieler (2004) for specific details concerning the International Marine Bivalve Workshop (IMBW-FL) sampling stations.

Taxa	Location	# of individuals sequenced	Catalog #
Family Gryphaeidae			
Subfamily Pycnodonteinae			
Parahyotissa mcgintyi	IMBW-FK-650	1	UMMZ 300092
Parahyotissa numisma	Guam	1	UMMZ 265996
Hyotissa hyotis	Guam	1	UMMZ 265995
Neopycnodonte cochlear	Maui, Hawaii	1	UMMZ 265997
Family Ostreidae			
Subfamily Ostreinae			
Teskeyostrea weberi	IMBW-FK-645	4	FLMNH 298644
Ostreola equestris	IMBW-FK-629	9	FLMNH 298643
Ostreola equestris	IMBW-FK-644	1	FLMNH 298645
Ostreola equestris	IMBW-FK-649	1	FLMNH 298640
Ostreola equestris	Skidaway River, Georgia	11	UMMZ 300093
Ostreola equestris	Cedar Key, Florida	10	UMMZ 300094
Ostrea aupouria	Hauraki Gulf, New Zealand	12	UMMZ 255404
Cryptostrea permollis	Panacea, Florida	2	UMMZ 255410
Subfamily Crassostreinae			
Crassostrea virginica	Skidaway River, Georgia	3	UMMZ 300095
Crassostrea virginica	Panacea, Florida	2	UMMZ 300096

Parahyotissa mcgintyi

Numerous specimens of the gryphaeid *Parahyotissa mcgintyi* were sampled (by L. Kirkendale and G. Steiner) from the superstructure epibenthos of the sunken vessel *Thunderbolt* (IMBW-FK-650; Table 1) – apparently this species' first record from the Florida Keys (Mikkelsen & Bieler, 2000). *Parahyotissa mcgintyi* is easily distinguished from other regional oysters by its frequently plicated shell margins, absence of clasper spines, typically pycnodonteinid vesicular shell structure (Fig. 2), and presence (in live adult specimens) of a bright orange pigment in ovarian tissue (Harry, 1985). In order to test Harry's (1985) taxonomic rearrangement of the Hyotissini, we sequenced a 941nt (post-alignment length) fragment of nuclear 28S rDNA, added it to Ó Foighil & Taylor's (2000) homologous 28S ostreoidean matrix, and analyzed the resulting dataset utilizing pterioid outgroups (Giribet & Distel, 2003). A complementary gryphaeid mt 16S rDNA data set was constructed and then phylogenetically analyzed using *Neopycnodonte cochlear*, a sister taxon to the Hyotissini (Ó Foighil & Taylor, 2000), as an outgroup.

Teskeyostrea weberi

Specimens of *Teskeyostrea weberi* were recovered (by L. Kirkendale) from one of our sampling sites: the ocean-side shore of Grassy Key (IMBW-FK-645; Table 1), where it was locally abundant attached to the underside of large boulders at depths of 1–3 m. Positive identification of this species was made not only on the basis of its shell characters – flat, thin apricot-colored shell ornamented with fine radial ribbing and thin lamellose extensions (Olsson, 1951; Harry, 1985) – but also on its lack of an anal appendage, a prominent anatomical feature of *Ostreola equestris* (Harry, 1985). To place *Teskeyostrea weberi* phylogenetically, we generated mt 16S sequences for four individuals, yielding two haplotypes, which were incorporated into Jozefowicz & Ó Foighil's (1998) brooding oyster 16S matrix. This matrix was further supplemented by 16S sequences (two haplotypes) generated from 11 Florida Keys *Ostreola equestris* specimens sampled from three locations in the Florida Keys (Table 1). These latter specimens collectively displayed a wide variety of shell morphs, including *T. weberi* look-alikes, but exhibited

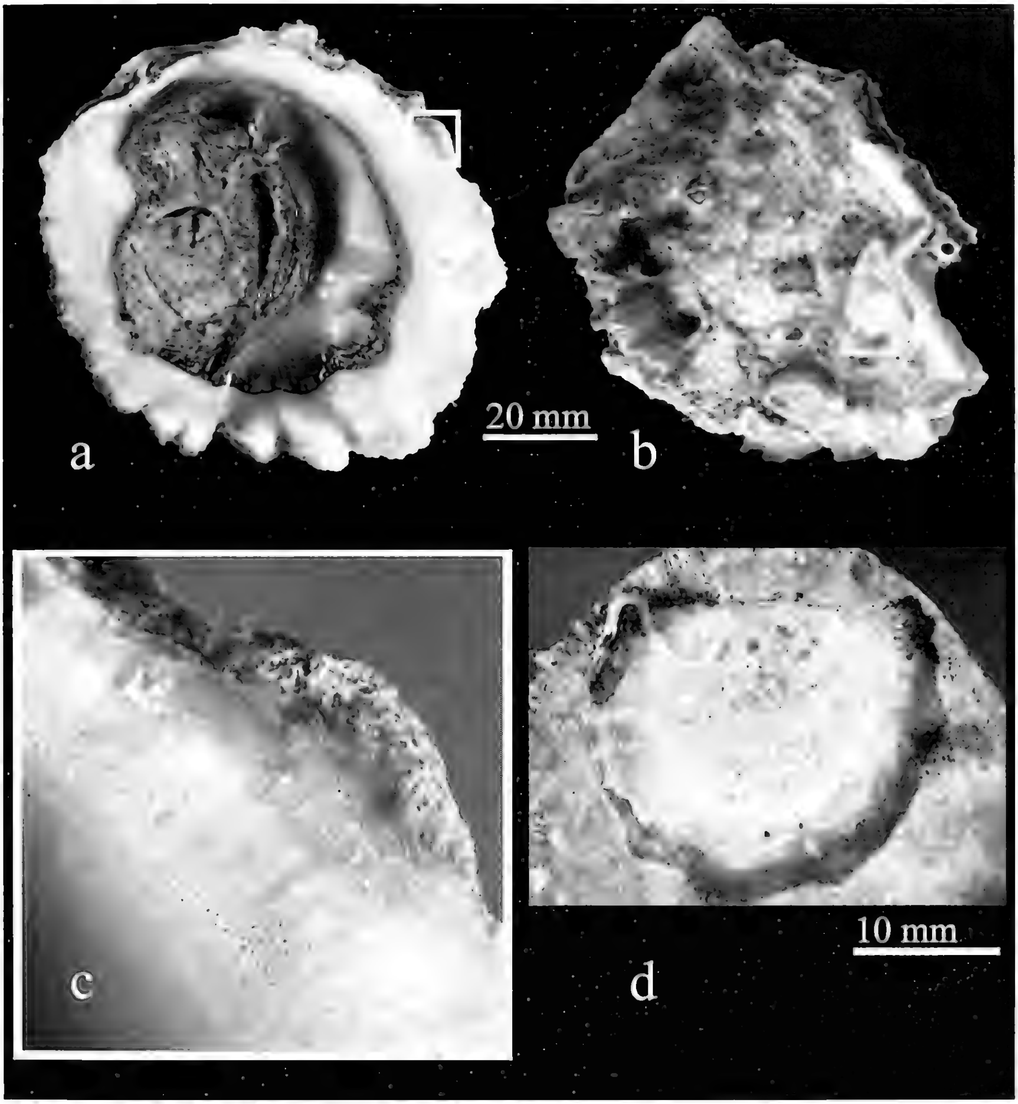

FIG. 2. Views of gross shell morphologies of adult and juvenile *Parahyotissa mcgintyi* specimens sampled from IMBW-FK-650. a, internal view of the left valve of an adult preserved in 95% ethanol after shucking (Note the prominent plication of the ventral valve margin); b, external view of the right valve of specimen depicted in 2a (Note the heavy fouling which obscures the valve outline); c, detail of anterio-dorsal inner edge of left valve of adult (see boxed area in 2a) showing the distinctive vesicular substructure characteristic of pycnodonteinid gryphaeids (Harry, 1985); d, external view of intact juvenile (note straight hinge line, flattened D-shaped profile and the vesicular substructure evident in abraded surface areas).

distinct anal appendages (mainly digitform, some more cardiform in outline). Finally, we added to the single available 16S haplotype of the sponge commensal *Cryptostrea permollis* by sequencing two additional specimens (Table 1).

Ostreola equestris

In order to more fully resolve the phylogenetic relationships of these geographically disjunct, polytomous (at least for 16S, Fig. 4), New Zealand/American tip taxa, a mt COI gene fragment (626 nt) data set was generated for a total of 44 individual oysters. Twelve New Zealand *Ostrea aupouria* – reliably distinguished by their possession of an anal appendage (Dinamani & Beu, 1981) from the co-occurring *Ostrea chilensis* (Philippi, 1844) – were sequenced, yielding 6 haplotypes, as were 32 *Ostreola equestris* specimens which collectively contained 15 haplotypes.

We were interested in establishing if *Ostreola equestris* exhibits a regional Gulf/Atlantic genetic break in southeastern Florida in common with many other co-occurring nearshore marine taxa (Avise, 1992, 2000; Cunningham & Collins, 1994) and, if so, how it might scale relative to the *equestris*/*aupouria* disjunction. In addition to Florida Keys specimens (N = 11, six haplotypes), our 32 *O. equestris* individuals sequenced for COI also included specimens from the northeastern Gulf of Mexico (Cedar Key, N = 11, seven haplotypes) and from the Atlantic coast of Georgia (Skidaway River estuary, N = 10, six haplotypes). To provide a phylogeographic yardstick, we also generated homologous COI sequences (598 nt) for a token number of replicate Gulf (Panacea, Florida Panhandle, N = 2, one haplotype) and Atlantic (Skidaway River, N = 3, 2 haplotypes) specimens of the cupped oyster *Crassostrea virginica*. This ecologically dominant regional oyster species displays a well-characterized Gulf/Atlantic mt disjunction centered on southeastern Florida (Reeb & Avise, 1990).

Molecular Methods

Specimens utilized in this study were processed for molecular characterization either at the University of Florida (by L. Kirkendale) or the University of Michigan (by T. Lee). As a result, there were some minor methodological distinctions associated with DNA template preparation and PCR amplification as referred to below. All novel DNA sequences were generated at the University of Michigan's DNA Sequencing Core and have been deposited in GenBank (Accession #s AY376596–AY376635).

Genomic extractions and amplifications of flat oyster samples collected during the Florida Keys Bivalve Workshop were conducted by L. Kirkendale at the Florida Museum of Natural History Molecular Phylogenetics Lab at the University of Florida (UF). Total genomic DNA was obtained from ethanol-preserved mantle tissue using modifications of standard protocols. Roughly 20–30 mg of tissue was finely cut, ground with a mortar and pestle and placed in 750 µL of DNAzol with 5–20 µL of 5–20 mg/ml proteinase K (Molecular Research Center, Inc.). Tissue was gently shaken overnight on an orbital shaker and following three rounds of ethanol extraction and centrifugation, the pellet was eluted in 100 mL ddH20 (for further details of DNAzol extraction procedure, refer to Chomczynski et al. 1997). Universal primers were used to amplify 16S and COI gene regions sequenced from the above-mentioned samples and were as follows: 16Sar 5'-CGCCTGTTTATCAAAAACAT-3' and 16Sbr 5'-GCCGGTCTGAACTCAGATCACGT-3' (Kessing et al. 1989) and LCO1490 5'-GGTCAACAAATCATAAAGATATTGG-3' and HCO2198 5'-TAAACTTCAGGGTGACCA AAAAATCA-3' (Folmer et al., 1994). Reactions included 1µL of genomic DNA template and 31.8 µL ddH2O, 5 µL of 10X TAQ PCR buffer (Perkin Elmer), 5 µL of dNTPS (10 mM stock), 2 µL of each primer (10 µM stock), 3 µL of MgCl2 solution (25 mM stock, Perkin Elmer) and 0.2 µL TAQ enzyme (Perkin Elmer). Reactions for 16S were initially denatured at 96°C for 150 sec, followed by 37 cycles of 94°C for 40 sec, 52°C for 35 sec, and 72°C for 60 sec. Reactions for COI were handled similarly except that the initial denaturation step was at 95°C for 120 sec and that 40 cycles of amplification were employed with a 40°C annealing temperature. All amplifications were run with positive and negative (no template) controls. PCR products were visualized by electrophoresis on 1% TBE agarose gels, stained with ethidium bromide solution and photodocumented. Successful PCR products were cleaned for cycle sequencing using Wizard PCR Preps (Promega), following described protocols. Verification of the cleaned PCR product occurred in the same manner as for initial PCR products.

Ostreola equestris samples from Cedar Key were extracted at UF, as above, but amplified at the Museum of Zoology, University of Michigan (UMMZ), by T. Lee, along with Skidaway River *O. equestris* samples, using specifically designed COI primers: 5'-GATATTGGACGGTTTT ATAT-3' and 5'-CCAAAAATCAAAACAATGCT-3' (Lee, unpublished). DNA template preparation methods utilized at the UMMZ are detailed in Lee & Ó Foighil (2003). Other target gene fragments amplified at the UMMZ were mt 16S from *Cryptostrea permollis* and from the four gryphaeid study species (Table 1) using Kessing et al. (1989) primers, 28S nuclear ribosomal domains 1–3 from *Parahyotissa mcgintyi* using Ó Foighil & Taylor's (2000) primer set, and mt COI from *Ostrea aupouria*, and *Crassostrea virginica* Gulf (Panacea) and Atlantic (Skidaway River) samples using Folmer et al. (1994) primers. A touchdown (Palumbi, 1996) protocol was used for all UMMZ PCR reactions [after 4 min denaturation at 94°C, the initial annealing temperature of 65°C was decreased by 2°C/cycle (40 sec denaturing at 94°C, 40 sec annealing and 1.5 min extension at 72°C) until the final annealing temperature (45°C for COI, 50°C for 16S and 52°C for 28S) was reached and subsequently maintained for an additional 30 cycles].

Phylogenetic Methods

Initial alignments were constructed using Clustal X (Thompson et al., 1997) using default parameters and then adjusted by eye to minimize mismatches in the ribosomal gene datasets. Phylogenetic analyses were conducted on each of six molecular datasets – (1) gryphaeid 28S, (2) gryphaeid 16S, (3) Ostreid/Lophinid 16S, (4) *Ostrea aupouria/ Ostreola equestris* COI, (5) *O. equestris* COI, and (6) *Crassostrea virginica* COI – under the maximum parsimony (MP) optimality criterion using PAUP*4.0b10 (Swofford 2002). While unrooted anayses were performed on COI datasets, the pterioid taxa, *Neopycnodonte cochlear*, and lophinid taxa were designated as outgroup for gryphaeid 28S, gryphaeid16S and ostreid 16S datasets respectively. MP analyses were performed using heuristic search option with 100 random stepwise additions and tree bisection-reconnection (TBR) branch-swapping. Gaps were treated as a missing state, character states were treated as unordered and equal weights were assumed. Branch support was estimated by bootstrapping (Felsenstein, 1985) (500 replicates, heuristic searches, 10 random additions each) and decay indices (Bremer, 1994), generated in TreeRot (Sorenson, 1996).

We wished to construct unrooted gene networks for three COI datasets (*Ostreola equestris* and *O. aupouria*; *O. equestris* alone, *Crassostrea virginica* alone) and took a Maximum likelihood (ML) approach because two of the three (*O. equestris* and *O. aupouria*; *O. equestris* alone) produced multiple equally most parsimonious trees. A MP tree was first used to estimate the log-likelihood scores using PAUP*. The best-fit ML model for each partition was then determined by hierarchical likelihood ratio tests (hLRTs) using Modeltest 3.06 (Posada & Crandall, 1998). ML analyses were conducted using a heuristic search option in which the parameter values under the best-fit model were fixed and a MP tree was used as a starting point for TBR branch swapping. The K81uf model [K81 model (Kimura, 1981) with unequal base frequencies] + Γ [gamma-distributed heterogeneity of the substitution rate across sites (Yang, 1994)] was chosen as the best-fit model for the combined *Ostreola equestris* and *O. aupouria* dataset. For the *O. equestris* and *C. virginica* COI datasets, the respective best-fit models chosen were K81uf and HKY (Hasegawa et al., 1985).

RESULTS

Systematic Placement of *Parahyotissa mcgintyi*

Figure 3 shows the most parsimonious gene tree obtained when a *P. mcgintyi* 28S genotype was added to, and analyzed with, Ó Foighil & Taylor's (2000) ostreoidean 28S dataset. We obtained a paraphyletic *Parahyotissa* and a robust terminal sister relationship for the two Pacific Hyotissini: *P. numisma* and *Hyotissa hyotis*. A congruent topology was recovered when the 16S sequences for the four gryphaeid taxa at our disposal (Table 1) were subjected to a maximum parsimony analysis (Fig. 3). The earlier study (Ó Foighil & Taylor, 2000) should be consulted for a detailed discussion of the ostreid clade topology.

Phylogenetic Status of *Teskyostrea weberi*

Figure 4 shows the strict consensus topology of the 54 most parsimonious trees obtained when the brooding oyster 16S matrix was analyzed using the lophine taxa as outgroups. Major elements of the topology are congruent with that obtained, and discussed at length, in an earlier study (Jozefowicz & Ó Foighil, 1998) and will not be reiterated here. The salient features of the topology concern the relative placement of the three Floridian flat oyster taxa (labeled in bold text). All three occur in distinct, well-supported terminal clades: *Teskeyostrea weberi* on its own, *Ostreola equestris* in a terminal polytomy with the New Zealand *Ostrea*

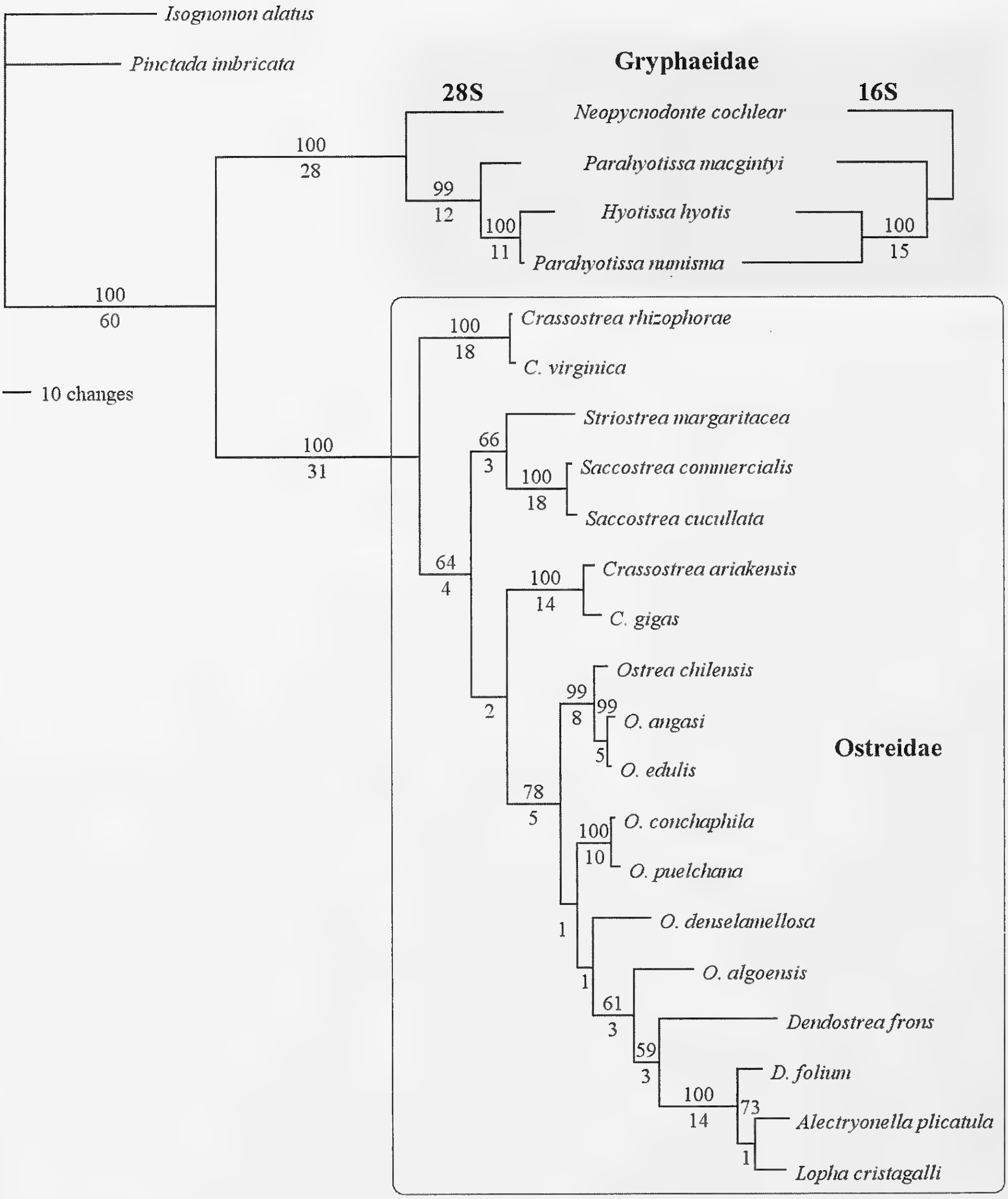

FIG. 3. The single most parsimonious tree (809 steps, CI = 0.668, RI = 0.779) obtained by heuristic unweighted searches of 28S genotypes for 22 oyster taxa, including 4 gryphaeid species, with the two pterioids, *Pinctada* and *Isognomon*, designated as outgroups. See also the juxtaposed single most parsimonious tree (173 steps, CI = 0.948, RI = 0.710) obtained by heuristic unweighted searches of gryphaeid mt 16S genotypes, in which *Neopycnodonte cochlear* was the designated outgroup. Numbers above the branches represent bootstrap values (> 50) and numbers below indicate decay index values.

aupouria, *Cryptostrea permollis* in a terminal polytomy with the Argentine *Ostrea puelchana*. A prominent basal ostreinid (+ *Dendostrea frons*) polytomy captures the branch supporting the *T. weberi* tip clade (Fig. 4), thereby obscuring its sister relationships.

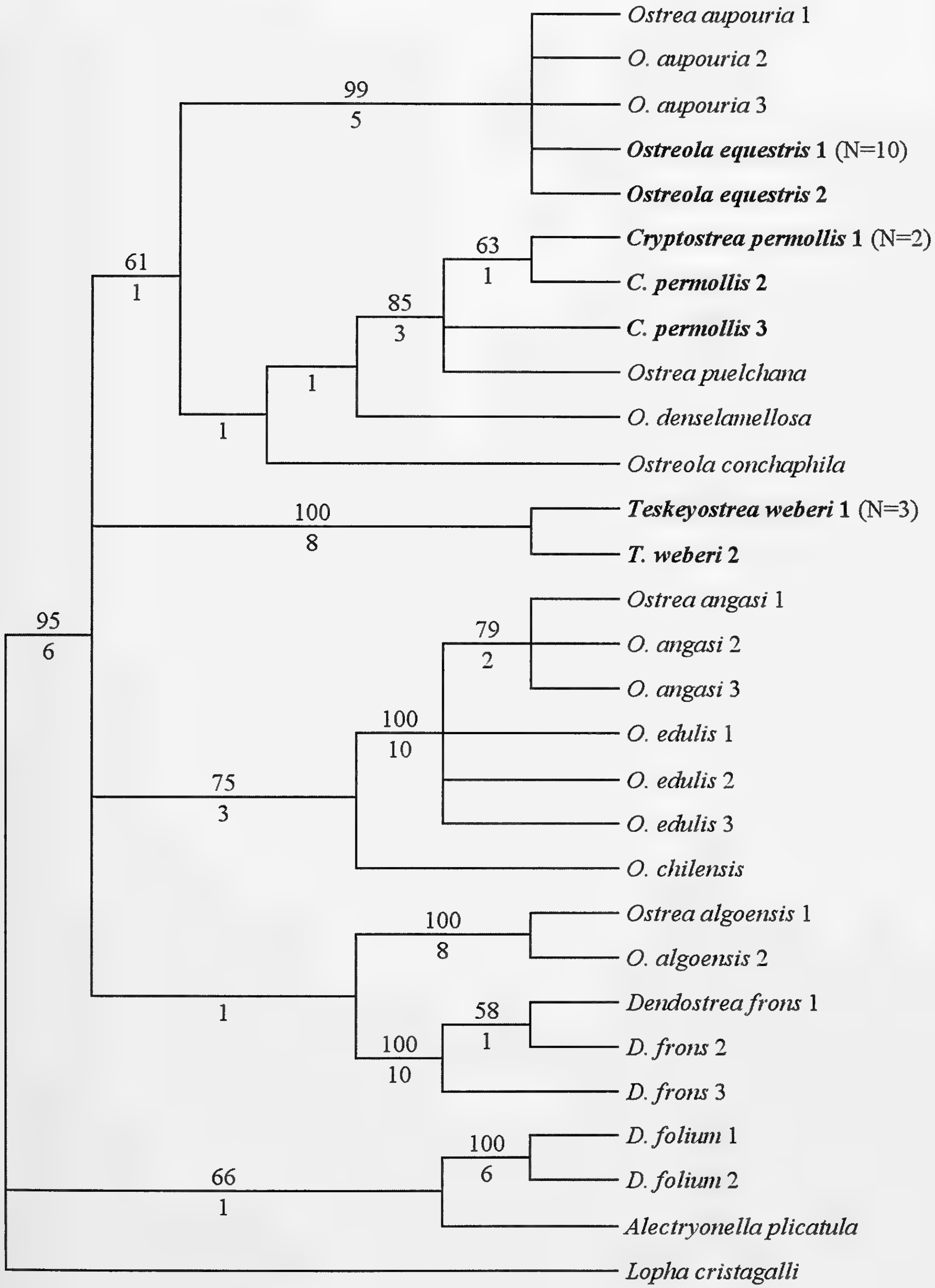

FIG. 4. Strict consensus of 54 equally most parsimonious trees (174 steps, CI = 0.6379, RI = 0.8437) resulting from heuristic unweighted searches of 29 brooding oyster 16S genotypes. The lophine taxa *D. folium*, *D. frons*, *A. plicatula* and *L. cristagalli* were designated as outgroups. Florida Keys ostreinid taxa are in boldface. Bootstrap values (> 50) and decay indices are shown above and below the branches, respectively.

Biogeographic Relationships of *Ostreola equestris* and *Ostrea aupouria*

A maximum-likelihood analysis of the combined American *Ostreola equestris* and New Zealand *Ostrea aupouria* COI dataset is shown as an unrooted network in Figure 5. New Zealand and American samples were reciprocally, and robustly, monophyletic. Note however, that the minimum cumulative branch lengths separating members of the two clades was less than that of the maximum branch lengths separating within-clade *O. equestris* haplotypes.

Figure 6 concerns only American taxa and shows the unrooted maximum-likelihood Gulf/Atlantic COI networks for both *Ostreola equestris* and *Crassostrea virginica*. The *Crassostrea virginica* Gulf/Atlantic phylogenetic split, estimated by Reeb & Avise (1990) from whole mt genome RFLP assays at approximately 2.5% divergence, was also recovered from our token sample of Gulf/Atlantic CO I gene fragment sequences (1.8%; 11 substitutions over 598 nt). In sharp contrast, no such disjunction was evident in *Ostreola equestris*. Two haplotypes were found in all three regional populations (Table 2, Fig. 6), including by far the most common mt COI genotype (AFG1; N = 13). This latter mt genotype was numerically predominant in both Gulf (Cedar Key, 6/11) and Florida Keys (5/11) samples of *Ostreola equestris*, but not among our Atlantic (Skidaway River sample; 2/10) specimens. If we consider the former two samples in isolation, the numerically predominant haplotype was centrally placed and connected to all but one (F4) of the

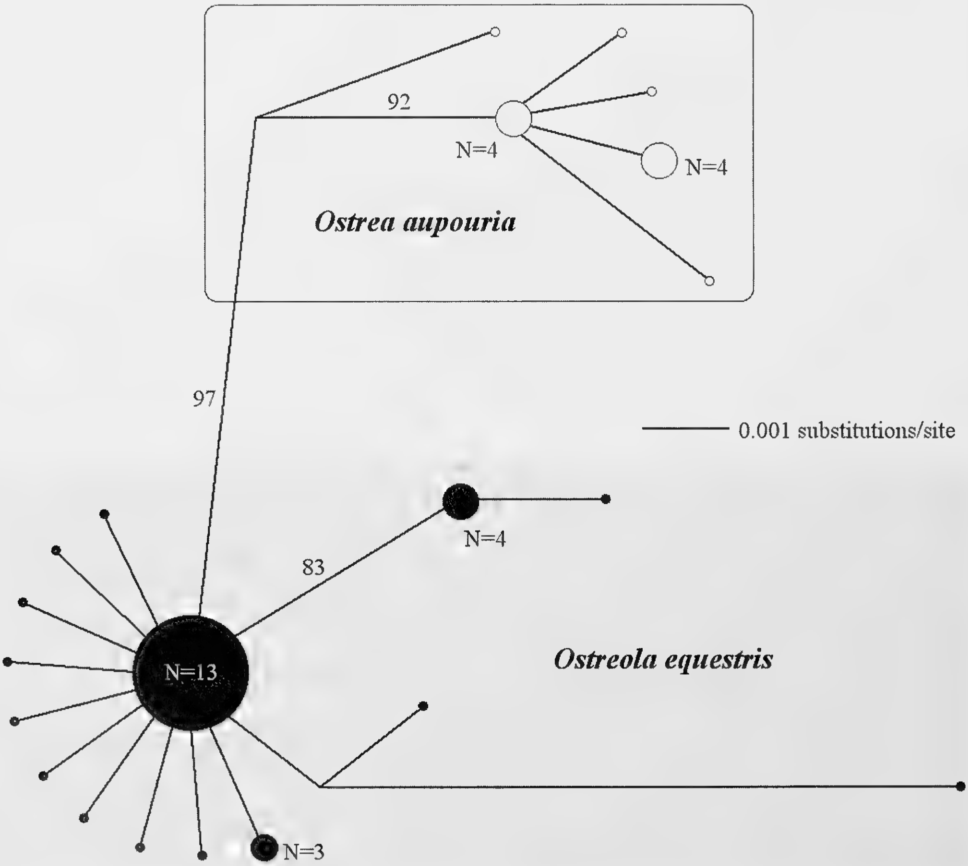

FIG. 5. Maximum likelihood network (-ln = 1073.4044) of *Ostrea aupouria* (New Zealand) and *Ostreola equestris* (American) COI haplotypes. Numbers on the branches are MP bootstrap values.

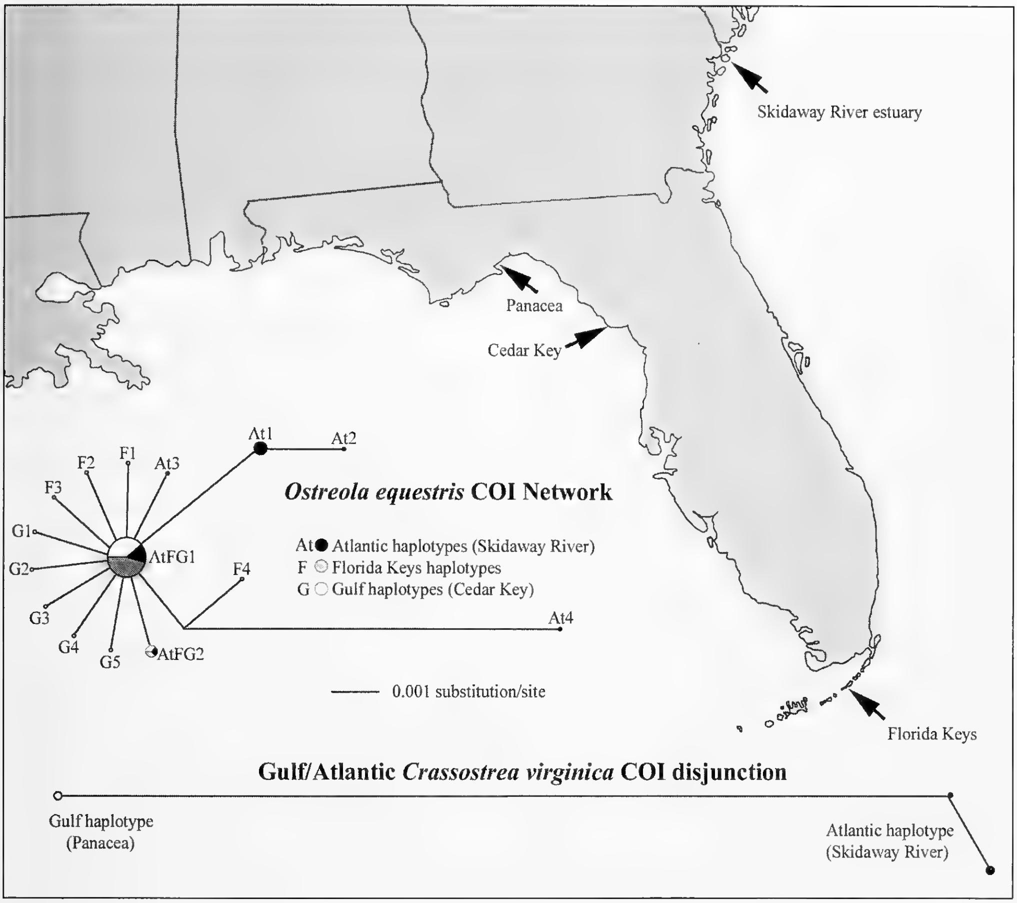

FIG. 6. Regional map showing our collection sites for Gulf/Atlantic *Ostreola equestris* and *Crassostrea virginica* samples and also the superimposed maximum likelihood networks of the resulting *O. equestris* (-ln = 985.5091) and *C. virginica* (-ln = 878.0842) COI haplotypes.

TABLE 2. Relative distribution of the 16 COI genotypes recovered from the three regional Gulf/Atlantic *Ostreola equestris* sampling locations. The prefixes At, F, G and AtFG, respectively indicate haplotypes found solely in the Atlantic (Skidaway River) site, solely in the Florida Keys sites, solely in the Gulf (Cedar Key) site, and finally, those recovered from all three sites. See Figure 6 for map showing sampling site locations and the inferred topological relationships among the COI haplotypes.

	AtFG1	AtFG2	At1	At2	At3	At4	F1	F2	F3	F4	G1	G2	G3	G4	G5	G6
Skidaway River	2	1	4	1	1	1	-	-	-	-	-	-	-	-	-	-
Florida Keys	6	1	-	-	-	-	1	1	1	1	-	-	-	-	-	-
Cedar Key	5	1	-	-	-	-	-	-	-	-	1	1	1	1	1	1

other 10 COI genotypes recovered from the Gulf (Cedar Key) and Florida Keys populations by single substitutions (Fig. 6). Our Atlantic (Skidaway River) sample exhibited a different topological pattern characterized by a relatively extensive network in which the constituent haplotypes showed more pronounced collective phylogenetic definition (Fig. 6).

Shell Phenotype Variation in *Ostreola equestris*

An impressive diversity of *O. equestris* shell phenotypes was recovered from the Florida Keys, and indeed also from single sampling sites, such as the Summerland Key Horseshoe. Intertidal Horseshoe specimens exhibited a shell morphology that is typically associated with this species: gray oval shells with raised crenulated margins (Abbott, 1974). Figure 7a shows a cluster of specimens showing this morphology, sampled in this particular case from the Skidaway River study population. Subtidal Florida Keys specimens were generally flatter in appearance, in some cases markedly so, and frequently incorporated a diversity of pigmentation colors and patterns, some of which are presented in Figure 7 (b–f). Exemplars spanning the range of *O. equestris* shell phenotypes found in the Horseshoe site, and other locations in the Keys, were genotyped using mt (16S and COI) markers and no evidence for genetic differentiation was evident among them. A minority of *O. equestris* individuals displayed shell phenotypes that resembled *Teskeyostrea weberi* in external appearance: very thin shells with golden brown pigmentation sculptured with fine radial ribbing and lamellose extensions (Fig. 7).

DISCUSSION

Systematic Placement of *Parahyotissa mcgintyi*

Our nuclear and mt ribosomal gene trees consistently recovered a paraphyletic *Parahyotissa* in which *P. mcgintyi*, the type species, was robustly sister to a tip clade containing *P. numisma* and *Hyotissa hyotis*. This topology implies that the character state used by Harry (1985) to distinguish *Parahyotissa* (closed left promyal passage) is plesiomorphic in extant Hyotissini, rather than a synapomorphy diagnosing a *Parahyotissa* clade, and that the condition in the monotypic genus *Hyotissa* (open but reduced left promyal passage) is autapomorphic. Based on available information, there seems to be no phylogenetic basis for Harry's *Parahyotissa*. Future research incorporating *P.* (*Parahyotissa*) *imbricata* (Lamarck, 1819) and *P.* (*Pliohyotissa*) *quercinus* (G. B. Sowerby II, 1871), may uncover more than one natural (i.e., monophyletic) group within the Hyotissini that can be defined by morphological synapomorphies and warrant generic status. Until then, we recommend that all hyotissinid taxa be returned to the genus *Hyotissa* Stenzel, 1971.

Phylogenetic Status of *Teskeyostrea weberi*

Our 16S strict consensus tree topology (Fig. 3) conclusively demonstrates that this species is not a free-living ecomorph of the sponge commensal *Cryptostrea permollis*, as thought by Abbott (1974), but is instead a distinct ostreinid lineage lacking (at present) any obvious candidate sister species. Olsson (1951) had proposed the eastern Pacific "*Ostrea iridescens*", synonymized with *Striostrea prismatica* (Gray, 1825) by Harry (1985), as a putative sister species to *T. weberi*, based on the similarity of the former's juvenile shell phenotype to that of the adult *T. weberi*. However, *S. prismatica*'s taxonomic placement in the cupped oyster subfamily Crassostreinae (Harry, 1985), which is supported by preliminary molecular data (Lee & Ó Foighil, unpublished), rules this out. A more comprehensive sampling of brooding oyster global diversity, including data from genes other than 16S, is required to better resolve *T. weberi*'s phylogenetic position within the Ostreinae/Lophinae.

Although *Teskyostrea weberi* and *Ostreola equestris* represent very distinct lineages (Fig. 3), they co-occur in the Florida Keys, and a fraction of latter species resemble *T. weberi* in their external appearance (Fig. 7). Fortunately, these *O. equestris weberi*-lookalikes can be distinguished upon dissection by their distinct anal appendage (Harry, 1985), and their relatively larger adductor muscle. Based on our preliminary observations, there may also be ecological and larval settlement differences among these two ostreinid taxa in the Florida Keys. All of the *T. weberi* specimens we encountered were attached to the underside of rocks (Harry, 1985: fig. 25) in an oceanside location, whereas *O. equestris* were commonly sampled from the exposed hard surfaces in bayside locations.

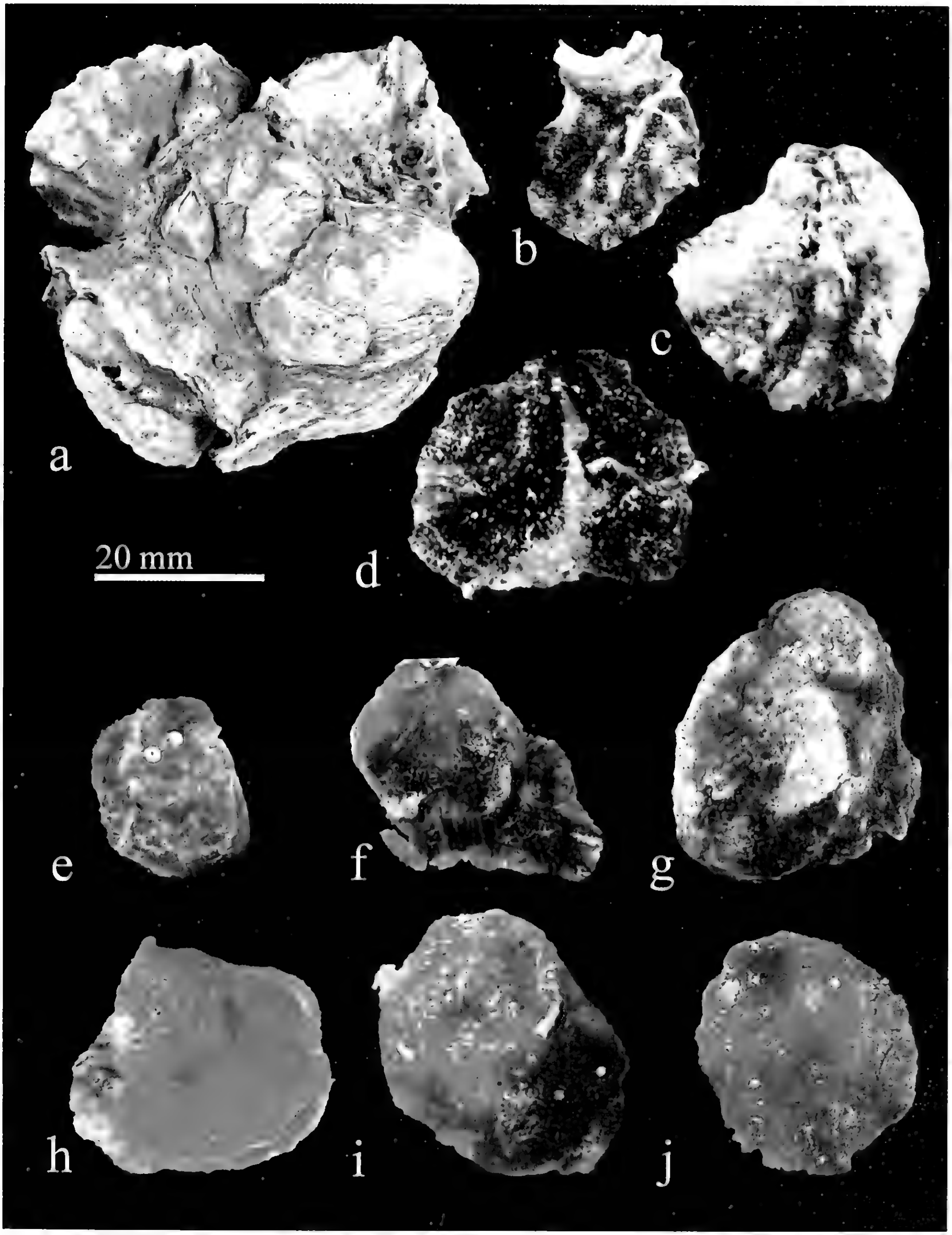

FIG. 7. Shell phenotypes. a–f, displayed by genotyped *Ostreola equestris* sampled from the Skidaway River, Georgia (a, cluster of individuals), and from 2 sites in the Florida Keys (b–e, IMBW-FK-629 from rock surfaces and f, IMBW-FK-649 epifaunal on *Pinna*); g, a specimen of *Ostrea aupouria*, New Zealand sister species of *Ostreola equestris* (UMMZ 255404); h, a specimen of the sponge commensal *Cryptostrea permollis* from Panacea, Florida Gulf Coast (UMMZ 255410); i and j, individuals of *Teskeyostrea weberi* sampled from IMBW-FK-645.

Biogeographic Relationships of *Ostreola equestris* and *Ostrea aupouria*

The COI gene tree topology (Fig. 5) demonstrates that our respective study populations of New Zealand *Ostrea aupouria* and Gulf/Atlantic *Ostreola equestris* are reciprocally monophyletic. This result is sufficient, at least for now, for retention of their respective specific status. Coan et al. (2000) rejected the separation of *Ostreola* from *Ostrea* based on morphological characters and the phylogenetic validity of Harry's (1985) *Ostreola* is questionable given that two of his three constituent species (*O. equestris* and *O. conchaphila*) are not sister taxa in our gene trees (Fig. 3). However, a definitive generic designation for *equestris* and *aupouria* requires data from the Mediterranean/African-Atlantic type species *Ostreola stentina* (Payraudeau, 1826).

Two lines of evidence indicate that the *Ostreola equestris*/*O. aupouria* disjunction results from evolutionarily recent dispersal rather than ancient vicariance. Maximum within-population COI genetic divergence for the Skidaway River sample exceeds the minimum New Zealand/American divergences obtained (Fig. 5). This result implies that the age of the *O. equestris*/*O. aupouria* disjunction may be less than the haplotypic lineage sorting time window for the Atlantic population of the *O. equestris*. Although we do not have a fossil-calibrated lineage-specific clock for any oyster, the well-studied Gulf/Atlantic *Crassostrea virginica* divergence has been dated, using "conventional calibrations" to approximately 1.2 myr (Reeb & Avise, 1990). Parsimony analysis of our token samples of Gulf/Atlantic *C. virginica* COI sequences found that they differed by 11 steps (1.83% of the 598 nt fragment). The minimum number of substitutions separating the New Zealand and American COI clades in parsimony analyses is six steps (0.95% of the 626 nt fragment). Although the resulting age estimate of 0.625 myr for the *O. equestris*/*O. aupouria* disjunction is undoubtedly crude, it is over two orders of magnitude less than the vicariant separation of New Zealand from Gondwanaland (Weissel & Hayes, 1977).

The *Ostreola equestris*/*O. aupouria* geographic disjunction is but one of three such cases involving tip taxa in the brooding oyster 16S gene tree (Fig. 3); the other two involve *Ostrea edulis*/*O. angasi* and *Crypytostrea permollis*/*Ostrea puelchana* and are discussed in Jozefowicz & Ó Foighil (1998). Although anthropogenic transoceanic oyster introductions have occurred on numerous occasions (Dinamani, 1971; Edwards, 1976; Buroker et al., 1979; Chew, 1990; Carlton & Mann, 1996; Boudry et al., 1998; Ó Foighil et al., 1998), we can, with some confidence, rule out such historic transfers among the New Zealand/American study populations (Fig. 4). This conclusion is based on their lack of shared COI haplotypes and on their reciprocal monophyly (Fig. 5), a phylogenetic relationship that is characteristic of populations that have not experienced evolutionary recent gene flow (Avise, 2000). It is possible, however, that such an event may have occurred involving yet-to-be-sampled, genetically differentiated portions of either species' ranges – according to Harry (1985), *O. equestris* occurs from North Carolina to Argentina.

Genetic Structuring of Gulf/Atlantic *Ostreola equestris* and *Crassostrea virginica*

Genetic characterization of near-shore marine taxa found on either flank of the Floridian peninsula have revealed cryptic phylogenetic disjunctions among diverse Gulf-Atlantic Carolinian faunal elements (Saunders et al., 1986; Bert, 1986; Avise et al., 1987; Bert & Harrison, 1988; Dillon & Manzi, 1989; Brown & Wolfingbarger, 1989; Cunningham et al., 1991; Sarver et al., 1992; Cunningham & Collins, 1994; Felder & Staton, 1994; Bert & Arnold, 1995; Duggins et al., 1995; Ó Foighil et al., 1996; Schizas et al., 1999; Avise, 2000; Collin, 2001, 2002), with by far the most intensively studied exemplar being the American oyster *Crassostrea virginica* (Reeb & Avise, 1990; Karl & Avise, 1992; McDonald et al., 1996; Hare & Avise, 1996, 1998; Hare et al., 1996). *Ostreola equestris* occurs in micro-sympatry with *C. virginica* throughout regional estuaries, although prior research has shown that *O. equestris* tends to be abundant only at high salinity portions of estuaries (Hoese, 1960). Surprisingly, our *O. equestris* mt COI data (Fig. 5, Table 2) show that this oyster species differs from *C. virginica*, and from a large fraction of the regional marine biota, in lacking a Gulf/Atlantic mt genetic disjunction. Absence of genetic structuring among Gulf and Atlantic populations is not unique to *O. equestris* (Gold & Richardson, 1998; Avise, 2000); however, our results indicate that these two co-occurring oyster species have experienced significantly different regional histories.

Another discrepancy among the two oyster mt datasets concerns the relative topological definition of Gulf and Atlantic populations. Beckenbach (1994) performed a cladistic analysis of Reeb & Avise's (1990) extensive (N = 232) *C. virginica* mt RFLP dataset and found that both Gulf and Atlantic populations were dominated by one or two common haplotypes. These occupied central positions in their respective clades and were separated by single steps from a large number of terminally positioned rare haplotypes. Our Gulf (Cedar Key) and Florida Keys samples of *Ostreola equestris* showed (either separately or jointly) essentially a similar topology; however, the Atlantic (Skidaway River) sample did not (Fig. 5). In the absence of significant homoplasy, the relative lengths of individual branches within a molecular phylogenetic tree topology are rough proxies for evolutionary time. In this context, it is interesting to note the markedly longer collective branch lengths interconnecting *Ostreola equestris* Atlantic haplotypes relative to the truncated area of the COI topology occupied by Gulf and Florida Keys haplotypes (Fig. 5). This topological distinction is consistent with an older evolutionary history for this species in the Atlantic section of its present-day regional range. The compact star-like haplotypic topology produced by Gulf (Cedar Key) and Florida Keys COI genotypes (Fig. 5) is characteristic of a population founded more recently by one ancestral type, presumably represented by the numerically predominant, topologically central, well-connected (Castelloe & Templeton, 1994) haplotype AFG1, found in all three study populations. Such a topology is also indicative of populations that have experienced a phase of rapid demographic growth, a process associated with lowered stochastic elimination of novel/rare lineages (Avise et al., 1984; Slatkin & Hudson, 1991; Moritz, 1996).

Our mt COI data for the three study populations of *Ostreola equestris* paint a regional history that differs in important respects from that of *Crassostrea virginica* and also from a large fraction of the local marine biota. The dominant regional theme is the presence of a Gulf-Atlantic phylogeographic break characterized by considerable geographic concordance in genetic structuring across diverse faunistic elements (Avise, 2000). This implies a coherent spatial patterning of vicariance and secondary contact events. In contrast, *O. equestris* shows no evidence of a vicariant imprint and our results imply that its present day Gulf/Atlantic distribution has been achieved by range extension from source Atlantic populations followed by a demographic growth pulse in the new Florida Keys/Gulf of Mexico habitats.

Shell Phenotype Variation in *Ostreola equestris*

Though forearmed with an awareness of the fabled xenomorphism of oysters, we were surprised at the extent to which *O. equestris*, the most commonly encountered ostreid in the Florida Keys, exhibited a multitude of shell phenotypes – a repertoire far from exhausted by our limited presentation in Figure 6. This facility is also a characteristic of *Ostrea aupouria*, its New Zealand sister taxon (Dinamani & Beu, 1981). Although genetic characterization is a reliable method for distinguishing co-occurring oyster species with overlapping shell morphs, the presence of a distinct anal appendage in *O. equestris* (Harry, 1985; but not all are digitiform) and in *O. aupouria* (Dinamani & Beu, 1981) is also particularily useful in this regard. It is unclear to what degree the phenotypic variation we observed in *O. equestris* reflects populational allelic diversity and/or local micro-environmental parameters, or what contribution this plasticity makes to the local ecological success of this small species – the numerically dominant Florida Keys oyster.

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HOW RELIABLE IS MORPHOLOGY BASED SPECIES TAXONOMY IN THE BIVALVIA? A CASE STUDY ON *ARCOPSIS ADAMSI* (BIVALVIA: ARCOIDEA) FROM THE FLORIDA KEYS

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ABSTRACT

A morphological study of *Arcopsis adamsi* was made on three populations from contrasting biotopes, supralittoral, sublittoral (1 m depth) and offshore (8–10 m depth). Shell morphometrics gave statistically significant differences and these were supported by subjective observations on shell sculpture, periostracum and haemoglobin content. The observations form the core of a discussion on the reliability of morphological characters when defining species taxonomy. It must still be recognised that bivalve growth can strongly affect shell morphology and that sculptural and anatomical differences can be the result of environmental differences. The influence of geographical separation or isolation of populations probably unduly influences taxonomic decision making. Such decision making requires consideration of ecological factors and should now be more widely supported by molecular studies at the population level.

Key words: *Arcopsis*, morphology, species taxonomy, growth effects.

INTRODUCTION

This paper is a result of a taxonomic training workshop organised under the U.S. National Science Foundation PEET Initiative and reflects on one issue of bivalve taxonomy, namely the reliability of morphological characters at the species level.

Current bivalve species taxonomy remains primarily based on morphological characters and species identification relies mostly on shell characters. Introducing students to bivalve taxonomy is often problematic because many characters, both shell and anatomical, are subtle parts of a continuum and not discreet. Compounding this are the widespread phenomena of ecophenotypic and geographic clinal variation.

Arcopsis adamsi (Dall, 1886) is a relatively common species inhabiting both intertidal and sublittoral biotopes (Abbott, 1974) and was chosen because it or similar taxa had already appeared in morphometric analyses (Marko & Jackson, 2001; Oliver & Cosel, 1992). In these instances, the comparisons were made across isolation barriers or along large geographical ranges. Analysing morphological variation at a much smaller geographical scale has not been done within the Arcoidea. *Arcopsis adamsi* is a common component of intertidal, sublittoral and offshore mixed rock and sand biotopes to recorded depths of 10 m. It is generally found attached by a weak byssus to the undersides of rocks resting on sand. It is widespread in the subtropical and tropical western Atlantic and Caribbean Sea ranging from Brazil to North Carolina. In the tropical eastern Atlantic it has a sister species, *Arcopsis afra* (Gmelin, 1791) (Figs. 8, 9), that occurs along with the closely related *Striarca lactea* (Linnaeus, 1758) (Figs. 14, 15). In the western Atlantic, in contrast, the genus *Striarca* is not represented in the Recent fauna. A similar situation occurs in the Pacific Panamic region where *Arcopsis solida* (Sowerby, 1833) is the sole representative of the Striaciinae. *Arcopsis* species may therefore fill a much broader niche in the Americas and may have radiated into cryptic species.

This study examines the biotope range of *Arcopsis adamsi* in the Florida Keys and compares the morphology of populations from different biotopes. The primary aim of this paper is to draw attention to issues that students will encounter when undertaking species-level taxonomy studies and is intentionally discursive in nature. Many questions about *Arcopsis* taxonomy are raised by this study and both authors are aware that the solutions are not provided although methodologies are proposed.

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MATERIALS AND METHODS

Materials

The materials used in the morphometric analysis are housed in the National Museum of Wales, Cardiff, under the specific numbers cited below. All additional materials are also housed in the National Museum of Wales under NMW.Z.2003.075.

Arcopsis adamsi was found in four biotopes.

(1) Supralittoral crevices

Collection site: IMBW-FK-629, 21 & 26-VII-02, “The Horseshoe” bayside of West Summerland Key, MM35, Monroe County, Florida Keys, 24°39.3’N, 81°18.2’W; NMW.Z.2003.075.1.

At the “The Horseshoe” site, the supralittoral fringe along the south side of the quarry consists in places of highly eroded friable limestones with many cavities and crevices that remained damp throughout the tidal cycle. These cavities were populated by many *Arcopsis* a few *Brachidontes* and the occasional *Arca imbricata* and *Isognomon*. The presence of the “terrestrial” snails *Laemodonta cubensis* (Pfeiffer, 1854) *and Truncatella pulchella* Pfeiffer, 1839, is highly indicative of the supralittoral environment.

(2) Shallow sublittoral rubble on sand and lower littoral

Collection site: IMBW-FK-629, 21 & 26-VII-02, “The Horseshoe” bayside of West Summerland Key, MM35, Monroe County, Florida Keys, 24°39.3’N, 81°18.2’W; NMW.Z.2003.075.2.

Other sites: IMBW-FK-622, IMBW-FK-657

On the north side of the Horseshoe quarry the very low vertical face drops onto a sloping face covered in muddy sand and blocks of quarry rubble. *Arcopsis* was found frequently attached to the undersides of the rubble blocks in 0.5 to 1.5 m water depth. This area was never exposed at low tide and can be considered sublittoral. The upper surfaces of the blocks were covered, predominantly by large *Chama*, *Arca,* and oysters. The lower surfaces were mostly bare with an assemblage of small gastropods, Rissoidae, Cerithidae, Muricidae.

Arcopsis can also be found attached to the undersides of rocks in the lower littoral often with *Acar domingensis*.

(3) Offshore coralline sands and rubble

Collection sites: IMBW-FK-651, 27-VII-02, “Samantha’s patch reef” 5 nmi S of Marathon, Monroe County, Florida, 24°39.49’N, 81°00.32’W, 7.6 m; NMW.Z.2003.075.3. IMBW-FK-641, 23-VII-02, Tennessee Reef Light, off Long Key, Monroe County, Florida, 24°44.75’N 80°46.95’E, 6.1 m; NMW.Z.2003.075.4. IMBW-FK-624, 20-VII-02, Horseshoe Reef, off Fat Deer Key, Monroe County, Florida, 24°39.91’N, 80°59.56’E, 7.3 m; NMW.Z.2003.075.5

These sites are all of patch reefs with sandy bottoms and rubble blocks. *Arcopsis* are found attached to the undersides of the blocks lying on sand.

(4) Sea grasses

Arcopsis were also collected from a number of sea grass biotopes but not in sufficient numbers for analyses. They were found attached to the base of shoots and exposed rhizomes.

Methods

Shell morphometric analyses were based on samples of at least 30 individuals, representing the total size ranges, taken from the supralittoral, sublittoral, and offshore sites. In the hand, specimens from each biotope had a different appearance generally in the apparent inflation and elongation of the valves. Parameters used focussed on these outward subjective views and included: shell length, shell height, and shell tumidity. The ligament appeared to be smaller in the offshore population, and the parameters inter-umbonal distance, ligament length, and number of ligament bands were measured. During the process, it was suspected that the inflation of the right and left valves was not equal and consequently left and right valve tumidity were included. This analysis was not applied to the small number offshore specimens available, as the separation of the valves would have destroyed the soft tissues, which were needed for anatomical study. Paired parameter comparisons were made rather than a multivariate approach in order to reveal specific differences. Arcoid bivalves are known to exhibit allometric growth of the ligament (Thomas, 1975, 1976) and it was decided that other shell parameters should be examined in relation to ontogeny. All data were analysed using Statview™.

Shell sculpture and structure were examined using a scanning electron microscope.

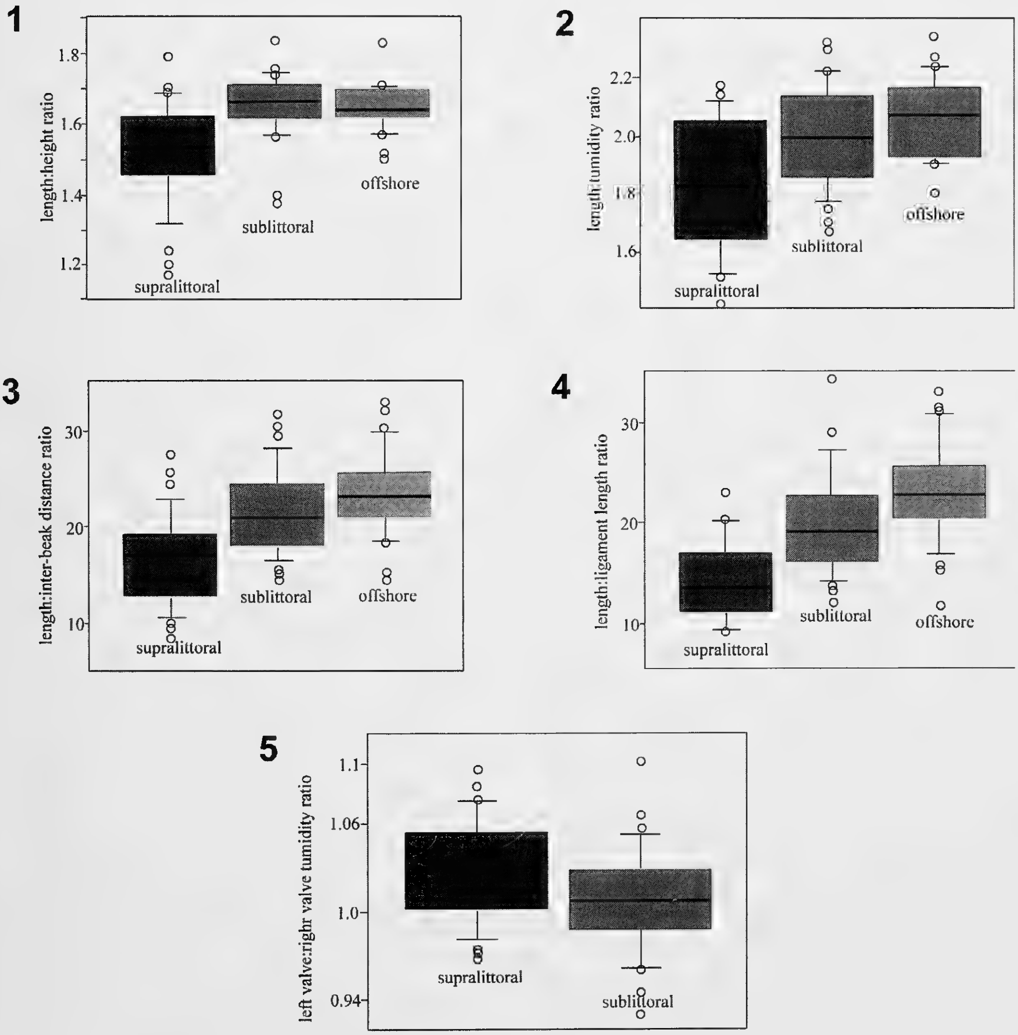
Anatomical comparisons were made from both living and preserved specimens.

RESULTS

Shell Morphometrics

Maximum size: The maximum size of the shells differed between samples with the largest shells occurring in the shallow sublittoral and reaching 13.5 mm in length. In the supralittoral the maximum size recorded was 10.5 mm and for offshore it was 9.5 mm. Sample sizes here for the supralittoral and sublittoral populations exceeded 100 individuals but for the offshore population only 30 were collected.

Comparisons of Shell Parameter Ratios: The most apparent difference in the hand was the shorter, more inflated form of the supralittoral shells, and to test this the length: height (Fig. 1) and length: tumidity (Fig. 2) ratios were compared. An ANOVA test (Fisher's PSLD) of the two ratios showed that the supralittoral population did have proportionately shorter and more tumid shells as compared to the other populations (significant at p = 0.0005 to < 0.0001) but that the difference between the sublittoral and offshore populations was not significant.



FIGS. 1–5. Box plots comparing shell morphometric ratios for populations of *Arcopsis adamsi* from the Florida Keys. FIG. 1: Shell length to shell height; FIG. 2: Shell length to shell tumidity; FIG. 3: Shell length to inter-umbonal distance; FIG. 4: Shell length to ligament length; FIG. 5: Left valve to right valve tumidity.

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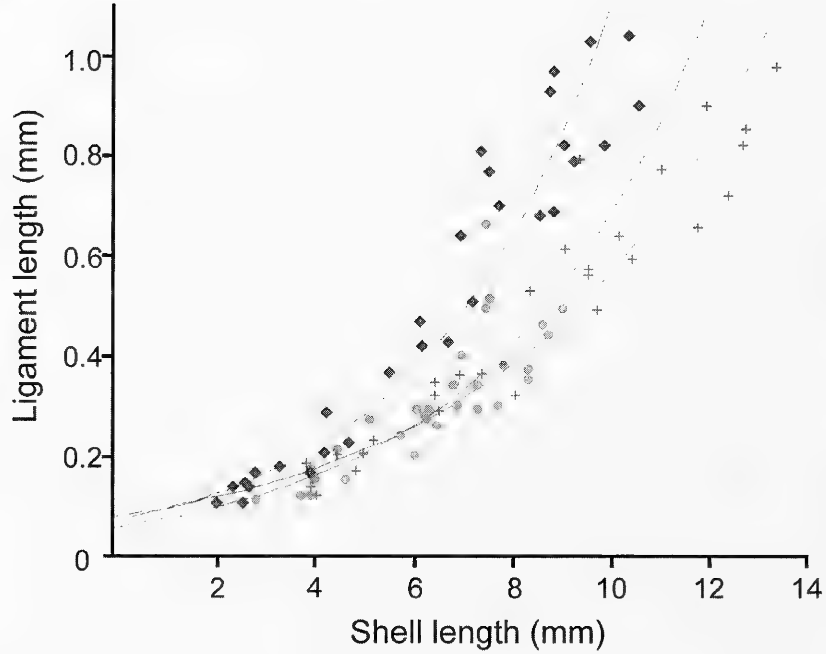

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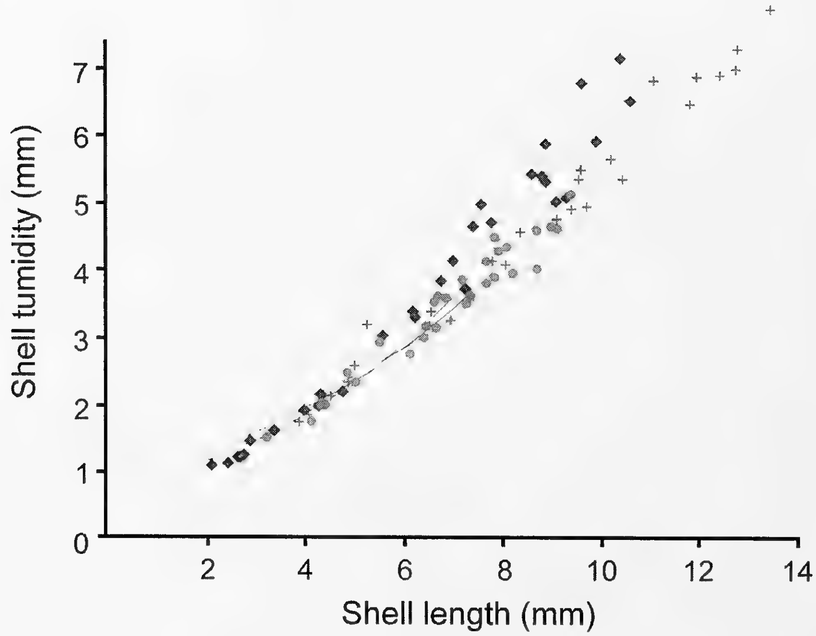


FIGS. 6, 7. Comparisons of growth curves in three populations of *Arcopsis adamsi* from the Florida Keys. FIG. 6: Plot of ligament length against shell length; FIG. 7: Plot of shell tumidity against shell length. Diamond, supralittoral; dot, offshore; +, sublittoral.

Comparisons of the inter-umbonal distance (length: inter-umbonal distance) gave the same pattern of results (Fig. 3) with significance at $p < 0.0001$. Comparison of the relative size of the ligament (length: ligament length) gave significant differences between all three populations (Fig. 4) except that this was less between the supra and sublittoral populations, p only 0.0106.

Comparing the tumidity of left and right valves did reveal that *Arcopsis adamsi* is slightly inequivalve (Fig. 5) and that the supralittoral population is significantly more inequivalve than the sublittoral population, $p = 0.02$.

Comparisons of Growth Curves: The regression plot of ligament length to shell length fits an exponential curve (Fig. 6) and confirms allometric growth of the ligament. Similar plots of tumidity (Fig. 7), interumbonal distance and number of ligament bands all reveal a similar pattern.

In all cases, the point at which the curve most rapidly climbs is at a smaller shell size in the supralittoral population. In the offshore populations the curves are least steep.

Shell Sculpture and Structures

Sculpture: On outward appearance the shells from the three biotopes have different aspects. The offshore shells (Figs. 10, 20) appear delicate, are clean with no apparent periostracum, white in colour with a sculpture of interlacing radial and concentric tracery. The density of the sculpture appears less in the offshore population, with the posterior area lacking the distinct semi-erect nodules seen in the sub and supralittoral populations. The sublittoral shells (Figs. 12, 18) are dirty with a pilose periostracum that retains fine sediment. The sculpture is partly obscured but when revealed appears primarily radial but is cancellate. The supralittoral shells (Figs. 13, 16) are grubby, dirty white with the periostracum either lacking or persistent around the margins only. The sculpture appears primarily radial but is cancellate.

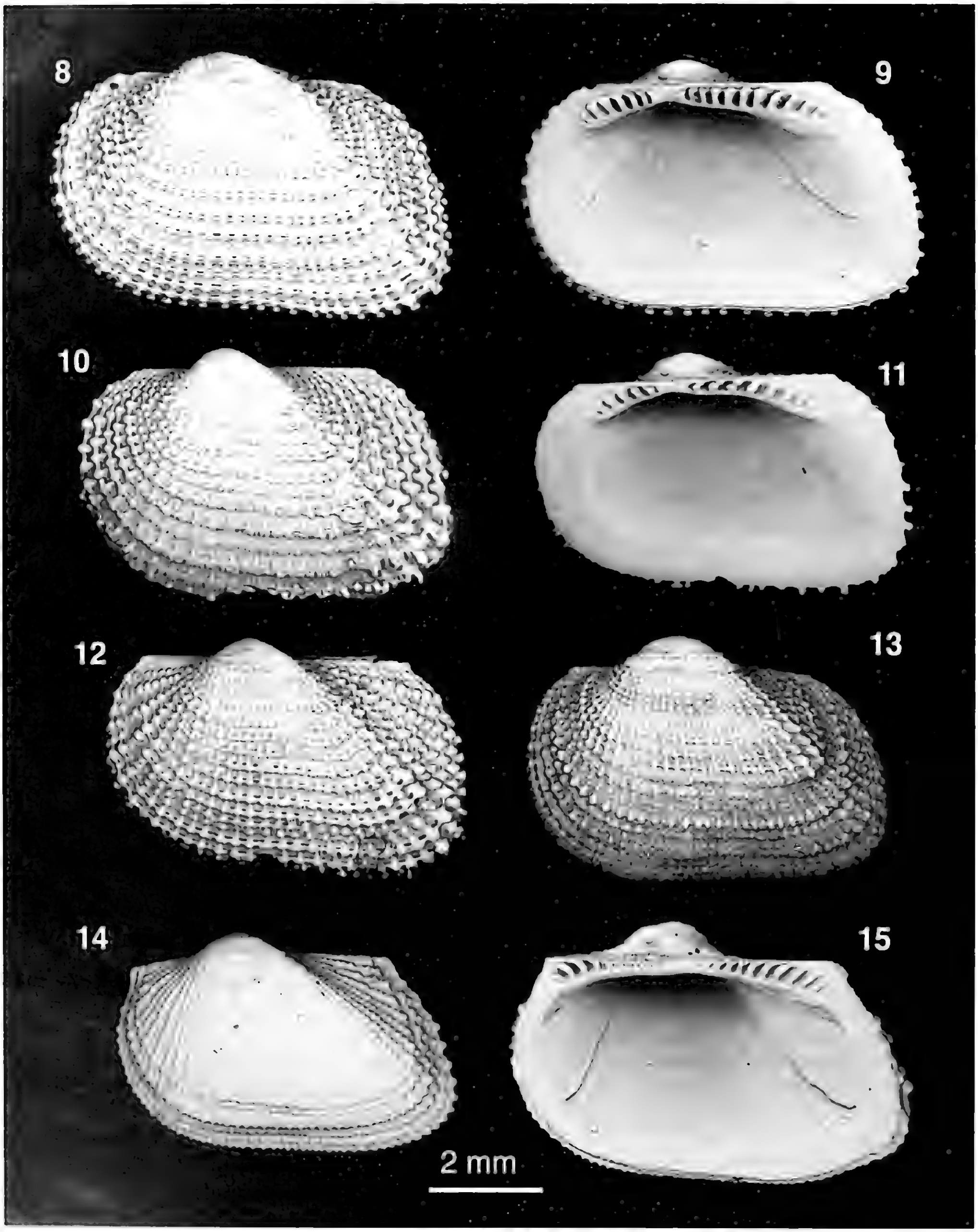
A detailed examination using the scanning electron microscope reveals that all three populations have the same sculptural pattern (compare Figs. 16, 18, 20) but that the apparent differences are related to the expression of the concentric element. The sculpture consists of radial rows of elongate teardrop shaped pustules, the expanded portion coinciding with the intersection of the concentric element (compare Figs. 17, 19, 21). The concentric sculpture consists of elevated bands attached to the radial elements but not to the interspaces, so when entire there is a lattice effect. The observed differences consequently appear to be related to the degree and rapidity of erosion of the non-attached interspace concentric cords.

Periostracum: The periostracum consists of flimsy concentric lamellae with fine hairs. In the offshore population, the periostracum is not apparent in the hand but, when magnified, appears as a thin concentrically striated covering expanded into thin lamellae along the lower edges of the concentric shell sculpture (Fig. 26). The lamellae bear thin, slightly thickened strap-like hairs at regular intervals. This contrasts with the obvious brown pilose covering on the sublittoral and supralittoral shells (Fig. 25) where both the adherent portion and the lamellae are more strongly developed.

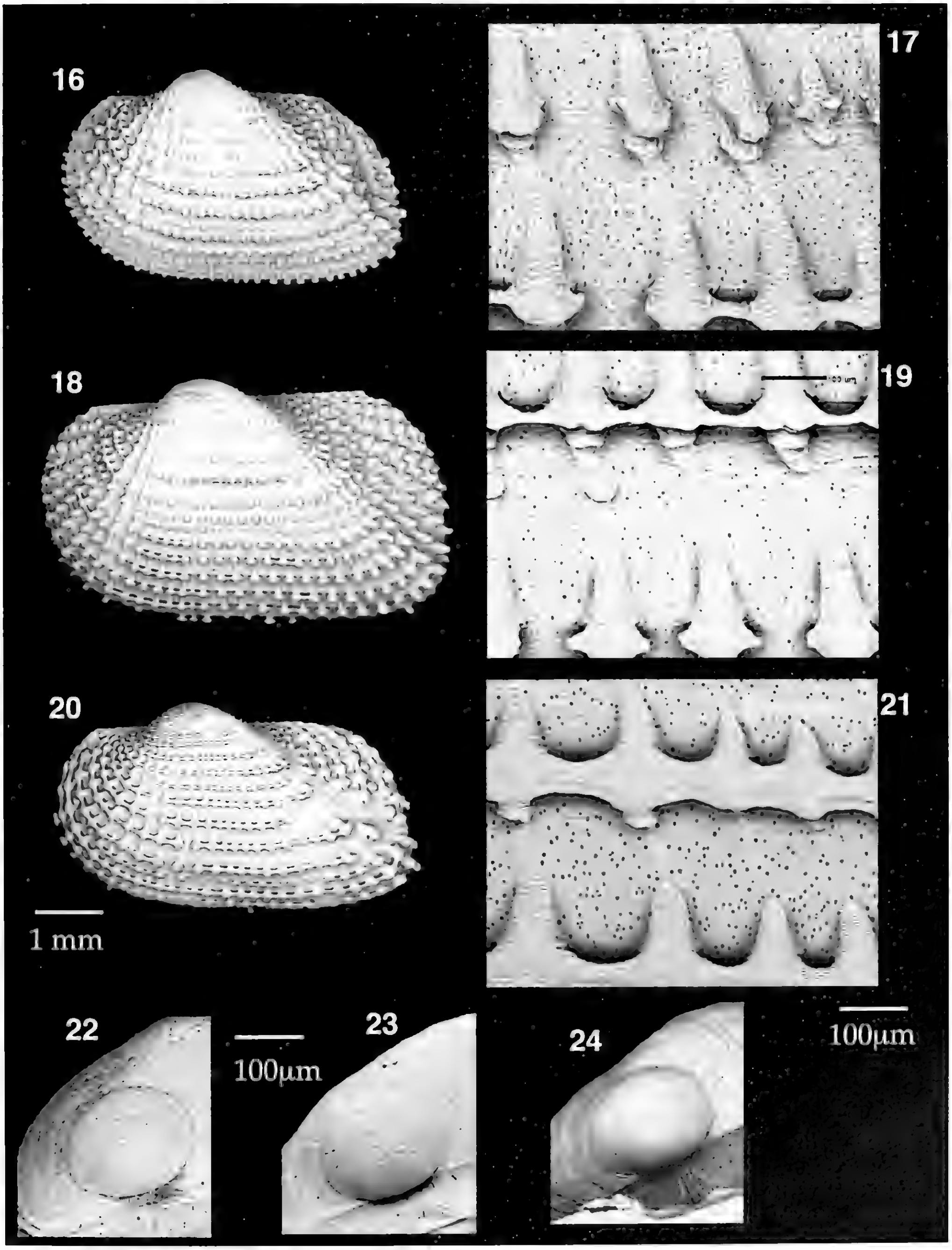
Shell Pores: As with other arcoid bivalves, *Arcopsis* valves possess numerous pores (caeca) (Reindl & Haszprunar, 1996). These tubules traverse the valves and can be observed on the inner and outer surfaces. On the external surface the pores are visible between the raised sculpture and under low magnification were most obvious in the supralittoral population. Scanning electron microscopy shows that the pores in all three populations are similar in size but that in the supralittoral shells the area around each pore is more heavily eroded and thus gives the appearance of being larger.

Pore density was also examined and was observed to vary over the shell with a radial pattern present and a decrease in density towards the ventral margins. Comparisons between populations were made by examining a strip on the internal surfaces directly below the ligament, and then at the same point on each strip (compare Figs. 27, 28, 29). A visual comparison suggests that the pore density is greater in the supralittoral population.

Larval Shell: The larval shells in all three populations are of the same form and same size (compare Figs. 22–24). There is a Prodissoconch I that is 105–106 µm in width and is smooth. There is a Prodissoconch II that is 174–178 µm in width and has concentric sculpture of widely spaced raised lines.



FIGS. 8–15. Scanning electron micrographs of *Arcopsis* and *Striarca* shells. FIGS. 8, 9: *Arcopsis afra* Angola. FIGS. 10, 11: *Arcopsis adamsi*, offshore population, IMBW-FK-651; FIG. 12: *A. adamsi*, sublittoral population, IMBW-FK-629; FIG. 13: *A. adamsi*, supralittoral population, IMBW-FK-629; FIGS. 14, 15: *Striarca lactea*, Banyuls, Mediterranean Sea.



FIGS. 16–24. *Arcopsis adamsi*, all scanning electron micrographs. FIGS. 16, 17: Cleaned supralittoral shell and detail of sculpture; FIGS. 18, 19: Cleaned sublittoral shell and detail; FIGS. 20, 21: Cleaned offshore shell and detail; FIGS. 22–24: Larval shells, supralittoral, sublittoral and offshore.

Anatomy

Gross Anatomy: The gross anatomy of *Arcopsis adamsi* is in all respects very similar to that of the Indo-Pacific, epibyssate *Striarca symmetrica* (Reeve, 1844) (Oliver, 1985) and the eastern Atlantic *Striarca lactea* (Oliver, pers.obs).

Offshore Population (Fig. 30) – The adductor muscles are approximately of equal size, both with quick and catch portions. The posterior pedal (byssus) retractor is prominent but not large, some 5 x the size of the anterior pedal retractor.

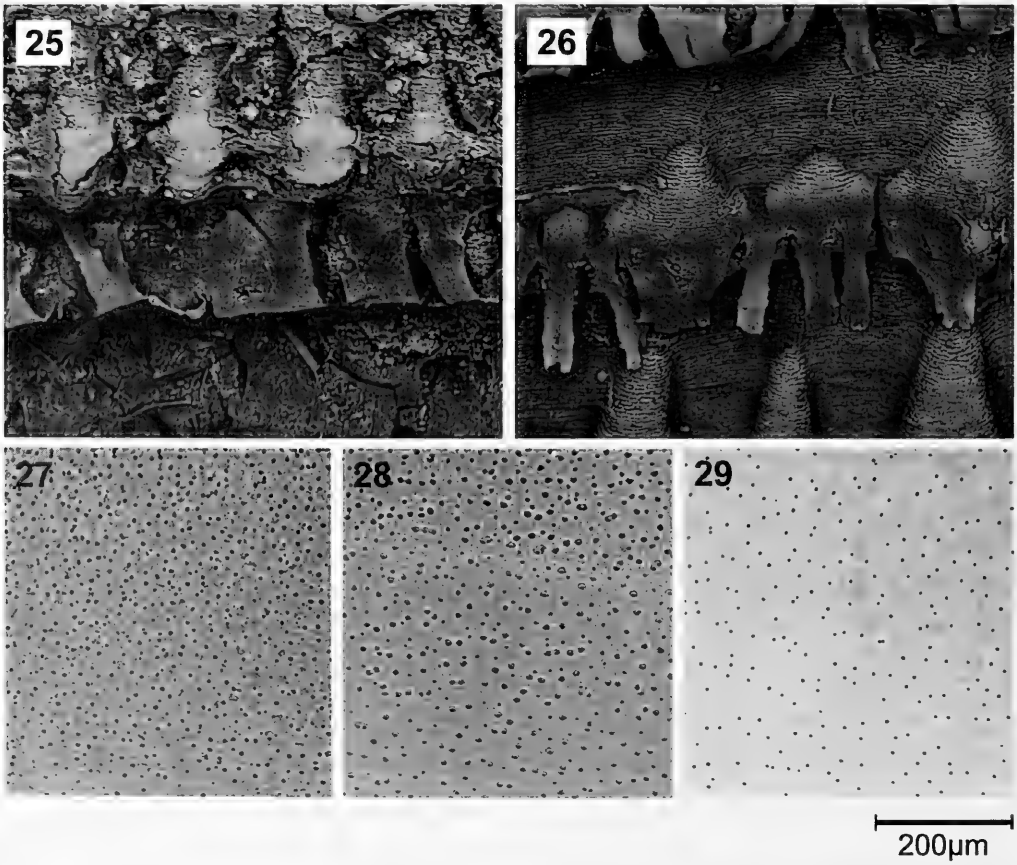
The mantle is thick, and the mantle edges are free, with the main inhalant and exhalant regions at the posterior; the frilled anterior mantle edge suggests that there is an anterior inhalant current.

The foot has a developed toe and a smaller heel; the byssal groove runs along the anterior and median regions.

The gills are paired, with both demibranchs well developed, the inner being larger than the outer. The labial palps are moderately large, with 12 to 15 well-developed palp ridges.

The anus is attached to the underside of the posterior adductor muscle and is accompanied by a pair of abdominal sense organs each in the form of a simple dome.

Sublittoral (Fig. 32) and Supralittoral (Fig. 31) Populations – As above, with the only apparent difference seen in the supralittoral population, where the inner demibranch is smaller and almost the same as the outer. It is not possible to discount differential contraction through the fixation process.



FIGS. 25–29. *Arcopsis adamsi*, SEM of periostracum. FIG. 25: Supralittoral shell; FIG. 26: Offshore shell; FIGS. 27–29: *Arcopsis adamsi*, SEM of shell pores at the median area below the beaks; FIG. 27: Supralittoral; FIG. 28: Sublittoral; FIG. 29: Offshore.

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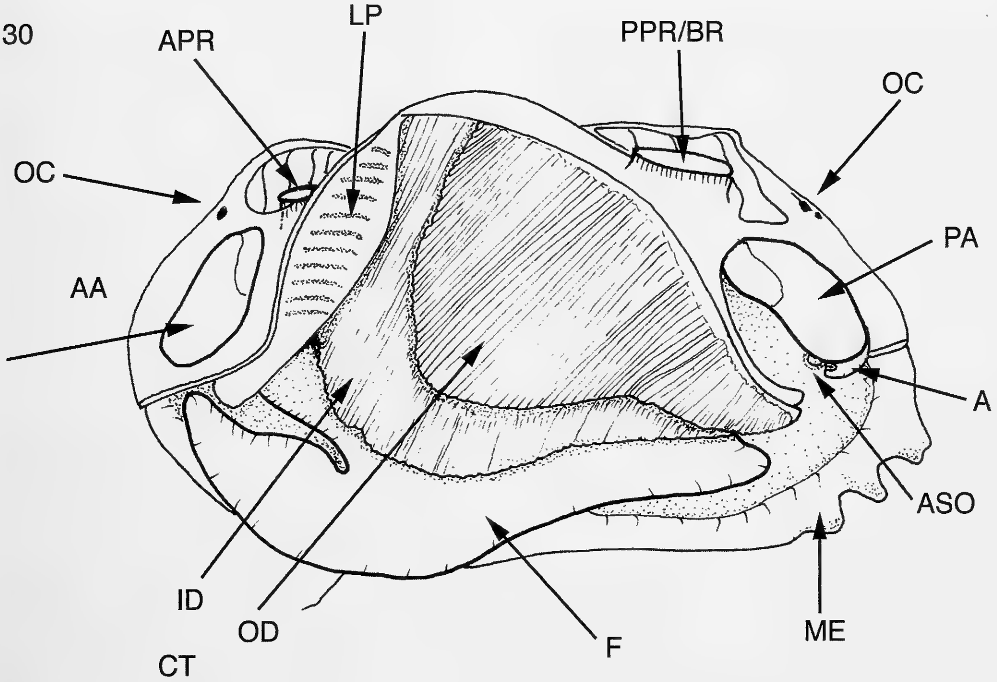

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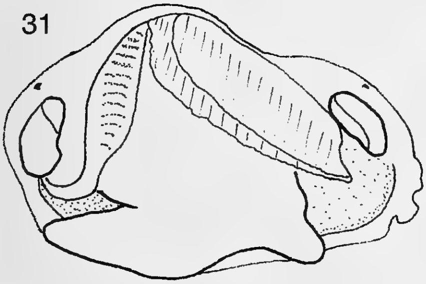

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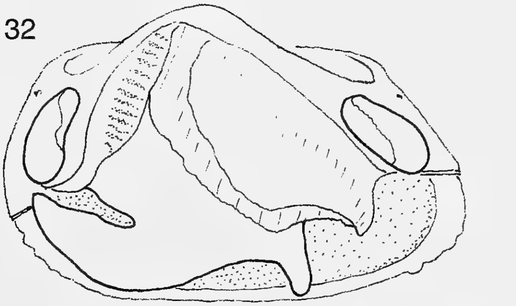

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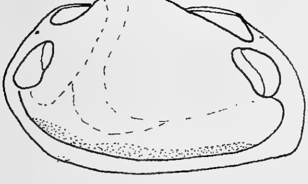

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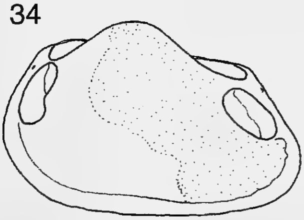

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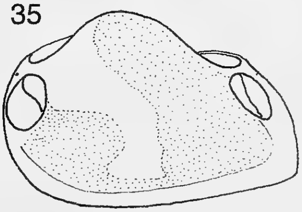

FIGS. 30–35. Anatomy of *Arcopsis adamsi*. FIG. 30: Gross anatomy (left mantle removed), Samantha's Patch Reef (offshore population). A, anus; AA, anterior adductor muscle; APR, anterior pedal retractor muscle; ASO, abdominal sense organ; CT, ctenidium; F, foot; ID. inner demibranch of ctedium; LP, labial palps; ME, mantle edge; OC, ocelli; OD, outer demibranch of ctenidium; PA, posterior adductor muscle; PPR/BR, posterior pedal/byssus retractor muscle; FIGS. 31, 32: Gross anatomy of supralittoral (FIG. 31) and sublittoral (FIG. 32) specimens; FIGS. 33–35: Left mantle after shell removal showing areas of haemoglobin staining (stippled areas); FIG. 33: Offshore; FIG. 34: Sublittoral; FIG. 35: Supralittoral.

Haemoglobin: The Arcoidea are one of the few bivalve superfamilies in which haemoglobin cells are a characteristic component of the haemocoelomic fluid. *Arcopsis adamsi* tissues, especially those of the mantle, are tinged pink to blood red indicating the presence of haemoglobin. The variation in colour intensity indicates that the haemoglobin concentrations differ between populations, but given the constraints of the workshop we were unable to measure the actual concentrations. We observed that the living tissues of the offshore population are scarcely tinged pink and in fixed material a rust coloured band is present only along the mantle edge (Fig. 33). This contrasts completely with the supralittoral population, in which the living tissues, primarily the mantle, are dark blood red and in the fixed state the pigmentation covers most of the mantle (Fig. 35). The sublittoral population is intermediate in appearance but very distinctly with haemoglobin and thus more like the supralittoral population (Fig. 34).

DISCUSSION

The question for the taxonomist is of the degree of significance of these observations, could they reflect different species or are they result of ecophenotypic variation related to the different biotopes inhabited by the *Arcopsis* populations?

Marko & Jackson (2001) using shell morphometrics concluded that the Pacific taxon *Arcopsis solida* was different from the Caribbean *A. adamsi*, but that this difference was primarily one of size rather than shape. Nevertheless, they nowhere suggested that the two were conspecific. Given that the two taxa are now isolated by the Panamanian isthmus, their conclusion to maintain them as separate species was probably influenced by the geographical separation of the taxa as much as the morphological differences. Marko (2002) later showed that at the molecular level his populations of *A. solida and A. adamsi* were distinct. The anatomy of *A. solida* and *A. adamsi* has been described by Heath (1941), but no direct comparisons were made, and his observations were inconclusive in relation to differences between these species.

Oliver & Cosel (1992), studying *Striarca lactea* populations along the West African coast, also used morphometrics to justify the erection of subspecies, giving outline and sculpture most credence. They did discuss the problems of erecting new taxa on such evidence but again were influenced by the geographical separation of the populations.

The morphometric data from these studies are comparable with those presented here but if they were used to create new taxa such decisions would be met with severe scepticism. The proximity of the populations and the data available would suggest to many that ecophenotypic variation was being observed. However, it is now widely accepted that, for example in the Littorinidae, that a number of species can live in adjacent microhabitats in close proximity to each other (Reid, 1986). This is accepted because the differences cited are from disjunct characters, such as the structures of the genitalia and radula, rather than being based on statistical analyses of gradients such as shell shape. Unfortunately, bivalves display few characters of this kind and one of the major problems in bivalve species taxonomy is the gradation of many characters. Greater character definition of these gradients would strengthen bivalve taxonomy, but in using statistical methods at what levels of significance do we attach a species level or population level distinction?

In 1992 Oliver & Cosel did discuss the affinities of the West African taxon *A. afra* and *A. adamsi*. They indicated sculptural differences, but given the variation now seen in *A. adamsi* such differences are not so conclusive. *Arcopsis afra* appears more umbonate with a stronger sculpture, but in most respects difficult to separate from *A. adamsi*. Once again, the geographic isolation of the two taxa is giving the weight to their separation.

It is therefore essential to examine in detail the possible causes of the morphological differences observed in populations that only show character gradients.

Thomas (1975, 1976; Thomas et al., 2000) showed that the allometric growth of the arcoid ligament was essential to maintain a functioning hinge. This allometry is expressed either in the progressive invasion of the ligament ventrally into the hinge plate or by further and further separation of the beaks. In *Arcopsis* the allometry is displayed in the separation of the beaks, and this allometry occurs at smaller shell length in the supralittoral population and is least marked in the offshore population. The growth function of the ligament is correlated not only to the relative inter-umbonal distance, ligament width and number of ligament bands, but probably also to the relative differences in shell tumidity and the degree of the inequivalve condition. Consequently, the morphometric data presented are all a function of growth and may be related to environmental parameters.

Of the three biotopes sampled, the supralittoral provides the most extreme conditions for a suspension feeding organism as feeding time is restricted to a short period at high tide times. Long periods of exposure will also cause potential stress from desiccation and restricted respiration. It is reasonable to suggest that restrictions in feeding time will reduce the growth rate in the supralittoral population and will result in the decrease in maximum size observed. If the allometry is age-related rather than size-related, then different growth rates will produce shells of different shapes where the parameters are linked to umbonal separation. The increased relative tumidity and inequivalve condition seen in the supralittoral population is likely to be growth-related and therefore ecophenotypic. However, the offshore population has a similar maximum size but shows little allometry and is smaller than the sublittoral population. If we were to use ecophenotypic variation as an explanation of morphological difference, then it would be supportive if we could link the differences to environmental parameters. The taxonomist, therefore, should also be aware of the ecology and habitats of the taxa under study. Here we can only speculate at the ecological differences between the habitats occupied by *Arcopsis*, but changes in growth rate and maximum size are likely to be controlled by food availability.

The function of the shell pores has been tentatively linked to respiration and haemoglobin is known to be a more efficient oxygen carrier than haemocyanin. The density of shell pores and the haemoglobin concentration are greatest in the supralittoral population and may be physiological responses to the greater time spent out of the water. When considering the sublittoral and offshore populations, it is more difficult to apply the same reasoning as both populations are permanently submerged. The sublittoral population lives under rocks embedded in muddy sand and may suffer oxygen depletion in the very warm surface waters along the margins of the Keys. At the offshore sites, the rocks sit on clean sand and water flow is probably much greater over the animals. These differences may account for the different densities of shell pores and haemoglobin seen in the two submerged populations.

Consequently, the characters that define the supralittoral population can all be related to environmental effects on growth rate and physiology, but a similar argument cannot explain all the differences between the offshore population and the two shallow populations. Additionally, it is difficult to explain the difference in periostracum simply through abrasion as that on the offshore population is not abraded only very thin. The sculptural density is also not readily explained by differential growth rates.

Without disjunct characters, the taxonomic process has been led more and more towards ecology and physiology and increasing attempts to discover the functionality of the characters under review. Most of the discussion above is subjective and would require substantial experimentation to confirm whether or not morphology and physiology were responding to environment. Taxonomists traditionally have not or were not able to support their decisions concerning species discrimination and intraspecific variation. Morphometric analyses do give statistical support to observations but do not resolve the issue. Environment does affect shell form and growth rate, and these may alter sculptural density reinforcing the need for the taxonomist to be aware of ecology. At least in the arcoids, the ligament growth is related to the expression of many other shell characters so that what may appear to be an array of characters is in reality a single one.

Although morphological characters are the traditional tools of the bivalve taxonomist they must be used carefully, because many are gradients and many are influenced by environment. Without additional data from ecology, including physiology and reproductive biology, the interpretation of characters is difficult. The application of molecular techniques needs to become routine especially when ecophenotypic or geographic variation is suspected. It must be recognised that most bivalve species taxonomy remains at the morphospecies concept and that a good species remains the product of a good taxonomist! A molecular study of the populations discussed here is in progress but the wider application of this technique now requires access to correctly preserved material, which precludes most of the collections in the worlds museums. Morphological based taxonomy will remain widespread as will the need to identify species based on readily observable characters. Although molecular techniques are necessary, the routine use of molecular characters for identification is probably a long way off.

CONCLUSIONS

Morphological characters in bivalves need careful assessment before conferring species level significance to differences in them.

Many characters form gradients and need statistical analyses to substantiate observations.

Statistical differences in gradient characters do not necessarily indicate species difference.

Many shell characters are inter-dependent and can all be altered by simple changes in growth.

Where possible, ecology should be an integral part of taxonomic studies.

Molecular techniques need to be applied to complex problems to give better resolution.

ACKNOWLEDGEMENTS

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ROCK AND CORAL BORING BIVALVIA (MOLLUSCA) OF THE MIDDLE FLORIDA KEYS, U.S.A.

Paul Valentich-Scott[1] & Grete Elisabeth Dinesen[2]

ABSTRACT

Eight species from three bivalve families were collected and/or observed in the Middle Florida Keys. Diagnoses based on shell characters are given for *Botula fusca*, *Lithophaga antillarum*, *L. aristata*, and *L. bisulcata* in the Mytilidae, and *Gastrochaena hians* in the Gastrochaenidae. Shell and anatomical comparisons are made for three members of the Petricolidae, *Petricola lapicida, Choristodon robustum*, and *Choristodon* sp. A, which is not attributable to a described Recent *Choristodon* species.

These bivalves bore into limestone and dead coral, and in one case into living coral. Observations substantiated previous findings of primary chemical boring processes in *Botula* and *Petricola*.

Key words: *Botula, Lithophaga, Petricola, Choristodon, Gastrochaena*, endolithic, boring bivalves, Florida Keys.

INTRODUCTION

As an expansion of the general bivalve biodiversity study initiated by Mikkelsen & Bieler (2000), we here describe the rock and coral boring bivalve fauna of the Middle Florida Keys. The goal of this publication is to provide a guide to the identification of the rock and coral boring bivalves in the Middle Keys region. Where possible, we have made observations and comparisons of the living animal, the anatomy, and the habitat of each species.

Middle Keys boring bivalves are represented in the families Mytilidae, Petricolidae, and Gastrochaenidae. Turner & Boss (1962) described the lithophagan mytilids throughout the western Atlantic, including the Florida Keys. Coan's (1997) treatment of the eastern Pacific Ocean Petricolidae discussed species that are also found in the Caribbean/Atlantic region. The taxonomy and biology of the Gastrochaenidae are well documented in Carter (1978). Carter also provided a list of coral boring bivalves from Soldier Key, Dade County, Florida, which is only 100 km north of the site of this study (West Summerland Key). Including members in the three aforementioned families, Kleemann (1980, 1990a) discussed the methods of chemical boring of these bivalves in the Caribbean, eastern Pacific Ocean and the Great Barrier Reef. Morton (1990) presented a global overview of coral-boring bivalves, including those in the western Atlantic Ocean.

MATERIALS AND METHODS

Limestone and coral habitats were examined for boring bivalves, intertidally and subtidally to 3 m in the Middle Florida Keys in July 2002 (Mikkelsen & Bieler, 2004, provide a station listing and map). Individuals were observed and/or collected primarily from the Florida Bay side of West Summerland Key (24°39'N). The limestone at this site is thought to be Key Largo Limestone, which in some cases is overlain by the Miami Oolite facies (M. Campbell, pers. comm., March 2003). Boring bivalves were collected from limestone and dead coral substratum with a rock hammer and chisel. Bivalves occurring in living coral were examined, but not collected. Field observations of the living animal and their burrows were made. In addition, bivalve borers were observed at Bahia Honda State Park (24°39'N), Fat Deer Key (24°40'N), Crawl Key (24°41'N), Grassy Key (24°44'N), Long Key (24°45'N), Planta-

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tion Key (24°50'N), and Lower Matecumbe Key (24°50'N).

Live animals were removed from their burrows, and relaxed in 7% $MgCl_2$. Observations of the shell, ligament, siphons, mantle, and foot were made while the living animal was in a relaxed state. The right shell valve was carefully removed with a scalpel inserted between the mantle margin and the shell. For selected species, the morphology of the labial palps, ctenidia, and siphons were recorded.

Relaxed specimens were placed in 4% formalin solution, and transferred to 70% ethyl alcohol. Ctenidial and labial palp filament counts were compared between living and preserved specimens.

Voucher specimens for all species collected in this study have been deposited at the Santa Barbara Museum of Natural History (SBMNH).

Each species description includes a short diagnosis, followed by an expanded description of the shell morphology and, where observed, the anatomy. Measurements and localities of specimens examined are given, along with habitats where the species were observed and collected. Additional literature citations are provided for each species, and when necessary additional remarks on the taxonomy or biology of the species are given.

The following abbreviations are used in the text: AMNH, American Museum of Natural History, New York, New York, USA; BMSM, Bailey-Mathews Shell Museum, Sanibel, Florida, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; SBMNH, Santa Barbara Museum of Natural History, Santa Barbara, California, USA. Station numbers listed in the following text refer to International Bivalve Workshop – Florida Keys (IMBW-FK) stations, as maintained by AMNH and FMNH (Mikkelsen & Bieler, 2004).

SYSTEMATIC ACCOUNT

Mytilidae Rafinesque, 1815
Botula fusca (Gmelin, 1791)
Figures 1–4

Diagnosis

Shell highly inflated; exterior dark brown; periostracum silky; beaks terminal, inturned, projecting beyond anterior margin; sculpture of commarginal striae only; without calcareous incrustations on exterior of shell; length of shell to 40 mm.

Description

Exterior – Lateral View: Shell subquadrate-elongate, slightly bent in the middle, slightly flaring posteriorly; beaks terminal, prosogyrate, inturned, pronounced, inflated; region ventral of umbones straight; posterior end rounded; broadly inflated from umbones to posterior margin, with rounded shoulders radiating from umbones to anteroventral and posterior regions, middle region slightly depressed; ventral margin incurved; byssus visible; sculpture of commarginal striae; periostracum chestnut brown, lighter brown in small specimens, strongly adherent; milky white mucus remnants attached to shell.

Dorsal View: Ligament sunken, long, dark brown portion of ligament split for much of length; shell highly inflated.

Ventral View: Umbones and prodissoconch visible from ventral side; ventral margin smooth; commarginal striae more pronounced near posterior margin.

Interior: Shell pearly white internally; periostracum covering hinge under beaks; long thin, sharp posterior lateral tooth; edentulous under umbones; ligament deeply sunken, attached to a rolled nymph on the anterior portion, and a shelf-like nymph posteriorly.

Anatomy

Dorsal View: Foot orange anteriorly, white posteriorly, depressed in an anterior posterior direction, with small heel; distal portion of foot triangular, black; byssus projecting from base of foot; mantle unfused for most of ventral length; posterior rim of mantle is dark brown, remainder of mantle milky white.

Lateral View (with left valve and mantle removed): Anterior adductor muscle large for size of shell; posterior adductor circular, larger than anterior; inner fold of mantle margin very muscular, middle fold thin; labial palps short.

Measurements

Length 29 mm, height 13 mm, width 15 mm; length 17 mm, height 8 mm, width 9 mm; both specimens from West Summerland Key, IMBW-FK-629, 24°39.3'N, 81°18.2'W, collected by P. Valentich-Scott and G. Elisabeth Dinesen (SBMNH 350547, 350548). Additional observations were made at Crawl Key and Bahia Honda State Park. Four additional lots of dry specimens from the Florida Keys were examined (SBMNH).

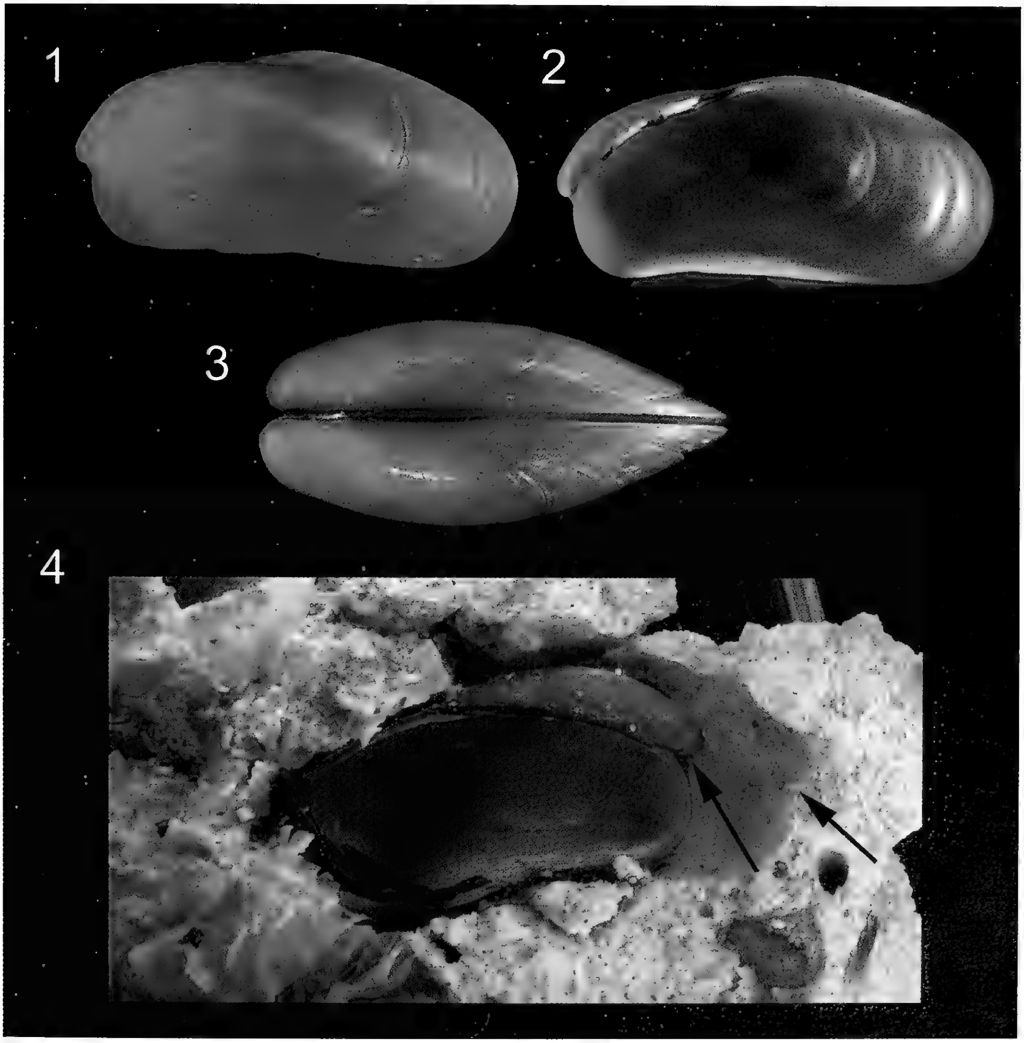
Habitat

In a mucus nest, boring in soft limestone. Carter (1978) reported in dead coral (*Diploria*).

Remarks

The limestone burrows of several specimens were found with dorsal keels, or with anterior notches in the limestone under the umbones (Fig. 4). Mechanical boring would not allow these keels or notches to be formed in the borehole. These findings correspond with Wilson & Tait (1984), who suggested that *Botula fusca* only uses chemical means for boring.

There has been much nomenclatural debate as to the correct name for the species in the western Atlantic Ocean. Wilson & Tait (1984)

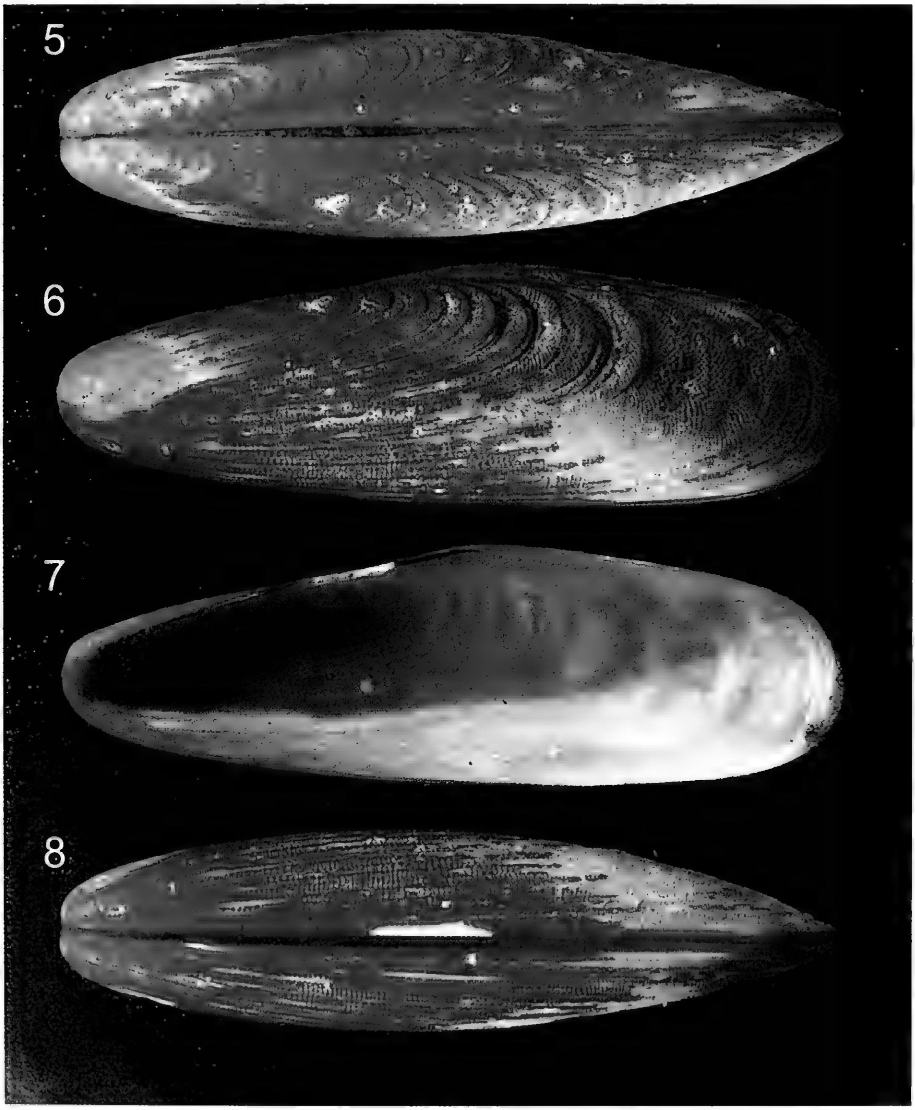


FIGS. 1–4. *Botula fusca*. FIGS. 1, 2: External left valve, internal right valve. West Summerland Key, Monroe County, Florida; 24°39.3'N, 81°18.2'W; subtidal; Station 629; length 28.8 mm; SBMNH 350546; FIG. 3: Dorsal view, Grassy Key, Monroe County, Florida; 24°45'46"N, 80°57'11"W; length 39.6 mm; SBMNH 53503; FIG. 4: In limestone substratum; arrows denote invagination below umbones and corresponding notch in limestone; locality data the same as figures 1–2; length 26.1 mm; SBMNH 350547.

used *Botula fusca* (Gmelin, 1791) as a single global species distributed in the Indian, Atlantic, and Pacific Oceans, and placed *B. cinnamonea* (Gmelin, 1791) in synonymy. Nielsen (1986) contrasted this viewpoint, seeing *B. cinnamonea* as valid, with a broad Northern Hemisphere distribution. In addition, Nielsen designated a lectotype for *B. cinnamonea*, and restricting the type locality of this species to the Nicobar Islands. Additional morphological, anatomical and genetic studies are needed to solve this global issue.

Literature

Abbott (1974: 436), Keen (1971: 74), Mikkelsen & Bieler (2000), Nielsen (1976), Redfern (2001: 201), Soot-Ryen (1955: 86), Wilson & Tait (1984).



FIGS. 5–8. *Lithophaga antillarum*. Missouri Key, Monroe County, Florida; 24°40.6'N, 81°14.3'W; length 77.9 mm; SBMNH 350549. FIG. 5: Dorsal view; FIG. 6: External left valve; FIG. 7: Internal right valve; FIG. 8: Ventral view.

Lithophaga antillarum (Orbigny, 1853)
Figures 5–8

Diagnosis

Shell elongate, cylindrical; beaks subterminal, but not extending past anterior end; periostracum light to medium brown, dehiscent; sculpture of fine vertical lines over most of shell, and heavy commarginal undulations posterodorsally; without calcareous incrustations on exterior of shell; length of shell to 120 mm.

Description

Exterior – Lateral View: Shell cylindrical, somewhat compressed laterally, sharply rounded anteriorly, broadly rounded posteriorly, slightly flaring in the middle portion; beaks subterminal, small; sculpture of fine vertical lines over entire surface except narrow region from beaks to posterior end, and irregular commarginal striae, commarginal undulations posterodorsally; large portions of shell eroded, especially anteriorly; periostracum dehiscent, medium brown; calcareous incrustations not present on shell, no encrusting extensions.

Dorsal View: Beaks small, not inflated or protruding; dorsal margin not gaping; ligament not visible from dorsal surface; with long narrow escutcheon; lunule not well demarcated; shell widest near midline, tapering posteriorly.

Ventral View: Shell tightly closing, except for very narrow, short pedal gape, and very slight posterior gape; ventral margin slightly beveled inward.

Interior: Interior pearly white, translucent; edentulous; ligament dark brown, deeply sunken, extending from umbones nearly to the shell midline.

Anatomy

Not examined.

Measurements

Length 85 mm, height 25 mm, width 21 mm; specimen collected by José Leal (26 July 2002) at West Summerland Key, IMBW-FK-629, 24°39.3'N, 81°18.2'W at 3 m depth, in soft limestone; deposited as a voucher specimen at the Zoological Museum, University of Copenhagen, Denmark. Also observed at Fat Deer Key. Eight additional lots examined from Missouri Key (24°40'N) (SBMNH 350549), Vaca Key (24°46'N), and Barbados (all SBMNH), and Lower Matecumbe Key and Townsend Island (BMSM).

Habitat

Boring into soft limestone. Carter (1978) reported in dead coral (*Diploria*), and Scott (1988a) observed in dead coral and rock.

Literature

Turner & Boss (1962), Kleemann (1983, 1984, 1990a, b, 1996), Mikkelsen & Bieler (2000), Morton (1990), Redfern (2001: 201), Warmke & Abbott (1971: 164).

Lithophaga aristata (Dillwyn, 1817)
Figures 9–11

Diagnosis

Shell inflated, cylindrical; beaks subterminal; with heavy calcareous incrustations over most of shell; elongated incrustations posteriorly, forming overlapping scissors-like “forceps”; length of shell to 33 mm.

Description

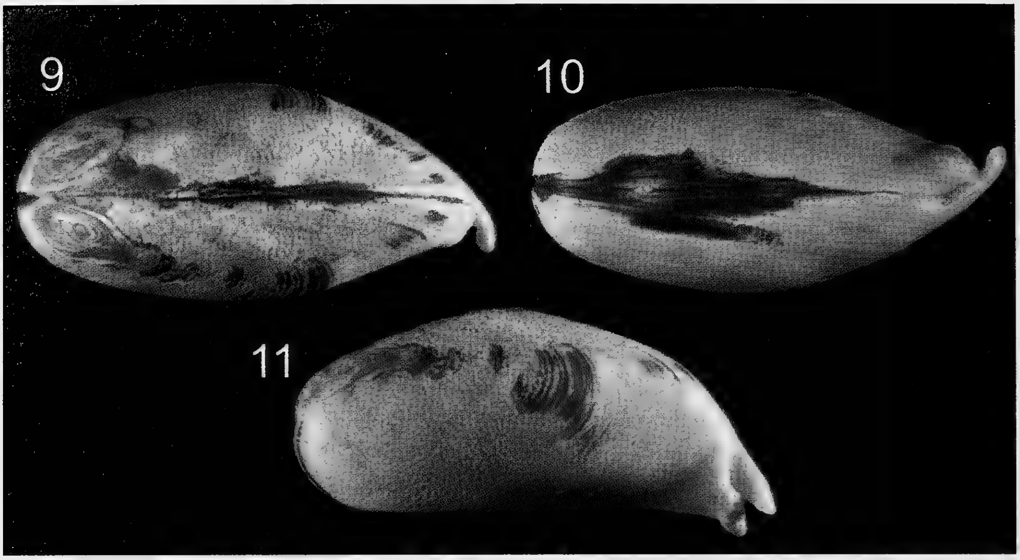
Exterior – Lateral View: Shell elongate ovate to cylindrical, sharply rounded anteriorly, tapering posteriorly; beaks subterminal, usually eroded; sculpture of fine commarginal striae; periostracum dark brown; heavy calcareous incrustations over entire surface, eroded in some spots; incrustations extending past the posterior end, forming overlapping, scissors-like projections.

Dorsal View: Beaks usually eroded, not extending past the anterior margin; ligament black, sunken anteriorly, becoming visible near shell midline.

Ventral View: Shell tightly closing, without visible pedal gape; ventral margin nearly straight; posterior scissors-like incrustations easily viewed from this orientation.

Interior: Shell very thin, fragile, translucent, slightly pearly white, slightly flaring dorsally; edentulous; posterior end of shell tapering, with calcareous extensions.

Anatomy not examined. Morton (1993) discussed various aspects of the anatomy, including a discussion on the formation of the scissors-like “forceps”.



FIGS. 9–11. *Lithophaga aristata*. West Summerland Key, Monroe County, Florida; 24°39.3'N, 81°18.2'W; subtidal; Station 629; length 9.9 mm; SBMNH 350550. FIG. 9: Dorsal view; FIG. 10: Ventral view; FIG. 11: External left valve.

Measurements

Length 9.9 mm, height 4.1 mm; specimen collected by Diarmaid O'Foighil (27 July 2002) at West Summerland Key, IMBW-FK-629, 24°39.3'N, 81°18.2'W (SBMNH 350550). Two additional Florida lots were examined, along with 50 lots from the eastern Pacific Ocean (all SBMNH).

Habitat

Boring into limestone and coral. Coan et al. (2000) reported boring into shell in the eastern Pacific Ocean.

Literature

Coan et al. (2000: 181), Keen (1971: 70), Kleemann (1983, 1990a, b, 1996), Mikkelsen & Bieler (2000), Morton (1993), Redfern (2001: 202), Turner & Boss (1962), Yonge (1955).

Lithophaga bisulcata (Orbigny, 1853)
Figures 12–15

Diagnosis

Shell cylindrical, with flare along dorsal margin, tapering posteriorly; with feathery calcareous incrustations along posterodorsal slope; incrustations extending evenly past posterior end of shell; length of shell to 45 mm.

Description

Exterior – Lateral View: Shell cylindrical, tapering posteriorly, anteriorly rounded; dorsal and ventral margin parallel for the anterior half of the shell, flaring posterodorsally and then tapering posteriorly; beaks broad, slightly projecting, near anterior end, not terminal; sculpture of fine commarginal striae, with broad keel running from just posterior of beaks to posterior end; periostracum chestnut dark brown; surface anterior of keel with fine granular concretions except in the umbonal region and ventral margin, posterior of keel with heavy concretions, concretions becoming heavier posteriorly, feathery concretions posteriorly, posterior concretion extension short with fine granules.

Dorsal View: Ligament deeply sunken in deep long escutcheon; anterior end triangular; gaping posteriorly; concretions along entire dorsal surface.

Ventral View: Ventral margin slightly incurved to slightly bowed, smooth; shell narrowly gaping posteriorly; posteroventral calcareous incrustations with zipper-like pattern.

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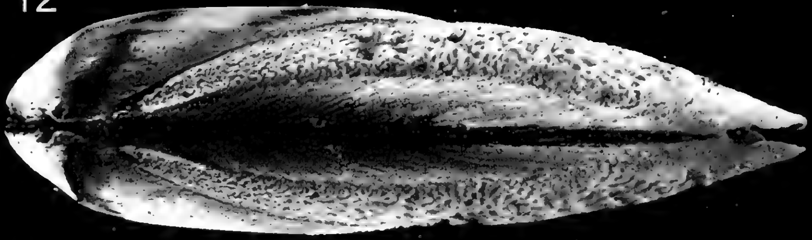

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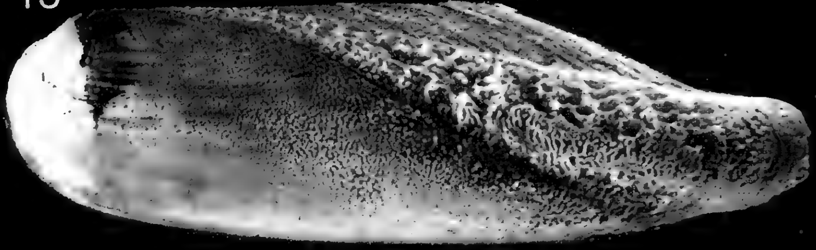

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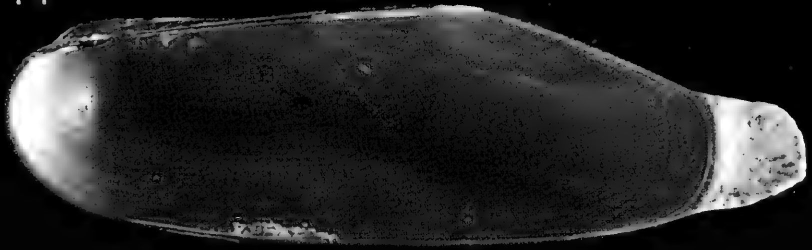

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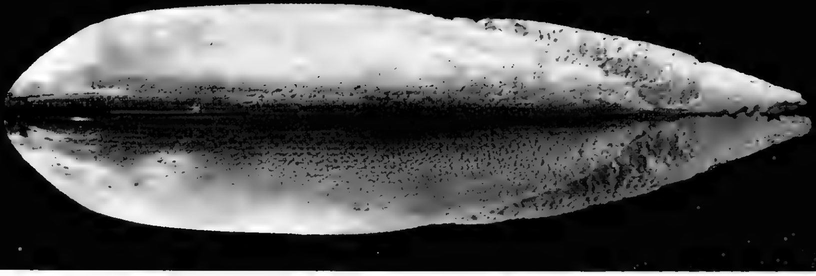


FIGS. 12–15. *Lithophaga bisulcata*. Missouri Key, Monroe County, Florida; 24°40.6’N, 81°14.3’ W; length 45.0 mm; SBMNH 350551. FIG. 12: Dorsal view; FIG. 13: External left valve; FIG. 14: Internal right valve; FIG. 15: Ventral view.

Interior: Shell dark brown, translucent, with slight sheen; edentulous; ligament deeply sunken, extending from beaks to the end of dorsal flare (well posterior of midline); beaks near anterior end, but not subterminal; anterior end broadly rounded, dorsal flaring, posterior tapering; calcareous incrustations straight off posterior end, not forming forceps.

Anatomy

Not examined. Scott (1988a) detailed much of the anatomy of this species.

Measurements

Length 21 mm (4 mm are the forceps concretions); height 6.5 mm; width 6 mm; specimen collected by Diarmaid O'Foighil (27 July 2002) at West Summerland Key, IMBW-FK-629, 24°39.3'N, 81°18.2'W. Six additional Florida lots examined (SBMNH), including specimens from Missouri Key (SBMNH 350551).

Habitat

Boring into limestone. Scott (1988a) reported from living and dead coral, and rock.

Literature

Kleeman (1983, 1990a, b, 1996), Mikkelsen & Bieler (2000), Morton (1990), Redfern (2001: 202), Scott (1985, 1988a, b), Turner & Boss (1962), Warmke & Abbott (1971; 164).

Petricolidae Orbigny, 1840

Choristodon robustum (G. B. Sowerby I, 1834)

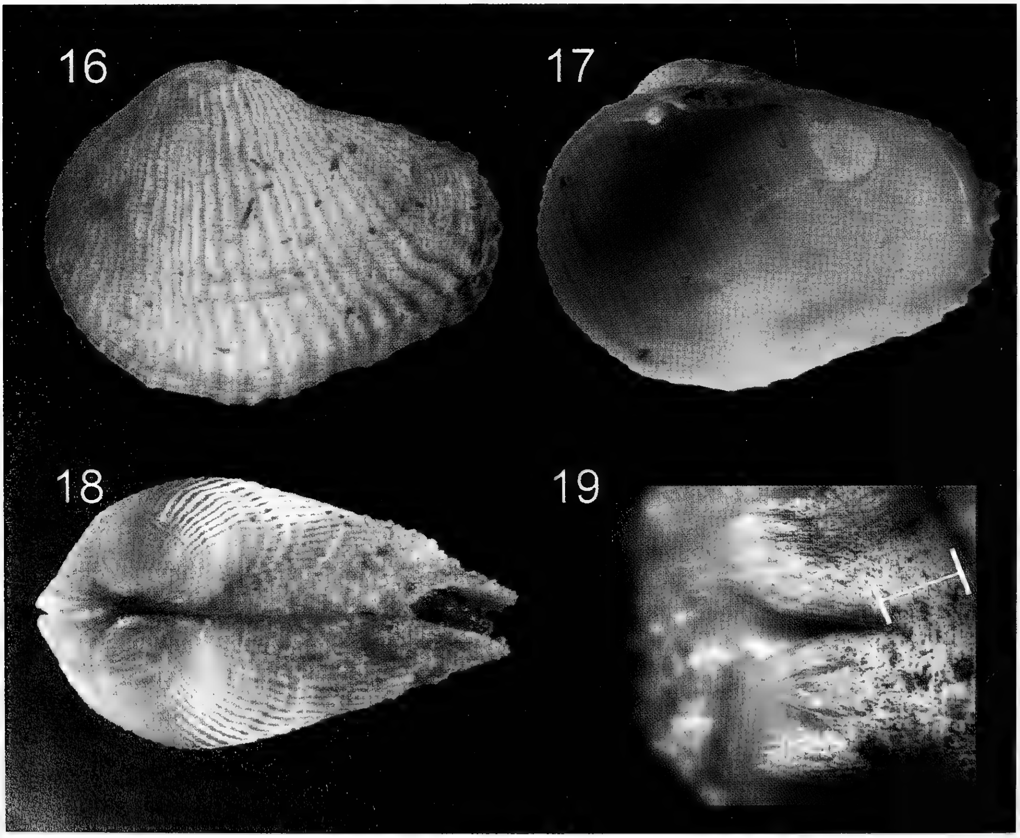
Figures 16–19, Table 1

Diagnosis

Shell ovate-elongate to trigonal, moderately inflated; inequilateral, posterior end much longer; anterior broadly rounded, posterior end tapering; sculpture of strong, irregular radial ribs, most prominent on the central portion of the shell; anterior and posterior ends gaping; siphons fused for nearly half length; length of shell to 43 mm.

Description

Exterior – Lateral View: Shell ovate to trigonal; moderately inflated; inequilateral, posterior end much longer; anterior end rounded, posterior end attenuate; umbones prosogyrate;



FIGS. 16–19. *Choristodon robustum*. West Summerland Key, Monroe County, Florida; 24°39.3'N, 81°18.2'W; subtidal; Station 629. FIGS. 16, 17: Length 20.2 mm; SBMNH 350554; FIG. 16: External left valve; FIG. 17: Internal right valve; FIG. 18: Length 19.8 mm; dorsal view; SBMMH 350553; FIG. 19: Siphons of living animal, demarcation showing region of siphonal fusion; SBMNH 350552.

TABLE 1. Characteristics of members of the Petricolidae from the Middle Florida Keys.

Species	Shell shape / sculpture	Exhalant siphonal tentacles	Inhalant siphonal tentacles	Siphonal fusion	Outer labial palps	Ctenidia color	Demibranch plicae	Foot
Choristodon robustum	ovate-elongate to trigonal, posterior end much longer; strong, irregular radial ribs	simple, white papillae along rim	short, simple papillae along rim	siphons fused for half length of inhalant siphon	light pink to yellow; small size, with 14 plicae	creamy white	inner demibranch: 20 plicae, outer demibranch: 20 plicae	white color, laterally compressed; long sole; toe small, sharp and pointed; heel small, pointed
Choristodon sp. A	ovate, subequilateral, anterior with flange; fine radial ribs anteriorly, becoming stronger posteriorly	simple, short papillae with dark brown spots; inner papillae are white, flower-like	simple, short papillae with dark brown spots; inner papillae are white, flower-like	siphons only fused at basal part	light orange; small size; 16 plicae	light pink to creamy white	inner demibranch: 16 plicae, outer demibranch: 12 plicae	white color; thick, broad; toe broad, short; without heel
Petricola lapicida	subquadrate; fine divaricate ribs, radial ribs posteriorly	tentacles are of several types, some simple bifurcations, others heavily branched	tentacles of two types, (1) simple, pointed, not bifurcate, with small lobes on side, (2) very short tentacle nobs	not fused	white; medium size; with 32 plicae	dark orange	inner demibranch: 52 plicae, outer demibranch: 40 plicae	peach color; compressed laterally; pointed toe

beaks broad, projecting; sculpture of irregular radial ribs, weak anteriorly, strong posteriorly; posterior ribs prominent, broad, rounded, groove between ribs shallow, broad; anterior ribs very weak, barely visible at anterior end; mid portion ribs gradually increasing in size and height, sharp, thin; commarginal striae closely spaced, making surface weakly cancellate, slightly lamellate posteriorly.

Dorsal View: Shell moderately inflated, slightly compressed posteriorly; shell inequivalve, right side larger; shell gaping anterior and posterior of beaks; ligament short, external, sunken, on nymph; lunule small, deep; prodissoconch large.

Ventral view: Widely gaping except for midline; terminal end of radial ribs intermesh at midline; right valve convex posteriorly; left valve concave posteriorly; posterior end twisted to the left; inequivalve, left valve smaller.

Interior: Hinge plate short; three cardinal teeth in left valve – two anterior teeth short, stout, posterior tooth larger, plate-like, pointing posteriorly; right valve with two cardinal teeth – anterior tooth short, wide, stout, posterior tooth very small, thin, plate-like; ligament in two parts, outer section beginning just below beaks, light brown, inner section attached to nymph, black.

Pallial sinus broad, shallow, not extending to beaks (about 1/3 distance between adductors); right valve pallial sinus slightly broader than that of left valve; pallial line continuous in sinus region, patchy along ventral margin; anterior adductor muscle scar long, moderate in width, pointed dorsally and ventrally; posterior adductor muscle scar nearly circular; left valve with two small pedal retractor scars posterodorsally; inside shell surface chalky; inner margin weakly and irregularly crenulate behind umbonal middline, inner margin non-crenulate anteriorly.

Anatomy (Table 1)

External View: Siphons translucent pale yellow/orange on outer section, milky white near mantle, with small white granules in tissue, and brown streaks and blotches; exhalant siphon much narrower than inhalant; inhalant siphon with short, simple papillae along rim; exhalant with simple papillae along rim; middle mantle fold light orange distally, rim plicate.

Internal View: Outer and inner mantle fold very thick milky white, middle fold plicate, light orange with sporadic white granules towards the siphons, middle mantle fold near siphons dark brown; mantle fused from siphons to line below umbones; pedal gape relatively short extending from below beaks to anterior margin; labial palps small, with 14 plicae; siphons fused for approximately half of their length; ctenidia creamy white; ctenidial plicae parallel to dorsal margin; outer demibranch 2/3 length of inner demibranch; plicae much larger and wider than *P. lapicida*, approximately 20 plicae on outer demibranch, about 20 on inner demibranch; foot white, laterally compressed, long sole, toe small, sharp, pointed; with small pointed heel.

Measurements

Length 19 mm, height 14 mm, width 10 mm; specimen collected by P. Valentich-Scott and G. Elisabeth Dinesen at West Summerland Key, IMBW-FK-629, 24°39.3'N, 81°18.2'W (SBMNH 350552).

Habitat

Shallow, unlined burrows in limestone rocks. Carter (1978) reported (as *Rupellaria typica*) in dead coral (*Diploria*).

Literature

Coan (1997), Keen (1971: 199), Lamy (1923), Redfern (2001: 240), Warmke & Abbott (1971: 199, as *Rupellaria typica*).

Choristodon sp. A

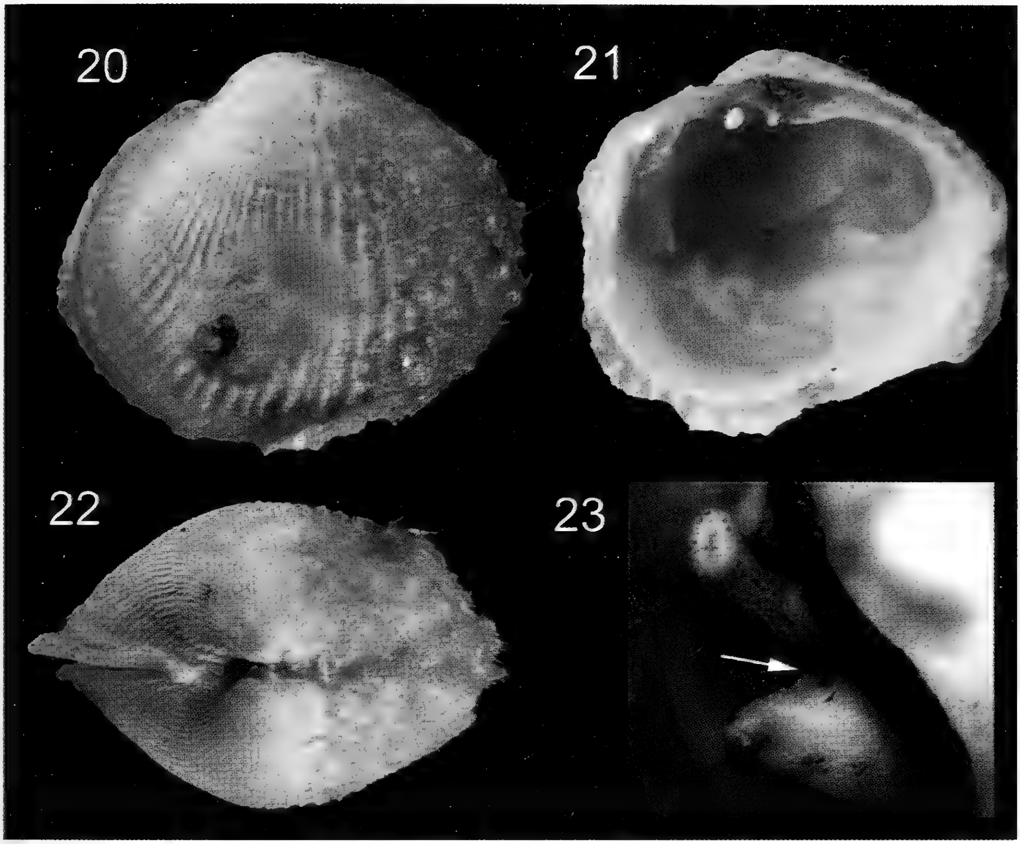
Figures 20–23, Table 1

Diagnosis

Shell ovate, inflated; subequilateral; anterior end with flange, extending well beyond inner shell margin; sculpture of fine radial ribs on anterior portion, stronger radial ribs posteriorly; anterior end slightly gaping, posterior end tightly closed; siphons only fused basally; length of shell to 23 mm.

Description

Exterior – Lateral View: Shell ovate, highly inflated, anterior end broad, posterior end slightly tapered; subequilateral, posterior end slightly longer; posterodorsal margin straight; anteroventral margin flared laterally; beaks broad, inflated, prosogyrate; lunule deep; sculpture of pronounced radial flat-topped ribs, interspaces deep, wide, overlain by fine commarginal striae.



FIGS. 20–23. *Choristodon* sp. A. West Summerland Key, Monroe County, Florida; 24°39.3'N, 81°18.2'W; subtidal; Station 629; length 22.8 mm; SBMNH 350556. FIG. 20: External right valve; FIG. 21: Internal left valve; FIG. 22: Dorsal view; FIG. 23: Siphons of the living animal, arrow showing fusion only at base of siphon (SBMNH 350555).

Dorsal View: Ligament deeply sunken, short; shell gaping anteriorly, but closed posteriorly; equivalve.

Ventral View: Anterior end slightly gaping, posterior end tightly closed.

Interior: Right valve with two cardinal teeth, with large stout anterior tooth, fairly large plate-like posterior tooth; left valve with 3 cardinal teeth, anterior tooth small, stout, middle tooth large stout, posterior tooth thin plate-like.

Anatomy (Table 1)

Siphons small, short; space between siphons dark brown, dorsal of exhalent siphon dark brown, remaining area around siphons white; rim of both siphons with simple, short papillae with dark brown spots; inner papillae white, flower-like; siphons only fused for a short distance beyond mantle; posterior portion of mantle very dark brown; outer fold thick, smooth; middle mantle fold thinner than outer, slightly plicate, pigmented towards siphons; inner mantle fold thick, milky white, smooth; pedal gape short anteriorly; inner mantle fold unfused along anterior margin, but fused for remainder of ventral margin; labial palps small, short, with 16 plicae; ctenidia pale pink to creamy white; outer demibranch with 12 plicae, inner demibranch with 16 plicae; foot thick, broad, without heel, with broad, short anterior end.

Measurements

Length 25 mm, height 20 mm, width 16 mm; specimen collected by P. Valentich-Scott and G. Elisabeth Dinesen at West Summerland Key, IMBW-FK-629, 24°39.3'N, 81°18.2'W (SBMNH 350555).

Habitat

Boring into limestone, adjacent to *Choristodon robustum*. We found many shells of this species to be heavily bored by sponges and polychaetes.

Remarks: Coan (1997) placed *Choristodon typica* Jonas, 1844, in synonymy with *C. robustum*, based on the figure provided by Jonas (Coan, 1997: fig. 43). The species we describe above is distinct, conchologically and anatomically, from *C. robustum* (e.g., shell outline and sculpture, siphonal fusion, siphonal tentacles). As yet, we have not found a described species to correspond with our material. However, our specimens are very similar to the species illustrated by Narchi (1974), which he identified as *C. typica*. The Florida Keys species is not the same at Redfern's (2001: 240) *Petricola* sp. from the Bahamas, nor *P. stellae* (Narchi, 1975) from Brazil (Narchi, 1975).

Table 1 compares anatomical characters of the two species of *Choristodon* found in the Middle Florida Keys, along with *Petricola lapicida*.

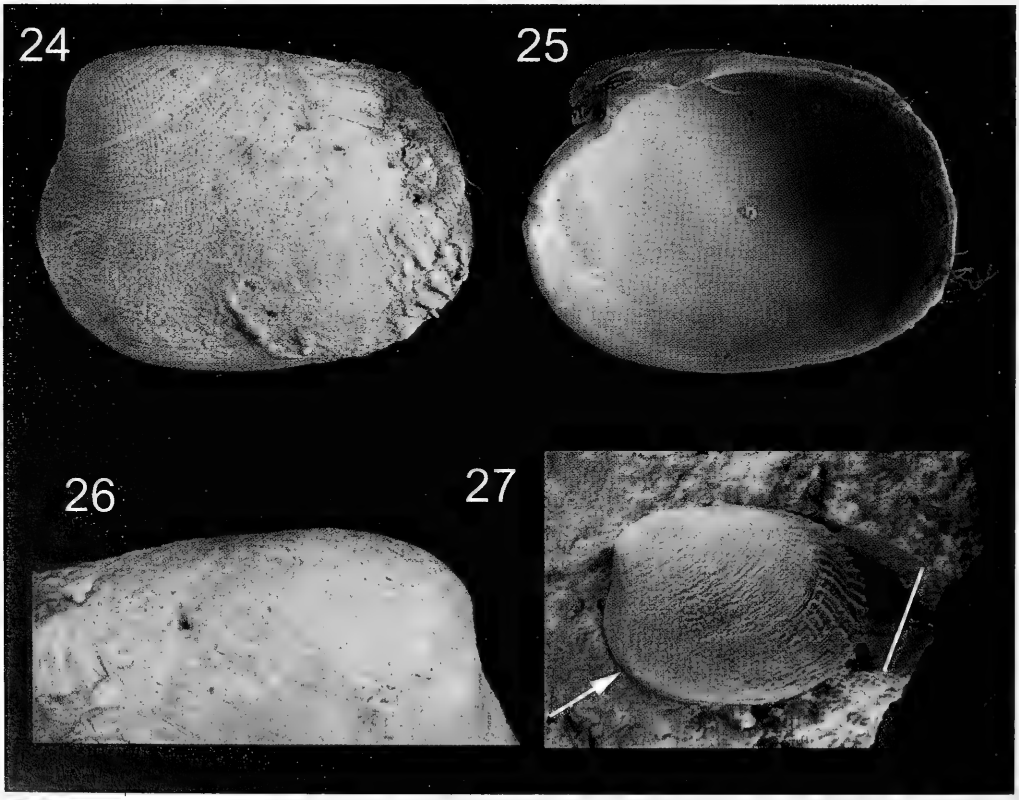
Literature

Narchi (1974).

Petricola lapicida (Gmelin, 1791)
Figures 24–27

Diagnosis

Shell subquadrate; inequilateral, posterior end much longer; sculpture of fine divaricate ribs over entire surface, and partial radial ribs near the posterior margin; siphons not fused; length of shell to 30 mm.



FIGS. 24–27. *Petricola lapicida*. West Summerland Key, Monroe County, Florida; 24°39.3'N, 81°18.2'W; subtidal; Station 629; length 27.3 mm; SBMNH 350343. FIG. 24: External left valve; FIG. 25: Internal right valve; FIG. 26: Detail of external of right valve showing divaricate markings; FIG. 27: Preserved animal in limestone burrow, arrows denote burrow tightly fitting around animal (anteriorly), and the constricted posterior portion of the burrow; SBMNH 350559.

Description

Exterior – Lateral View: Shell subquadrate, strongly prosogyrate, beaks broad, inflated; inequilateral, posterior end much longer, beaks almost at anterior end; anterior end rounded; posterior end truncate; posterodorsal margin nearly straight; sculpture very fine, divaricate ribs over most of surface (Fig. 26); posterodorsal region with few pronounced, sharp radial ribs, terminating before margin, sometimes wavy near ventral margin (eroded in some), interspaces between radial ribs wide, flat.

Dorsal View: Inflated anteriorly, more compressed posteriorly; equivalve; ligament deeply sunken, short; lunule deeply excavated posteriorly beneath ligament.

Ventral View: Without ventral gape.

Interior: Hinge plate short, triangular; periostracum in lunular region; ligament deeply sunken, seated on a elongate infolded nymph, in two sections, both dark brown; left valve with two teeth, anterior tooth large, rectangular, posterior tooth small, thin, plate-like; right valve with two teeth, anterior small peg-like, posterior larger but plate-like; pallial sinus very broad, shallow, not reaching beaks; ventral pallial line slightly patchy, continuous in sinus area; anterior adductor muscle scar long, narrow (slightly broader than *C. robustum*); posterior adductor circular.

Anatomy (Table 1)

Mantle fused from beak to anteroventral margin, small fusion just anterior of inhalant siphon; mantle open over entire ventral region from inhalant siphon to anterior margin; mantle without papillae; most of mantle milky white, except near siphons where it is dark brown in color; mantle swollen anteroventrally, possibly a pallial gland; outer mantle fold very thin; middle fold muscular, tapering on margin, wavy, inner fold thin; mantle filled with white granules; labial palps white, medium length, pointed ventrally, with 32 plicae; smooth dorsally and anterior portion of palp; ctenidia dark orange; plicae parallel to dorsal surface; outer demibranch extending to middle of inner demibranch; plicae number on demibranchs – inner 52, outer 40; siphons transparent dark gray, with embedded white granules; exhalant siphon circular in outline with tentacles of several types, some with simple bifurcations, others heavily branched; inhalant siphon elongate-ovate, gray with white spots; inhalant siphonal tentacles of two types, large compared to exhalant, simple, pointed (not bifurcate), with small lobes on side; also very short tentacle nobs projecting; inhalant siphon three times as large in diameter as exhalant; siphons barely extending beyond shell margin; foot compressed laterally, peach color, very flexible, pointed at tip.

Measurements

Length 27 mm, height 20 mm, width 13 mm, specimen collected by P. Valentich Scott and G. Elisabeth Dinesen at West Summerland Key, IMBW-FK-629, 24°39.3'N, 81°18.2'W (SBMNH 350558).

Remarks

Field observations of the burrow of *Petricola lapicida* have shown it lives in a constricted, flat burrow (Fig. 27). This strongly suggests the species burrows through chemical means only, and agrees with the findings of Morton & Scott (1988) and Morton (1990). Comparisons between the functional morphology of *P. lapicida* and *P. pholadiformis* were presented by Purchon (1955).

Habitat

Shallow burrow in limestone. Carter (1978) reported this species in dead coral (*Diploria*).

Literature

Abbott (1974), Bromley (1978), Kleemann (1990a), Lamy (1923), Morton (1990), Morton & Scott (1988), Redfern (2001: 240), Robertson 1963, Warmke & Abbott (1971: 191).

Gastrochaenidae Gray, 1840
Gastrochaena hians (Gmelin, 1791)
Figures 28–30

Diagnosis

Shell ovate, white; incurved and widely gaping ventrally; widely gaping posteriorly; beaks terminal.

Description

Exterior – Lateral View: Shell inflated, ovate elongate; posterior end rounded, flaring; anterior end narrow pointed; beaks terminal, pointed, prosogyrate; prodissococh large, smooth; widely gaping anteroventrally, invaginate; shell color translucent white; sculpture of commarginal striae, stronger anteroventrally, without radial elements; shell thicker along ventral gape.

Dorsal View: Highly inflated, more compressed posteriorly; right valve overlapping the left; left valve slightly concave posteriorly; ligament external, protruding, long, one third of shell length; valves slightly gaping posterior to ligament.

Ventral View: Periostracum thin, milky white, translucent, dehiscent; outer mantle fold thick, projecting beyond valve margin, wide gape, not fused for half shell length; middle mantle edge fused except for small pedal gape near shell midline; posterior end tightly closed, right valve overlapping left; posteriorly periostracum projecting beyond shell margin.

Interior: Not examined.

Anatomy

See Carter (1978) for discussion of *Gastrochaena* anatomy and shell features, along with diagnostic characters of related species.

Measurements

Length 11 mm, maximum height 6 mm, width 4.5 mm, ligament length 4.5 mm, gape length 8 mm, gape width 4 mm; specimen collected by Lisa Kirkendale on 27 July 2002, at Fiesta Key, IMBW-FK-644, 24°50.4'N, 80°47.0'W (SBMNH 350345). Three additional specimens were collected by the authors from West Summerland Key, IMBW-FK-629.

Habitat

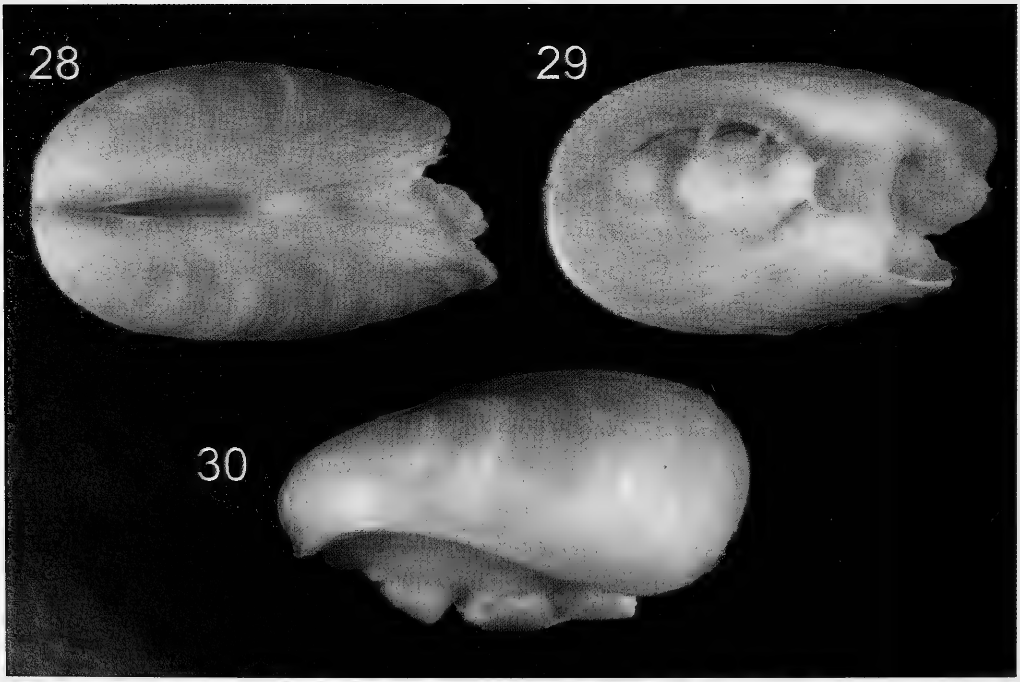
In calcareous lined burrows in living and dead coral, and limestone. Carter (1978) reported in dead coral (*Diploria*).

Remarks

Coan, et al. (2000: 494, left specimen) illustrated a Florida specimen of *Gastrochaena* as *G. ovata*, but this specimen is actually *G. hians*.

Literature

Carter (1978), Morton (1983, 1990), Redfern (2001: 242).



FIGS. 28–30. *Gastrochaena hians*. Fiesta Key Causeway, Monroe County, Florida Keys; 24°50.4'N, 80°47.0'W; subtidal; station 644; length 11.8 mm; SBMNH 350345. FIG. 28: Dorsal view; FIG. 29: Ventral view; FIG. 30: Lateral view of left side.

DISCUSSION

The rock and coral boring bivalves of the Middle Florida Keys are diverse and numerous. With a modest sampling effort, eight species representing three families were observed and collected. While quantitative studies were not undertaken, several limestone rocks had more than 50 individuals/m^2. However, there was a distinct patchiness to the distribution of these borers, even with seemingly identical substrata in adjacent areas. Often, large limestone boulders were completely void of bivalve borers, where adjacent rocks were riddled with petricolids, mytilids, and gastrochaenids.

Careful examination of the living bivalves and boreholes has confirmed the boring mechanisms of two species. In agreement with Wilson & Tate (1984) and Kleemann (1990a), our observations indicate that *Botula fusca* is a chemical borer (Fig. 3). Similarly we have found strong indications of chemical boring in *Petricola lapicida* (Fig. 27), concurring with Morton & Scott (1988). Lithophagans were relatively rare in our sampling areas, and we were unable to make definitive conclusions on habitat or boring mechanisms of these species.

Far outside the scope of this paper are conclusions about the localized or global distributions of many boring bivalve species. Among the different lineages of boring bivalves, several are thought to be represented by a single genus with one or only a few species, and distributed worldwide (Morton, 1990). Morton further discussed the evolutionary events and implications, which could explain both the presence of true cosmopolitanism of some species and restricted regional distribution of other species.

Nomenclatural inconsistency by researchers may account for confusion between cosmopolitan distributions and localized endemism within the boring bivalve lineages. This is easily understood, as the majority of boring bivalve species names (and most marine bivalves) were originally designated exclusively based on shell characters. The shell morphology of boring bivalves has shown intraregional variation as large as interregional variation (Coan, 1997). This could be due to worldwide conspecifity, as has been suggested for *Botula fusca* by Wilson & Tait (1984), with shell plasticity as a consequence of individual morphometric adaptation to their boring habitat. The use of shell features to discriminate between the species within different lineages of boring bivalves still needs confirmation from other methods (e.g., gross anatomy and histology, molecular sequencing and analyses).

ACKNOWLEDGEMENTS

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COMPARATIVE MORPHOLOGICAL STUDY OF FOUR SPECIES OF *BARBATIA* OCCURRING ON THE SOUTHERN FLORIDA COAST (ARCOIDEA, ARCIDAE)

Luiz Ricardo L. Simone[1] & Anton Chichvarkhin[2]

ABSTRACT

A detailed study on the morphology of the arcid genus *Barbatia s.l.* is performed, based on the common species occurring in Florida, complemented by samples from Brazil. The species are: *B. cancellaria, B. candida, B. dominguensis*, and *B. tenera*. The primary goal of this project is to collect comparative morphological data (especially on the internal anatomy) suitable for use in phylogenetic analysis. A complete descriptive and systematic treatment of these species is presented. A small phylogenetic analysis, based on nine characters (19 states) and seven taxa, demonstrates a closer relationship of *B. cancellaria* with *B. candida*, and of *B. dominguensis* with *B. tenera*. *Barbatia s.l.* is found to be monophyletic.

Keywords: specific differentiation, phylogeny, distribution, systematics.

INTRODUCTION

It is often thought that bivalve anatomy is very conservative and therefore of limited use for resolving systematic problems. To test this hypothesis, a study including four sympatric species that most malacologists consider to belong to a single arcid genus was undertaken. The genus is *Barbatia* Gray, 1842 (type species *Arca barbata* Linné, 1758, by subsequent designation of Gray, 1857, from the Mediterranean). The four species examined are commonly collected in intertidal and subtidal areas of rocky environments on the Florida coast, as well as in the tropical western Atlantic. Additional information about arcid biology and systematics was provided by Lamy (1907), Reinhart (1935), Heath (1941), Sullivan (1961), Coelho & Campos (1975), and Boyd (1998).

The taxonomy of the various members of Arcidae is mostly based on conchology, as the anatomical knowledge is sparse and present in few papers (e.g., Heath, 1941). The four *Barbatia* species studied here are commonly allocated in different subgenera, with *B. cancellaria* and *B. candida* mostly referred to the subgenus *Barbatia s.s.* (alternatively, *B. candida* has been placed in *Cucullaearca* Conrad, 1865; type species: *Byssoarca lima* Conrad, 1848, by the subsequent designation of Stoliczka, 1871; Upper Cretaceous, eastern United States), *B. dominguensis* to the subgenus *Acar* Gray, 1865 (type species: *Arca gradata* Broderip & G. B. Sowerby I, 1829, by the subsequent designation of Stoliczka, 1871; eastern Pacific), and *B. tenera* to the subgenus *Fugleria* Reinhart, 1937 (type species by original designation: *F. pseudoillota* Reinhart, 1937; Pliocene of Florida). Our paper provides detailed comparative descriptions of the morphology of some arcid representatives, taxonomic treatments, and a preliminary application of these data in a small phylogenetic study.

The objective of this paper is to perform a detailed anatomical study, developing the analysis of the data under a comparative scenario, showing that the study of the anatomy is valuable in comparative biology and important source of data.

MATERIALS AND METHODS

The specimens were collected during snorkeling and scuba dives in several localities of the Florida Keys (Mikkelsen & Bieler, 2004: fig. 1), and were maintained alive for several days. Some of the specimens were narcotized using magnesium hydroxide in the field laboratory and subsequently dissected. Other specimens were fixed in 96% ETOH, and after some days transferred to 70% ETOH for dissection at MZSP or FMNH. The dissections were performed using standard techniques, with specimens immersed in sea water or fixative. Images

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were obtained using a standard digital camera directly or though a microscope; drawings were made with the aid of a camera lucida. For shell measurements, length indicates the anteroposterior distance; lateral indicates the maximum inflation of the articulated valves; height indicates the dorsoventral distance originating from highest region of the umbo.

The phylogenetic analysis was performed using the computer program Hennig86 (Farris, 1988) by means of the interface Tree Gardener (Ramos, 1998). Two arcid species were also included to test monophyly of the genus *Barbatia*:

(1) *Arca zebra* (Swainson, 1833). U.S.A.; Florida; Florida Keys, Monroe County, 24°39.3'N, 81°18.2'W, "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), 4 specimens, MZSP 36100 (FK-626, Simone coll. 26/vii/02).

(2) *Anadara notabilis* (Röding, 1798). BRAZIL; Bahia; Salvador, Ribeira beach, MZSP 28481, 15 specimens (Simone coll., 24–27/ii/1997).

A non-arcid filibranch was used as an outgroup: *Isognomon bicolor* (C. B. Adams, 1845), Isognomonidae (Martins, 2000). This species is operationally used as the outgroup (rooting), the other two arcids (*A. zebra, A. notabilis*) are operationally analyzed as part of the ingroup. This procedure is undertaken for testing the monophyly of the genus *Barbatia*, as represented here. The anatomical study of these three non-*Barbatia* species was performed in detail similar to that of the *Barbatia* species described herein.

The following abbreviations are used in the figure captions: aa, anterior adductor muscle; an, anus; ao, abdominal organ; ap, anterior pedal protractor muscle; ar, anterior retractor muscle of foot; au, auricle; bf, byssal furrow of foot; by, byssus; ce, cerebral ganglion; cp, central gastric pad; cv, ctenidial vein; dd, ducts to digestive diverticula; dh, dorsal hood; er, esophageal rim; es, esophagus; ey, eye of mantle edge; ft, foot; ga, gill edge attached by cilia; gi, gill; gm, gill longitudinal muscle; gp, gill projection; gs, gastric shield; hi, hinge; ia, intestinal and style sac apertures; id, inner demibranch; if, inner fold of mantle edge; ih, inner hemipalp; in, intestine; ki, kidney; mb, mantle border; mf, middle fold of mantle edge; ml, mantle lobe; mo, mouth; ne, nephrostome; nv, nerve; od, outer demibranch; of, outer fold of mantle edge; oh, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pe, periostracum; pg, pedal ganglion; pm, pallial muscle; pp, palps; pr, posterior retractor muscle of foot; pt, pedal tentacle; rt, rectum; sa, gastric sorting area; sh, shell; ss, style sac and proximal portion of intestine; st, stomach; tm, connective between cerebral-pleural ganglia with visceral ganglion; ty, pair of typhlosoles separating intestine and style sac; um, umbo; ve, ventricle; vg, visceral ganglia; vm, visceral mass.

Abbreviations of institutions: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; MNRJ, Museu Nacional da Universidade Federal do Rio de Janeiro; MZSP, Museu de Zoologia da Universidade de São Paulo.

SYSTEMATICS

Barbatia cancellaria (Lamarck, 1819)

(Figs. 1–7, 33–36, 43–51)

For additional synonymy, see Lamy (1907: 55).

?Barbatia barbata: Heath, 1941: 294, pl. 5, figs. 2, 7; pl. 15, fig. 12 (*non* Linné, 1758).

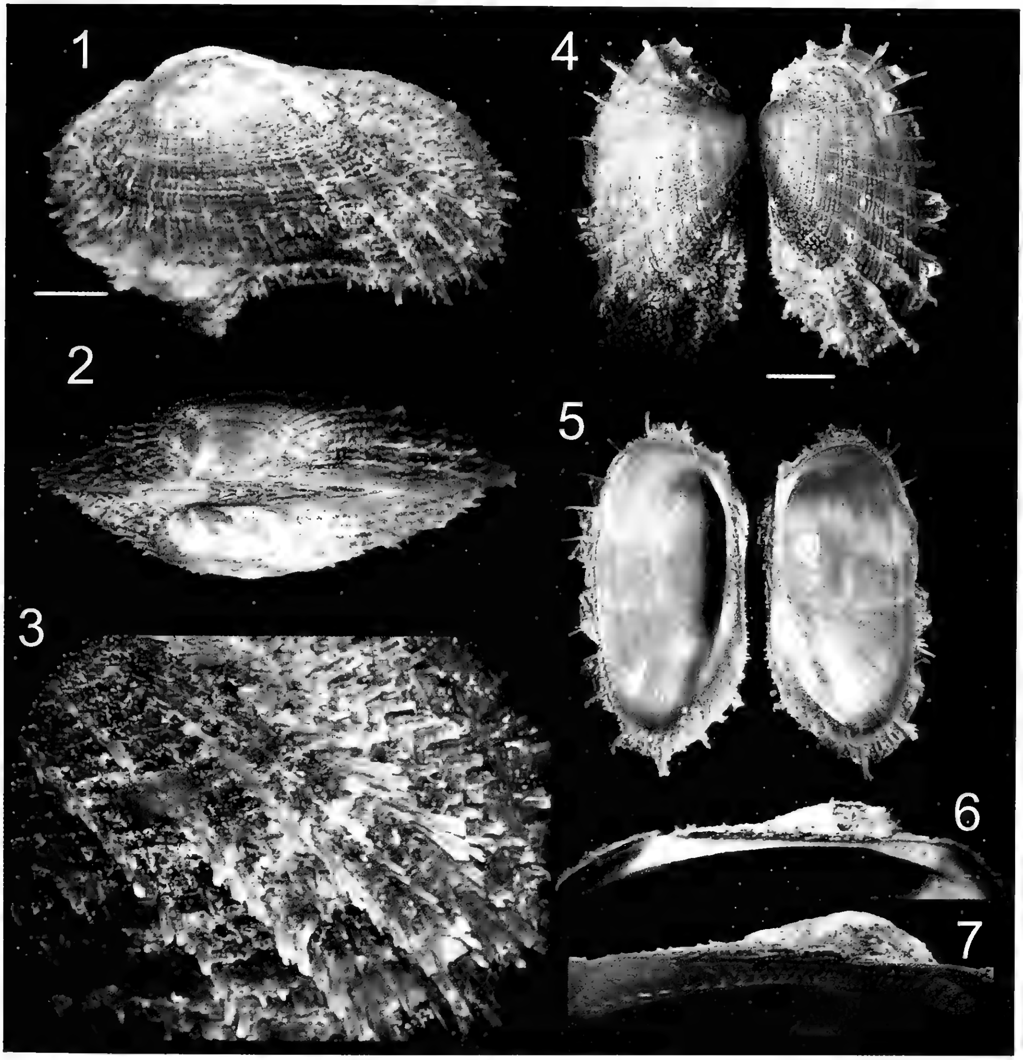
Barbatia (Barbatia) cancellaria: Warmke & Abbott, 1962: 158, pl. 30, fig. j; Rios, 1970: 151; Andrews, 1971: 150, fig.; Abbott, 1974: 421–422, fig. 4966; Rios, 1975: 192, pl. 61, fig. 939; Humfrey, 1975: 210, pl. 23, fig. 11; Rios 1985: 208, pl. 75, fig. 1061; 1994: 230, pl. 80, fig. 1136; Redfern, 2001: 203, pl. 83, fig. 831.

Barbatia cancellaria: Diaz & Puyana, 1994: 46, fig. 24.

Description

Shell (Figs. 1–7). Medium to large size, to 100 mm. Color pale reddish brown. Main sculpture composed of narrow radial threads, separated from each other by furrows of approximately same width as threads (Fig. 3); commarginal sculpture weak, composed mainly of undulations. Periostracum somewhat thick, with many scales along radial threads; scales longer close to shell border. Most specimens with a pattern (most clear in posterior region) of one row of long scales followed by five rows of short scales (Figs. 1–5). Periostracum extending beyond shell edges (Fig. 5). Umbos flat, located between anterior and middle thirds of hinge. Inner surface glossy, brownish violet on borders, becoming paler towards umbo. Hinge variable, but generally with about 30 teeth located just anterior to umbo and posteriorly (Figs. 5–7); three anteriormost teeth broader, weakly arched, tilted towards anterior; next three teeth with similar shape to those described, but narrower; following 8–10 teeth abruptly different, shorter, narrower, situated perpendicularly to outer edge of hinge, gradually becoming thicker, slightly longer and more tilted towards posterior; last 5–6 teeth broader, almost horizontal.

Soft Part Color (Figs. 33–36): Mantle border with a mixture of dark and pale brown spots, being darker towards edge (Fig. 33); some pale cream spots randomly distributed mostly along middle region of border. Posterior region of mantle border more pigmented than more anterior region, including inner surface to base of gills; this posterior-inner surface pigmented uniform beige, having irregularly sized, randomly distributed white spots (Fig. 33). This pattern also covering posterior and dorsal surface of posterior adductor muscle and rectum; anal papilla



FIGS. 1–7. *Barbatia cancellaria* shell. FIG. 1: Left view, MZSP 36105; FIG. 2: Same, dorsal view; FIG. 3: Same, detail of sculpture in posterior region; FIG. 4: Outer view of both valves, MZSP 32336; FIG. 5: Same, inner view; FIG. 6: Right valve; MZSP 36105, detail of hinge; FIG. 7: Same, MZSP 36211. Scale bars = 5 mm.

abruptly preceded by a white region. Foot and ventral region of visceral mass pigmented by a mosaic of brownish purple, coalescent spots, in a pale cream base (Fig. 36). Gills uniformly colored pale purple; their posterior, projected region colored by brownish purple, having small to large white spots randomly distributed, more concentrated along middle region (Figs. 33, 34). Remaining regions of soft parts lacking any special pigmentation.

Main Muscle System (Figs. 43, 44): Anterior adductor muscle elliptical in cross-section, located in anterodorsal region. Posterior adductor muscle rounded in cross-section, located in posterodorsal region, almost twice as large as anterior adductor muscle. Pair of pedal protractor muscles very narrow, originating in middle region of ventral edge of anterior adductor muscle, running towards posterior attached to inner surface of integument splayed insertion area near anterior foot base. Pair of anterior retractor muscles of foot narrow; originating in a small area just posterior and ventral to anterior adductor muscle, running towards posterior and ventral close to median line, inserting in anterior region of foot. Pair of posterior retractor muscles of foot very large and thick, occupying about 2/3 of visceral mass volume; originating in umbonal cavity just anterior to posterior adductor muscle, extending about twice adductor muscle area towards anterior; running towards ventral and anterior closely attached to one another (except for a narrow dorsal area along median line); inserting along middle and posterior regions of foot. Visceral wall of visceral cavity thickly muscular, serving as base for foot. Gill muscles running in a pair along ventral surface of ctenidial vein, between two demibranchs (Fig. 48).

Foot and Byssus (Figs. 36, 43, 44): Foot somewhat narrow and long. Byssal furrow deep and broad, running all along its ventral surface to pedal tip (Fig. 36), in median-posterior region of foot becoming broader, contouring byssus. A pair of pedal tentacles located preceding this broader region, close to byssus (Figs. 36, 43: pt); this pair of tentacles absent in some specimens or represented by a pair of flaps in others. Each tentacle slender, stubby, located in byssal furrow edge. Byssus composed of several fused fibers (similar to Figs. 37–39); their dorsal region forming a deep concavity, its edge formed by several, aligned, flat, free filaments, which fuse with each other after some distance; left series of filaments separated from right series by deep anterior and posterior furrows; these free portions remaining deeply introduced in byssal gland and compressed by posterior retractor muscles of foot, each filament encased in special folds of a central, large convexity (similar to Fig. 41). Middle region of byssus forming a single, solid stem. Distal portion of byssus irregularly splayed, attached to hard substrata.

Mantle: Edge of each mantle lobe entirely free (except in dorsal region). Mantle edge thick, mostly tri-folded (Fig. 49). Color as described above. Middle fold shorter, covered by inner and outer folds; inner fold tall, undulating, typically situated towards median line, touching its pair. Remaining mantle areas very thin and transparent. Flap of mantle fitting inside hinge flat and short.

Pallial Cavity (Figs. 43, 46, 48): Pallial cavity surrounding most of outer region, except a narrow area anterior to posterior adductor muscle. Gill large, filibranch, having thousands of narrow, uniform filaments. Inner and outer demibranch of equal size. Anterior 2/3 of gill attached to visceral mass, outer basal edge of outer demibranch and inner basal edge of inner demibranch attached, respectively, to mantle and visceral mass, by means of cilia (Fig. 48: ga). Posterior 1/3 of each gill attached dorsally to a long, muscular, mobile stalk (Figs. 33, 43, 46). These stalks originating side by side from ventral surface of posterior adductor muscle, relatively broad, tapering distally and posteriorly; in this region, outer basal edge of outer demibranch and inner basal edge of inner demibranch with capacity of attaching, respectively, to mantle and to its pair, by means of cilia. These stalks pigmented as described above.

Visceral Mass (Fig. 44): Visceral mass broad, thick, posterior half entirely filled by posterior pedal retractor muscles. Anterior half filled by visceral organs. Gonad pale beige, mostly located externally, surrounding digestive diverticula and tubes. Digestive diverticula brownish green, located surrounding stomach, below umbonal cavity.

Circulatory and Excretory Systems: Heart relatively small, located just anterior to origin of posterior retractor muscle of foot, in umbonal cavity (Fig. 44). Auricles originating in middle portion of gill ctenidial vein, with narrow anterior and posterior portions of ctenidial vein. Each auricle connected to accessory auricles as expansions of ventricle (Fig. 50) in middle region of a broad outer surface, gradually tapering and inserting in ventricle. Ventricle narrow, surrounding intestine. Kidney mostly solid, brown, located along posterior half of gill insertion on visceral mass, on their inner edge (Fig. 46), gradually becoming broader, crossing to region dorsal to gill on visceral mass. Nephrostome a small slit located in anterior extremity of each kidney (Fig. 46: ne).

Digestive System (Fig. 44): Palps located contouring anterior edge of pallial cavity, just posterior to anterior adductor muscle (Figs. 34, 35), surrounding anterior edge of gill. Palps dorsoventrally very long, anteroposteriorly short; dorsal end somewhat rounded, of uniform width along their length. Palp outer surface smooth. Palp inner surface with a special arrangement of folds similar in outer and inner hemipalps (Figs. 35, 45); folds of dorsal half of palp transverse, situated perpendicular to posterior palp edge; folds gradually curving, situated longitudinally; ventral palp half with longitudinal (dorsoventral) folds restricted to region close to intersection of both hemipalps, running parallel to one another towards mouth. Palps' ventral connection with each other broad, forming a sac that covers anteroventral region of visceral mass (Figs. 43, 45). An inner smooth area contouring entire posterior edge of palps, broader in ventral half (Fig. 45). Mouth located at anterior end of ventral connections between palps. Esophagus running close to posterior surface of anterior adductor muscle, almost its entire length, relatively narrow, inner surface with low, narrow longitudinal folds. Stomach dorsoventrally elongated, situated transversely in middle region of visceral mass; stomach dorsal region spherical, positioned horizontally, abruptly curving towards ventral, narrowing gradually, continuing as style sac. Gastric inner surface (Fig. 51) separated from esophageal surface by ventral, narrow, low rim, which extends toward posterior in right side; immediately posterior to rim a broad, concave sorting area, bearing several transverse (situated anteroposteriorly) uniform folds; aperture to digestive diverticula as two pairs, each positioned between these folds, two on each side; gastric central pad located transversely, in mid-ventral gastric surface, as posterior limit of previously described sorting area; central pad possessing longitudinal (left to right) low, uniform folds, left region of central pad fitting in dorsal hood, anterior and right borders somewhat tall, posterior border connected to typhlosole, which runs towards intestine. Pair of typhlosoles incompletely separating intestine from style sac; anterior typhlosole originating broadly, attached to central pad; posterior typhlosole narrow, originating as low, weak fold; a low, narrow fold dorsally surrounding aperture of style sac and intestine, located in posterior-left side of ventral gastric surface. Gastric shield located in middle region of posterodorsal gastric inner surface. Dorsal hood low, located in middle-left side of gastric dorsal surface. Digestive diverticula as described above. Intestine as continuation of style sac, curving abruptly towards right, performing three strong, but short loops located along right surface of style sac. Intestine broad in region after style sac, abruptly becoming relatively narrow, with uniform width along its length. After these loops, intestine running posterodorsally to pericardial region; running horizontally though ventricle and narrowly between both posterior retractor muscles of foot. Rectum exposed in excurrent chamber (although covered by integument), running in dorsal and posterior surface of posterior adductor muscle. Anal papilla (Figs. 43, 46, 47) a long projection towards posterior, narrowing gradually to a pointed tip; located in posteroventral region of adductor muscle; anal aperture long, subterminal, ventral, possessing a small transverse fold in anterior end.

Central Nervous System: Pair of cerebral-pleural ganglia located compressed between esophagus and anterior adductor muscle posterior surface, situated laterally at broad distance from each other. Pair of pedal ganglia large, located close to each other in anterior surface of visceral mass (Fig. 44), just dorsal to anterior adductor muscle; their connective with cerebral-pleural ganglia very thin, relatively short. Pair of visceral ganglia located in base of both gill projections (Fig. 46) in anterior region of posterior adductor muscle, close to each other and to median line; a broad nerve running along gill projection axis; their connective with cerebral-pleural ganglia very thin, running close to integument. A conspicuous pair of nerves originating from posterior end of visceral ganglia, running along gill stalks to their distal ends. Abdominal organ as a pair of bulging masses covering ventral surface of posterior adductor muscle, just posterior to visceral ganglia.

Measurements of Dissected Specimens (length, lateral, height in mm): MZSP 36105(1): 47.8 by 19.4 by 26.4; (2): 47.3 by 22.4 by 28.0; MZSP 36258(4): 34.4 by 13.5 by 18.7.

Distribution

North Carolina, USA, to Bahia, Brazil.

Habitat

Rocky, from intertidal zone to about 10 m depth.

Material Examined

U.S.A.; Florida; Florida Keys; Monroe County, roadside quarry N of Keys Marine Laboratory, 24°49.78'N, 80°48.51'W, 2–5 m depth, MZSP 36105, 6 specimens (Simone coll. 22/vii/2002); "Long Key Artificial Reefs", oceanside of Long Key, 24°44.78'N, 80°50.00'W, 7 m depth, MZSP 36277, 4 specimens (FK-621, Simone coll., 17/vii/2002); W side of Pigeon Key, 24°42.2'N, 81°09.3'W, MZSP 26171, 2 specimens (sta. 647, Simone coll., 28/vii/2002); Bahia Honda State Park, oceanside, just E of old bridge, 24°39.25'N, 81°16.83'W, MZSP 36268, 1 specimen (FK-632, Simone coll., 22/vi/2002); Old Dan Bank, bayside of Long Key, 24°50.45'N, 80°49.63'W, MZSP 36258, 4 specimens (FK-620, Simone col, 16–18/vii/2002); "The Billboard" site, oceanside, Lower Matecumbe Key, MM 74.5, 24°51.4'N, 80°43.7'W, MZSP 36261, 4 specimens (FK-642, Simone coll., 23/vii/2002); oceanside off Craig Key, 24°49.81'N, 80°45.73'W, MZSP 36197, 2 specimens (FK-640, Simone coll., 23/vii/2002); "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), MM 35, 24°39.3'N, 81°18.2'W, MZSP 36211, 4 specimens (FK-629, Simone & Leal coll., 21–25/vii/2002), MZSP 36101, 7 specimens (FK-629, Simone coll., 26/vii/2002). BRAZIL; Pernambuco, Fernando de Noronha Archipelago (Simone & Souza coll.); Porto Beach, MZSP 31205, 2 specimens, 4 shells, MZSP 31247, 1 shell (17/vii/1999); Atalaia Beach, MZSP 31166, 1 specimen (18/vii/1999); Buraco do Inferno, Rata Island, MZSP 31071, 21 specimens (19/vii/1999); Bahia; Abrolhos Archipelago, MZSP 39837, 1 specimen (Luiz Pinni Neto coll., v/1958); Coroa Vermelha, MZSP 23698, 1 specimen (L. Pinni NT. Coll., ii/1957); Pedra da Lixa, Parcel de Paredes, MZSP 32336, 5 specimens (Souza & Gonçalves coll., i/2000).

Barbatia candida (Helbling, 1779)
(Figs. 8–14, 26, 32, 37–39, 52–59)

For additional synonymy: Coelho & Campos (1975: 40).

Barbatia (Barbatia) candida: Warmke & Abbott, 1962: 158, pl. 30, fig. i; Rios, 1970: 150–151; Andrews, 1971: 150–151, fig.; Abbott, 1974: 421, fig. 4965; Humfrey, 1975: 210, pl. 23, fig. 6; Redfern, 2001: 203, pl. 83, fig. 832.

Barbatia (Cucullaearca) candida: Heath, 1941: 294, pl. 5, figs. 4, 5; pl. 7, fig. 9; Rios, 1975: 192, pl. 62, fig. 940; 1985: 209, pl. 75, fig. 1063; 1994: 230, pl. 80, fig. 1138.

Barbatia candida: Merlano & Hegedus, 1994: 46, fig. 23.

Description

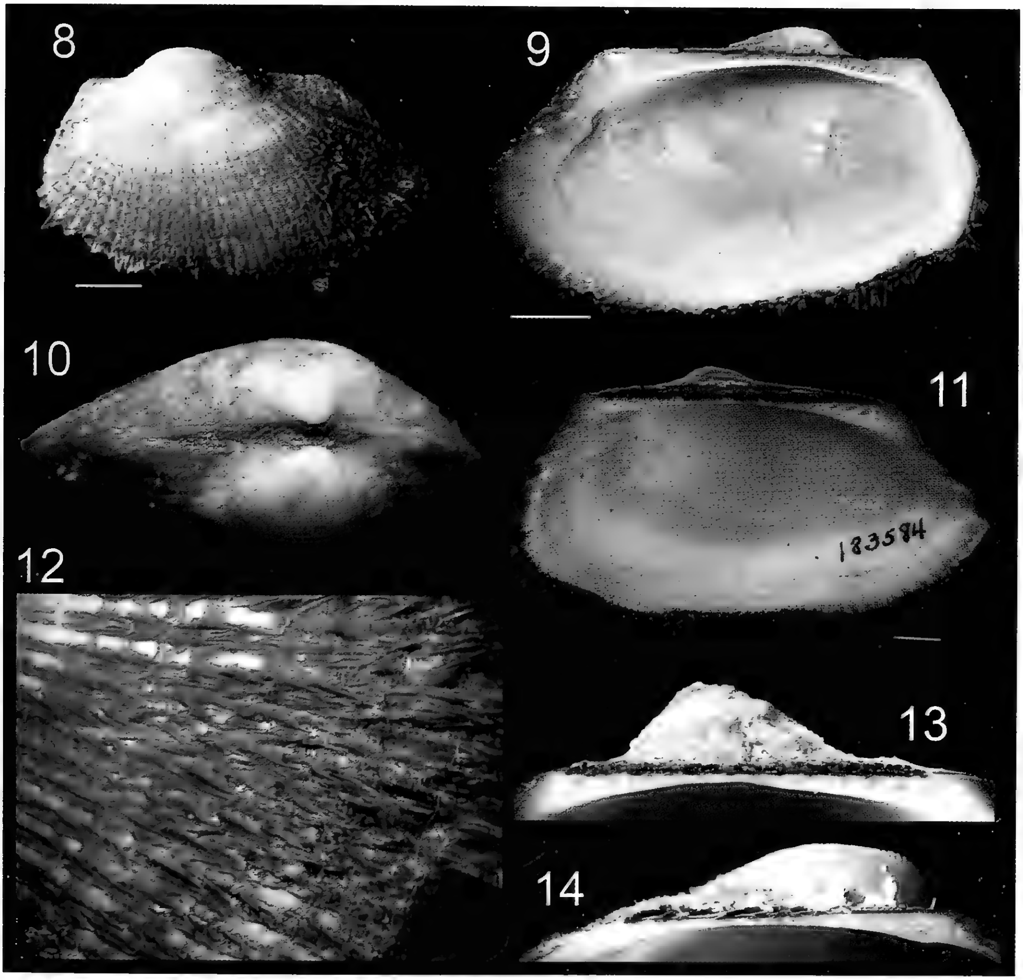
Shell (Figs. 8–14, 32): Medium to large size, to 100 mm. Color beige to pale brown. Main sculpture composed of narrow radial threads (Figs. 8, 12, 32) separated from each other by furrows of approximately same width as threads; commarginal sculpture of only growth lines; threads relatively uniform in size, except posterior threads somewhat broader. Periostracum relatively thick, with many scales along radial threads, scales longer close to shell border, varying in shape from simple (in southern specimens, Fig. 32) to bifid (in northern specimens, Fig. 12). Periostracum extending beyond shell edges, mainly in region between threads (Figs. 9, 11). Umbos flat to tall, located between anterior and middle thirds of hinge (Fig. 10). Inner surface glossy, white (Figs. 9, 11). Hinge (Figs. 9, 11, 13, 14) variable, but generally with about 30 teeth located both anterior and posterior to umbo; three anteriormost teeth broader, straight, weakly tilted towards anterior; posteriorly a series of similar-shaped teeth, becoming gradually smaller until umbo level, afterwards gradually increasing towards posterior, becoming weakly tilted posteriorly; last 5–6 teeth broader, strongly tilted posteriorly.

Soft Part Color: Mantle border gill stalks and exposed portion of foot with similar coloration to those of *B. cancellaria*, differing in being paler, with beige base color beige.

Main Muscle System (Fig. 54): Essentially as in *B. cancellaria*. Other details in Heath (1941: pl.7, fig. 9).

Foot and Byssus (Figs. 37–39). As in *B. cancellaria*, except pair of pedal tentacles absent, and with distinct color as described above. Foot convexity for byssal accommodation (Fig. 41) similar to that in *B. cancellaria*.

Mantle (Figs. 52, 55): Mantle edge thick but thinner than that in *B. cancellaria*, mostly trifolded. Color as described above. Middle fold shorter, covered by inner and outer folds; inner fold tall, undulated, typically situated towards median line, touching its pair. Most



FIGS. 8–14. *Barbatia candida* shell. FIGS. 8–10: AMNH 298092; FIG. 8: Left valve, outer view; FIG. 9: Same, inner view; FIG. 10: Whole specimen, dorsal view; FIGS. 11, 12: FMNH 183584; FIG. 11: Right valve, inner view; FIG. 12: Detail of sculpture and periostracal scales in posterior region; FIGS. 13, 14: Detail of hinge; FIG. 13: Right valve, MZSP 32304 from Bahia, Brazil; FIG. 14: Left valve, MZSP 32336. Scale bars = 5 mm.

specimens with a short portion with clear undulations in ventral region of incurrent canal and in mid-ventral region.

Pallial Cavity: As in *B. cancellaria*, except as follows. Muscular and mobile stalk of gill narrower and differently pigmented (as described above). Gill filaments of each demibranch maintained in their position by a transverse membrane restricted to ventral half of filament, this membrane connecting inner branch of each filament to outer branch in both inner and outer demibranchs (Figs. 42, 57).

Visceral Mass: As in *B. cancellaria*.

Circulatory and Excretory Systems (Fig. 58): As in *B. cancellaria,* except in having shorter and paler-colored kidney.

Digestive System (Fig. 53): Most characters as in *B. cancellaria*, except as follows. Palps with same location and outer features, including sac-like ventral region preceding mouth (Figs. 52, 56); inner folds arrangement with longer portion with transverse (antero-posterior) folds, ventral portion smooth, lacking folds (Fig. 56). Gastric inner surface (Fig. 58) with esophageal rim surrounding entire esophageal aperture, additionally with a branch at right surrounding a distinct duct to digestive gland, being broader, forming a small dorsal chamber. Central pad narrower, originating from right branch of esophageal rim, passing anteriorly to aperture of dorsal hood; central pad disconnected from anterior typhlosoles. Anterior typhlosole with about same width as posterior typhlosoles, and originating from a longitudinal, low, narrow fold running along left gastric surface. Posterior typhlosole as continuation of fold separating gastric and style sac chambers. Intestine as continuation of style sac, abruptly curving towards anterior, performing thereafter a single wide loop located anterior and to right of style sac. Intestine relatively narrow, of uniform width along its length. Following these loops, intestine running posterodorsally to pericardial region close to style sac; running horizontally though ventricle and narrowly between both posterior pedal retractor muscles. Anal papilla (Figs. 52, 59) as a long projection towards posterior, narrowing gradually to a pointed tip; located in posteroventral region of adductor muscle; its aperture wide, from its insertion in adductor muscle to its apex (Fig. 59).

Central Nervous System: As in *B. cancellaria*.

Measurements of Dissected Specimens (length, lateral, height in mm): MZSP 32304: 46.0 by 20.0 by 31.8.

Distribution

North Carolina, USA, to Santa Catarina, Brazil.

Habitat

Rocky, from intertidal zone to about 10 m depth.

Material Examined

U.S.A.; Florida; Miami; Miami Causeway, FMNH 183584, 1 shell (Koto coll., 1940); Soldier Key, FMNH 183583, 2 shells (Koto coll. 1940); Florida Keys; due E of New Ground, near Tower, 24°40'51"N, 82°16'02"W, 12.2 m depth, AMNH 298092, 2 specimens (FK-080, otter trawl; Mikkelsen et al. coll.; 22/iv/1997); Monroe County, east Turtle Shoal, ocean side off Grassy Key, 24°43'15"N, 80°55'42"W., FMNH 279038, 1 shell (FK-242, Bieler & Mikkelsen coll., 04/viii/1999); Looe Key, FMNH 279041, 1 shell (FK-275, Bieler et al. coll., viii/1999); 24°32.87'N, 81°24.41'W, less than 3 m depth, FMNH 279040, 3 shells (FK-276, Bieler et al. coll., 21/viii/1999); 24°32.77'N, 81°24.23'W, 7 m depth, FMNH 279039, 3 shells (FK-262, Bieler & Mikkelsen coll., 11/viii/1999); 24°32.87'N, 81°24.41'W, less than 3 m depth, FMNH 279052, 1 shell (FK-276, Bieler et al. coll., 21/viii/1999); Coffins Patch coral reef, 24°41'05"N, 80°57'28"W, 5 m depth, FMNH 279043, 2 shells (FK-236, Bieler et al. coll., 2/viii/1999); Molasses Reef, 25°00.55'N, 80°22.58'W, FMNH 279042, 1 shell (FK-200, Bieler & Mikkelsen coll., 07/iv/1999); Key Vaca, FMNH 155511, 1 shell (Nelson coll.); Missouri Key, FMNH 183596, 7 shells, FMNH 183580, 1 shell (Koto coll.). BRAZIL; Bahia; Salvador, Banco da Panela, 16–20 m depth, MZSP 28459, 1 specimen (Simone coll., 26/ii/1997); Farol da Barra, MZSP 28539, 1 specimen (Simone coll., 22–28/ii/1997); Parcel de Paredes, Pedra da Lixa, 1–5 m depth, MZSP 32304, 5 specimens, 3 shells (Souza Jr. & Gonçalves col, i/2000); Abrolhos Archipelago, MZSP 28988, 1 specimen (R. Moura coll., 9–15/i/1998); Rio de Janeiro; Arraial do Cabo, Prainha, MNRJ 9775, 2 specimens (Simone & Costal col, 27/ii/2003); Cabo Frio, MZSP 35243, 4 specimens (P. Gonçalves coll., v/2002); Niterói, Itaipu Beach, MZSP 28739, 5 specimens (Simone coll. 12/vii/1997); Angra dos Reis, Vila Velha Beach, MZSP 18353, 25 specimens; São Paulo, Ubatuba, MZSP 23681, 1 specimen (Klappenbach coll.); Saco da Ribeira, MZSP 23679, 1 specimen (Montouchet coll., 20/vii/1967); Ilha Bela, São Sebastião canal, MZSP 28663, 3 specimens (F.L.Silveira coll., 17/v/1997); São Sebastião, Baraqueçaba Beach, MZSP 30892, 4 specimens (Simone coll., 27/ix/1998); Ilha Alcatrazes, 8 m depth, MZSP 28314, 2 specimens (Simone coll., ix/1996).

Barbatia dominguensis (Lamarck, 1819)
(Figs. 15–25, 60–65)

For additional synonymy: Lamy (1907: 80–82).

?Acar reticulata: Heath, 1941: 294, pl. 6, fig. 9; pl. 7, fig. 8 (*non* Gmelin, 1791).

Barbatia (Acar) dominguensis: Warmke & Abbott, 1962: 158, pl. 30, fig. d; Rios, 1970: 151; Andrews, 1971: 151, fig.; Abbott, 1974: 422, fig. 4967; Rios, 1975: 192, pl. 62, fig. 941; Humfrey, 1975: 210, pl. 23, fig. 5); Rios, 1985: 208–209 (pl. 75, fig. 1062); 1994: 230, pl. 80, fig. 1137; Diaz & Puyana, 1994: 46, fig. 25; Redfern, 2001: 203, pl. 83, fig. 833.

Description

Shell (Figs. 15–20): Small to medium size, to 25 mm. Color pale beige. Sculpture composed of well-developed radial and commarginal threads, both of equal strength or with commarginal threads more weakly developed; with small nodes at intersections of radial and commarginal threads. Periostracum thin, transparent, lacking scales, restricted to shell edges. Umbos flat, located from between anterior and middle thirds of hinge to middle portion of it. Inner surface glossy, white (Fig. 17). Hinge with about 15–20 teeth located just anterior to umbo and posteriorly; 3–4 anteriormost teeth larger, tilted towards anterior; immediately following posterior teeth abruptly changing in size and slightly more dorsally located, these teeth small, perpendicular to dorsal edge, gradually becoming larger and tilted towards posterior (Figs. 17, 20).

Soft Part Color: Mostly pure white or pure pale cream. Some pale purple pigmentation in posterior region of gill and posteroventral region of mantle border (Figs. 23–25). Mantle border surrounded externally by a series of minute, black eyespots, located in somewhat regular distance from each other (Figs. 23–25, 60); eyes more developed in posterior region (about 20 in each mantle lobe), scarce in ventral and anterior regions.

Main Muscle System (Fig. 62): Similar to those in *B. candida*, with the following differences. Posterior adductor muscle proportionally larger. Pair of anterior pedal protractor muscles thicker and separated from integument, running immersed in gonad.

Foot and Byssus: Both structures very similar to those in *B. cancellaria,* with the following remarkable features. Extra-byssal portion of foot lacking pigmentation and proportionally smaller (Fig. 60). Byssus shorter, lacking posterior furrow separating left and right series of dorsal byssal bands (Figs. 21, 22).

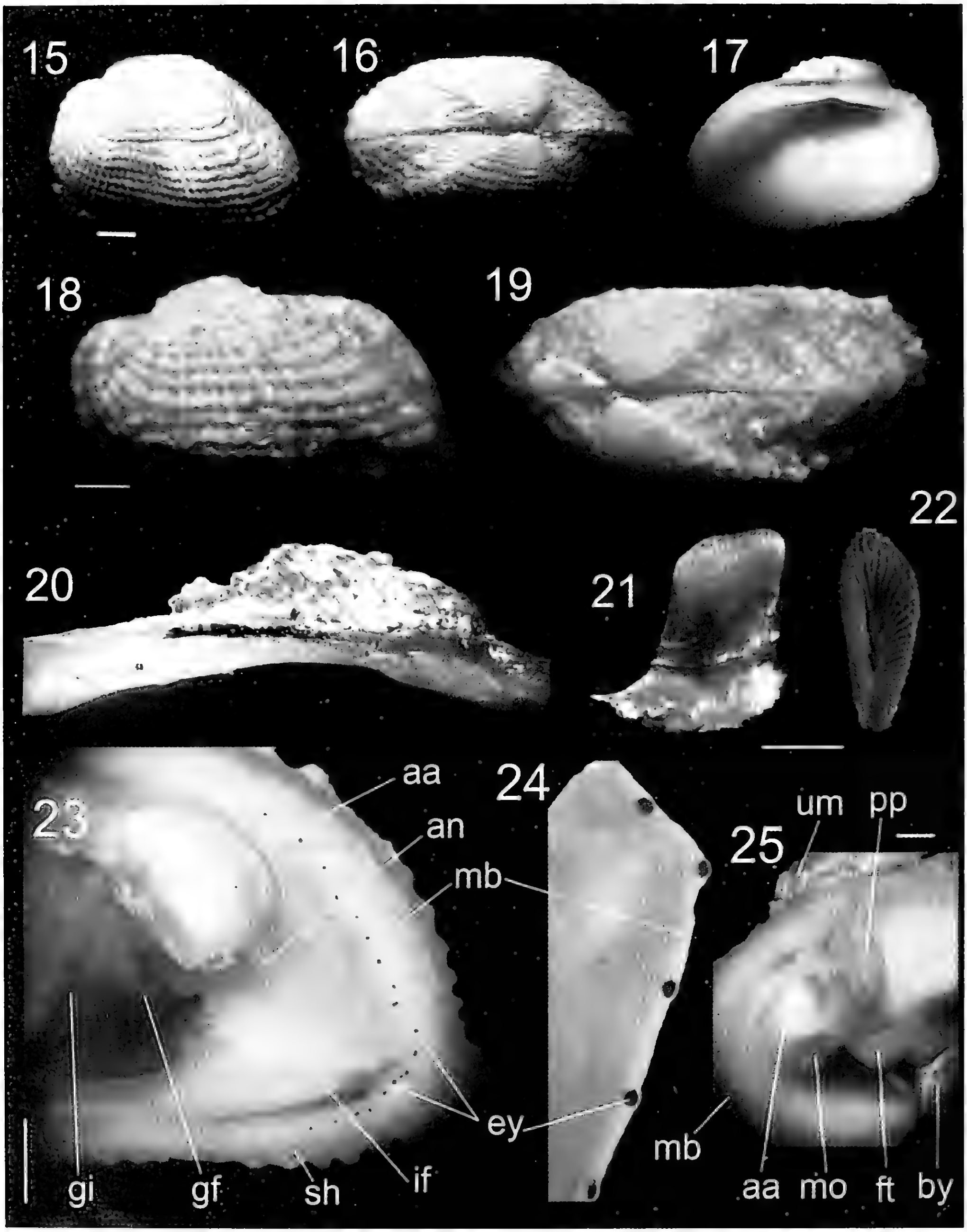
Mantle: Mantle edge features broadly similar to those in *B. cancellaria*, but of different color. Edge relatively thinner (Fig. 65); posteroventral portion thicker, possessing a taller and thicker median pigmented fold. Outer fold bearing a series of minute, black-colored eyespots all along its length, on both mantle lobes (Figs. 23, 24, 60). Each eye located at a regular distance from next, equivalent to about five times its width. Larger eyes located at posterior edge, ventral eyes smaller, sometimes absent (Figs. 23, 25). Each eye composed of a spherical distal portion, black pigmented, followed by a very short stalk, positioning it subterminally in outer mantle edge fold (Fig. 24). More details of compound eyes described by Jan-Olof (1998: fig. 1).

Pallial Cavity: General features similar to those in *B. cancellaria*, with the following notable characters. Gill coloration different. Gill stalks supporting posterior third of gill proportionally more slender, and originating more anteriorly in posterior adductor muscle (Figs. 23, 60).

Visceral Mass: As in *B. candida*.

Circulatory and Excretory Systems: No notable distinctions to those described for *B. cancellaria*.

Digestive System (Fig. 62): General organization similar to that in *B. cancellaria*, with the following differences. Palps' inner surface with a special arrangement of folds similar in outer and inner hemipalps (Fig. 61);



FIGS. 15–25. *Barbatia dominguensis* shell and anatomy. FIG. 15: Left view, MZSP 36167; FIG. 16: Same, dorsal view; FIG. 17: Same, inner view of left valve; FIG. 18: Left view, MZSP 36144; FIG. 19: Same, dorsal view; FIG. 20: Detail of hinge, left valve, MZSP 36147; FIG. 21: Isolated byssus, left view; FIG. 22: Same, apical view; FIG. 23: Detail of posterior region, left view, left valve and mantle lobe removed; FIG. 24: Detail of mantle border of incurrent region; FIG. 25: Detail of anterior region, left view, left valve and mantle lobe removed. Scale bars = 2 mm.

folds of dorsal third of palp transverse, situated perpendicular to posterior palp edge; folds gradually becoming oblique in middle third; ventral palp third smooth, lacking longitudinal (dorsoventral) folds; region preceding mouth narrow, simple (lacking sac-like morphology). Esophagus running close to posterior surface of anterior adductor muscle, almost its entire length, relatively narrow, inner surface with low, narrow longitudinal folds. Gastric inner surface (Fig. 63) with esophageal rim restricted to lateral and dorsal region of esophageal insertion; another transverse fold, narrow, long, running ventrally just anterior to esophageal rim, longer at right. Concave anteroventral sorting area lacking left ducts to digestive diverticula; left duct to digestive diverticula single, located dorsal to a transverse fold which separates it from sorting area. Another small sorting area located in middle region of gastric dorsal surface. Central part smooth, lacking folds and any connection to anterior typhlosole. Anterior typhlosole narrow, surrounding posterior edge of central pad; posterior typhlosole weakly developed. Gastric shield large, occupying most of posterior gastric surface. Dorsal hood located in posterior region of stomach, its aperture narrow, probably containing a sphincter. Intestine curving gradually towards right and anterior, performing a single, broad loop. Intestine relatively narrow, with uniform width along its length to pericardial region; running horizontally though ventricle and narrowly between both posterior retractor muscles of foot. Anal papilla (Fig. 64) a long projection towards posterior, narrowing gradually to a pointed tip; located in posteroventral region of adductor muscle; anal aperture long, subterminal, ventral, possessing thick edges.

Central Nervous System: As in *B. cancellaria,* except in pair of connectives between cerebral-pleural ganglia and visceral ganglia being broader, running through visceral mass, gonad and digestive diverticula.

Measurements of Dissected Specimens (length, lateral, height in mm): MZSP 36279: 23.0 by 11.0 by 13.6; MZSP 36167: 14.5 by 7.7 by 10.1; MZSP 26375: 18.0 by 9.3 by 11.4.

Distribution

North Carolina, USA, to Bahia, Brazil.

Habitat

Rocky, from intertidal zone to about 10 m depth.

Material Examined

U.S.A.; Florida; Florida Keys; "Long Key Artificial Reefs", oceanside of Long Key, Monroe County, 24°44.78'N, 80°50.00'W, MZSP 36279, 2 specimens (FK-621, Simone coll. 17/vii/2002); Pigeon Key, 24°42.2'N, 81°09.3'W, MZSP 36167, 1 specimen (FK-657, Simone coll., 28/vii/2002); "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), MM 35, 24°39.3'N, 81°18.2'W, MZSP 36144, 1 specimen (FK-629, Simone coll., 26/vii/2002); Tennessee Reef Light, 24°44.75'N, 80°46.95'W, 4–7 m depth, MZSP 36147, 9 specimens (FK-648, Simone coll., 26/vii/2002); Old Dan Bank, bayside of Long Key, 24°50.45'N, 80°49.63'W, MZSP 36260, 1 specimen (FK-620, Simone coll., 16–18/vii/2002). BRAZIL; Bahia; Abrolhos Archipelago, MZSP 26375, 2 specimens, MZSP 15566, 9 specimens (L. Pinni Nt. Coll., v/1958).

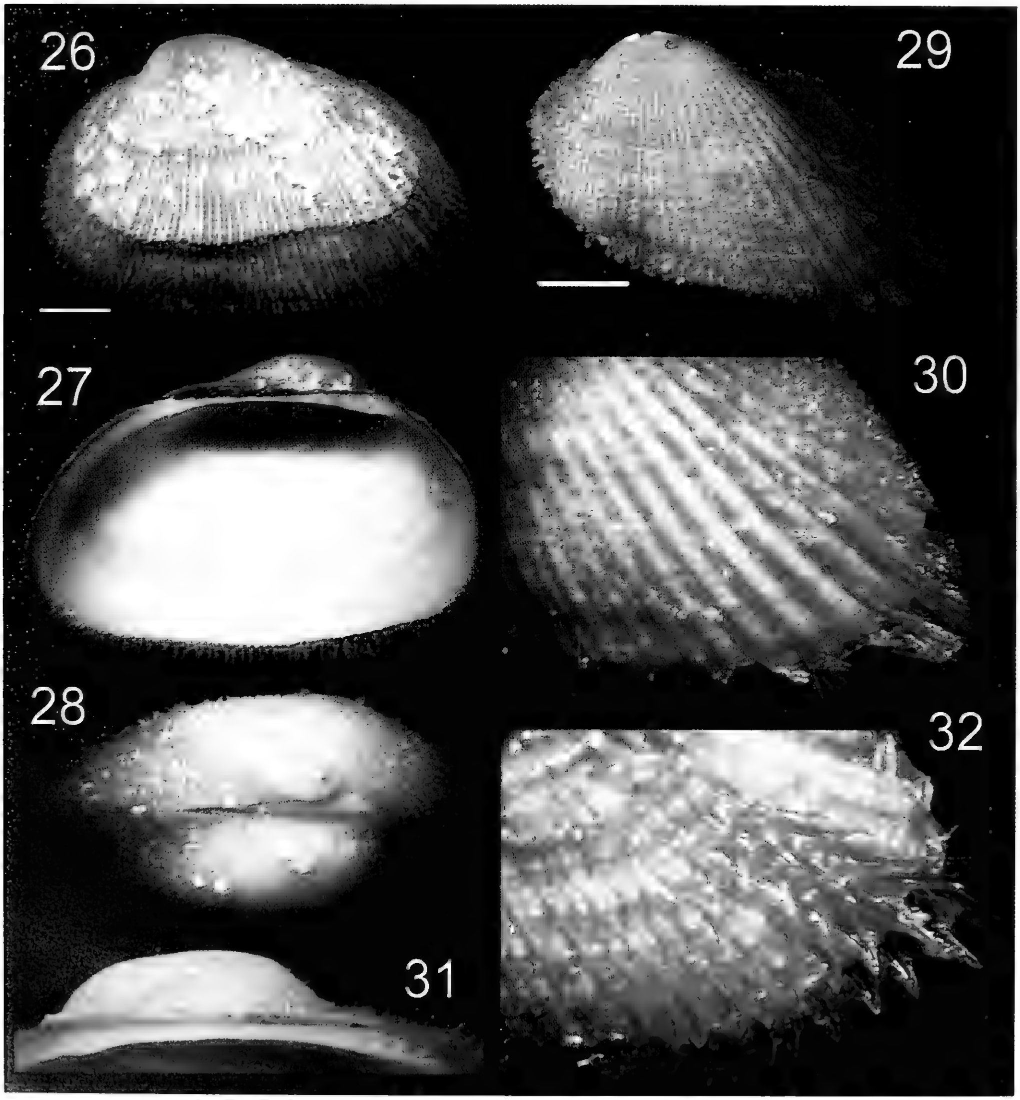
Barbatia tenera (C. B. Adams, 1845)
(Figs. 26–31, 40–42, 66–73)

Barbatia (Fugleria) tenera: Warmke & Abbott, 1962: 158, pl. 30, fig. g; Andrews, 1971: 151–152, fig.; Abbott, 1974: 422; Rios, 1975: 192, pl. 62, fig. 942; Rios, 1985: 209, pl. 76, fig. 1064; 1994: 231, pl. 80, fig. 1140; Diaz & Puyana, 1994: 47, pl. 3, fig. 26; Redfern, 2001: 203, pl. 83, fig. 834.

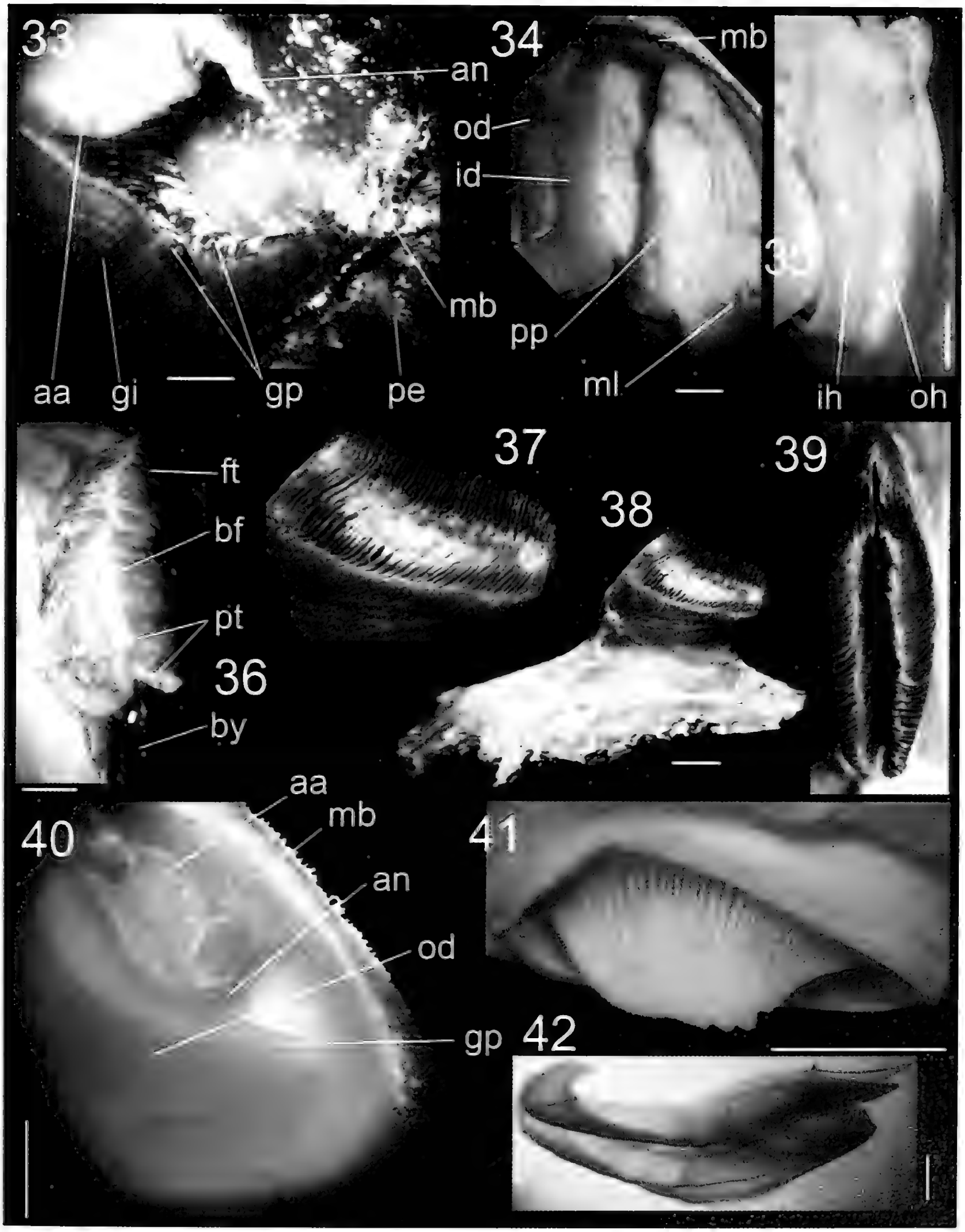
Description

Shell (Figs. 26–31): Of medium size, to 50 mm. Color pale beige. Outline trapezoidal. Sculpture composed of well-developed radial and weakly developed commarginal threads; a small node at intersection of radial and commarginal threads; posterior threads broader than anterior threads. Periostracum relatively thick, with many scales between radial threads, scales longer close to shell border; scales brush-like in shape (Fig. 30), divided into 4–7 pointed projections. Umbos flat, located from between anterior and middle thirds of hinge to middle portion of it. Inner surface glossy, white (Fig. 27). Hinge with about 15–25 teeth located just anterior to umbo towards posterior; 3–4 anteriormost teeth larger, tilted towards anterior; next posterior teeth abruptly changing in size and slightly more dorsally located, these teeth small, perpendicular to dorsal edge, gradually becoming larger and tilted towards posterior (Figs. 27, 31).

Soft Part Color (Fig. 40–42): Mantle border uniform pale orange or yellow. Posterior region of mantle border more weakly pigmented than more anterior region. This pattern also covering posterior and dorsal surface of posterior adductor muscle and rectum; anal papilla abruptly preceded by a white region. Foot (Fig. 41) and ventral region of visceral mass pigmented uniform orange or yellow. Gills uniformly colored pale yellow (Fig. 42), including their posterior,



FIGS. 26–32. *Barbatia* shell. FIGS. 26–31: *Barbatia tenera* shell; FIG. 26: Left view, MZSP 36278; FIG. 27: Same, right valve, inner view; FIG. 28: Same, dorsal view; FIG. 29: Left view, MZSP 36146; FIG. 30: Detail of sculpture and periostracal scales in posterior region, MZSP 36146; FIG. 31: Detail of hinge, right valve, MZSP 36278; FIG. 32: *Barbatia candida*, MZSP 28314, detail of sculpture and periostracal scales in posterior region (for comparison). Scale bars = 5 mm.



FIGS. 33–42. Details of *Barbatia* anatomy. FIGS. 33-36: *Barbatia cancellaria*; FIG. 33: Detail of posterior region, left view, left valve and mantle lobe removed; FIG. 34: Region of right palp, right view, right valve removed, right mantle lobe deflected; FIG. 35: Same, outer hemipalp deflected to show inner surface; FIG. 36: Foot, ventral view; FIGS. 37-39: *Barbatia candida*; FIG. 37: Byssus, left view, detail of apical region; FIG. 38: Same, whole left view; FIG. 39: Same, apical view; FIGS. 40-42: *Barbatia tenera*; FIG. 40: Detail of posterior region, left view, left valve and mantle lobe removed; FIG. 41: Foot, left view, detail of byssal groove; FIG. 42: Left gill isolated, ventral view. Scale bars = 3 mm.

projecting region. Remaining regions of soft parts lacking any special pigmentation.

Main Muscle System (Figs. 40, 66, 68): Similar to those in *B. dominguensis*, with following differences. Posterior adductor muscle slightly larger than anterior adductor muscle. Pair of anterior pedal protractor muscles thin, fused with integument; their origins thin, surrounding ventral edge of anterior adductor muscle insertion in each valve.

Foot and Byssus (Figs. 41, 66–68): Very similar to those in *B. cancellaria*, with the following differences. Extra-byssal portion of foot lacking pigmentation (Fig. 41) and proportionally smaller than that in *B. cancellaria* (Figs. 66, 68). Byssus shorter, lacking posterior furrow separating left and right series of dorsal byssal bands.

Mantle: Mantle edge features broadly similar to those in *B. cancellaria*. Color different, as described above (Fig. 40). Edge relatively thinner; posteroventral portion thicker, possessing a taller, thicker median fold (Figs. 66, 70).

Pallial Cavity (Figs. 66, 67): General features similar to those in *B. cancellaria*, with the following notable characters. Different gill coloring as described above (Fig. 42). Gill stalks supporting posterior third of gill proportionally more slender, originating more anteriorly on posterior adductor muscle (Figs. 66–68). Gill filaments with ascendant and descendant branches almost free from each other (Fig. 72).

Visceral Mass (Fig. 68): As in *B. dominguensis*.

Circulatory and Excretory Systems (Figs. 67, 73): No notable distinctions to those described for *B. cancellaria*.

Digestive System (Figs. 68, 71, 73): General organization similar to those in *B. cancellaria*, with following differences. Inner folds of palps (Fig. 69) transverse in dorsal and middle thirds, situated perpendicular to posterior palp edge; folds gradually becoming weakly oblique in ventral third; region preceding mouth narrow, simple (lacking sac-like morphology), inner surface smooth. Esophagus relatively narrow, inner surface with low, narrow longitudinal folds. Gastric inner surface (Fig. 71) with esophageal rim indistinguishable, a very deep transverse (slightly oblique) furrow located at short distance posterior to esophageal insertion, 2–3 pairs of ducts to digestive diverticula originating from this furrow; central pad broad, located in central portion of gastric ventral surface, occupying about half of ventral surface area; a broad fold surrounding central pad anterior, right and posterior edges; anterior edge forming border of transverse furrow, posterior edge surrounding anterior border of combined intestine-style sac origin; this fold extending transversly on left-dorsal gastric surface, surrounding anterior edge of gastric shield; a small, anteroposteriorly elongated sorting area located in ventral surface of esophageal insertion, flanked by pair of narrow, low folds that unite in posterior region bulging against right edge of central pad; another sorting area in dorsal-right gastric region adjacent to dorsal hood; gastric shield occupying posterior and dorsal regions of stomach. Dorsal hood located obliquely in dorsal region of stomach, low, amply opened to stomach. Intestine and style sac running ventrally and, in region dorsal to foot base, curving anterodorsally in a narrow loop; intestine free from style sac in ascendant branch of this loop; in middle level of its preceding loop, intestine abruptly performing a 360° curve, running adjacent to and at right of preceding loop; this ascendant branch of intestine becoming slightly separated from style sac, passing at some distance posterior to stomach, penetrating pericardium. Intestine relatively narrow, with uniform width along its length to pericardial region; running horizontally though ventricle and narrowly between both posterior pedal retractor muscles. Anal papilla (Figs. 67, 68: an) short, located on posterior region of ventral surface of posterior adductor muscle, with a narrow and short distal projection.

Central Nervous System (Figs. 67, 68): As in *B. cancellaria*, except in having broad connectives between cerebropleural and visceral ganglia, running through gonad and digestive diverticula.

Measurements of Dissected Specimens (length, lateral, height in mm): AMNH 298090: 1) 23.2 by 10.6 by 15.0; 2) 20.0 by 9.8 by 13.7.

Distribution

Florida, USA, to Ceará, Brazil.

Habitat

Rocky, from intertidal zone to about 10 m depth.

Material Examined

U.S.A.; Florida; Florida Keys; off Key Vaca, 24°39.30'N, 81°01.30'W, AMNH 298090, 8 specimens (FK-131, R/V "Floridays"; Bieler & Cipriani coll.; 07/viii/1997); Monroe County, "Long Key Artificial Reefs", oceanside of Long Key, 24°44.78'N, 80°50.00'W, 7 m depth, MZSP 36278, 3 specimens (FK-621, Simone coll., 17/vii/2002); Tennessee Reef Light, 24°44.75'N, 80°46.95'W, 4–7 m depth, MZSP 36146, 8 specimens (FK-648, Simone coll., 26/vii/2002); W side of Pigeon Key, 24°42.2'N, 81°09.3'W, MZSP 36164, 1 specimen (FK-659, Simone coll., 28/vii/2002); between Marquesas Keys & Dry Tortugas, 24°50'36"N, 82°28'25"W to 24°48'17"N, 82°28'42"W, 30 m depth, FMNH 279044, 2 shells (FK-081, Bieler et al. coll., 22/iv/1997); East Washerwoman Shoal, 24°40'N, 81°04.3'W, to 2.7 m depth, FMNH 295616, 3 specimens (FK-115, Mikkelsen & Bieler coll. R/V "Floridays", 12/vii.1997); off Marathon, MM 50, 24°39.53'N, 81°00.90'W, 7 m depth, FMNH 295615, 2 specimens (FK-121, Mikkelsen & Bieler coll., 21/vii/1997); Looe Key coral reef, 24°32.77'N, 81°24.23'W, FMNH 295617, 1 specimen (FK-262, Bieler & Mikkelsen coll., 11/viii/1999); Missouri Key, FMNH 183739, 4 shells, FMNH 183740, 9 shells (Koto coll., 1939), FMNH 159758, 1 shell (Bales coll.); Molasses Key, FMNH 183741, 2 specimens (Koto coll., 1955).

DISCUSSION OF CHARACTERS

The shell obviously has been the main subject of most morphological studies on the arcids. However, the shell of these sessile animals is greatly subject to ecophenotypic variation, enlarging with growth to fit into the concavities in the rocks where it lives. For example, the outline can be flattened or wide; the anteroposterior or dorsoventral distances can be short or long. As a result, the outline can vary in a single species from almost symmetrical (Fig. 26) to asymmetrical (Fig. 29), or from almost straight (Fig. 18) to arched (Fig. 15). For this reason, the shell can be misleading, particularly in specimens of *Barbatia cancellaria* and *B. candida*. The color pattern, however, can be useful in such cases; the interior of the shell of *B. cancellaria*, for example, is purple (Figs. 1–7), whereas those of the other three species are pale beige to white (Figs. 20–26).

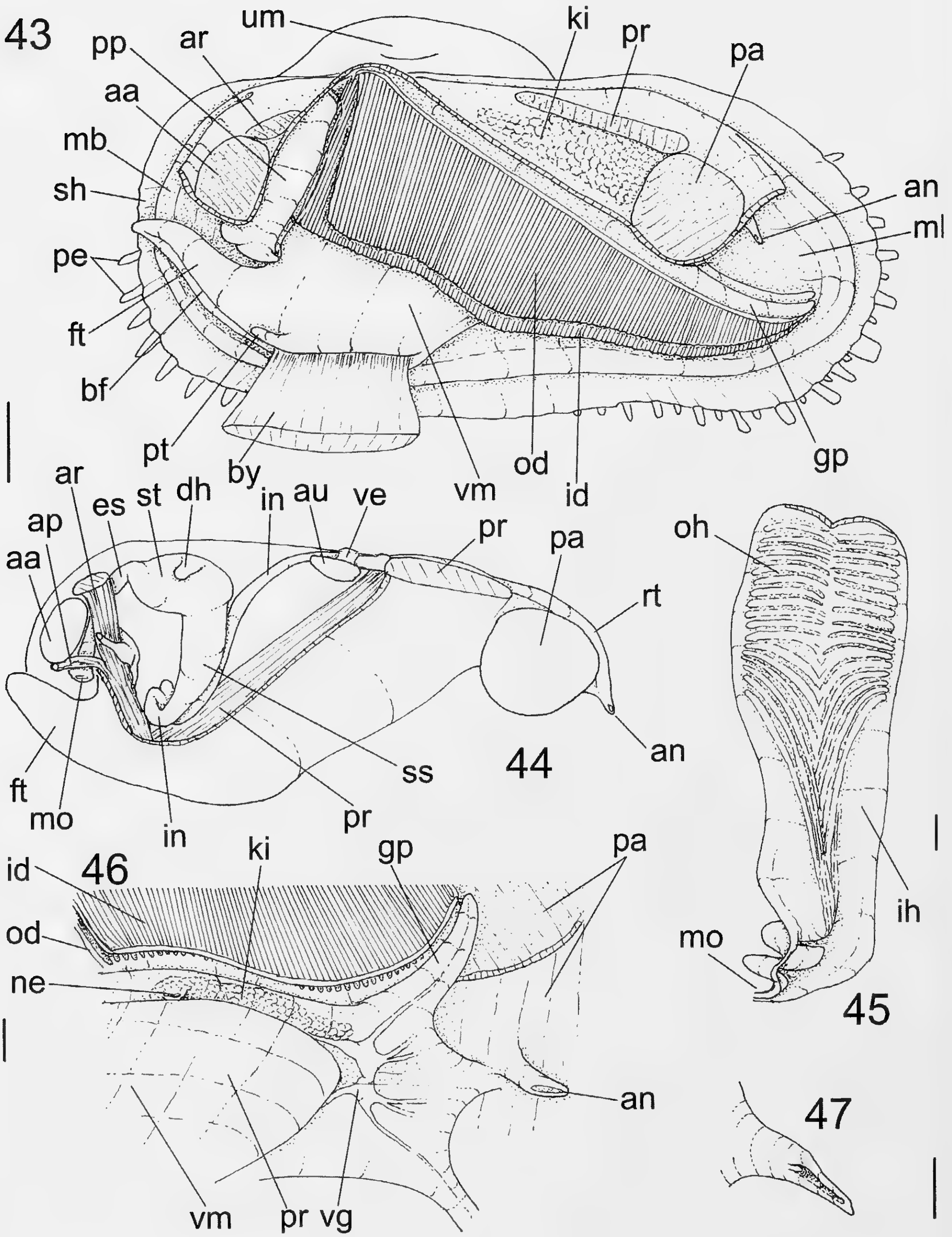
(1) Periostracum: 0 = glabrous (without scales); 1 = with scales but not extending beyond shell edges (*A. notabilis*); 2 = with scales extending beyond shell edges (*B. cancellaria, B. candida, B. tenera, A. zebra*) (additive).

The periostracum of *B. cancellaria, B. candida* and *B. tenera* bears well developed scales, which extend beyond the shell edge, mainly in the region between the radial ribs (Figs. 4, 5, 27, 29–32). This feature is shared with *Arca zebra*. *Anadara* species, on the other hand, normally have small, velvet-like hairs in the periostracum, as present in *A. notabilis* and most other species of the genus, except *A. brasiliana* (Lamarck, 1819). The periostracum of *B. dominguensis*, however, is glabrous, smooth, transparent, and does not extend beyond the shell edge. This state has been found in most bivalves and was initially considered plesiomorphic. However, according to the analysis presented herein, the state in *B. dominguensis* is a reversion.

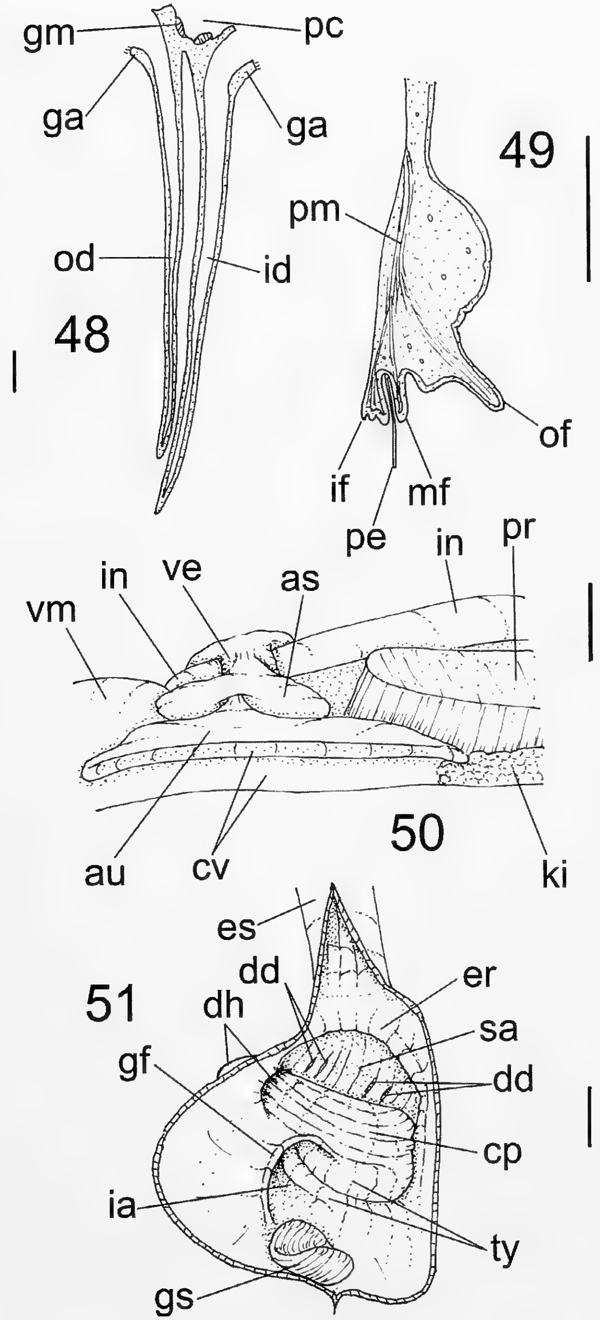
The periostracum can be destroyed by the cover of epibionts that attach to the shell, as well as by wave abrasion. An interpretation of the periostracum must therefore be preceded by special care with the selection of specimens. In *B. candida*, an interesting variation is found in the different populations observed. In northern specimens, the periostracal scales are mostly bifid, resembling a snake's tongue (Fig. 12), whereas in southern specimens the scales are simple and somewhat pointed (Fig. 32). For identification purposes, the types of periostracal scales are very informative in the separation of *B. candida* and *B. tenera*, because in both species the conchological attributes are very similar.

(2) Ligamental area: 0 = wide; 1 = narrow (*Barbatia*).

The ligamental area of the arcids possesses a generally weak ligament, being constricted in its growth pattern to an increase in umbonal area either by horizontal growth, which pushes the beaks apart, or by ventral growth,



FIGS. 43–47. *Barbatia cancellaria* anatomy. FIG. 43: Whole left view, left valve and mantle lobe removed; FIG. 44: Main muscular system and digestive tubes as in situ, left view; FIG. 45: Left palp, left view, outer hemipalp deflected to show inner surface; FIG. 46: Posterior region of visceral mass, ventral view, both gills deflected; FIG. 47: Detail of anus, ventral view. Scale bars = 5 mm (Figs. 43, 44), 1 mm (Figs. 45–47).



FIGS. 48–51. *Barbatia cancellaria* anatomy. FIG. 48: Left gill, mid-transverse section; FIG. 49: Mantle border, transverse section between middle and posterior regions; FIG. 50: Detail of pericardial region, left view, dorsal pericardium and left gill removed; FIG. 51: Stomach, dorsal view, dorsal wall sectioned longitudinally and deflected, inner surface exposed. Scale bars = 1 mm.

which invades the hinge plate (Thomas, 1976). The structure of the ligament also varies in producing a few rather wide chevrons (in some *Anadara* and *Barbatia*) or many narrow chevrons (in *Arca*). All ligamental characters in the present sample resulted in autapomorphies, except ligamental width, which separated the ingroup from the remaining arcids.

(3) Hinge teeth: 0 = mostly perpendicular; 1 = mostly tilted (*Barbatia*).

The narrow ligamental area, when compared to other arcids, has long been recognized as a distinctive character of *Barbatia*. The narrow ligamental area is associated with the inclination of the hinge dentition (Reinhart, 1935: 20, pls. 1, 2). This character is found in the examined species, however, the dentition was very variable. Younger specimens generally possess a more typical hinge (Figs. 7, 17) that is disfigured during ontogeny and development. Sometimes the more central teeth are reduced or lost (Figs. 6, 14), whereas in other cases the more anterior and posterior teeth become horizontal (Fig. 14). *Barbatia dominguensis* has as the distinctive feature of a sudden change of the hinge axis at the cardinal level (Figs. 17, 20), which is one of the features used by some authors (e.g., Reinhart, 1935) to substantiate the subgeneric separation of *Acar*. A similar situation also occurs in *B. tenera*, which is mostly referred to the subgenus *Fugleria*.

Another special feature of the arcids is the nature of the byssus. In the examined arcids the byssus has fused fibers, forming a single, thick bundle. Vestiges of the fibrous nature of this structure are only found in the dorsal area, where the byssus attaches to the foot. In this region, the byssal bundle has a special arrangement as a concavity ornamented by a series of parallel folds. This concavity fits into a special protuberance in the posterior region of the byssal groove, which has furrows for the folds. This byssal morphology is apparently exclusive to the arcids and would be a strong synapomorphy if some genera (e.g., *Anadara*) did not lack the byssus. *Arca notabilis*, for example, has a byssal furrow comparable to that found in other byssate bivalves and can produce a typical byssus with separated fibers. The presence or absence of a thick byssus was also used in arcid classification (Lamy, 1907; Reinhart, 1935; Coan et al., 2000). *Barbatia dominguensis* differs in byssal morphology compared to other *Barbatia* species (Fig. 39) and to *Arca*, as it lacks an anterior notch in the dorsal concavity (Fig. 22). This lack of an anterior notch is an autapomorphy in the present study; this character could not be fully examined in *B. tenera*, because no fully preserved byssi of this species were available.

Although normally the color patterns of the soft parts are very variable in mollusks, the species studied here maintained a constant differentiation in the color of most regions of soft parts. *Barbatia cancellaria* has a greater richness of pigmentation, with dark brown, beige and white spots, which also occur in *B. candida*, but in paler patterns; *B. tenera* is in general almost invariably orange, while *B. dominguensis* is mostly pale to dark purple.

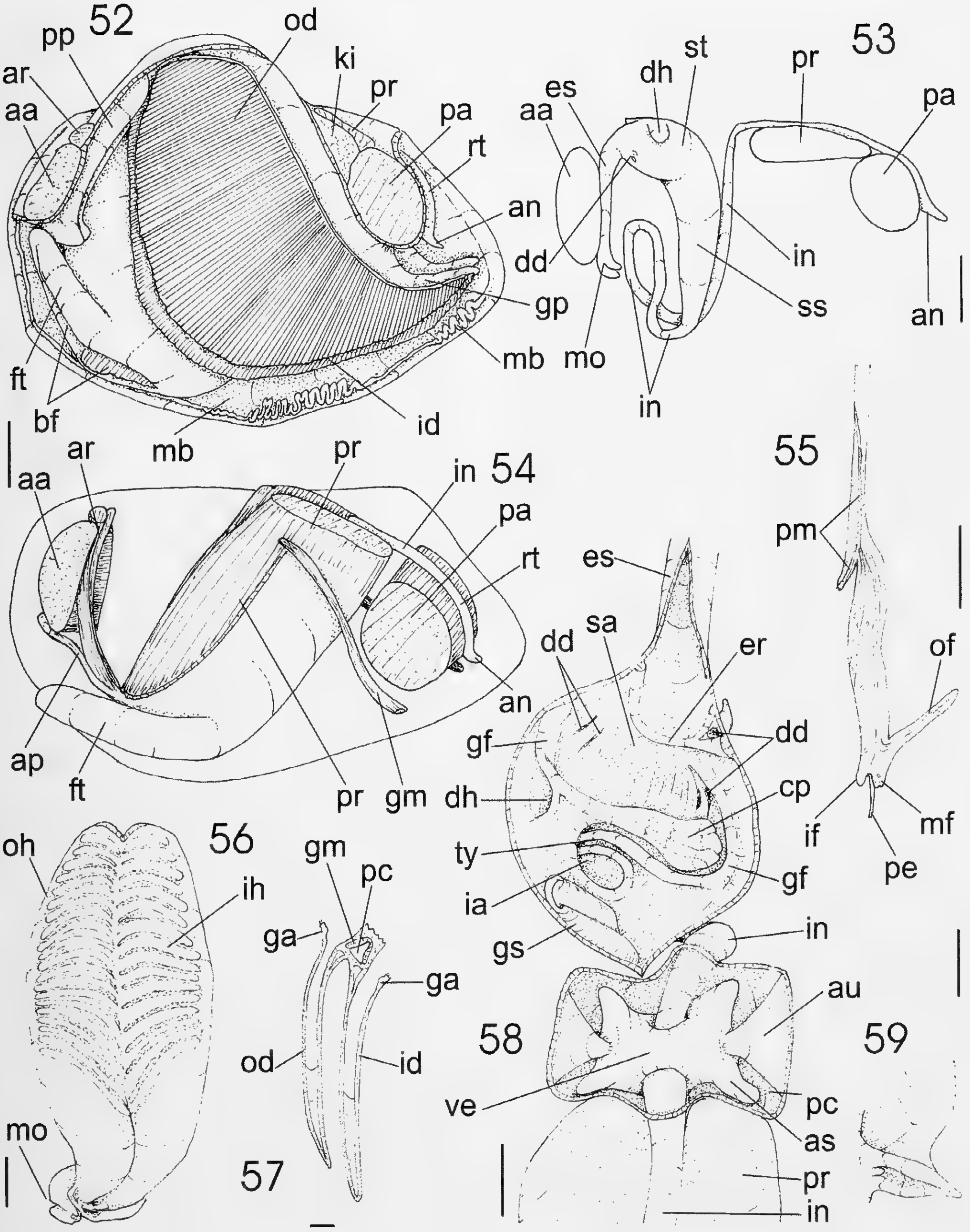
(4) Origin of pair of pedal protractor muscles: 0 = in restricted area in posteroventral region of anterior adductor muscle; 1 = surrounding ventral edge of anterior adductor muscle (*B. dominguensis, B. tenera*).

The two indicated species differ from the other included species in having the pair of pedal protractor muscles apparently as part of the integumental anterior area, and their origin is along the ventral edge of the origin of the anterior adductor muscle, in a dorsoventrally narrow, but anteroposteriorly broad, region. In this state, the ventral edge of the shell scar normally attributed only to the anterior adductor muscle, actually also belongs to the pedal protractors.

The main musculature of the examined ingroup species has the typical arcid morphology. *Barbatia dominguensis*, however, is distinct in having enlarged pedal protractor muscles, which are detached from the integument crossing through visceral glands.

(5) Mantle edge inner fold: 0 = simple; 1 = tall (*Barbatia*).

The mantle edge of the four *Barbatia* species studied herein is of the basic complement, with three folds. This morphology has been also found in *Anadara trapezia* (Deshayes, 1840) (Sullivan, 1961: fig. 4). However, the species studied here present a greater development of the inner fold, forming an undulated membrane in some specimens (Figs. 49, 55, 65, 70: of). Another attribute of the examined species is the presence of well-developed eyes along the mantle edge in *B. dominguensis* (Figs. 23–25), which



FIGS. 52–59. *Barbatia candida* anatomy. FIG. 52: Whole left view, left valve and mantle lobe removed; FIG. 53: Digestive tubes, left view, seen as in situ, with some adjacent structures; FIG. 54: Main muscular system, left view; FIG. 55: Mantle border, transverse section between middle and posterior regions; FIG. 56: Left palp, left view, outer hemipalp deflected to show inner surface; FIG. 57: Left gill, mid-transverse section; FIG. 58: Stomach and pericardium, dorsal view, dorsal wall of stomach sectioned longitudinally and deflected, inner surface exposed, dorsal pericardial wall removed; FIG. 59: Detail of anus, ventral and slightly left view. Scale bars = 5 mm (Figs. 52–54), 1 mm (Figs. 55–59).

are present on the outer fold (Fig. 65), covered by the periostracum. This feature is possibly related to the transparency and simplicity of its periostracum. Although the presence of ocelli is a common feature of the arcid mantle edge (Boss, 1982), a well-developed eye with a lens (Jan-Olof, 1998) is presently an autapomorphy of *B. dominguensis*.

The gill of the examined species is of typical arcid morphology (Atkins, 1936; Sullivan, 1961) (Figs. 42, 48), although *B. candida* is distinct in having a membrane on the ventral half of each filament, holding it in a determinate position (Fig. 57). The gill projection or stalk, inserted into the ventral region of the posterior adductor muscle, and projecting the posterior region of each gill posteriorly (Figs. 43, 46, 52, 60: gp), has been clearly illustrated by some of authors (e.g., Rost, 1955; Sullivan, 1961; Boyd, 1998; Coan et al., 2000). However, no one has either named or called attention to this structure.

The kidneys are separated from each other and are closely similar in all examined arcids. A distinct nephrostome is located at the anterior end of the branchial surface of the kidney, apparently surrounded by muscles, forming a low papilla.

The heart of the examined arcids is distinct in having the accessory auricles as clear expansions of the ventricle. The remaining region of the ventricle is small and surrounds the intestine. The aortae emanate from this portion of the ventricle. The accessory auricles are very expansive, almost as large as the auricle itself. Heath (1941) and Sullivan (1961: fig. 1C) clearly show the accessory auricles, however, they did not pay any special attention to them, simply calling them ventricles. Boss (1982) described the arcid heart as having two lateral cavities, each one with a ventricle and an auricle.

(6) Palps' ventral region preceding mouth: 0 = simple; 1 = wide, forming a sac (*B. cancellaria, B. candida*).

The labial palps of arcids are unlike those of other bivalves in being dorsoventrally elongated, with their anterior edges attached to the visceral mass. This palp morphology is apparently present in all arcids we have seen in the literature (e.g., Lamy, 1907; Reinhart, 1935; Sullivan, 1961), and could be characteristic of the family. The inner folds, which typically are distributed along the entire inner surfaces of the palps, are mostly restricted to the dorsal halves in the arcids (Sullivan, 1961: fig. 3C; this study). This apparently is another distinctive feature of the family. *Barbatia cancellaria*; however, is unique in having some longitudinal folds on the ventral halves of the palps, concentrated on the inner borders between the two hemipalps. *Barbatia cancellaria* and *B. candida* are distinct as a pair in having the region preceding the mouth very broad and flaccid, forming a cover on the anterior region of visceral sac, with a sac in the ventral region of the palps (Figs. 35, 43, 45, 52, 56).

(7) Stomach with anterior typhlosole forming a fold posterior to central pad: 0 = absent; 1 = present (*Barbatia*).

See discussion under character 8.

(8) Anterior typhlosole surrounding right and posterior edge of central pad: 0 = absent; 1 = present (*B. cancellaria, B. candida*) (Figs. 51, 58: ty).

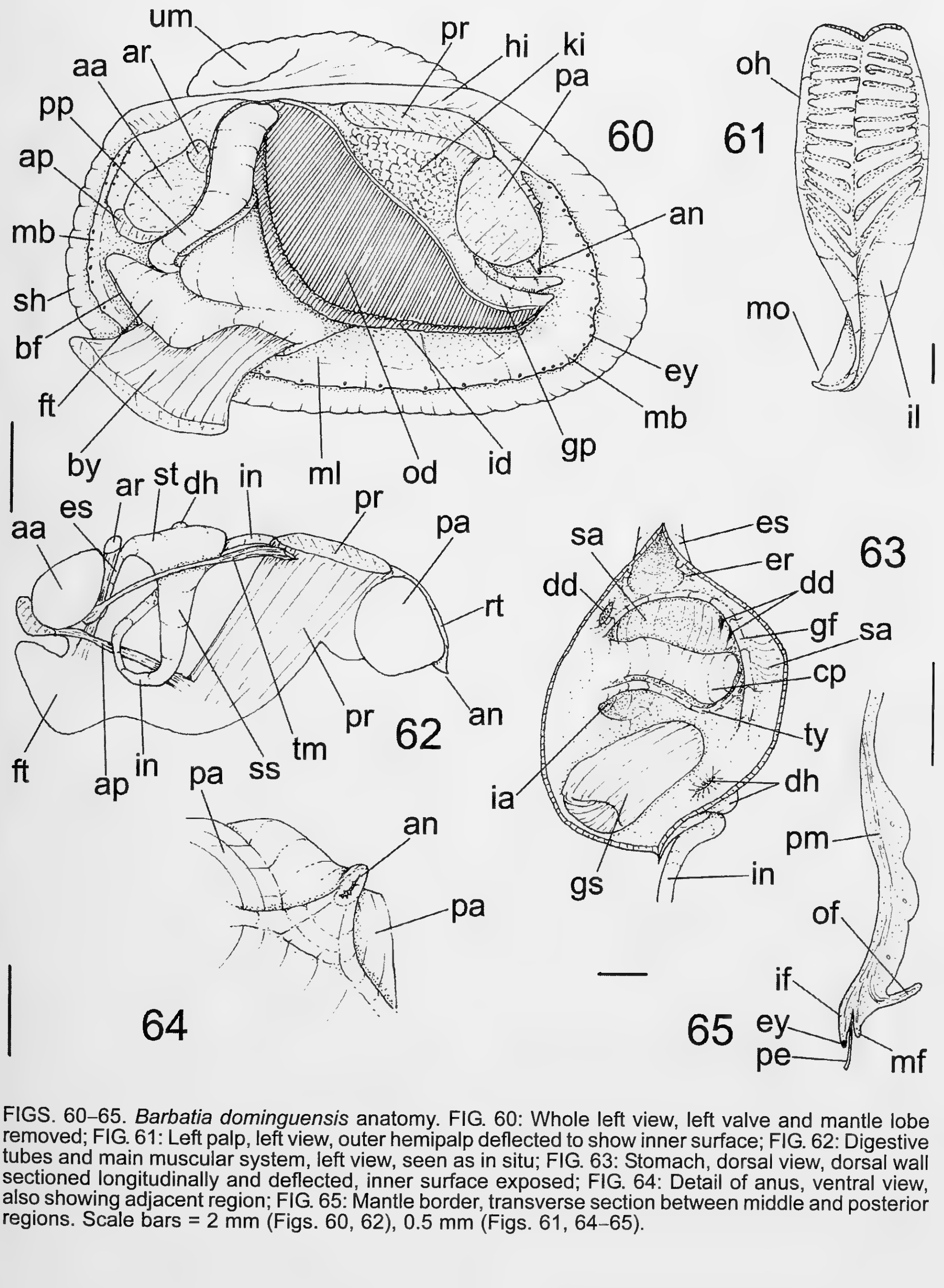
The stomachs of the examined species are somewhat similar to one another, referred to as type III (Purchon, 1957; Boss, 1982). Although they differ in a number of details, only two of these are coded as characters in the present phylogenetic analysis. Several other characters are considered autapomorphies in the present study. One such character is the position of the dorsal hood, which is in the middle region of the gastric dorsal wall in *B. cancellaria* and *B. candida*, but more posteriorly in *B. dominguensis*; besides, it is widely opened in *B. tenera*. The dorsal hood is located more anteriorly in *Anadara trapezia* (Sullivan, 1961). In addition, *B. candida* has a duct to the digestive gland located in the dorsal-right region, which is exceptionally large and can be confused with the dorsal hood, which is somewhat reduced in this species.

The arcids generally possess few intestinal loops, and the intestine is narrow, running close to the style sac. In *B. cancellaria*, on the other hand, the intestine is slightly broader, forming a close zigzag in the style sac end, forming almost a secondary intestinal chamber. This is an autapomorphy in present study.

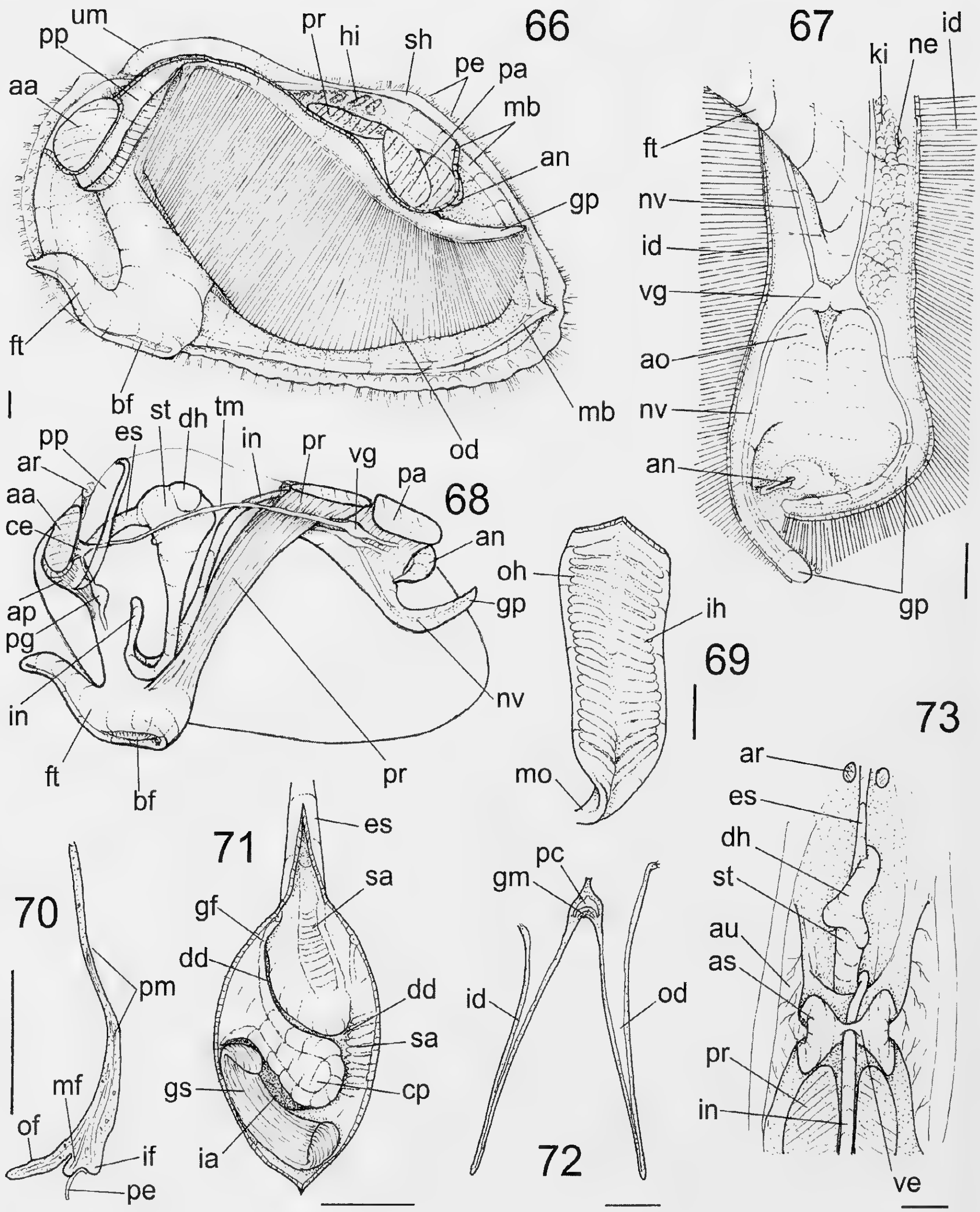
The anus of the examined species is notable in being siphoned, that is its aperture is located at the tip of a muscular stalk (Figs. 47, 64), which has the capacity for movement and protraction. However, *B. candida* is unique in having the anal aperture posterior to this stalk base (Fig. 59).

(9) Connective between cerebropleural ganglia and visceral ganglia: 0 = broad, running through visceral glands; 1 = thin, running close to integument (*B. cancellaria, B. candida*).

The pair of connectives uniting the cerebropleural ganglia with the visceral ganglia is normally easy to distinguish in dissection, as conspicuously iridescent cords running al-



FIGS. 60–65. *Barbatia dominguensis* anatomy. FIG. 60: Whole left view, left valve and mantle lobe removed; FIG. 61: Left palp, left view, outer hemipalp deflected to show inner surface; FIG. 62: Digestive tubes and main muscular system, left view, seen as in situ; FIG. 63: Stomach, dorsal view, dorsal wall sectioned longitudinally and deflected, inner surface exposed; FIG. 64: Detail of anus, ventral view, also showing adjacent region; FIG. 65: Mantle border, transverse section between middle and posterior regions. Scale bars = 2 mm (Figs. 60, 62), 0.5 mm (Figs. 61, 64–65).



FIGS. 66–73. *Barbatia tenera* anatomy. FIG. 66: Whole left view, left valve and mantle lobe removed; FIG. 67: Posterior region of visceral mass, ventral view, both gills deflected; FIG. 68: Digestive tubes, central nervous system and main muscular system, left view, seen as in situ, palp shown as a transparent structure; right gill stalk also shown; FIG. 69: Left palp, left view, outer hemipalp deflected to show inner surface; FIG. 70: Mantle border, transverse section between middle and posterior regions; FIG. 71: Stomach, dorsal view, dorsal wall sectioned longitudinally and deflected, inner surface exposed; FIG. 72: Mid-transverse section of gill; FIG. 73: Visceral mass, dorsal view, with dorsal portion of integument and mantle, visceral glands covering stomach, and part of pericardium removed. Scale bars = 1 mm.

TABLE 1. Character matrix for four *Barbatia* species studied here and three outgroups (see text for description of characters).

Character/taxon	1	2	3	4	5	6	7	8	9
Barbatia cancellaria	2	1	1	0	1	1	1	1	1
Barbatia candida	2	1	1	0	1	1	1	1	1
Barbatia dominguensis	0	1	1	1	1	0	1	0	0
Barbatia tenera	1	1	1	1	1	0	1	0	0
Arca zebra	2	0	0	0	0	0	0	0	0
Anadara notabilis	1	0	0	0	0	0	0	0	0
Isognomon bicolor	0	0	0	0	0	0	0	0	0

most straight through the visceral glands (gonad and digestive diverticula) (Fig. 62: tm). However, in *B. cancellaria* and *B. candida* this pair of connectives is less distinct, being very thin and running close to the inner surface of the integument. This state is interpreted as apomorphic. On the other hand, the enlargement of these connectives in *B. dominguensis* is autapomorphic and could be coded as a third, state, a presently autapomorphy. The remaining features of the central nervous system and primary sense organs of the examined species are similar to those described in the literature (e.g., Sullivan, 1961). It is interesting to note the location of the visceral ganglia, at the base of the posterior projections of the gills (Fig. 46), normally they are located slightly anterior to them.

ANALYSIS OF THE CLADOGRAM

A cladistic analysis based on the matrix in Table 1 resulted in a single most parsimonious tree (Fig. 74). We emphasize, however, that a search for family characters was not performed, which would demand a wider analysis. The main concern is to compare the four species of *Barbatia* studied herein and to test how the analysis of the anatomy is useful in phylogenetic estimation. Although the matrix is admittedly very restricted, based on the result, *B. cancellaria* and *B. candida* are closer to each other than to the other two *Barbatia* species, as are *B. dominguensis* and *B. tenera*; the first is a branch supported by three synapomorphies (node 4), whereas the second is supported by a single synapomorphy

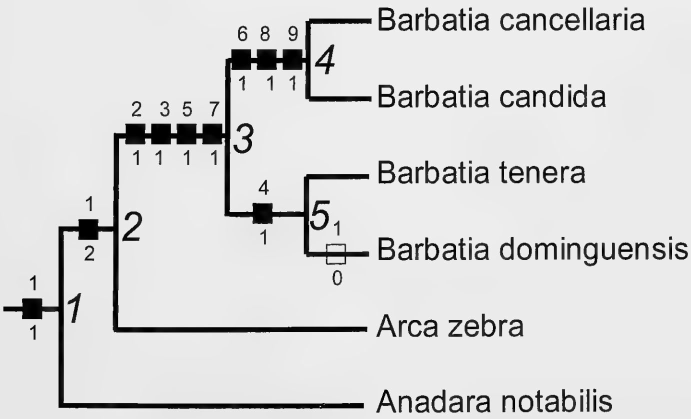


FIG. 74. Cladogram showing the relationship of the examined species and the two arcid outgroups (below). Squares represent synapomorphies (black square = not homoplastic; empty square = reversion), superior number refers to the character, inferior number indicates the state. Larger numbers in italics are node numbers referred to in the text (length = 12; consistency index = 0.81; retention index = 0.85).

(node 5). The genus *Barbatia s.l.* is also well supported by four synapomorphies (node 3), which separates them from the other arcids, being monophyletic. Additionally, it was possible to see that *Arca* is more closely related to *Barbatia* than *Anadara*. The single homoplasy detected in the analysis was the reversion in the periostracum of *B. dominguensis* from scaly with extensions to smooth (lacking scales) (character 1). Although all autapomorphies were excluded of the present analysis, they would be useful in a wider analysis, including more species and more genera. An example is the composed eyes in the mantle border of *B. dominguensis*; they could be character of the species, of the subgenus *Acar*, or something else.

As stated in the synonymy listing, *Barbatia cancellaria* and *B. candida* have been considered as members of the subgenus *Barbatia s.s.* by several authors. However, *B. candida* is sometimes considered in the subgenus *Cucullaearca* Conrad, 1865 (e.g., Rios, 1994). *Barbatia dominguensis*, on the other hand, has been placed consistently in the subgenus *Acar*, whereas *B. tenera* has been referred to *Fugleria*. An analysis of the subdivision of the genus, and/or the elevation of the subgenera to generic level is considered premature at this present level of knowledge.

A recent paper (Marko, 2002) presented a molecular phylogenetic analysis of a pool of arcids that coincidently includes all species studied here, in addition to a number of Pacific species. The results of that analysis (Marko, 2002: figs. 1–5) are difficult to compare with those obtained here, since they differ almost totally. The combined cladogram of CO1 and H3 sequences, despite excluding some of the presently studied species, revealed a closer relationship of *Barbatia candida* with *Anadara* spp., and the same for *Arca imbricata* with *B. dominguensis*.

CONCLUSIONS

(1) In this analysis of four species attributed to *Barbatia s.l.*, *Barbatia cancellaria* and *B. candida* are found to be sister taxa, as are *B. dominguensis* and *B. tenera*.
(2) *Barbatia s.l.* is a monophyletic group.
(3) Morphological characters, including those from conchology and internal anatomy, are useful in phylogenetic analysis, even of closely related bivalve species.

ACKNOWLEDGMENTS

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RECENT CHAMIDAE (BIVALVIA) FROM THE WESTERN ATLANTIC OCEAN

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ABSTRACT

The International Marine Bivalve Workshop, Florida Keys, July 2002, initiated an examination of the bivalve genera *Chama* and *Pseudochama*. Unraveling the systematics of the seven species collected during the workshop necessitated a review of literature and collections for the fossil and Recent chamid taxa of the western Atlantic. Subsequent discovery of a small population *P. inezae* Bayer, 1943, enabled detailed observation of variation within a previously rare species. Given the 50:50 ratio of right-attached to left-attached specimens and the characteristic *Chama* prodissoconch, *P. inezae* is transferred to the genus *Chama. Pseudochama radians* (Lamarck, 1819) is returned to the genus *Chama* based on a complex of morphological characters and molecular data. We discuss the morphology of eight *Chama* and one *Arcinella* species.

Nucleotide sequence data of the ITS region (ITS1 + 5.8S rRNA + ITS2) and the 16S rRNA gene were obtained for six species of *Chama* collected during the workshop. *Chama congregata* Conrad, 1833, appears to include multiple species based on morphological details and molecular data. One specimen of *C. congregata* had two alleles of ITS elements, which is the first demonstrated case of multiple alleles within the Bivalvia. Molecular phylogenetic reconstructions containing *C. congregata* will be more complicated because gene trees and species trees may not be identical due to incomplete lineage sorting. *Chama sarda* Reeve, 1847, appears to include multiple species based on morphological data. Populations of several other fossil and recent species need to be examined for the range of variation within nominate species.

Key words: Chamidae, *Chama*, *Pseudochama*, *Arcinella*, Neogene, Atlantic, attachment, transposition.

INTRODUCTION

This revision of the Recent Chamidae from the western Atlantic was undertaken to determine the systematics of seven chamid species collected during the International Marine Bivalve Workshop (IMBW), Florida Keys, July 2002. Recent western Atlantic chamid species are found in tropical and subtropical seas at shallow to moderate depths, from Brazil to Cape Hatteras, North Carolina. Neogene distribution ranged from the Miocene of Argentina to the Miocene of New Jersey. The earliest stratigraphic records of Chamidae are from the upper Cretaceous (Keen, 1969; Kennedy et al., 1970). In the Recent, eight species of *Chama* and *Pseudochama* are recognized from current literature for the western Atlantic, all of which occur in the study area. Four are also found north to Cape Hatteras, seven range south to the Lesser Antilles, and five reach Brazil. Three species of *Arcinella* have been reported from the western Atlantic basin, but two occur only south of the Florida Keys. Consequently, a thorough literature review of the Floridian species requires a larger, western Atlantic focus. Lamy (1928) is an important but often overlooked reference containing much critical detail concerning Recent Chamidae from all oceans.

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MATERIALS AND METHODS

Material Examined

Living specimens of *Chama congregata*, *C. macerophylla*, *C. florida*, *C. sinuosa*, *C. radians*, *C. sarda*, and *C. inezae* were collected during the International Marine Bivalve Workshop (Table 1). The field collections are listed in the introduction to this volume (Mikkelsen & Bieler, 2004). The identifications of these seven species are based on the morphological descriptions in Abbott (1974), Bayer (1943), Dall (1886), and Redfern (2001), as well as comparison with specimens from the Florida Museum of Natural History (FLMNH) and the University of South Carolina Spartanburg (USCS). Mikkelsen & Bieler (2000) also reported *C. lactuca* and *Arcinella cornuta* from the Florida Keys, and these are included in this review.

Molecular Methods

We determined sequences of the nuclear ITS1 + 5.8S rRNA + ITS2 region and of the mitochondrial 16S rRNA genes of four specimens of *Chama macerophylla,* two specimens of *C. congregata,* and of single specimens of *C. sarda*, *C. florida*, *C. inezae*, and *C. radians* (Table 2). Two specimens of an unidentified *Chama* species from the Seychelles served as the outgroup. The other available bivalve sequences of the ITS genes are too divergent to be reasonably aligned.

Living specimens were removed from their shells and dehydrated in 96% ethanol. The tissues were washed in distilled water prior to DNA extraction. Total DNA was isolated with CTAB (Winnepenninckx et al., 1993) or with CHELEX resin (Sigma) (Steiner & Hammer, 2000).

The target sequence, including ITS1, 5.8S rRNA, and ITS2, was amplified using the primers ITS-F2 (5´-taa caa ggt atc cgt agg tga a-3´) and ITS-R2 (5´-tgc tta aat tca gcg ggt-3´) or in two fragments using internal primers 5.8-R (5´-cag ctg gct gcg ctc ttc tac gac-3´) and 5.8-F (5´-gtc gta gaa gag cgc agc cag ctg-3´) when necessary. The 16S rRNA sequence was amplified with the primers 16Sf (5´-ctc gcc tgt tta wca aaa aca t-3´) and 16Sr (5´-acg ccg gtc tka act cag-3´). The PCR-reactions were run on a Personal Cycler (Biometra) in 30 µl reaction mixes containing 1.75–3.0 mM $MgCl_2$, each dNTP at 250 µM, each primer at 0.1 µM, 0.6 units Taq polymerase (Biotaq Red, Bioline) and the supplied reaction buffer at 1 x concentration. The standard PCR cycle conditions were: initial denaturation step of 2 min at 94°C, 35 cycles of 40 sec denaturation at 94°C, 40 sec annealing at 46°C, and 75 sec primer extension at 72°C, followed by a final primer extension step of 10 min at 72°C. Touchdown PCR was often more successful than the standard protocol. It included stepwise lowering annealing temperatures from 56°C to 42°C within 10 cycles and a subsequent return to 56°C within the remaining 25 cycles. PCR products were purified with the Concert Rapid PCR Purification System (Life Technologies) and sequenced with the PCR primers on an ABI 3700 at VBC-Genomics Bioscience Research GmbH, Vienna. Heterogeneous PCR products were subcloned with the TOPO cloning kit (Invitrogen), and three clones sequenced.

Sequences were aligned manually and with CLUSTAL X 1.8 (Thompson et al., 1997) using default parameters for the ITS sequences. The only change for aligning the 16S rRNA sequences was setting the gap opening penalty to 20. Phylogenetic analyses were run with PAUP* 4.0b10 (Swofford, 1998) on an IBM-PC

TABLE 1. Stations where Chamidae were collected live during the IMBW. For full station data, see introduction to this volume (Mikkelsen & Bieler, 2004).

	Station								
Species	624	625	629	630	631	641	644	650	651
Chama congregata	1	1	11	1	-	2	1	4	-
Chama macerophylla	-	1	13	-	-	-	1	5	-
Chama florida	-	-	-	-	-	2	-	1	-
Chama sarda	-	-	1	-	-	-	1	-	-
Chama sinuosa	1	-	-	-	-	1	-	-	1
Chama inezae	2	-	-	-	-	-	-	-	1
Chama radians	6	3	1	-	1	8	-	2	1

and on the Schrödinger 1 Linux-Cluster at the Central Informatics Service, University of Vienna. Unweighted maximum parsimony analyses (MP) included an exhaustive search and 1,000 bootstrap replicates, each with three random sequence additions. Gaps were treated as missing. For maximum-likelihood analyses (ML), the most parsimonious trees (MPT) were used as starting trees for the calculation of the model parameters and subsequent branch swapping. Empirical nucleotide frequencies and the parameters for the transition/transversion ratio and the gamma shape value were estimated under the HKY85 model with rate heterogeneity and four categories of substitution rates following a gamma distribution (HKY85+G model) as recommended by the likelihood ratio test implemented in MODELTEST (Posada & Crandall, 1998). The resulting values were then set for subtree-pruning-regrafting (SPR) branch swapping. The two phylogenetic markers were analysed both separately and combined in a single matrix. The latter analysis is justified, although the taxon samples for the individual analyses are not identical, because the resulting trees were congruent.

RESULTS

Molecular Genetics and Phylogeny

We obtained both the near-complete ITS1 + 5.8S rRNA + ITS2 and partial 16S rRNA sequences from seven specimens collected in the Florida Keys belonging to *Chama macerophylla* (3), *C. congregata*, *C. sarda*, *C. florida*, and *C. radians*, and two specimens of *C.* sp. from the Seychelles. An additional specimen of *C. congregata* yielded two different alleles of the ITS region but no 16S sequence. *Chama macerophylla* and *C. inezae* are also represented by one additional specimen each with only the 16S sequence (Table 1).

We faced considerable difficulties amplifying and sequencing the target sequences. Although we applied two different extraction protocols, PCR reactions were inhibited by some components of the DNA extract of certain specimens. Other specimens of the same species subjected to identical protocols worked well. In several reactions the PCR yielded at least two different products. In addition to the *Chama* sequence, these were identified by BLAST searches as products from parasites, *Perkinsus* sp. (Apicomplexa, Protista) and a parasitic flatworm. In the case of *C. congregata* 625-1a and 1b, the two products were polymorphic copies of the ITS elements.

The amplified sequence lengths for the ITS region ranged from 910 bp in *Chama congregata* to 1,072 bp in *C. florida*, resulting in an alignment with 1,058 positions (the autapomorphic 5´-end of the *C. florida* sequence was truncated) of which 234 were parsimony informative. The 16S rRNA sequences varied in length from 659 bp in *C. sarda* to 825 bp in *C. macerophylla*. The sequence of *C. florida* was incomplete and consisted of 364

TABLE 2. List of species and specimens sequenced for ITS1 + 5.8 rRNA + ITS2, and 16S rRNA with AMNH or FMNH catalog numbers, sampling locations and Genbank Accession numbers.

Species	Catalog Number	Station-Specimen	Genbank Accession Number	
			ITS	16S
Chama macerophylla	AMNH 306419	625-3	AY230078	AY388507
Chama macerophylla	FMNH 301423	629-22	AY230079	AY388511
Chama macerophylla	AMNH 306415	625-4	AY230080	AY388506
Chama macerophylla	FMNH 301291	Palm Beach, FL	-	AY388509
Chama congregata	AMNH 306412	624-1a	AY230081	-
Chama congregata	AMNH 306412	624-1b	AY230082	-
Chama congregata	FMNH 301422	629-9	AY230083	AY388512
Chama florida	AMNH 306410	641-1	AY230084	AY388508
Chama sarda	AMNH 306411	629-26	AY230085	AY388505
Chama radians	AMNH 306414	624-6	AY230086	AY388510
Chama inezae	FMNH 301292	Palm Beach, FL	-	AY388513
Chama sp.	-	Seychelles	AY230087	AY388514
Chama sp.	-	Seychelles	AY230088	AY388515

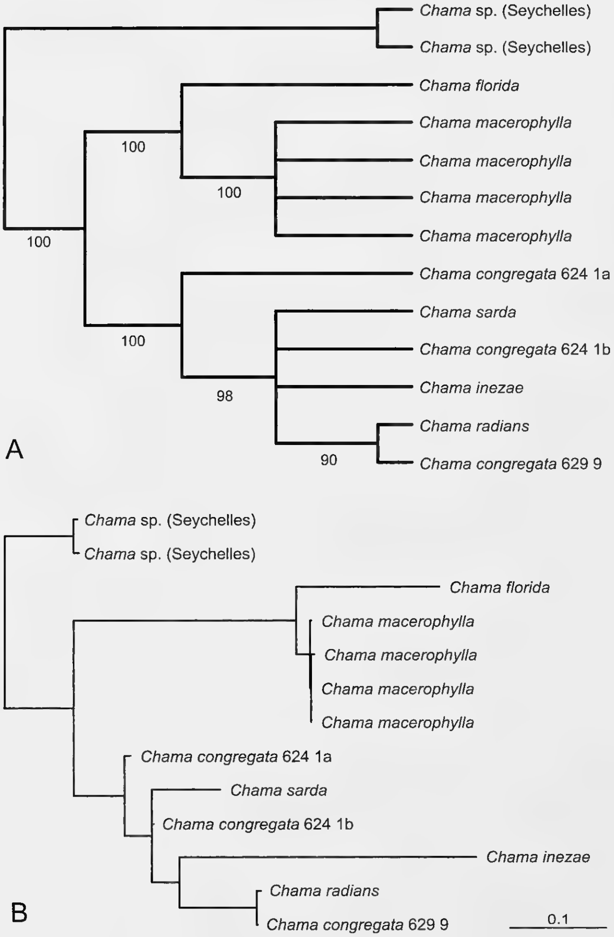

FIG. 1. Phylogenetic analysis of the combined molecular data ITS1 + 5.8S + ITS2 and 16S rRNA sequences. A: Strict consensus tree of 50 most parsimonious trees (length = 879, CI = 0.89, RC = 0.82). Values below branches indicate bootstrap support; B: One of four maximum likelihood trees (HKY85+G model, logL = 3416.604, ti/tv ratio = 0.771, gamma shape = 0.89824). The other trees differ only in the branching order of the *Chama macerophylla* sequences.

bp of the 3´ end only. The alignment had 813 positions, of which 355 were parsimony informative.

Parsimony analysis of the ITS data returned six parsimonious trees (length = 304, CI = 0.93, RC = 0.89), whereas the 16S rRNA data yielded a single most parsimonious tree (length = 575, CI = 0.87, RC = 0.76). Except for the taxa present in only one of the data sets the ITS strict consensus tree and the 16S rRNA tree were fully congruent. The combined analysis returned 50 shortest trees (length = 879, CI = 0.89, RC = 0.82). The strict consensus tree (Fig. 1A) separated two major groups: one contains *Chama macerophylla* and *C. florida*, the other *C. sarda*, *C. congregata*, *C. inezae*, and *C. radians*. Bootstrap support for the branches in the strict consensus tree was generally high (≥ 90) except for the branching order of *C. congregata* 624-1b, *C. sarda*, and *C. inezae*.

Similar congruence was found for the maximum likelihood trees of the two data sets, although they differed slightly in the position of *Chama florida* nesting in *C. macerophylla* in the ITS tree (logL = 3416.604, ti/tv ratio = 0.771, gamma shape = 0.89824) as opposed to basal to it in the 16S rRNA tree (logL = 3314.612, ti/tv ratio = 2.576, gamma shape = 0.41149). Four maximum likelihood trees, differing only in the branching pattern of the *C. macerophylla* specimens, resulted from the analysis of the combined data (Fig. 1B; logL = 7101.247, ti/tv ratio = 1.146, gamma shape = 0.648739).

Both genes supported the same basic branching pattern, independent of the phylogenetic method employed. The *Chama macerophylla* specimens from three different localities form a robust monophyletic clade with *C. florida* as sister taxon. In contrast, the *C. congregata* sequences – even if from the same individual, are polyphyletic. The weak support in this area of the tree may also be due to the missing 16S data for *C. congregata* 624-1 and the missing ITS data for *C. inezae*.

Morphological Characters

"The mutations within the species of *Chama* are quite marked. They comprise color variations which are often quite striking, as lemon-yellow and pale or dark purple in *C. macerophylla*, profuse, sparse, or obsolete foliation, and such changes of form as are due to the object upon which they are fixed. In discriminating species these fluctuations should be taken into account by the student, but it will also be found that there are features which are tolerably constant and which, after due discrimination, will be found to serve as guides to specific identity" (Dall, 1903: 1397).

In the Chamidae, large, adult shells from wrecks, buoys, or protected portions of quiet-water reefs are the most diagnostic specimens for deriving species concepts. Such material is rare, but spectacular of form, color, and ornament. By contrast, the encrusted, subadult specimens typical of reef and dredge samples can be a challenge to identify. Among the genus or species level discriminators given in literature are right or left valve attachment, size and shape of the prodissoconch, hinge patterns, absolute size, presence or absence of internal margin crenulations, pattern of pallial line attachment to muscle scars, color or color pattern, patterns of sculpture, and relative inflation of attached and free valves.

Chamids live with either their left or right shell cemented to a hard substratum, which can considerably influence shell shape and surface ornament. In current literature, species which attach exclusively by the left valve; species which typically attach by the left valve, but may occasionally attach by the other (Lamprell & Whitehead, 1992; Matsukuma, 1996); and species which attach indiscriminately to produce a roughly 50:50 balance (Yonge, 1967) are all assigned to the genus *Chama*. The Indo-Pacific genera *Eopsuma* and *Carditachama* are separated by their primitive hinge, retaining cardinal and lateral teeth. *Eopsuma* includes both species that attach by the right valve only, and by right or left indiscriminately (Matsukuma, 1996). Spiny, equilateral chamids, attaching by the right valve as juveniles, can be assigned to *Arcinella*.

Classification of the exclusively right attached chamids with a typical *Chama* hinge was problematic. Depending upon the author, such species represent either a valid, monophyletic clade assigned to *Pseudochama,* a form genus using *Pseudochama* for convenience, or represent *Chama* with reversed attachment, synonymizing *Pseudochama* with *Chama* (e.g., Yonge, 1967). The concept of *Pseudochama* has been controversial since its introduction (Odhner, 1919; Yonge, 1967; Matsukuma et al., 1997). Most authors who use *Pseudochama* apply it as a form genus. Used in this sense, *Pseudochama* are most diverse in the tropical eastern Pacific, with Keen (1971) documenting six *Pseudochama* species sympatric with eight *Chama* species.

An intriguing feature is the transposition of hinge teeth. Dentition usually is not determined by the left-right symmetry as in other bivalves, but by which valve attaches to the substratum. Thus, an attached valve, whether right or left, almost always exhibits the same dentition. Odhner (1919) placed great emphasis on differences in the hinge formulas of *Chama* and *Pseudochama*, making the hinge a key argument for separation of the genera, but these differences appear to be nothing more than the mirror image reversals achieved by transposition (Davis, 1935; Kennedy et al., 1970). Very rarely specimens have been found with transposed shell attachment but normal dentition (Matsukuma et al., 1997).

Starobogatov (1992) argued for separating *Arcinella* and *Pseudochama* into an entirely different superfamily, Arcinelloidea Scarlato & Starobogatov, in Nevesskaya et al. (1971: 17), in the rudist suborder Hippuritoidei, based on the supposed lack of heterodont dentition. However, the nepionic shell in *Pseudochama* has two cardinal teeth before metamorphosis

(Keen, 1971: 151). Kennedy et al. (1970: 406–410) compared in detail chamid shell and dentition with every family of rudists, and rejected the hypothesis of a rudist ancestry.

Maximum adult size appears to be a species-specific trait within a given fauna. In the Florida Keys we found small (*Chama sarda*), medium (*C. congregata*), and large taxa (*C. macerophylla*). Maximum size has been frequently cited as a discriminating character, for example in separating the Late Pliocene fossil *C. willcoxii* Dall from the Miocene to Recent *C. macerophylla* Gmelin. However, Allen (1977: 258) found evidence for a three-year lifespan in *C. gryphoides,* and Epstein & Lowenstam (1953: 432) documented that *C. macerophylla* in Bermuda produced shell growth only in the warmest season of the year. Consequently, it appears that maximum size has both genetic and environmental components. More tropical, central to southern Caribbean *C. macerophylla* may be 20 to 40 mm larger than typical Floridian material (Pilsbry & McGinty, 1938), perhaps reflecting a greater number of days warm enough for shell growth across a brief lifespan. In turn, the greater size of *C. willcoxii* may reflect the milder Florida winters during mid- to late Pliocene seas. Maximum size proves helpful when dealing with adult specimens, but subadult specimens of the larger taxa are often conformable to and easily confused with the smaller species.

The presence or absence of internal margin crenulations is frequently cited as a species-level discriminator (Dall, 1903; Abbott, 1974). In our study, we have found no smooth-margin species, with an occasional crenulate individual. One specimen of *Chama inezae* (USCS collections) adjusted a wide, shell-edge lamella by pleating the inner edge, but careful examination revealed no true crenulations. We have examined over 100 specimens each of the fossil species *C. congregata* Conrad, 1833, and *Pseudochama corticosa* (Conrad, 1833), and find them to be consistently crenulate. However, five of 40 specimens of the Recent *C. radians* lacked the crenulations typical of that species. We conclude that presence or absence of crenulation is a constant factor in some western Atlantic species, but is variable in others. Consequently, individual specimens, including holotypes, may or may not express the normative pattern. This caution also applies to the identification of single specimens from a fossil site or dredge haul.

Chamid ontogeny expresses a break in shell growth corresponding to larval settlement and a second break corresponding to cementation to a hard substratum (Kennedy et al., 1970: 382–384). Some authors (Odhner, 1919, 1955; Kennedy et al., 1970; Bernard, 1976; Matsukuma, 1996) used the term “prodissoconch” to refer exclusively to larval growth, and the terms “dissoconch” or “dissoconch I” for shell growth between larval settlement and cementation. Other authors (Cox et al., 1969; Waller, personal communication, March 2003) apply the term “prodissoconch” to all shell growth before cementation. Here we follow the latter usage.

The size and shape of the prodissoconch have been used to separate *Chama* from *Pseudochama*, with *Chama* species having a rounded prodissoconch of less than 1 mm but *Pseudochama* species having a rectangular prodissoconch of greater than 2 mm (Odhner, 1919). Subsequent investigation indicates that these characters do not appear to be definitive at the genus level in western Atlantic chamids. Most larger chamid specimens are encrusted, abraded, or bored, and the prodissoconch is destroyed. Smaller, post-metamorphic shells (5–7 mm in diameter) in many cases preserve the prodissoconch, but at that size they have not established diagnostic morphology, and the species can be difficult to identify. Prodissoconch form remains undescribed for most chamid species. Among the few *Chama* and *Pseudochama* species for which the prodissoconch has been described, there are overlapping ranges of variation. *Chama* species that preserve this early growth stage often have a round to oval prodissoconch, 0.5 to 2 mm in diameter, which is smooth or has radial sculpture. In contrast, documented *Pseudochama* and *Arcinella* generally have an oval to rectangular prodissoconch that is 1.5 to 2.5 mm in diameter, and has concentric lamellar sculpture before cementation (Odhner, 1919; Matsukuma, 1996). Odhner (1919: pl. 1, fig. 7) illustrated a “definitive” prodissoconch for *P. ferruginea*, a synonym of *C. radians,* and Redfern (2001) illustrated a large, rectangular prodissoconch for *C. radians.* However, Ferreira & Xavier (1981: fig. 4) illustrated a similar large, oval prodissoconch for *C. macerophylla,* and Dall (1903: 1395) reported a 2-mm prodissoconch for *C. lactuca*. Odhner (1919: 14) first invoked misidentification as the explanation for Dall’s (1903) report of *Chama* prodissoconchs larger than 1 mm, and later described a “transition” zone in the metamorphosis of *Chama* (Odhner, 1955) to maintain the supposed size differ-

TABLE 3. Stratigraphic and geographic distribution of *Chama* and *Pseudochama* in the western Atlantic Ocean: New Jersey to Florida and Gulf of Mexico, Lower Miocene to Upper Pliocene.

Distribution	Lower & Middle Miocene	Upper Miocene	Lower & Middle Pliocene	Upper Pliocene
New Jersey to Maryland	*C. congregata*	-	-	-
Virginia to north of Cape Hatteras, NC	-	-	*C. congregata* *C. emmonsi* *P. corticosa*	*C. congregata* *C. emmonsi*
North Carolina to northern Florida	*Chama* sp.	-	*C. congregata* *C. emmonsi* *P. corticosa*	*C. congregata* *C. emmonsi*
Southern Florida and Florida Keys	-	-	*C. congregata* *C. emmonsi* *Chama*. sp. *P. caloosana*	*C. congregata* *C. emmonsi* *C. heilprini* *C. willcoxii* *P. caloosana*
Western Florida and Gulf of Mexico	*C. chipolana* *P. draconis* *P. corticosa*	-	*C. congregata* *C. emmonsi*	-

ences. Kennedy et al. (1970: pl. 71) illustrated a circular, cancellate prodissoconch for *C. pellucida*, an oval, lamellar prodissoconch for *A. arcinella*, and a small, circular lamellar prodissoconch for *Chama* sp. We conclude that a small, round prodissoconch is more typical of *Chama*, and that a larger, rectangular stage may represent "*Pseudochama*" of authors, or *Arcinella*. The overlap is considerable and is non-definitive. We have been unable to

TABLE 4. Stratigraphic and geographic distribution of *Chama* and *Pseudochama* in the western Atlantic Ocean: Cuba and Greater Antilles to Argentina, Lower Miocene to Upper Pliocene.

Distribution	Lower & Middle Miocene	Upper Miocene	Lower & Middle Pliocene	Upper Pliocene
Cuba, Greater Antilles, Bahamas	-	*C. caimitica* *C. involuta* *P. riocanica*	*C. macerophylla* *C. involuta*	-
Lesser Antilles	-	-	-	*C. macerophylla* *Pseudochama* sp. aff. *P. caloosana*
Central America	-	-	*C. macerophylla*	-
Panama	*C. strepta*	*C. berjadinensis*	-	-
Colombia, Venezuela	*C. berjadinensis* *P. buchivacoana*	*C. berjadinensis* *P. corticosaformis* *P. quirosana* *P. scheibei*	-	-
Brazil	-	-	-	-
Argentina	-	*C. paschauli* *P. lazai*	-	-

TABLE 5. Stratigraphic and geographic distribution of *Chama* and *Pseudochama* in the western Atlantic Ocean: North Carolina to Central America, Lower Pleistocene to Recent.

Distribution	Lower Pleistocene	Upper Pleistocene	Recent
North Carolina to northern Florida	-	*C. macerophylla*	*C. congregata* *C. macerophylla* *C. radians* *C. lactuca*
Southern Florida and Florida Keys	*C. congregata* *C. macerophylla* *C. emmonsi*	-	*C. congregata* *C. macerophylla* *C. florida* *C. sinuosa* *C. radians* *C. lactuca* *C. sarda* *C. inezae*
Western Florida and Gulf of Mexico	-	-	*C. congregata* *C. macerophylla* *C. radians* *C. lactuca*
Cuba, Greater Antilles, Bahamas	-	*C. congregata* *C. macerophylla* *C. florida* *C. sinuosa* *C. radians*	*C. congregata* *C. macerophylla* *C. florida* *C. sinuosa* *C. radians* *C. sarda*
Lesser Antilles	-	-	*C. congregata* *C. macerophylla* *C. florida* *C. sinuosa* *C. radians* *C. lactuca* *C. sarda*
Central America	-	-	*C. congregata* *C. macerophylla* *C. florida* *C. sinuosa* *C. radians* *C. sarda*

find any published description of the prodissoconch of *C. cristella* Lamarck, 1819, type species of *Pseudochama.*

The adductor muscle scars in the Chamidae are large, elongate, and are often described as reniform. In most species, the muscle scars are subequal, and are connected by a simple pallial line with no sinus. Attachment of the pallial line typically is at the center of the ventral margin of the adductor scars, but considerable variation exists within conspecific populations. Pallial line attachment can meet the ventral margin at the outer edge, inner edge, or center; or the pallial line can extend dorsally and attach to the outer or inner lateral margin of the adductor muscle scar. The latter condition has been erroneously described as a pallial sinus. Bayer (1943) cited attachment at the ventral margin of the anterior adductor muscle scar for *Chama florida* and attachment at the outer lateral margin of the scar as characteristic of *C. sarda*. Although we find this attachment pattern more common in *C. sarda*, it is not a consistent trait at the species level.

TABLE 6. Stratigraphic and geographic distribution of *Chama* and *Pseudochama* in the western Atlantic Ocean: Panama to Argentina, Lower Pleistocene to Recent.

Distribution	Lower Pleistocene	Upper Pleistocene	Recent
Panama	-	-	*C. congregata* *C. macerophylla* *C. florida* *C. sinuosa* *C. radians* *C. sarda*
Colombia, Venezuela	*C. sinuosa* *C. radians*	*C. macerophylla* *C. florida*	*C. congregata* *C. macerophylla* *C. florida* *C. sinuosa* *C. radians*
Brazil	-	*C. macerophylla*	*C. congregata* *C. macerophylla* *C. florida* *C. sinuosa* *C. radians*
Argentina	-	*C. iudicai*	-

Systematics

Zoogeographic and stratigraphic distributions are given from literature (Tables 3–6). Authority for particular distribution records can be found in the literature cited in the synonymies, and is generally not repeated in the Distributions. Institutional abbreviations for specimens examined or illustrated are as follows: AMNH, American Museum of Natural History, New York, New York, USA; ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; FLMNH, Florida Museum of Natural History, Gainesville, Florida, USA; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; MNHG, Museum of Natural History of Geneva, Switzerland; USCS, University of South Carolina Spartanburg, South Carolina, USA.

Family Chamidae Lamarck, 1809

Genus *Chama* Linnaeus, 1758

Type species: *Chama lazarus* Linnaeus 1758 (ICZN Opinion 484, 1957). *Chama lazarus* is from the Indo-Pacific, not the Mediterranean, as cited by Abbott (1974: 466).

Matsukuma (1996: 29) gave the following characters for *Chama*: "Shells usually attached by the left valve, entirely aragonitic, with outer crossed-lamellar layer, middle myostracal layer, and inner complex crossed-lamellar layer. Nepionic shell small, less than 1.2 mm long, prodissoconch without ornament, early dissoconch having minute sculpture of closely spaced radiating striae, punctations and somewhat more distant commarginal riblets. Hinge of the nepionic shell and adult 'pachydont'-type; hinge formula of the nepionic shell: 3a, 3b, LPI in the right valve and 2, 4b, LPII in the left; each tooth somewhat parallel to the hinge plate. Adult free right valve: single long, narrow cardinal (3a) + 3b, a wide ventral socket below the cardinal, parallel to hinge plate, denticles (5b) below nymph, and a posterior lateral (LPI); adult attached left valve: a broad anterior cardinal (2) parallel to the hinge plate, a dorsal socket, a weak, long, narrow, posterior cardinal (4b), and a posterior lateral (LPII)."

Genus *Pseudochama* Odhner, 1917

Type species (subsequent designation: Gardner, 1926): *Chama cristella* Lamarck, 1819 (Figs. 11, 12). Lamarck's original handwritten label stated a locality of "Océan des grandes indes". A more recent label with the type specimen indicated "Ocean indien" (= Indian Ocean).

The holotype of *Chama cristella* Lamarck is from the Delessert collection (Fig. 11; MNHG

1087/6). In Lamarck's description, he made an incidental reference to Chemnitz (1786: fig. 993). Odhner (1917, 1919) based his type concept of *Pseudochama* on specimens of "*Chama cristella* Lamarck", but did not designate a type species, listing *P. cristella* (Lamarck) and *P. similis* Odhner, 1917, in the genus. He hypothesized that all species with a typical chamid hinge and right valve attachment should be placed in *Pseudochama*. Gardner (1926) designated *C. cristella* Lamarck, 1819, as the type species, a designation independently given by Prashad (1932: 295) (Nicol, 1952a, b). Sandberg & Warén (1993: 120) cited the type species of *Pseudochama* Odhner, 1917, as *P. similis* by original designation. However, Odhner implied but did not state a type species, an opinion confirmed by Warén (personal communication, August 2003).

Despite the extensive debate over the validity of *Pseudochama*, we have been unable to locate any illustration of undoubted *P. cristella* published subsequent to the mid-nineteenth century. Lamy (1928: 347) noted the nomenclatural confusion involving *Chama cristella* Lamarck, 1819; *C. sinistrorsa* Bruguière, 1792; and Chemnitz (1786: figs. 992 and 993). Lamy (1928) cited Chemnitz (1786) for a locality of West Indies (St. Croix) for figure 992, and of West Indies for figure 993. Bruguière (1792: 392) cited Chemnitz figure 992 and a locality of the Greater Antilles for his new species *C. sinistrorsa*. Lamarck (1819: 96) described *C. radians* based on a specimen in his collection (Fig. 7A; MNHG 1087/3), and referenced Chemnitz figure 992 as conspecific. Similarly, Lamarck described *C. cristella* based on a specimen in the Delessert collection (Fig. 11; MNHG 1087/6) and also referenced Chemnitz figure 993. In Lamarck's description, he noted that *C. radians* was a different species from *C. sinistrorsa* Bruguière, 1792. Lamy concluded that *C. cristella* Lamarck, 1819, and *C. sinistrorsa* Bruguière, 1792, were conspecific with Chemnitz' figure 993, leaving Chemnitz figure 992 as conspecific with *C. radians* Lamarck, 1819. Lamy listed "*Chama sinistrorsa* ?Bruguière, 1792", as a synonym under the more recently described *C. cristella* Lamarck, 1819. Resolution of this problem is beyond the scope of this study.

Bucquoy et al. (1892: 312) thought that Chemnitz's figure 992 could depict *Chama ruppelli* Reeve, 1847, but Lamy (1928) stated that *C. ruppelli* Reeve was a distinct species from Chemnitz's figure 992. Clessin (1889: 38, pl. 16, figs. 3, 4) thought that *C. cristella* as figured in Reeve (1847) differed from *C. cristella* Lamarck, 1819. Clessin named Reeve's figure *C. reevana* Clessin, 1889, and applied Lamarck's species *C. cristella* to a shell from Puerto Rico. However, Lynge (1909: 265) said that the figure of Reeve (1847) was conspecific with *C. cristella*, and the Clessin 1889 specimen from Puerto Rico was not *C. cristella*. Lynge (1909: 265) quoted Reeve (1847): "the example here figured has been satisfactorily identified with Lamarck's original specimen in the collection of M. Delessert."

The type specimen of *Chama cristella* Lamarck (Fig. 11) appears to be very close, if not conspecific with *Pseudochama similis* Odhner, 1917, as figured by Matsukuma et al. (1997: 229, figs. 7a–d). Reeve (1846: pl. 3, fig. 10b) figured a right-attached specimen, BM(NH) 1950.11.1.50, and a left-attached specimen (his fig. 10a), BM(NH) 150.11.1.49 as two syntypes of *C. pulchella* Reeve, 1846. An unfigured syntype, BM(NH) 150.11.1.51, is also a left-attached specimen of *C. pulchella* Reeve, 1846. Odhner (1917) described *P. similis* based on the right-attached specimen BM(NH) 1950.11.1.50 (Reeve, 1846, pl. 3, fig. 10b). Lamprell & Whitehead (1992: pl. 23, fig. 149) synonymized *P. similis* with *C. pulchella,* but Matsukuma (1996: 36) argued that Reeve's figure 10b represented a valid right-attached species. Matsukuma et al. (1997, figs. 7a–d, 8a–d, 9) illustrated the three Reeve (1846) syntypes for *C. pulchella*, with *P. similis* as figures 7a–d. They cited a second possible specimen of *P. similis* from Tonga. Matsukuma et al. (1997) argued that Odhner correctly separated the right-attached syntype as *P. similis*, because its sculpture pattern distinctly contrasted with the two left-attached syntypes. Higo et al. (2001) also illustrated this right-attached British Museum syntype, but gave its number as BM(NH) 150.11.1.49, identifying it as a syntype of *Chama pulchella* Reeve.

Matsukuma (1996) followed Odhner (1919) in emphasizing anatomical differences between *Chama* and *Pseudochama*. Matsukuma (1996: 46) listed the following characters for *Pseudochama*: "animal without lateral caecal appendage of the stomach, nephridia with the pericardial tubes not covered on their median side by distal sacs; shell usually attached by the right valve; nepionic shell sculptured just as in *Arcinella* Schumacher, 1817, with rather distantly spaced commarginal lamellae, and no or very fine punctuations or only traces of radiating riblets; the size of early dissoconch more considerable, length up to 1.0–2.5 mm;

hinge formula of the nepionic shell: 1, 3b, LPI in the right valve and (2a), 2b, (4b), LPII in the left; hinge formula of adult shell: 1 + 3b, 5b, LPIII in the right valve and (2a), 4b, LPII in the left." We add no anatomical details, but note that Kennedy et al. (1979) had documented left-attached species with lateral appendages on the stomach and left-attached species without lateral appendages on the stomach.

Matsukuma (1996) discussed "normal" and "reverse" attachment, and the various chamid genera and species in which both forms occur. He restricted the genus concept of *Pseudochama* to *P. cristella*, the type species of the genus, and to those species in strict conformity of valve attachment, hinge form, shell form, prodissoconch, and anatomy to this type species. However, prodissoconch form remains unknown for *P. cristella*.

Odhner (1917, 1919) based his type concept of *Pseudochama* on specimens of "*Chama cristella* Lamarck" which Dr. Mjoberg brought from the northwestern coast of Australia. Lamprell & Whitehead (1992) and Lamprell & Healy (1998) did not recognize *P. cristella* from Australian waters, but noted several species which are typically or occasionally right-attached. Slack-Smith (1998: 308, figs. 8.1d, e) illustrated as "*Pseudochama* sp." a specimen from Australian waters that resembles *P.* sp. cf. *P. cristella* (ANSP 54808) from Java (Figs. 12A–C). Most authors who cite *P. cristella* in current literature limit its distribution to Thailand and Indonesia. Lamy (1928) cited a distribution of Indonesia, Thailand, the Indian Ocean, and possibly South Australia for *P. cristella*.

The holotype of *Chama cristella* Lamarck, 1819 (Fig. 11), contrasts with specimens from Java identified as *Pseudochama cristella* and housed in the Academy of Natural Sciences Philadelphia collection (Figs. 12A–C). In both the holotype and the ANSP Javan specimens, the attached valves show a similar attachment pattern, strong fluting adjacent to the line of attachment, more subdued fronds or low fluting adjacent to the posterior edge, and rare to common granular nodes between the two rows of fluting. General details of the interior of the valves are conformable for both lots, although Javan specimens show a stronger knob on the hinge. However, the external sculpture of the free valves differs markedly. The holotype of *P. cristella* shows a free valve with large, widely spaced lamellae that are scalloped into large flutes. This fluting contrasts with the three Javan specimens that show a consistent pattern of fine, crowded lamellae broken up into scale-like fronds. At the other extreme, the sculpture of the type of *P. similis*, from Matsukuma et al. (1997: 229, fig. 7a–d) is even more fluted and elaborate, but the pattern matches that of the *P. cristella* holotype. The question remains whether the Javan specimens are *P. cristella* with subdued and more crowded sculpture, or whether they represent a distinct species. Such range of variation is present for some chamid species, but not in others. Given the rarity of the taxa in question, we suggest that the ANSP lot from Java be referenced as *Pseudochama* sp. cf. *P. cristella*. Resolution of these questions is essential in defining the range of variability within the type species of the genus *Pseudochama* Odhner, 1917, but a conclusion is beyond the limits of this study.

Kilburn & Rippey (1982: 174, pl. 39, fig. 9) reported *Pseudochama cristella* (Lamarck) from "Indo-Pacific to western Transkei". They described and figured a small (to 30 mm), right-attached form, the size, color, and sculpture of which differ considerably from Lamarck's holotype. This South African taxon is probably not *P. cristella*.

Odhner's (1919) hypothesis of a pervasive, monophyletic *Pseudochama*, defined by a typical chamid hinge and right valve attachment, can be no longer supported. In the western Atlantic, right-attached taxa first appeared in the Middle Eocene, and continued as a scarce element into the Recent tropical and subtropical faunas. The right-attached condition appears to have arisen independently by valve transposition several times in western Atlantic and eastern Pacific fossil and Recent faunas. For example, the Californian *P. exogyra* (Conrad, 1837) and sympatric *Chama arcana* (Bernard, 1976) (= *C. pellucida* of authors, *non* Broderip, 1835) differ in valve attachment, but share an otherwise rare outer shell layer of calcite (Kennedy et al., 1970: 388–389) from which they were judged to be closely related.

We agree with Matsukuma (1996) that a valid concept of *Pseudochama* must conform rigorously to the type species, but many uncertainties surround *P. cristella* and congeneric status with *Chama radians* cannot be presently established. In the western Atlantic, there are no extinct *Pseudochama* species with right attachment that are morphologically an obvious ancestor of *C. radians*. Pilsbry & McGinty (1938) observed that certain *C. radians* appear to be mirror images of Recent *C. congregata*. *Chama radians* is consistently right-attached, and has a rectangular prodissoconch of about 2 mm. In our molecular analysis of the ITS gene, *C. radians* falls within a cluster of *Chama* species. The hypothesis of a right-attached monophyletic clade predicts that all species of "*Pseudochama*" should stand apart. Even Odhner (1919: 81–82) informally divided his genus into a *P. cristella* "group" and a *P. radians* "section". While recognizing that more systematic and molecular work needs to be done, including analysis of multiple individuals of several different "*Pseudochama*" species, we are returning *P. radians* to the genus *Chama*.

CHAMID SPECIES OF SOUTHERN FLORIDA

Chama congregata Conrad, 1833
Figures 2A–C

?*Chama foliacea* Gmelin, *auctt.*, *non* Gmelin, 1791: 3304, based on Lister, 1685: pl. 215, fig. 51.

Chama congregata Conrad, 1833: 341; Dall, 1903: 1400–1401; Glenn, 1904: 342, pl. 91, figs. 1–3; Olsson, 1922: 218, pl. 28, fig. 11; Lamy, 1928: 329; Bayer, 1943: 120, pl. 12, fig. 3; Weisbord, 1964: 235–238, pl. 31, figs. 11–14, pl. 32, figs. 5, 6 (extensive synonymy); Hoerle, 1970: 58; Waller, 1973: 41, 48; Abbott, 1974: 466, pl. 21, fig. 5385; Cerridwen & Jones, 1991: 100; Campbell, 1993: 30, pl. 8, fig. 76; Díaz & Puyana, 1994: 74–75, pl. 16, fig. 152; Rios, 1994: 260, species 1266, pl. 89; Redfern, 2001: 214, species 876, pl. 89.

Chama congregatoides Maury, 1917: 200, pl. 33, fig. 8.

Type Locality

Miocene, James River, Virginia "near Smithfield" (Conrad, 1833: 341). Emended by Campbell (1993): Pliocene, Yorktown Formation, James River, Virginia. Numerous outcrops were available to Conrad in the riverbanks near Smithfield, such as Rock Wharf, a known Conrad locality with a high molluscan diversity.

Remarks on Early Literature

Dall (1903: 1401) said of Recent *Chama congregata*: "This appears to be the species said to be abundant in Cuba, which is cited by Arango (1878–1880: 272) as *Chama foliacea* Gmelin, based chiefly on Lister's figures. It is, however, too uncertain to be adopted even if the specific name was not so glaringly inappropriate." *Chama foliacea* Gmelin, 1791, was originally described from "Mediterranean and Americas," based on Lister (1685: pls. 215–217, figs. 51, 53). Lister had fossil specimens from Colonial Virginia (Campbell, 1993), and modern "Colonial Williamsburg" gravels its paths with *C. congregata*. Lister (1685) sometimes gave localities, for example, plate 215, figure 50, portrayed a *Chama* with radiating color bands (probably *C. florida*) from "Barb. jamaic" (Barbados and Jamaica). Some of his Virginia fossils have the designation of "virg". However, no Lister (1685) locality information accompanied figures 51 and 53, and the two are not conspecific. Lister's figure 51 was copied by Klein (1753: pl. 12, fig. 81), a reference also cited by Gmelin (1791). Figure 51 is an upper valve of a *Chama*, showing the radial grooving of typical *C. sinuosa*, but lacking in all variations of *C. congregata* (see below). Figure 53 depicts an upper valve not showing the radial grooving. It is larger, and shows considerable bioerosion of the ventral margin. Such damage is unusual for *C. congregata*, but common in larger chamid specimens. The third citation given by Gmelin (1791) is Chemnitz (1783: pl. 52, fig. 521). Chemnitz figured a *Chama* with a very low, appressed beak, and with the attached valve hardly larger than the free valve. *Chama congregata* possesses a high, "naticiform" beak, and is clearly not conspecific with that figure. The last figure cited by Gmelin (1791) is Lister (1685) plate 215, figure 50, which was considered above. Consequently, we concur with Dall (1903) in rejecting *C. foliacea* (Gmelin) as a senior synonym for *C. congregata*. Bruguière (1792) proposed *C. rugosa* on essentially the same concepts, citing Lister (1685: fig. 53), Klein (1753: fig. 81), and "Martini" [= Chemnitz], fig. 521, along with two other references not given by Gmelin. Consequently, whatever *C. foliacea* is, *C. rugosa* would appear to be a synonym. Lamy (1928: 327) noted that *C. foliacea* Quoy & Gaimard (1835) is a junior homonym of *C. foliacea* Gmelin.

A second complicating element to the species concept of *Chama foliacea* Gmelin from the older literature concerns *C. lamellosa* Lamarck, 1806. Lamarck (1806: 348) listed fossil species of *Chama*, beginning with *C. squamosa* (Brander, 1766 [= Solander]), which he renamed *C. lamellosa*. This usage has con-

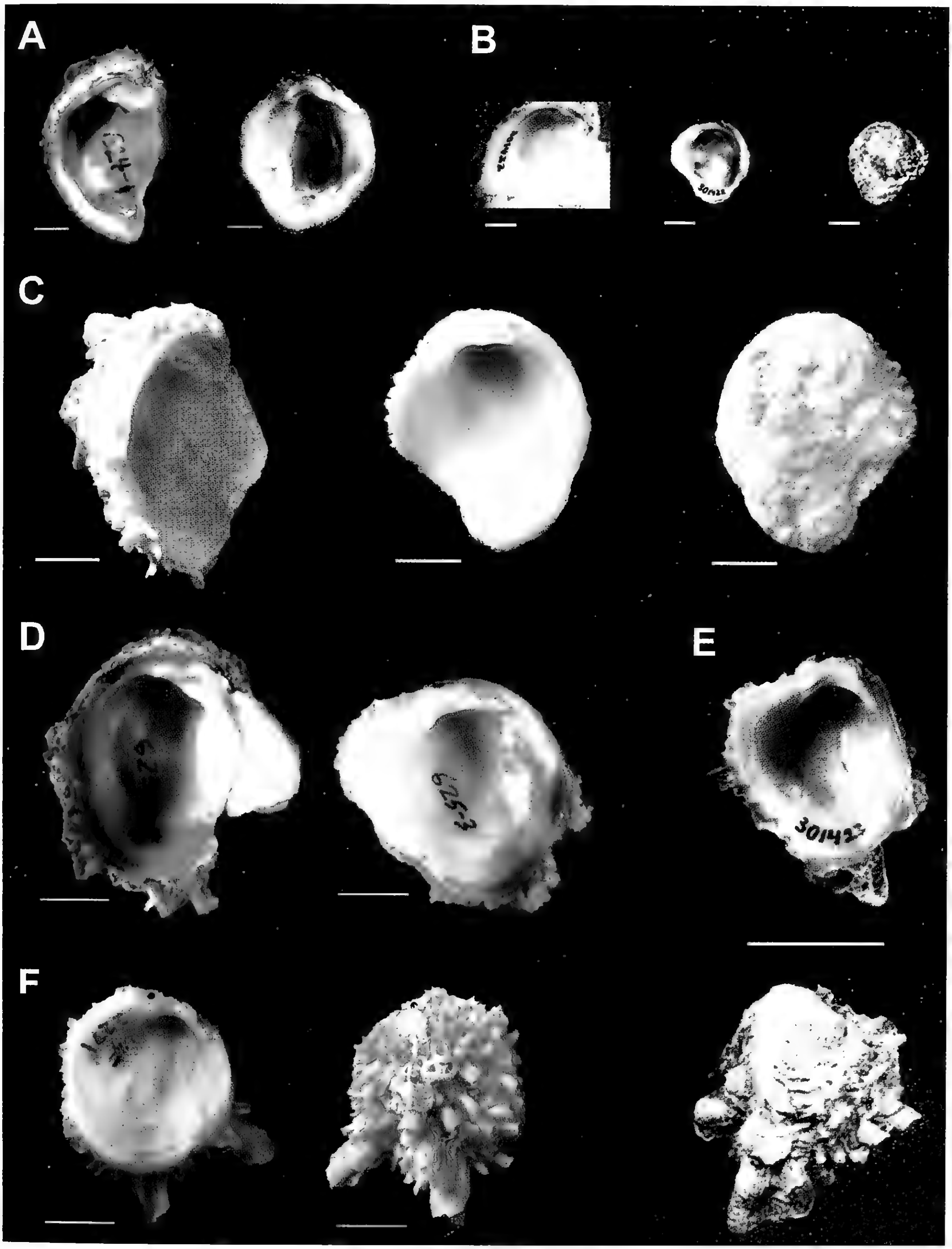

FIG. 2. *Chama* spp. A: *Chama congregata*, right and left valves, IMBW-FK-624, Horseshoe Reef, off Fat Deer Key, Florida, 7.3 m (AMNH 306412); B: *C. congregata*, right and left valves, IMBW-FK-629, "The Horseshoe" site, West Summerland Key (Spanish Harbor Keys), Florida (FMNH 301422); C: *C. congregata*, right and left valves, Missouri Key, Monroe Co., Florida, (FLMNH 127093); D: *C. macerophylla*, right and left valves, IMBW-FK-625, Coffins Patch Sanctuary Preservation Area, off Crawl Key, Florida, 6.4 m (AMNH 306419); E: *C. macerophylla*, right valve, IMBW-FK-629 (FMNH 301423); F: *C. macerophylla*, right valve, Key Largo, Florida (FLMNH 2271). Scale bars = 5 mm (A–C); 10 mm (D–F).

tinued. Brander's species was from the Eocene Barton beds at Hampshire, England (Natural History Museum, 1975). Brander's illustration portrayed a medium-sized *Chama* with a high, strongly recurved, "naticiform" attached valve, similar to *C. congregata*. This being the only work cited by Lamarck, 1806, the species concept of *C. lamellosa* should be uniquely tied to *C. squamosa,* and become a junior synonym. However, Lamarck (1819: 98) later expanded the concept of *C. lamellosa* to include *C. rugosa* Bruguière, 1792 [*non* Linnaeus, 1771] and Chemnitz (1783: pl. 52, fig. 521), which Gmelin included in *C. foliacea*. As none of the taxa from the 1819 expansion appear conspecific with *C. squamosa* (Brander), they may be rejected from *C. lamellosa* (*sensu stricto*). *Chama squamosa* (Brander) (= *C. lamellosa* Lamarck) is convergent, but not conspecific, with *C. congregata.*

Remarks on *Chama congregata*

Three or more fossil and Recent morphospecies appear to be present under the name "*Chama congregata*". Additionally, we report under molecular systematics that DNA sequencing of multiple specimens of *C. congregata* within the Recent Florida Keys population indicates that multiple cryptic species may be present. Here we treat each form separately and, for the present, retain all forms under the traditional name.

Chama congregata Conrad, 1833, original lot of nine fossil syntypes from the James River, Yorktown Formation, Pliocene of Virginia.

Description

Small to medium sized (to 25 mm, rarely to 30 mm); both valves with small, short, flat, smooth scales arranged in radial rows; attached valve with very small attachment area, mostly free growth, producing a deeply cupped, "naticiform" valve; upper valve circular, somewhat inflated, lacking or with only the slightest hint of a depressed central radial furrow; inner margin crenulated.

Distribution

Miocene, Kirkwood beds, New Jersey; Miocene, Calvert Formation, Maryland. Glenn (1904) figured specimens from the Calvert that appear conspecific with Yorktown material. Lower Pliocene, Yorktown Formation, Zone 1 and Zone 2, Virginia, Yorktown Formation, North Carolina; Goose Creek Limestone, Raysor Marl, Duplin (at Natural Well); Jackson Bluff Formation, western Florida; Pinecrest bed 7, Sarasota, Florida; Upper Pliocene, Waccamaw Formation, Carolinas; Caloosahatchee Formation, southern Florida. We are not aware of any Recent specimens conformable with Conrad's Yorktown Formation types.

Discussion

Calvert specimens from Plum Point, Maryland (USCS collections), are larger, have raised lamellar sculpture, and are wider than high. This latter form is probably an undescribed species. A similar form was illustrated by Ward (1992) from the Belgrade Formation of the Upper Oligocene of North Carolina. Ward (1992) used the name "*Chama chipolana* Dall, 1903", for these specimens, but Ward's illustrated topotypes do not appear conspecific with Dall's illustrated syntypes of *C. chipolana*, nor with Chipola specimens on loan from the Florida Museum of Natural History. Given the possibility of multiple species, all Kirkwood and Calvert Formation records of *C. congregata* need to be critically reexamined.

Although Conrad's types were from the south bank, along the north bank of the James River at King's Mill (another Conrad locality), and in several localities around Williamsburg, Virginia, *Chama congregata* is the dominant element in bioherms or reefs 5–10 m thick and 200 m or more wide. The millions of complete specimens found in these reefs give context to Conrad's name for the species. In the *Chama* reefs, individuals were unattached or were loosely attached to their neighbors. Other shell substrata, such as large valves of *Chesapecten, Mercenaria*, and *Ostrea*, were common in these reefs and on the Yorktown sea floor, but appear unexploited as attachments by this form. Similar concentrations of paired *C. congregata* with no reef development have been found in Early Pliocene deposits near Lynchburg and Florence, South Carolina.

"*Chama congregata*" of Upper Pliocene to Recent deposits, North Carolina and South Carolina to Florida and the West Indies.

Description

Shell small to medium-sized (15 to 20 mm, rarely to 30 mm), usually attached to rock, coral, or shell substrata; attachment area large, with specimens typically having the anterior edge of attached valve in contact with substratum, giving right (unattached) valve a semicircular outline; attached valve shallow-cupped, not "naticiform"; sculpture suppressed and scaly in the furrow, but coarsely frondose on the flanks; shell outline somewhat rectangular; inner margin crenulated. Bayer (1943: pl. 12, fig. 3), Weisbord (1964: pl. 32, figs. 1, 2), and Redfern (2001: pl. 89, figs. 876A, B) illustrated large specimens in which the unattached valve has a very broad and depressed central radial furrow.

Distribution

Upper Pliocene, lower and upper Waccamaw Formation at Calabash, North Carolina. Late Pliocene, Nashua Formation, northeastern Florida. Early Pleistocene, Bermont beds, southern Florida. Upper Pleistocene, Venezuela and Grand Cayman. Recent, shallow to mid-shelf, Cape Hatteras, North Carolina, to Florida, Texas, Bermuda, and the West Indies. Redfern (2001: 214) reported this morphology as common in two to five m depth in the Bahamas.

"*Chama congregata*" Recent of Brazil

Description

"Valves rounded (35 x 28 mm), grayish to red in color. Right valves smaller than the left. Surface with axial, wavy corrugations. Ventral margins slightly crenulated. Attached to rocks, corals, and other shells, usually in colonies at low tide and on mangrove roots" (Rios, 1994: 260). Pilsbry & McGinty (1938: 75) cited a maximum size of 36 mm.

Discussion

The large size and subdued sculpture suggest that Recent "*Chama congregata*" of Brazil is a different species. Both attributes may be a consequence of living in shallow subtidal, higher energy waters. The larger size could also be related to the effects of water temperature on shell growth (Epstein & Lowenstam, 1953; Lowenstam, 1954), or a combination of these factors. Alternatively, this may prove to be a Recent extension of *C. iudicai* Pastorino, 1991, from the Pleistocene of Argentina.

Chama macerophylla Gmelin, 1791
Figures 2D, 3A

Chama gryphoides (*ex parte*) Linnaeus, 1767: 1139.
Macerophylla, Flos Maris Chemnitz, 1783: 101, 149, pl. 52, figs. 514, 515.
Chama macerophylla Gmelin, 1791: 3304; Dall, 1903: 1403; Woodring, 1925: 104–105, pl. 12, figs. 18, 19; Lamy, 1928: 308 (extensive synonymy); Weisbord, 1964: 238–241, pl. 33, figs. 1, 2 (extensive synonymy); Richards et al., 1969: 4; Hoerle, 1970: 58; Scoffin, 1972: 1281; Waller, 1973: 41, 48; Abbott, 1974: 466, pl. 21, fig. 5384; Cerridwen & Jones, 1991: 100; Donovan & Littlewood, 1993: 37–38; Paulay, 2003: 223, 234.
Chama citrea Gmelin, 1791: 3305.
Chama imbricata Lamarck, 1801: 131; Krebs, 1864: 117, *non* Broderip, 1835: 149.
Chama lazarus Linnaeus – Lamarck, 1819: 93, *non* Linnaeus, 1758.
Chama macrophylla [sic] Gmelin – Hanley, 1843: 226.
Chama bicornis Linnaeus – Krebs, 1864: 117, *non* Linnaeus, 1758: 692.
Chama macerophylla var. *purpurascens* Poulsen, 1878: 15.
Chama macerophylla var. *sulphurea* Poulsen, 1878: 15, fig. 14, *non* Reeve, 1846.
not *Chama macerophylla* Gmelin – Melvill & Standen, 1907: 840, *non* Gmelin, 1791.
Chama cf. macerophylla Gmelin Jung, 1969: 362, pl. 24, figs. 1, 2.
?*Chama bermudensis* Heilprin, 1890: 141, pl. 8, figs. 1, 1a (see Waller, 1973: 48).

Type Locality

Recent, "oceano americano" (Gmelin, 1791).

Description

Large, very foliaceous, with profuse, erect fronds that are radially striate; fronds small and abundant, or fewer, larger, longer within a single population; left valve not deeply cupped; attachment area extensive; inner margin is crenulated; colors may be uniform or combinations of white, lemon yellow, and/or purple; interior ventral margin almost always stained with a band of brownish purple (Fig. 2D).

In dredge sample or reef-survey, this species may identified by the combination of striate fronds, internal color band, and crenulate margin.

Distribution

Miocene and Pliocene, Dominican Republic (Woodring, 1925: 104–105); Pliocene, Bowden beds, Jamaica. Pliocene (?), Trinidad (Jung, 1969). Pliocene, Limon, Costa Rica (Woodring, 1925: 104–105). Early Pleistocene, Bermont beds, southern Florida. Late Pleistocene, Grand Cayman (Cerridwen & Jones, 1991); Jamaica (Donovan & Littlewood, 1993), the Antilles and Curacao (Woodring, 1925: 104–105), Bermuda, North Carolina, Florida, Cuba, Dominican Republic, St. Kitts, Curacao, Aruba, and Venezuela. Recent, Bermuda, Cape Hatteras, North Carolina to Brazil. Louisiana record from Garcia & Lee (2002). Paulay (2003: 223, 234) documented this species as a Pacific invasive in the waters around Guam.

Discussion

Chama macerophylla Gmelin, 1791, is common on rock, reefs, wrecks, and sea walls. Woodring (1925: 104–105) recorded it from shallow water to 525 m. The radial striations are visible and pervasive. *Chama sinuosa* and other associated species may have an occasional frond showing radial striae, but that is the exception. Small, encrusted specimens of *C. macerophylla* may appear convergent with *C. congregata,* but in *C. macerophylla* the interior ventral margin is almost always stained brownish purple (Fig. 2D), a color absent in *C. congregata.*

Lamy (1928) provided an extensive synonymy. He concluded that *Chama macerophylla* Gmelin of Melvill & Standen (1907: 840) from the Persian Gulf was not *C. macerophylla* Gmelin and instead probably was *C. damaecornis* Lamarck, 1819, a junior synonym of *C. lazarus* Linnaeus, 1758. Lamy (1928) also stated that *C. imbricata* Lamarck, 1801, was a synonym of *C. macerophylla* Gmelin, 1791. (*Chama imbricata* Lamarck, 1801, is a senior homonym of *C. imbricata* Broderip, 1835, from the Red Sea and Indian Ocean.)

Chama macerophylla was present in the Late Miocene of the Dominican Republic, and in the Middle Pliocene of Venezuela and southern Florida. These earliest populations were probably ancestral to *C. willcoxii* Dall, 1903, which was endemic to the Plio-Pleistocene Caloosahatchee Formation of southern Florida. *Chama willcoxii* was larger, and the fused fronds were more than twice the width of those of *C. macerophylla*. In *C. willcoxii*, the fronds were appressed, contrasting with the erect sculpture of *C. macerophylla*.

Waller (1973: 48) documented heavy, deeply cupped specimens of *Chama macerophylla* from Walsingham Pond, Bermuda, which he compared with *Chama bermudensis* Heilprin, 1890. Abbott (1974: 466) followed Bayer (1943: 122) in placing *C. bermudensis* as a form of *C. sinuosa* Broderip. Pending re-examination of Heilprin's type, we tentatively retain *C. bermudensis* within *C. sinuosa*.

Chama florida Lamarck, 1819

Figures 3B, C

Chama florida Lamarck, 1819: 94; Dall, 1903: 1404; Lamy, 1928: 376 (extensive synonymy); Pilsbry & McGinty, 1938: 74; Bayer, 1943: 117, 119, 123, pl. 12, fig. 6; Weisbord, 1964: 241–242, pl. 33, figs. 3, 4 (extensive synonymy); Abbott, 1974: 467.

?*Chama sarda* Reeve – Díaz & Puyana, 1994: 74, pl. 16, fig. 154; Rios, 1994: 260, pl. 89.

Type Locality

Recent, Dominican Republic.

Description

Small to medium-sized, with crowded, concentric rows of small, fluted fronds; upper valve typically white, with a variable number of radial rows of red dots, often stained internally with red or pink; inner margin crenulated; sculpture uniform or stronger with continued growth, as illustrated by Bayer (1943: pl. 12, fig. 6).

A specimen from Soldier Key (FLMNH 146889) shows first-year growth with erect, recurved scales. Second-year growth remains erect, but points ventrally. Spine wear and epizoan growth suggest a three-year life span.

Distribution

Pleistocene, Cuba and Venezuela (Weisbord, 1964: 242). Recent, southeastern Florida and West Indies, eastern Brazil, 9 to 80 m (Abbott, 1974: 467).

Discussion

Brazilian specimens were described by Rios (1994) as having white, tubular spines, and Díaz & Puyana (1994) illustrated such a specimen from the Atlantic coast of Colombia. Rios (1994) and Díaz & Puyana (1994) placed this southern material in *Chama sarda*, but the Díaz & Puyana (1994) illustration most resembled the Bayer (1943) figure of *C. florida*. This Colombian material shows larger fronds with down-turned margins. Pilsbry & McGinty (1938: 74) suggested synonymizing *C. sarda* and *C. florida*. Bayer (1943: 117) argued for separate species, and noted that the pallial

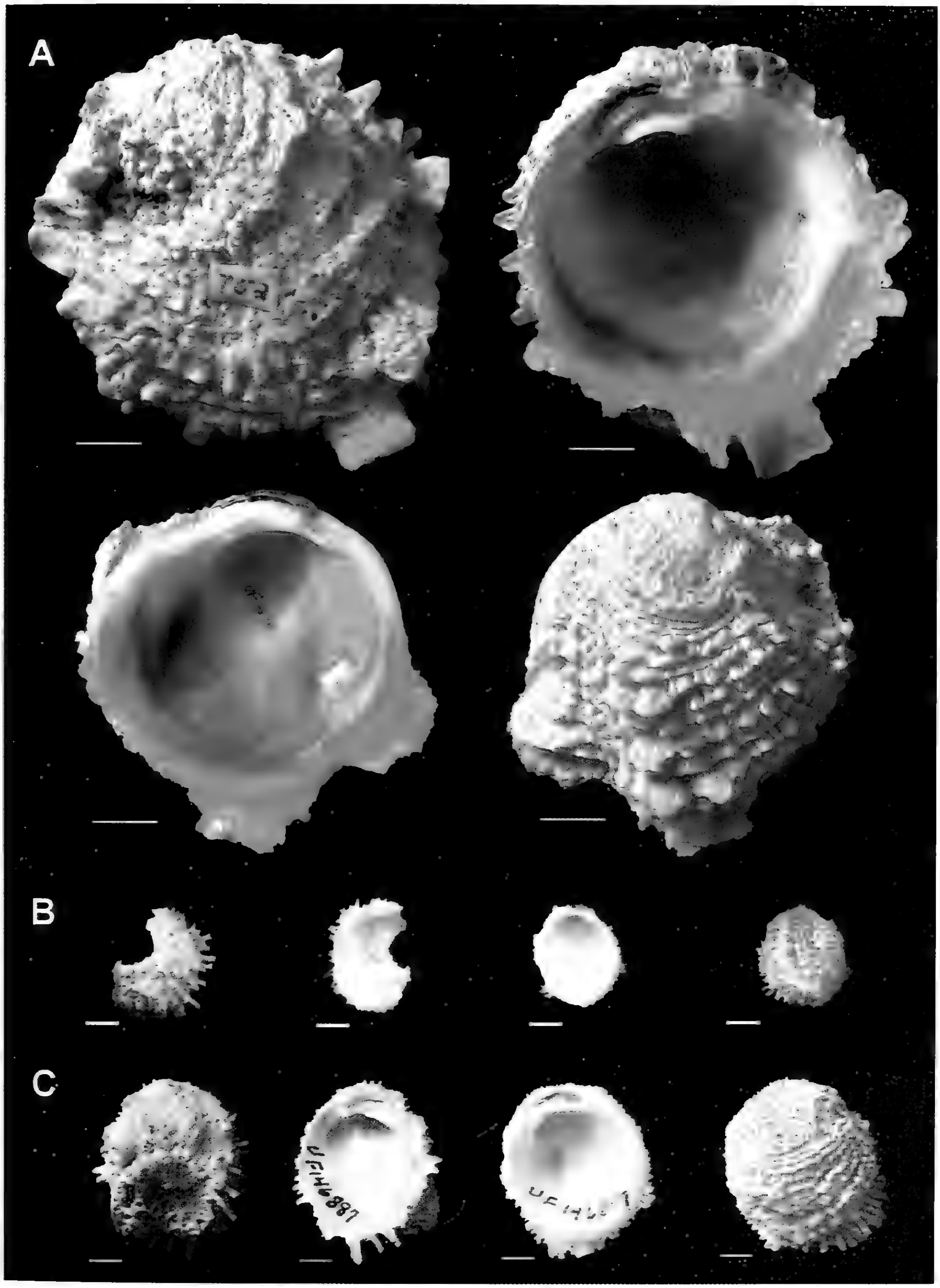

FIG. 3. *Chama* spp. A: *Chama macerophylla*, right and left valves, Bear Cut, Dade County, Florida (FLMNH 238239); B: *C. florida*, right and left valves, IMBW-FK-641, Tennessee Reef, off Long Key, Florida, 7 m (AMNH 306410); C: *C. florida*, right and left valves, Sand Key Light, Key West, Florida (FLMNH 146887). Scale bars = 10 mm (A); 5 mm (B–C).

line attaches to the bottom of the anterior adductor muscle scar in *C. florida*, but attaches higher on the margin in *C. sarda*. Based on our examination of fifteen to thirty specimens of each (FLMNH), we find all *C. florida* specimens consistent with Bayer's observation, but *C. sarda* shows considerable variation in the position of pallial line attachment.

Deshayes, in Lamarck et al. (1835: 583) noted that *Chama florida* Lamarck could be a variety of "*C. cornuta* Chemnitz" (Chemnitz, 1783: pl. 52, fig. 518). Clessin (1889) accepted this synonymy. Lynge (1909: 265) examined Chemnitz's specimen and decided that it was a young individual, worn and hard to identify, from the Nicobar Islands, India, in contrast to *C. florida* from the Dominican Republic. Hanley (1843) thought some of the original specimens of *C. florida* resembled the figure of *C. spinosa* Broderip, 1835. Lamy (1928) decided that the specimens were too poorly preserved for definitive identification, and that Chemnitz' figure 518 could be *C. spinosa* Broderip 1835, a synonym of *C. asperella* Lamarck, 1819.

Lamy (1928) examined five boxes of specimens labeled by Lamarck as *Chama florida*. He concluded that the specimens in the first box were too poorly preserved for definitive identification. The second and third boxes contained juvenile *C. macerophylla* Gmelin. The fourth box contained a large (45 mm), rounded discolored shell labeled as "*Chama florida*? old individual". The fifth box contained five valves of *C. florida* that matched Reeve's illustrations of that species (1847).

Lamy (1928) rejected the comparison by Broderip (1835) of *Chama florida* with *C. pacifica* Broderip, 1835, and rejected the synonymy by Dall (1903) of *C. sarda* Reeve, 1847, with *C. florida* Lamarck, 1819. Lamy (1928) concluded that the figures in Chenu (1846) for *C. florida* were inadequate and instead resembled *C. chinensis* Chenu, 1846.

Chama sinuosa Broderip, 1835
Figures 4–6

Chama sinuosa Broderip, 1835: 303, pl. 39, fig. 11; Dall, 1903: 1403 (in synonymy with *C. macerophylla*); Lamy, 1928: 311 (extensive synonymy); Pilsbry & McGinty, 1938: 76, pl. 7, fig. 9; Abbott, 1974: 466, text fig. 5386, pl. 21, fig. 5386; Cerridwen & Jones, 1991: 100.
Chama cistula Reeve, 1847: pl. 9, fig. 51.
Chama tumulosa Reeve, 1847: pl. 9, fig. 52.
Chama lamarckiana Clessin, 1889: 42, pl. 5, figs. 1, 2.
?*Chama bermudensis* Heilprin, 1890: 141, pl. 8, figs. 1, 1a.
Chama sinuosa firma Pilsbry & McGinty, 1938: 76, pl. 7, fig. 1; Bayer, 1943: 121, pl. 13, fig. 11.
Chama sinuosa bermudensis Heilprin – Bayer, 1943: 118, 122, 123, pl. 14, fig. 26; ?Weisbord, 1964: 242–243, pl. 32, figs. 10, 13.

Type Locality

Recent, Brazil (Broderip, 1835).

Description

Medium to large, thin to heavy, with large, fluted, smooth (or rarely striate) fronds in typical expression; unattached valve with central, radial, depressed band, the edges of which are deep, narrow grooves; grooves visible even on surf-worn valves devoid of all other sculpture; no internal margin crenulations present.

A 57 mm specimen (FLMNH 15877), labeled *C. sinuosa firma*, shows two years growth with surface sculpture removed by a variety of shell-degrading endolithic species (Fig. 5). The onset of third year growth provides a fringe of fresh, undamaged fronds and lamellae, the pattern that defines the variety.

Distribution

Early Pleistocene, Venezuela (Weisbord, 1964). Late Pleistocene, Grand Cayman (Cerridwen & Jones, 1991); Cockburn Town, San Salvador, Bahamas (Hagey, 1991). Recent reef species, southern half of Florida, West Indies, Bermuda, and Brazil (Abbott, 1974: 466).

Discussion

The variety *Chama sinuosa firma* Pilsbry & McGinty, 1938, has reduced sculpture except for some large fronds at the margin, is larger, and more deeply cupped (Fig. 5). That trend, taken to an extreme, produces *C. s. bermudensis* Heilprin, 1890, in which the shell is very large, thin to very thick; the ventral valve very deep, and the beak high and strongly coiled (Fig. 6). The latter morphology parallels the Pliocene *C. heilprini*. The Venezuelan fossils referred to *C. s. bermudensis* by Weisbord (1964) more closely resemble *C. s. firma*. Waller (1973: 41, 48) found no specimens of *C. sinuosa* in his survey of Bermu-

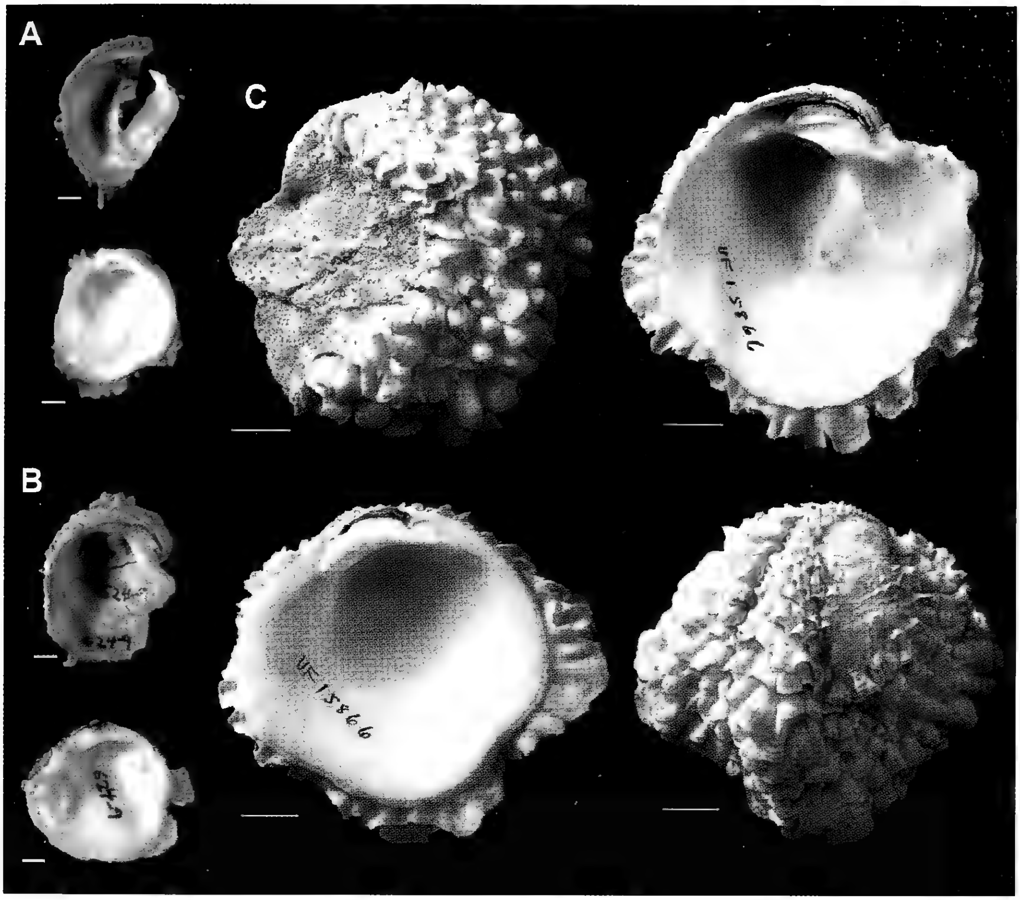

FIG. 4. *Chama sinuosa*. A: Right and left valves, IMBW-FK-641, Tennessee Reef, off Long Key, Florida, 7 m (AMNH 306936); B: Right and left valves, IMBW-FK-624, Horseshoe Reef, off Fat Deer Key, Florida, 7.3 m (AMNH 306938); C: Right and left valves, off Yamoto, Palm Beach, Florida, 73 m (FLMNH 15866). Scale bars = 5 mm (A–B); 10 mm (C).

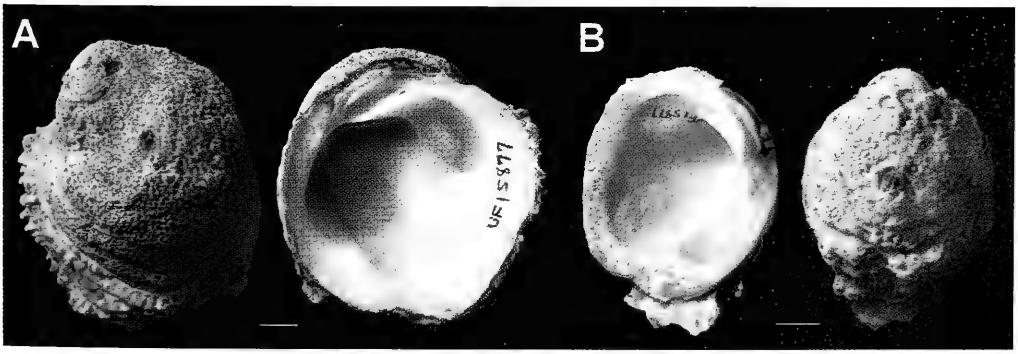

FIG. 5. *Chama sinuosa firma,* in moat, Fort Jefferson, Dry Tortugas, Florida (FLMNH 15877). Scale bar = 10 mm. A: Right valve; B: Left valve.

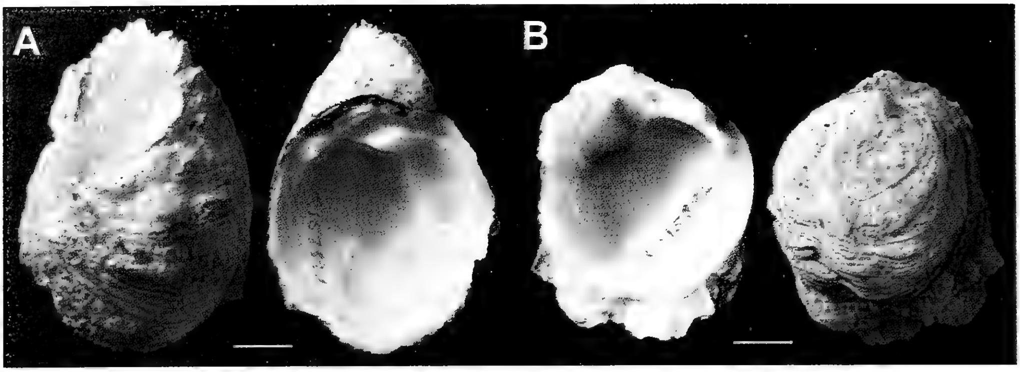

FIG. 6. "*Chama sinuosa bermudensis*" (Bayer 1943, label), in moat, Fort Jefferson, Dry Tortugas, Florida (FLMNH 15882). Scale bar = 10 mm. A: Right valve; B: Left valve.

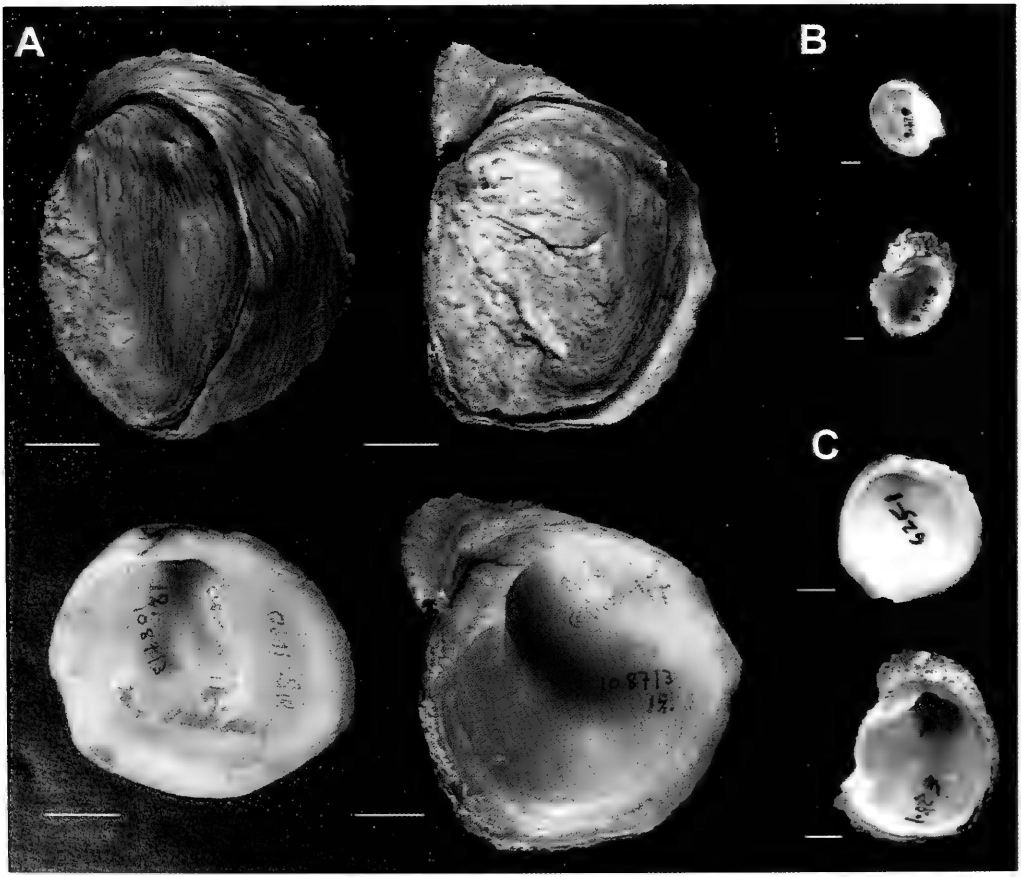

FIG. 7. *Chama radians*. A: Holotype, right and left valves (MNHG 1087/3, photographs courtesy of Yves Finet). The original label had no locality data, and a more recent label said "Oc. indien?"; B: Right and left valves, IMBW-FK-624, Horseshoe Reef, off Fat Deer Key, Florida, 7.3 m (AMNH 306414); C: Right and left valves, IMBW-FK-625, Coffins Patch Sanctuary Preservation Area, off Crawl Key, Florida, 6.4 m (AMNH 306418). Scale bars = 10 mm (A); 5 mm (B–C).

dian molluscs, but did find heavy specimens of *C. macerophylla* that strongly resembled Heilprin's taxon. Waller's specimens of *C. macerophylla* had crenulated margins. Neither Heilprin's text nor figures expressed the internal margin crenulations characteristic of *C. macerophylla*. The figure showed chipping of the shell margin that can remove crenulations in large *Chama* specimens. Heilprin (1890: 141) had a population of *C. bermudensis* "dredged in large quantities in Harrington Sound". We tentatively retain *C. bermudensis* within *C. sinuosa* pending re-examination of the type material.

Tryon (1872) synonymized the dextral *Chama cistula* Reeve with the sinistral species *C. appressa* Reeve. However, based on Reeve's (1847) descriptions and figures, we synonymize *C. cistula* with *C. sinuosa,* and *C. appressa* with *C. radians* Lamarck.

Lamy (1928: 311) noted that *Chama lamarckiana* Clessin, 1889 (p. 42, pl. 5, figs. 1, 2), from St. Thomas, Virgin Islands, was so badly eroded that it was difficult to identify. Benthem Jutting (1927) considered *C. lamarckiana* Clessin to be a variety of *C. sinuosa* Broderip, 1835. She also treated *C. bermudensis* Heilprin, 1890 as a synonym of *C. sinuosa* Broderip, 1835.

Lamy (1921, 1928) reported that Jousseaume had identified a *Chama* from Djibouti, Indian Ocean, as *C. sinuosa* Broderip. However, Lamy thought this specimen matched *C. prætexta* Reeve, 1847, figured by Reeve (1847) and Clessin (1889) from the Indian Ocean.

Chama radians Lamarck, 1819
Figures 7, 8

Chama radians Lamarck, 1819: 96, also referencing Chemnitz, 1786: 145, pl. 116, fig. 992.
Chama ferruginea Reeve, 1846, pl. 4, sp. 21; Dall, 1903: 1404.
Chama variegata Reeve, 1847a: 118; 1847b, pl. 9, fig. 50; Dall, 1903: 1404.
Chama appressa Reeve, 1847b: pl. 9, fig. 55.
Chama ruderalis Lamarck – Guppy, 1877: 86, *non* Lamarck, 1819: 96.
Pseudochama ferruginea Reeve – Odhner, 1919: 39.
Pseudochama radians (Lamarck) – Lamy, 1928: 375 (extensive synonymy); Pilsbry & McGinty, 1938: 77; Weisbord, 1964: 243–246, pl. 33, figs. 5, 6, pl. 34, figs. 1–6; Waller, 1973: 41, 48; Abbott, 1974: 467, pl. 21, fig. 5395; Cerridwen & Jones, 1991: 100; Donovan & Littlewood, 1993: 37; Redfern, 2001: 215, pl. 90, figs. 880A–D.
Pseudochama radians variegata Reeve – Pilsbry & McGinty, 1938: 77, pl. 7, figs. 3–5; Bayer, 1943: 122, pl. 12, fig. 4.

Type Locality

Recent, uncertain; possibly St. Croix, West Indies (*fide* Lamy, 1928: 376, see below).

Description

Medium to large, thin to heavy, attached along the anterior edge of right valve, commonly from umbo to ventral margin (Abbott, 1974, pl. 21, fig. 5395); left, unattached valve obliquely oval in specimens with an extended attachment surface, more circular in specimens with a small attachment area and greater free growth; sculpture of rough, closely packed concentric lamellae often broken into low fronds or scales; red-brown to purple stain varying in extent on the inside of attached valve; interior margin crenulated in most specimens, but five of the forty specimens examined lacked crenulations.

Distribution

Early Pleistocene, Bermont beds, southern Florida, and the Abisinia Formation, Venezuela. Late Pleistocene, Jamaica (Donovan & Littlewood, 1993), and Grand Cayman (Cerridwen & Jones, 1991). Recent, North Carolina to Florida, Texas, West Indies, Bermuda, and to Brazil (Abbott, 1974: 467), Louisiana record from Garcia & Lee (2002). Indian Ocean references (Clessin, 1889; Lamy, 1928) unlikely.

Discussion

The type locality is unknown. Yves Finet (e-mail, 3 March 2003) examined the labels with the holotype of *Chama radians* Lamarck, 1819 (Fig. 7A; MNHG 1087/3). The original label had no locality data; a more recent label said "Oc. indien?". Lamy (1928: 376) cited Chemnitz (1786) as indicating West Indies (St. Croix) as the locality for his plate 116, figure 992.

Unpigmented white shells of *Chama radians* are known from Eleuthra, Bahamas. A lot of six live-taken pairs of *C. radians* (FLMNH 127267; Grassy Key, Florida) possess a bizarre and confusing morphology, in which lateral expansion of the shell was halted at a length of 25 mm and height of 30 mm (Fig. 8C), with subsequent growth by shell thickening and body cavity inflation. The largest pair spans 37 mm width across both valves and is superficially convergent with certain rudists. Surface detail of the free valve is chemically leached, possibly from exposure to fresh water at low tide.

Pilsbry & McGinty (1938: 77–78) restricted *Chama radians variegata* (Reeve) to Florida (Fig. 8A), and suggested that *C. r. radians* and *C. r. ferruginea* are more typically West Indian taxa. However, Honduras was Reeve's (1847) type locality for *C. variegata*. Most current authors consider these to represent a single, variable species. Molecular sequencing could test the validity and affinities of these forms.

Lamy (1928: 312) said that *Chama ferruginea* Reeve was similar to *C. macerophylla* Gmelin. Lamy cited Tryon (1872) as synonymizing *C. ferruginea* with *C. sinuosa* Broderip, and Lamy said that Tryon cited a Broderip figure that did not exist. Clessin (1889: 48, pl. 19, figs. 1–3) described *C. rotunda* as a sinistral species from Veracruz, Mexico. Lamy said that the Clessin figures were insufficient and showed a worn specimen, but that *C. rotunda* was probably a synonym of *C. ferruginea* Reeve.

Chama appressa Reeve, 1847, represented a large specimen of *C. radians* with a small attachment surface, freeing it for more circular growth. Tryon (1872) combined the dextral species *C. cistula* Reeve, 1847, with the sinistral species *C. appressa* Reeve, 1847. Here

FIG. 8. *Chama radians*. A: Right and left valves, South of Boyton Inlet, Palm Beach, Florida (FLMNH 135589); B: Right and left valves, Marco, Collier County, Florida (FLMNH 199101); C: Right and left valves, Grassy Key (Gulf side), Monroe County, Florida (FLMNH 127267). Scale bars = 10 mm (A–B); 5 mm (C).

we synonymize *C. appressa* Reeve, 1847, with *C. radians* Lamarck, 1819, and *C. cistula* Reeve, 1847, with *C. sinuosa* Broderip, 1835.

Clessin (1889) and Lamy (1928: 376) identified specimens from the Indian Ocean and Aden, Red Sea as *Chama radians* Lamarck. Lamy (1928: 376) noted that this was in contrast to the West Indies distribution cited in Chemnitz (1786). *Chama sinistrorsa* Bruguière, 1792, may be an older name for *C. radians*. Deshayes, in Lamarck et al. (1835: 587) synonymized *C. sinistrorsa* Brocchi, 1814, *non* Bruguière, 1792, with *C. gryphina* Lamarck, 1819 (see Discussion under *Pseudochama cristella*).

Chama lactuca Dall, 1886
Figure 9A, B

Chama lactuca Dall, 1886: 268, 1903: 1404; Pilsbry & McGinty, 1938: 74; Bayer, 1943: 120–121, pl.12, figs. 1, 2; Abbott, 1974: 467, text fig. 5391.

Type Locality

Recent, Barbados (Dall, 1886).

Description

Small, white, sometimes with brown bands; attached valve deeply cupped, “naticiform”, sculptured with concentric lamellae; lamellae most often entire, but in some specimens cut into broad fronds; upper valve with radiating and concentric, small, short, spine-like fronds; lamellae of attached valve and fronds of free valve with radial grooving underneath.

Distribution

Recent, North Carolina to Florida, Gulf of Mexico, and to Barbados; 25–200 m or more. Louisiana record from Garcia & Lee (2002).

Chama sarda Reeve, 1847
Figures 9C–F, 13A

Three different recent forms appear under this name in current literature. Apart from some red pigmentation and small size, they have little in common.

Chama sarda Reeve, 1847 (attached valve shallow, stained deep red)

Chama sarda Reeve, 1847b: pl. 7, fig. 40; Dall, 1903: 1404; Lamy, 1928: 379 (extensive synonymy); Pilsbry & McGinty, 1938: 74; Bayer, 1943: 119, pl. 14, figs. 15, 16; Waller, 1973: 41, 48; Abbott, 1974: 466, pl. 21, fig. 5387.
Chama sarda lutea Lamy, 1928: 380.

Type Locality

Recent, Honduras (Reeve, 1847b).

Description

“Shell somewhat orbicular, both valves peculiarly faintly obliquely striated, with sharp remote short scales; bright coral-red within and without. Hab.: Honduras (attached to coral). Rich in colour and very characteristic in sculpture, being crossed in an oblique direction throughout with faint striae, and roughened here and there with short scales like the asparaties of a coarse file” (Reeve, 1847b).

Reeve described a rather variable, often misshapen small *Chama* with the attached valve shallow and extensively secured to the substratum. The attached valve is partially or completely stained bright, deep red. The right, unattached valve is commonly shades of red, red-pink, or cream, with low concentric corrugations, and in some cases, white, flat fronds near the edge of adult growth.

Distribution

Recent, Bermuda, northern Florida (H. Lee, personal communication, July 2003) to Florida Keys and from Bahamas at least to Honduras and the Dominican Republic.

Discussion

This is the form described by Reeve, and clearly illustrated by Bayer (1943), Abbott (1974), and Redfern (2001). Lamy (1928) rejected the synonymy by Dall (1903) of *Chama sarda* Reeve, 1847, with *C. florida* Lamarck, 1819. Lamy (1928) noted that previous reports were from the Antilles, and then reported 11 specimens from Île du Prince, West Africa, with a yellow specimen from there indicated as “variété jaune”.

Two lots from the Florida Museum of Natural History – ten pairs from Key Largo (FLMNH 135580) and six pairs from off Palm Beach (FLMNH 127241) – clarify and extend the range of morphologies possible in this species. The Key Largo specimens show first- and second-year growth reaching about 20 mm (Fig. 9D). The paired shells are wedge-

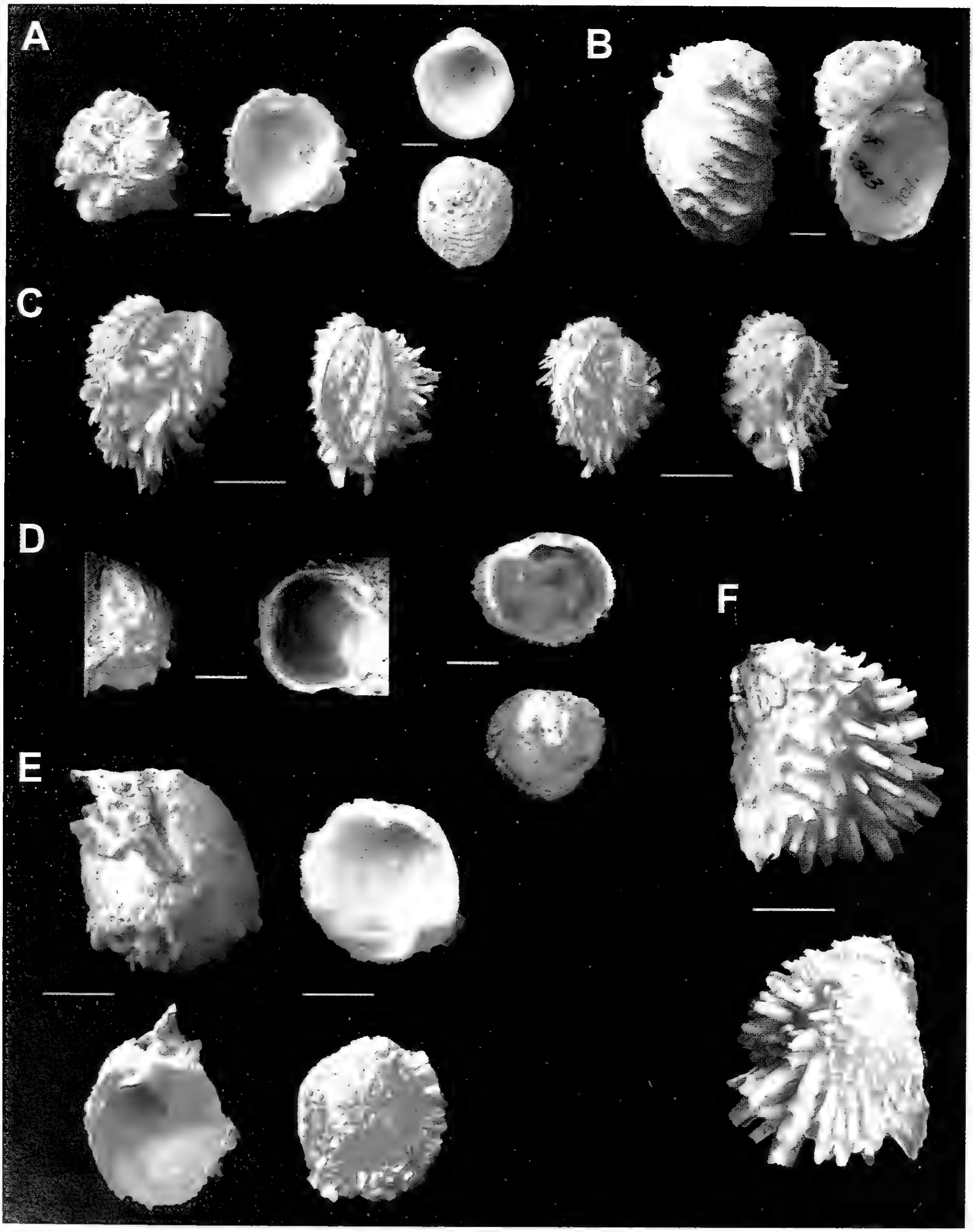

FIG. 9. *Chama* spp. A: *Chama lactuca*, right and left valves, off Dodge Estates, Palm Beach, Florida, 45 m (FLMNH 135481); B: *C. lactuca*, left valve, off Radio tower to Breakers Hotel, Palm Beach County, Florida, 137 m (FLMNH 186363); C: *C. sarda*, four pairs, right and left valves, Key Largo, Florida, 11 m (FLMNH 135580); D: *C. sarda,* right and left valves, IMBW-FK-629, "The Horseshoe" site, West Summerland Key (Spanish Harbor Keys), Florida (AMNH 306411); E: *C. sarda,* right and left valves, Boynton Beach, Palm Beach County, Florida, on beached gorgonian after storm (FLMNH 135582); F: *C. sarda*, right and left valves, Key West, Florida, SW Channel (FLMNH 246260). Scale bars = 5 mm (A, B, D); 10 mm (C, E, F).

shaped. Color ranges from uniform red or yellow, to red-and-white, to nearly white shells. Clusters of long, typically white spines may flank the posterior radial groove on both valves, with shorter spines covering the remaining shell. The Palm Beach lot exhibits more standard chamid morphologies. The largest specimen reaches a maximum elevation of 38 mm, but most specimens are less than 25 mm. The radial lines mentioned by Reeve, 1847, are weakly developed on some of the attached valves, but are lacking on the free valves. The irregular form and limited spine development (Reeve, 1847) seem most typical of first year growth, but sometimes persist with continued growth. More typically, spine development becomes more frequent and regular with second-year growth.

Kennedy et al. (1970: 395, text fig. 6) illustrated the chamid microstructure, noting that myostracal pillars may extend from the pallial myostracum through the inner shell layer and create bosses or bumps on the inner surface of the shell. These bosses are common to a number of species, including *Chama radians* and *C. macerophylla*, but we find them to be particularly large and frequent in young *C. sarda*.

"*Chama sarda* Reeve, 1847" (attached valve deeply cupped with ventral sulcus)
Figure 13A

Chama sarda Reeve, 1847 – Abbott, 1974: 466 (in part, deep cupped morphologies); Rehder, 1981: 729, fig. 654.

Description

Small, with the attached valve deeply cupped, and with a square, box-like outline due to a strong ventral sulcus, so that in outline it resembles the fossil species *Chama emmonsi* Nicol, 1953; left valve with a small attachment surface, allowing for much free growth; shell uniformly cream colored, with none of the red blotches typical of *C. sarda*, and with radial rows of tightly appressed, narrow, red fronds that may become erect at the margin of adult growth; upper valve cream color, with finer and more numerous radial rows of red rectangular appressed fronds, some of which elevate into low scales; upper valve with two radial furrows, a wider central one that merges with the ventral sulcus, and a smaller, narrower posterior furrow; myostracal pillars fused into linear radial ridges bordering inner edge of pallial line.

Distribution

Bahia, Brazil, and Caribbean, precise localities uncertain.

Discussion

The smaller, but uniform size, consistent quadrate outline with ventral sulcus, appressed sculpture, and lack of red blotching separate this form from typical *Chama sarda*. Typical *C. sarda* has myostracal pillars that form elevated oval bosses on the shell interior, not the fused, linear patterns found in this form. Rehder (1981) illustrated the diagnostic outer surface of the attached valve of this form.

Olsson & Harbison (1953: 76) reported a Recent *Chama* (ANSP 84720) from Bahia, Brazil, resembling their new species *C. gardnerae* (= *C. emmonsi* Nicol, 1953). Paul Callomon located this lot and provided illustrations (Fig. 13A; ANSP 84720). The label reads: "*C. linguafelis* Rve." crossed out and replaced with "*C. florida* Lam. (ballast) Bahia, Brazil. J. G. Malone, 1903". The two pairs are conspecific with our lot of 16 specimens (USCS collections) of uncertain Caribbean locality and with Rehder's field guide specimen of unstated provenance.

Based on the material in hand, this could be a previously unrecognized, distinct species with a distribution from Florida to Brazil. A search of museum collections will be necessary to determine its distribution and full range of variation. A review, especially of the 19th century literature, will be necessary to ascertain if it is undescribed.

"?*Chama sarda* Reeve" (tubular spine form)

Chama sarda Reeve, 1847; Díaz & Puyana, 1994: 74, pl. 16, fig. 154; Rios, 1994: 260, pl. 89.

Discussion

The taxon identified as *Chama sarda* by Rios (1994: 260) and by Díaz & Puyana (1994: 75) is probably *C. florida*, as discussed above under that species.

Chama inezae (Bayer, 1943)
Figure 10

Pseudochama inezae Bayer, 1943: 22, pl. 15, figs. 1–4; Abbott, 1974: 467, species 5396; Mikkelsen & Bieler, 2000: 372.

Type Locality

Recent, Carysfort Reef, Key Largo, Florida Keys, Florida (Bayer, 1943).

Description

Large, thin, with very thin, widely spaced, concentric, erect, ruffled lamellae; sculpture on both valves of broad, concentric draperies, or of lamellae becoming frondose at outer margins, or of very wide, fused fronds; broad, flaring lamellae most spectacular on smaller, apparently second-year, fresh-growth individuals; full-grown, third year specimens typically with wide lamellae trimmed by bioerosion; radial lines and threads sometimes present on the lamellae, but are of varied and limited extent; shell alabaster-white, lacking interior margin crenulations; early prodissoconch circular, about one millimeter in diameter, punctate, a pattern more typical of the genus *Chama*.

A population from Palm Beach, Florida of 16 specimens has eight right-attached and eight left-attached individuals.

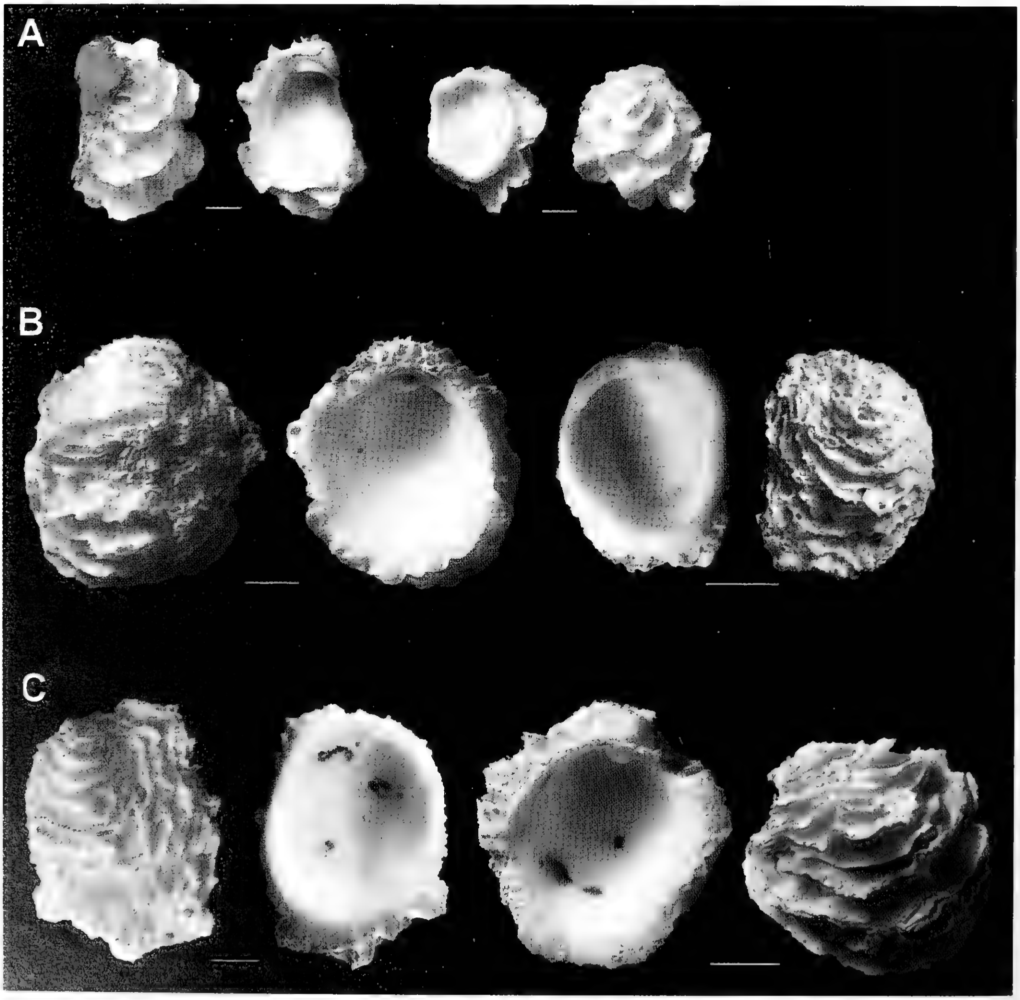

FIG. 10. *Chama inezae*. A: Right and left valves (FLMNH 135544); B: Right attached and left free valves, off Palm Beach, Florida, 20 m, under coral ledges (AMNH 308078); C: Right free and left attached valves, off Palm Beach, Florida, 20 m, under coral ledges (AMNH 308077). Scale bars = 5 mm (A); 10 mm (B–C).

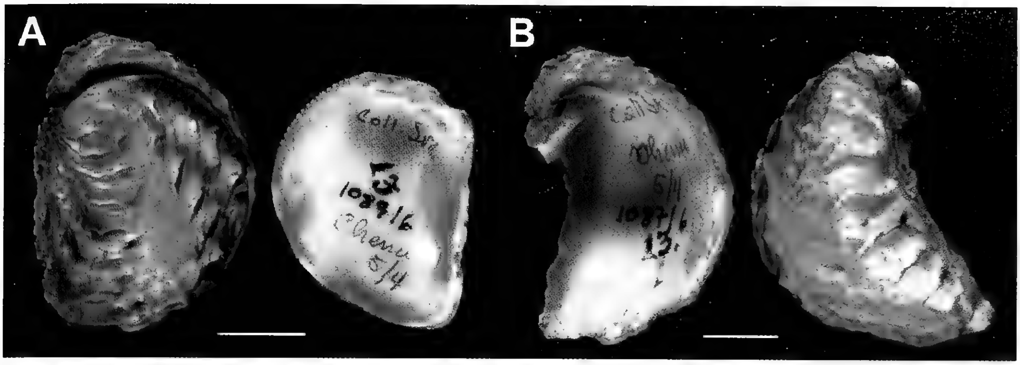

FIG. 11. Holotype, *Pseudochama cristella*, (MNHG 1087/6, photographs courtesy of Yves Finet). Lamarck's original handwritten label stated "Océan des grandes indes". A more recent label indicated "Ocean indien" (= Indian Ocean). Scale bar = 10 mm. A: Right valve; B: Left valve.

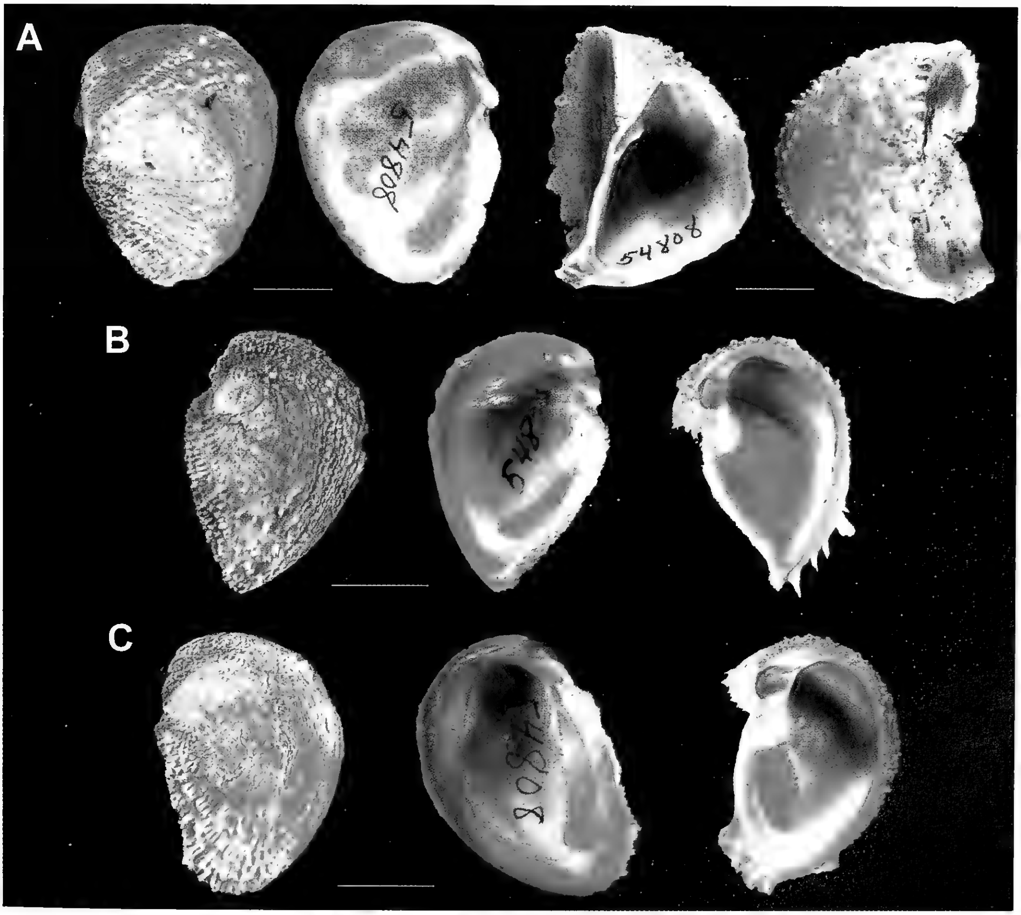

FIG. 12. *Pseudochama* sp. cf. *P. cristella*. A–C: Three pairs, right and left valves, Java (ANSP 54808, photographs courtesy of Paul Callomon). Scale bars = 10 mm.

Distribution

Recent, southeastern Florida (Abbott, 1974); Palm Beach County to Florida Keys.

Discussion

Chama inezae was originally based on a right-attached, unique holotype, and remains a rare, endemic species of mid-depth reefs, hard grounds, and wrecks off Florida. Bayer assigned his species to *Pseudochama* because of the right attachment. However, the specimen of *C. inezae* in the Florida Museum of Natural History (Fig. 10A; FLMNH 135544) proved to be left-attached. Two contrasting specimens are insufficient to define the normal attachment pattern, and we began a search for additional specimens of this rare species. We learned that Tom Honker had discovered a small population in 20 m under dead coral ledges off Palm Beach, Florida. Our 16 specimens (AMNH 308077-308078; USCS collections) were collected by Tom Honker in May 2002, and showed a 50:50 ratio of right valve and left valve attachment (Figs. 10B, C). This is the first known example of this attachment pattern for a Recent species from the western Atlantic. Yonge (1967) reported 50:50 ratios in the Indo-Pacific *Chama ruderalis* Lamarck, 1819, in Australia. Fossil species preserving similar ratios of right and left attached valves are known from Mississippi and France. Prevaling interpretation in literature places such specimens in the genus *Chama.* Left-attached specimens of *C. inezae* express the typical *Chama* hinge pattern, having the same arrangement of teeth and sockets as found in *C. sarda* and *C. macerophylla.* Right-attached specimens show that transposition of the hinge is linked to transposition of the shell in this species. Examination of the hinge in a right-attached valve demonstrates that the teeth and sockets are mirror images of those in a left-attached valve, but are less vigorously developed.

The presence of both right and left valve attachment patterns complicates identification. Any small to large, all white, Recent Floridian right-attached chamid lacking marginal crenulations may be referred to *Chama inezae.* Among left-attached species, *C. inezae* is strikingly alabaster-white, has broad, widely spaced lamellae, and has concentric sculpture dominant on both valves. Most of the other "white" *Chama* species in the region are cream, multicolored, or dirty white. The attached valve of *C. lactuca* has similar concentric lamellae, but the lamellae are proportionally shorter, and the valve is more deeply cupped and is internally crenulate. *Chama lactuca* is also much smaller than *C. inezae. Chama macerophylla* may be alabaster-white, but the crowded, frondose sculpture sets it apart from *C. inezae.*

Genus *Arcinella* Schumacher, 1817

Type species by tautonomy: *Chama arcinella* Linnaeus, 1767.
Not preoccupied by *Arcinella* Oken, 1815, rejected by ICZN Opinion 417 (1956).
Synonym: *Echinochama* P. Fischer, 1887.

"Shell attached to the substrate only in the early stages of growth. Lunule prominent, bordered by an incised line. Sculpture of radial rows of thin spines" (Abbott, 1974: 467). All Recent species, including *Arcinella cornuta, A. arcinella* from the central Caribbean to southern Brazil, and *A. brasiliana* (Nicol, 1953), from southeastern Brazil, attach by the right valve in early growth stages, are pitted between rows of spines, and are nearly equivalve (Nicol, 1953). In contrast, fossil species of *Arcinella* have a wider range of morphologies and sculptures and may lack a lunule, may lack spines, and/or may be strikingly inequivalve. J. Gibson-Smith & W. Gibson-Smith (1979) provided a review of the western Atlantic species.

Arcinella cornuta Conrad, 1866
Figure 13B

Arcinella cornuta Conrad, 1866: 105; Abbott, 1974: 467, pl. 21, fig. 5400; J. Gibson-Smith & W. Gibson-Smith, 1979: 18, pl. 3, figs. 13–15.
Chama arcinella Linnaeus – Tuomey & Holmes, 1856: 22–23, pl. 7, figs. 4–6; Mansfield, 1916, pl. 113, figs. 11, 12.
Echinochama arcinella (Linnaeus, 1767) – Dall, 1903: 1405–1406; Mansfield, 1932: 92–93: pl. 18, figs. 1, 4.
Pseudochama (*Echinochama*) *arcinella* (Linnaeus) – Gardner, 1926: 94–95, pl. 17, figs. 14–16.
Echinochama arcinella cornuta (Conrad) – Pilsbry & McGinty, 1938: 78–79, pl. 7, fig. 7.
Echinochama cornuta (Conrad) – Nicol, 1952c: 809–810, pl. 118, fig. 2, pl. 119, fig. 7.

Type Locality

Pliocene, Royal Landing, Waccamaw River, South Carolina (Tuomey & Holmes, 1856).

Description

Large, quadrate, equivalve, with a pronounced lunule, and typically with 7–9 radial rows of large spines.

Distribution

Middle Miocene, Shoal River Formation, western Florida. Lower Pliocene, Goose Creek Formation and Raysor Marl, South Carolina; *Ecphora* zone, Jackson Bluff Formation, western Florida; Tamiami Limestone, southern Florida. Middle Pliocene, Duplin Formation, North and South Carolina; *Cancellaria* zone, Jackson Bluff Formation, western Florida; Pinecrest beds, southern Florida. Upper Pliocene, Waccamaw Formation, North and South Carolina; Nashua Formation, northeastern Florida; Caloosahatchee Formation, southern Florida. Recent, Cape Hatteras to Florida and Texas to northern Yucatan, Mexico.

Discussion

Arcinella cornuta differs principally from the more southern *A. arcinella* in having fewer spine rows across the posterior half of the shell. *Arcinella cornuta* from shallow, high energy environments have stubby spines; specimens from deep, quieter waters may develop strikingly long, thin, recurved spines. The species is remarkably long-lived, ranging from the Middle Miocene to Recent. No specimens were recovered during the

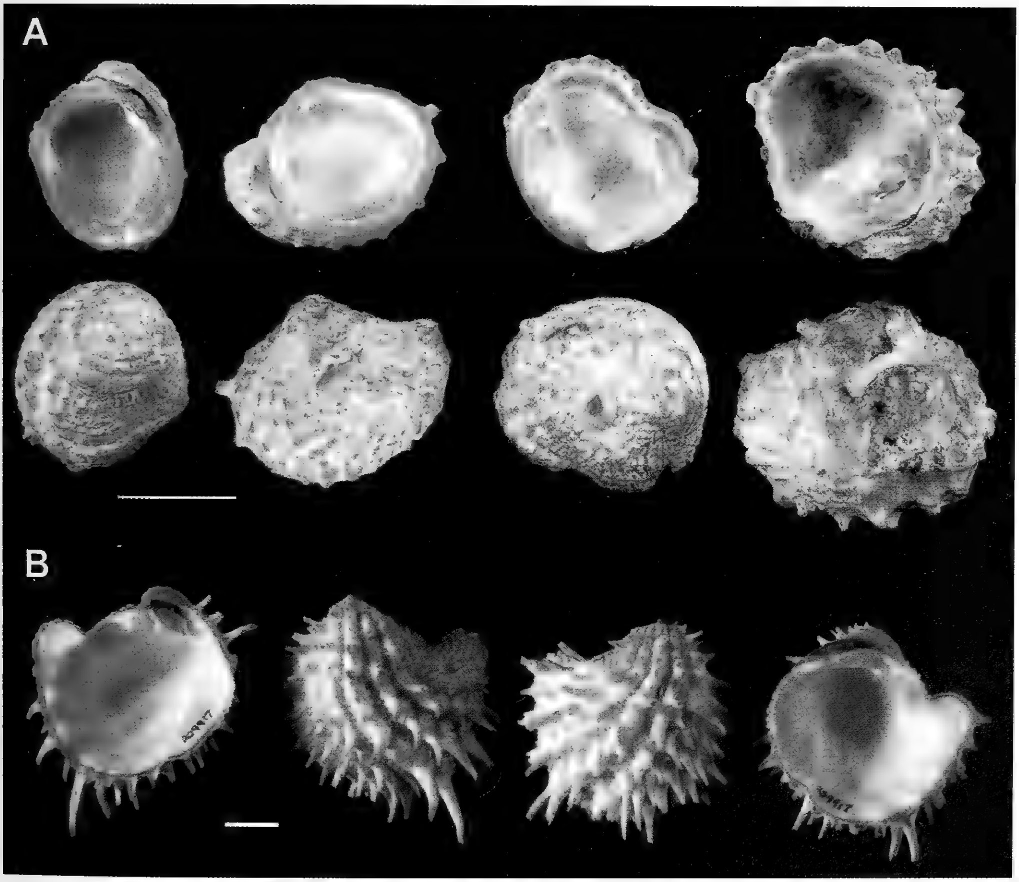

FIG. 13. Chamidae. A: *Chama sarda* deeply cupped form, right and left valves, ballast, Bahia, Brazil (ANSP 84720, photographs courtesy of Paul Callomon); B: *Arcinella cornuta,* right and left valves, Bahia Honda Key, Florida, collected live on ocean side (AMNH 209917). Scale bars = 10 mm (A–B).

Bivalve Workshop, but it is well documented from the Florida Keys (Mikkelsen & Bieler, 2000). The J. Gibson-Smith & W. Gibson-Smith (1979: 18) reference to *A.* (*Nicolia*) *cornuta* in their figure caption to Plate 3 was a lapse with no bearing on the affinity of the species. Nicol (1952c) found one left-attached shell among over 1,000 normal specimens.

Dubious or erroneous reports of *Chama* and *Pseudochama* species from the western Atlantic Ocean

Chama lobata Broderip, 1835, is a large, trapezoidal species based on syntypes he labeled "Nevis Island, Leeward Island, West Indies". Tryon (1872) repeated this locality information. Reeve (1847b) figured a specimen of this species and stated; "Mr. Broderip has recorded the 'Island of Nevis, West Indies' as the habitat of this very characteristic species; this must surely be an error for there are several well-authenticated specimens in the British Museum, brought from China by John Reeves, Esq. and I cannot learn that it has been received from any other locality." Lamy (1928) and Matsukuma (1996: 34, 45, figs. 16a–b) noted the original locality data and confirmed Reeve's correction.

Chama lazarus Linnaeus was listed as being from the Carolinas by Kurtz (1860). This record is typical of a common misidentification in nineteenth century literature.

Clessin (1889: 30) reported *Chama rubea* Reeve, 1847, from the Gulf of Mexico. Lamy (1928: 318–319) decided that Clessin's figures included not only true *C. rubea* Reeve from the Philippines but also a specimen of *C. producta* Broderip, 1835. Lamy noted that *C. producta* Broderip was a Pacific species, in contrast to the locality given by Clessin (1889).

Clessin (1889: 38, pl. 16, figs. 3, 4) reported *Chama cristella* Lamarck, 1819, from Puerto Rico. Lynge (1909) said that the Clessin Puerto Rico specimen was not *C. cristella*.

Vanatta (1914) reported *Chama lingua-felis* Reeve, 1847, from a Pleistocene deposit near Sierra Nueva, Dominican Republic. This record is not *C. lingua-felis* Reeve, described from the Recent of Guimaras, Philippines. Peile (1926: 96) said that *C. lingua-felis* as recorded by Rice (1884) from Bermuda was probably a juvenile *C. macerophylla*.

Chama coralliophaga in the index for Maury (1917) referred to *Coralliophaga coralliophaga* (Gmelin, 1791).

Chama crassa Chenu, 1846 (pl. 5, fig. 3) is a Recent taxon with no locality data. (Chenu figured Recent taxa, including *C. crassa* in color, and fossil taxa in black and white – Gary Rosenberg, e-mail, 25 March 2003.) The listing of *Chama crassa* Chenu as a Florida fossil in Kennedy et al. (1970: 391) undoubtedly is a lapse for *C. crassa* Heilprin, 1886, and both are junior homonyms of *C. crassa* Smith, 1817. *Chama crassa* Heilprin, 1886, was renamed *C. heilprini* by Nicol (1953).

DISCUSSION

Although the present molecular results are limited, they allow drawing some preliminary conclusions. Both the nuclear ITS sequences and the mitochondrial ribosomal sequences support the same basic topology. All trees show four distinct sequence clusters, the *Chama* species from the Seychelles, the *C. macerophylla* group, *C. florida*, and the *C. congregata–C. sarda–C. inezae–C. radians* group. *Chama congregata* is polyphyletic and also shows different alleles of ITS elements in one individual. The difference between these two alleles is greater than that between *C. sarda* and *C. congregata* 624 1b indicating that the origin of the allelic difference predates the speciation. The one sequence from *C. radians* clusters with one of the *C. congregata* sequences and they form the sister group to *C. inezae*. This suggests that the genus *Pseudochama* as defined by attachment pattern is polyphyletic, but additional sequence data are needed to confirm this tentative result.

The presence of different alleles of ITS elements in a single specimen was reported for several species of the vetigastropod genus *Haliotis* by Coleman & Vacquier (2002). Our report of allelic differences in *Chama congregata* is the first demonstrated case for the Bivalvia, but not unique for the Mollusca. Gene trees and species trees may not be identical due to incomplete lineage sorting, which will complicate phylogenetic reconstructions. The significance and impact on phylogenetic reconstructions remain to be determined by a broad assessment of this feature in chamids.

Bayer (1943) provided the most recent review of Recent *Chama* and *Pseudochama* in the western Atlantic Ocean, and he did not include fossil taxa. Dall (1903) was the last to review fossil species. Subsequent authors have doubled the number of nominal fossil species. We intend to publish a review of the fossil taxa in a separate paper. Including Miocene to Recent taxa, there are eighteen species of *Chama* and nine species of "*Pseudochama*" in this region (Tables 3–6). Ten species of *Chama* are known only from the fossil record, with *C. chipolana* Dall, 1903; *C. strepta* Woodring, 1982; *C. berjadinensis* F. Hodson, 1927; *C. paschuali* Brunet, 1986; *C. caimitica* Maury, 1917; *C. involuta* Guppy, 1873; *C. heilprini* Nicol, 1953; *C. emmonsi* Nicol, 1953; and *C. willcoxii* Dall, 1900, from the Neogene and *C. iudicai* Pastorino, 1991, from the Pleistocene. Additionally, *C. emmonsi* has one doubtful record from the Recent. Five species, *C. congregata*, *C. macerophylla*, *C. florida*, *C. sinuosa*, and *C. radians* are known from both the fossil record and the Recent. Three species, *C. lactuca, C. sarda*, and *C. inezae* are known only from the Recent.

Nine species of *Pseudochama*, *P. draconis* (Dall, 1903); *P. buchivacoana* (F. Hodson, 1927); *P. corticosaformis* (Weisbord, 1929); *P. lazai* Brunet, 1986; *P. quirosana* (F. Hodson, 1927); *P. scheibei* (Anderson, 1929); *P. riocanica* (Maury, 1917); *P. corticosa* (Conrad, 1833); and *P. caloosana* (Dall, 1903) are known only from the Neogene fossil record.

In the genus *Pseudochama*, many species do not have obvious phylogenetic affinities with other fossil or Recent taxa from the region. *Pseudochama corticosa* and *P. caloosana* do not appear to be closely related to *C. radians*. Lineages are lacking.

The taxa described from the Neogene of Panama, Venezuela, Argentina, Colombia, and the Dominican Republic (*Chama strepta*, *C. berjadinensis*, *C. paschuali*, *C. caimitica*, *Pseudochama buchivacoana*, *P. corticosaformis*, *P. lazai*, *P. quirosana*, *P. scheibei*, and *P. riocanica*), are in need of further study, more detailed morphological descriptions, and more precise stratigraphic data.

CONCLUSIONS

The species *Chama congregata*, *C. macerophylla*, *C. florida*, *C. sinuosa, C. radians*, *C. sarda*, and *C. inezae* were collected during the International Marine Bivalve Workshop held in the Florida Keys, U.S.A., 19–30 July 2002. Mikkelsen & Bieler (2000) also reported *C. lactuca* and *Arcinella cornuta* from the Florida Keys.

The genus-level characters cited by Matsukuma (1996), particularly soft anatomy, prodissoconch and hinge structure, need further testing among taxa in this region. Prodissoconch characters overlap to some degree in western Atlantic species historically assigned to *Pseudochama* and *Chama*. Based on the small prodissoconch and on equal numbers of right-attached and left-attached specimens, *P. inezae* Bayer, 1943, is reassigned to the genus *Chama*. *Chama inezae* (Bayer) is the first Recent species reported from the western Atlantic Ocean with a roughly 50:50 ratio of right-attached to left-attached specimens. *Chama radians* Lamarck is returned to the genus *Chama* based on morphologic, hinge, and ITS and 16S rRNA sequence data. *Chama congregata* appears to include multiple species based on morphological and molecular data. One specimen of *C. congregata* had two alleles of ITS elements, the first demonstrated case for the Bivalvia of ITS allelic differences within an individual. Molecular phylogenetic reconstructions containing *C. congregata* will be complicated because incomplete lineage sorting could cause differences between gene trees and species trees. *Chama sarda* also appears to include multiple species based on morphological data. Additional morphological and molecular study is needed for populations of both species.

Western Atlantic chamids are taxonomically challenging. Our study underscores the necessity of reviewing both the fossil and the Recent literature, and the necessity of synthesizing morphological and molecular data.

Several taxa require further population analyses across a broad range of distribution in space and time. These include the Recent taxa *Chama congregata*, *C. sarda*, *C. radians*, and the more obscure forms described by Reeve (1846–1847). Such studies should clarify whether odd morphologies, named varieties and subspecies, and various synonyms represent variation along a continuum or stand apart as separate species.

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SIZE AT FIRST MATURITY, OOCYTE ENVELOPES AND EXTERNAL MORPHOLOGY OF SPERM IN THREE SPECIES OF LUCINIDAE (MOLLUSCA: BIVALVIA) FROM FLORIDA KEYS, U.S.A.

Gregorio Bigatti[1], Melita Peharda[2] & John Taylor[3]

ABSTRACT

Gonads in the tropical lucinid bivalves *Ctena orbiculata, Codakia orbicularis*, and *Lucina pensylvanica* are located in the cephalopodial mass above the foot and behind the gills. Age estimates for *Lucina pensylvanica* suggest that individuals less than one year old are immature, as also is *C. orbicularis*, and that both males and females mature at two years. For *Ctena orbiculata,* we have no age data, but we consider that this species may also have early development. In July 2002 when water temperatures were high, mature individuals of all three species were spawning or in resorption, and oocyte envelopes were present. Parasites were found in the digestive diverticula of *C. orbiculata* and *L. pensylvanica*. External ultrastructure of the spermatozoon shows differences between the three species. *Codakia orbicularis* and *L. pensylvanica* have a long-headed spermatozoa, whereas *Ctena orbiculata* has a middle-size head. *Codakia orbicularis* possesses a flagellum with a lateral undulating membrane, absent from the two other species.

Key words: Lucinidae, reproduction, oocytes, sperm.

INTRODUCTION

The Lucinidae is the most diverse and geographically widespread of the bivalve families possessing chemoautotrophic sulphide-oxidising bacteria (Distel, 1998). Species live in a wide variety of marine habitats ranging from intertidal mangrove muds to hydrothermal vents, and the family has a long and rich fossil history (Taylor & Glover, 2000). Many tropical lucinids live in close association with shallow water seagrass beds and are particularly diverse in the Florida Keys area, where 21 species have been recorded from all depths and habitats (Mikkelsen & Bieler, 2000). Of these, ten species were found living in the shallow water habitats of the Middle Keys sampled during the International Marine Bivalve Workshop (IMBW) in 2002 (Mikkelsen & Bieler, 2004). Three species, *Ctena orbiculata* (Montagu, 1803), *Codakia orbicularis* (Linnaeus, 1758), and *Lucina pensylvanica* (Linnaeus, 1758) were sufficiently abundant and present in a range of size classes to attempt an investigation of some aspects of their reproductive biology. The objectives of this study were to determine the size of maturity, the presence of oocyte envelopes and to describe the external morphology of their sperm. Additionally, the maturation sizes of *L. pensylvanica* were related to the age of the individual as estimated from acetate peel replicas of sections through the shell.

Previous research on Lucinidae has primarily focused on aspects of functional anatomy, chemosymbiosis and evolution, and there are few studies of their reproductive biology. The exception is *Codakia orbicularis,* one of the most studied species. General aspects of the reproductive biology of this large, edible clam have previously been studied by Alatalo et al. (1984), Berg & Alatalo (1984), and Prieto et al. (1999), larval development by Gros et al. (1997), and sperm morphology by Mouëza & Frenkiel (1995). The potential role of chemosynthesis in molluscan mariculture has also been investigated for this species (Berg & Alatalo, 1984).

Many invertebrates possess oocyte envelopes with different layers. An inner protein-polysaccharide layer (vitelline envelope) can be formed by the Golgi apparatus of the oo-

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cyte itself and deposited at the outer surface by exocytosis (Jong-Brink et al., 1983; Huebner & Anderson, 1976). When present, a thick jelly coat covers the outer surface of the vitelline envelope, and appears as a loose association of striated fibrous material (Hodgson & Eckelbarger, 2000). Follicle cells are also believed to produce secondary compounds or cellular egg envelopes around oocytes (Eckelbarger, 1994). In *Codakia orbicularis*, the jelly coat that covers the oocyte is formed by an inner layer (the vitelline envelope) and an outer layer (Gros et al., 1997). In another lucinid, *Phacoides pectinata* (Gmelin, 1791), this jelly coat is made up of glycoproteins and proteoglycans (Frenkiel et al., 1997), synthesized by the oocyte during vitellogenesis (Frenkiel, unpubl.). No information exists concerning the composition and formation of oocyte envelopes in *Ctena orbiculata* and *L. pensylvanica*, and the reproductive biology of these species has received no attention probably due to their smaller size and lack of commercial importance.

MATERIAL AND METHODS

The lucinid bivalves *Codakia orbicularis, Ctena orbiculata* and *Lucina pensylvanica* were collected between July 2002, at different localities in Florida Keys, USA, during the International Marine Bivalve Workshop 2002. Sampled habitats included sandy bottoms at 6 m depth (sampled by scuba diving) and shallow subtidal sandy substrata colonized by the seagrasses *Thalassia*, *Halodule, Syringodium* and *Halophila*. Most of the seagrass-covered sediments were anoxic with hydrogen sulphide concentrations detectable by smell. Bivalves were collected by digging and sieving sediment through 2 mm mesh screens. Sampling localities included a number of oceanside intertidal and shallow water sites in the Middle Keys (IMBW-FK-622, 628, 635, 638, 642, 647, 649; Mikkelsen & Bieler, 2004: fig. 1 for map). *Ctena orbiculata* was most abundant at inshore bayside sites in sparsely vegetated sand patches; *Codakia orbicularis* at several oceanside sites with thick *Thalassia* growths, and *Lucina pensylvanica* was found commonly only at oceanside Station IMBW-FK-642 on Lower Matecumbe Key in shallow sand on rock.

Twenty individuals of each species were sexed macroscopically observing the texture of gonads (females had granulose and males homogeneous texture) and their shell parameters measured. A preliminary scale of gonad maturation was compiled from light microscope observations of fresh tissue, and this was used for comparison with thin sections of gonads prepared later. External gonad morphology was described from fresh animals. Samples of gonad tissue were fixed in Bouin´s solution for 48 h and stored in 70% alcohol. In order to determine the first maturation stage and the presence of oocyte envelopes, sections of the gonads were cut at 6 μm with a Leitz microtome and stained with hematoxilin and eosin. We use the term oocyte or egg envelope for the inner layer and jelly coat for the outer layer of the oocyte. For scanning electron microscopy (SEM) of spermatozoon ultrastructure, pieces of male gonad were cold fixed in 2.5% glutaraldehyde solution in Sorenson's phosphate buffer. Slices of gonad were then cut with a razor blade, dehydrated through an ascending acetone series, critical point dried, sputter coated with gold, and examined by scanning electron microscopy (SEM) with a Philips XL30 field emission SEM operated at 5kV.

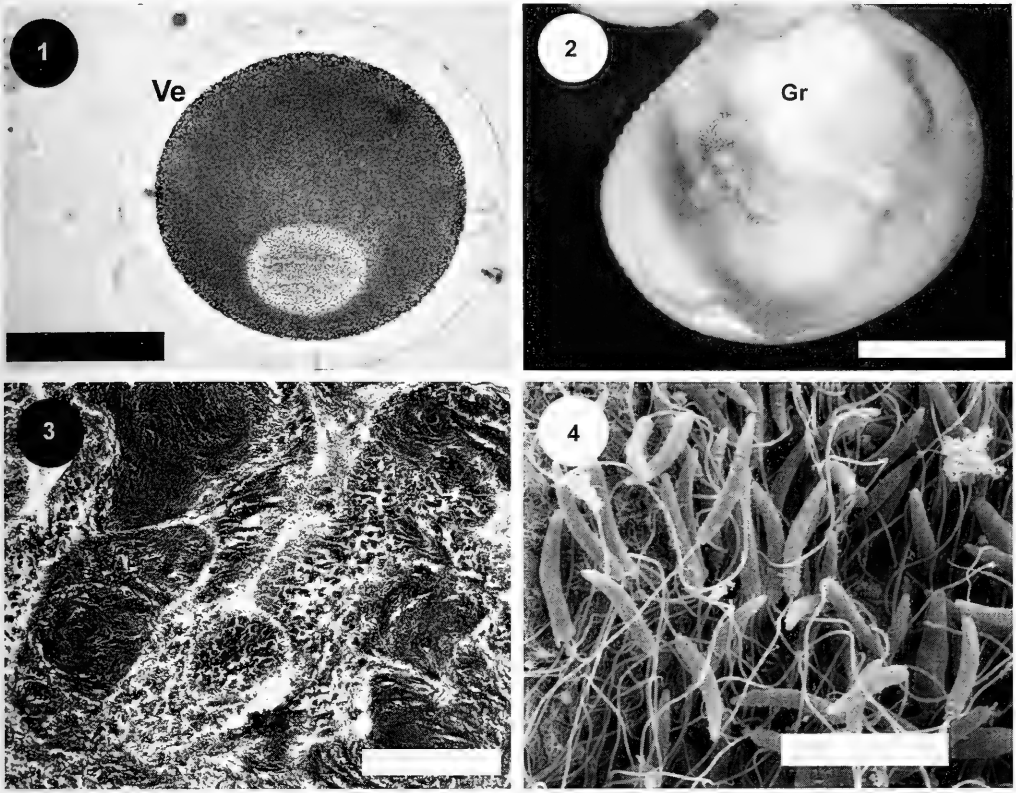
For age determination, 20 dry shell valves of *Lucina pensylvanica* were embedded in MET20 resin (Struers Ltd), sectioned from the umbo to the ventral edge, ground, polished, and etched for 20 min in 0.01M HCl and acetate peel replicas prepared (Richardson, 2001). The age of each shell was estimated by three observers using the major growth lines present in acetate peels of the umbonal region and the outer prismatic shell layer (Richardson, 2001). These major growth lines were treated as annual lines by comparison with the results of a study of *Codakia orbicularis* from the Bahamas by Berg & Alatalo (1984). Data were fitted to the von Bertalanffy growth function $L_t = L_\infty(1-e^{-k(t-t0)})$ using the Fisheries Programme "Fisat".

Voucher specimens of the species studied are deposited in the Mollusca collections of the Department of Zoology, The Natural History Museum, London.

RESULTS

Ctena orbiculata

Specimens collected measured between 5.5 mm and 13.8 mm in length. No gonad development was observed in individuals smaller than 5.6 mm. All males larger than 5.6 mm

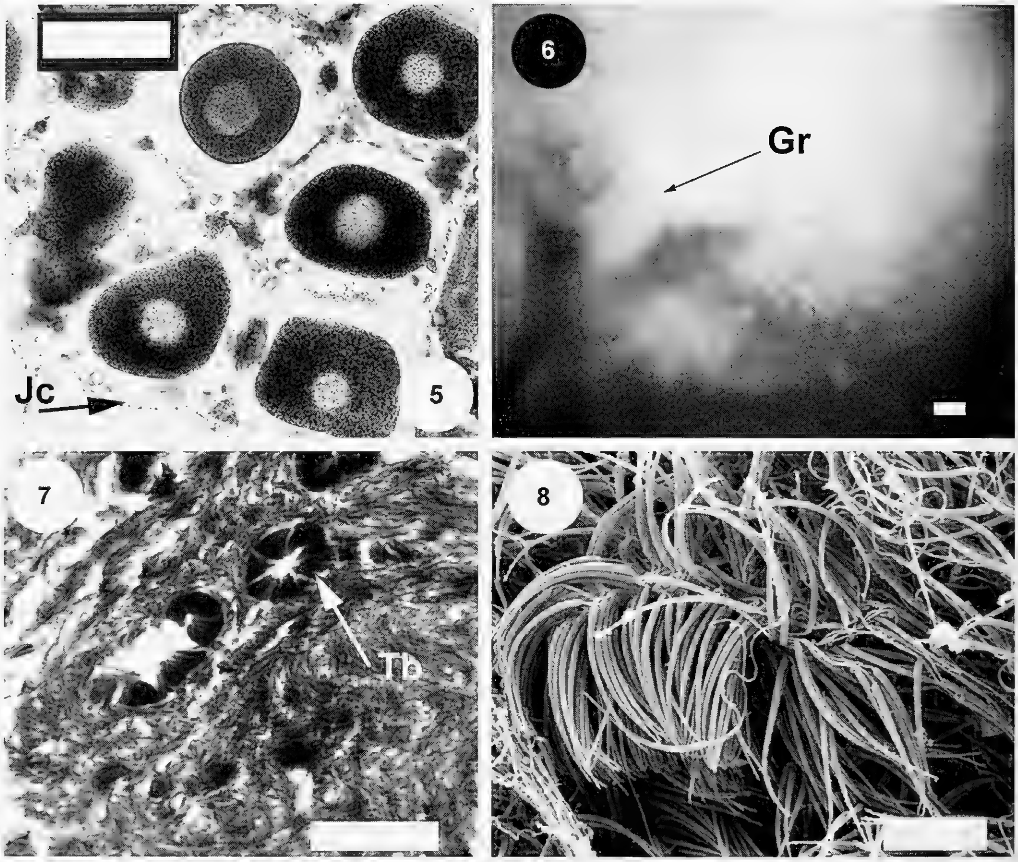


FIGS. 1–4. *Ctena orbiculata*. FIG. 1: Living mature oocytes covered by the vitelline envelope. Scale bar = 50 µm; FIG. 2: Female gamete release. Scale bar = 3 mm; FIG. 3: Sperm in follicles. Scale bar = 100 µm; FIG. 4: SEM image of sperm. Scale bar =10 µm. Gr, gamete release; Ve, vitelline envelope.

were mature. The spermatozoa were contained in follicles and orientated in relation to the lumen of the follicle (Fig. 3). Females less than 7.1 mm in length were immature; oocytes of individuals of 7.1 mm had a mean diameter of 20 mm (SD = 1.8) and no envelope was present. Developing oocytes were present in specimens between 7.2 mm and 7.8 mm length with maturity reached at 7.9 mm. Some individuals were spawning at this size, but no resorption was observed. The maximum oocyte diameter measured was 137.5 mm, with an oocyte envelope width of 10 mm, with no jelly coat covering it. When the gonad is ripe, an egg mass full of gametes forms a thin layer, that covers the ctenidia and sometimes all of the pallial cavity (Fig. 2). The egg mass has no defined organization. At this stage, the oocytes are sticky and covered by a jelly coat and have a total mean diameter of 360 µm (Fig. 1). This corresponds to the time of gamete release and possibly the oocytes are retained by mucus in the pallial cavity until fertilization. After release, the oocytes are covered by the jelly coating and this probably provides protection to the egg until fertilization occurs. No evidence of either protandry or simultaneous hermaphroditism was found in this species.

Male gametes are released as sperm strings comprising hundreds of sperm attached to each other at the head. SEM images (Fig. 4) show that sperm cells are relatively short-headed, with a long, cylindrical flagellum. The heads are cylindrical and tapering, slightly curved with a visible, short acrosome. Heads have a mean length of 7.5 µm and a width of 1–1.2 µm, with the acrosome about 0.6 µm long and the mid piece 0.9 µm. The tail measures around 28 µm, giving a total length for the sperm cell of around 36 µm.

Parasites were observed in the digestive diverticula lying adjacent to the gonad follicles

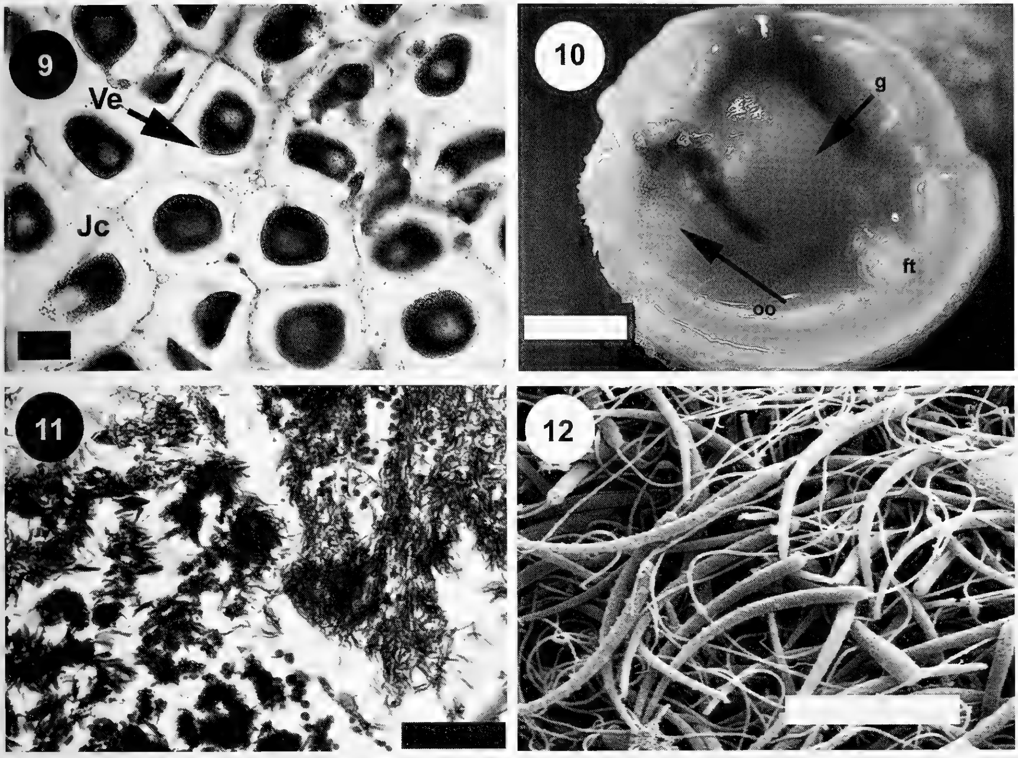


FIGS. 5–8. *Codakia orbicularis*. FIG. 5: Mature oocyte with jelly coat. Scale bar =100 µm; FIG. 6: Female gamete release. Scale bar =500 µm (arrow shows the finger-shaped mass); FIG. 7: Sperm ready to spawn. Scale bar = 50 µm; FIG. 8: SEM image of sperm. Scale bar = 10 µm. Gr, gamete release; Jc, jelly coat; Tb, tubules.

(Fig. 13). They are probably cercaria of the digenean family Monorchiidae (D. Gibson, personal communication). We also found yellow granules in the digestive diverticula, fluxing to the gonads.

Codakia orbicularis

The bivalves sampled measured between 11.3 mm and 64.8 mm shell length. Individuals less than 12.5 mm were immature, while one individual of 12.6 mm had started to form follicles. Males larger than 13.2 mm had begun to mature with some sperm visible. All males larger than 25.9 mm were mature. In individuals larger than 46 mm, sperm were observed in tubules ready to spawn (Fig. 7). All females sampled had already spawned with visible oocyte resorption. Females larger than 46.8 mm had oocytes of 100 µm average diameter (SD = 5.8), covered by an oocyte envelope of about 7.5 µm thick. The largest male sampled was 47.1 mm in length. Unfortunately, no larger-sized *Codakia* were available to determine if protandry occurs in this species. No hermaphrodites were found. Release of female gametes occurs in a mucous mass held within the mantle cavity similar to that of *Ctena orbiculata*, but in *C. orbicularis* it is finger shaped (Fig. 6). At this stage, the oocytes are sticky and slightly negatively buoyant. Upon release from the gonads, oocytes are spherical and covered by a 50 µm thick jelly coat that, together with the oocyte envelope, forms the external envelope (Fig. 5). Further expansion of the envelopes results in an egg with a total diameter of around 200 µm.



FIGS. 9–12. *Lucina pensylvanica*. FIG. 9: Mature oocyte with irregular jelly coat. Scale bar = 100 µm; FIG. 10: Ova release. Scale bar = 5 mm; FIG. 11: Mature sperm in gonads. Scale bar = 50 µm; FIG. 12: SEM image of sperm cells. Scale bar = 10 µm. ft, foot; g, gonad; Jc, jelly coat; Oo, oocyte; Ve, vitelline envelope.

The sperm have long, slender, tapering, curved heads (Fig. 8) with a long flagellum that possesses a narrow, lateral, undulating membrane to either side (Fig. 14). The head measures around 14–15 µm in length with a width of 0.8 µm at the posterior end. The lengths of the flagella were difficult to measure in our preparations, but were at least 25 µm long, with the undulating membrane having a width of 0.42 µm.

Lucina pensylvanica

Individuals sampled measured between 12.8–42.6 mm shell length. No gonad development was observed in individuals of less than 13 mm. Sexual differentiation with incipient follicular formation begins at a size of 13.8 mm (specimens of one to two years old). Individuals larger than 15.9 mm had well-developed gonads; males were all mature and females exhibited different maturity stages. Male gametes are released as sperm strings comprising hundreds of sperm attached at the head as in *Ctena orbiculata* (Fig. 11). Females begin maturation at a shell length of 17.7 mm and reach maturity at around 26.6 mm. Individuals having oocytes with a mean diameter of 130 µm (SD = 6.7) with an oocyte envelope of approximately 10 µm were classified as mature females. Release from the gonads occurs as a finger-shaped mucous mass containing the ova, similar to that of *Codakia orbicularis* (Fig. 10). After release from the gonad, oocytes are spherical with an irregular jelly coat (Fig. 9). This jelly coat is approximately 47 µm thick, covering the ova, which has an external maximum diameter of 245 µm.

Sperm have long, curved, tapering heads (Fig. 12), with a long flagellum without a lateral membrane. The mean length of the head

FIG. 13. Parasite found in the digestive diverticula of *C. orbiculata* and *L. pensylvanica*. Scale bar = 100 µm.

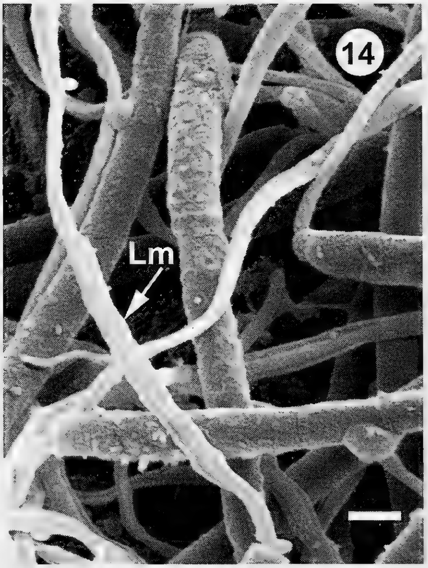


FIG. 14. SEM image showing the lateral undulating membrane (Lm) of the flagellum of *C. orbicularis*. Scale bar = 1 µm.

is 15.5 µm and the width at the posterior end is 1.1 µm. Flagella measured around 33 µm in length. Cercaria similar to those of *Ctena orbiculata* were found as parasites in the digestive diverticula adjacent to the gonad follicles.

From the analysis of major growth halts observed in shell sections, the oldest individual studied had attained an age of 5 years. Analysed shells showed individual variations in growth (Taylor et al., 2004). The asymptotic shell length was 38.37 ± 9.36 mm (Fig. 15).

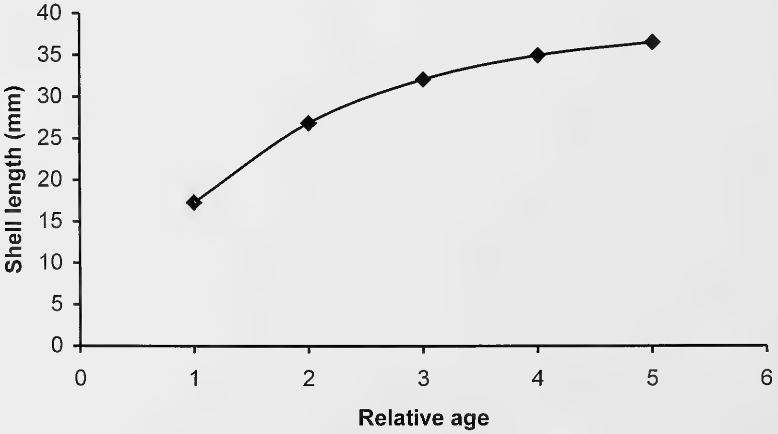


FIG. 15. Growth curve for *Lucina pensylvanica* fitted using the Von Bertalanffy growth equation: $L=38.37\ (1-e^{-0.60t+0.37})$.

DISCUSSION

It should be emphasised that this was a very short-term study conducted over a period of only two weeks. Nevertheless, the results show that interesting similarities and differences exist in the reproductive biology among the three coexisting lucinid species.

For mature individuals of the three lucinid species studied, the gonads were ripe, spawning or in resorption in July 2002. This spawning period corresponds to the hottest time of the year, and surface water temperatures measured by the National Data Buoy Center (LONF1, Long Key, Florida) ranged between 29–30ºC for the period 20–30 July. At the sampling sites, temperatures reached around 35°C in water depths of between 0.5–1 meter.

According to Berg & Alatalo (1984), the annual size classes of *Codakia orbicularis* at Grand Bahama Island are 12, 29, 42, 52 and 63 mm for years 1 to 5, respectively. By comparison with these results, our data suggest that *C. orbicularis* from the Florida Keys are immature at less than one year old, with males maturing between 1 and 2 years and females spawning at 3 years. In the Bahamian *Codakia*, shell growth was not continuous throughout the year, as evidenced from sharp growth rings on the external surface of the shell, and the number of these external growth rings coincided with annual year classes predicted from the von Bertalanffy growth equation (Berg & Alatalo, 1984). Spawning and recruitment of *C. orbicularis* occur over a long period, with variation in individual growth rates, and at Grand Bahama Island growth rates decreased during winter months. Follicular development in *C. orbicularis* was first observed at a shell length of 19.8 mm, corresponding to an age of 1.5 years, and the smallest animal with fully developed gametes measured 25.4 mm (Berg & Alatalo, 1984*).* In our study, we were unable to record the size of first maturity for females, but one individual of 12.6 mm length was observed with incipient follicular formation. According to Berg & Alatalo (1984), this corresponds to an individual of about one year old. They also recorded three hermaphrodites from a total sample of 224 bivalves analysed. We recorded no hermaphrodites in our Florida Keys sample, but all individuals examined less than 46.6 mm long were males, with the larger sizes all females. This result suggests protandry for this population, but more data are needed for confirmation. The observation from the Bahamas that most animals greater than 30 mm were ripe during the summer months indicates the same maturity pattern for this species as at Florida Keys, for we found maturity at sizes above 25.9 mm length. Animals within the population at Gold Rock Creek, Bahamas, did not spawn completely, nor simultaneously, but appeared to continue spawning over a period of at least a month (Berg & Alatalo, 1984). The spawning season for *C. orbicularis* in Bahamas (Alatalo et al., 1984) and in Venezuela, Sucre State (Prieto et al., 1999), agrees with our results for July 2002 in Florida Keys. In our case, we found spawned females towards the end of July, with oocyte resorption visible, but only in individuals greater than 46.8 mm. Observations on animals of both smaller and larger sizes are necessary to complete this study.

Parasites observed in the digestive diverticula of *Ctena orbiculata* and *Codakia orbicularis* resembling the general body form of *Cercaria caribbea* LXIV of Cable (1963) were previously recorded from the lucinid bivalve host *Ctena pectinella*. Cable suggests that the adult is a species of *Proctotrema* that occurs in the porkfish *Anisotremus virginicus*. The cercaria were observed only *in vivo*, and further studies are needed to confirm this. The yellow granules found in the digestive diverticula of *Ctena orbiculata* could be sulphur granules, related to the chemoautotrophic habits of this species.

Our age estimates for *Lucina pensylvanica* suggest that individuals less than one year old are immature, as in *C. orbicularis*, and that both males and females mature at two years. For the smallest species, *Ctena orbiculata,* we have no age data, but from the size range we consider that this species may also have early development. Selection for rapid gonad development could assure the recruitment of new spat when environmental conditions are favourable. Unfortunately, no further data is available concerning reproductive biology of *Ctena orbiculata* and *L. pensylvanica.*

Another lucinid from the western Atlantic, the large *Phacoides pectinata*, a protandric species inhabiting mangrove swamps and reducing mud, has permanently mature gonads (Frenkiel et al., 1997). This reproductive strategy, which, in addition to the sulphur oxidising bacterial endosymbionts and high bacteriocyte haemoglobin concentration, is considered an adaptation to a high-stress environment. Resorption of oocytes and recovery of metabolites through the follicular cell lysosomal function appears to be the most efficient means to minimize the metabolic cost of maintaining the state of maturity. In the cases of *Ctena orbiculata* and *L. pensylvanica*, resorption of oocytes was found, suggesting the same reproductive strategy in these species also living in similar hypoxic habitats. In the case of *C. orbiculata*, we observed only females spawning, but larger sizes were not found. Probably the same strategy occurs in this species, as a possible adaptation to reducing substrata.

We consider the oocyte envelope as a vitelline envelope. The composition and location of its synthesis is still unknown for *Ctena orbiculata* and *Lucina pensylvanica*. For *Codakia orbicularis,* Gros et al. (1997) considered that the jelly coat is made up of glycoproteins and proteoglycans synthesised by the oocyte itself during vitellogenesis. After spawning, it is swollen by hydration of the proteoglycan components. In *Phacoides pectinata*, the same jelly coat is observed and the glycoproteins are likely to support recognition receptors for sperm (Frenkiel et al., 1997). In bivalves from Antarctica, such as *Laternula elliptica* (King & Broderip, 1832), a similar oocyte envelope is observed, allowing storage of mature oocytes for the whole year until environmental conditions are favourable (Bigatti et al., 2001). This vitelline envelope and the jelly coating protect the embryos of *Codakia orbicularis* in the veliger stage (Alatalo et al., 1984) and are digested by enzymes from the larva (Gros et al., 1997). This is another possible adaptive response to a high-stress environment. For *Ctena orbiculata* and *Lucina pensylvanica*, studies concerning oogenesis and the origin and composition of oocytes envelopes are needed, but as they are members of the same family and live in similar environments, a similar pattern could be expected.

For the Florida lucinids, our observations of the release of gametes adhering within the pallial cavity suggests that these species retain oocytes until fertilization. However, this observation does not suggest the existence of a brood chamber, such as occurs in *Ostrea* spp. (Morriconi & Calvo, 1979), because no embryos or divided cells were identified. Probably the oocytes were recently spawned when we observed them. This could be another adaptation that enhances reproductive success after the eggs are released to the exterior environment.

Electron microscopy of molluscan sperm has provided an important set of characters for phylogenetic studies (Healy, 1995, 1996). Most detail is provided by TEM studies, but scanning microscopy of external features reveals a set of morphological characters useful for generic and specific differentiation. Our observations show that *Lucina pensylvanica* and *Codakia orbicularis* have similarly proportioned large sperm with long, curved, tapering heads, but the latter differs in having an undulating membrane to the flagellum. By contrast, *Ctena orbiculata* sperm have much shorter and less tapering heads.

The length of the spermatozoa of *Lucina pensylvanica* and *Codakia orbicularis* is comparable with that of *Scrobicularia plana* (da Costa, 1778) (Souza et al., 1989), which is the longest described spermatozoon in bivalves. TEM studies show that *Codakia orbicularis* sperm have a short acrosome (Mouëza & Frenkiel, 1995), as does *Codakia punctata* (Linnaeus, 1758) (Healy, 1995) and *Loripes lucinalis* (Lamarck, 1818) (Johnson et al., 1996). It has been suggested by Mouëza & Frenkiel (1995) that occurrence of this feature, along with long tapering heads, in species having large oocytes with a gelatinous coat might be adaptations to facilitate penetration of the spermatozoa through this coating and the vitelline envelope.

The undulating lateral membrane of the flagellum in *C. orbicularis* (Fig. 14), previously described by Mouëza & Frenkiel (1995), is an unusual feature of bivalve sperm, although well-developed undulating membranes appear characteristic of corbiculid sperm (Komaru & Konishi, 1996; Konishi et al., 1998). Mouëza & Frenkiel (1995) suggest that the structure is somehow related with sperm locomotion prior to fertilization. The sperm of too few lucinid species has been studied to evaluate the possible systematic significance of this feature.

Finally, longer-term studies of the reproductive biology of *Lucina pensylvancia* and *Ctena orbiculata* are necessary to confirm and expand our preliminary findings based on the two-week survey. Both of these species are abundant, but poorly studied, chemosymbiotic bivalves inhabiting the shallow waters of the Florida Keys and the populations are highly vulnerable to environmental disturbance of these fragile habitats.

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PERIGLYPTA LISTERI (J. E. GRAY, 1838) (BIVALVIA: VENERIDAE) IN THE WESTERN ATLANTIC: TAXONOMY, ANATOMY, LIFE HABITS, AND DISTRIBUTION

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ABSTRACT

Periglypta listeri (J. E. Gray, 1838), one of the largest and most distinctive western Atlantic venerids, and the only Atlantic member of the genus, is redescribed based on original material from the Florida Keys, museum specimens, and literature records. Conchologically, this species agrees with previously described venerids in having a well-developed escutcheon and lunule, and a hinge with three cardinal teeth in each valve. Within the genus, it is unique in having internal purplish brown coloration, and in the frequent presence of a purplish brown "hinge dot" on the anterior lateral tooth. This is the first anatomical study for any species in the genus *Periglypta*, and the most complete so far for any member of Venerinae. *Periglypta listeri* agrees with previously described venerids in most anatomical characteristics, and notably features an undulating mantle edge that can close in "zipper" fashion, tentacles at the anterior mantle edge, and branching tentacles at the tips of the unfused siphons, type B mantle fusion, type C(2) ctenidia, and a type V stomach. Although empty shells are commonly collected, *P. listeri* unusually (for venerids) lives cryptically in rubble or sand among rocks, and/or in reef settings. Thus far, the presence of an anterior lateral hinge tooth is the sole morphological feature separating the subfamily Venerinae from the closely allied Chioninae.

Key Words: Florida Keys, Mollusca, Caribbean, infaunal, clam, sanctuary.

INTRODUCTION

Veneridae is the largest marine family of bivalves, with many of the more than 500 living species forming key components in the world's clam fisheries. The nominate subfamily Venerinae currently comprises 14 genus-group taxa (e. g., *Venus, Periglypta, Globivenus, Ventricoloidea*; Keen, 1969) with more than 140 nominal extant and fossil species. Members of this subfamily live in a wide range of benthic habitats, in coarse sand, mud, or gravel between tide lines to depths over 150 m, and from temperate to tropical seas. Delimiting shell characteristics are the presence of both radial and concentric sculpture and an anterior lateral tooth in the left valve (Keen, 1969; see hinge discussion below). The nominal subfamily Chioninae, another large group comprising such genera as *Chione, Mercenaria*, and *Protothaca*, has recently been synonymized with Venerinae by some authors (Coan & Scott, 1997; Coan et al., 2000). Relationships between these and among other venerid subfamilies remain unresolved, due to a surprising paucity of comparative morphological work. Despite their relative abundance and commercial importance, only about 50 venerid species have some published anatomical data. Most publications focus on a few species traditionally grouped in the Chioninae, such as representatives of *Mercenaria* (Kellogg, 1892, 1903, 1915; Morse, 1919; Jones, 1979), *Chione* (Kellogg, 1915; Jones, 1979; Narchi & Gabrieli, 1980), *Timoclea* (Ansell, 1961; Narchi, 1980), *Lirophora* (Jones, 1979), *Tawera* (Burne, 1920), *Chamelea* (Odhner, 1912; Ansell, 1961), *Anomalocardia* (Narchi, 1972; Purchon, 1985), *Bassina* (Morton, 1985; Purchon, 1985), *Protothaca* (Guerón & Narchi, 2000), and *Clausinella* (Ansell, 1961). Anatomical details for members of other nominal venerid subfamilies are much sparser, with data available for individual species of Gouldiinae [= "Circinae"] (Pelseneer, 1911; Ansell, 1961; Fishelson, 2000), Cyclininae (Purchon, 1985), Dosiniinae (Thiele, 1886; Ansell, 1961; Guéron & Coelho, 1989; Fishelson, 2000); Gemminae (Morse,

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1919; Sellmer, 1967; Narchi, 1971), Meretricinae (Kellogg, 1915; Narchi, 1972; S. Gray, 1982; Narchi & Dario, 2002), Pitarinae (G. B. Sowerby II, 1854; Thiele, 1886; Pelseneer, 1911; Kellogg, 1915; Morse, 1919; Narchi, 1971; F. R. Bernard, 1982; S. Gray, 1982; Fishelson, 2000; Morton, 2000), and Tapetinae (G. B. Sowerby II, 1854; Carrière, 1879; Pelseneer, 1894, 1897, 1911, 1923, 1931; Berkeley, 1959; Ansell, 1961; Nielsen, 1963; Joshi & Bal, 1965a, b; Morton, 1985; Fishelson, 2000).

The morphological diversity of the nominate subfamily, Venerinae, remains largely unexplored, with published anatomical data restricted to *Circomphalus casina* (Linnaeus, 1758) (Ansell, 1961), *Venus verrucosa* Linnaeus, 1758 (type species of *Venus* Linnaeus, 1758, and of *Clausina* Brown, 1827; Pelseneer, 1894, 1897), and *Globivenus toreuma* (Gould, 1850) (Pelseneer, 1911). The current paper focuses on a venerine species currently classified in the genus *Periglypta* Jukes-Brown, 1914, a group not previously studied anatomically. *Periglypta listeri* (J. E. Gray, 1838), also known as "Lister's venus" or "princess venus", is the second largest Caribbean venerid species, only exceeded in shell size by *Mercenaria campechiensis* (Gmelin, 1791), which ranges from the mid-Atlantic coast to the Gulf of Mexico and extends into the Caribbean. A shallow-water species with a very conspicuous shell, *P. listeri* had at one point even been declared the type species of the genus *Venus* (Stoliczka, 1871: xvii; *Venus verrucosa* Linnaeus, 1758, was subsequently fixed as the type by ICZN Opinion 195, 1954). Empty shells of *P. listeri* are commonly collected, but living specimens are less frequently encountered, due in part to their relatively cryptic infaunal habitat in seagrass areas and algae-covered rubble near reefs.

This paper reviews the taxonomy and geographic distribution of this species, its anatomy, and life habits, based on original information from living specimens from the Florida Keys, together with a re-evaluation of existing literature and selected museum data. Comparisons are drawn with sympatric large-bodied venerids in the western Atlantic, with selected worldwide species of *Periglypta*, and with known anatomical data for the family.

MATERIALS AND METHODS

This study is part of an ongoing investigation of marine molluscan biodiversity in peninsular Florida and the Florida Keys, formally initiated by RB and PMM in 1994. Consecutively numbered stations comprising these collections are preceded by an "FK" acronym in the following text. Living animals and empty shells were collected by hand mainly during scuba diving on coral reefs and shallow-water (2–10 m) patch reefs, rubble areas, and ledges. The majority of live observations were made on specimens from the "Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), comparable to stations IMBW-FK-629 and -637 reported by Mikkelsen & Bieler (2004). Interpretations of distribution records based Henderson's *Eolis* expeditions are taken from the recent compilation by Bieler & Mikkelsen (2003).

Specimen photography used a variety of equipment and techniques. *In situ* photographs of living animals (Fig. 24) were taken using a Nikonos V underwater camera with close-up lens. Other living animals (Figs. 25, 26) were photographed in aquaria using standard 35 mm single-lens reflex or electronic cameras. Whole-valve and detail light micrography (Figs. 3–12, 31, 32) used a Microptics® micro/macro imaging system based on a high-resolution Nikon® single-lens reflex digital camera. Excised preserved tissues were prepared for scanning electron microscopy (SEM) by critical point drying and gold sputter coating, then viewed at beam acceleration voltages of 10kV on a Amray 1810 scanning electron microscope at FMNH.

For anatomical observation, specimens were relaxed by chilling in a household refrigerator assisted by the addition of magnesium sulfate crystals (Epsom salts) to their seawater supply, or in an isotonic aqueous magnesium chloride solution. Ciliary currents were studied using carmine particles. Anatomy was observed under a dissecting microscope; preserved tissues were dyed for better contrast with neutral red or methylene blue. Voucher FK specimens were fixed in 5% formalin, later transferred to 70% ethanol, and are deposited in the Field Museum of Natural History (FMNH), Chicago, and the American Museum of Natural History (AMNH), New York.

All measurements and meristics were taken from the left valve whenever possible. Shell measurements, taken with calipers or with ocular micrometer on a stereomicroscope, include: maximum height from umbo to farthest distal point on free edge, and maximum length (= width) perpendicular to axis of height. Size is expressed as shell length unless otherwise noted. Radial ribs were counted at the growth edge on the main body of the shell. For morphometric analyses (length to height ratio), 32 shells were measured and the linear regression calculated using Microsoft® Excel 2000.

Other cited repositories include:

ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania, U.S.A.
BMNH	The Natural History Museum [= British Museum (Natural History)], London, United Kingdom
BMSM	Bailey-Matthews Shell Museum, Sanibel Island, Florida, U.S.A.
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.
DMNH	Delaware Museum of Natural History, Wilmington, U.S.A.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MTD	Staatliche Naturhistorische Sammlungen, Museum für Tierkunde, Dresden, Germany
NCSM	North Carolina State Museum of Natural Sciences, Raleigh, North Carolina, U.S.A.
NTM	Northern Territory Museum of Arts and Sciences, Darwin, Australia
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, California, U.S.A.
UMML	Rosenstiel School of Marine and Atmospheric Science [= University of Miami Marine Laboratory], University of Miami, Florida, U.S.A.
USNM	National Museum of Natural History. [= United States National Museum], Smithsonian Institution, Washington, DC., U.S.A.
ZMB	Museum für Naturkunde [= Zoologisches Museum, Berlin], Humboldt-Universität, Berlin, Germany

Other abbreviations:

alc	fluid-preserved (alcohol) specimen
frag	shell fragment
juv	juvenile or subadult
LV	left valve
pair	an empty (dead) complete shell (2 valves)
RV	right valve
spm	a live-collected specimen
valve	an empty (dead) single valve

RESULTS

Veneroidea: Veneridae: Venerinae Rafinesque, 1815: 146 (as Veneridia)

Periglypta Jukes-Brown, 1914: 72

Type species, by original designation: *Venus puerpera* Linnaeus, 1758. *Periglypta* was introduced as a subgenus of *Antigona* Schumacher, 1817, by Jukes-Brown (1914: 72).

Cytherea Röding (1798), *non* Fabricius, 1794 (Diptera: Bombylidae). Type species (subsequent designation of Dall, 1902): *Venus puerpera* Linnaeus.

Periglypta listeri (J. E. Gray, 1838)

Selected synonymy:

?"pectunculus admodum crassus ..." Lister, 1687: Liber III, fig. 178 [pl. 341, fig. 178 in later editions].

[unlabelled figure] – Lamarck, 1797: pl. 378, fig. 2a–b.

Venus puerpera (2) Var. – Lamarck, 1818: 584–585 [referring to Lister (1687) and Lamarck (1797) figures; *non Venus puerpera* Linnaeus, 1771].

Venus puerpera Var. 2 – Deshayes, 1832: 1112 [referring to Lister (1687) and Lamarck (1797) figs.]; – Deshayes, 1835: 335.

Venus puerpera – Schramm, 1869: 20.

Dosina Listeri J. E. Gray, 1838: 308.

Venus listeri – Hanley, 1843, in 1842–1856: 110; – Deshayes, 1853a: 106 [distribution (Philippines, Australia) erroneous]; – G. B. Sowerby II, 1853 [in part]: 705, pl. 152, fig. 8 [excluding figs. 7, 9; distribution (Philippines, Australia) erroneous]; – Reeve, 1863: no. 14, pl. 5, fig. 14 ["Hab. Philippine Islands; Cuming" erroneous]; – Krebs, 1864: 97; – Pfeiffer, 1869: 141, pl. 8, figs. 8, 9 [distribution (Nicobares, Philippines) erroneous]; – Simpson, 1889: 64; – F. C. Baker, 1891: 47; – Cockerell, 1894: 118; – Benthem Jutting, 1927: 34; – McLean, 1936b: 119; – Dance, 1974: 263–264, fig.; – Fischer-Piette, 1975: 36–37; – Dance, 1977: 264, fig.

Venus (Periglypta) listeri – Lamy, 1929: 205.

Omphaloclathrum listeri – Mörch, 1853: 24.

Venus (Chione [Omphaloclathrum]) listeri – Römer, 1867: 32 ["Insulae Philippinae" in error].

Venus crispata – Dall, 1889: 54 [*non Venus crispata* Deshayes, 1853b].

Cytherea (Cytherea) listeri – Dall, 1902: 372.

Cytherea listeri – Dall, 1903: 1275–1276, 1279; – Maury, 1920: 103.

Antigona (Periglypta) listeri – Jukes-Brown, 1914: 72; – Warmke & Abbott, 1961: 185, pl. 38 fig. L; – Humfrey, 1975: 248, pl. 30, fig. 3.

Antigona (Dosina) listeri – Palmer, 1927: 337 [129]; – Palmer, 1929: pl. 28, figs. 2, 11; – Abbott, 1954: 404, pl. 32, fig. m; – Abbott, 1958: 129.

Antigona listeri – Weisbord, 1926: 83; – Johnson, 1934: 48; – Lermond, 1936: 6; – Clench & McLean, 1936: 166; – McLean, 1936a: 41; – Clench & McLean, 1937: 39–40; – M. Smith, 1937: 53, pl. 21, fig. 11; – M. Smith, 1940: 110, fig. 1445; Jaume & Perez Farfante, 1942: 39 [Pleistocene]; – Jaume, 1946: 101; – Aguayo & Jaume, 1949: 1; – Pulley, 1952: 150, pl. 13, fig. 7; – Nowell-Usticke, 1959: 14; – Abbott, 1961: 162; – Weber, 1961: 58; – Rice & Kornicker, 1962: 382, pl. 7, fig. 6a–b; – Moulding, 1967: 83; – Brooks, 1968: 8; – J. A. Baker, 1969: 3–4; – Ross, 1969: 8; – Voss et al., 1969: 71; – Abbott, 1970: 162; – Stanley, 1970: 160, pl. 21, figs. 12, 13; – McGinty, 1970: 58 [Lower Pleistocene]; – Magnotte, [1970–1979]: 63, fig. 12; – Woods, 1970: 2–3; – McGinty & Nelson, 1972: 13; – Godcharles & Jaap, 1973: 37; – Zischke, 1973: 35; – Zischke, 1977a: 29; – Zischke, 1977b: 338, fig. A.14–67; – Romashko, 1974: 49, fig. 17; – Ekdale, 1974: 657; – Eisenberg, 1981: 169, pl. 151, fig. 16; – Abbott, 1986: 230, fig. 5; – Sutty, 1990: 92, fig.; – Prieto et al., 2001: 593.

Antigona (Antigona) listeri – McLean, 1951: 82, pl. 15, fig. 5.

Periglypta aff. *listeri* – Weisbord, 1964: 300–302, pl. 43, figs. 7, 8 [Pliocene].

Periglypta listeri – Morris, 1973: 58, pl. 24, fig. 13; – Abbott, 1974: 521, color pl. 24, fig. 5852; – Emerson & Jacobson, 1976: 429, pl. 42, fig. 18 [AMNH 106142; seen by authors]; – Parodiz, 1976: 20 [Mayan ruins]; – Lozet & Pétron, 1977: 129, fig. 247; – Edwards, 1980: 3; – Theroux & Wigley, 1983: 47, fig. 85 (map); – Voss et al., 1983: 316, 429; – Romashko, 1984: 96, fig. p. 97; – H. E. Vokes & E. H. Vokes, 1984: 43, pl. 45, fig. 9; – Abbott, 1984: 54, fig. 9; – Lipe & Abbott, 1991: 76, fig. 9; – Lawson, 1993: 53; – Espinosa et al., 1994: 123; – Díaz M. & Puyana H., 1994: 78, pl. 18, fig. 170; – Abbott & Morris, 1995: 60, pl. 30; – Lyons & Quinn, 1995: J-13; – Alvarez, 1998: 103 ff.; Pointier & Lamy, 1998: 214, fig.; – Tremor, 1998: 7; – Turgeon et al., 1998: 48; – Mikkelsen & Bieler, 2000: 379; – Redfern, 2001: 236, pl. 101, fig. 965.

Periglyphus (*sic*) *listeri* – Voss et al., 1983: 79, 183.

Distribution (Figs. 1, 2)

North Carolina, southeastern and western Florida, including the Florida Keys, Texas, the West Indies, Caribbean Central America and northern South America; apparently not reaching Brazil. It appears to have a largely Caribbean island (as opposed to Gulf of Mexico or mainland North or South American) distribution. It is rare off Texas and other Gulf of Mexico locations. It extends along the entire island chain of the Florida Keys, from Key Largo to the Dry Tortugas.

Localities (*= unverified): **North Carolina* (Pulley, 1952). *Florida*: east coast (AMNH, ANSP, FMNH, USNM; Dall, 1902; M. Smith, 1937; Pulley, 1952; Stanley, 1970; McGinty & Nelson, 1972), Florida Keys (AMNH, ANSP, BMSM, CMNH, DMNH, FMNH, USNM, this study; Simpson, 1889; Dall, 1902; Palmer, 1927; Lermond, 1936; M. Smith, 1937; Pulley, 1952; Abbott, 1961; Brooks, 1968; Ross, 1969; Abbott, 1970; Magnotte, 1970–1979; Woods, 1970; Godcharles & Jaap, 1973; Zischke, 1973, 1977a, b; Edwards, 1980; Voss et al., 1983; Lyons & Quinn, 1995; Tremor, 1998; W. G. Lyons, pers. comm.), Dry Tortugas (USNM, this study), *west coast (M. Smith, 1937; Pulley, 1952); *Texas* (ANSP); *Caribbean*: Bahamas (AMNH, ANSP, FMNH, USNM; Clench & McLean, 1936; McLean, 1936b; Clench & McLean, 1937; McLean, 1938; Moulding, 1967; J. A. Baker, 1969; Lawson, 1993; Redfern, 2001), Cuba (ANSP, FMNH, MTD, USNM); McLean, 1936a; Aguayo & Jaume, 1949; Pulley, 1952), Cayman Islands (ANSP; Abbott, 1958), Jamaica (USNM), Hispaniola – Haiti and Dominican Republic (AMNH, ANSP, USNM; Palmer, 1927), Puerto Rico (ANSP, USNM; Clench & McLean, 1937; McLean, 1951; Warmke & Abbott, 1961), Virgin Islands (AMNH, ANSP, FMNH, USNM; Krebs, 1864; Dall, 1902; McLean, 1951; Nowell-Usticke, 1959; Weber, 1961), Antigua (USNM), *Martinique (Lamy, 1929; Fischer-Piette, 1975); *Guadeloupe (Schramm, 1869; Pointier & Lamy, 1998); Grenada (ANSP); Netherlands Antilles (DMNH, FMNH, USNM; Benthem Jutting, 1927); *Central America*: Mexico (AMNH; F. C. Baker, 1891; Weisbord, 1926; Jaume, 1946; Rice & Kornicker, 1962; Ekdale, 1974; Parodiz, 1976 [Mayan ruins]; H. E. Vokes & E. H. Vokes, 1984); Belize (ANSP, USNM), Honduras (USNM; Alvarez, 1998); Costa Rica (USNM); Panama (USNM); *South America*: Colombia (AMNH, FMNH, USNM; Díaz M. & Puyana H., 1994), *Venezuela (Prieto et al., 2001); *French Guyana (Femorale, 2003).

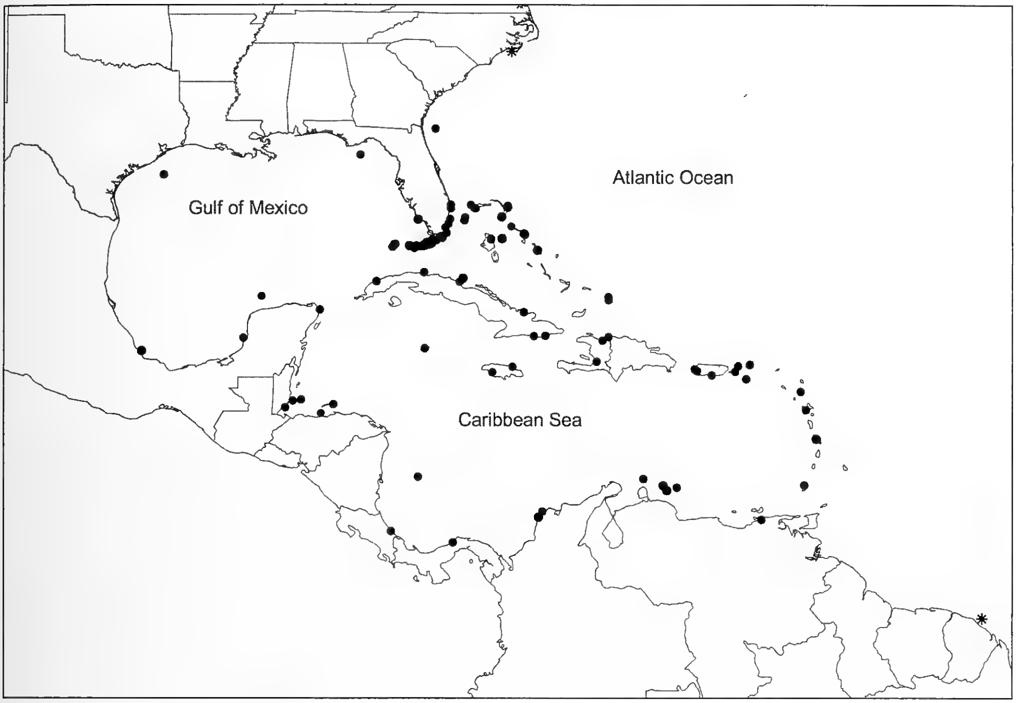


FIG. 1. Distribution of *Periglypta listeri*; * denotes record for region, without details.

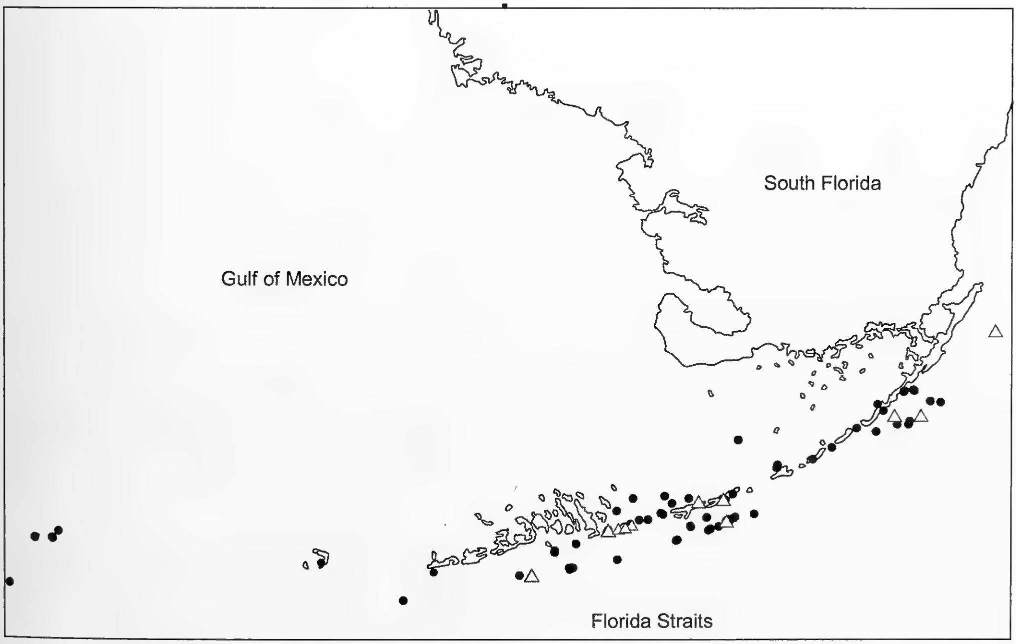


FIG. 2. Distribution of *Periglypta listeri* in the Florida Keys; (•) living records, (△) dead records.

Fossil Record

Lower Pleistocene (McGinty, 1970: 58) and Upper Pleistocene (M. Campbell, in lit., Feb. 2003) of southern Florida; Pleistocene of Cuba (Jaume & Perez Farfante, 1942) and Santo Domingo [Hispaniola] (Dall, 1903). It was collected from Mayan archaeological sites (but not from concurrent Recent collections) in Yucatan, Mexico, by Parodiz (1976). Weisbord (1964: 302) noted that the species was "reported from the Pleistocene of ... Barbados, and the Island of Tortuga, Venezuela", but did not include source citations for these records; Weisbord examined additional fragments from the Lower Mare formation (Pliocene, possibly Lower Pliocene) at Quebrada Mare Abajo, northern Venezuela.

Cassab (1984) recorded the eastern Pacific *P. multicostata* (G. B. Sowerby I, 1835) from several Tertiary western Atlantic locations – the Chipola Formation (Lower Miocene) of Florida, the Pirabas Formation (Lower Miocene) of Para State, Brazil, and the Middle Miocene of Costa Rica; verification of the species-level identity of these materials, which date prior to the closure of the Panamanian landbridge, is warranted. All post-closure western Atlantic *Periglypta* records should most definitely be reconsidered against *P. listeri*; Dall (1903: 1279) noted that *P. multicostata* "has been enumerated as one of the reef Pleistocene fossils of St. Domingo, but doubtless through a misidentification, perhaps of [*P.*] *listeri.*" A large-shelled form described as *P. tamiamensis* Olsson & Petit, 1964, from Florida's Late Miocene and Pliocene Tamiami formation seems closely related. The relationship of *P. listeri* to extinct western Atlantic species from older geological formations [e.g., *Antigona dominica* Palmer, 1928 (= *A. caribbeana* Anderson, 1927), Miocene of Santo Domingo, *fide* Hertlein & Strong, 1948; *P. tarquinia* (Dall, 1900), Oligocene of western Florida and Santo Domingo, called a small "precursor" of *P. listeri* by Dall, 1903; *P. mauryae* (H. E. Vokes, 1938), Upper Miocene of Trinidad], awaits a more comprehensive review of the genus.

Type Material

No original material located (see Taxonomic Remarks, below).

Material Examined

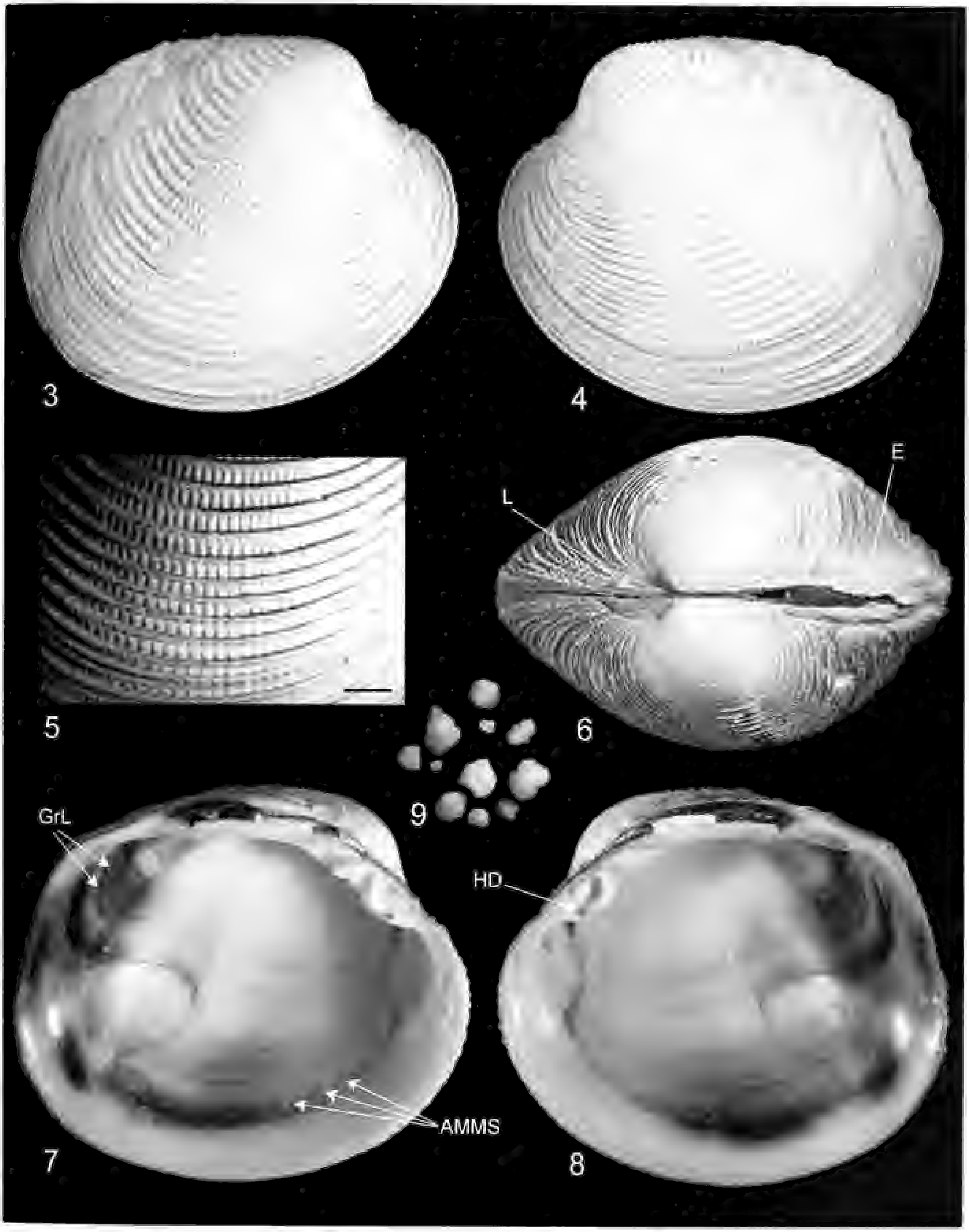
See Appendix 1.

Diagnosis

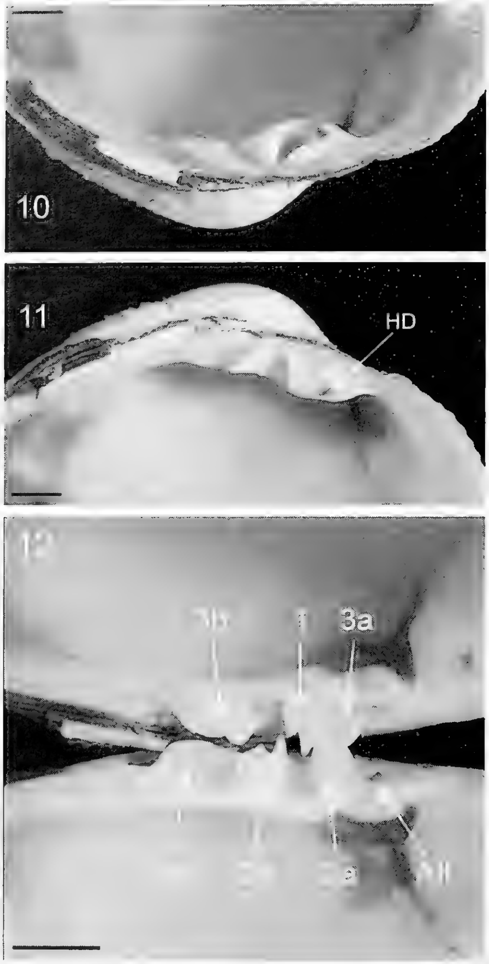
Large western Atlantic venerid, with thick-walled, inflated, trapezoid shell, with external sculpture of erect commarginal ridges crenulated by underlying radial sculpture, and with posterior end vertically truncated. Exterior cream-colored, with scattered brown speckles, blotches, or flames. Interior yellowish white with more-or-less strongly developed purplish brown stain around posterior adductor muscle scar, posterior margin, and above the pallial line. Anterior lateral hinge tooth often with a purplish brown "hinge dot".

Description

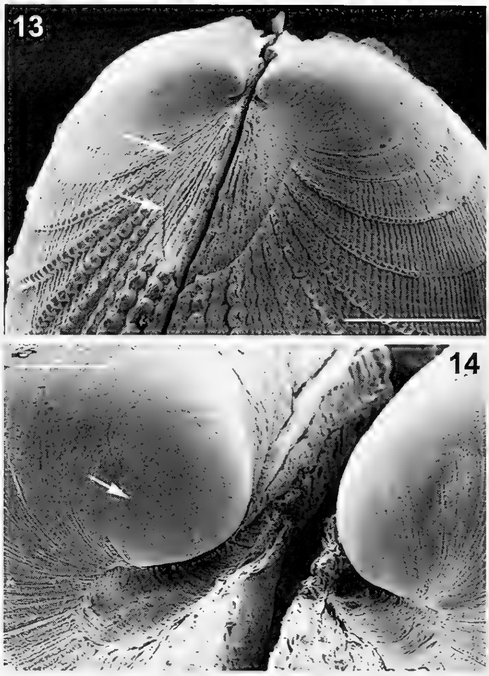
Shell relatively heavy, equivalve, longer than high, trapezoid, with nearly straight dorsal margin and bluntly truncated posterior margin; inequilateral with low, rounded umbones approximately 1/3 of the shell length from the anterior end (Figs. 3, 4). Length to height ratio very regular throughout lifespan ($R^2 = 0.9929$, $n = 32$). Inflated, with posterodorsal slope somewhat concave. External sculpture consisting of prominent erect commarginal ridges, regularly spaced, reflected umbonally, those along posterior margin higher and not reflected; ridges more-or-less alternating in strength at anterior and posterior margins as well as on later growth of shells (beginning at 2.5–3 cm or after first 15–25 commarginal ridges); ridges crenulated by underlying radial sculpture consisting of uniform flattened ribs separated by narrow grooves approximately 1/2–1/3 width of ribs (Fig. 5). Lunule broadly spindle- to teardrop-shaped (Figs. 6, 13), with deeply incised margins, asymmetric, right half slightly larger than left, with many very fine commarginal lamellae (continuing the much coarser ridge pattern of the anterior shell), without radial elements. Escutcheon distinct (Fig. 6), delimited by a marginal groove, right half overlapping left in the posteriormost third, both halves finely obliquely grooved. Externally cream-colored with brown speckles, blotches, or flames, sometimes darker posterodorsally, occasionally radially merging into (often three) broadening radial stripes; escutcheon and lunule with color of surrounding shell. Internal margin finely crenulated, continuing onto lunular margin. Anterior adductor muscle scar oval; posterior adductor muscle scar bean-shaped, somewhat flattened dorsally; posterior scar larger and more curved than anterior;



FIGS. 3-9. *Periglypta listeri*, Florida Keys specimens. FIGS. 3, 4: External shell; FMNH 176372, Little Duck Key, 75 mm; FIG. 5: Sculptural detail of shell in Fig. 3. Scale bar = 5 mm; FIG. 6: Umbonal aspect; FMNH 296695, Rachel Bank, 66 mm; FIGS. 7, 8: Internal shell; FMNH 296695, Rachel Bank, 62 mm; FIG. 9: Loose pearls from 78 mm shell; AMNH 295199, Spanish Harbor Keys, largest pearl with maximum dimension of 5.8 mm. (AMMS, accessory mantle muscle scars; E, escutcheon; GrL, pigmented growth lines on posterior adductor muscle scar; HD, hinge dot; L, lunule).

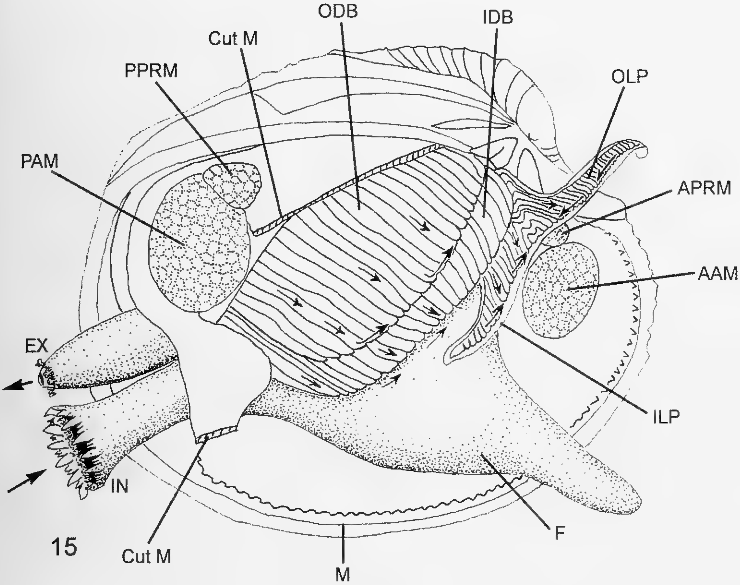


FIGS. 10–12. *Periglypta listeri,* details of specimen in Figs. 7, 8. FIGS. 10, 11: Close-up of hinge teeth; FIG. 12: Articulated shells. (1, right middle cardinal tooth; 2a, left anterior cardinal tooth; 2b, left middle cardinal tooth; 3a, right anterior cardinal tooth; 3b, right posterior cardinal tooth; 4b, left posterior cardinal tooth; HD, hinge dot; AII, left anterior lateral tooth). Scale bars = 5 mm.



FIGS. 13, 14. *Periglypta listeri,* details of umbo and prodissoconch; AMNH 296531, Looe Key reef, Florida Keys, 9.5 mm. FIG. 13: Anterior aspect with lunule. Arrows point to transition from wide commarginal lamellae on surface to fine striae on lunule; FIG. 14: Transition between prodissoconch I and II (arrow). Scale bars = 1 mm (Fig. 13), 100 µm (Fig. 14).

dorsalmost portion of posterior scar formed by pedal retractor muscle scar, separated by faint demarcation. Anterior pedal retractor muscle scar on ventral side of hinge plate, dorsomedial to anterior adductor muscle scar, just below anterior cardinal tooth (Fig. 12: 3a). Pallial line entire (Figs. 7, 8); pallial sinus wide, roundly pointed anteriorly. Accessory pallial muscle scars just inside pallial line, more-or-less regularly spaced. Internal color yellowish white with purplish brown stain around posterior adductor muscle scar and posterior margin, extending dorsally above the pallial line, sometimes also ventrally below, occasionally also surrounding anterior adductor and pedal retractor muscle scars; additional faint purplish brown "lines" often extending toward umbo from anterior limits of pallial sinus and anterior pedal retractor muscle scar (Figs. 7, 8). Live-collected specimens that are pure white internally also noted (e.g., USNM 464243, 890543, 890776). Color pattern within posterior adductor muscle scar sometimes showing distinct growth lines (Fig. 7). Hinge teeth of left valve (Figs. 11, 12) comprising minute anterior lateral [*AII*] (see Discussion below), prominent triangular anterior cardinal (*2a*), slightly smaller bifid middle cardinal (*2b*; with posterior part 1/4–1/3 less prominent), and lamellate posterior cardinal (*4b*). Hinge teeth of right valve (Figs. 10, 12) comprising well-defined, relatively small anterior cardinal (*3a*), larger bifid middle cardinal (1; with posterior part narrower and smaller),



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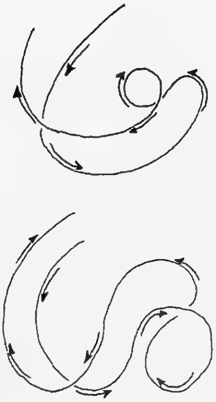

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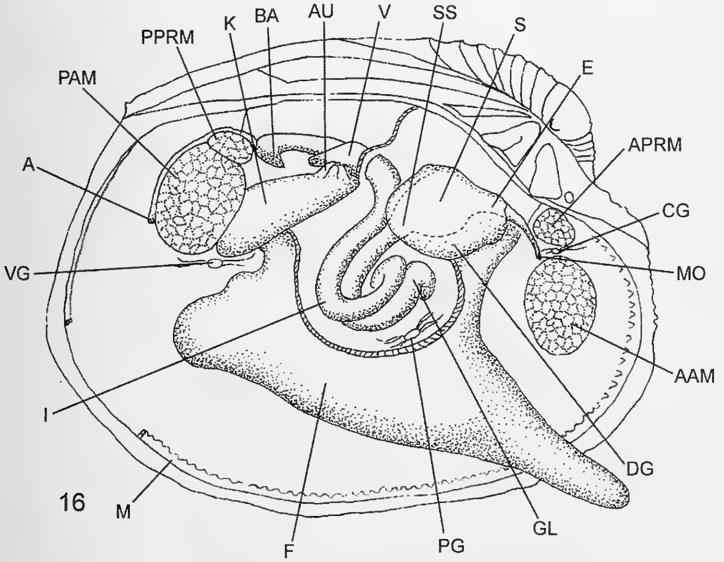

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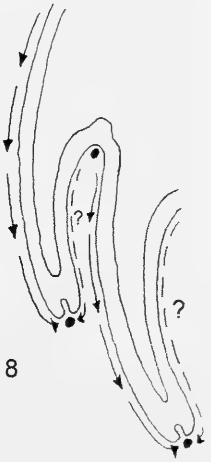

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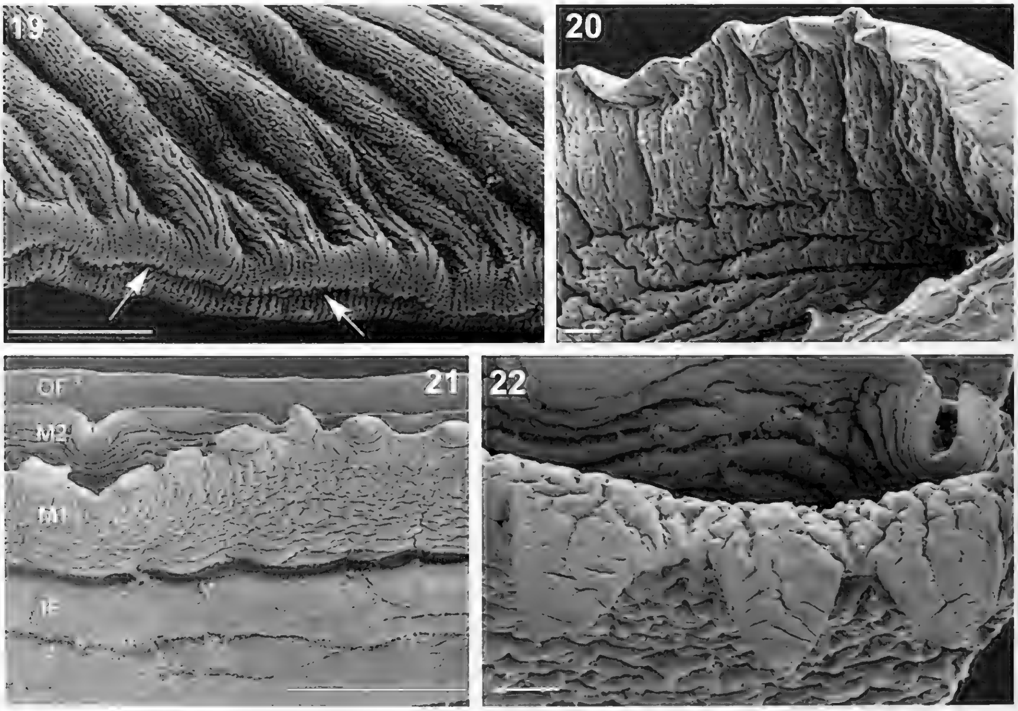
FIGS. 15–18. Diagrammatic anatomy of *Periglypta listeri*. FIG. 15: Organs of the mantle cavity, with RV and most of right mantle removed. Arrows on gills and labial palps indicate direction of particle flow. Outer labial palp (OLP) is reflected to show structure and particle flow over palps; FIG. 16: General dissection of alimentary system, with RV and right mantle, siphons, gills and labial palps removed; FIG. 17: Gut-loop variation in two additional dissected specimens (FK-273, FK-357); FIG. 18: Vertical section through gill, illustrating direction of food currents along inner and outer demibranchs. (A, anus; AAM, anterior adductor muscle; APRM, anterior pedal retractor muscle; AU, auricle of heart; BA, bulbus arteriosus; CG, cerebral ganglia; Cut M, cut mantle edge; DG, digestive gland; E, esophagus; EX, excurrent siphon; F, foot; GL, gut loop; I, intestine; IDB, inner demibranch; ILP, inner labial palp; IN, incurrent siphon; K, kidney; M, mantle edge; MO, mouth; ODB, outer demibranch; OLP, outer labial palp; PAM, posterior adductor muscle; PG, pedal ganglia; PPRM, posterior pedal retractor muscle; S, stomach; SS, style sack; V, ventricle of heart; VG, visceral ganglia).

and prominent, wide, equally bifid posterior cardinal (*3b*). Anterior lateral tooth at base of anterior cardinal of LV, and its corresponding socket in RV, often each with purplish brown "hinge dot" (Figs. 8, 10, 11).

Prodissoconch I visible at tip of umbo (Figs. 13, 14), 155 µm in length (n = 1; AMNH 296531, FK-269). Uncertain border between prodissoconch II and juvenile shells (at about 1.3 mm). Juvenile sculpture (Figs. 13, 23) initially smooth, followed by fine commarginal ridges with wide bands of radial ribs between. Surface pattern of brown to orange speckles particularly noticeable on juvenile shell (Fig. 23).

Foot large (Fig. 15), with brown pigment (in living specimens) between muscular part and visceral mass, with pedal gland opening slightly anterior of midpoint; pedal groove extending from ventral posterior end toward anterior third. Mantle muscles attaching mantle to shell, some extending dorsalward to produce so-called accessory muscle scars dorsal to pallial line (approx. 1.5 mm dorsal, in larger specimens). Attachment of anteriorly pointed siphonal retractor muscles producing (and reflecting shape of) pallial sinus on shell. Anterior and posterior adductor muscles (AAM, PAM, respectively) oval; PAM slightly larger than AAM. Posterior pedal retractor muscle (PPRM) round, arising anterodorsal to PAM. Fibers of PAM differently colored in living material, with posterior third darker than remainder. Anterior pedal retractor muscle (APRM) attaching to underside of anterior hinge plate and inserted into anterodorsal part of foot a short distance posterior to AAM. Visceral retractor muscle attached to inner surface of umbo behind hinge plate, inserting into roof of visceral mass.

Mantle with four mantle folds as previously described for other venerids (Ansell, 1961; Yonge, 1957). Ventral mantle margins distinctly wavy (Figs. 15, 20, 26) in living and preserved specimens; capable of closing in "zipper" fashion and held closely appressed in living indi-



FIGS. 19–22. *Periglypta listeri*, scanning electron micrographs of critical-point dried tissues; AMNH 295199, West Summerland Key, 73.2 mm. FIG. 19: Mid-ventral portion of the outer demibranch, with food groove (arrows); FIG. 20: Ventral mantle margin with wavy inner median mantle fold; FIG. 21: Anteriormost portion of mantle margin with all four mantle folds; FIG. 22: Detail of anterior mantle margin with triangular tentacles. (IF, inner mantle fold; M1, inner middle mantle fold; M2, outer middle mantle fold; OF, outer mantle fold. Scale bars = 100 µm (Figs. 20, 22), 1 mm (Figs. 19, 21).

viduals at rest. Pedal gape extending ventrally from base of incurrent siphon to AAM. Anterior 1/8 of inner median mantle fold with small triangular tentacles (Figs. 21, 22). Siphons separated (Figs. 15, 26), each with distinct black pigment (persisting in preserved specimens) between tentacles internally and externally; pigment stronger at terminal margin and fading toward basal region; internally with densely placed yellow-white surface papillae; each siphon with terminal digitate tentacles and basal siphonal membrane consisting of a thin tissue flap narrowing the lumen, with membrane of incurrent siphon forming a double ridge. Siphonal mantle fusion of type B (Yonge, 1957, 1982); union of inner and middle folds exposing outer surface of middle folds, with common outer ring of sensory tentacles. Incurrent (ventral) siphon slightly larger in diameter and length than excurrent (dorsal) siphon (Figs. 24–26); excurrent siphon tapering to narrower terminal diameter than wider, slightly flaring incurrent

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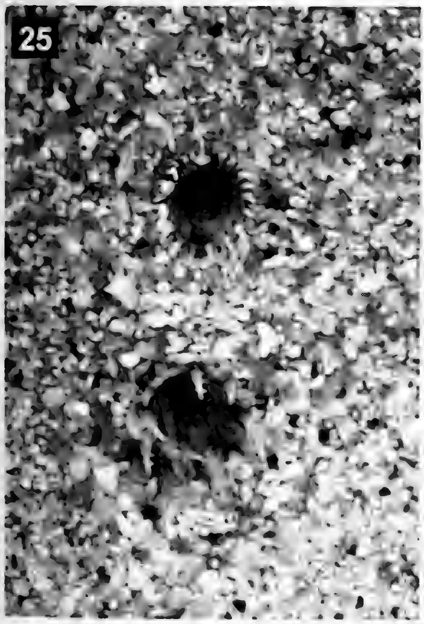

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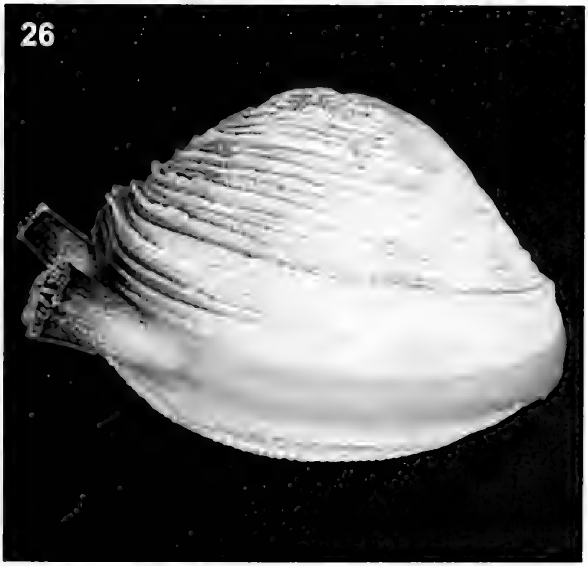
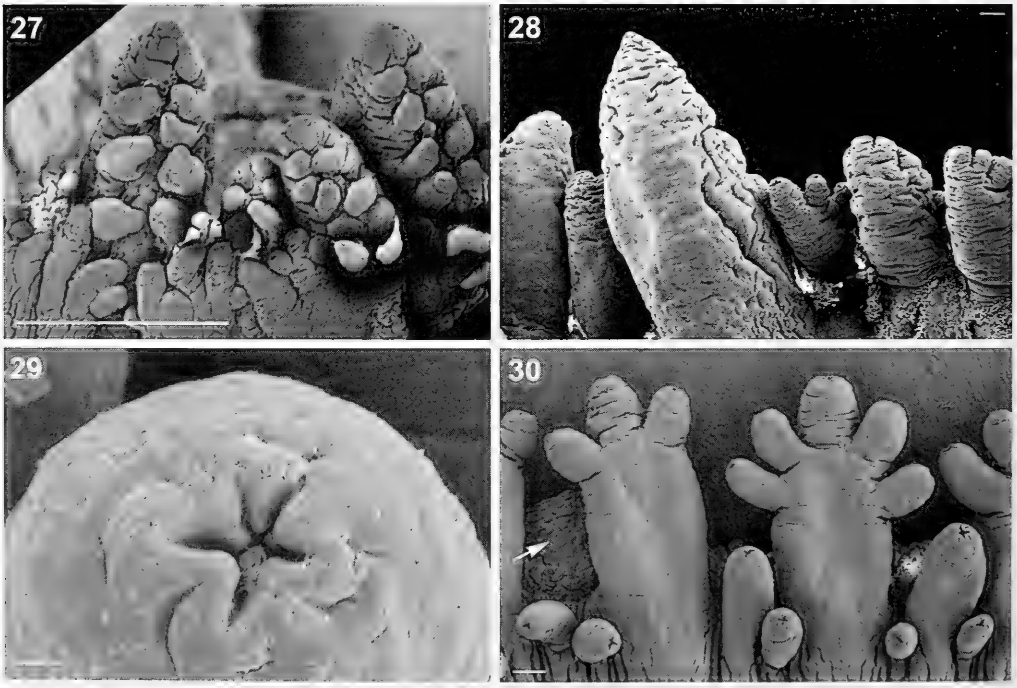


FIGS. 23–26. *Periglypta listeri*, juvenile shell and living specimens. FIG. 23: Juvenile shell with color pattern; FMNH 296719, West Summerland Key, Florida Keys, 7.2 mm; FIG. 24: Siphons of living specimen *in situ*, muddy sand and algal cover, 2 m depth; West Summerland Key, not collected; FIG. 25: Siphons of living specimen in sand in laboratory tank; FMNH 301448, West Summerland Key, 56 mm; FIG. 26: Living specimen in laboratory tank; FMNH 295706, off Stirrup Key, Florida Keys, 59 mm.

siphon. Siphonal tentacles digitate, those on incurrent siphon with 5–11, on excurrent with 3–5, lateral papillae, interspersed with additional small, simple tentacles; both kinds of tentacles on excurrent siphon with distal opening of unknown function (Figs. 29, 30); complex tentacles on incurrent siphon (Figs. 24–28) 30–75% larger, slightly more pointed and more numerous (approx. 40 tentacles of various sizes in 73 mm specimen, FK-273; AMNH 295199) than those on smaller excurrent siphon (approx. 30 tentacles, same specimen; Figs. 24–26, 29–30). Distal end of excurrent siphon with pointed dome-shaped valve surrounded by ring of tentacles, presumably allowing control of current (Figs. 24–26, 30).

Demibranchs smooth (not plicated; Fig. 15), with axes nearly vertical dorsoventrally; inner demibranch slightly larger than outer, each with numerous interlamellar junctions. Surface currents moving particles ventrally on the outer surface of each demibranch; currents on inner surfaces uncertain. Food grooves at distal edges of inner and outer demibranchs (Figs. 18, 19), with oralward currents, indicating gills and ciliation of type C(2) (Atkins, 1937); longitudinal oralward current also found between bases of adjacent demibranchs. Triangular palps with narrow lamellae on inner surface (33–37 lamellae, n = 2; FK-273, AMNH 295199, 73 mm; FK-352, FMNH 283534, 67 mm); margins smooth at ventral and dorsal side; outer surface smooth. Acceptance currents on palps along lamellae directed ventrally, and on ventral boundary oralward. Rejection currents counter-oralward on smooth ventral and dorsal margins of palps. Ctenidial/labial palp association of type II (Stasek, 1963); anteroventral tips of inner demibranch inserted and fused to distal oral groove between labial palps.

Esophagus relatively short, with 7–8 longitudinal rugae, leading into anterior part of stomach (Fig. 16); stomach embedded in di-



FIGS. 27–30. *Periglypta listeri*, scanning electron micrographs of critical point dried siphonal papillae; AMNH 295199, West Summerland Key, 73.2 mm. FIG. 27: Digitate tentacles on incurrent siphon, exterior aspect of siphon; FIG. 28: Same, viewed from interior of siphon; FIG. 29: Detail of simple tentacle of excurrent siphon with orifice of unknown function; FIG. 30: Digitate tentacles on excurrent siphon in front of flap-like valve (arrow). Scale bars = 1 mm (Fig. 27), 100 µm (Figs. 28, 30), 10 µm (Fig. 29).

gestive diverticula, located posterior to labial palps. Stomach of type V (Purchon, 1985), with two caeca. Right caecum with seven ducts; left caecum with 11 ducts opening into digestive diverticula; four ducts of digestive diverticula opening into left pouch. Major typhlosole (MT) and intestinal groove extending from intestine into stomach, penetrating right caecum; MT crossing stomach floor beneath esophageal opening into left caecum; MT continuing from stomach into intestine, ending just after gut loop. Minor typhlosole projecting into stomach but ending close to midgut opening. Gastric shield located opposite crystalline style sac at roof and left side of stomach, with flanges that pass into dorsal hood and left pouch. Dorsal hood with left and right sorting areas, located over esophageal opening. Style sac combined with midgut, together exiting posteroventrally from posterior end of stomach, then turning anteriorly and coiling on ventral side of stomach, turning again posteriorly and crossing style sac, then ascending (as hindgut, penetrating pericardium, ventricle and bulbus arteriosus) to continue dorsally and posteriorly across surface of PAM (Fig. 16). Gut loops varying somewhat (Fig. 17) in configuration between individuals, but always including a single ventral loop.

Ventricle of heart surrounding intestine, with lateral auricles connecting to outer limbs of kidney (Fig. 16). Kidney positioned along ventral edges of pericardium and anterior to PAM (Fig. 16). Three pairs of ganglia (Fig. 16), with cerebral ganglia between APRM and AAM, joined by supraesophagal commissure; visceral ganglia ventral and slightly anterior to PAM; pedal ganglia extensively fused, anteroventral to the ventral gut loop. Gonad surrounding stomach and intestine within visceral mass; reproductive system not otherwise investigated.

Dimensions and Maximum Recorded Size

Median length approximately 65 mm, ranging 13–100 mm (mean 63.3 ± 14.7 mm SD, n = 103). Maximum 100.2 mm, St. Thomas, Virgin Islands; AMNH 31868 [registered specimen, K. Hutsell (San Diego, California), Registry of World Record Size Shells]. Largest Florida Keys specimen, 96 mm, FK-601, FMNH 296718.

Habitat and Ecology

Based on observations in southeastern Florida's Biscayne Bay, Stanley (1970: 160) described this species as "widespread in intertidal and shallow subtidal settings, in large numbers; it is generally restricted to coarse substrate and grassy areas". Voss et al. (1969: 71) reported the species, for the same region, from the highly unlikely habitat of "rocks; pilings; seawalls" as well as from seagrass beds, open sand, and lagoonal patch reefs. Other habitat records include sand (FMNH, this study; Abbott, 1974; Humfrey, 1975; Dance, 1977; Tremor, 1998), mud (Humfrey, 1975), loose rock/rubble (this study; Godcharles & Jaap, 1973; Zischke, 1973; Voss et al., 1983), and seagrass (this study; Clench & McLean, 1937; Zischke, 1973; H. E. Vokes & E. H. Vokes, 1984). Clench & McLean (1937: 39) noted that *P. listeri* was "exceedingly abundant" in Savannah Sound (Eleuthera, Bahamas) but generally uncommon elsewhere. At Savannah Sound, they lived buried 5–10 cm below the surface of seagrass-covered sand bars; native Bahamians were observed using "a short stick as a probe [to locate the clams] ... [they are not] eaten by the natives though they are gathered in this way for fish bait" (Clench & McLean, 1937: 37). In the present study, one living specimen was found nestled in red algae within the cavity of a large barrel sponge at 8 m depth (FK-395), although the favored habitat for the species seems to be sand with loose rubble. It undoubtedly is a shallow-water species, in contrast to the analysis by Theroux & Wigley (1983: 47) who placed this species based on two dredge records "in the 50–99 m depth range grouping". Collecting records of all (living and dead) material range from shallow water to 84 m (Theroux & Wigley, 1983), with the deepest confirmed live-collected specimen in this study from 8 m (FK-395). Stanley (1970: 160) described the slow burrowing process of this species and noted that (in Biscayne Bay) the depth of burial is to some extent dependent upon interference by the subsurface rhizomes of surrounding turtlegrass (*Thalassia testudinum* König). In the laboratory, when permitted to burrow in its native sediment with the seagrass removed, a 5.8 cm-long animal assumed a position with the posterior shell margin 4.5 cm beneath the sediment surface. Specimens observed in the present study were often found hindered from deep burrowing by rubble, and had their shells barely covered by substratum. In addition to an herbivorous diet, evidenced through the presence of a crystalline style, *P. listeri* appears to opportunistically ingest zooplankton: two copepods were found in the stomach of one individual (FK-352). In Puerto Rico, this species is a "favourite food of the Slipper Lobster" (Sutty, 1990: 92). In the Florida Keys, empty shells have been frequently found associated with octopus middens at scuba depths, or with beveled drill holes, the latter indicative of predation by naticid gastropods.

Pearls

A single living animal was found with a series of loose pearls lining the center of the inside shell, apparently in response to the remains of an intruding worm-shaped organism (Fig. 9). The 78 mm specimen (FK-273, AMNH 295199) contained 11 irregular pearls, the largest with a maximum dimension of 5.8 mm. This is the first record of pearls from *Periglypta*; both free and attached pearls have previously been reported from several other venerids, especially *Mercenaria* spp. (Haas, 1931; Shirai, 1994; Hill, 1996; Landman et al., 2001; Mienis, 2001).

Taxonomic Remarks

Although there is general consensus in the recent literature of applying the species name "*listeri*" to this western Atlantic taxon, the taxonomic history of that name is not without complications. *Dosina listeri* was introduced by J. E. Gray (1838: 308). He placed it in an unnamed section of *Dosina* J. E. Gray, 1835, characterized by "anterior lateral tooth small, sometimes obliterated", together with three previously described species: *Venus verrucosa* Linnaeus, 1758 (as "*Dosina veerrucosa* [*sic*], *Venus veerruicosa* [*sic*], Linn."); *Venus reticulata* Linnaeus, 1758; and *Venus puerpera* Linnaeus, 1771. While other species in the same article were expressly identified as new species descriptions (labeled as "n.s.", accompanied by a textual description and including an indication of the originating collection; e.g., as done for *Grateloupea cuneata* J. E. Gray, 1838: 304), the name *D. listeri* appears as a new name referring to prior literature data (1838: 308). The complete "description", cryptic by today's standards, introducing the name *listeri* for a previously unnamed variety of *Venus puerpera* Linnaeus, 1771, reads as follows: "*Dosina Listeri*, *V. puerpura* [*sic*] *var.*, Linn. Sow. Gen. f. Ency. Meth. t. 278, f. 2". *Venus puerpera* was introduced by Linnaeus (1771: 545), in the *Mantissa*. Linnaeus himself did not mention varieties in the original description and referred to two prior illustrations – Gualtieri (1742: pl. 83, fig. F) and Argenville (1742: pl. 26, fig. F). In Hanley's words (1855: 453): "Neither of the very dissimilar figures referred to bears the least resemblance to the shell which has been universally accepted for the species." In any case, *Venus puerpera* clearly is an Indo-Pacific, not Atlantic, species (Fig. 31). Lamarck (1818: 584–585) and Deshayes (1832: 1112) distinguished two varieties of *V. puerpera*; their "*Venus puerpera* var. 2" referred to the cited figure of Lister (1687), as well as to an illustration by Lamarck (1797: pl. 278, fig. 2a, b) in the *Encyclopédie Méthodique*.

J. E. Gray (1838) had named *Dosina listeri* for Martin Lister, author of the *Historia Conchyliorum* (1685–1692). The first reference to a figure by Lister in conjunction with *Venus puerpera*, and the first reference to a distinct variety of this species (as γ), appeared in the 13th edition of Linnaeus' *Systema naturae*. The latter was authored by Gmelin (1791: sp. 3276), and it is the entry in this work that Gray seemed to have meant with his "var., Linn.". The indicated Lister figure (1687: pl. 341, fig. 178) is in agreement with today's concept of *Periglypta listeri*, but lacks detail to distinguish it from similar bivalve shells.

J. E. Gray's (1838) introduction of the new name *Dosina listeri* included references to two works. As outlined above, he did not seem to have actual specimens before him, and it appears that only the specimens referred to in these two works (and, possibly, Lister's original material) qualify as the type series (ICZN, 1999: Art. 72.4). One reference, and the only one indicated by Gray with actual plate and figure numbers, was to Lamarck's figures (1797: pl. 278, fig. 2a, b) as cited earlier by Lamarck (1818) and Deshayes (1832) for "variety 2" of *Venus puerpera*. The latter are excellent illustrations of an external right valve and of the external hinge area of an articulated specimen. Lamarck's illustration matches today's concept of western Atlantic *Periglypta listeri*. Somewhat confusingly, Deshayes (1835: 334) stated that Lamarck's specimen of "var. 2" and the figure 2a, b of the *Encyclopédie* fit well with the typical *V. puerpera* of Linnaeus. Lamy & Fischer-Piette (1938: 292) agreed and considered all such Lamarck material in the MNHN collection to represent *V. puerpera* [as well as (from a specimen agreeing with figs. 1a, b of *Encyclopédie* pl. 278) *Venus magnifica* Hanley, 1845]. The interior features of the shell, particularly its coloration, are unknown; the specimen on which Lamarck's excellent illustrations were based cannot currently be located (B. Metivier, 10/2002 in lit.).

The other work, cited by J. E. Gray as "Sow. Gen. f.", is G. B. Sowerby I's *Genera of Recent and fossil shells* (1834). In it, figure 1 of the *Venus* plate shows detailed color illustrations of the inside valves of a species identified as *V. puerpera*. However, the illustrated valves lack the brown or purple stains usually present in *Periglypta puerpera* and *P. listeri* and instead are shown with extensive orange coloration below the umbo. The illustrated specimen or specimens (considerable differences in the shape of mantle line and muscle scars indicate that these drawings of valves might originate from different individuals) have not been located in the BMNH collection. The orange interior coloration is matched by a specimen of *P. puerpera* from J. E. Gray's collection (BMNH 1991135, unknown locality, 49 mm; seen by authors). However, this shell differs considerably from Sowerby's illustrations in having dark brown markings at the shell margin, oval (not angular) anterior muscle scars, and a much more angular posterior shoulder. Another specimen at BMNH, furnished as a potential syntype of *Dosinia listeri* (K. Way, 02/2003 in lit.; BMNH 1840.7.1.41, 76 mm, no locality, old British Museum collection; see Appendix*)*, is a member of *P. listeri* in today's sense, but likewise not a shell illustrated by G. B. Sowerby I (1834). It is here, for reasons outlined above, not considered part of the syntypic series. Because the identity of *P. listeri* is not currently in dispute, and the figured specimens of Lamarck and Sowerby cannot be located at present, we refrain from designating a lectotype (or neotype) in the context of this study and defer to a future genus-wide revision.

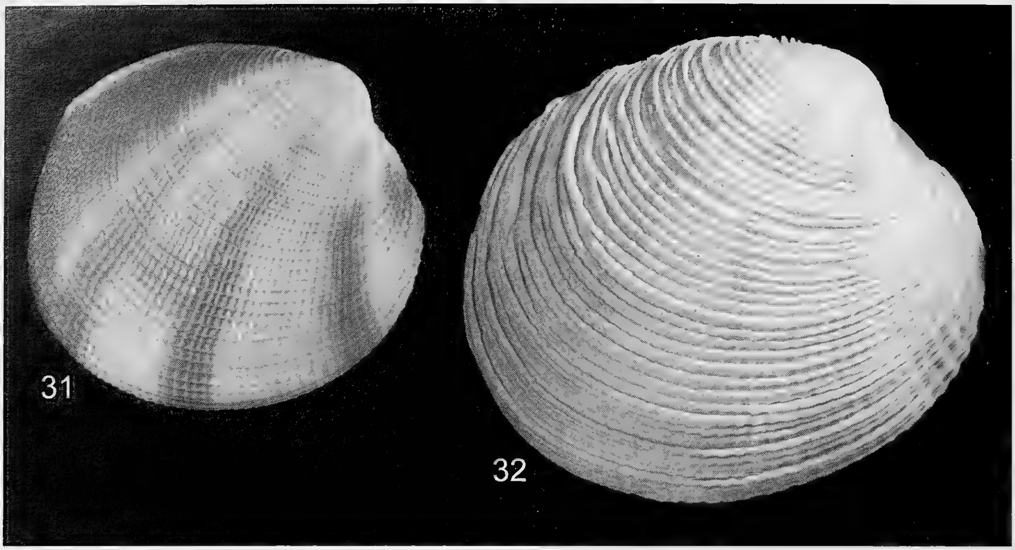
Subsequent British authors, particularly Hanley (1843, in: 1842–1856: 110) and G. B. Sowerby II (1853: 705), referred to *Venus listeri* as a species distinct from *V. puerpera*. However, their concept of this nominal species was broader and included differently colored forms with dark rayed patterns on the shells, as evidenced by the range of included illustrations. *Venus listeri* was thought to hail from the "Indian Seas", from the Philippines and Australia. Nevertheless, G. B. Sowerby II (1853: 705) expressly endorsed Lamarck's oft-cited illustration for *V. listeri* by stating "The figure in the Encyclopaedia is very exact for the type." Reeve (1863: pl. 5, no. 14) narrowed the interpretation of *V. listeri* to shells that are "fulvous-white, obscurely freckled with flesh-brown", but still assumed the waters near the Philippines Islands as its home. It was in the context of an Indo-Pacific interpretation of *V. listeri* that Reeve (1863: pl. 3) stated that he doubted that eastern Pacific *Periglypta multicostata* "is anything more than a variety of *V. listeri*, in which the ribs are more timidly thickened and recurved." Fischer-Piette (1975) assigned most of the Indo-Pacific records of *Venus/Dosinia/Chione/Cytherea/Antigona listeri* to *P. puerpera* and restricted *P. listeri* to Atlantic records.

Comparative Remarks

Periglypta listeri is one of the largest western Atlantic venerids, second only to *Mercenaria campechiensis* in maximum adult size. Its sculpture, of flattened radial ribs between sharp commarginal ridges (which are further crenulated by the radials), renders it distinct from other sympatric venerids: *M. campechiensis* lacks discernible sculpture between the commarginals, whereas *Globivenus* (formerly *Ventricolaria) rugatina* (Heilprin, 1886), *G. rigida* (Dillwyn, 1817), and *Circomphalus strigillinus* (Dall, 1902) have fine concentric striae between the commarginal ridges and are also rounder in general shell shape.

Periglypta listeri is part of a worldwide complex of morphologically similar species, the relationships of which far exceed the scope of this paper. Römer (1867: 32, here translated) referred to similarities so great "that the differences often can barely be put into words" when comparing "*Venus*" *listeri* to other nominal species of *Venus* – *Venus lacerata* Hanley, 1845; *V. clathrata* Deshayes, 1853; *V. crispata* Deshayes, 1853; *V. multicostata* G. B. Sowerby II, 1853; *V. laqueata* G. B. Sowerby II, 1853; *V. resticulata* G. B. Sowerby II, 1853; *V. chemnitzii* Hanley, 1844; *V. sowerbyi* Deshayes, 1853; *V. reticulata* Linnaeus, 1758; and *V. monilifera* G. B. Sowerby II, 1851. Citing a high degree of variability, E. A. Smith (1885: 120–121) considered "*Venus*" *resticulata, V. aegrota* Reeve, 1863, *V. lacerata* Hanley, *V. sowerbyi*, *V. clathrata*, *V. crispata*, *V. puerpera*, *V. listeri*, and probably also *V. multicostata* and *V. magnifica* Hanley, 1845, as "races" of a single biological species, although he fell short of formalizing this action in not placing these names in synonymy under *V. puerpera*. Modern revisionary treatment of the Indo-Pacific taxa is urgently needed.

Periglypta listeri is the only living member of the genus in the Atlantic Ocean. It differs from



FIGS. 31, 32. Contrasting shell morphology in *Periglypta* spp. FIG. 31: *P. puerpera*; FMNH 82478, Mindanao, Philippines, 59 mm; FIG. 32: *P. multicostata*; FMNH 165936, Pacific Panama, 111 mm.

the Indo-Pacific *P. puerpera* (Fig. 31), type species of the genus, in general shell shape and coloration. *Periglypta puerpera* is less anteroposteriorly elongated, and generally more rounded in outline. Its external sculpture appears smoother, a result of its less prominent commarginal ridges. Externally it is cream-colored, with or without scattered radial brown flecks, often with 1–3 darker brown rays, one almost always extensively covering the posterior third. Internally it is white with a bright purple (not purplish brown) stain at the posterior margin below the PAM, sometimes also with a yellow or peach-colored flush at the center (although internally pure-white specimens also occur). As earlier noted by E. A. Smith (1885: 120–121), *P. puerpera* has a "V-shaped purple mark upon the apex of the umbones", referring to two radial color bands on the prodissoconch and earliest juvenile stage; this is lacking in examined specimens of *P. listeri*.

Weisbord (1964: 302) called *Periglypta listeri* the western Atlantic analog of Panamic *P. multicostata*, citing a difference in the outline of the posterior end (obliquely vertical and truncated in *P. listeri*, subtruncated and more rounded in *P. multicostata*; see Fig. 32); although based on many museum specimens (AMNH, n = 31), this difference is only obvious among the largest specimens. *Periglypta multicostata* attains a larger size (maximum observed 120 mm, AMNH 248600, Baja California Norte, Mexico) than *P. listeri*. Externally, the commarginal ridges of *P. multicostata* are decidedly coarser and more prominently dorsally reflected than those of *P. listeri*, rendering the crenulations and radial ribs less obvious. Internally, *P. multicostata* is white (or very occasionally flushed with pink, not purplish brown, either centrally or in an oblique posterior streak from umbo to margin, but not prominently surrounding the posterior muscle scars) and marginal crenulations are less noticeable or absent in the largest specimens (although the latter are quite prominent in specimens < 65 mm).

DISCUSSION

Periglypta listeri agrees with previously described venerids in conchological features, such as a well-developed escutcheon and lunule, and a hinge with three cardinal teeth in each valve (Keen, 1969). Although Lamprell (1998) cited differences in the shape of the pallial sinus, we found that distinguishing characters at the species level reside in sculpture and color/color pattern. So far as is known, the pattern of the internal purplish brown coloration and the purplish brown "hinge dot" are unique to *P. listeri* within the genus.

This paper presents the first anatomical study for any species in the genus *Periglypta*, and is arguably the most extensive anatomical description yet available for any member of the subfamily Venerinae. Anatomical information is published for only three other venerines. Pelseneer (1894, 1897) provided minor details about the anatomy of *Venus verrucosa* (tongue-shaped foot without byssus, very small labial palps, siphons more or less fused). He later (Pelseneer, 1911) presented similarly cursory details (siphons short and united, with retractors; short "byssal" groove on posterior foot; very narrow external demibranch) for *Venus* (now *Globivenus*) *toreuma.* Ansell (1961: fig. 8) illustrated (but did not extensively discuss) the gross anatomy and stomach structure of *Circomphalus casina* (Linnaeus, 1758), which are closely similar to those in *P. listeri* with respect to the gills, labial palps, foot, stomach, and adductor muscles, as well as the flow of particles over the gills and labial palps. Like *P. listeri, C. casina* features a structurally complex ventral mantle edge, but its function was not mentioned. Its siphons appear short, unlike the longer, separated siphons of *P. listeri*. Ansell (1961; also Pelseneer, 1911) considered the degree of siphonal fusion to vary greatly within Veneridae, and from these minimal data this could also be true within Venerinae.

The anatomy of *Periglypta listeri* agrees with these and other previously described venerids in most features. As elaborated by Yonge (1957), Ansell (1961), and Narchi (1971), the mantle edge has four folds (outer, OF; inner middle, M1; outer middle, M2; and inner, IF). The periostracum is secreted between OF and M2. In *P. listeri,* M1 is undulating, with its anterior part elaborated into distinctly triangular tentacles. The wavy structure and tentacles can close in "zipper" fashion (Fig. 26), presumably to protect the organs of the mantle cavity from intrusion of particles and small organisms. At the anterior end of the pedal gape, OF fuses with M2, and M1 fuses with IF. At the posterior end, M1 and IF are fused to form the siphons; this configuration typifies venerids of type B fusion (Yonge, 1948, 1957, 1982; Ansell, 1961). The conical valve on the tip of the excurrent siphon is the elaborated IF, while the ring of tentacles on the siphon represents M1 (Yonge, 1957; Ansell, 1961; Jones, 1979). The tentacles on the incurrent siphon are not distinguishable into inner and outer rings of tentacles, in contrast to Jones' (1979) findings in members of *Chione, Mercenaria*, and *Austrovenus*. The siphonal tentacles of *P. listeri* are long and digitate, serving as an effective screen to block intrusion of particles. Ansell (1961) contrasted the digitate tentacles of *Circomphalus, Timoclea, Clausinella, Venerupis*, and *Gafrarium* spp., which live in gravelly and stony bottom habitats, against the simple tentacles of *Chamelea* and *Dosinia* spp., which live in cleaner sand or gravelly bottoms. *Periglypta listeri* is not congruent with this pattern; it carries digitate tentacles but lives in a gravel and sand habitat without a high amount of detritus in suspension.

At the proximal end of each siphon, *Periglypta listeri* has a siphonal membrane or valve comprised of thin tissue flaps, as described for other venerids (Ansell, 1961; Jones, 1979). That of the incurrent siphon consists of a basal double ridge; Ansell (1961) described this double ridge in *Circomphalus casina* and, like others (Kellogg, 1915; Jones, 1979; Narchi & Dario, 2002) postulated that such a valve can be opened to admit water inflow, or closed to direct water ventrally and flush out accumulated pseudofeces.

The anterior end of the gill in *Periglypta listeri* is inserted into the distal oral groove, in the midline of the labial palps to which the gill is fused (Stasek, 1963). The ctenidia, with food grooves on the edges of both demibranchs, correspond to Atkins' (1937) type C(2) along with members of *Paphia, Mercenaria, Chione, Tivela*, and *Saxidomus*. Other venerines, such as *Venus verrucosa* and *Circomphalus casina,* as well as other venerids (in *Clausinella, Dosinia, Gafrarium, Chamelea,* and *Paphia*), lack a groove on the outer demibranch and have therefore been assigned to type C(1b). However, it must be noted that Atkins (1937) found this character variable within genera (e.g., *Paphia*) and species (e.g., only one of four specimens of *C. casina* had a groove on the outer demibranch), indicating that this character requires larger sample sizes and further research.

The circulatory and nervous systems are broadly similar to the species studied by Jones (1979), as is the general plan of the digestive system and configuration of the gut loop. The type V stomach of *P. listeri* agrees overall with the descriptions by numerous authors (Ansell, 1961; Dinamani, 1967; Narchi, 1971, 1972; Jones, 1979; Purchon, 1987; Narchi & Dario, 2002) for other members of the family. A combined style sac and midgut is typical of venerids, except for *Placamen tiara* (Dillwyn, 1817), in which the openings, although close together, lead into separate tubes (Dinamani, 1967). The numbers of ducts entering the left and right caeca vary among species and range, respectively, from a minimum of one and two in *Nutricola tantilla* (Gould, 1853) to a maximum of 13 and seven in *Venerupis pullastra* (Montagu, 1803) (Purchon, 1987); *P. listeri* is at the high end of this range with 11 and seven ducts. Four additional ducts open into the left pouch in *P. listeri,* in contrast to two or three in *Meretrix, Katelysia, Placamen, Sunetta*, and *Irus* spp. (Dinamani, 1967), five ducts in *Tivela* and *Gafrarium* spp., or eight in *Dosinia* spp. (Purchon, 1987). No additional ducts enter the stomach near the right caecum in *P. listeri,* unlike in *Clausinella* and *Callista* spp. (Purchon, 1987).

Periglypta listeri lives in rubble or sand among rocks, and/or in reef settings (as opposed to soft bottoms like most other venerids). This is also true for the similar eastern Pacific *P. multicostata,* aptly named "giant reef clam", described as a common species in 3–6 m depth in Baja California Sur (García-Domínguez et al., 1998), and noted from sand among rocks (Keen, 1971). Other *Periglypta* species recorded for rocky or reef habitats are *P. puerpera* and *P. reticulata* (*fide* Whitehead, 1983; Graham, 1995).

Periglypta was originally described as a subgenus of *Antigona*, and Harte (1998: 358) maintained that that is its proper placement. However, although *Antigona* Schumacher (type species by original designation, *A. lamellaris* Schumacher, 1817, Indo-Pacific) shares radial threads between the commarginal shell ridges with *Periglypta*, its members have radial ribs extended onto the lunule, no groove around the escutcheon, a more triangular pallial sinus, and hinge teeth with a much wider *3b* and smaller *2b*. *Periglypta* also differs from *Dosina* J. E. Gray (type species, *D. zelandica* J. E. Gray, 1835, South Pacific, by subsequent designation of Frizzell, 1936), in which *P. listeri* was originally described, by the predominantly concentric sculpture (Keen, 1969) and a weakly or undeveloped escutcheon in that genus (pers. obs.).

Most authors (e.g., Keen, 1969) refer to an anterior lateral tooth in the left valve as characteristic of venerines, but an anterior lateral tooth is also present in members of other venerid subfamilies (e.g., Gouldiinae [= "Circinae"], Sunettinae, Meretricinae, Pitarinae, and Dosiniinae; Keen, 1954). There are indications that such lateral teeth result from different ontogenetic pathways and might not be homologous. Félix Bernard (1895: 127) presented an ontogenetic series of hinge development for a Miocene species of *Gouldia*, which (together with its numbering system) became the model for tooth development in the "corbiculoid" hinge type *sensu* Cox (1969: N54). According to this model, the venerine anterior lateral tooth of the left valve (designated as *AII*) derives from lamella *II*. Whereas F. Bernard (1895: 127) noticed differing hinge morphologies of other venerids, such as *Macrocallista*, he still recognized the anterior lateral tooth in the latter as a lamella *II* derivative, and thus an *AII*. Marwick (1927: 598–599), in another ontogenetic comparison, showed that the Oligocene venerine *Kuia vellicata* (Hutton, 1873) displayed the same *AII* development as shown in F. Bernard's *Gouldia* study. However, Marwick (1927: 598) maintained that the left anterior lateral tooth of *Macrocallista*, a continuation of a low ridge proceeding from below the umbo, is "in no way connected with the anterior cardinal". Some subsequent authors (Frizzell, 1936) followed Marwick's argument of non-homologous anterior lateral teeth in the Veneridae; Grant & Gale (1931: 316) referred to the venerine *AII* of *Antigona* as a "pseudolateral", in contrast to the situation in groups such as *Macrocallista*. It appears that venerid "anterior lateral teeth" might variously be derived from either lamella *II* or *IV* and homology assumptions of these structures need closer scrutiny.

Chionines do not have anterior lateral or pseudolateral teeth even though their overall shell morphology is very similar to that of venerines. Anatomical studies carried out by Jones (1979) showed that chionine siphons are usually fused along their length in contrast to the unfused siphons of *Periglypta listeri* seen in this study; the high degree of variability in siphonal fusion, as well as the presumably fused siphons in the venerine *Circomphalus casina* (see above) render this a weak distinguishing character. At present, the presence of an *AII* lateral hinge tooth is postulated as the only reliable morphological feature separating these two nominal subfamilies. Although recently synonymized by Coan & Scott (1997), preliminary molecular studies (16S gene; I. Kappner, unpubl.) indicate a distinct grouping that might warrant retention of these subfamilial units. Studies of additional taxa, and more anatomical and molecular characters are needed for resolution of subfamilial synapomorphies.

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APPENDIX 1: Material Examined

Material examined (this study, Florida Keys)

RB unnumb., N of Bahia Honda State Park, shallow water, sand, 25 Mar 1989 (1 spm alc, FMNH 288810); FK-018, "The Stakes", off Middle Florida Keys, scuba, 20 ft (6.1 m), patch reef/ledges, sand patches, M/V SITE FINDER, 08 July 1995 (1 pair, AMNH 308088); FK-035, Indian Key Fill, 24°53'25"N, 80°40'28"W, bayside, *Thalassia* seagrass bed, 1 m, shovel/sieve, 10 March 1996 (1 juv valve, AMNH 296528); FK-039, Crawl Key, 24°44'36"N, 80°58'47"W, oceanside, beach inside channel, shallow sand, seagrass, seawall, by hand and hand dredge, 12 March 1996 (1 spm alc, FMNH 301424); FK-047, Channel marker 50A off Ramrod Key, 24°35.80'N, 81°27.24'W, rubble and patch reef, 15 ft (4.6 m), scuba, M/V THE SNAIL, 21 September 1996 (1 pair, 1 valve, AMNH 295179); FK-068, bayside of West Summerland Key (Spanish Harbor Keys), 24°39'19"N, 81°18'13"W, bayside, shovel/sieve in *Thalassia* + beach combing, 0.5–1 m, 18 April 1997 (3 valves, 1 frag, FMNH 279531); FK-069, Channel marker 50A off Ramrod Key, 24°35.80'N, 81°27.24'W, rubble and patch reef, 18 ft (5.5 m), scuba, R/V FLORIDAYS, 19 April 1997 (1 pair, FMNH 279521); FK-090, Garden Key, Dry Tortugas, 24°37'50"N, 8252'20"W, sand beach with stone pilings, 2.5 m, by hand and snorkeling, 23 April 1997 (1 pair, AMNH 296520), FK-091, Fort Jefferson, Garden Key, Dry Tortugas, 24°37'50"N, 82°52'24"W, beach at mote and mote wall, by hand and snorkeling, 23 April 1997 (2 pair, AMNH 290122); FK-115, East Washerwoman Shoal (Channel Marker 49), off Marathon, 24°40'N, 8104.3'W, 9 ft (2.7 m), scuba, R/V FLORIDAYS, 12 July 1997 (1 valve, FMNH 279523); FK-117, Key Vaca, channel west of Stirrup Key, 24°44.19'N, 81°02.92'W, bayside, in channel, 15 ft (4.6 m), plus in surrounding shallow *Thalassia*/sand, scuba, 14 July 1997 (1 spm alc [photographed alive], FMNH 295706); FK-119, "The Slabs" patch reef between "outer patches" and "coral humps" off Marathon, 24°39.53'N, 81°00.90'W, scuba, 23 ft (7.0 m), R/V FLORIDAYS, 20 July 1997 (1 valve, FMNH 279528); FK-121, "The Slabs" patch reef between "outer patches" and "coral humps" off Marathon, 24°39.53'N, 8100.90'W, 23 ft (7.0 m), scuba, R/V FLORIDAYS, 21 July 1997 (1 pair, 3 valves, AMNH 296525); FK-131, off Key Vaca, oceanside, "outer patches" south of Hawk Channel, 24°39.30'N, 81°01.30'W, rubble, gorgonians, sponges, 21 ft (6.4 m), scuba, R/V FLORIDAYS, 07 August 1997 (3 valves, AMNH 296530); FK-135, east of Bethel Bank, Florida Bay, 2443.86'N, 81°07.41'W to 24°43.60'N, 81°07.47'W, sand/sparse seagrass, 8 ft (2.4 m), dredge, R/V FLORIDAYS, 07 August 1997 (1 valve, FMNH 279525); FK-149, exposed flats outside channel off Crawl Key, 24°44'29"N, 80°58'24"W, oceanside, clean sand + *Thalassia/Syringodeum* seagrass, *Penicillus*, 0.5 ft (0.15 m), by hand, R/V FLORIDAYS, 22 August 1997 (2 valves, FMNH 279530); FK-169, Tavernier Creek, near bayside entrance, west side (Plantation Key), 25°00.76'N, 80°32.68'W, sand/*Thalassia*, 6–8 ft (1.8–2.4 m), ponar grab and dredge, R/V FLORIDAYS, 17 September 1998 (1 valve, AMNH 296522); FK-171, just off mouth of Tavernier Creek, oceanside, near marker #7, 24°59.67'N, 80°31.72'W, sand, *Thalassia/Syringodeum* seagrass, 0–3 ft (0–0.9 m), snorkeling/sieving, R/V FLORIDAYS, 17 September 1998 (observed pair); FK-178, east end of Rodriguez Key, oceanside of Key Largo, 25°03.13'N, 80°26.49'W, *Thalassia* seagrass, sand, small rubble, 2–3 ft (0.6–0.9 m), snorkeling, R/V FLORIDAYS, 20 September 1998 (2 pair, 1 valve, AMNH 295178); FK-179, Lower Matecumbe Key, 24°51'24"N, 80°43'40"W, oceanside, from beach front 3 days after Hurricane Georges, in *Thalassia* droves (1–3 ft deep) washed ashore by storm, 28 September 1998 (1 valve, FMNH 279529); FK-205, Carysfort Reef, 25°13.25'N, 80°12.78'W, coral rubble, sand patches, coral heads, 6–15 ft (1.8–4.6 m), scuba, R/V FLORIDAYS, 10 April 1999 (1 spm alc, AMNH 298893); FK-207, east end of Rodriguez Key, 25°03.13'N, 80°26.49'W, sand, seagrass, rubble, 1–2 m, snorkeling, R/V FLORIDAYS, 11 April 1999 (3 pair, AMNH 296519); FK-228, Old Dan Bank, bayside off Long Key, 24°49.66'N, 80°50.18'W, *Thalassia/Porites/Halimeda*, 2–4 ft (0.6–1.2 m), snorkeling, R/V FLORIDAYS, 31 July 1999 (2 pair, AMNH 296521); FK-233, Old Dan Bank, bayside of Long Key, north of marker 2X, 24°49'57"N, 80°49'45"W, *Thalassia* seagrass, *Halimeda, Porites*, 2–4 ft (0.6–1.2 m), snorkeling/sieving, R/V FLORIDAYS, 01 August 1999 (2 pair, AMNH 296527); FK-236, Coffins Patch, oceanside of Grassy Key, 24°41'05"N, 80°57'28"W, algae-covered coral reef, 16 ft (4.9 m), scuba, R/V FLORIDAYS, 02 August 1999 (3 valves, FMNH 279522); FK-244, bayside of West Summerland Key (Spanish Harbor Keys), 24°39'19"N, 81°18'13"W, bayside, rock wall and sand slope, 23 ft (7.0 m), scuba, 05 August 1999 (1 valve, AMNH 296524); FK-246, bayside of West Summerland Key (Spanish Harbor Keys), along inner shore of western arm of horseshoe, 24°39'19"N, 81°18'13"W, beach, 05 August 1999 (1 frag, AMNH 296523); FK-255, Friend Key Bank, bayside of Bahia Honda Key, north side at crest of bank, 24°42.58'N, 81°16.77'W, *Thalassia/Syringodeum* seagrass, sand patches, 0.5–2 ft (0.15–0.6 m), snorkeling, R/V FLORIDAYS, 09 August 1999 (3 valves, FMNH 279520); FK-260, Looe Key coral reef, oceanside of Ramrod Key, 24°32.80'N, 81°24.80'W, spur and groove reef, 24–25 ft (7.3–7.6 m), scuba, R/V FLORIDAYS, 10 August 1999 (1 valve, FMNH 279526); FK-268, Looe Key back reef, 24°32.79'N, 81°24.33'W, seagrass, sand patches, rubble, 2–8 ft (0.6–2.4 m), snorkeling, R/V FLORIDAYS, 19 August 1999 (1 valve, FMNH 279527); FK-269, Looe Key back reef, 24°32.79'N, 81°24.33'W, sediment sample, 8 ft (2.4 m), snorkeling, R/V FLORIDAYS (1 juv pair, AMNH 296531); FK-273, bayside of West Summerland Key (Spanish Harbor Keys), at outermost point of western arm of horseshoe, 24°39.35'N, 81°18.22'W, 1–4 ft (0.3–1.2 m), snorkeling, hand collecting, 19 August 1999 (3 spm alc [1 dissected, 1 with pearls, 1 SEM, AMNH 295199; 1 partial animal alc [body of spm with pearls, see prior; DNA], FMNH 296696; 1 juv pair, AMNH 296526); FK-275, Looe Key back reef, 24°32.87'N, 81°24.41'W, 5–10 ft (1.5–3.0 m), snorkeling and hand-collecting, R/V FLORIDAYS, 20 August 1999 (1 valve, FMNH 279524); FK-287, bayside of West Summerland Key (Spanish Harbor Keys), inside outermost arm of horseshoe, 24°39.35'N, 81°18.22'W, shallow subtidal, by hand, snorkeling, 10 April 2000 (1 spm alc, FMNH 289982; 1 live-collected pair, FMNH 301426; 9 pair, FMNH 289939); FK-298, Looe

Key National Marine Sanctuary, southwest, ca. 24°32.5'N, 81°24.7'W, 30 ft (9.1 m), scuba, R/V EUGENIE CLARK, 02 July 2000 (1 juv pair; AMNH 308080); FK-350, Looe Key National Marine Sanctuary, southwest corner of core area, 24°32.61'N, 81°24.66'W, 32 ft (9.7 m), scuba, R/V EUGENIE CLARK, 07 July 2000 (1 valve, 1 juv valve, AMNH 299545); FK-351, Looe Key back reef, 24°32.87'N, 81°24.41'W, rubble, 3–7 ft (0.9–2.1 m), snorkeling, R/V FLORIDAYS, 08 July 2000 (1 pair, AMNH 299489); FK-352, bayside of West Summerland Key (Spanish Harbor Keys), south arm, 24°39'19"N, 81°18'13"W, bayside, rubble, to 1.5 m, snorkeling, 08 July 2000 (3 spm alc [dissected], FMNH 283534; 6 juv pair, 1 valve, 2 juv valves, AMNH 299467); FK-357, American Shoals, northwest of lighthouse, 2431.54'N, 81°31.26'W, *Thalassia* seagrass with large coral rubble, 9–11 ft (2.7–3.3 m), scuba, R/V FLORIDAYS, 09 July 2000 (3 spm alc [1 dissected], FMNH 301428); 1 frag, AMNH 299581); FK-359, American Shoals, 24°31.56'N, 81°31.10'W, *Thalassia/Syringodeum* seagrass with rubble, rocks, 11–12 ft (3.3–3.6 m), scuba, R/V FLORIDAYS, 10 July 2000 (observed spm; 2 pair, 2 valves, AMNH 299421); FK-360, coral lumps off Newfound Harbor Keys, off Big Munson Key, 24°36.96'N, 81°23.64'W, sand, seagrass, patch reef, gorgonians, 9 ft (2.7 m), scuba, R/V FLORIDAYS, 11 July 2000 (1 pair, AMNH 299520); FK-363, east end of Rodriguez Key, oceanside of Key Largo, 25°03.27'N, 80°26.66'W, *Thalassia* seagrass, sand, small rubble, 6 ft (1.8 m), snorkeling, R/V FLORIDAYS, 07 October 2000 (2 pair, AMNH 307612); FK-364, Dove Key (just southwest of Rodriguez Key), oceanside of Key Largo, 25°02.94'N, 80°28.27'W, sand, algae, sponges, *Sargassum*, 2–6 ft (0.6–1.8 m), snorkeling, R/V FLORIDAYS, 07 October 2000 (1 pair, AMNH 307613); FK-367, northeast corner of Conch Reef, oceanside of Key Largo, 24°57.895'N, 80°27.248'W, rubble, *Thalassia* seagrass, 9 ft (2.7 m), snorkeling, R/V FLORIDAYS, 08 October 2000 (1 frag, AMNH 307736); FK-392, Lower Matecumbe Key, 24°51'24"N, 80°43'40"W, oceanside, by hand in wrack line, 20 October 2000 (9 valves, FMNH 301429); FK-395, Snappers Ledge reef, 24°58.88'N, 80°25.36'W, in cavity of large sponge with red algae, 26 ft (7.9 m), scuba, M/S REPUBLIC IV, 27 March 2001 (1 pair, FMNH 301430); FK-459, Ft. Zacchary Taylor State Park, Key West, beach, shells washed ashore among rubble, 02 May 2001 (1 frag, AMNH 307737); FK-463, American Shoals, 24°31.541'N, 81°33.218'W, 5 ft (1.5 m), *Thalassia/Syringodium* seagrass and rubble, scuba, R/V FLORIDAYS, 20 July 2001 (3 pair, 4 valves, 2 frag, FMNH 301431); FK-499, Sand Key, 24°27.18'N, 81°52.79'W, beach to 16 ft (4.9 m) under ship, sand, rocks, patch reef, snorkeling, R/V EUGENIE CLARK, 24 July 2001 (2 frag, AMNH 307738); FK-539, south of Bahia Honda Key, west of Looe Key reef, 24°34.24'N, 81°16.64'W, 30.2–34.1 m (99–112 ft), sand and rubble, pipe dredge and triangle dredge, R/V EUGENIE CLARK, 28 July 2001 (1 juv valve, AMNH 308089); FK-547, Looe Key reef, 24°32.809'N, 81°24.158'W, 25 ft (7.6 m), spur and groove reef, scuba, R/V FLORIDAYS, 30 July 2001 (2 valves, AMNH 307614); FK-559, south beach of Loggerhead Key, Dry Tortugas, 24°37.790'N, 82°55.400'W, wrack line to 7 ft (2.1 m), by hand and snorkeling, R/V CORAL REEF II, 15 April 2002 (3 valves, FMNH 301432); FK-581, north shore of Loggerhead Key, Dry Tortugas, 24°37.871'N, 82°55.447'W, wrack line and shallow subtidal, by hand and snorkeling, R/V CORAL REEF II, 16 April 2002 (5 valves, FMNH 301433); FK-601, Hospital Key, Dry Tortugas, 24°38.970'N, 82°51.284'W, patch reef, sand, 16 ft (4.9 m), scuba and snorkeling, R/V CORAL REEF II, 18 April 2002 (1 valve, 3 frag, AMNH 307615; 1 pair, FMNH 296718); FK-606, southwest of Dry Tortugas, 24°30.009'N, 82°59.914'W to 24°29.970'N, 82°59.687'W, 28 m, triangle dredge, R/V CORAL REEF II, 18 April 2002 (1 frag, AMNH 307616); FK-615, Cosgrove Shoal, 24°27.486'N, 82°11.039'W, 9.7 m (32 ft), patchy rubbly reef with sponges, gorgonians, overhangs, sand flat, scuba, R/V CORAL REEF II , 20 April 2002 (2 pair, 3 valves, AMNH 307617); FK-620, Old Dan Bank, bayside of Long Key, 24°50.45'N, 80°49.63'W, *Thalassia* seagrass with *Halimeda, Porites*, sponges, hydroids, patches of sand/*Halimeda* hash, 1–2 ft (0.3–0.6 m), by hand, R/V FLORIDAYS, 16 and 18 July 2002 (2 valves, FMNH 301445); FK-622, directly off Keys Marine Laboratory, bayside of Long Key, 24°49.5'N, 80°48.9'W, seagrass bed with coral rubble, snorkeling, sieving, by hand, 0–1.5 m, 20 July 2002 (valves observed); FK-624, Horseshoe Reef, off Fat Deer Key, 24°39.91'N, 80°59.56'W, patch reef with sandy bottom, 24 ft (7.3 m), scuba, M/V SHUTTERBUG II, 20 July 2002 (3 valves, FMNH 301446); FK-625, Coffins Patch Sanctuary Preservation Area, off Crawl Key, 24°40.92'N, 80°58.26'W, patch reef with sand patches, gorgonian, pillar coral, 21 ft (6.4 m), scuba, M/V SHUTTERBUG II, 20 July 2002 (5 valves, FMNH 301447); FK-629, bayside of West Summerland Key (Spanish Harbor Keys), 24°39.3'N, 8118.2'W, among rocks along arms of quarry, to ca. 1 m, by hand, snorkeling, 21 and 26 July 2002 (1 spm alc [siphons photographed in sand, dissected], FMNH 301448; 5 pair, 4 valves, 2 juv valves [incl. photo voucher], FMNH 296719); FK-639, Coral Gardens inshore patch reef, oceanside of Lower Matecumbe Key, 24°50.23'N, 80°43.77'W, snorkeling, 1215 ft (3.6–4.6 m), Keys Marine Laboratory boat, 23 July 2002 (valves observed); FK-647, west side of Pigeon Key, 24°42.2'N, 81°09.3'W, *Thalassia/ Halodule/Syringodeum* seagrass on sand/ rubble, concrete bridge piers, 0.5–1 m, by hand, snorkeling, shovel/sieving (1 pair, NTM); FK-649, Sprigger Bank, bayside, just W of Everglades National Park border, 24°54.75'N, 80°56.24'W, *Thalassia/ Syringodeum* seagrass, 1–3 ft (0.1–0.9 m), snorkeling, shovel/sieving, Keys Marine Laboratory boat, 27 July 2002 (2 pair, 1 valve, FMNH 301449); FK-659, Pigeon Key, 24°42.2'N, 81°09.3'W, seagrass, scuba, 2–4 ft (0.6–1.2 m), 28 July 2002 (valves observed); FK-660, Old Dan Bank, bayside of Long Key, 24°50.08'N, 80°49.63'W, *Thalassia* seagrass with *Halimeda, Porites*, sponges, hydroids, patches of sand/*Halimeda* hash, 1–5 ft (0.3–1.5 m), snorkeling, R/V LAST MANGO, 28 July 2002 (2 pair, 5 valves, 3 frag, FMNH 301450); FK-661, Molasses Keys, south of center of Seven-Mile Bridge, north of westernmost island, 24°41.070'N, 81°11.483'W, sandy bottom, coral rubble, *Thalassia* seagrass, hot water (> 30°C), snorkeling, 1–6 ft (0.3–1.8 m), R/V FLORIDAYS, 04 August 2002 (5 valves [2 with breakage by predator], FMNH 301434); FK-662, Sombrero Reef, vicinity of buoy SO-3, 5 nmi south of Knights Key, 24°37.619'N, 81°06.528'W, sandy bottom adjacent to coral reef; scuba, 17–23 ft (5.2–7.0 m), R/V FLORIDAYS, 05 August 2002 (1 valve, 1 frag, FMNH 301435); FK-664, Molasses Keys, south of center of Seven-Mile Bridge, north of westernmost island, 24°41.070'N, 81°11.483'W, sandy bottom, coral rubble, *Thalassia* seagrass, strong current, snorkeling, 2–5 ft (0.6–1.5 m), R/V FLORIDAYS, 06 August 2002 (2 valves, FMNH 301436); FK-665, Coffins Patch pillars, south of Crawl Key, 24°40.899'N, 80°58.246'W, coral reef, sand plains, some *Thalassia* seagrass, scuba, 18–23 ft (5.5–7.0 m), R/V FLORIDAYS, 07 August 2002 (2 valves, FMNH 301437); FK-668, Money Key, oceanside of west end of Seven-Mile Bridge, off north and west ends of island, 24°41.009'N, 81°12.955'W, "ironshore" beach rock, sand, *Thalassia* seagrass, snorkeling, 0–5 ft (0–1.5 m), R/V FLORIDAYS, 09 August 2002 (1 pair, FMNH 301444); FK-672, John Sawyer Bank, 3 nmi north of western part of Key Vaca, bayside, 24°45.498'N, 81°06.621'W, coral rubble, *Thalassia* seagrass, strong current over shoal, snorkeling, 2–6 ft (0.6–1.8 m); R/V FLORIDAYS, 11 August 2002 (1 pair, 2 valves, 1 fresh frag, FMNH 301438); FK-673, Bethel Bank, 2 nmi N of Knights Key Channel, 24°43.796'N, 81°07.588'W, bayside, coral rubble, *Thalassia* seagrass, strong current over shoal, 3–5 ft (0.9–1.5 m), snorkeling, R/V FLORIDAYS, 11 August 2002 (1 valve, FMNH 301439); FK-674, Sombrero Reef, southwest area of lighthouse reef, 24°37.555'N, 81°06.729'W, spur and groove reef, rubble, scuba, 22–26 ft (6.7–7.9 m), R/V FLORIDAYS, 12 August 2002 (4 valves, 1 fresh frag, FMNH 301440); FK-675, Red Bay Bank, 3 nmi north of Pigeon Key, bayside, 24°45.1000'N, 81°08.647'W, very diverse habitat: coral, seagrass, many algae, snorkeling, 1–6 ft (0.3–1.8 m), R/V FLORIDAYS, 13 August 2002 (2 spm, 2 valves, FMNH 301441); FK-676, Rachel Bank, 2 nmi north of Key Vaca, bayside, 24°44.714'N, 81°04.599'W, muddy sand, seagrass, coral rubble, snorkeling, 35 ft (0.9–1.5 m), R/V FLORIDAYS, 13 August 2002 (5 spm, 7 valves, 1 fresh hinged frag, FMNH 296695); FK-677, Doughnut Reef, oval reef mass east of Coffins Patch (off Crawl Key), 24°41.507'N, 80°56.835'W, sand flat at reef edge, scuba, 23 ft (7.0 m), M/V SHUTTERBUG II, 13 August 2002 (1 valve, FMNH 301442); FK-678, bayside of West Summerland Key (Spanish Harbor Keys), 24°39.3'N, 81°18.2'W, inside western arm, scuba, 3–10 ft (0.9–3.0 m), 14 August 2002 (1 spm alc [dissected], 4 valves, FMNH 301443); FK-688, Conch Reef, oceanside of Key Largo, 24°57.380'N, 80°29.428'W, algae-covered reef, vertical walls and adjacent sand plains, max. 28 ft (8.5 m), scuba, R/V FLORIDAYS, 05 June 2003 (1 V, FMNH 302086; 2 LV, AMNH 308081); FK-689, northeast of Dove Key, oceanside of Key Largo, 25°03.055'N, 80°28.220'W, hard bottom with silty sand, sponges, gorgonians, 0.5–1.0 m, snorkeling, R/V FLORIDAYS, 06 June 2003 (1 juv pair, AMNH 308084); FK-692, Hen and Chickens patch reef, oceanside of Plantation Key, 24°56.099'N, 80°32.920'W, max. 21 ft (6.4 m), scuba and snorkeling, R/V

FLORIDAYS, 08 June 2003 (1 RV, 1 LV, AMNH 308087); FK-693, off Dove Key, oceanside of Key Largo, 25°03.039'N, 80°28.151'W, silty *Thalassia* seagrass and sand, 3–5 ft (0.9–1.5 m), snorkeling, R/V FLORIDAYS, 08 June 2003 (3 pair, 1 RV, 1 LV, AMNH 308083); FK-696, Sand Island (near Molasses Reef), 25°01.116'N, 80°22.046'W, patch reef with rubble, max. 22 ft (6.7 m), scuba, R/V FLORIDAYS, 10 June 2003 (1 pair, AMNH 308085); FK-698, Wolfe mooring buoy (near Three Sisters Reef), 25°01.311'N, 80°23.774'W, patch reef with adjacent *Thalassia* seagrass, max. 16 ft (4.9 m), scuba, R/V FLORIDAYS, 11 June 2003 (2 RV, 1 fragment, AMNH 308082); FK-701, off Dove Key, oceanside of Key Largo, 25°03.011'N, 80°28.163'W, silty *Thalassia* seagrass and sand, 1–2 ft (0.3–0.6 m), snorkeling, R/V FLORIDAYS, 12 June 2003 (5 pair, 1 RV, 1 LV, AMNH 308086). FK-702, seagrass flat off Yellowtail Inn, oceanside of Grassy Key, mile marker 58.3, 24°45.494'N, 80°57.179'W, 1–5 ft (0.3–1.5 m), snorkeling, 5–23 August 2003 (1 pair, 1 LV, FMNH 302071); FK-703, patch reef with sand pockets in vicinity of mooring buoy near "the Stake", Coffins Patch coral reef, oceanside of Grassy Key, 24°41.159'N, 80°57.836'W, 8–18 ft (2.4–5.5 m), snorkeling, R/V FLORIDAYS, 7 August 2003 (1 pair, 1 RV, FMNH 302079); FK-704, Sombrero Reef, vicinity of buoy SO-4, 5 nmi S of Knights Key, 2437.591'N, 81°06.563'W, sandy bottom immediately adjacent to spur & groove coral reef; scuba, 17–25 ft (5.2–7.6 m); R/V FLORIDAYS, 08 August 2003 (1 LV, FMNH 302072); FK-705, Doughnut Reef, oval reef mass E of Coffins Patch (off Crawl Key); 24°41.439'N, 80°56.862'W, patch reef surrounded by sand flats, scuba, 24 ft (7.3 m); M/S SEAFARI, 09 August 2003 (1 LV, FMNH 302073); FK-706, Elbow Reef, E of Coffins Patch (off Crawl Key); 24°41.551'N, 80°56.789'W, patch reef surrounded by sand flats, scuba, 19 ft (5.8 m); M/S SEAFARI, 09 August 2003 (1 RV, FMNH 302074); FK-710, "Porkfish" and "Hammer Ledge" reefs, E of Coffins Patch (off Conch Key); 24°42.038'N, 80°53.578'W, scuba, 19–25 ft (5.8–7.6 m); M/S SEAFARI, 11 August 2003 (2 RV, 2 frag, FMNH 302075); FK-711, patch reef with sand pockets in vicinity of mooring buoy 9, Coffins Patch coral reef, oceanside of Grassy Key, 24°41.131'N, 80°57.818'W, 18–20 ft (5.5–6.1 m), scuba; R/V FLORIDAYS, 12 August 2003 (1 LV, FMNH 302076); FK-714, vicinity of mooring buoy 1 at "Marker 48" patch sand and seagrass; 24°41.505'N, 81°01.528'W, 16–24 ft (4.9–7.3 m), scuba; R/V FLORIDAYS, 17 August 2003 (1 pair, 5 LV, FMNH 302077); FK-719, beach near moat wall, Fort Jefferson, Garden Key, Dry Tortugas, 24°37'50"N, 82°52'24"W, by hand, 21 August 2003 (1 RV, FMNH 302078);

Other Material Examined

Florida: Boynton, Lake Worth, T. L. McGinty! ANSP 195919 (1 pair); Lake Worth Inlet, C. T. Simpson! UMML 28.1729 (1 pair); South Lake Worth near Boynton, Kline! July 1944, DMNH 72175 (1 pair); Lake Worth, Lermond! August 1941, DMNH 153846 (3 pair); Lake Worth, south end, dredged in 6 ft (1.8 m), Lermond! 14 September 1937, DMNH 153848 (2 pair); Lake Worth, south end, Doremus! 1942, DMNH 63779 (2 pair); Lake Worth, south end, F. Lyman family! Summer 1944, FMNH 144097 (1 pair); Lake Worth, South Inlet, oyster reef, F. M. Bayer! USNM 890543 (1 pair with tissue); Boynton in Lake Worth, E Fal, sand pocket in rock reef, T. L. McGinty! June 1940, USNM 599285 (1 pair); Lake Worth, White collection, USNM 153360 (1 pair); Lake Worth, Singer Bridge, F. M. Bayer! USNM 890617 (2 juv pair); opposite Lemon City, C. T. Simpson! UMML 28.1731 (1 LV); Bal Harbor, Broad Causeway, dredgings, Poh! June 1975, DMNH 118270 (1 pair, 1 valve); Coral Gables, FMNH 54675 (1 pair); off Cape Florida, Florida, Finger Channel flats, Crovo! 05 April 1970, DMNH 30152 (1 pair); Cape Florida, Biscayne Bay, T. L. McGinty! 1937, ANSP 264016 (1 pair); Miami Bay area, flats off Cape Florida, Ingalls Family! 12 March 1967, AMNH 140432 (1 pair); Miami area, Biscayne Bay, flats off Cape Florida, W. E. Old! 12 March 1967, AMNH 136053 (2 pair); Cape Florida, T. L. McGinty! FMNH 26427 (2 valves); Cape Florida, near Miami, T. L. McGinty! June 1936, USNM 599308 (1 pair); Bear Cut, Key Biscayne, Miami, W. S. Bitler! 1963, AMNH 142323 (1 pair); Bear Cut, Key Biscayne, S. Sokoloff! 18 November 1961, AMNH 261423 (1 pair); Bear Cut, April 1939, UMML 28.45 (1 pair); Bear Cut, Hepler! DMNH 45331 (2 pair); Caesar Creek, Whitney! November 1956, DMNH 97311 (1 pair); Florida Keys, Lermond! DMNH 153830 (1 pair); Angelfish Creek [north of Key Largo, connecting Card Sound and Atlantic Ocean], Wisoff Collection, AMNH 120395 (1 pair); Key Largo, Nelson collection, FMNH 155544 (1 pair); Key Largo, T. L. Moise! August 1950, ANSP

193815 (1 juv pair); Key Largo, F. M. Bayer! June 1940, USNM 890827 (1 pair); Windley Key, Whale Harbor Channel, near bridge in 5–10 ft (1.5–3.0 m), T. R. Waller! Sta. 3, 31 August 1971, USNM 707750 (1 valve); Upper Matecumbe Key, Islamorada, on beach, 13 January 1978, BMSM 26108 (5 pair); Indian Key, D. V. Stingley! May 1959, BMSM 26109 (1 pair); Lower Matecumbe Key, Hausman! AMNH 133675 (1 pair); Conch Key, south end, J. J. Parodiz & Winters! 08 July 1976, CMNH 43728 (4 pair); Grassy Key, M. & S. Snyder! July 1966, ANSP 309750 (2 pair); Grassy Key, Minzak! February 1972, DMNH 93337 (3 pair); Crawl Key, 24°44’36"N, 80°58’47"W, beach, P. M. Mikkelsen & R. Bieler! 22 September 1996, AMNH 295180 (1 pair); Crawl Key, Richardson! DMNH 85844 (1 pair); Crawl Key, shallow water, J. M. Bijur! May 1964, AMNH 248309 (1 pair); Crawl Key, bayside, on flats at 1 ft (0.3 m), Raeihle! November 1961, AMNH 106142 (1 pair, figured Emerson & Jacobson, 1976: pl. 42, fig. 18); Crawl Key, bayside, on beach, D. Raeihle! November 1973, AMNH 179278 (1 pair); Crawl Key, bayside, D. Raeihle! AMNH 116658 (1 pair); Crawl Key, bayside, November 1959, Raeihle! AMNH 307848 (3 pair, 1 valve, live-collected); Crawl Key, G. Dingerkus & L. D. Uhler! 06 January 1977, AMNH 267424 (1 spm alc); Crawl Key, bayside, edge of borrow pit ½ mi north of mile marker 56, in weeds, M. J. de Maintenon! 24 June 1985, AMNH 307571 (1 pair); Bonefish Key, A. Koto! AMNH 133664 (1 pair) and FMNH 176293 (1 pair, 1 valve); Marathon Key, Florida Straits, K. C. Vaught Collection, AMNH 250783 (1 pair); Marathon, 1959, BMSM 26110 (2 pair); Marathon Key, south end, Jensen! 1962, DMNH 42547 (1 pair); Sombrero Reef, 25–30 ft (7.6–9.1 m), P. S. Mikkelsen! 21 May 1980, DMNH 180066 (2 valves); Washerwoman’s patch reef, 24°39’54"N, 81°04’14"W, M. Snyder! August 1966, ANSP 398069 (1 pair); Pigeon Key, 24°42’N, 81°09’W, M. Snyder! July 1966, ANSP 398068 (2 pair); Little Duck Key, A. Koto! 1955, FMNH 176330 (1 pair) and FMNH 176372 (1 pair [photo voucher]); Little Duck Key, shallow water, sand, F. Schilling! July 1968, FMNH 288716 (1 pair); Missouri Key, Richardson! DMNH 85835 (1 pair), Missouri Key, snorkeling, A. D. Barlow! 05 March 1967, AMNH 243914 (2 pair); Missouri Key, sand, F. Schilling! 16 July 1970, FMNH 288718 (1 pair); Bahia Honda State Park, Germer Collection, 11 July 1973, AMNH 269541 (1 pair); north of Bahia Honda State Park, shallow water, sand, R. Bieler & P. M. Mikkelsen! 25 March 1989, FMNH 288810 (1 spm alc); Bahia Honda Key, BMSM 26111 (1 pair); Spanish Harbor Key, beach, Piech! July 1980, DMNH143838 (1 pair); West Summerland Key, at entrance to dredge hole, L. Scheu Collection, 1984, AMNH 230097 (2 pair); Newfound Harbor Keys, living in shallow water, sand, November 1968, Raeihle! AMNH 307849 (1 pair); Torch Key channel, C. T. Simpson! UMML 28.1716 (4 pair); Sugarloaf Key, J. B. Clark! 23–24 May 1921, ANSP 9634 (1 juv pair); Boca Chica Key, H. A. Pilsbry! ANSP 100273 (1 valve); Stock Island, F. R. Kirtland! 1936, ANSP 167777 (1 pair); Key West, A. Koto! FMNH 176402 (1 pair); Key West, Nelson! FMNH 166745 (1 pair); Key West, coral banks at low tide, J. W. Milner! USNM 127385 (1 pair); Key West, Hawk Channel, 3–20 ft (0.9–6.1 m), *Eolis* sta. 65, J. B. Henderson Jr.! 15 May 1913, USNM 448344 (2 juv valves); Key West, reefs, rare, H. Hemphill! USNM 95672 (2 pair); Key West, Smith Shoals, *Eolis* sta. 335, J. B. Henderson Jr.! 1916, USNM 448343 (1 juv pair); Key West, N side, beach collecting, *Eolis* sta. 35, J. B. Henderson Jr.! 30 May (or 6 June) 1911, USNM 48340 (1 juv pair); Key West, USNM 406825 (2 pair); Key West, H. Hemphill! ANSP 52199 (2 pair); Key West, H. A. Pilsbry! March-April 1940, ANSP 175943 (1 pair); Key West, Sand Point, B. R. Bales! 1946, DMNH 21225 (2 pair) and ANSP 285406 (6 pair); Key West, at low tide, 3–4 ft (0.9–1.2 m), F. Schilling! 21 June 1967, FMNH 288719 (1 pair); Key West, C. T. Simpson! UMML 28.1748 (1 pair); Sand Key, Key West, Ostheimer! DMNH110654 (3 pair); near Boca Grande Key, UMML 28.1740, C. T. Simpson! (1 pair); Tortugas, Stm.! USNM 36403 (4 pair, 1 valve); Dry Tortugas, off Loggerhead Key, north end, beach collecting, *Eolis* sta. 367, J. B. Henderson Jr.! 13 June 1911, USNM 448347 (1 valve); Dry Tortugas, Garden Key, 3 mi out from red sea buoy, 5 dredge hauls, 14–15 fms (25.6–27.4 m), *Eolis* sta. 34, J. B. Henderson Jr.! 09 June 1911, USNM 448341 (4 pair, 1 valve); Tortugas, Bush Key, F. M. Bayer! USNM 890776 (1 pair); off Carabelle [Franklin County, panhandle of Florida], 29°15’N, 84°40’W, 90–100 ft (27.4–30.5 m), dredged, J Moore! ex M. & B. Naide, August 1966, ANSP 402130 (1 pair).

Texas: off Freeport, 28°13’N, 94°51’W, 27 ft (8.2 m), dredge, A. Kight! ANSP 338392 (1 pair).

Bahamas: Bahamas, J. B. Henderson Jr.! USNM 448342 (2 pair); PMM-1047 (wp277-R rubble), off Andros, 24°54'44.42"N, 77°53'51.80"W, rubble in back reef pavement zone with gorgonians, 7 ft (2.1 m), scuba, P. M. Mikkelsen, et al.! 29 August 2000, AMNH 305616 (1 valve); PMM-1090 (wp415-R), off Andros, 24°53'32.2"N, 77°53'51.4"W, thick *Thalassia* seagrass, 12 ft (3.6 m), scuba/snorkeling, P. M. Mikkelsen, et al.! 04 September 2000, AMNH 305617 (1 pair), FMNH 301425 (1 spm alc [95%]); PMM-1079 (wp427-R), off Andros, 24°55'24.8"N, 77°55'19.8"W, sand/algal plain, 5 ft (1.5 m), scuba/snorkeling, P. M. Mikkelsen, et al.! 02 September 2000, FMNH 296720 (1 pair); PMM-1063 (BH-R seagrass), oceanic blue hole off Blue Hole Cay, off Andros, 24°53'55.2"N, 77°55'12.1"W, *Thalassia* seagrass, 4 ft (1.2 m), scuba/snorkeling, P. M. Mikkelsen, et al.! 31 August 2000, AMNH 307572 (1 pair); East Andros Island, Calabash Bay, Abbott! February 1971, DMNH 29242 (1 pair); East Andros Island, Small Hope Bay, Abbott! DMNH 41253, March 1971 (1 valve); Chub Cay, Berry Islands, Moise! ANSP 193106 (1 pair); Chub Cay, Periwinkle Beach, K. C. Vaught Collection, April 1977, AMNH 250782 (1 pair); Grand Bahama Island, 26°31'N, 78°46'30"W, J. N. Worsfold! ANSP 375213 (2 pair); Grand Bahama Island, 26°31'00"N, 78°46'30"W, J. N. Worsfold! ANSP 375212 (1 juv valve); Grand Bahama Island, Running Mon Canal, 26°29'45"N, 78°41'45"W, J. N. Worsfold! ANSP 369788 (1 pair); Grand Bahama Island, C. C. Allen! 1922-1923, ANSP 133697 (1 pair); Grand Bahama island, Bottle Bay Canal, 26°39'30"N, 78°57'00"W, sediment, 5 ft (1.5 m), J. Worsfold! ANSP 371908 (1 pair); east end of Grand Bahama Island, Deep Water Cay, ca. 2.5 mi northwest of Sweetings Cay Light, intertidal sand and rocks, V. O. Maes! January 1965, ANSP 307688 (1 juv pair); Grand Bahama Island, F. H. Low Collection, AMNH 113790 (1 pair); Nassau, New Providence Island, Wards! (before 1893), FMNH 2741 (1 pair, 1 valve); Nassau, New Providence Island, Pope! FMNH 187147 (2 valves); Nassau, C. C. Allen! USNM 36617 (1 pair); New Providence Island, Dicks Point, McLean & Russell! July 1936, ANSP 169917 (2 valves); New Providence [Island], Lyford Cay, AMNH 80763 (2 pair); north coast of Hog Island, north of New Providence Island, R. Robertson! 11 September 1955, ANSP 299657 (1 juv pair); Great Abaco Island and Green Turtle Key, Abaco Islands, Cherokee flats, Great Abaco and Mendelson's flats, Heilman! DMNH 37728 (3 pair); Great Abaco Island and Green Turtle Cay, Cherokee flats, DMNH 37977 (5 pair); Great Abaco, Mendelson's flats, Heilman! February 1958, DMNH 86223 (5 pair, 2 valves); Great Abaco, Parrot Cays, west of Elbow [Little Guana] Cay, near octopus hole, R. Robertson! 14 August 1953, ANSP 299066 (3 pair); Great Abaco, west coast of north end of Elbow [Little Guana] Cay, mud/sand, *Halimeda* remains, *Thalassia* seagrass, 0.5–3 ft (0.15–0.9 m) and near octopus hole, R. Robertson! 04 September 1953, ANSP 298847 (1 pair, 1 juv pair); Abaco Island, Green Turtle Cay, Gwillim Bay, on sand on exposed sand bar at low tide, A. & A. Taxson! 10 June 1964, AMNH 111921 (4 pair) and AMNH 269540 (2 pair, ex D. Germer Collection); Abaco, Crab Cay, 2–4 ft (0.6–1.2 m), E. I. Wright! 1974, USNM 846377 (1 pair); Abaco, Marsh Harbor, O. Bryant! USNM 180541 (1 pair); east-central Eleuthera, north end of Half Sound, 25°07'45"N, 76°09'00"W, R. Robertson! 18 April 1984, ANSP 359292 (2 pair); Eleuthera, Savannah Island, Santy Point, W. J. Clench! May 1936, ANSP 173811 (3 pair); Eleuthera, Savannah Sound, Sandy Point, Cora Staples Collection, AMNH 306250 (1 pair); Eleuthera, Current, Current Club, A. Ross! 29 July 1963, AMNH 100174 (1 valve); Eleuthera Island, Doremus! DMNH 63778 (2 pair); Eleuthera Island, Sandy Point, Savannah Sound, Doremus! May 1936, DMNH 63780 (2 pair); Harbour Island, N end Eleuthera Island, Loc.114, Kline! 17 June 1949, DMNH72173 (1 pair); Eleuthera, N end Half Sound, E central Eleuthera Island, Abbott! June 1976 DMNH 115333 (1 valve); Exuma Island, Rolle Town, Loc.16, Kline! 11 July 1951, DMNH 72174 (1 pair); southern Exuma Cays, north of Leaf Cay, R. Robertson! 07 July 1957, ANSP 285738 (1 pair); Bimini, near Bailey Town, Bimini Lagoon, R. Robertson! 1957–1958, ANSP 326271 (1 valve); South Bimini, east of Nixon's Harbour, R. Robertson! 1957–1958, ANSP 325603 (1 pair); Bimini, 1.75 mi southeast of Orange Cay, 23 ft (7.0 m), R. Robertson! 1957–1958, ANSP 325698 (1 juv valve); Bimini, South Cat Cay, grassy, T. L. Moise! ANSP 193577 (1 pair); Bimini, around Risty Causeway, Pigeon Cay, Steger! April 1956, DMNH 107635 (1 pair); San Salvador Island, W Pigeon Creek, beach, Piech! February 1977, DMNH 143251 (1 pair).

Turks and Caicos: Providenciales, Water Cay, beach, Piech! February 1978, DMNH 144123 (1 pair).

Cuba: east of Tarallones de Arena, near Santiago, sand beach, R. E. Dickerson! ANSP 182932 (3 valves); Paradise Island, Oriente, Christofferson! 17 April 1949, FMNH 144071 (4 valves); west of Guardalavaca, eastern shore near Playa Esmeralda, Province Holguin, K. & Ch. Schniebs! December 2001, 1 pair, MTD 43828; Guantanamo, E. O. Mitchell et al.! 1930, USNM 405334 (1 valve); Cayo Hutia Reef, *Barrera* Expedition sta. 218, USNM 448345 (2 pair); Esperanza, 2–3 fms (3.6–5.5 m), *Barrera* Expedition sta. 210, USNM 448346 (1 pair); Varadero Beach, *Barrera* Expedition sta. 213, USNM 448348 (1 juv valve).

Cayman Islands: Grand Cayman Island, Gun Bay, near Blakes', mud and turtlegrass flats, A. J. Ostheimer III! ANSP 199513 (1 pair); Grand Cayman, North Sound, Jensen! August 1970, DMNH 39561 (1 pair).

Jamaica: Harboreale, near Annotta Bay, St. Mary, Orcutt! USNM 440717 (1 valve); Black River, St. Elizabeth, Orcutt! USNM 441413 (1 valve).

Hispaniola: Haiti, off Port-au-Prince, southeast side of Grand Bans, east side of reef, G. Goodfriend! 25 June 1972, AMNH 177703 (1 pair); Haiti, Cape Haitien, American Haitien Dev. Company, Krieger! USNM 487861 (1 valve); Santo Domingo, Monte Christi, W. J. Clench et al.! July 1937, ANSP 173105 (2 valves); Santo Domingo, Monte Cristi, Doremus! July 1937, DMNH 63777 (2 pair).

Puerto Rico: Puerto Rico, Stearns! USNM 54091 (1 pair); El Deseches Island, Mayaguez B., F. A. Gallardo! USNM 464243 (1 valve); Bahia Bramadero [south of Mayaguez], G. L. Warmke! November 1956, ANSP 222755 (1 valve); Puerto Rico, Richardson, DMNH-85845 (2 pair).

U.S. Virgin Islands: St. Thomas, W. A. Haines Collection, pre-1895, AMNH 31868 (9 pair, including largest recorded specimen); St. Thomas, M. Petit! USNM 250151 (1 pair); St. Thomas, Petit collection, USNM 530502 (1 pair, 2 valves, 1 juv valve); St. Thomas, Lindberg Beach, D. M. Barringer! 1936, ANSP 166919 (1 valve); St. Thomas, Swift Collection, ANSP 53580 (5 pair, 2 juv pair); St. Thomas, ZMB-104283 (1 pair); St. Thomas, ZMB-104287 (1 pair).

British Virgin Islands: Peter Island, Little Harbour, R. H. Pine! July 1976, FMNH 197453 (1 valve); Seal Dog Islands, R. H. Pine! August 1976, FMNH 197476 (1 pair); Tortola, east of Roadtown, H. G. Richards! ANSP 244999 (1 juv valve); Tortola, Kjaer! USNM 3208 (1 pair); Tortola, K. Lamprell! 25 September 1980, AMNH 303476 (1 pair); Gorda Island, Colquhon Reef, Bredin-Smithsonian Expedition sta. 37–58, Schmitt et al.! 07 April 1958, USNM 735909 (1 pair).

Antigua: Falmouth Harbor, beach, SUI Expedition, J. B. Henderson Jr.! 1918, USNM 500994 (1 pair).

Grenada: South Grenada, Little Bacaye Harbor, silt, *Thalassia* seagrass, sand patches, R. Ostheimer and Buerk! 23 January 1964, ANSP 297064 (1 pair).

Mexico: Isla Mujeres, K. C. Vaught Collection, AMNH 250781 (1 pair).

Belize: east-southeast of Punta Negra, 16°16'15"N, 88°32'10"W, R. Robertson! 23 August 1961, ANSP 281836 (1 juv valve); north of Tarpon Cay, shallow *Acropora cervicornis* reef, 16°37'05"N, 88°09'05"W, R. Robertson! 17 August 1961, ANSP 282574 (1 valve); Glovers Reef, NE Cay, R. S. Houbrick! USNM 771205 (1 pair).

Honduras: NW shore Bonacca Island, L. Kornicker! July 1963, USNM 667961 (4 valves).

Costa Rica: Port Limon, Wailes! USNM 187276 (1 pair).

Panama: Payardi Island, NW end, W. P. Woodring! 13 December 1959, USNM 67821 (1 valve); Payardi Island, NW end, 6 mi NE of Colon, suction dredge at refinery site, W. P. Woodring! 13 December 1959, USNM 637931 (1 valve); Payardi Island, Minas Bay, E of Colon, R. H. Stewart! USNM 734522 (3 valves).

Colombia: Old Providence Island, Sid Anderson! January–March 1966, AMNH 138019 (1 pair); San Andres Island, S. Anderson! January 1966, AMNH 137541 (1 valve, 1 frag); vicinity of Cartagena, T. A. Link! USNM 364301 (3 valves); Cartagena, R. Pfaff! 1959, FMNH 78686 (1 pair).

Netherlands Antilles: Aruba, M. R. Barnes! USNM 619369 (1 valve); Bonaire, Abbott! November 1972, DMNH 72707 (1 pair); Bonaire, Abbott! February 1973, DMNH 72794 (1 pair); Curaçao, N. Dearborn! 1908, FMNH 12764 (1 valve, subfossil?).

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ANATOMY AND SYSTEMATICS OF NORTHWESTERN ATLANTIC *DONAX* (BIVALVIA, VENEROIDEA, DONACIDAE)

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ABSTRACT

A morphological examination of two nominal species of northwestern Atlantic donacids, *Donax fossor* and *D. variabilis*, was performed to resolve current taxonomic discrepancies. Specimens from New Jersey, South Carolina, and Florida were studied confirming the typical anatomical bauplan for the family as previously reported. Detailed investigation of all organ systems revealed a series of differences, mainly in the shell, mantle border papillae, siphonal tentacles and papillae, and digestive system, supporting separation of the two species. Other shared morphological features, such as the gill muscle, pallial muscles of the siphonal chamber, the glandular dorsal gastric caecum, and length of the style sac, have potential value for further functional and systematic studies.

Key words: *Donax fossor*, *Donax variabilis*, differentiation, distribution, western Altantic.

INTRODUCTION

The systematics of the genus *Donax* along the Atlantic coast of the United States has been problematic for the last three decades. The nomenclature of *Donax variabilis* Say, 1822, which occupies the intertidal zone of sandy beaches from Virginia to Mississippi, has been particularly confusing. *Donax variabilis* became a primary junior homonym when *Latona variabilis* Schumacher, 1817, was proposed as a new name for *Donax cuneatus* Linnaeus, 1758 (Morrison, 1971). Because *Latona* is considered a subgenus of *Donax*, the name *D. variabilis* Say is thus preoccupied. Morrison's (1971) revision of the group identified the next available name for this species, *D. protracta* Conrad, 1849. Morrison considered *D. protracta*, from the southeastern coasts of the United States and eastern Gulf of Mexico, to be a subspecies of *D. roemeri* Philippi, 1849, from the northern and western Gulf of Mexico. Based on morphological differences between the two forms, Morrison designated the eastern forms as *D. roemeri protacta* Conrad, 1849, and the western forms as *D. roemeri roemeri* Philippi, 1849, because the publication date of *D. roemeri* was five months prior to that of *D. protracta*. Later, Boss (1970) proposed conservation of the name *D. variabilis* Say, 1822, to the International Commission on Zoological Nomenclature and it was subsequently conserved (Melville, 1976).

In addition to his recognition of *D. roemeri roemeri* and *D. roemeri protacta,* Morrison (1971) recognized four other species of *Donax* inhabiting the eastern shores of the United States: *Donax fossor* Say, 1822, from Cape Hatteras, North Carolina, to New Jersey and occasionally the southern shores of Long Island; *D. parvula* Philippi, 1849, from North Carolina to southern Florida; *D. dorotheae* Morrison, 1971, along the shores of the northeastern Gulf of Mexico; and *D. texasianus* Philippi, 1847, along the shores of Louisiana, Texas and Mexico.

Subsequent analysis of RAPD DNA markers failed to support Morrison's distinction between the subspecies *D. roemeri roemeri* and *D. roemeri protractra* (Adamkewicz & Harasewych, 1996). The analysis also demonstrated that *D. parvula* was indistinguishable from *D. fossor*, and *D. dorotheae* was indistinguishable from *D. texasianus*, with the latter of each pair having taxonomic priority. That analysis simplified the biogeography of *Donax*; *D. variabilis* shares the Atlantic coast with *D. fossor* and the Gulf coast with *D. texasianus.*

Even in older literature, taxonomic problems are notable. Say (1822) described two similar species of *Donax*, *D. fossor* ("the digger"), a northern form inhabiting the coasts of New Jersey and Maryland, and *D. variabilis* ("highly

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variable"), a southern form from the coasts of Georgia and eastern shores of Florida. Based on the original species descriptions, differentiating the two species is quite difficult. Size, color, sculpture, and thickness of the shell valves are most often used to differentiate the two species (Say, 1822; Chanley, 1969). *Donax variabilis* reaches a length of 19 mm, exhibits an wide variety of colors, and displays radial shell sculpture that is more pronounced on the posterior slope (Say, 1822; Chanley, 1969; Morrison, 1971). *Donax fossor* reaches 13 mm length, exhibits only "yellowish" or "whitish" colors, has smooth radial sculpturing over the entire shell and exhibits thickened valves at the anterior end to produce "lips" (Say, 1822; Chanley, 1969; Morrison, 1971). The escutcheon area of *D. variabilis* juveniles of about 5 mm in length is more rounded toward the vertical, whereas in *D. fossor*, the same is regularly sloping parallel to the rounded posterior ridge (Morrison, 1971). *Donax fossor* is believed to inhabit the surf and subtidal zones in the winter, while *D. variabilis* inhabits the intertidal zone throughout the year (Morrison, 1971).

These two species are so similar that the populations of New Jersey have often been labeled *D. variabilis* (e.g., Johnson, 1927; A. E. Wood & H. E. Wood, 1927; McDermott, 1983; Alexander et al., 1993), which exacerbates taxonomic confusion in the northern limit of *Donax* on the Atlantic coast of North America. Some authors accept the validity of these two species (e.g., Johnson, 1934; Morris, 1947; Miner, 1950; Morrison, 1971; Abbott & Morris, 1995), while others suggest that the two are conspecific (Abbott, 1954, 1974; Chanley, 1969). For example, Chanley (1969) suggests that *D. fossor* is merely a summer range extension of *D. variabilis*, based on sporadic populations of *Donax* on Long Island, New York, that do not overwinter. Chanley (1969) hypothesized that these northern populations were actually *D. variabilis* recruited from larvae swept north of the sustainable species range due to fortuitous warm-water currents, and that conchological differences between the two species are merely ecophenotypic. However, Morrison's (1971) revision of Chanley's specimens concluded that *D. fossor* is not a summer range extension of *D. variabilis*, further supporting the distinction between the two species.

According to Morrison (1971), *Donax variabilis* is not found north of Virginia Beach, Virginia, and *D. fossor* is not found south of Nag's Head, North Carolina. Thus, their ranges do not overlap until Virginia Beach, Virginia. The objective of this study was to compare the anatomy of specimens from Florida and South Carolina (supposedly *D. variabilis*) to that of specimens from Avalon, New Jersey (supposedly *D. fossor*), to provide evidence for confirming or refuting the biological validity of the two species along the east coast of the United States.

Anatomical investigations have been performed for about ten species of donacids (e.g., Ridewood, 1903; Pelseneer, 1911; Graham, 1934; Yonge, 1949; Duval, 1963; Nakazima, 1965; Wade, 1969; Narchi, 1972, 1978; Mouëza & Frenkiel, 1974, 1976, 1978; Odiete, 1981; Hodgson, 1982; Ansell, 1983; Salas-Casanova & Hergueta, 1990; Passos, 1998), however, none has been published on the species analyzed here. Those papers provide a secure scenario for discussion of the anatomical characters at the species and family level.

MATERIAL AND METHODS

Specimens were collected and fixed directly in 70% ethanol. Gross dissections were performed with the specimen immersed in fixative under a stereomicroscope. Histological 5-µm serial sections of partial regions were stained with Mallory's tristain. All drawings were made with the aid of a camera lucida.

Abbreviations used in figures: am, anterior adductor muscle; an, anus; au, auricle; cm, cruciform muscle; cv, ctenidial (efferent) vessel; dd, ducts to digestive diverticula; dg, digestive diverticula; dh, dorsal hood; di, inner demibranch; do, outer demibranch; dv, dorsal portion of outer demibranch covering visceral mass; es, esophagus; fe, foot elevator muscle; ff, fecal furrow; fm, posterior foot retractor muscle; fp, foot protractor muscle; fr, anterior foot retractor muscle; ft, foot; gf, ventral gastric fold; gm, gill retractor muscle; go, gonad; gs, gastric shield; id, insertion of outer demibranch in mantle; in, intestine; ip, inner hemipalp; is, septum in siphonal base separating infra- and suprabranchial chambers; ki, kidney; mb, mantle border; mm, mantle muscles of siphonal chamber; mp, mantle papillae; op, outer hemipalp; pa, posterior adductor muscle; pc, pericardium; pd, dorsal caecum; pp, palp; sc, siphonal chamber; se, excurrent siphon; ri, ridge in esophageal insertion in stomach; rt, rectum; sh, shell; si, incurrent siphon; sm, siphonal retractor muscle; ss, style sac; st, stomach; ty, typhlosole; um, fusion between left and right mantle lobes; ve, ventricle; vg, visceral ganglia; vm, visceral mass.

Abbreviations of institutions: FMNH, Field Museum of Natural History, Chicago; MZSP, Museu de Zoologia da Universidade de São Paulo, Brazil; USNM, National Museum of Natural History [United States National Museum], Washington, DC.

SYSTEMATICS

Donax fossor Say, 1822

(Figs. 1–5, 11, 12, 14, 16–26)

Synonymy (for additional references, see Morrison, 1971: 456):

Donax fossor: Abbott, 1974: 509 (as form of *D. variabilis*); Emerson & Jacobson, 1976: 415–416, pl. 43, fig. 15; Abbott & Morris, 1995: 91; Adamkewicz & Harasewych, 1996: 97–103.

Donax variabilis: McDermott, 1983: 529–538; Alexander et al., 1993: 289–303.

Diagnosis

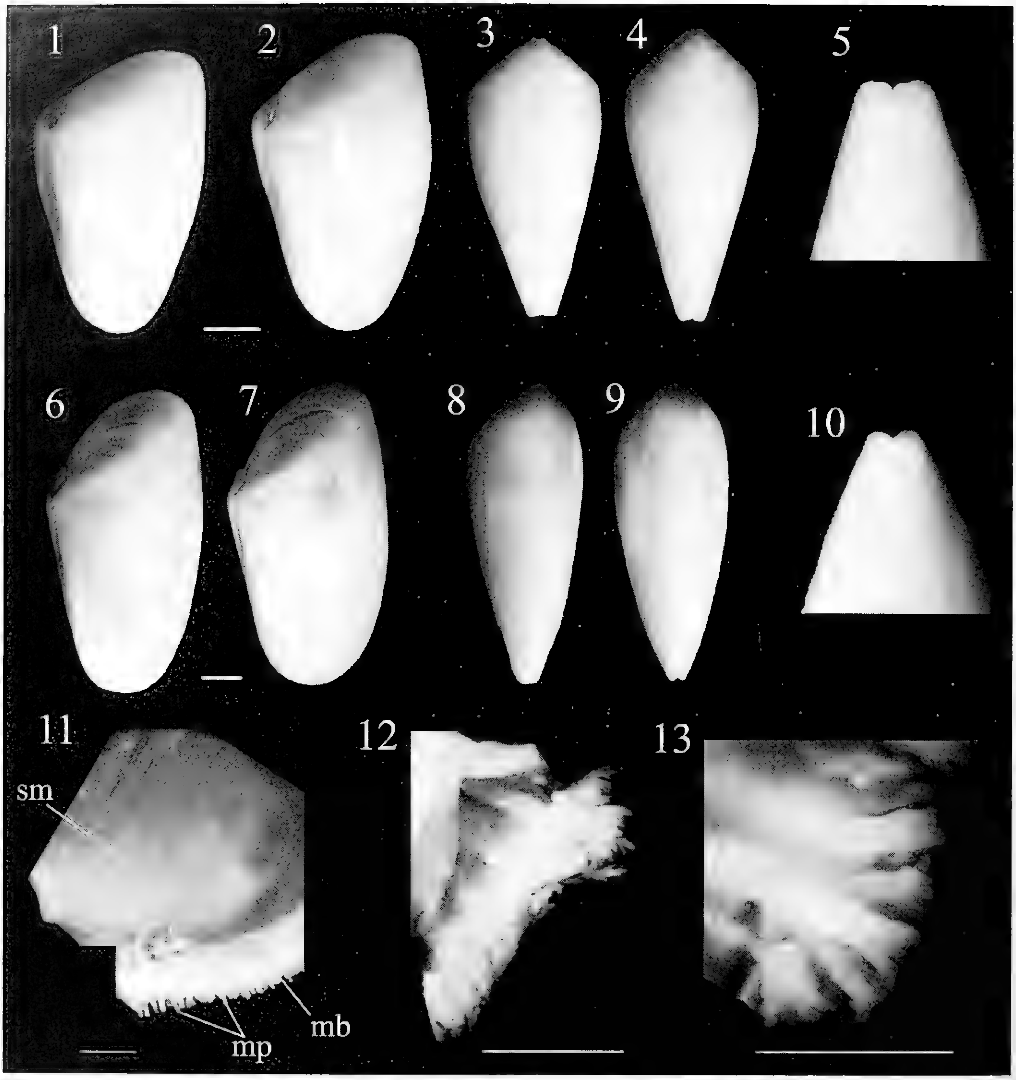
Shell triangular; anterior (pedal) edge very thick; posterior region flattened, with a flattened posterior margin. Mantle edge and siphons with large number of papillae. Gastric style sac almost straight, with distal region positioned in ventral region of visceral sac. Intestine bearing few undulations.

Description

Shell (Figs. 1–5, 14): Up to 13 mm length. Color varying from pure white to yellowish. Outline somewhat triangular; general shape cuneiform; anterior region with very thick edge, producing a strong slope. Umbo located in posterior third of hinge, weakly protruded, rounded. Outer surface smooth, bearing only concentric undulations. Hinge with three teeth in left valve, including small tooth just anterior to umbo, another two cardinal teeth at posterior level of ligament (Fig. 14, arrows) of similar size, transverse, separated by short depression. Right valve with single small, transverse tooth articulating between two cardinal teeth of left valve; also bearing sockets for teeth of left valve.

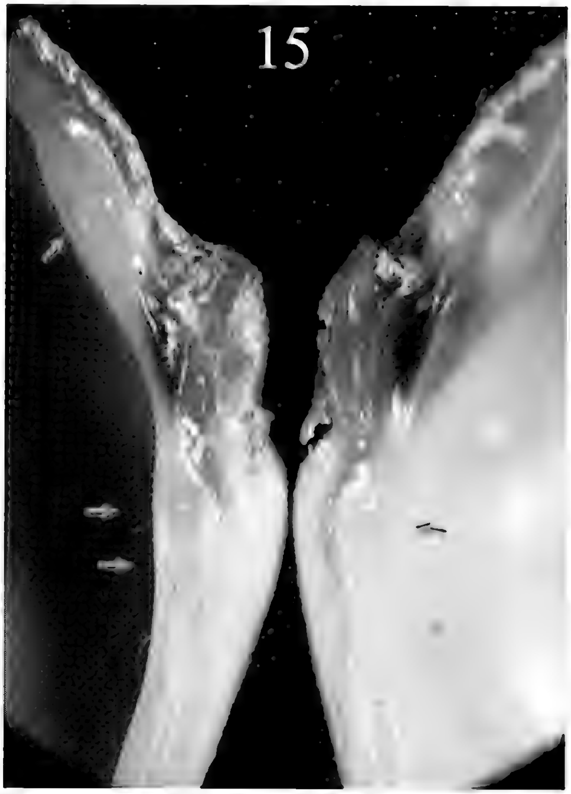
Mantle: Mantle border of somewhat uniform width along its length; mostly not fused, except in siphonal area and short portion ventral to them (Figs. 18, 20, um). Mantle border with two folds, each with series of small papillae of uniform size; each papilla long, slender (Figs. 11, 18, 20), with longitudinal, narrow furrow along outer side; tip concave, edges slightly projecting. Siphons separated from each other, similarly sized (Figs. 18, 20), each protected by cavity formed by mantle, depth about one-quarter of animal's length. Siphonal walls thickly muscular, basal region thinner, with muscle fibers arranged radially like a fan (Figs. 11, 20), originating from pallial sinus of shell. Incurrent siphon with 6–7 larger folds projecting inwardly, each bearing several papillae on outer surface (Figs. 12, 16, 17, 20), smaller and simpler tentacles among large papillae (Figs. 16, 17). Excurrent siphon with simpler tentacles than incurrent siphon (Fig. 20); tentacles narrow, with 2–3 papillae on distal end; fecal groove narrow, shallow, running longitudinally along internal ventral surface of excurrent siphon (Fig. 20, ff), terminating in a furrow on siphonal edge between two tentacles. Cruciform muscle located on ventral edge between middle and posterior thirds of mantle edge, at base of incurrent siphon (Figs. 18, 20), inside mantle fusion (Fig. 21); anterior branches longer and narrower, inserted on shell tangentially; posterior branches broader, shorter, inserted on shell almost perpendicularly (Fig. 21). Several radial muscle fibers connecting posterior edge of posterior adductor muscle with mantle border, becoming successively larger ventrally, abruptly terminating in middle region of siphonal area; ventral fibers thicker, branched distally (Fig. 23).

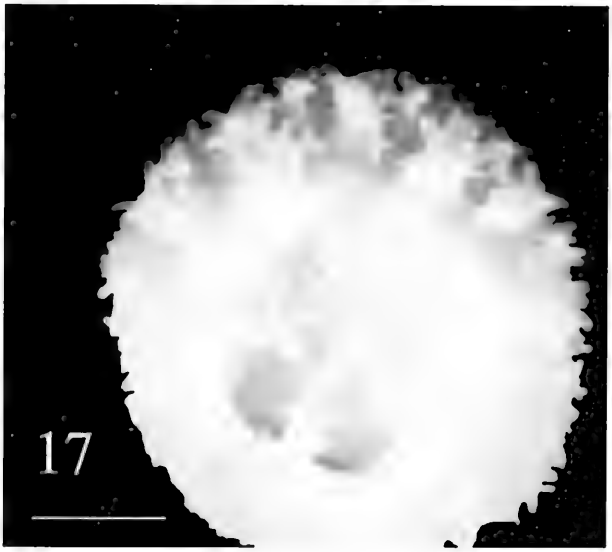
Mantle Organs: Pallial cavity very ample (with only narrow dorsal portion not covered by cavity) (Fig. 18). Gills small, occupying about one-third of pallial cavity (Fig. 18). Outer demibranch shorter than inner demibranch anteriorly, gradually becoming about same width posteriorly. Both demibranch ventral edges simple, lacking food grooves (Figs. 18, 19). Gill insertion on visceral mass between demibranchs, that of inner demibranch (on visceral mass) more ventral; outer demibranch with portion dorsal to gill insertion, covering visceral mass (Fig. 19), with shallow longitudinal furrow separating



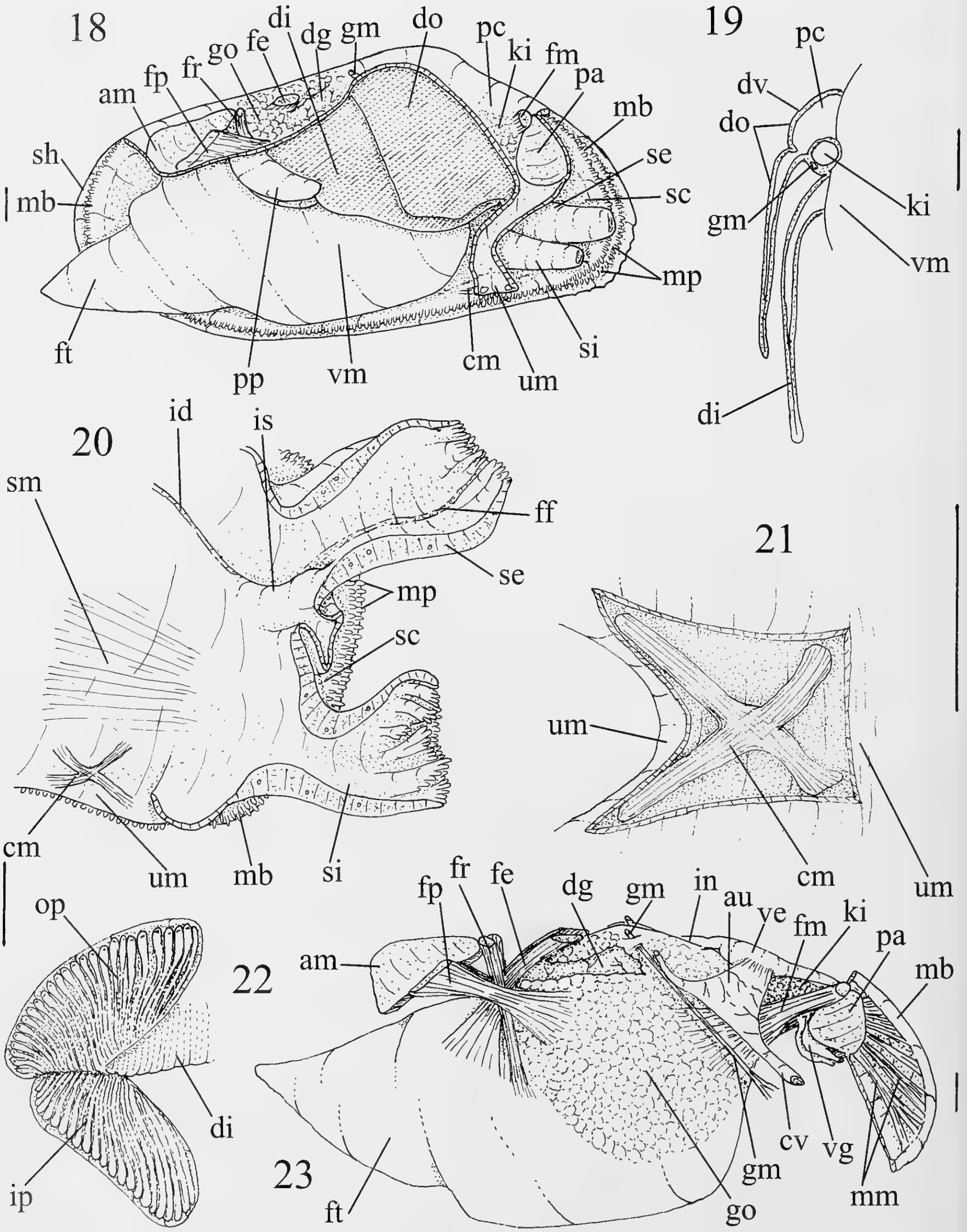
FIGS. 1–13. *Donax* shells and mantle. FIGS. 1–5: *Donax fossor* shells, two specimens MZSP 36508 (New Jersey); FIGS. 1, 2: Right lateral view; FIGS. 3, 4: Ventral view; FIG. 5: Detail of anterior region of Fig. 4; FIGS. 6–10: *Donax variabilis* shells, two specimens MZSP 36509 (South Carolina); FIGS. 6, 7: Right lateral view; FIGS. 8, 9: Ventral view; FIG. 10: Detail of anterior (foot) region of Fig. 9; FIG. 11: *D. fossor*, left mantle lobe, inner view, detail of siphonal basal region; FIG. 12: *D. fossor*, incurrent siphon, detail of apical region opened longitudinally, showing tentacles and papillae on inner edge; FIG. 13: Same for *D. variabilis*, showing more weakly developed tentacles and papillae. Scales = 2 mm.

this portion from remaining demibranch, connecting to visceral mass far dorsal of gill insertion. Gill dorsal and ventral connections to visceral mass cilial only. Gills connected to one another posterior to visceral mass in median line; no other anatomical gill connection, either with mantle (only by cilia) or with posterior adductor muscle. A communication between infra- and suprabranchial chambers remaining in contracted gill condition (Fig. 20). Mantle transverse septum in ventral base of excurrent siphon, separating infra-





FIGS. 14–17. *Donax* hinges and siphons. FIG. 14: *Donax fossor* hinge, left valve at left, arrows indicating teeth. Scale = 1 mm; FIG. 15: Same for *D. variabilis*; FIG. 16: *D. fossor*, extended incurrent siphon, dorsal-slightly apical view. Scale = 0.5 mm; FIG. 17: Same, apical view, showing fully extended tentacles and papillae. Scale = 0.5 mm.



FIGS. 18–23. *Donax fossor* anatomy. FIG. 18: Whole specimen, left view, left mantle lobe partially removed (except for portion in siphonal base); FIG. 19: Left gill, transverse section at mid-region, with some adjacent structures; FIG. 20: Siphonal region, left view, both siphons opened longitudinally along their left side; FIG. 21: Detail of posteroventral union of mantle lobes, at base of incurrent siphon, inner view, with inner layer of tissue removed; FIG. 22: Left labial palp, outer hemipalp deflected, with adjacent region of inner demibranch; FIG. 23: Foot and visceral mass, left view, emphasizing main muscle system, pericardial structures, topology of visceral glands, gill muscle and mantle muscles shown in situ. Scale bars = 1 mm.

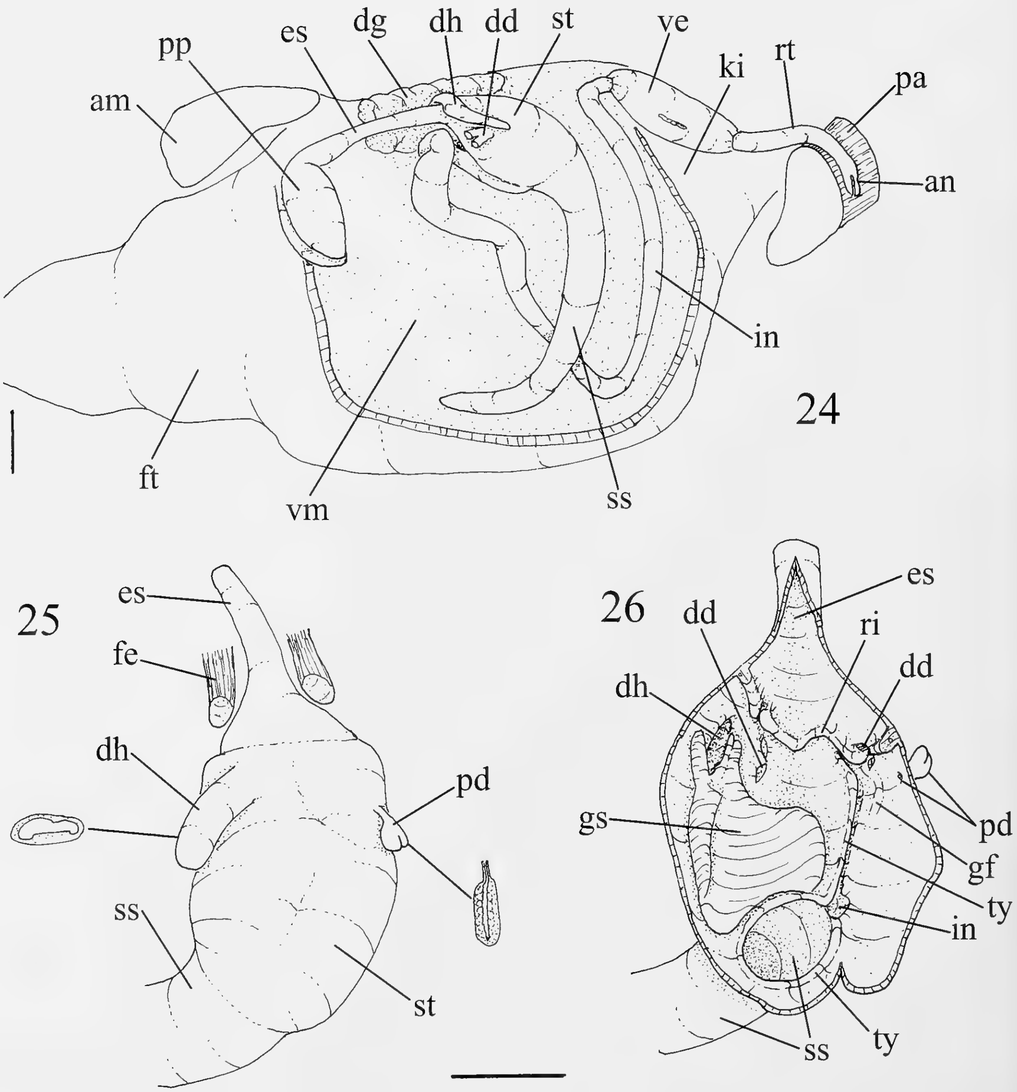
and suprabranchial chambers, somewhat short (Fig. 20, is). Palps long, curved, slightly triangular, located in anteroventral corner of inner demibranch, relatively small (Fig. 18); outer surface smooth; inner surface (Fig. 22) with several uniform transverse folds, somewhat parallel to palp posterodorsal edge; dorsal portion of folds very narrow, ventral portion broader, a short transverse whitish furrow located in distal end of each fold of outer demibranch (Fig. 22, op); folds ending short distance from palp inner edge, producing a narrow smooth margin. Palps and palp folds gradually becoming shorter toward anterior, a smooth inner area in palp portion surrounding mouth.

Foot and Main Muscle System: Foot large, about half of body size; triangular, tip broadly pointed, laterally flattened, bent in retracted condition (Figs. 18, 23). Adductor muscles similarly sized (Figs. 18, 23); each with ventral region somewhat circular, dorsal somewhat pointed. Anterior adductor muscle close to anterodorsal shell edge. Posterior adductor muscle at middle level of posterior shell edge. Paired anterior protractor muscles broad, thin, flat, originating in posteroventral edge of anterior adductor muscle, passing posteroventrally to insert fan-like on lateral wall of visceral mass (Figs. 18, 23, fp). Paired anterior pedal retractor muscles (Figs. 18, 23, fr) long, flat, narrow, slender, originating on shell just posterior to anterior adductor muscle, internally crossing anterior protractor muscles, passing superficially posteroventrally, inserting fan-like in middle region of transitional area of foot-visceral mass. Paired pedal levator muscles (Figs. 18, 23, 25, fe) narrow, long, cylindrical, originating in umbonal cavity at some distance posterior to anterior adductor muscle, running ventrally and anteriorly close to median line and close to one another, covered laterally by anterior retractor muscles, inserting in transitional area of foot-visceral mass. Paired posterior pedal retractor muscles (Figs. 18, 23, fm) originating on shell just dorsal to posterior adductor muscle, passing anteroventrally, narrow in posterior half, gradually becoming broad in anterior half, inserting on outer surface of posterior region of visceral mass. Paired gill retractor muscles very narrow, thin (Figs. 18, 19, 23, gm), originating on very small area of umbonal cavity at some distance posterior to levator muscles, penetrating pallial cavity between demibranchs, passing along gill to posterior end, becoming thinner and more diffuse (Fig. 23).

Visceral Mass: Internal organs visible by transparency only in narrow dorsal umbonal region (Fig. 18). Digestive diverticula pale green in preserved specimens, somewhat small, surrounding gastric area in dorsal region of visceral cavity. Gonad very large (Fig. 23), cream-colored, occupying most of visceral cavity, surrounding all visceral structures except renopericardial organs and some portions of digestive diverticula.

Circulatory and Excretory Systems: Pericardial cavity relatively small, located just anterior to posterior adductor muscle (Figs. 18, 23). Paired auricles triangular, with thin, transparent walls, central region connecting directly to gill, anterior and posterior vertices connecting to relatively short efferent gill vessels (Fig. 23). Auricles connecting to ventricle laterally. Ventricle surrounding intestine. Kidney whitish, mostly solid, located ventral to pericardium, compressed by posterior pedal retractor muscles, gonad and posterior adductor muscle.

Digestive System: Mouth somewhat small, in central region between palps. Esophagus relatively long, dorsoventrally flattened, away from anterior adductor muscle (Fig. 24). Stomach (Figs. 24–26) ovoid, located in umbonal region of visceral mass totally surrounded by digestive gland. Gastric dorsal hood narrow, about half of stomach length, originating close to median line, situated on left side covering dorsal surface of stomach (Figs. 24, 25, dh); inner surface smooth, except for broad, low longitudinal fold on ventral surface (Figs. 25–26). Dorsal gastric caecum (Figs. 25, 26, pd) small, generally bifid; walls whitish, glandular, with inner space narrow; connecting to stomach by very narrow duct to anterior third of stomach left-dorsal side (Fig. 25). Inner surface of posterior esophagus smooth; esophageal junction with stomach marked by tall, transverse typhlosole almost entirely surrounding this insertion, except at two narrow portions in lateroventral region where pair of furrows begin, running toward ducts of digestive diverticula (Fig. 26). Digestive diverticular apertures located lateroventrally in anterior gastric region. Dorsal hood aperture just dorsal of left apertures of digestive diver-



FIGS. 24–26. *Donax fossor* anatomy. FIG. 24: Visceral mass showing digestive system in situ, left view, with some adjacent structures; left wall of visceral sac, gonad and part of digestive diverticula removed; FIG. 25: Stomach, dorsal view, with some adjacent structures; with transverse sections of dorsal hood and dorsal caecum; FIG. 26: Same, left wall sectioned longitudinally and deflected, exposing inner surface. Scale bars = 1 mm.

ticula; transverse, low fold (closer to dorsal hood aperture) separating the two digestive diverticula apertures, bearing short projection of gastric shield (Fig. 26). Aperture of gastric dorsal caecum immediately dorsal to right aperture of digestive diverticula; deep, narrow furrow running posteriorly from right aperture of digestive diverticula, along ventral-right inner gastric surface, to intestinal origin. Gastric shield occupying about one-third of inner gastric surface, located in ventral and left inner regions (Fig. 26). Intestine and style sac origins adjacent (that of intestine right-anterior); narrow low fold almost entirely surrounding style sac origin, except for short portion adjacent to intestinal origin (Fig. 26). Style sac entirely separated from intestine, very long (longer than dorsoventral height of visceral cavity), passing ventrally, gradually narrowing, with tip somewhat pointed, curved forward (Fig. 24). Intestine mostly narrow, from origin in posteroventral region of stomach, to right of style sac, passing anteriorly, contouring ventral gastric region to left-anterior side, abruptly twisting towards right, passing sinuously posteroventrally, crossing right side of style sac ventral third; in posteroventral region of visceral cavity curving dorsally, to region just posterior to stomach; curving abruptly toward anterior, crossing pericardium and posterodorsal surface of posterior adductor muscle (Fig. 24). Anus in middle region of posterior adductor muscle, bearing short longitudinal, narrow notch on median line (Fig. 24, an).

Genital System: Gonad apparently dioecious.

Central Nervous System: Not seen in detail, except for pair of large visceral ganglia (Fig. 23) close to one another on posteroventral surface of posterior adductor muscle.

Measurements (length x dorsoventral height x lateral width, in mm): MZSP 36508: no. 7, 16.5 x 9.1 x 5.8; no. 8, 10.4 x 6.0 x 3.6.

Material Examined: U.S.A.: New Jersey; 66th St., Avalon, MZSP 36508, 13 specimens (Joanne Dougherty, coll., 01/ix/2001).

Donax variabilis Say, 1822
(Figs. 6–10, 13, 15, 27)

Synonymy (for additional references, see Morrison, 1971: 550–551):

Donax variabilis: Boss, 1970: 205–206; Tiffany, 1971: 82–85; Melville, 1976: 19–21; Abbott, 1974: 509, fig. 5753; Emerson & Jacobson, 1976: 414, pl. 43, fig. 14; Mikkelsen, 1981: 230–239; Leber 1982: 297–301; Mikkelsen, 1985: 308–311; Vega & Tunnell, 1987: 97–135; Ruppert & Fox, 1988: 158, pl. B28; Estes & Adamkewicz, 1991: 321–332; Bonsdorff & Nelson, 1992: 358–365; Nelson et al., 1993: 317–322; Adamkewicz & Harasewych, 1994: 97–103; Meinkoth, 1995: 556, pl. 321; Ellers, 1995a: 120–127; 1995b: 128–137, 1995c: 138–147; Abbott & Morris, 1995: 91, pl. 4, fig. 37; Adamkewicz & Harasewych, 1996: 97–103; Wilson, 1999: 61–83; Manning & Lindquist, 2003: 415–422.

Diagnosis

Shell elongated-elliptic; anterior (pedal) edge thin; posterior region compressed, anterior slope weak. Mantle edge and siphons with few weakly branched papillae. Gastric style sac curved, with distal region positioned in anterodorsal region of visceral sac. Intestine bearing several loops.

Description

Shell (Figs. 6–10, 15): Up to 20 mm. Color very variable, from pure white to yellowish, grayish, brownish and reddish (see Morrison, 1971, for further comments). Outline somewhat elongated and elliptical; general shape weakly cuneiform, somewhat compressed; anterior (pedal) region with edge about half as thin as that of preceding species. Umbos located between middle and posterior third of hinge, weakly protruded, rounded. Remaining characters similar to those of *Donax fossor*, differing in: (1) larger size; (2) surface with more developed radial sculpture; (3) anterior pedal region thinner, narrowing gradually, with a more rounded anterior margin (Figs. 8–10); (4) posterior siphonal slope longer (Figs. 6, 7), less abrupt than in *D. fossor*. This last difference is reflected in the position of umbo, which is in posterior quarter of dorsal edge in *D. fossor*, between middle and posterior third of dorsal edge in *D. variabilis*; (5) cardinal teeth shorter (Fig. 15), total hinge somewhat narrower.

Mantle: Features similar to those of *D. fossor*, with the following differences: Mantle border entirely bearing single series of papillae on inner fold; outer fold double, smooth or with very small, low papillae between papillae of inner fold, with two series of papillae in region of siphonal chamber similar to those in *D. fossor*. Mantle border papillae similar to those of *D. fossor*, but smaller. Distal end of incurrent siphon with 5–6 folds proportionally smaller than those of *D. fossor*, bearing fewer papillae on outer surface (Fig. 13); that of excurrent siphon with 4–5 folds lacking papillae or bearing few, very small papillae; fecal furrow also present (Fig. 27, se).

Mantle Organs: Similar to those of *D. fossor*, including characters of gill and palps (Fig. 27).

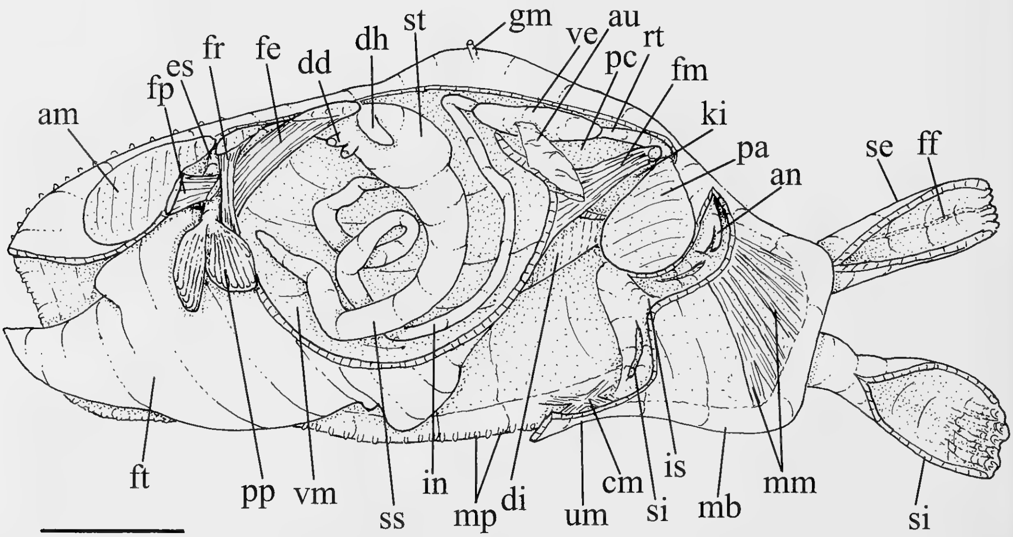


FIG. 27. *Donax variabilis* anatomy, whole specimen, left view, left mantle lobe partially removed (except at siphonal base), left gill, left wall of visceral sac, gonad and digestive diverticula removed, palps deflected. Scale = 2 mm.

Foot and Main Muscle System, Visceral Mass, and Circulatory and Excretory Systems: Similar to those of *D. fossor* (Fig. 27).

Digestive System: General organization similar to that of *D. fossor*, with following differences. Dorsal gastric caecum proportionally larger, with glandular portion more greatly developed. Gastric style sac proportionally longer (Fig. 27, ss), passing surrounding ventral border of visceral sac, decreasing gradually, in mid-ventral region of visceral mass ascending anteriorly, slightly sinuously, with distal end in mid-dorsal region of visceral sac at short distance from mouth. Intestine more convolute (Fig. 27, in), bearing a strong loop in region ventral to stomach.

Measurements (length x dorsoventral height x lateral width, in mm): MZSP 36509: no. 1, 12.4 x 7.5 x 5.5; no. 3, 17.7 x 7.8 x 5.5.

Material Examined: U.S.A.: South Carolina; Pawleys Islands, south end, MZSP 36509, 15 specimens (David Bushek, coll., 11/viii/2002). Florida; Franklin County, south corner of St. George Island, MZSP 36507, 12 specimens (Harry G. Lee & R. L. Whipple, coll., 29/vii/2002); Florida Keys; Monroe County, Matecumbe Key, FMNH 202068, 17 shells, 202070, 12 shells, 202071, 3 shells (A. Koto, coll.).

DISCUSSION

Donax fossor and *D. variabilis* are very similar in their morphology. The most significant difference in the shell is the pedal region, which is thicker and with a narrow slope in *D. variabilis* (Fig. 5), whereas in *D. fossor* is of a shape more typical of donacids, and with a thinner shell border (Fig. 10). The outline is also different; *D. fossor* has a more developed posterior slope and this region is shorter and more blunt (Figs. 1–2, 6–7). *Donax fossor* has many more papillae both at the mantle border and the siphons, with two series of somewhat long papillae (Fig. 11), while most specimens of *D. variabilis* have a single row, although some bear very small and short papillae on the outer mantle border fold. The incurrent siphon of *D. fossor* (Figs. 14, 15) has larger apical folds with proportionally more papillae on the outer surface than in *D. variabilis* (Figs. 12, 13). The tip of the excurrent siphon generally lacks papillae in *D. variabilis* (Fig. 27), or has very small papillae, while that of *D. fossor* has well-developed papillae (Fig. 20). The gastric style sac is longer in *D. variabilis*, being curved and slightly sinuous, with its distal end close to the mouth (Fig. 27); in *D. fossor*, the style sac is almost straight, with the distal end in the ventral region of the visceral mass (Fig. 24).

It is important to emphasize that the style sac proportions were consistent among specimens of different sizes of both species. The intestine of *D. variabilis* is more highly looped than that of *D. fossor*, mainly in its proximal region ventral to the stomach (Fig. 27).

Both *Donax* species show anatomy consistent with previous reports for the family, such as the siphons being separated from each other beginning at their base, the presence of a cruciform muscle, and the separation of the gastric style sac from the adjacent intestine. The circulatory system is very similar to that of *Donax trunculus* (Linnaeus, 1758) (Mouëza & Frenkiel, 1978). The cruciform muscle (Fig. 21) is cited as a character of the superfamily Tellinoidea (Yonge, 1949); it matches that previously reported in both species studied (Mouëza & Frenkiel, 1974: figs. 2–5).

The siphonal constitution is also similar to those described for other species of the family, with a clear siphonal septum separating supra- and infrabranchial chambers (Mouëza & Frenkiel, 1978; Hodgson, 1982). This septum (Fig. 20, id) aids in directing water flow to the gills, because the gills are not anatomically connected to the siphons. This study is the first report of a fecal furrow (Figs. 20, 27, ff) in any donacid species. The shape, number and constitution of the siphonal tentacles and papillae (Figs. 11, 12) are obviously associated with the high energetic environment that donacids normally inhabit; their differences have been very useful in comparative analysis among sympatric species (e.g., Ansell, 1981; 1983: fig. 6). Species of the genera *Iphigenia* (Narchi, 1972) and *Egeria* (Purchon, 1963) have weakly developed siphonal papillae and inhabit low energy environments. The well-developed radial pallial muscles connecting the posterior edge of the posterior adductor muscle with the mantle edge (Figs. 22, 27, mm) is a unique feature of the two species studied herein, and has not been described for any other species. The more dorsal of these muscles is short and thin, gradually becoming thicker, longer and more distinct ventrally, where it abruptly terminates.

A portion of the outer demibranch covering the visceral sac (Fig. 19, dv) is as previously reported in other donacids; this portion has been called supra-axial extension of the ctenidium (Ansell, 1983). The two species studied here differ from other known donacids in lacking a food groove on the ventral edge of the inner demibranch; this groove has been found in other species (Purchon, 1963; Yoloye, 1977; Ansell, 1981; Passos, 1998). Another interesting feature is the well-developed gill muscle (Fig. 22, gm), which occurs in both studied species, originating inside the umbonal cavity (Figs. 18, 27) and penetrating the mantle along the gill just between the demibranchs. The posterior region of the gill muscle is more diffuse and thin. Only one similar structure has been reported in the literature on donacids, the so-called "demibranch muscle" in *Donax gouldii* Dall, 1921, studied by Pohlo (1967). However, some confusion with the levator muscle of the foot exists in that description (Pohlo, 1967: 330). The gill muscle could be an exclusive feature of the three species (*D. fossor, D. variabilis, D. gouldii*).

The stomach of *Donax variabilis* and *D. fossor* (Figs. 25, 26) is also typical of donacids, having a transverse typhlosole in the esophageal insertion and a dorsal hood at left. However, the dorsal caecum found on the right side of stomach can be absent in some species (Nakazima, 1965) and has been called a stomach appendix (Pohlo, 1967; Wade, 1969; Narchi, 1972, 1978; Passos, 1998) or posterodorsal caecum (Yonge, 1949; Purchon, 1963; Mouëza & Frenkiel, 1976; Salas-Casanova & Hergueta, 1990). These last authors demonstrated that in *D. venustus* (Poli, 1795) sand grains and similar coarse particles pass by the dorsal caecum; in the present species the caecum appears to be a gland, because it is almost entirely filled by glandular tissue and has a narrow duct separating it from the stomach (Figs. 25, 26, pd). Dorsal caeca have been reported in members of other tellinoidean families (Yonge, 1949: figs. 28–29), but they differ from those of donacids in being larger and amply opened to the stomach. The species studied here also lack tall gastric typhlosoles as those reported in the above-mentioned papers. The highly curved style sac is a unique feature of *D. variabilis* (Fig. 27); however, Mouëza & Frenkiel (1976) showed a long style sac for *D. trunculus*, figuring it as a semi-circle.

The configuration of the intestinal coils is also useful for species distinction (e.g., Ansell, 1983: fig. 7) reinforcing the distinction between the two species studied here. The donacid intestine is normally weakly coiled, however, *Egeria radiata* (Lamarck, 1804) is an exception (Purchon, 1963: fig. 10).

CONCLUSIONS

(1) Specimens from New Jersey (attributable to *Donax fossor*) and South Carolina and Florida (attributable to *D. variabilis*) are confirmed as separate species, distinguishable by morphological features of shell and soft parts, in agreement with the molecular findings of Adamkewicz & Harasewych (1996).

(2) Morphological study of *Donax fossor* and *D. variabilis* confirmed the typical bauplan of the family as revealed by previous authors. Detailed investigation of all organ systems showed useful distinguishable differences that are consistent in each sample and sufficient for specific separation.

(3) At the present time, the radial pallial muscles of the siphonal chamber are unique to *Donax fossor* and *D. variabilis*, not having been described for any other donacid species. The gill muscle is an exclusive feature of these two species and *D. gouldii*.

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PINCTADA LONGISQUAMOSA (DUNKER, 1852) (BIVALVIA: PTERIIDAE), AN UNRECOGNIZED PEARL OYSTER IN THE WESTERN ATLANTIC

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ABSTRACT

Pinctada longisquamosa (Dunker, 1852) is redescribed based on original collections from the Florida Keys, type material, and other museum specimens. Conchological and anatomical features support its transfer from the genus *Pteria* (originally *Avicula*) to the genus *Pinctada*. A unique periostracal structure, with elements corresponding to the individual prismatic structures of the outer shell layer is described and illustrated. Comparison is made between this species and *Pinctada imbricata* and *Pteria colymbus*, with which it co-occurs and has often been confounded. Its preferred habitat in Florida Bay is seagrass, often intermixed with macroalgae, to which individuals byssally attach substantially off the silt-laden bottom. Quantitative and qualitative data from Florida Bay populations show fluctuating population densities, from absence to over 300 individuals/m^2, sometimes within a few months. These pronounced changes could be seasonal and/or influenced by the extremes of high and low salinity that sometimes occur in the Florida Bay estuarine system.

Key words: Florida Keys, Florida Bay, sanctuary, *Pteria,* Mollusca, systematics, anatomy.

INTRODUCTION

Members of the bivalve family Pteriidae, including pearl oysters and wing oysters, are characterized by obliquely ovate shells with a triangular wing-like projection both anterior and posterior to the straight hinge line. They are monomyarian and epibyssate, their shells inequivalve, inequilateral, and interiorly nacreous. Hinge teeth are small to obscure, and the exterior surface is often adorned with layers of overlapping lamellae arranged in radial rows. The fossil record extends from the Triassic. Three extant genera (*Pteria* Scopoli, 1777; *Pinctada* Röding, 1798; *Electroma* Stoliczka, 1871; Hertlein & Cox, 1969) and about 50 living species are currently recognized. Mainly tropical and subtropical in distribution, pteriids are relatively common and well-recognized bivalves by virtue of their historical and current roles as sources of nacre (mother-of-pearl) and natural or cultured pearls (Landman et al., 2001). Despite this familiarity, anatomical characters have received little attention and detailed work has mostly been restricted to a few species of commercial interest mainly in the genus *Pinctada* (Shiino, 1952; Hynd, 1955; Shirai, 1994). No phylogenetic framework yet exists for the family.

In the tropical western Atlantic, Pteriidae is represented mainly by the Atlantic pearl oyster, *Pinctada imbricata* Röding, 1798 (which some authors, e.g., Shirai, 1994, consider circumtropical), and the Atlantic wing oyster, *Pteria colymbus* (Röding, 1798). One other species of *Pinctada, P. margaritifera* (Linnaeus, 1758), widespread throughout the Indo-Pacific, has been introduced to Florida (Chesler, 1994; Carlton, 1996; Camp et al., 1998), but without evidence of established reproductive populations. One unidentified *Electroma* species was reported as well established in coastal Colombia (Borrero & Díaz, 1998), also presumably introduced from the Indo-Pacific. Three other nominal species of *Pteria, P. vitrea* (Reeve, 1857), *P. hirundo* (Linnaeus, 1758), and *P. longisquamosa* (Dunker, 1852), have also been reported as

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indigenous western Atlantic species (Hayes, 1972; Rios, 1994; Turgeon et al., 1998), but are far less represented in the literature and collections. This paper reviews the taxonomy and geographic distribution of one of these poorly known species, *P. longisquamosa*, establishing its generic placement, and describing its anatomy and life habits, based on original collections of living specimens from the Florida Keys together with a re-evaluation of existing literature and selected museum data. Comparisons are drawn with sympatric pteriids within its geographical range and with known anatomical data for the family.

MATERIALS AND METHODS

This study is part of an ongoing investigation of marine molluscan biodiversity in peninsular Florida and the Florida Keys, formally initiated by PMM and RB in 1994. Consecutively numbered stations comprising these collections are preceded by an "FK" acronym in the following text and Appendix. Living animals and empty shells of *Pinctada longisquamosa* were collected mainly by hand during snorkeling on shallow-water (2–10 m) seagrass flats; the majority of observations on living specimens were made from beds of *Thalassia testudinum* König and *Syringodium filiforme* Kützing in Florida Bay off the Upper Florida Keys. *Pinctada imbricata* and *Pteria colymbus* were collected for comparative purposes from locations throughout the Florida Keys. Voucher FK specimens were fixed in 5% formalin, later transferred to 70% ethanol (or fixed directly in 95–100% ethanol for potential molecular investigation), and are deposited in the American Museum of Natural History (AMNH), New York, and Field Museum of Natural History (FMNH), Chicago.

Our attention was first drawn to this species by its prominent occurrence in a study conducted by the Florida Marine Research Institute (FMRI) to assess the responses of molluscan populations to changes in salinity in Florida Bay during periods of drought and floods. Results, provided here by WGL, were obtained during quantitative sampling conducted at 101 sites spaced evenly throughout Florida Bay (Fig. 30) during the summers of 1994 (a drought year; salinity range at sites 14.8–51.8 ppt) and 1996 (year following a flood year; site salinity range 0.8–40.9 ppt). Fifteen samples were taken using a large-bore coring device at each site, with 0.27 m^2 of bottom area collectively sampled during each site visit. Sampling and analytical techniques were described by Lyons (1998), and a preliminary summary of results was presented by Lyons (1999). Live-collected specimens from this study are stored

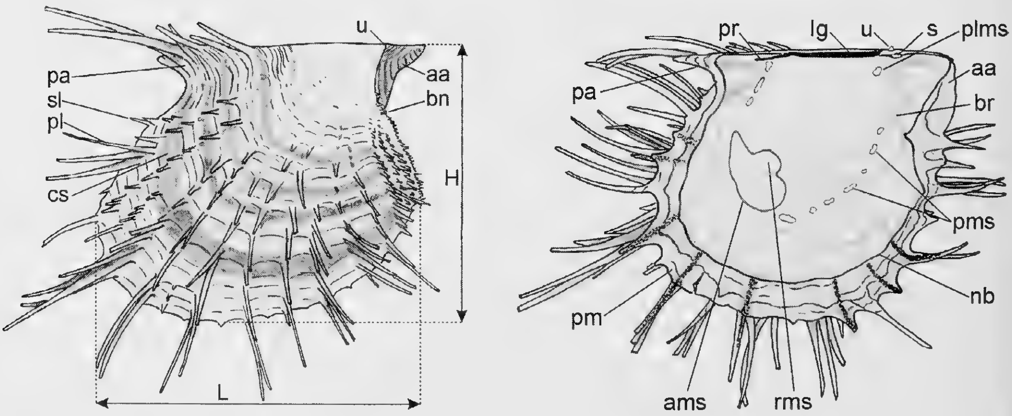


FIG. 1. Diagrammatic shells of *Pinctada longisquamosa,* showing general exterior (left) and interior (right) features and methods of shell measurement. (aa, anterior auricle; ams, adductor muscle scar; bn, byssal notch; br, byssal ridge; cs, commarginal stripe; lg, ligament; nb, border of nacreous layer; pa, posterior auricle; pl, primary lamella; plms, pedal levator muscle scar (anterior pedal levator muscle scar not shown, situated within ambonal arch); pm, prismatic margin; pms, pallial muscle scars; pr, posterior ridge; rms, pedal retractor muscle scar; s, socket of anterior dentition (corresponding to tooth in RV, not shown); sl, secondary lamella; u, umbo).

in 70% ethanol in the Specimen Reference Collection of the Florida Marine Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg (FSBC I).

Living specimens used for anatomical observations in the field were relaxed by chilling in a household refrigerator assisted by the addition of magnesium sulfate crystals (Epsom salts) to their seawater supply, or in an isotonic aqueous magnesium chloride solution. The anatomy of preserved specimens was studied using a combination of histology and gross dissection in various planes. For histology, shells were removed manually from formalin-fixed, ethanol-preserved specimens; tissues were dehydrated through a graded ethanol series, followed by clearing in xylene substitute, and embedding in paraffin. Complete 7-µm serial sections were produced for intact individuals in transverse and sagittal planes, and stained with PAS (Alcian Blue/Periodic Acid/Schiff's) trichrome stain. Dried shells and excised preserved tissues were prepared for scanning electron microscopy (SEM) by critical point drying (for tissues only) and gold-palladium sputter coating, and were then viewed on a Zeiss DSM-950 scanning electron microscope at AMNH.

Specimen photography used a variety of equipment and techniques. Laboratory photographs of living animals (Fig. 4) were taken in aquaria or finger bowls with a 35 mm single-lens reflex camera and electronic flashes; *in situ* underwater photos (Fig. 29) were accomplished with the same equipment in an underwater housing. Whole-valve and detail light micrography (Figs. 5–9) used a Microptics® micro/macro imaging system based on a high-resolution Nikon® single-lens reflex digital camera.

Shell measurements (taken with digital calipers or with ocular micrometer on a stereomicroscope) and meristics were taken from the right valve. Maximum shell height was measured perpendicular to the hinge line to the most distal point of the ventral shell margin; maximum shell length was taken parallel to the hinge line (Fig. 1). Primary radial sculptural elements were counted on the main body of the shell. Size is expressed as shell length unless otherwise noted. Although the hinge teeth of pteriids have been called "cardinal" and "lateral" teeth by some authors (e.g., Hayes, 1972), we use the phrases "anterior dentition" and "posterior dentition" to avoid unsupported assumptions of homology with the teeth of heterodont bivalves.

Other cited repositories include: ANSP – Academy of Natural Sciences of Philadelphia, Pennsylvania; BMNH – The Natural History Museum, London [= British Museum (Natural History)]; BMSM – Bailey-Matthews Shell Museum, Sanibel Island, Florida; DMNH – Delaware Museum of Natural History, Wilmington; HMNS – Houston Museum of Natural Sciences, Texas; UMML – Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida [= University of Miami Marine Laboratory]; USNM – National Museum of Natural History, Smithsonian Institution, Washington, DC [= United States National Museum]; and ZMB – Institute of Systematic Zoology, Museum für Naturkunde, Berlin, Germany [= Zoologisches Museum Berlin].

Other abbreviations and conventions used in the text (other than figure labels, explained in the figure legends) are: alc – fluid-preserved (alcohol) specimen; D – "diameter" or shell inflation; frag – shell fragment; H – shell height; juv – juvenile or subadult; L – shell length (often called "width"); LV – left valve; pair – an empty (dead) complete shell (2 valves); RV – right valve; spm – a living specimen; and valve – an empty (dead) single valve.

SYSTEMATIC RESULTS

Pterioidea J. E. Gray, 1847 (1820)

Pteriidae J. E. Gray, 1847: 199 [as Pteriadae] (1820)

Aviculidae Goldfuss, 1820, is an available older name, but was replaced before 1961 when the name *Avicula* Bruguière, 1792, was deemed a junior synonym of *Pteria* Scopoli, 1777. Because Pteriidae has won general acceptance, it is maintained under ICZN (1999) Art. 40.2.

Pinctada Röding, 1798: 166 (pearl oysters)

Synonyms: *Margaritiphora* Megerle von Mühlfeld, 1811; *Margarita* Leach, 1814; *Perlamater* Schumacher, 1817; *Meleagrina* Lamarck, 1819 (for further information on these and other synonyms; see Hertlein & Cox, 1969: N304).

Type species by subsequent designation (Iredale, 1915: 305): *Mytilus margaritiferus* Linnaeus, 1758.

Pinctada longisquamosa (Dunker, 1852)
(scaly wing oyster)

Synonymy

Avicula (Meleagrina) longisquamosa Dunker, 1852: 76–77; 1872: 12, pl. 2, fig. 6.

Avicula longisquamosa Dunker. – Petit de la Saussaye, 1856: 151 [name only]; – Beau, 1858: 21 [name only]; – Dall, 1885: 34 [name only, citing Dunker (1852), Petit de la Saussaye (1856), Beau (1858), and Krebs (1864)].

Avicula longisqvamosa Dunker [error pro *longisquamosa*]. – Krebs, 1864: 131–132 [name only, citing Beau, 1858].

Meleagrina longisquamosa "d'Orbigny." – Arango y Molina, 1878–1880: 268 [name only].

Pteria longisquamosa (Dunker, 1852). – Hayes, 1972 [unpubl.]: 52–58, pl. 2, fig. 2, pls. 6–8, 11f; – Abbott, 1974: 440, no. 5121; – Abbott & Dance, 1982: 301, fig.; – Espinosa et al., 1994: 114 ["rare", name only, citing Arango y Molina, 1878–1880]; – Camp et al., 1998: 9 [name only]; – Brewster-Wingard et al., 2001: 210–212, 214–216, 218, 220, 223–225, 227, 228, 230; Trappe & Brewster-Wingard, 2001: fig. 3, table 1.

Pinctada longisquamosa (Dunker, 1852). – Mikkelsen & Bieler, 2000: 376 (table 1).

Pteria viridizona Dall, 1916a: 15 [*nomen nudum*]; 1916b: 403; – Abbott, 1974: 440, no. 5119; – Keen, 1937: 25 ["extralimital" to eastern Pacific fauna].

Pteria viridozona [error pro *viridizona*] Dall, 1916. – Dall, 1921: 17; – Oldroyd, 1925: 48; – Burch, 1944: 8 ["Specimens in the Golisch collection taken from the backs of deep sea crabs off San Pedro ... a very questionable species with no member of the club sure of what it is"]; – Burch, 1945: 5 [name only; "questionable member of our [eastern Pacific] fauna"].

Pteria xanthia Schwengel, 1942: pl. 3, fig. 1, 1a [July, *nomen nudum*], 64 [October]; – Aguayo & Jaume, 1948a: 1; – Fischer-Piette, 1982: 174.

Pinctada xanthia (Schwengel, 1942). – McGinty & Nelson, 1972: 11 ["rare"; name only].

Pinctada sp. – Brewster-Wingard & Ishman, 1999: 374 ["important Florida Bay faunal constituent"].

Pinctada radiata [*non Pinctada radiata* (Leach, 1814)]. – Smith, 1937: pl. 5, fig. 6; – Pulley, 1952b: pl. 4, fig. 14; – ?G. L. Voss & N. A. Voss, 1955: 226; – ?Abbott, 1958: 115; – Hudson et al., 1970: 7; – Turney & Perkins, 1972: 7, 9, 10, 12–16, 30, 31, figs. 6, 8, table 3; – Wingard et al., 1995: 7; – Ishman et al., 1996: table 2; – Brewster-Wingard et al., 1996: 18, 19, 21, 22, tables 3, 4; 1997: 9, 11, table 2; 1998a: 164, 166; 1998b: 6, 9, 12, 14, table 2, figs. 5, 6; – Brewster-Wingard & Ishman, 1999: 374–376, fig. 4.

Pteria colymbus [*non Pteria colymbus* (Röding, 1798)]. – Tabb & Manning, 1961: 584.

Material Examined

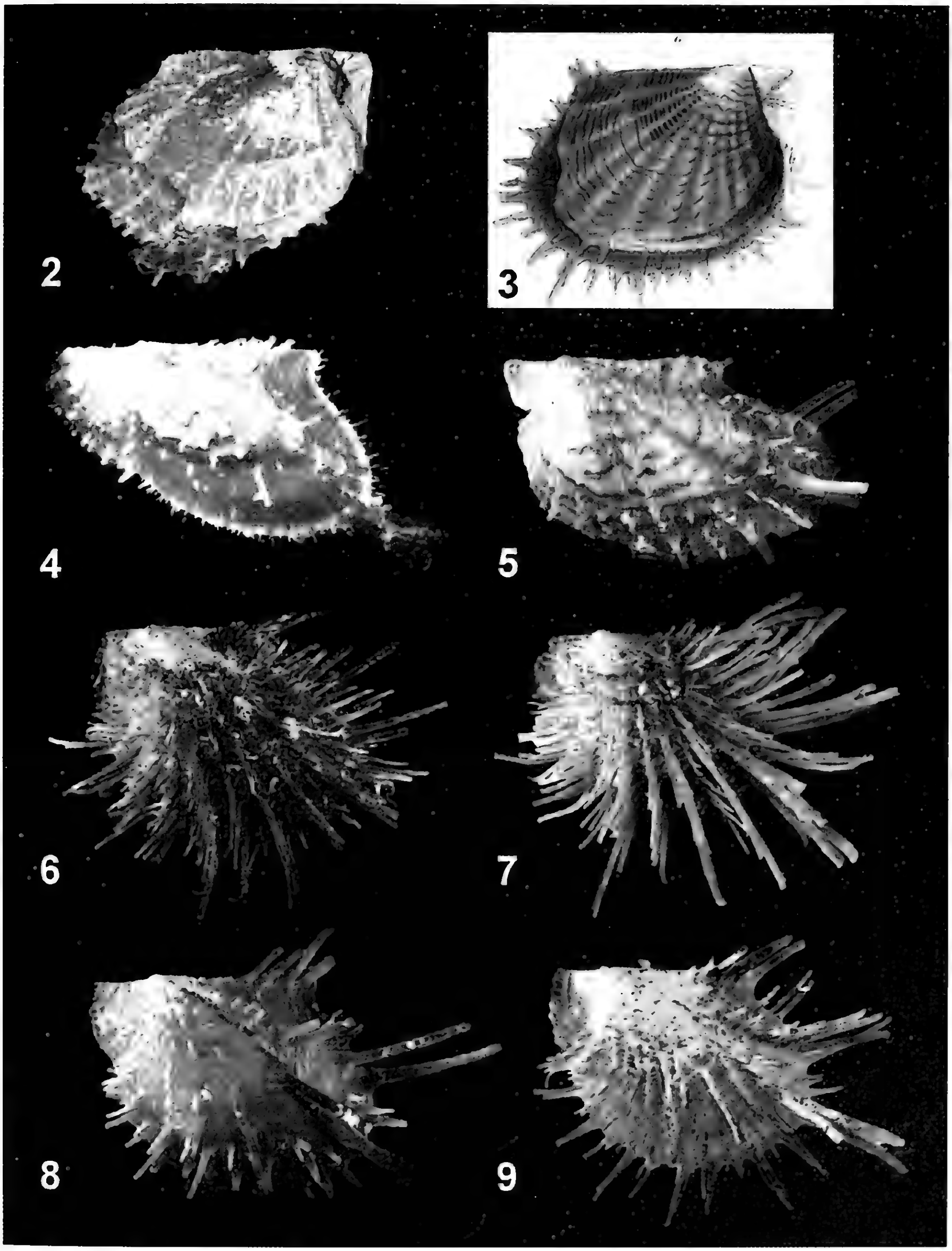
Type Material: *Avicula longisquamosa* Dunker, 1852, holotype (1 pair, olive green [as originally described/figured by Dunker, 1872] with byssus attached to RV; RV 27.6 mm H, 35.9 mm L; LV 34.0 mm H, 40.2 mm L [figured by Dunker, 1872: pl. 2, fig. 6, given in text as 33 mm H, 46 mm L, probably referring to LV with lamellae]; broken and repaired according to a note by R. Kilias, dated 1972), ZMB Moll. 101 674, from "Venezuelan beach at Puerto Cabello" (Dunker, 1852: 77, here translated). *Pteria viridizona* Dall, 1916b, 5 syntypes USNM 172600 (vidi, "holotype" L 25 mm, H 13 mm, D 5 mm, figured by Hayes, 1972: pl. 7), Long Beach, California [erroneous, according to Hayes, 1972], H. N. Lowe!. *Pteria xanthia* Schwengel, 1942, holotype ANSP 178717 (L 35 mm, H 18 mm, exclusive of projecting lamellae; figured by Schwengel, 1942 [July]: pl. 3, figs. 1–1a, and Hayes, 1972: pl. 10), dredged off Captive [error pro Captiva] Island, Florida, Alice D. Miner!, December 1941.

Other Material Examined: See Appendix.

Distribution

Bermuda, Florida (from St. Augustine to the Florida Keys to the panhandle), Texas, Bahamas, Greater and Lesser Antilles, Caribbean coast of Mexico, Colombia, and Venezuela.

Localities (*= unverified): *Bermuda* (USNM; Hayes, 1972; Abbott, 1974). *Florida*: east Florida [including St. Johns County (AMNH), Volusia County (HMNS), *Palm Beach County (Hayes, 1972), *Broward County (McGinty & Nelson, 1972), *Dade County (Pulley, 1952b; Hayes, 1972)], Florida Keys (AMNH, ANSP, BMSM, DMNH, FMNH, FSBC I, UMML, USNM, this study; Hudson et al., 1970; Hayes, 1972; Abbott, 1974), Dry Tortugas (USNM, this study; Hayes, 1972), west Florida (Smith, 1937) [including Lee County (AMNH, Schwengel, 1942; Hayes, 1972), Sarasota County (AMNH); Hillsborough County (AMNH, USNM; Hayes, 1972), Wakulla County (USNM; Hayes, 1972),



FIGS. 2–9. *Pinctada longisquamosa*, showing variation in ornamentation and shell coloration. FIG. 2: Holotype (ZMB Moll. 101 674, 35.9 mm); FIG. 3: Dunker's (1872: pl. 2, fig. 6) original illustration of the holotype; FIG. 4: Living animal (FMNH 295709, 23.5 mm total L), showing tentacles at shell margin and extreme elongation of posteroventral lamella; FIGS. 5–9: Representative Florida specimens, showing variation in shell shape, ornamentation, and color. FIG. 5, AMNH 264528, 23.7 mm; FIG. 6: AMNH 308109, 27.7 mm; FIG. 7: AMNH 308109, 23.3 mm; FIG. 8: AMNH 308109, 21.9 mm; FIG. 9: AMNH 308109, 29.2 mm.

Franklin County (USNM; Hayes, 1972), *Okaloosa County (Hayes, 1972)]. *Texas* (HMNS, USNM). *Caribbean*: Bahamas (AMNH, USNM; Hayes, 1972); Cuba (AMNH, USNM; Arango y Molina, 1878-1880; Aguayo & Jaume, 1948a; Hayes, 1972; Espinosa et al., 1994), *Grand Cayman Island (?Abbott, 1958), Jamaica (HMNS; Hayes, 1972), Puerto Rico (AMNH), Virgin Islands (AMNH), *Guadeloupe (S. Petit, 1856; Beau, 1858; Krebs, 1864), *Dominica (Hayes, 1972), Netherlands Antilles (USNM). *Caribbean Central America*: Mexico (USNM; Hayes, 1972). *Caribbean South America*: *Colombia (Hayes, 1972), Venezuela (AMNH, HMNS, ZMB; Dunker, 1852).

Dimensions and Maximum Recorded Size

Mean dimensions (from a single population, AMNH 308109, n = 195: length 16.34-29.75 mm, mean 23.31 ± 2.64 mm SD, median 23.38 mm, mode 23.92 mm; height 14.55–25.10 mm, mean 19.86 ± 2.00 mm SD, median 19.87 mm, mode 16.79 mm). Largest recorded specimen 39.34 mm L, 28.66 mm H (AMNH 308234).

Diagnosis

Small western Atlantic pteriid, with radial rows of narrow shell lamellae, generally bright coloration (commonly green to yellow), nacre thin (allowing external color and ornamentation to show through shell), a relatively strong ridge interiorly delimiting anterior auricle of LV, and anterior dentition with tooth in RV and corresponding socket in LV; intestine with twisted loop within visceral mass and passing dorsal to heart; pallial tentacles simple.

Description

Shell (Figs. 2–10) obliquely ovate to round, thin-shelled, fragile (especially when dried), compressed, inequivalve with LV more strongly convex. Hinge line straight, extended into anterior and posterior auricles. Anterior auricle of RV small, triangular, with slightly concave anterior edge, strongly demarcated from anterior shell margin by groove; that of LV extending ventrally past right auricle, although flattened, not clearly demarcated from anterior margin and continuous with it. Prolonged posterior auricles relatively small, slightly sinuated, supporting elongated lamellae. Byssal notch very narrow, present in RV only. Anterior margin (just posterior to anterior auricle and byssal notch) straight or slightly concave; ventral and posterior margins rounded convex and continuous with posterior auricle. Ventral margin (distal to nacreous layer) of RV flexible, capable of bending during closure to create tight seal against LV, with no gap present when shell is closed. Valves concordant in color, usually green with variants to yellow or brown (Figs. 6–9; from single population, AMNH 308109, n = 195: 88.7% green, 9.2% yellow, 1.5% white, 0.5% purple-brown), with commarginal (sometimes zigzag) green, brown, and/or yellow stripes of varied thickness generally corresponding to valve color but darker; sometimes indistinct. Juveniles often with opaque white randomly distributed, irregular blotches, and without conspicuous lamellae (Fig. 10). Commarginal growth lamellae inconspicuous. Umbones just posterior to anterior auricle, prosogyrous, slightly projecting beyond hinge margin, with

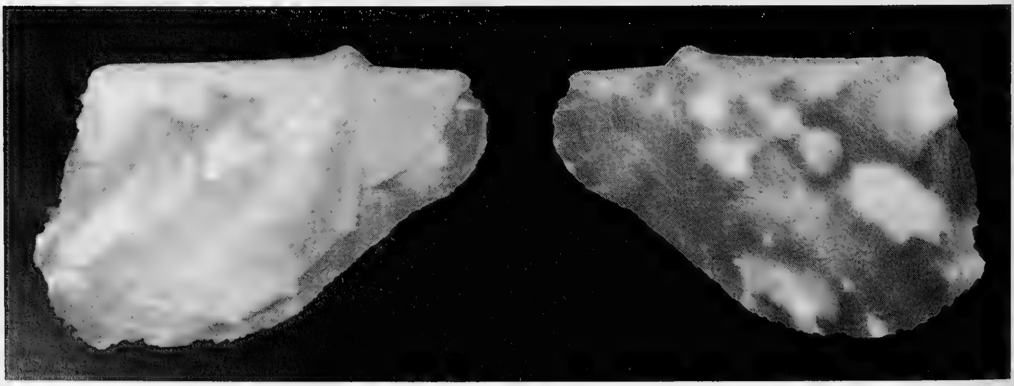


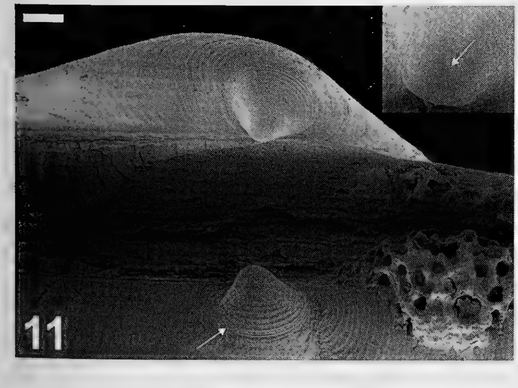
FIG. 10. *Pinctada longisquamosa,* juvenile shell, showing color pattern and absence of radial lamellae (AMNH 296429, 3.7 mm).

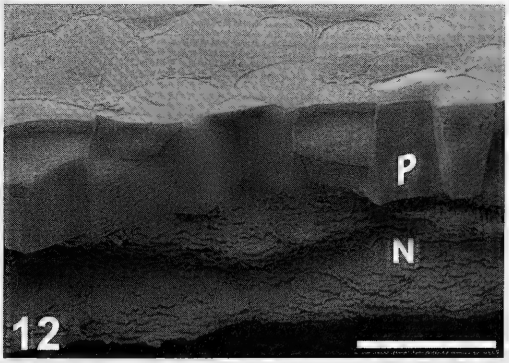
that of LV projecting slightly more dorsally than that of RV. Umbones often without color pattern, turning opaque white as shell abrades with age. Prodissoconch I (Fig. 11, inset) approximately 50 µm L. Subtriangular prodissoconch II with regularly spaced commarginal growth lines, slanting slightly posteriorly, 178.1–184.4 µm H, 212.5–225.0 µm L, (mean 218.8 ± 8.8 µm, n = 2) (Fig. 11); presumably aragonitic (as shown for *P. fucata martensii* (Dunker, 1872) by Kobayashi, 1980).

Outer shell layer simple, prismatic, comprised of single layer of regular, vertical, polygonal (mostly hexagonal) prisms, each 30 µm wide, assumed calcitic as shown for other pteriids (Carter, 1990) (Fig. 12). Periostracum with concentric rings of uniform thickness, with one roughly outlining each prism (Figs. 12, 13–17). Periostracal rings close to shell margin varying in shape and size, not closely adjacent to one another (Fig. 17); more proximally, reaching subequal size and shape (closely reflecting diameter of prisms), and becoming more regularly and densely arranged (Fig. 16); periostracum progressively wearing off toward older part of shell (Figs. 14–15), ultimately absent in umbonal region exposing prismatic layer (Fig. 13).

Each valve externally ornamented with roughly equal number of radial rows of flat, thin, elongated, flexible lamellae, from approximately mid-valve to distal edge, typically approximately 9 major rows per RV (from single population, AMNH 308109, n = 186: range 6–14, mean 9.1 ± 1.50 SD, median 9, mode 9; given as 10–12 by Dunker, 1872), relatively regularly spaced; progressively increasing in length toward shell margin. Lamellae usually of same color as valves but darker and often speckled with small brown dots. Rows adjacent to anterior margin and on auricles much more narrowly spaced and comprised of very small, semitransparent lamellae more densely packed in RV than LV. Shorter lamellae in mid-valve typically oriented toward distal shell margin parallel to valve surface or at slight angle (few almost perpendicular to valve surface), especially those in posterior region. Lamellae along ventral limit extending beyond shell margin and curving medially, interdigitating with those of other valve; those along posterior auricle and posterior margin also extending beyond shell margin but flaring laterally (with only few interdigitating) and directed slightly dorsally. Secondary or intermediate rows often present between major rows, composed of shorter and narrower lamellae, beginning and extending more distally than major rows, terminating at margin thereby producing "fringed" edge. Single row of lamellae terminating at posteroventral "corner" frequently bearing distally flaring lamellae (versus distally tapering lamellae in all other rows), often noticeably wider and longer than lamellae of other major rows (Fig. 4), sometimes conspicuously colored differently from valve (usually dark green or dark brown) (Fig. 8), often distinct only in one valve. In general, posterior lamellae longer than those on remaining part of valve, especially on dorsal margin of posterior auricle.

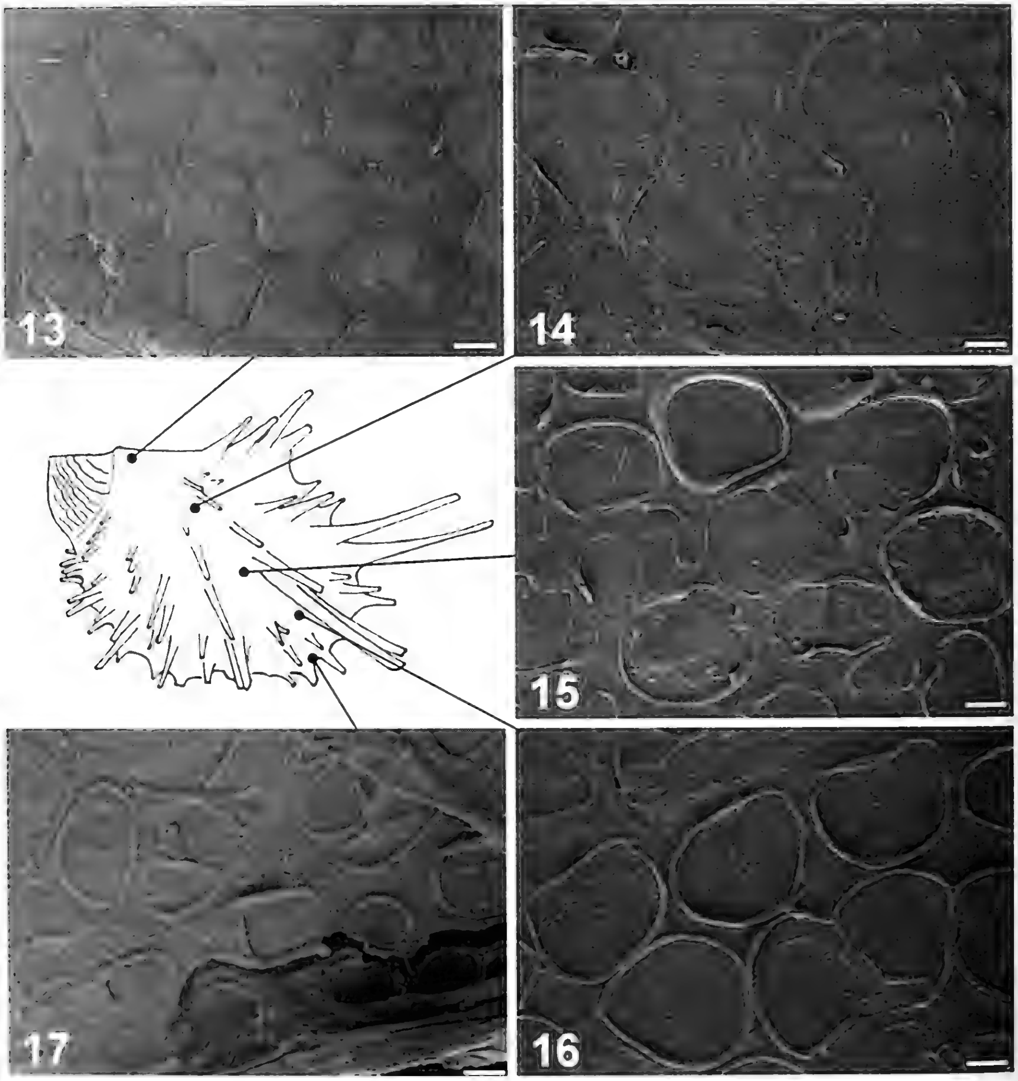
Interior shell layers nacreous, iridescent, but thinly so with external color visible through





FIGS. 11, 12. *Pinctada longisquamosa*, details of prodissoconch and shell microstructure (SEM; AMNH 308118, 10.7 mm). FIG. 11: Left (top) and right (bottom) prodissoconch; arrow indicates prodissoconch II border. Inset, closeup of left prodissoconch, showing prodissoconch I border (arrow); FIG. 12: Shell microstructure, showing prismatic layer (P) and nacre (N). Scale bars = 100 µm (Fig. 11), 50 µm (Fig. 12).

nacreous layer. Non-nacreous prismatic margin widest ventrally, approximately 1/5 of shell height, often considerably wider in RV (possibly to allow flexure during tight shell closure). Hinge plate narrow, widest in anterior part slightly posterior to umbo and gradually tapering toward posterior auricle. Ligament alivincular (restricted to hinge area), internal, lying in depression in hinge plate extending from area slightly posterior to umbones to posterior auricle. Anterior dentition (Fig. 18) represented by single rounded crenule in RV and complementary socket in LV. Posterior dentition in LV represented by single elongated ridge oriented nearly parallel to hinge line originating under posterior end of ligamental pit; complementary socket in RV comprised of two ridges oriented in same fashion. Anterior auricle interiorly often delimited on LV by very strong ridge extending from umbo to ventral



FIGS. 13–17. *Pinctada longisquamosa*, exterior surface of LV, sequence from umbo to margin showing gradual wear of periostracum to reveal surface of prismatic layer, with shell diagram indicating relative position (SEM; AMNH 308118, 9.5 mm). Scale bars = 10 μm.

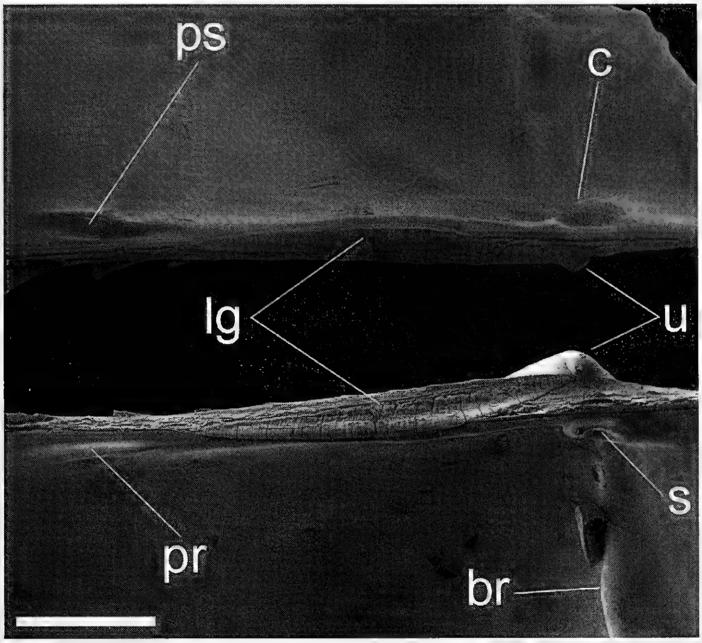


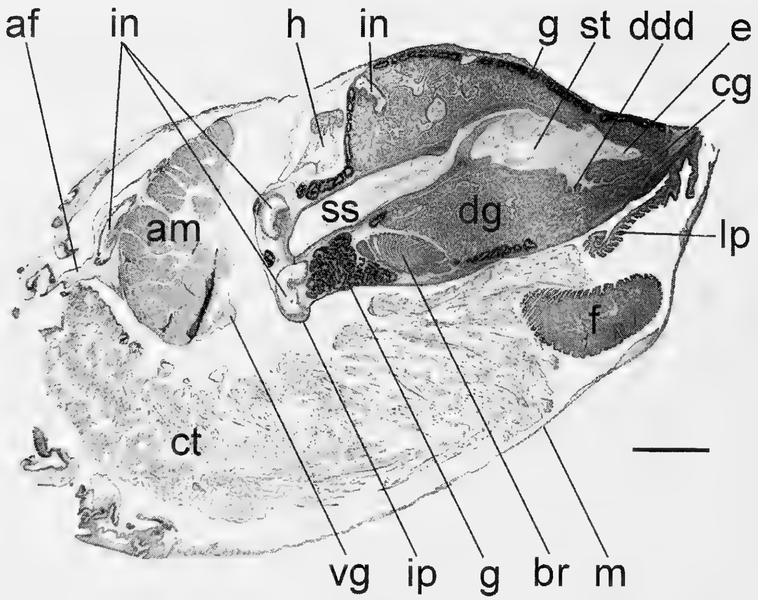
FIG. 18. *Pinctada longisquamosa,* hinge (RV top, LV bottom) (AMNH 308118, 10.3 mm); (br, byssal ridge; c, crenule of anterior dentition; lg, ligament; pr, ridge of posterior dentition; ps, socket of posterior dentition; s, socket of anterior dentition; u, umbo). Scale bar = 1.0 mm.

edge of byssal notch; corresponding ridge in RV much less conspicuous; two ridges together nearly closing byssal gape when valves are closed.

Adductor muscle scar (and corresponding adductor muscle) bean- to kidney- to crescent-shaped, with tapering dorsal end and widely rounded ventral end. Circular pedal retractor muscle and scar inset within adductor muscle and scar, producing fused three-lobed scar located subcentrally along dorsoventral axis, slightly posterior to anteroposterior axis (Fig. 1). Variable number of small discontinuous pallial muscle scars of irregular shape extending (a) from dorsal extremity of large adductor-retractor scar dorsally to area ventral to posterior dentition, and (b) from anteroventral extremity of large adductor-retractor scar along curve leading to pedal levator muscle scars. Two small, distinct, round pedal levator muscle scars, one within umbonal arch, other slightly ventral and posterior to umbo.

Adductor muscle heterogeneous, comprised of subequal anterior and posterior lobes corresponding to "quick" and "catch" muscles respectively, the former comprised of denser and finer transverse fibers in cross-section (Figs. 19, 20). Two anterior pedal levator muscles narrowing distally, extending from visceral mass at posterior side of base of foot to attachment sites in umbonal arches of each valve. Left levator much stronger than right levator and passing anterior to the latter. Two posterior pedal levators branching off anterior pedal levators just dorsolateral to mouth, passing posteriorly, attaching to valves posteroventral to umbones. Two symmetrical pedal retractor muscles extending from root of byssal gland to valves in concavity of adductor muscle scar. Pallial muscles radiating fan-like within the mantle to its edge from attachments at pallial muscle scars on inner valve surfaces.

Mantle points of attachment including pallial muscles, adductor and retractor muscles, pedal levator muscles, dorsal posterior part of labial palps, dorsal edge of outer demibranchs, and lateral surface of visceral mass. Mantle lobes fused dorsally, anterior and posterior to ligament along length of hinge line; remaining mantle margin free; inner and middle folds each equipped with single row of generally



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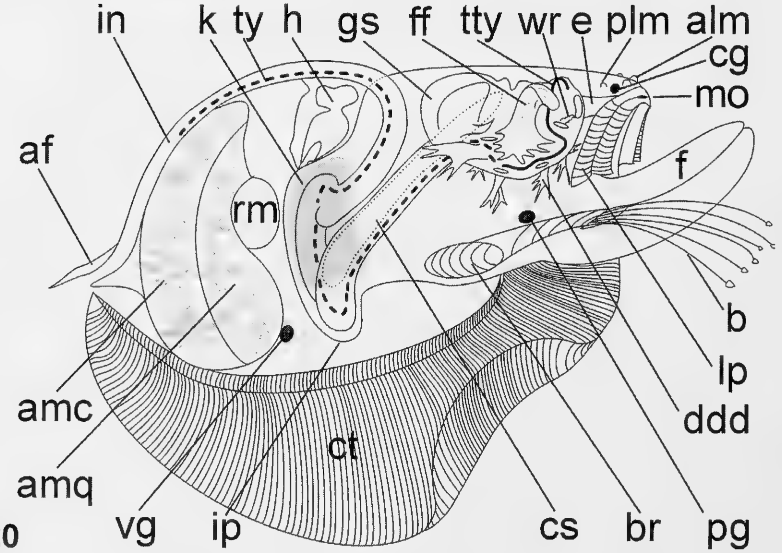

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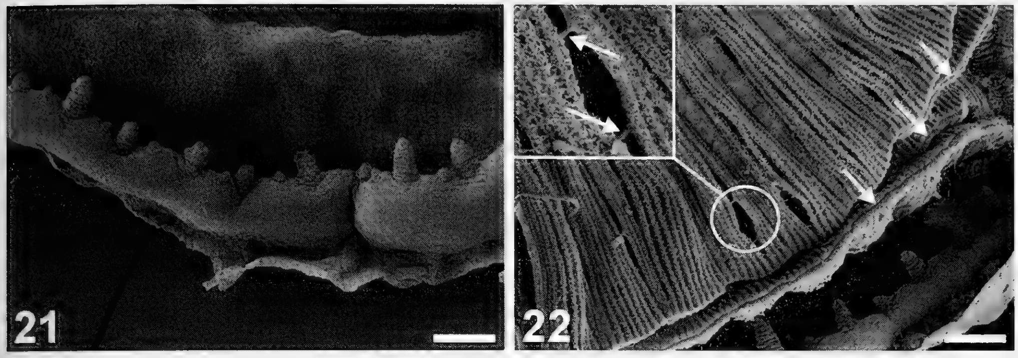
FIGS. 19, 20. *Pinctada longisquamosa*, internal anatomy. FIG. 19: Histological longitudinal section, close to midline, anterior at right (7 μm, PAS stain; AMNH 298904, 18.1 mm). Scale bar = 1 mm; FIG. 20: Diagrammatic anatomy from right side, with shell, mantle, and right ctenidia removed; stomach opened from right side; other structures (foot, intestine) depicted as though transparent; (af, anal funnel; alm, anterior levator muscle; am, adductor muscle; amc, adductor muscle ("catch" portion); amq, adductor muscle ("quick" portion); b, byssus; br, byssal root; cg, cerebral ganglia; cs, crystalline style; ct, ctenidia; ddd, duct of digestive diverticula; dg, digestive gland; e, esophagus; f, foot; ff, fleshy fold; g, gonad; gs, gastric shield; h, heart; in, intestine (dashed line indicates extent of typhlosole); ip, intestinal pouch; k, kidney; lp, labial palps; m, mantle; mo, mouth; pg, pedal ganglia; plm, posterior levator muscle; rm, pedal retractor muscle; ss, style sack; st, stomach; ty, typhlosole; tty, tongue of typhlosole; vg, visceral ganglia; wr, wavy ridge).



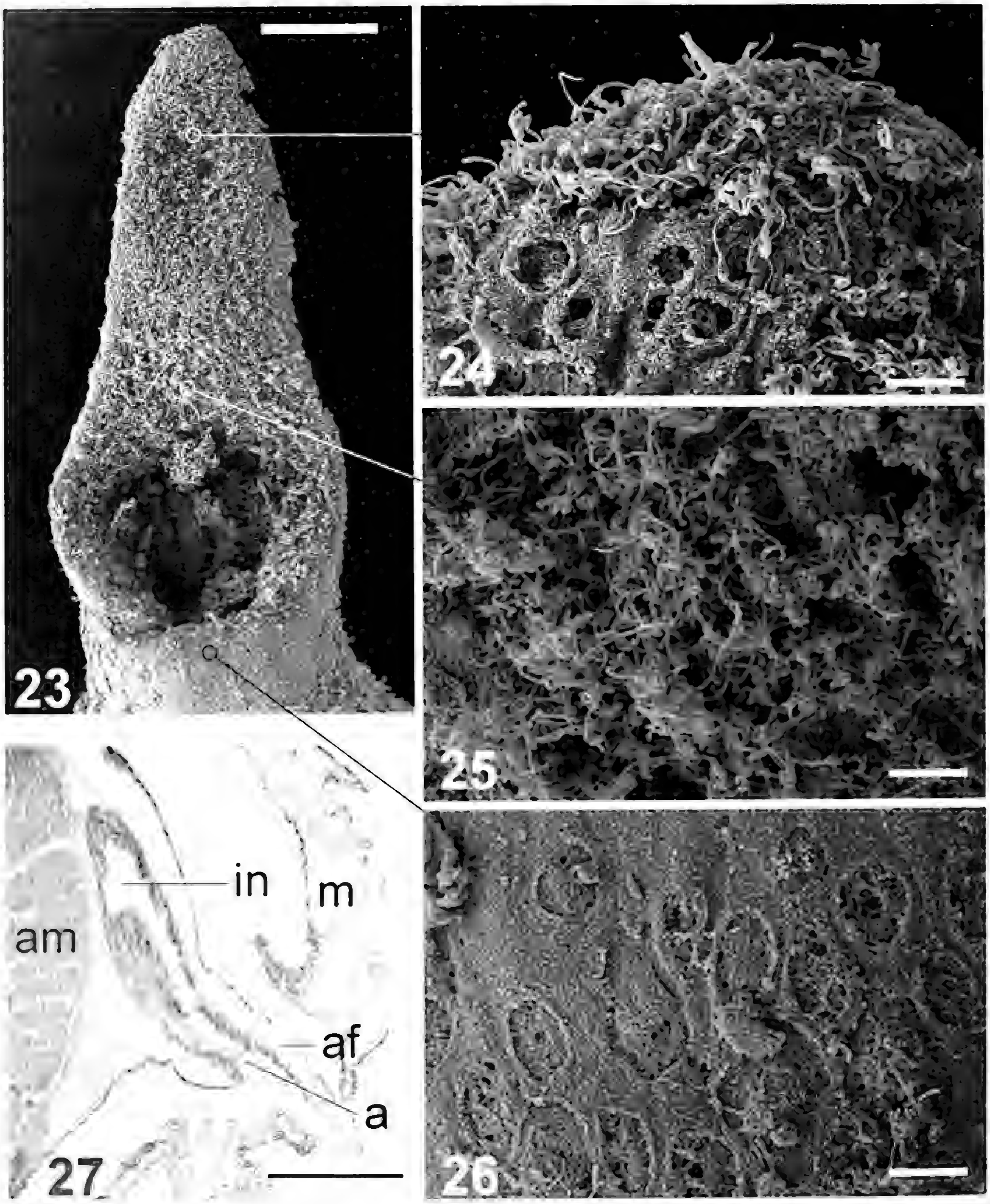
FIGS. 21, 22. *Pinctada longisquamosa*, mantle margin and ctenidia (SEM; AMNH 298903, 9.7 mm). FIG. 21: Mantle margin showing simple pallial tentacles; FIG. 22: Mid-ventral portion of the ctenidia, showing food grooves on both inner and outer demibranchs (arrows). Inset, closeup of gap in outer demibranch (circle) showing interlamellar tissue connections (arrows). Scale bars = 250 μm (Fig. 21), 1 μm (Fig. 22).

alternating large and small simple tentacles (Fig. 21), creating fringed pallial veil. Pallial veil translucent in living animals with alternating bars of black and white blotches; irregular blotches of brown-orange pigment often present on and between inner and middle mantle folds. Remaining mantle lacking pigmentation and effectively translucent. Pallial fold directed toward tips of ctenidia on posterior side of mantle lobes. Tentacles of inner fold longer than those of middle fold. Larger tentacles with short pointed lateral processes in larger animals (Fig. 21). Larger inner fold tentacles in living specimens frequently with brown-orange blotches at base, this color pattern retained in preserved specimens. Periostracum secreted from deep groove between outer and middle folds.

Labial palps projecting dorsoventrally on either side of anterodorsal visceral mass surrounding mouth area; each consisting of pair of elongated folds, wider at base, smooth on exterior surface and plicated by about 15 transverse lamellae on inner surface (Figs. 19, 20). Association of labial palps and ctenidia of Category III of Stasek (1963), characterized by anterior filament of inner demibranch not inserted into distal oral groove. Ctenidia large, plicate, broadly sickle-shaped, encircling ventral half of pallial cavity. Inner and outer demibranchs subequal, each with marginal food groove (Fig. 22); eulamellibranch with regularly spaced interfilamental connections; heterorhabdic with regularly spaced (occurring at intervals of 4–7 plica), large, U-shaped (in cross-section) principal filaments connected by interlamellar septa extending full height of demibranch and often but not always marked by brown pigmentation on dorsal edge. Neighboring filaments predominantly connected by continuous stretches of tissue; junctions also mediated by ciliated disks. Filaments of corresponding ascending and descending lamellae joined by regularly spaced interlamellar junctions, varying in number depending on filament length, reaching maximum of nine in outer and six in inner demibranch. Dorsal edges of inner demibranchs connected medially via ciliated junctions from point immediately ventral to foot to posteriormost extremity; dorsal edges of outer demibranchs attached laterally to mantle by ciliated junctions. Color of ctenidial ventral edge in life sometimes matching that of pallial veil (i.e., with white and dark bars), in other specimens, edge of outer demibranchs white along entire length while inner demibranchs translucent anteriorly and darker posteroventrally; such variability in color pattern can occur between ctenidia in single individual. Overall gill morphology corresponding to Type B (1b), characterized by frontal currents dorsalward in plical grooves and ventralward on crests (Atkins, 1937).

Muscular foot emerging anteriorly from visceral mass, with tip pointing dorsally and byssal groove on ventral side, extending from base to tip (Fig. 20). Foot curving noticeably to the left (observed in preserved specimens), possibly to accommodate foot extension and byssus deposition through byssal notch (RV only). Foot speckled dorsally and laterally with brown spots persisting after preservation that become darker and denser on dorsal side. Byssal gland in posteroventral portion of foot

(Figs. 19, 20). Golden to green shiny byssus emerging from groove in foot base, comprised of discrete threads extending outward; internal portion (within foot) bundled into twisted mass of partially fused threads, oval in cross-section. Byssal threads oval in cross-section, each terminating in subtriangular flat fan with rounded corners oriented perpendicular to thread axis.



FIGS. 23-27. *Pinctada longisquamosa*, anal funnel. FIGS. 23–26: Surface, showing various degrees of surface ciliation at tip (Fig. 24), mid-region (Fig. 25) and base (Fig. 26); FIG. 27: Cross-section (7 µm, PAS stain; AMNH 298904, same specimen as Fig. 19); a, anus; am, adductor muscle; f, anal funnel; in, intestine; m, mantle. Scale bars = 100 µm (Fig. 23), 5 µm (Figs. 24–26), 0.5 mm (Fig. 27).

Small living specimens very active in laboratory conditions, extending very agile foot to drag shell across surface of finger bowl. One museum label (AMNH 133648) noted, "when they were first put into a collecting jar full of salt water they moved their shells in and out, much like a bird flapping its wings"; this behavior not confirmed in this study.

Mouth concealed by dorsal and ventral lips produced, respectively, by outer and inner folds of labial palps. Esophagus connecting mouth to anterior stomach located asymmetrically in left portion of visceral mass. Overall stomach morphology corresponding to Type III of Purchon (1957) (Figs. 19, 20). "Wavy ridge" structure [as described for *Pinctada vulgaris* (Schumacher, 1817); Purchon, 1957], on ventral side of esophageal orifice but not extending downward toward left anterior group of ducts to digestive diverticula. Stomach lumen divided into anterior and posterior parts by fleshy fold extending from mid-dorsal to mid-ventral section along left wall. Marginal groove on right side marking division between anterior and posterior regions, extending toward right side from posteroventral region above embayments leading to ducts of digestive diverticula anterior to partition wall. Posterior part of partition wall extending anteriorly and toward right wall, emerging from ventral side of orifice of co-joined style sac and midgut on posteroventral wall of stomach, connected to posterior part of fleshy fold by a ridge. Minor and major typhlosoles emerging from right-ventral side of style sac/midgut; minor typhlosole fusing to ventral side of partition wall; major typhlosole passing along edge of partition wall to terminate at its ventral-most part. From this point, tongue of major typhlosole accompanied by intestinal grooves on each side, passing on ventral side from area to left of embayments, making a loop around ciliated finger-like extensions of fleshy fold (interpreted as food-sorting area by Purchon, 1957), turning left just anterior to fleshy fold, and passing along left wall to apex of ciliated food-sorting caecum. Gastric shield on left wall of posterior stomach consisting of dentate and membranous parts divided by cleft opening into stirring hollow; bordered anteriorly by dorsal hood, separated from fleshy fold by dorsal groove that branches off marginal groove in mid-lateral part of right wall, lining stomach roof, descending into stirring hollow just posterior to fleshy fold on left ventral side. Five groups of ducts to digestive diverticula exiting stomach: (1) one on ventral side of left pouch of posterior region (below gastric shield) extending posteriorly and leftward; (2–3) two from embayments at anterior part of partition wall, branching posteriorly, ventrally, and rightward; (4) one from ventral region just posterior and to left of esophageal orifice, extending anteriorly and laterally; and (5) one located sub-centrally on ventral wall of anterior stomach, leading ventrally and rightward. Intestine descending ventrally from posteroventral stomach wall into small intestinal pouch, turning left, twisting over itself, ascending to posterodorsal extremity, exiting visceral mass, passing dorsal to pericardial cavity, descending to anus along posterodorsal midline of adductor muscle. Intestine terminating in posteriorly oriented membranous process (anal funnel; Figs. 23–27) surrounding anus. Anal funnel flat, with tapering tip, facing ventrally, perpendicular to posterior surface of adductor muscle; anal opening at base. Distal inner surface of funnel (facing anal opening) ciliated; base smooth (Figs. 24–26).

Digestive gland occupying most of visceral mass. Gonadal alveolar tissue underlying epithelium and enveloping visceral mass from anteriormost region just above esophagus to posteriormost visceral mass to anterior area ventral to foot.

Heart (Fig. 28) within pericardium located posterior to visceral mass, dorsal to intestinal pouch (produced slightly posteriorly), anterior to upper part of adductor muscle; consisting of thick-walled ventricle attached to intestine at dorsal extremity, plus two symmetrical auricles situated ventral to ventricle, each with membranous extensions connecting with ventral pericardium and efferent blood vessels entering from posteroventral visceral mass. Major blood vessels including (1) anterior and posterior aortae, the former directed anteriorly, passing to dorsal midline over left side of intestine, branching into visceral mass and most anteriorly dividing into two pallial arteries along mantle edge; the latter passing backward along right side of intestine, branching into interior of adductor muscle above anus, (2) paired branchial afferent and efferent vessels passing longitudinally through ctenidial axis at dorsal junction of inner and outer demibranchs. Paired nephridia laterally compressed, on either side of posterior visceral mass below heart, connected to pericardium by wide ducts at dorsal extremity. Ventral edge fused with axis of dorsal junction of inner and outer demibranchs.

Nervous system conforming to general bivalve bauplan, with three pair of ganglia (Figs. 19, 20): (1) cerebropleural ganglia surrounding esophagus, (2) fused pedal ganglia at base

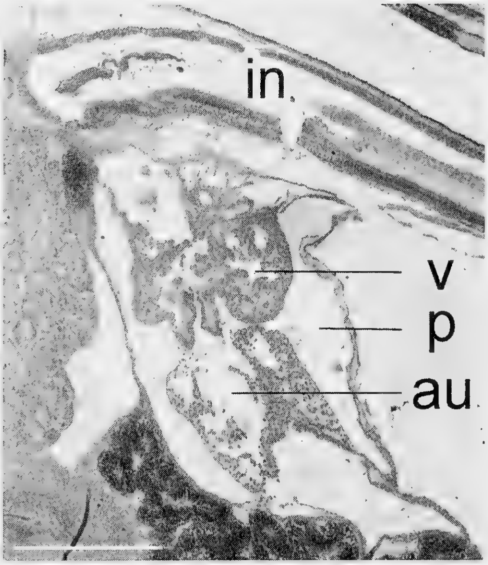


FIG. 28. *Pinctada longisquamosa,* histological section of heart, showing relative position of intestine (7 µm, PAS stain; AMNH 298904, same specimen as Fig. 19); (au, auricle; in, intestine; p, pericardial cavity; v, ventricle). Scale bar = 0.5 mm.

of foot, and (3) visceral ganglia at anteroventral side of adductor muscle. Cerebropleural ganglia connected to visceral ganglia by cerebrovisceral connectives and to pedal ganglia via cerebropedal connectives. Branchial nerves passing dorsally to blood vessels of ctenidial axis at dorsal junction of inner and outer demibranchs; pallial nerves transversing mantle edge.

Habitat and Ecology

In the Florida Keys, *Pinctada longisquamosa* is more typical of shallow Florida Bay than of areas off the Atlantic Ocean side of the islands. It occurs on the oceanside, but only in nearshore shallows (agreeing with Abbott & Dance, 1982), not on the patch or other coral reefs. It has been found most often associated with shallow (1–2 m) *Thalassia testudinum* seagrass beds, but has also been recorded in *Halimeda* clumps, in mixed algae on mangrove roots and rocks, associated with sponge and gorgonian stalks, an artificial reef, or attached to floating *Sargassum* that had washed ashore. Living specimens from "eelgrass" at Rock Harbor (AMNH 133956) and Teatable Key (AMNH 308111) in the Upper Florida Keys (also reported by Hayes, 1972) are reinterpreted here as from turtlegrass, *Thalassia testudinum*; true eelgrass, *Zostera marina* Linnaeus, extends only to northern Florida (Kaplan, 1988). Individuals byssally attach, usually substantially off the silt- or sand-laden sea bottom. Hayes (1972: 146) noted that one collector described their attachment to *Thalassia* in Rock Harbor as "attached [by] its byssus to 3 blades ... at the point of crossing, holding the grass in the position of an elongated X." Their predominantly green color has been noted as "the same as the marine plants to which they were attached" (label data, USNM 129177). Brewster-Wingard et al. (2001: 223), in reference to its occurrence on benthic macroalgae (especially *Chondria* and *Laurencia*), construed that the species "has the ability to camouflage itself to match the color of the vegetation to which it attaches." The deepest record for living specimens in FK samples is 4 m off the bayside of Tavernier (FK-170; in agreement with Hayes, 1972, ranging 1–4 m). Empty shells are a frequent component of beach drift, and were also found in one shallow offshore sediment sample from 12 m (FK-296), perhaps due to the transport qualities of its lightweight shell. *P. longisquamosa* was reported in a dredge sample from 10 fms (18.3 m) off Broward County, Florida (McGinty & Nelson, 1972, as *Pinctada xanthia*), although the condition of the specimens (live-collected or empty shells) was not indicated; empty shells are also known from a dredge sample (5.5–6.1 m) in Apalachee Bay, Florida (HMNS 38564).

Pinctada longisquamosa populations show some indication of seasonality at certain locations. Hayes (1972: 149) noted that the species was scarce in February 1971 in an area of Biscayne Bay, Dade County, Florida, where according to collectors the species had been abundant during the previous November; she attributed its absence to "drastic changes in environmental conditions" caused by dredging or pollution. During the present study, a similar situation was noted near Pigeon Key, off the Florida Bay side of Tavernier, Key Largo [not to be confused with the better-known Pigeon Key near the center of the Seven Mile Bridge], where an especially abundant population was sampled in September and October 1998 (FK-165, 183) and again in October 2000 (FK-368). Following a particularly cold spring, no living specimens were located at this site in April 2003 (FK-680), although numerous small (> 17 mm) specimens were again present two months later (FK-684, 691, 700; salinity 35 ppt) in macroalgal clumps

FIG. 29. *Pinctada longisquamosa,* living juvenile *in situ* on macroalgae (off Pigeon Key [bayside of Tavernier], Florida Keys, FK-700, approximately 10 mm).

within the seagrass bed (mixed *Thalassia testudinum* and *Syringodium filiforme*) (Fig. 29); population density in this newly recruited population was measured at 324 and 342 spm/m^2 (n = 2). One of the largest recorded specimens was found concurrently on a dead gorgonian stalk at 1.5 m oceanside of Key Largo in June 2003 (FK-693) suggesting that populations in more environmentally stable offshore locations might serve as recruitment sources for the bay. From this anecdotal evidence, *P. longisquamosa* densities at this location might be fluctuating in response to seasonal temperature or salinity changes; the population fluctuations noted by Hayes (1972) might be similar phenomena. Such a hypothesis, however, has not been rigorously investigated.

More compelling evidence exists for the effect of changing salinity on the presence and local abundance of *Pinctada longisquamosa*. Brewster-Wingard et al. (2001: 223, 224) included *P. longisquamosa* among eight mollusks considered to be important biological indicators of environmental conditions in Florida Bay. Their "*Pteria* assemblage" (centered on *Pinctada longisquamosa*) was "typically found on the sides of mudbanks (40-150 cm of water) in dense *Thalassia* beds, relatively clear water, and salinities between 20 and 40 ppt." They noted that the species "seems unable to survive in water of diminished quality", and believed distribution of the assemblage to be "controlled by a combination of salinity, substrate, water depth, and water clarity." Those authors reported a mean salinity of 29.3 ppt, based on 62 field observations of *P. longisquamosa* sites. In the 1994–1996 FMRI study, living *P. longisquamosa* was found in salinities from 18–42 ppt (mean 32 ppt; 65 observations). Its distribution seemed strongly influenced by the availability of suitable salinity. During the drought year of 1994, when hyperhaline conditions (salinity > 40–52 ppt) occurred throughout central Florida Bay (Lyons, 1998), *P. longisquamosa* was found only at 18 sites in the eastern bay, where more moderate salinities (18–30 ppt) prevailed (Fig. 30, top). In 1996, *P. longisquamosa* was found at 34 sites (Fig. 30, bottom), the increase attributed almost entirely to expansion into the central bay, where salinities returned to more moderate conditions. During both years of sampling, the species was most abundant immediately north of central Key Largo, where the highest density for the species (396 spm/m^2) was recorded in 1996 in a sample site immediately northeast of that containing Pigeon Key sampled by Mikkelsen/Bieler (Fig. 30, bottom). A secondary center of abundance was recorded in the central bay, where density was 156 spm/m^2 at one site, also in 1996. The five greatest densities recorded for *P. longisquamosa* in 1994 ranged from 41–74 spm/m^2 at sites of salinity 36.8–41.0 ppt (mean 38.4 ppt); the five greatest densities in 1996 (41–396 spm/m^2), including the two maxima mentioned above, occurred at sites of substantially lower salinity (27.0–33.4 ppt, mean 30.4 ppt). Similar patterns of retracting and expanding populations in response to increasing and decreasing salinity were discerned for several other Florida Bay mollusks, principally bivalves (Lyons, 1998).

Brewster-Wingard et al. (2001) questioned whether the occurrence of *Pinctada longisquamosa* in relatively clear water indicates that the species favors clear water, or that the water is cleared by the filtering activity of *P. longisquamosa*. Both explanations could be valid, especially in very shallow water. However, *P. longisquamosa* in the FMRI study was relatively abundant at several deeper (2.5–3.1 m) sites in northeastern Florida Bay. Water clarity at those sites was generally excellent, but similar levels of clarity also occurred nearby at sites where *P. longisquamosa* was uncommon or absent. In that area of the bay, high water clarity could be as much a factor of nutrient scarcity in the water column as it is a factor of bivalve abundance.

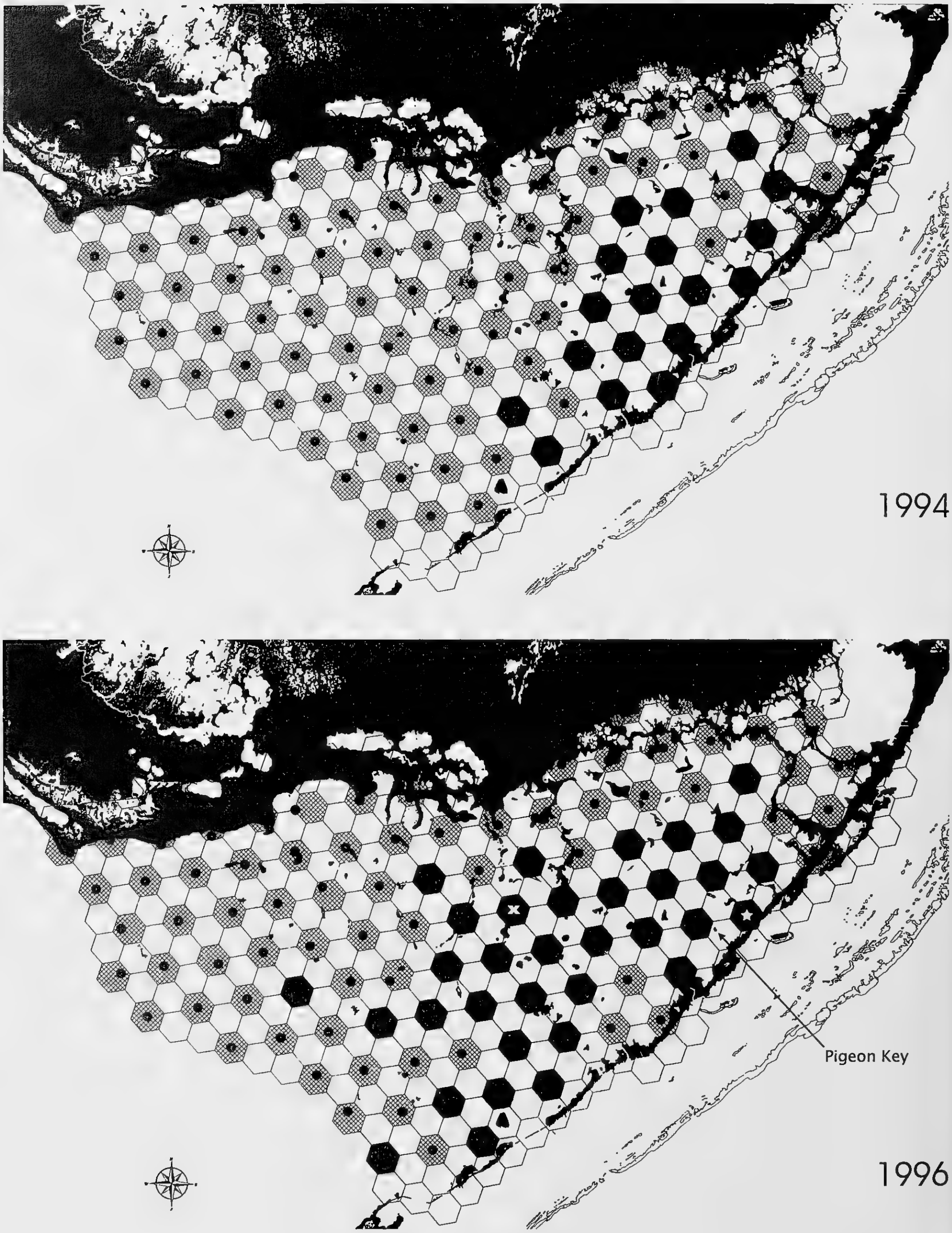


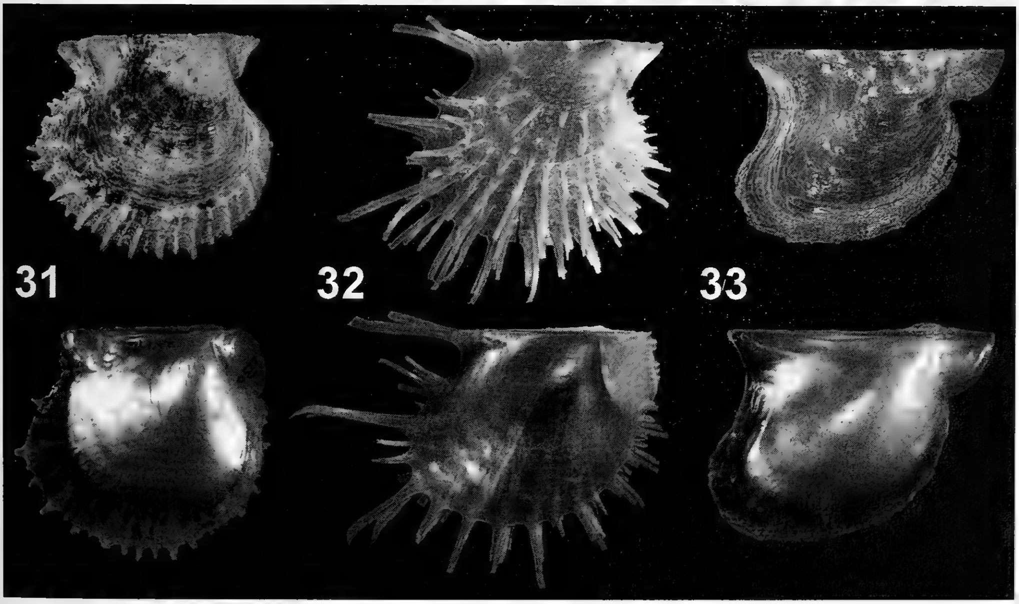
FIG. 30. Distribution of living *Pinctada longisquamosa* in Florida Bay in 1994 (top, drought year) and 1996 (bottom, year following flood year). Florida mainland is at top of each map, with Cape Sable at upper left. Cross-hatched hexagons represent 101 quantitative sites sampled by FMRI (clear hexagons not sampled); solid black hexagons are sites at which living *P. longisquamosa* was collected. White star and white “x” indicate sites of highest (396 spm/m^2) and second highest (156 spm/m^2) recorded densities, respectively.

DISCUSSION

Pinctada longisquamosa has most frequently been placed in the genus *Pteria* likely due at least in part to its oblique shell shape. In collections, it is frequently misidentified as one of the two other common western Atlantic pteriids, *Pinctada imbricata* and *Pteria colymbus* (Figs. 31–33). Its confusion with the former no doubt stems from its sculpture of radial lamellae. Aguayo & Jaume (1948b) included *P. longisquamosa* as a synonym of *Pinctada radiata* (Leach, 1814), a species generally recognized today as synonymous with *P. imbricata*.

Conchological, anatomical and ecological data for *Pinctada longisquamosa, P. imbricata,* and *Pteria colymbus* are presented in Table 1. These data reveal character sets that appear consistent at the generic level (I. Tëmkin, unpubl. data). Most informative are anterior and posterior dentition (tooth/socket in RV or LV), ornamentation (shell or periostracal), intestinal loop (with or without twist), intestinal path (dorsal to or through heart), shape of the adductor muscle (bean-shaped or oval), and byssal structure (filamentous or stalk-like). *Pinctada longisquamosa* shares these characters in common with *P. imbricata* and other examined species of *Pinctada,* and on this basis is here transferred to the genus *Pinctada*. Molecular data based on the 18S rDNA gene also support this conclusion, and will be reported in context of a larger analysis elsewhere.

For routine identification purposes, *Pinctada longisquamosa* can be distinguished from *Pteria colymbus* by the genus-level features (dentition, ornamentation) discussed above. It is separable from *Pinctada imbricata* by thinner and denser radial lamellae, and by thinner nacre, allowing external color and ornamentation to show through the valve. This latter character is useful in comparison with both *P. imbricata* and *P. colymbus,* even in small subadults. The prodissoconch of *P. longisquamosa* is noticeably smaller in length than that of *P. imbricata* (as reported by Waller & Macintyre, 1982; Table 1), although these data are based on very few specimens in both cases. The prodissoconch of *Malleus candeanus* (Orbigny, 1842) (Pterioidea, Malleidae) is remarkably similar in size and overall morphology (Waller & Macintyre, 1982: fig. 213).



FIGS. 31–33. Contrasting shell morphology in the three common western Atlantic Pteriidae. FIG. 31: *Pinctada imbricata* (FMNH 227467, Ohio-Missouri Key Channel, Florida Keys, coral rocks, 57.2 mm); FIG. 32: *Pinctada longisquamosa* (FMNH 302080, 40.1 mm including lamellae); FIG. 33: *Pteria colymbus* (FMNH 183297, Missouri Key, 56.0 mm).

TABLE 1. Comparative morphological and ecological characteristics of the three common western Atlantic Pteriidae.

	Pinctada imbricata	*Pinctada longisquamosa*	*Pteria colymbus*
Size	large (ca. 60 mm)	small-medium (mean 23 mm)	large (ca. 80 mm)
External shell color	light brown to yellow, with marginal black/white bands	primarily green	predominantly brown (periostracum), often encrusted
Ornamentation	radial rows of relatively wide shell lamellae	radial rows of long, narrow shell lamellae	relatively smooth shell with concentric and radial periostracal ridges
Prodissoconch (mean L, µm)	306 (Waller & Macintyre, 1982)	219	unknown
Anterior dentition	tooth in RV, socket in LV	tooth in RV, socket in LV	tooth in LV, socket in RV
Posterior dentition	ridge in LV, socket in RV	ridge in LV, socket in RV	ridge in RV, socket in LV
Adductor muscle scar	bean-shaped	bean-shaped	oval
Nacre	thick	thin, allowing color and ornamentation to show through shell	thick
Intestinal loop	with twist	with twist	without twist
Intestinal path	dorsal to heart	dorsal to heart	through heart
Pallial tentacles	branched	simple	branched
Byssal structure	filamentous	filamentous	stalk-like
Habitat	rock, shell, etc., near substratum	seagrass/algae, substantially off-bottom	gorgonians and other structures, substantially off-bottom

The type locality of *Pinctada longisquamosa* is Venezuela, the southernmost point of the species' geographical range. Several standard references on the malacofauna of Venezuela (Work, 1969; Lodeiros S. et al., 1999) do not list *Pinctada longisquamosa*, although they include *P. imbricata* and *Pteria colymbus*. Three additional specimens from Venezuela have been examined (AMNH 203057, HMNS 30309, the latter topotypes); they differ from the type specimen by a somewhat smaller size and having a zigzag pattern of commarginal ornament. This degree of variation is within that noted for Florida specimens.

Pteria viridizona, clearly conspecific with *Pinctada longisquamosa* but based on specimens supposedly from Long Beach, California, was previously determined to be based on specimens with erroneous locality data (Hayes, 1972; Coan et al., 2000). Prior to that determination, Fischer-Piette (1982) listed *P. viridizona* as a synonym of *Pteria sterna* (Gould, 1851), in turn treated by that author as a subspecies in a circumglobally distributed *Pteria colymbus*.

Pteria xanthia is a distinctive cadmium yellow color variant of *Pinctada longisquamosa*. Hayes (1972: 57) noted that some collectors have labeled such specimens as *Avicula crocata* (Swainson, 1831), a yellow-shelled species described from Ceylon that has been synonymized with *P. imbricata* (see Ranson, 1961; Shirai, 1994).

Pinctada longisquamosa is similar to *Pteria vitrea* (Reeve, 1857), "which it most nearly resembles, though it is not as oblique, the color is yellow instead of opaque white, and the laminations are much longer, though not as profuse" (Schwengel, 1942: 64). Hayes (1972: 58) also noted that *P. vitrea* has an extended posterior auricle, whereas *P. longisquamosa* has a short posterior auricle adorned with elongated lamellae. The differences in hinge teeth and ornamentation, discussed below in a generic context, also serve to distinguish these two nominal species as separate.

Avicula guadalupensis Orbigny (1842: pl. 28, figs. 23, 24), from Guadeloupe (Beau, 1858), was investigated as a possible earlier name for *Pinctada longisquamosa*. Hayes (1972: 87) deemed the description of *A. guadaloupensis* inadequate and the figure too stylized for positive identification. Examination of the holotype (BMNH 1854.10.4.611, 1 pair), which is off-white to gray in color, indicated that d'Orbigny's drawing, schematic as it is, is accurate in showing overlapping commarginal fringes of short, well-preserved prismatic scales continuous across the shell surface that are alternately arranged, as opposed to the long, radially arranged lamellae of *P. longisquamosa*. We therefore do not consider it conspecific. Full systematic revision of this and other nominal western Atlantic pteriids awaits a more comprehensive review of the genus, currently underway.

The unusual periostracal structure revealed by SEM during this study does not appear to have been previously reported. This configuration could have resulted from the growing shell prisms pushing aside the still-fluid periostracum as they increase in diameter (J. Carter, in lit., July 2003).

The general anatomical features of *Pinctada longisquamosa* was described and illustrated by Hayes (1972: figs. 6–8). Our results agree in all respects except in the presence of the catch component of the adductor muscle that Hayes (1972) stated as being absent.

Anatomical characteristics of *Pinctada longisquamosa* correspond well to those described for other pteriid species, with some notable variation. In the gills of *P. longisquamosa*, interfilamental junctions consist of tissue plus ciliated connections, as was previously reported for *Pteria argentea* (Reeve, 1857) (Ridewood, 1903), *Pinctada margaritifera* (see Atkins, 1938), and *Pinctada vulgaris* (see Herdman, 1904, 1905). However, interfilamental junctions in *Pteria hirundo* are exclusively cilial except for the area uniting principal and ordinary filaments in the dorsal part of a demibranch (Atkins, 1936, 1938). The presence of laterofrontal tracts of cilia on the gill filaments and the varied nature of interfilamental connections in these species led Atkins (1938) to consider pteriid gills as an intermediate grade between filibranch and eulamellibranch types. However, the extensive organic fusion in *Pinctada longisquamosa* is characteristically eulamellibranch.

The ciliated lateral attachment of the dorsal inner demibranch margins with the mantle is as described for other pteriids (Herdman, 1904; Atkins, 1936). The degree of fusion varies among individuals from complete attachment to entire absence, possibly indicating an inherent weakness of the cilial junctions leading to easy dissociation of the structures with minimal force. Herdman (1905: 226) described a similar condition in *Pinctada vulgaris*, noting that "slight pressure with dissecting-needles is generally sufficient to force the parts asunder, and they are seen to separate with clean-cut broad edges or seams and leave no appearance of tearing."

Overall stomach morphology closely resembles that of other pteriids (Herdman, 1904; Purchon, 1957, 1985; Kuwatani, 1965). As in *Pinctada martensii* (but not in *P. vulgaris*; Purchon, 1957; Kuwatani, 1965), the major typhlosole does not enter a blind pocket on the right stomach wall before turning ventrally.

Our histological study of the anal funnel of *Pinctada longisquamosa* confirmed previous observations in *P. imbricata* and *Pteria colymbus* (Hayes, 1972) that it consists of membranous loose connective tissue covered by thin epithelium; no muscular bundles or glands are present. In *P. longisquamosa*, the anal funnel is comparatively large and extends at a right angle from the intestine and posterior surface of the adductor muscle, passing beyond the gills and mantle margin. This suggests that it plays a role in directing the passage of fecal pellets, preventing their deposition in the pallial cavity, as proposed by Hayes (1972).

The distributional range of this species is in part difficult to establish. Because we have found it routinely confounded with *Pteria colymbus* and *Pinctada imbricata* in museum collections, we conclude that records of its occurrence in the literature cannot be trusted without verification through voucher specimens or published illustrations. A good example is the presence of *Pinctada longisquamosa* in Texas, currently the westernmost point of its range and only U. S. record outside of Florida. Pulley's (1952b) unpublished dissertation on Gulf of Mexico bivalves figured *P. longisquamosa* under the name *P. radiata* (now *P. imbricata*), but the figure caption gave that specimen as from Coconut Grove, Florida, and the accompanying description could refer to either nominal species. Pulley's (1952a: 130, pl. 7, figs. 3, 4, as *P. radiata*) Texas checklist definitely illustrated *P. imbricata* "occasionally found on Mustang and Padre Islands", providing no support that Pulley saw *P. longisquamosa* specimens west of Florida. Other standard works on the mollusks of Texas (Odé, 1979; Andrews, 1981, and earlier editions) did not list or illustrate this species. One museum lot (USNM 465343) of *P. longisquamosa* was verified, but with an indeterminate locality ("Texas coast"). Finally, the HMNS collection, well known for Texas and Gulf of Mexico material, provided the needed confirmation in the form of two lots from South Padre Island (HMNS 14589, 41598).

Several other published records suggest misidentified *Pinctada longisquamosa* but defy confirmation. Abbott (1958: 115, as *P. radiata*) described *P. imbricata* from Grand Cayman Island as "in shallow, inshore waters ... under one inch in length, very fragile and quite oblique in shape". This is most similar to *P. longisquamosa*, although it cannot be confirmed in the absence of a published figure. Voucher specimens for Abbott (1958) are at both ANSP and USNM (and MCZ, not seen), yet none identified as *P. longisquamosa* were confirmed by Hayes (1972), who used the USNM collection extensively, or by the authors during this study. Ekdale's (1974: 653, as *P. radiata*) description of *P. imbricata*'s habitat as "common in lagoons attached to *Thalassia* grass blades" in Yucatan, Mexico, is more similar in our experience to that of *P. longisquamosa* than *P. imbricata*, although the referenced figure (Warmke & Abbott, 1961: pl. 32, fig. b) is definitely that of *P. imbricata*. The same argument can be made about G. L. Voss & N.A. Voss (1955: 226) who listed *P. radiata* "living on *Thalassia*" off the southeast quadrant of Soldier Key off Biscayne Bay, Florida.

A substantial body of literature (see synonymy & literature cited) has reported the occurrence and importance of a species in Florida Bay reported principally as *Pinctada radiata*. However, Brewster-Wingard et al. (2001) established that the extensive records of Turney & Perkins (1972) and by Brewster-Wingard herself in earlier papers (Brewster-Wingard & Ishman, 1999; Brewster-Wingard et al., 1996, 1997, 1998b; Ishman et al., 1996; Wingard et al., 1995) were actually of *P. longisquamosa*, and a photographed shell by Turney & Perkins (1972: 12, fig. 6) supports that contention. Lyons (1998; unpublished) and Brewster-Wingard and her collaborators made several hundred collections of mollusks at sites throughout Florida Bay during several years in the 1990s. *Pinctada longisquamosa* was encountered during every year and every season (as both living specimens and dead shells in sediment cores dated to the mid-1800s), but no other pteriid species was encountered in the bay. Given this dominance by *P. longisquamosa*, it is reasonable to conclude that other Florida Bay records (e.g., Tabb & Manning, 1961; Hudson et al., 1970) also represent *P. longisquamosa*.

Pinctada longisquamosa appears highly (although not exclusively) specific to seagrass habitats. In shallow Florida Bay, this complex three-dimensional habitat provides a refuge for the thin-shelled species against larger predators, and also provides attachment places substantially off the substratum, away from gill-fouling sediment. The pallial tentacles of *P. longisquamosa* have few branches compared to the dendritic tentacles of larger-bodied species (e.g., *Pteria colymbus, Pinctada imbricata*), although it is uncertain if this is a factor of habitat, where highly branched tentacles can serve as a screen against siltation. Nevertheless, such a shallow-water habitat undergoes serious physical stresses associated with changing water temperatures, aerial exposure during low tide, stagnation causing low dissolved oxygen levels, and nutrient-loading eutrophication (natural and anthropogenic) during hot Florida summers (Sousa, 2001; Williams & Heck, 2001), and salinity extremes (Lyons, 1998; Brewster-Wingard et al., 2001). Anecdotal observations on populations during this study also suggest that unusually cold Florida winters are similarly impactful. Regardless of the effect of these factors on the pteriids themselves, seasonal sloughing off of older *Thalassia* blades probably influences the size and structure of *P. longisquamosa* populations on a nearly annual cycle. The aperiodic die-offs of *Thalassia* beds that have occurred in Florida Bay in recent years (Robblee et al., 1991) must have been accompanied by local extirpation of pteriids and other seagrass dwellers from those affected areas.

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APPENDIX. Material examined.

Florida Keys Diversity Study: FK-021, Lake Surprise, Key Largo, mile marker 107.5, NE end of U.S. Rte. 1 causeway across lake, 25°10.9'N, 80°23'W, off mangroves at side of road, hand dredge in sediment/algae, ca. 1.5 m, and by hand on shallow subtidal rocks, S = 22 ppt, 09 July 1995 (6 juv valves, AMNH 296437); FK-032, "Billboard" site, Lower Matecumbe Key, mile marker 74.5, oceanside, 24°51.4'N, 80°43.7'W, hand picked from flats and wrack line, 08 March 1996 (1 juv pair, AMNH 308210); FK-035, Indian Key Fill, mile marker 79, bayside, 24°53.4'N, 80°40.5'W, *Thalassia*, 1 m, shovel and sieve, 10 March 1996 (1 pair, AMNH 296438); FK-036, same as FK-032, hand scooped from wrack line on beach, 10 March 1996 (1 pair, 8 juv valves, AMNH 308209); FK-043, same as FK-021, off mangroves at side of road, shovel/sieve in sediment/algae (ca. 1.5 m) + shallow subtidal rocks by hand, 19 September 1996 (1 valve, FMNH 279467); FK-064, center of Coupon Bight, bayside off Big Pine Key/Newfound Harbor, 24°38.6'N, 81°22.2'W, 1.5 m, mud/*Thalassia*, bottom grab, R/V FLORIDAYS, 15 April 1997 (1 juv spm alc, FMNH 295709; 4 valves, FMNH 279466); FK-126, on old lobster traps being sold near "Billboard" site, Lower Matecumbe Key, mile marker 74.5, traps formerly used in "Florida Keys waters", 24 July 1997 (1 pair, AMNH 308099); FK-128, Rachel Shoal, bayside off Key Vaca, 24°45'N, 81°05'W, sand with algae/sponges, 1.5 m, dredge (2 tows), R/V FLORIDAYS, 25 July 1997 (1 pair, FMNH 279462); FK-136, E of Bethel Bank, bayside, 24°44.8'N, 81°04.7'W to 24°44.7'N, 81°04.7'W, sand/sparse seagrass, gorgonians, algae, 1.8–2.1m, 10 min dredge, R/V FLORIDAYS, 07 July 1997 (1 valve, AMNH 296433); FK-163, Tavernier, Key Largo, bayside, 25°03.6'N, 80°30.0'W to 25°03.5'N, 80°30.2'W, sandy mud/*Thalassia*/chicken liver sponge/*Dasycladus*, 1.7 m, dredge, R/V FLORIDAYS, 12 September 1998 (13 juv spm alc, AMNH 298903; 22 pair, 34 valves, AMNH 296432); FK-165, off W shore of Pigeon Key (bayside of Tavernier), 25°03.3'N, 80°30.8'W, *Thalassia*, 1.4 m, scuba, by hand, R/V FLORIDAYS, 13 September 1998 (32 spm alc, 2 valves alc, AMNH 298904); FK-166, Tavernier, Key Largo, bayside, mile marker 95.5, 25°03.2'N, 80°29.1'W, on *Acetabularia* on rocks, 0–1 m, by hand, 14 September 1998 (2 spm alc, FMNH 295714); FK-168, Tavernier Creek, near bayside entrance, west side (Plantation Key), 25°00.7'N, 80°32.7'W, mangrove root scrapings, snorkeling, R/V FLORIDAYS, 17 September 1998 (1 spm alc, FMNH 295715); FK-170, Hawk Channel, E of mouth of Tavernier Creek, 24°58.8'N, 80°30.9'W to 24°58.7'N, 80°30.8'W, *Thalassia* droves, 3.3–4.0 m, dredge, two tows of 3 min each, R/V FLORIDAYS, 17 September 1998 (2 juv spm alc, FMNH 295718); FK-172, Cowpens Anchorage, bayside of Plantation Key, 24°59.1'N, 80°34.4'W, grey soupy mud/*Thalassia*, 1.8–2.1 m, ponar grab and dredge, R/V FLORIDAYS, 18 September 1998 (4 spm alc, FMNH 295716; 2 pair, 4 valves, AMNH 296428; 9 valves, FMNH 288688); FK-174, same as FK-165, *Thalassia*, 1.4 m, scuba, by hand, R/V FLORIDAYS, 18 September 1998 (12 spm alc, AMNH 298902; 100 spm [empty] alc, FMNH 290099); FK-181, Rock Harbor, Key Largo, mile marker 98, bayside, 25°04.7'N, 80°27.7'W, shallow water off beach, seagrass/sand/shell gravel, snorkeling, 08 October 1998 (11 spm alc, FMNH 288839); FK-183, N of Key Largo, S end of Pigeon Key, bayside, 25°03.3'N, 80°30.6'W, dense to sparse seagrass, 0.3–1.5 m, snorkeling, R/V FLORIDAYS, 10 October 1998 (20 spm alc, FMNH 288845); FK-184, off Key Largo, W side of North Nest Key, bayside, 25°09.1'N, 80°30.8'W, seagrass flats near dock, R/V FLORIDAYS, 12 October 1998 (spm obs, 6 pair, FMNH 288613); FK-186, NW of Plantation Key, Cowpens Cut, bayside, 24°59.8'N, 80°33.6'W, seagrass beds, 1.2–1.8 m, hand-sieving, R/V FLORIDAYS, 14 October 1998 (1 spm alc, FMNH 288867); FK-188, Blackwater Sound, east of Bush Point, 25°08.8'N, 80°25.3'W, seagrass, 1.8 m, bottom sample, R/V FLORIDAYS, 14 October 1998 (13 spm alc, FMNH 288844); FK-191, Key Largo, bayside, small mangrove key off Hammer Point, near border of Everglades National Park, 25°02.0'N, 80°31.3'W, wrackline to 0.3 m, at extreme low tide, mats of brown and green algae, R/V FLORIDAYS, 31 March 1999 (7 juv alc, AMNH 298905; 4 pair, AMNH 296435); FK-192, same as FK-184, clay and sand beach, mangroves, by hand, R/V FLORIDAYS, 01 April 1999 (5 pair, FMNH 279460); FK-193, off Key Largo, bayside, E of Buttonwood Sound, Swash Keys, E shore of unnamed middle key between Whaleback Key and Shell Key, 25°07.3'N, 80°28.8'W, clay and sand beach, mangrove roots with oysters, by hand, R/V FLORIDAYS, 01 April 1999 (3 pair, AMNH 296431); FK-201, Key Largo, bayside, mile marker 95.5, 25°03.2'N, 80°29.1'W, sand/wrack line, intertidal, by hand, 06–13 April 1999 (8 juv pair, AMNH 296429); FK-209, same as FK-191, intertidal algae/seagrass/mangrove roots, by hand, R/V FLORIDAYS, 11 April 1999 (9 juv spm alc, 1 juv pair, FMNH 295717); FK-210, same as FK-032, beach drift, 13 April 1999 (1 pair, AMNH 296430); FK-211, unnamed bay between Shark Key and Big Coppitt Key, bayside, 24°36.4'N, 81°39.2'W, *Thalassia*, bottom sample, R/V FLORIDAYS, 17 April 1999 (1 juv valve, FMNH 279470); FK-224, W end of Missouri Key, oceanside, 24°40.5'N, 81°14.3'W, rocks and beach line, 0–1 m, by hand, 20 April 1999 (1 pair, FMNH 279465); FK-226, Saddlebunch Harbor, off W tip of Saddlebunch Keys, 24°35.2'N, 81°37.9'W, sand with various algae and sponges, *Thalassia*, 0.3 m, hand dredge, R/V FLORIDAYS, 20 April 1999 (1 frag, FMNH 279463); FK-249, E end of Ohio Key, oceanside, mile marker 39, 24°40.3'N, 81°14.5'W, beachcombing in wrack line, 05 August 1999 (3 valves, AMNH 308098); FK-255, Friend Key Bank, bayside of Bahia Honda Key, N side at crest of bank, 24°42.6'N, 81°16.8'W, *Thalassia/Syringodium* with sand patches, 0.15–0.6 m, snorkeling, R/V FLORIDAYS, 09 August 1999 (1 alc, FMNH 289986); FK-258, Friend Key, bayside of Bahia Honda Key, off N shore, 24°43.4'N, 81°17.3'W, sparse *Thalassia* with sponges and sand patches, 0.3–0.6 m, snorkeling, R/V FLORIDAYS, 09 August 1999 (1 valve, AMNH 296434); FK-270, Ohio Key campground, mile marker 39, bayside, 24°40.5'N, 81°14.7'W, mangrove shore, by hand, 19 August 1999 (1 pair, 3 valves, AMNH 296436); FK-278, Ohio Key, ocean side, beach facing Seven Mile bridge, 24°40.3'N, 81°14.5'W, beach drift, algae, silt-covered platform exposed at low tide, by hand, 06 April 2000 (1 pair, AMNH 308101); FK-286, same as FK-201, by hand, sand/wrack line, intertidal, 09 April 2000 (2 juv valves, AMNH 308103); FK-289, Cowpens Anchorage, bayside of Plantation Key, 24°58.7'N, 80°34.5'W, sand/sparse seagrass/*Penicillus,* 1.7 m, petit ponar grabs, M/V PATCH HAPPY, 11 June 2000 (8 valves, AMNH 308100); FK-353, "Horseshoe" site (outside S arm), Spanish Harbor Keys, 24°39.3'N, 81°18.2'W, gulf side, to 1.5 m, hand dredge, *Thalassia/Halodule* seagrass, 08 July 2000 (1 valve, AMNH 299574); FK-357, American Shoals, NW of lighthouse, 24°31.5'N, 81°31.2'W, *Thalassia* with large coral rubble, 2.7–3.3 m, scuba, R/V FLORIDAYS, 09 July 2000 (1 pair, AMNH 299590); FK-368, off W shore of Pigeon Key (bayside of Tavernier), 25°03.3'N, 80°30.7'W, live-collected in *Thalassia* and *Syringodium* seagrass, 0.3–0.9 m, snorkeling, R/V FLORIDAYS, 08 October 2000 (ca. 400 spm, AMNH 308109 and FMNH 302080); FK-392, same as FK-032, wrack line, by hand, 20 October 2000 (1 valve, AMNH 308102); FK-428, Infaunal Mollusk Survey, Windley Key transect sta. W-14-FK-428, 24°53.3'N, 80°31.5'W, 46.9 m, shelly mud, small pipe scoop, M/V STRANGE BRU, 25 April 2001 (1 valve, 1 fragment, AMNH 296439); IMBW-FK-629, "The Horseshoe" site, bayside of West Summerland Key (Spanish Harbor Keys), mile marker 35, 24°39.3'N, 81°18.2'W, among rocks along arms of quarry, by hand, snorkeling, to ca. 1 m, 21 and 26 July 2002 (2 pair, AMNH 308106); IMBW-FK-649, Sprigger Bank, bayside, just W of Everglades National Park border, 24°54.7'N, 80°56.2'W, *Thalassia/Syringodium*, snorkeling, shovel/sieving, 0.1–

0.9 m, Keys Marine Laboratory boat, 27 July 2002 (1 juv pair with dried tissue, AMNH 308105); IMBW-FK-652, Long Key State Park, oceanside, 24°48.7'N, 80°49.7'W, seagrass bed (predominantly *Thalassia*) on muddy sand, > 1 m, wading, shovel/sieving, 27 July 2002 (1 pair, AMNH 308107); IMBW-FK-656, mangrove channel off South Layton Drive, oceanside of Long Key, 24°49.4'N, 80°48.8'W, red mangrove roots, snorkeling, 0.6–1.2 m, 28 July 2002 (4 spm alc, AMNH 305172); FK-680, W of Pigeon Key (bayside of Tavernier), 25°03.304'N, 80°30.715'W, 2 ft (0.6 m), sweepnet through mixed algae on *Thalassia* seagrass, R/V FLORIDAYS, 12 April 2003 (1 valve, AMNH 308097); FK-681, bayside of Tavernier, off small mangrove island near border of Everglades National Park, 25°01.95'N, 80°31.17'W, 2 ft (0.6 m), pavement with sand, sparse to thick *Thalassia* seagrass, snorkeling, by hand, R/V FLORIDAYS, 12 April 2003 (26 pair, 40 valves, AMNH 308496; 7 pair, FMNH 296727); FK-683, W of Tavernier Creek, bayside, fast-flowing mangrove-lined tidal channel in midst of Cross Bank leading into Cowpen's Cut, 25°00.345'N, 80°33.468'W, 0.5–1.0 m, snorkeling, *Thalassia* seagrass, R/V FLORIDAYS, 03 June 2003 (1 juv pair, 60 juv valves, AMNH 308120); FK-684, W of Pigeon Key (bayside of Tavernier), 25°03.304'N, 80°30.715'W, 0.6 m, snorkeling, dipnet, mixed algae on *Thalassia* seagrass, R/V FLORIDAYS, 03 June 2003 (12 alc, 11 juv pairs, 1 fragment, AMNH 308119/308235/308236); FK-690, E of Pigeon Key (bayside of Tavernier), 25°03.400'N, 80°30.617'W, 0.9 m, snorkeling/dipnet, sparse *Thalassia/Halodule* seagrass with algae, some *Gracilaria*, R/V FLORIDAYS, 07 June 2003 (2L alc, AMNH 308231); FK-691, W of Pigeon Key (bayside of Tavernier), 25°03.304'N, 80°30.715'W, 0.6 m, snorkeling, dipnet, mixed algae on *Thalassia* seagrass, R/V FLORIDAYS, 07 June 2003 (89 alc, 25+ pair, 100+ valves, AMNH 308233); FK-693, off Dove Key, oceanside of Key Largo, 25°03.039'N, 80°28.151'W, 0.9–1.5 m, snorkeling, silty *Thalassia* seagrass and sand, at top of dead gorgonian stalk, R/V FLORIDAYS, 08 June 2003 (1 alc, largest recorded specimen, AMNH 308234); FK-700, W of Pigeon Key (bayside of Tavernier), 25°03.287'N, 80°30.693'W, 0.3–0.6 m, snorkeling, seagrass with algae, R/V FLORIDAYS, 12 June 2003 (1 pair, 2 valves, AMNH 308104; 70+ juvs alc, FMNH 302081).

Other material examined:

Bermuda: Bermuda, entrance of Harrington Sound, H. G. Richards! 29 June 1932 (2 pair, USNM 422492). *Florida*: Florida, Velie!, "the color when living is green – the same as the marine plants to which they were attached" (4 pair with tissue, 3 pair, USNM 129177). *Eastern Florida*: 20 mi S of St. Augustine, live-collected on beach in seaweed, May 1968, Miriam K. Hicks! (2 juv pair, AMNH 249011); S of Matanzas Inlet, on seaweed at high tide mark, Fall 1970, Miriam K. Hicks! (2 pair, AMNH 248983); Ormond Beach, 1955 (3 pair, HMNS 27356); off Ormond Beach, Betty Allen! 1977 (3 pair, HMNS 19433); Coconut Grove, at Pan Am Airport, 4 ft (1.2 m), Fostor! 1936 (1 spm, 1 valve, HMNS 201); Chicken Key, 6 mi S of Coconut Grove, R. Foster! (1 pair with piece of sponge (presumed substratum), AMNH 200267). *Florida Keys*: Broad Creek, Bean! 24 December 1906 (1 pair with tissue, USNM 198115); Cormorant/Jew Points, mangrove roots among *Caulerpa verticillata* Agardh, 07 October 1978, P. M. and P. S. Mikkelsen! (1 juv spm, DMNH 179666; 6 juv alc, 8 juv pair, AMNH 308498); lower part of Barnes Sound, Harry Balknap! (2 pair, AMNH 67013); Barnes Sound, H. A. Rehder! 20 April 1947 (2 pair, USNM 778259); Key Largo, February 1944 (4 pair, AMNH 200266); Key Largo, Atlantic side, shallow, "found feeding on grass of bay", J. M. Bijur collection (6 pair, AMNH 232620); Key Largo, May 1940, J. Donovan! Grace G. Eddison collection (2 pair, AMNH 293718); NW Key Largo, mangrove channel, on mangrove roots, P. S. Mikkelsen! 07 October 1978 (3 alc); PSM-811, Key Largo, N of Rock Reef Motel, *Thalassia* seagrass and algae, by hand, 0.7–1.5 m, P. S. Mikkelsen! 8 and 10 February 1982 (12 juv alc, 3 juv pair, AMNH 308500); Key Largo Sound, J. M. Bijur collection (3 pair, AMNH 232622); Key Largo, Largo Sound, 08 December 1956, Craig and Fanny Phillips! (1 pair with tissue, FMNH 62888); Key Largo, Molasses Reef (1 pair, AMNH 100868); Key Largo, 2 mi W of Rock Harbor, Florida Bay, alive on eelgrass (*sic*), 2 ft (0.6 m), firm sand bottom, November 1961, D. Raeihle! A. D'Attilio Colln (2 pair, AMNH 133956); Key Largo, 2 mi S of Rock Harbor, Florida Bay, alive on turtlegrass, 2–3 ft (0.6–0.9 m), firm sand bottom, November 1961, D. Raeihle! (9 pair, AMNH 106140); Florida Bay, Bottlepoint [now Bottle] Key, R. P. Allen! (1 pair, USNM 533677); Key Largo, Harris Beach, W.

S. Bitler! (3 pair, AMNH 308211); Key Largo, bar on gulf side, opposite Tavernier, Vilas! (7 pair, BMSM 26118); Key Largo, bar on gulf side, opposite Tavernier, Vilas collection (1 pair, BMSM 26119); Florida Bay, May 1964–July 1965, Tabb and Manning! (many small pairs, UMML 30.8885, 8890, 8893, 8916, 8922, 8930, 8936); Upper Matecumbe, oceanside, on beach, HC Porreca! (5 pair, AMNH 139428); Islamorada, Florida Straits, H. S. Feinberg! (5 pair, AMNH 308207); Islamarada (*sic*), 1967, Alice Denison Barlow! (5 pair, AMNH 244070); Islamarada (*sic*), March 1963, Mrs. Ward!, H. C. Porrecca collection (1 pair, BMSM 26117); east of Teatable bridge, living on eelgrass (*sic*), 1959, Raeihle collection (2 pair, AMNH 308111); Lower Matacumbe (*sic*) Key, 1956, Elinor Townsend!, Dale V. Stingley collection (2 pair, BMSM 26116); Islamorada, off mangrove roots, Eleanor Townsend! (10 pair, AMNH 139427); Lower Matacumbe (*sic*) Key, February 1952, Mary Brevillier! Dale V. Stingley collection #593 (6 pair, BMSM 26114); Lower Matecumbe Key, January 1965 and 1966, H. C. Porreca! (9 pair, BMSM 26123); Matecumbe Key, Wisoff collection (1 pair, AMNH 120106); Matacombe (*sic*) Key, February 1965, Bert Porrecca! (7 pair, BMSM 26113; 8 pair, BMSM 26121; 16 pair, BMSM 26122); Key Vaca, Marathon, B. R. Bales collection, donated by J. Schwengel 1958 (1 pair, ANSP 222085); Marathon, Mrs. H. McGill! via T. L. Moise (1 pair, ANSP 193909); off Marathon, on old rope (2 pair, FMNH 159957); Marathon, ocean[side], ropes of lobster traps, E. M. Malone collection (1 juv pair, BMSM 26120); Marathon (1 pair, BMSM 26115); N of Knight's Key [bayside], channel, 11 fms (20.1 m), U.S. Fish Commission *Fishhawk* sta. 7412 (1 pair with tissue, USNM 198142); Lower Florida Keys, 1947, A. Koto! ex Wickham (1 pair, FMNH 183214); PSM-786, Big Pine Key, seawall off Bogie Channel, subtidal attached algae, by hand and sieving, 0.2 m, P. S. and P. M. Mikkelsen! 16 August 1981 (1 juv alc, AMNH 308501); Boca Chica, H. A. Pilsbry! (2 pair, ex ANSP 100274); Boca Chica, fresh-dead in drift of turtlegrass, November 1963, Raeihle collection (6 pair, AMNH 308110); Key West, pulled onto boat on seaweed while fishing, A. D. Barlow collection (5 pair, AMNH 244074); Key West, 1937, A. Koto! (5 pair, FMNH 288737); Key West, South Beach, 18 February 1947, Mrs. Ward Brown!, ex J. D. Parker (2 pair, ex ANSP 182650); Key West, especially E side, Jan.–Feb 1958, M. Bogart! (14 pair, AMNH 184816); Key West, December 1938, Dr. and Mrs. Julius Wisof! (1 pair, AMNH 308208); Key West, Mrs. Eshnaur! (3 pair, 1 valve, USNM 404236); Key West, A. E. Mehring! sta. 6-B-5, 29 December 1949 (8 pair, USNM 700383); Key West, A. D. Clark!, June 1958 (1 pair, HMNS 199); SW of Tortugas, 35 fms (64.0 m), Schmitt! 14 August 1933 (1 pair, USNM 421671). *Western Florida*: Sanibel Island, D. Germer! (11 pair, AMNH 264528); Manasota Key, Butler!, Johnstone collection (1 juv pair, AMNH 210312); Tarpon Springs, brought in by sponge fishers, "sent in for identification by William Rhodes, School for the Blind, Indianapolis, Indiana" (1 pair, AMNH 70803); Tarpon Springs, P. Bartsch! 1936 (5 pair, USNM 428700); Apalachee Bay, dredged, 18–20 ft (5.5–6.1 m), near artificial reef, Gleeson, Keeler & Loftin! 30 April 1987 (1 pair, HMNS 38564); off Live Oak Island, Wakulla County, on scallop shells, J. Rudloe! 11 November 1970 (1 valve, USNM 70690); Gulf coast, Apalachicola, sta. 304/305, A. S. Pearse! June 1935 (1 pair with tissue, USNM 467928). *Texas*: Texas coast, J. D. Mitchell! (8 pair, 3 valves, USNM 465343); Port Isabel (gulf beach on South Padre Island), ex Betty Allen via C. E. Boone! (2 pair, HMNS 14589); South Padre Island, beach drift, W. W. Sutow! August 1966 (1 juv valve, HMNS 41598). *Bahamas*: Bahamas, 1904, Prof. W. M. Wheeler! (26 pair, 3 valves, with tissue, AMNH 27897); Bahamas, Prof. W. Wheeler! (6 pair with tissue, 3 valves, AMNH 27808); Andros, sta. wp126-Q5, transect from 24°54.8'N, 77°53.3'W to 24°54.8'N, 77°53.2'W, quadrat #5, *Thalassia*, 10 ft (3.0 m), scuba, P. M. Mikkelsen and G. Hendler! 03 September 2000 (1 valve, AMNH 308117); Andros, sta. wp126-R, 24°55.4'N, 77°54.4'W, *Thalassia*, 10 ft (3.0 m), scuba/snorkeling, P. M. Mikkelsen et al.! 03 September 2000 (3 spm alc, AMNH 308499); Andros, sta. wp415-R sediment, 24°53.5'N, 77°53.8'W, thick *Thalassia*, 12 ft (3.6 m), scuba/snorkeling, P. M. Mikkelsen et al.! 04 September 2000 (2 juv valves, AMNH 308497); Andros, sta. PMM-1039, on beach in front of Forfar Field Station, on *Sargassum* washed ashore, by hand, P. M. Mikkelsen! 28 August 2000 (12 pair, AMNH 308118); Andros, inside Golding Key, P. Bartsch! 03 May 1912 (1 pair with tissue, USNM 269347); Spanish Wells, across from Galliot Cay, NW end of Cape Santa Maria, Long Island, Mrs. J. Stout! 12-18 March 1967 (1 pair, AMNH 136184); Eleuthera, M. Bogart! (1 pair, AMNH 184885);

shores E of Fox Hill, Nassau, February 1928, William S. Treator! (1 pair, AMNH 270630); W shore of North Bimini, near entrance to Cavelle P[on]d, on tips of mangrove roots out of water at very low tide, W. Schwarting, 20 April 1950 (2 pair with tissue, AMNH 87385). *Cuba*: on flats between Cuba and Isle of Pines, live-collected on sea weed, 1 ft (0.3 m), F. H. Low! (7 juv pair, AMNH 113648); Santa Lucia, NW Cuba, 2–4 fms (3.6–7.3 m), *Barrera* Expedition sta. 200 (7 pair, USNM 456990); Punta Tolete, NW Cuba, 2–3 fms (3.6–5.5 m), *Barrera* Expedition sta. 205 (5 pair, USNM 45683); sand bar off Arroyos, NW Cuba, *Barrera* Expedition sta. 206 (1 pair with tissue, 1 pair, 7 valves, USNM 457007); Santa Rosa, NW Cuba, 3–6 fms (5.5–11.0 m), *Barrera* Expedition sta. 209 (14 pair, 43 valves, USNM 456989); Cape Cajon, NW Cuba, *Barrera* Expedition sta. 211 (7 pair with tissue, 4 pair, 14 valves, USNM 456987); Varadero Beach, Cuba, *Barrera* Expedition sta. 213 (1 pair, USNM 456985); Esperanza, NW Cuba, 4–6 ft (1.2–1.8 m), *Barrera* Expedition sta. 217 (1 pair, USNM 456986); Bay of Santa Rosa, NW Cuba, 1–3 fms (1.8–5.5 m), *Barrera* Expedition sta. 219 (2 pair, USNM 456982); Los Arroyos, NW Cuba, 3 fms (5.5 m), *Barrera* Expedition sta. 229 (1 pair, USNM 456988). *Jamaica*: Kingston, south shore, Betty Walden! September 1956 (1 valve, HMNS 15401). *Puerto Rico*: Mangrove Island, W of Magueyes (sic) Island, on *Rhizophora mangle*, 13 September 1962, H. E. Coomans! (1 pair with tissue, AMNH 109620); E of Carib Cayo, 5.5–8.75 fms (10–16 m), 25 June 1915, R. C. Osburn! (1 juv pair, AMNH 1036). *Virgin Islands*: St. Thomas, Alice Denison Barlow! (2 pair, AMNH 244072). *Mexico*: in bay E of larger island S of village, Mujeres Island, Quintana Roo, dredged, eelgrass bottom, Bredin-S.I. Expedition sta. 26–60, 31 March 1960 (4 pair with tissue, 1 valve, USNM 662550); Allen Point, Ascension Bay, Quintana Roo, Bredin-S. I. Expedition sta. 68–80, Schmitt! 13 April 1960 (1 pair with tissue, USNM 736070); shore of small bay behind Halfway Point, N end Ascension Bay, Quintana Roo, Bredin-S.I. Expedition sta. 76–60, Bousfield and Rehder! (2 valves, USNM 736096); shore near Halfway Point, N end Ascension Bay, Quintana Roo, Bredin-S.I. Expedition sta. 77+93, Schmitt et al.! 15, 18 April 1960 (1 pair with tissue, USNM 736157). *Netherlands Antilles*: Curaçao, Spaanse water near Brakkeput Ariba, on *Isognomon alatus* in mangroves, K. B. Meyer! 07 February 1971 (3 pair, USNM 702277). *Venezuela*: Chichiribiche, live-collected on algae washed ashore, August 1975, Edo. Falcón! F. Fernández H. collection (2 pair, AMNH 203057); Puerto Cabello, R. W. Barker! October 1949 (1 pair, HMNS 30309).

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MARINE BIVALVES OF THE FLORIDA KEYS: A QUALITATIVE FAUNAL ANALYSIS BASED ON ORIGINAL COLLECTIONS, MUSEUM HOLDINGS AND LITERATURE DATA

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ABSTRACT

Marine bivalve biodiversity in the waters surrounding the Florida Keys, an island archipelago off southern Florida, including the Florida Keys National Marine Sanctuary, was studied from ten years of original collections as well as from a critical review of museum specimens and literature data. A database of more than 12,000 records representing 389 species (half of which were ranked as abundant or common) was assembled and analyzed, resulting in a 139% increase of the known bivalve fauna of this region compared to the most recent prior (1995) checklist. Of the 389 species, 42% have not been positively recorded as live-collected, and 12.5% are represented only as singletons or doubletons. Using multivariate non-metric statistics and a priori geographic groupings along the island chain (Upper, Middle, Lower Keys; Dry Tortugas) and across the island chain (Florida Bay, shallow Atlantic waters [< 35m], deeper Atlantic waters [35–300 m]), the data showed distinct differences in benthic community structure across several spatial gradients. A pronounced northeast-to-southwest gradient was found on the Florida Bay-side of the island chain, although none was evident along the oceanside in either shallow or deep depth zones. Although they shared dominant species, the shallow-water communities of bayside and oceanside differed significantly in the percentage distributions of co-occurring species. In contrast, the deeper oceanside community differed substantially from both shallow-water groups in supporting a different set of species. A comparison of the bivalve fauna of the Keys with other well-documented faunas of the western Atlantic indicated that the Florida Keys fauna groups more closely to the Gulf of Mexico and Cuba than to eastern peninsular Florida, Yucatan, or the Bahamas. The impact of the heterogeneous nature of the dataset (live-specimen, dead-shell; and original collections, museum, and literature) is discussed and compared to analyses based on live-only data: the latter resulting in less spatial resolution but the same general patterns. In a comparison of data sources (original collections, museum records, gray literature and traditional literature), original collections were least effective (51%) in capturing the total species list despite representing approximately half of the total records. Literature was most successful (90%) in capturing the list but only when gray literature was included. Rapid assessment methods contrasted against the long-term results showed effectiveness when based on a range of sample types and habitats.

Key words: spatial patterns, community analysis, western Atlantic, Florida Keys National Marine Sanctuary, inventory, rapid assessment.

INTRODUCTION

Type of Analysis

Regional diversity can be assessed in different ways. Community ecologists use a “sample and estimate” approach, extrapolating species diversity from standardized sampling data. Systematists, on the other hand, often prefer a “find-them-all” approach and use a variety of information sources. In the case of shelled mollusks, the two academic approaches usually also differ in that benthic ecologists restrict their analyses to living or-

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ganisms, whereas systematists integrate data from both live-collected animals and empty "recently dead" shells. The current study, on extant marine bivalves of the Florida Keys, is systematically focused – we have compiled all accessible data to produce a "baseline" inventory that can be analyzed for its internal content as well as externally with other faunal results.

Any attempt to document and analyze a fauna, regardless of approach, depends on a sound taxonomic foundation. This naturally pertains to identification of field and museum material, in this case particularly for juvenile or small-adult "little white clams", and also plays an important role in critical interpretation of "legacy" literature data. While monographic and illustrated descriptions are easily verified, unfigured references, even if deemed of trustworthy authority, must be interpreted in taxonomic and historic contexts. This not only involves actual nomenclatural synonymies, but also "traceable" misidentifications, for example, misapplication of the name of a morphologically similar eastern Pacific or eastern Atlantic species to specimens from Florida. Deliberation is often also necessary in cases of incomplete or enigmatic geographic information, especially with names like "Sombrero", "Sand Key", or "Long Key", each of which applies to multiple locales in the subtropical western Atlantic. To make such decisions transparent and to allow subsequent corrections where necessary, we have documented our interpretations of literature data used in this study in a separate publication (Mikkelsen & Bieler, 2004b).

In contrast to most other animal groups, it is useful and often necessary to include skeletons, (i.e., empty shells) in a molluscan biodiversity study. Many cryptic, burrowing, stenoecious (e.g., parasitic), or seasonal species are rarely encountered alive, and in fact many species are known exclusively from empty shells (or have never been explicitly indicated, in literature or collections, as having been collected alive). Shell assemblages, with their usually high preservation potential, provide a time-averaged record that could only be mirrored by extremely intensive and long-term studies of living individuals. A labor-intensive molluscan diversity study in New Caledonia (Bouchet et al., 2002), involving 400 person-days of collecting effort of live and dead specimens, showed that about 30% of the total recorded molluscan fauna was never encountered alive. The inclusion of empty shells raises, however, three key issues. First, recent studies have explored the question of whether relative abundances in live-assemblages are reflected in their respective dead-assemblages. Kidwell (2001) found that dead-collected species occur in statistically similar rank-order abundance to that found in the local living community as measured by a single census. Live-dead agreement (at least for specimens larger than 1.5 mm) was found to remain stable or improve as information on the composition of the living fauna increased through prolonged or otherwise intensified sampling. Bouchet et al. (2002) agreed with the ecological fidelity of dead-assemblages and stressed the improbability of large-scale dead-shell transport into their study area. As in Bouchet's study, we placed considerable effort in collecting living specimens in original collections (because of our research interest in morphology), and, where possible, we have contrasted live-only data with the findings of the overall analysis including live plus empty shells. Second, geological age also becomes an issue when older strata are deliberately or accidentally sampled (e.g., by corers or bottom dredges). Data exist for Florida Bay that largely alleviate this concern: coring data for sites within (Bob Allen Keys) or immediately north of our study region (Whipray Basin) demonstrate a rapid sedimentation rate about 0.5 cm per year, so that shells from shallow digging or accidentally exposed deeper layers still date from very recent depositions (Wingard et al., 1995; Trappe & Brewster-Wingard, 2001). During this study, we made efforts to collect only uppermost layers and otherwise exclude subfossils from the study. Third, the collection of empty shells has been demonstrated to substantially increase the species-level capture of a biotic inventory. Bouchet et al. (2002) found that 28.5% of the total molluscan fauna in the New Caledonia study was only represented by dead shells. This is remarkably similar (25%) to the results of Kidwell's (2002) meta-analysis of multiple molluscan diversity studies. This percentage is even higher in our study, as will be demonstrated below.

From the onset, we were aware of different levels of data reliability in our study:

(1) *Original Project Collections*: Our original collections provide data for individual collecting events, clearly delimited in time and space. Specimens are fully vouchered in permanent and publicly accessible museum collections (AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural

History, Chicago), and precise locations have been recorded by Global Positioning System (GPS) in the field.

(2) *Previous Collections*: Specimens in existing (museum or private) collections have been taxonomically verified as part of this study, but vary in their degree of data reliability, as well as in their accuracy of distributional and temporal information. Some specimen series have the same data quality as our project collections, while others obviously contain pooled specimens collected at different times. Many museum series have incomplete collection data, ranging from simply lacking a collection date (a very common omission in malacological collections that hampers reconstructing past faunas) to solely indicating a broad place name (e.g., "Florida Keys").

(3) *Literature*: Monographic works, especially when images are provided, often deliver the same data quality as originally collected specimens. However, literature data in general show the greatest range in data reliability. Distributional information is often pooled (copied or summarized from earlier authors), and temporal information can sometimes only be interpreted as "some time before the publication date". Faunal checklists (e.g., Lermond, 1936; Lyons & Quinn, 1995) have been of critical importance to this project, yet works such as these usually provide the poorest supporting data, to the extent that the basis for a species' inclusion on a given checklist can be enigmatic.

Similar to the time-averaging effect of accumulated shell material, the pooling of literature and museum-label data that have accumulated over decades might (1) hide changes over time (such as local extinctions or invasions), and (2) make a few chance occurrences add up to appear as established members of the local fauna. Here we have the opportunity to compare our original fieldwork data with documented prior collecting efforts and to investigate any discrepancies. The pooled data provide the background (i.e., "all Recent bivalve species ever recorded in this region") against which the original fieldwork results can be discussed. Any discrepancies must be the result of (1) actual changes in faunal composition, (2) overlooked species (then or now), (3) rare visitors or human-transplanted material, or (4) taxonomic misidentification or other technical problems.

Although we are able to make coarse abundance inferences and have collected ecological data during our own field research, we emphasize that ours is necessarily a qualitative study, in order to take advantage of the range of data sources. Because of the widely varying habitats (from intertidal mangrove root communities to mud bottoms and coral reefs), great range of individual size and life mode (ranging from a cemented 18-cm gryphaeid oyster to an infaunal nuculid clam measuring 1 mm), and different techniques employed (e.g., collecting by hand or with a bottom grab), the collecting/observation events are not directly comparable. Many of the statistical methods that have been previously used, for instance, for standardized soft-bottom grab samples or for person-hours invested in sampling along a transect, cannot be applied to this type of analysis.

Project Region – the Florida Keys

The Florida Keys (Fig. 1) form a curved chain of Pleistocene limestone islands, mud islands, and reefs at the southernmost tip of the continental U.S.A., extending about 360 km from Key Largo to Key West and westward to the Dry Tortugas Archipelago (about 24°20'–25°21'N and 80°–83°W). The limestone islands that stretch from Key Largo to Key West are characterized by two principal surficial stratigraphic units: Key Largo Limestone in the Upper and Middle Keys, and the oolitic facies of the Miami Limestone in the Lower Keys (Hoffmeister & Multer, 1968). The islands in Florida Bay and the islands west of Key West (Marquesas Keys, Dry Tortugas) are not formed of limestone but are mostly accumulations of modern sediment, carbonate mud, sand, and mangrove peat (Randazzo & Halley, 1997). The Middle Florida Keys are characterized by large tidal channels that allow for significant water exchange between Florida Bay and the Atlantic Ocean. A semi-continuous series of offshore bank reefs forms the Florida Reef Tract that demarcates the southern edge of the Floridian Plateau, about 5–11 km from shore. Between the reef tract and the island chain is Hawk Channel, a wide V-shaped basin of 5–12 m depth that parallels the island chain and contains various shoals and patch reefs. Ecologically, the "Keys", situated at the intersection of Florida Bay, the Gulf of Mexico, and the Atlantic Straits of Florida, comprise diverse marine habitats including hypersaline ponds, mangrove thickets, seagrass meadows, mud banks and tidal channels, sandbars, coral reefs, patch reefs, deep sand plains, and hard bottoms.

A unique natural resource that includes North America's only living barrier reef, the third longest in the world following those of Australia and Belize (albeit discontinuous and perhaps more correctly a "bank reef system"; Jaap, 1984), the Keys are host to about three million visitors annually. More than a dozen preservation areas have been established for conservation and management of local historical and ecological resources. By far the largest of these, the Florida Keys National Marine Sanctuary (FKNMS), was established in 1990 with about 10,000 km^2 encompassing the entire island chain out to the 91-m (300-ft or 50-fm) isobath (NOAA, 1996, also http://floridakeys.noaa.gov/). This management area surrounds the Dry Tortugas National Park in the west and borders on the Everglades National Park and the Biscayne National Park in the east. Our project area encloses nearly the entire FKNMS (Fig. 1). For further description and regional subdivision of the project region, see Materials and Methods, below.

Molluscan Diversity Research in the Keys

The relative ease of access to tropical species has made the Florida Keys a popular collecting site, and many formal and informal publications, including the many popular shell books by R. Tucker Abbott, have included Keys taxa. But despite its rich history of popular and professional mollusk collecting, and a vast accumulation of Florida Keys material in many museum and private collections, formal scientific inventorying in this region began late and with great difficulty. This has resulted in the paradoxical situation of the Florida Keys

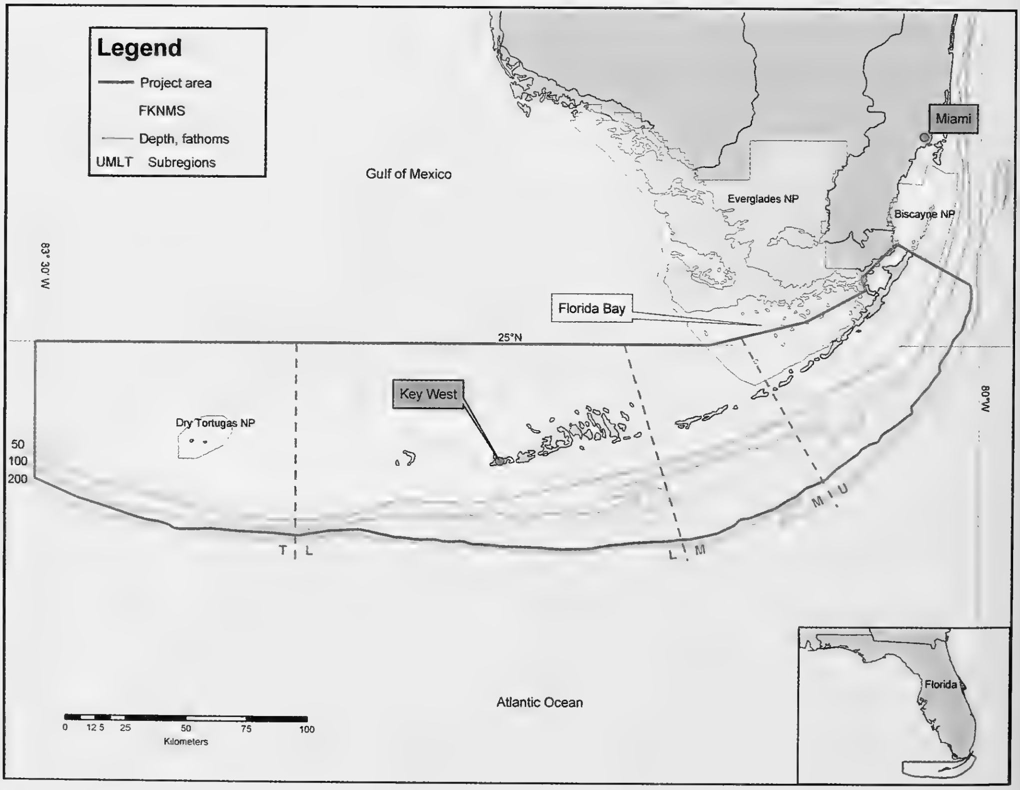


FIG. 1. The Florida Keys. The project area of approximately 28,000 km^2 corresponds in size to the combined areas of the U.S. states of Massachusetts, Delaware, and Rhode Island, and is only slightly smaller than the country of Belgium. U, M, L, and T indicate the Upper Keys, Middle Keys, Lower Keys, and Dry Tortugas subregions, respectively, as employed in the study. In an alternative approach, the Lower Keys area west of Key West was united with the Dry Tortugas subregion into a Western Keys unit.

as one of the most sampled, but also most poorly inventoried, regions of the North American coast. A first comprehensive attempt was made in the late 1860s by William Stimpson of Chicago's Academy of Sciences, who accumulated all available records and loan material from various collections. This included the extensive holdings of the Smithsonian Institution and the original collections from the Straits of Florida and the Pourtales Terrace off the Florida Keys obtained by Count Louis Francois de Pourtales (of the Museum of Comparative Zoology, Harvard University) during the U.S. Coast Survey expeditions of the 1860s (Dall, 1896; Rehder, 1999). Tragically this material, together with Stimpson's near-completed manuscript, was lost in the Great Fire that devastated Chicago in 1871 (Dall, 1883), and Stimpson never attempted to recreate the research. William Healey Dall (1883) made a second attempt, beginning by discussing the results of collecting efforts of amateur conchologist Henry Hemphill and by analyzing the works of James C. Melvill (1881; who reported on material obtained mainly in Key West during 1871–1872) and of W. W. Calkins (1878; who collected in the Keys during 1875 and 1877). Charles Torrey Simpson (1887–1889) produced the first effective Florida Keys checklist by including a separate column in his tabulation of Florida mollusks; this included 98 bivalve species names, now recognized as 86 valid taxa. Concurrently, Dall described the renewed dredging efforts off southern Florida by the U.S. Coast Survey (Dall, 1886, 1889b), culminating in a preliminary species catalog (Dall, 1889a, revised in 1903) that tabulated 225 species from the Florida Keys (plus 15 species now regarded as synonyms and 34 species out of the range of this survey). From 1910 to 1915, amateur collector John B. Henderson, Jr., sampled the molluscan fauna of the Florida Keys with his yacht *Eolis*, resulting in a massive collection of more than 31,000 specimen series now housed in the National Museum of Natural History, Washington, DC (Bieler & Mikkelsen, 2003). No comprehensive taxonomic treatment of the *Eolis* efforts was ever published, although numerous *Eolis* specimens have been cited in scattered systematic papers. A privately issued checklist by Lermond (1936) reported 247 nominal bivalve species for the shallow waters of the Keys, 214 of which are here considered as valid. No other comprehensive attempt at summarizing the Keys fauna was made until the inception of the Florida Keys National Marine Sanctuary in the 1990s, when a taxon list including 163 bivalve species appeared in the FKNMS Draft Management Plan (Lyons & Quinn, 1995). This last total was surprisingly low given the previous checklists (perhaps confounded by the plethora of archaic and synonymous names used by Simpson, Dall, and Lermond) and was, like them, undocumented as to source and specific Keys location.

In 1999, we completed a preliminary assessment of marine bivalve diversity in the Florida Keys based on a dataset of 6,000 records critically researched from literature, taxonomically updated museum holdings and five years of original collections from 1994 to 1999 (Mikkelsen & Bieler, 2000). That paper emphasized the importance of this fauna to studies of zoogeography, malacology, and conservation efforts of the Florida Keys National Marine Sanctuary. 325 species were documented, representing a 100% increase over the previous tally (Lyons & Quinn, 1995), largely attributable to a critical review of museum-held specimens. Literature sources (especially when non-traditional newsletters and agency reports were excluded) or original collections alone were found to be less effective in capturing the total fauna; these results questioned the effectiveness for inventory work of ecological and other studies that are so restricted in sampling effort.

Since 1999, our effort to document species occurrences has continued, adding 186 original stations over another five years of collecting throughout the Florida Keys (including the Dry Tortugas, the region least represented in the previous analysis) and, importantly, capturing data from 280 additional literature sources that mention bivalves in the Keys. This has culminated, in our tenth year of study, in a database more than twice as large as that used in our prior analysis. The newly surveyed literature includes important early checklists (Calkins, 1878; Simpson, 1887–1889; Lermond, 1936), results of substantial ecological surveys (e.g., Turney & Perkins, 1972; Brewster-Wingard et al., 2001), and many detailed Florida Keys collecting reports by amateurs in publications such as Frank Lyman's *Shell Notes* and the Palm Beach, Florida, Shell Club's newsletter *Seafari*. The full annotated bibliography appears elsewhere in this proceedings issue (Mikkelsen & Bieler, 2004b).

Goals

This paper addresses four major issues:

(1) Characterization of the bivalve fauna of the Florida Keys, for which a complete ("ever recorded") annotated checklist is provided.

(2) Analysis and discussion of species-level similarity patterns within the Florida Keys, both in terms of geographic subregions (Upper, Middle, Lower Keys, and Dry Tortugas) and in relative position to the island chain (bayside or oceanside, the latter further divided into shallow and deep records).

(3) Comparison of the total Keys bivalve fauna to other regional faunas in the western Atlantic.

(4) Discussion of the respective utility of the different kinds of major data sources (original collections, museum holdings, and literature sources), and of the results obtained by "all shells" versus live-collected records alone.

MATERIALS AND METHODS

Study Area

The "Florida Keys" project area is here defined as the waters surrounding the entire island chain from Broad Creek (about 25°21'N, 80°15'W) at the northern end of Key Largo (including Card and Barnes Sounds but not Biscayne Bay, southwest of but not including Old Rhodes Key) to west of the Dry Tortugas (at 83°30'W). The southern half of Florida Bay is included (with a northern border at the levels of, from east to west, the northern end of the Nest Keys, Russell Key, and the northern limit of Rabbit Key Basin), eliminating that part of the bay that is more properly considered the southern extent of the Florida Everglades (Fig. 1). To facilitate analysis of the Keys fauna by a priori selected subregions, traditional boundaries were employed but explicitly defined as Upper Keys [Key Largo to Craig Key], Middle Keys [Fiesta Key to the western end of Seven-Mile Bridge], and Lower Keys [Little Duck Key to Rebecca Shoal (west of the Marquesas)]; the Dry Tortugas Archipelago was treated separately. These subregions are roughly equivalent to those recently used in other diversity/monitoring studies, such as that by Wheaton et al. (2003) on stony corals. An alternative scheme, that draws the western border of the Lower Keys at Key West and combines all those remaining westward with the Dry Tortugas into a Western Keys subregion, has been used in water circulation/exchange studies (e.g., Lee et al., 2003) and in several of our analyses we recoded our data to include this grouping. Depth categories used were based upon sampling techniques: shallow = wading to diving depth (0–35 m), and deep = beyond normal scuba depth (i.e., > 35 m or 100 ft); these are as previously employed (Mikkelsen & Bieler, 2000), but an oceanward depth limit has now been set at the 300 m (= 164 fms or 984 ft) isobath (a restriction which eliminated seven previously included species). Nearby records were combined into 59 land-based locations (usually a representing single island or small cluster of neighboring keys) so that each location was represented by at least 25 records (fewer for the live-only analysis, see below). Each location was then coded for its general exposure (bayside of the island chain, i.e. in Florida Bay/Gulf of Mexico; oceanside, shallow or deep), and its position in the Upper, Middle, Lower Keys, or the Dry Tortugas. For analyses of the (considerably fewer) live-collected records, all stations represented by single records were combined with neighboring stations where feasible, otherwise they were eliminated (resulting in a total of 63 stations).

Data Sources and Quality

Literature sources are as described in the catalog and annotated bibliography elsewhere in this volume (Mikkelsen & Bieler, 2004b). In addition to the nine museum collections previously listed (Mikkelsen & Bieler, 2000), the full bivalve holdings of the Houston Museum of Natural Sciences (HMNS) and the Rosenstiel School of Marine and Atmospheric Sciences (UMML; University of Miami, Florida) were surveyed and identifications confirmed for this analysis. Original collecting methods are as described earlier (Mikkelsen & Bieler, 2000). All collection lots were interpreted and recorded as dead-collected unless soft tissue was still attached to the specimen, or unless the labeling explicitly indicated live-collection. Nomenclature, initially based on Turgeon et al. (1998), has been substantially modified according to subsequent systematic research, the latter partly a result of the 2002 International Marine Bivalve Workshop (this issue; Mikkelsen & Bieler, 2004a). Synonyms and misidentifications used in the literature in the past 160 years have been carefully researched and documented (Mikkelsen & Bieler, 2004b).

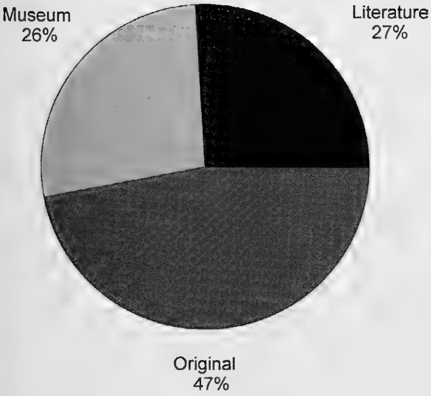
Analyses

The new Florida Keys bivalve dataset is more than twice that previously analyzed (12,382 versus 6,145 records), and provides a better-balanced analysis of all three data sources, comprising 3,385 records from the literature, 3,231 records from museum lots, and 5,768 records from original collections (Fig. 2). The dataset was compiled as a Microsoft Excel® spreadsheet in the form of a square matrix (species by location). Coding within the database was as previously described (Mikkelsen & Bieler, 2000), including data partitioning into the aforementioned geographically defined subregions. While Dry Tortugas remained less sampled, as in the previous analysis, the Upper, Middle, and Lower Keys subregions provided relatively equal proportions of the database records (Fig. 3).

It is important to note that efforts were made not to duplicate records in the database. For example, literature records describing lots that were subsequently verified in a museum collection were scored as museum records, that is, as the "original" (and more reliable) source. Literature records that were judged to be based on the same material were entered into the database only once, as the earliest publication. As has become customary in community analyses, we are employing the terms "singleton" and "doubleton" for species that were encountered only once or twice (here referring to species represented only once or twice in the database). Literature and museum records that provided only "Florida Keys" as locality data were not entered into the database (giving rise, e.g., to "0" record entries and singletons from multiple locations in Table 1). Of the 15,296 records generated during this study from all sources, 2,914 (19%) were not entered into the database because of incomplete identification, species of uncertain status, poor locality data, or duplication.

Although this was a qualitative study, the number of collecting events or the frequency of encounters (= records-per-species in the database) is a fair approximation of species commonness or rarity. In this context, species were scored as abundant (> 50 records), common (10–49 records), and rare (< 10 records), regardless of source. These data are also reflected by a histogram of the frequency distribution of occurrences, plotting number of taxa versus number of occurrences ($\log_2$) binned to full integers.

Within the database, records were entered as "live" if at least one specimen in the lot was live-collected (regardless of additional dead-collected specimens). The heterogeneous nature of these records is also evident in this regard. While conservation-minded collectors might preferentially collect empty shells even if live specimens were present, morphologists, anatomists, and systematists would preferentially collect live specimens, perhaps also leaving behind empty shells at the same site. Literature records and museum labels often do not indicate whether specimens were collected living or dead, and museum specimens are often so efficiently cleaned as to remove all traces of tissue. In all uncertain and un-



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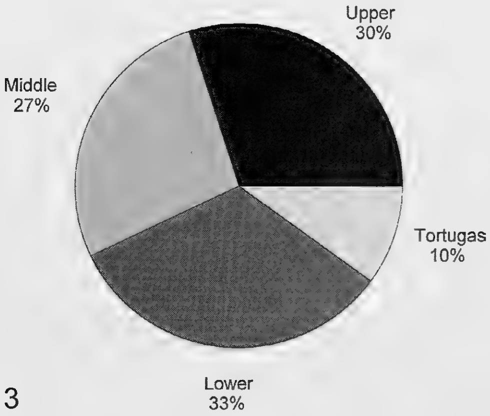

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FIGS. 2, 3. Percent of records in the database. FIG. 2: From each of the three data sources (literature, museum holdings, original collections); FIG. 3: From the Upper, Middle, Lower and Dry Tortugas regions of the Florida Keys.

TABLE 1. Florida Keys bivalves, with categories reflecting distribution and occurrence in this study, and inclusion in five earlier Florida checklists.

Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
Anomiidae	*Anomia simplex* d'Orbigny, 1842	OML	UMLT	47	SD	OB	17	–	x	x	–	x
	Pododesmus rudis (Broderip, 1834)	OML	U–LT	7	SD	O–	1	–	x	x	–	–
Arcidae	*Acar domingensis* (Lamarck, 1819)	OML	UMLT	120	SD	OB	35	x	x	x	x	x
	Anadara baughmani Hertlein, 1951	–ML	––LT	5	–D	O–	3	–	–	–	–	x
	Anadara floridana (Conrad, 1869)	OML	U–LT	15	SD	OB	4	–	x	x	–	x
	Anadara notabilis (Röding, 1798)	OML	UMLT	130	SD	OB	23	x	x	x	x	x
	Anadara transversa (Say, 1822)	OML	UMLT	13	S–	OB	3	x	x	x	–	x
	Arca imbricata Bruguière, 1789	OML	UMLT	218	SD	OB	41	x	x	x	x	x
	Arca zebra (Swainson, 1833)	OML	UMLT	171	SD	OB	43	x	x	x	x	x
	Barbatia cancellaria (Lamarck, 1819)	OML	UMLT	297	SD	OB	84	x	x	x	x	x
	Bathyarca glomerula (Dall, 1881)	–ML	––LT	2	–D	O–	0	–	x	–	–	x
	Bathyarca inaequalis (Dall, 1927)	–M–	–––T	1	–D	––	0	–	–	–	–	–
	Bentharca sagrinata (Dall, 1886)	––L	––––	0	––	––	0	–	x	–	–	–
	Cucullaearca candida (Helbling, 1779)	OML	UMLT	59	SD	OB	10	x	x	x	–	x
	Fugleria tenera (C. B. Adams, 1845)	OML	UMLT	35	SD	O–	13	–	–	–	x	–
	Lunarca ovalis (Bruguière, 1789)	–ML	–M––	3	––	––	0	–	x	x	–	x
	Scapharca brasiliana (Lamarck, 1819)	–ML	U–L–	2	––	––	1	x	x	x	–	–
	Scapharca chemnitzii (Philippi, 1851)	––L	––––	0	––	––	0	–	x	x	–	–
Astartidae	*Astarte crenata subequilatera* G. B. Sowerby II, 1854	––L	U–L–	2	––	––	0	–	x	–	–	–
	Astarte globula Dall, 1886	–ML	––L–	1	–D	O–	0	–	x	–	–	–
	Astarte nana Dall, 1886	–ML	U––T	6	–D	O–	2	–	x	x	–	x
	Astarte smithii Dall, 1886	OML	–ML–	3	–D	O–	0	–	x	–	–	–

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
Cardiidae	*Acrosterigma magnum* (Linnaeus, 1758)	OML	UMLT	24	SD	O–	0	–	x	x	x	x
	Americardia guppyi (Thiele, 1910)	OML	UMLT	32	SD	OB	2	–	–	–	x	x
	Americardia media (Linnaeus, 1758)	OML	UMLT	112	SD	OB	10	x	x	x	x	x
	Dinocardium robustum (Lightfoot, 1786)	–ML	––L–	1	––	––	0	–	–	–	–	–
	Laevicardium laevigatum (Linnaeus, 1758)	OML	UMLT	206	SD	O–	34	x	x	x	x	x
	Laevicardium mortoni (Conrad, 1830)	OML	UMLT	205	S–	OB	67	–	–	–	x	x
	Laevicardium pictum (Ravenel, 1861)	OM–	U–LT	10	SD	OB	1	–	–	–	–	x
	Laevicardium sybariticum (Dall, 1886)	–ML	UMLT	5	S–	O–	2	–	–	–	x	x
	Nemocardium peramabile (Dall, 1881)	OML	UMLT	24	–D	O–	6	–	x	x	–	x
	Nemocardium tinctum (Dall, 1881)	–ML	–MLT	6	–D	O–	0	–	x	–	–	x
	Papyridea lata (Born, 1778)	OML	–MLT	18	SD	OB	0	–	–	–	–	–
	Papyridea semisulcata (Gray, 1825)	OML	UMLT	29	SD	OB	7	x	x	x	x	x
	Papyridea soleniformis (Bruguière, 1789)	OML	UMLT	52	SD	O–	1	–	x	x	x	x
	Trachycardium egmontianum (Shuttleworth, 1856)	OML	UMLT	66	SD	OB	6	–	x	x	x	x
	Trachycardium muricatum (Linnaeus, 1758)	OML	UMLT	99	SD	OB	14	–	x	x	x	x
	Trigoniocardia antillarum (d'Orbigny, 1842)	––L	––––	0	––	––	0	–	x	x	–	–
Carditidae	*Carditamera floridana* Conrad, 1838	OML	UMLT	186	S–	OB	67	x	x	x	x	x
	Glans dominguensis (d'Orbigny, 1842)	OML	UMLT	17	SD	OB	10	–	x	–	x	x
	Pleuromeris tridentata (Say, 1826)	OML	UMLT	44	SD	OB	13	–	–	–	x	x
	Pteromeris perplana (Conrad, 1841)	OML	–MLT	10	SD	OB	0	–	–	–	x	x
Chamidae	*Arcinella cornuta* Conrad, 1866	OML	U–LT	40	SD	OB	6	–	x	x	x	x
	Chama congregata Conrad, 1833	OML	UMLT	122	SD	OB	23	–	–	x	x	x
	Chama florida Lamarck, 1819	OML	UMLT	39	SD	OB	6	–	–	–	–	x
	Chama inezae (F. M. Bayer, 1943)	OML	UM––	4	S–	O–	2	–	–	–	–	x
	Chama lactuca Dall, 1886	OML	UML–	8	SD	OB	1	–	–	–	x	x

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Family	Species	Data Sources[*]	Fla. Keys Distrib.[†]	Recs[**]	Depth[‡]	Side[§]	Live[††]	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995[‡‡]	M&B, 2000[§§]
	Chama macerophylla Gmelin, 1791	OML	UMLT	167	SD	OB	40	x	x	x	x	x
	Chama radians Lamarck, 1819	OML	UMLT	75	SD	OB	28	–	–	–	x	x
	Chama sarda Reeve, 1847	OML	UMLT	15	SD	OB	2	–	x	x	x	x
	Chama sinuosa Broderip, 1835	OML	UMLT	15	S–	OB	6	–	–	–	x	x
Condylocardiidae	*Carditopsis smithii* (Dall, 1896)	OML	UMLT	22	SD	OB	2	–	–	–	x	x
Corbiculidae	*Polymesoda maritima* (d'Orbigny, 1842)	OML	UML–	58	S–	OB	12	x	x	x	x	x
Corbulidae	*Caryocorbula caribaea* (d'Orbigny, 1842)	OML	UMLT	15	SD	OB	5	–	x	x	–	x
	Caryocorbula chittyana (C. B. Adams, 1852)	–ML	–––T	1	––	––	1	–	x	x	–	–
	Caryocorbula contracta (Say, 1822)	–ML	––LT	5	–D	O–	3	–	–	x	–	x
	Caryocorbula cymella (Dall, 1881)	––L	––––	0	––	––	0	–	x	x	–	–
	Caryocorbula dietziana (C. B. Adams, 1852)	OML	U–LT	10	SD	OB	0	–	x	x	–	x
	Juliacorbula aequivalvis Philippi, 1836	––L	––––	0	––	––	0	–	x	–	–	–
	Varicorbula disparilis (d'Orbigny, 1842)	OML	U–LT	34	SD	OB	9	–	–	x	–	x
	Varicorbula krebsiana (C. B. Adams, 1852)	––L	––––	0	––	––	0	–	x	–	–	–
	Varicorbula philippii (E. A. Smith, 1885)	OM–	––LT	7	SD	O–	3	–	–	–	–	x
Crassatellidae	*Crassinella dupliniana* (Dall, 1903)	OML	–MLT	5	SD	O–	0	–	–	–	–	x
	Crassinella lunulata (Conrad, 1834)	OML	UMLT	32	SD	OB	15	–	x	x	x	x
	Crassinella martinicensis (d'Orbigny, 1842)	–ML	––LT	11	–D	OB	10	–	–	–	x	x
	Eucrassatella speciosa (A. Adams, 1852)	OML	U–LT	13	SD	O–	1	–	x	x	–	x
Cuspidariidae	*Cardiomya alternata* (d'Orbigny, 1842)	––L	––L–	1	–D	O–	0	–	–	–	–	–
	Cardiomya costellata (Deshayes, 1830)	O–L	–ML–	3	S–	OB	1	–	x	x	–	x
	Cardiomya glypta (Bush, 1885)	–M–	–––T	1	––	––	0	–	–	–	–	x
	Cardiomya ornatissima (d'Orbigny, 1842)	O––	––LT	2	SD	–B	0	–	–	–	–	x
	Cardiomya perrostrata (Dall, 1881)	O–L	––LT	6	–D	O–	3	–	x	–	–	x
	Cardiomya striata (Jeffreys, 1876)	–ML	––L–	8	–D	O–	1	–	x	–	–	–

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(Continued)

Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Cuspidaria obesa (Lovén, 1846)	–ML	––L–	1	–D	––	0	–	x	–	–	–
	Cuspidaria rostrata (Spengler, 1793)	–ML	––LT	4	–D	O–	2	–	x	–	–	x
	Myonera gigantea (A. E. Verrill, 1884)	–M–	––L–	1	––	––	0	–	–	–	–	x
	Myonera lamellifera (Dall, 1881)	––L	––––	0	––	––	0	–	x	–	–	–
	Myonera paucistriata Dall, 1886	–ML	–––T	1	S–	––	0	–	–	–	–	–
	Plectodon granulatus (Dall, 1881)	–ML	U––T	2	–D	O–	2	–	x	–	–	x
Cyrenoididae	*Cyrenoida floridana* (Dall, 1896)	–ML	UML–	6	S–	–B	4	x	x	–	–	x
Donacidae	*Donax variabilis* Say, 1822	–ML	UML–	5	––	––	0	x	x	x	–	x
	Iphigenia brasiliana (Lamarck, 1818)	–ML	U–––	2	––	––	0	–	x	x	–	x
Dreissenidae	*Mytilopsis leucophaeata* (Conrad, 1831)	O––	U–––	2	S–	–B	1	–	–	–	–	x
	Mytilopsis sallei (Récluz, 1849)	O–L	U–––	1	S–	–B	0	–	–	x	–	x
Entoliidae	*Pectinella sigsbeei* (Dall, 1886)	––L	––––	0	––	––	0	–	x	–	–	–
Galeommatoidea	*Kellia suborbicularis* (Montagu, 1803)	–ML	U–––	1	–D	O–	1	–	–	–	–	x
	Lasaea adansoni (Gmelin, 1791)	OML	–MLT	8	S–	OB	4	x	–	–	–	x
	Mysella planulata (Krause, 1885)	O–L	UMLT	12	SD	–B	1	–	–	–	–	x
	Orobitella floridana (Dall, 1899)	OML	UMLT	5	S–	OB	4	–	–	–	–	x
Gastrochaenidae	*Gastrochaena hians* (Gmelin, 1791)	OML	UMLT	31	SD	OB	13	–	x	x	x	x
	Gastrochaena ovata G. B. Sowerby I, 1834	OML	UMLT	19	SD	OB	11	x	x	x	x	x
	Spengleria rostrata (Spengler, 1783)	OML	UMLT	14	SD	OB	4	x	x	x	x	x
Glycymerididae	*Glycymeris americana* (DeFrance, 1829)	–ML	–––T	1	–D	––	0	–	–	x	–	x
	Glycymeris decussata (Linnaeus, 1758)	OML	UMLT	53	SD	O–	5	–	–	x	x	x
	Glycymeris spectralis (Nicol, 1952)	O–L	U–L–	4	SD	O–	2	–	–	–	–	–
	Glycymeris undata (Linnaeus, 1758)	–ML	U–––	2	––	O–	0	–	x	x	x	x
	Tucetona pectinata (Gmelin, 1791)	OML	UMLT	241	SD	OB	67	–	x	x	x	x
Gryphaeidae	*Hyotissa mcgintyi* (Harry, 1985)	OML	–MLT	10	SD	O–	3	–	–	–	–	–

(Continues)

(Continued)

Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Neopycnodonte cochlear (Poli, 1795)	OM–	U–L–	4	SD	O–	1	–	–	–	–	x
Hiatellidae	*Hiatella arctica* (Linnaeus, 1767)	OML	UMLT	10	SD	O–	7	–	x	–	–	x
	Hiatella azaria (Dall, 1881)	––L	––––	0	––	––	0	–	x	–	–	–
Isognomonidae	*Isognomon alatus* (Gmelin, 1791)	OML	UMLT	104	S–	OB	45	x	x	x	x	x
	Isognomon bicolor (C. B. Adams, 1845)	OML	UMLT	103	SD	OB	51	–	–	x	x	x
	Isognomon radiatus (Anton, 1839)	OML	UMLT	62	SD	OB	26	–	–	x	x	x
Limidae	*Ctenoides miamiensis* Mikkelsen & Bieler, 2003	–M–	––LT	2	–D	–B	2	–	–	–	–	–
	Ctenoides mitis (Lamarck, 1807)	OML	UMLT	122	SD	OB	27	x	x	x	x	x
	Ctenoides planulatus (Dall, 1886)	–M–	––L–	1	–D	––	0	–	–	–	–	x
	Ctenoides sanctipauli Stuardo, 1982	–ML	–MLT	5	SD	–B	1	–	–	–	–	x
	Ctenoides scaber (Born, 1778)	OML	UMLT	95	SD	OB	23	x	x	x	x	x
	Divarilima albicoma (Dall, 1886)	––L	––––	1	–D	––	0	–	x	–	–	x
	Lima caribaea d'Orbigny, 1842	OML	UMLT	138	SD	OB	31	x	x	x	x	x
	Limaria locklini (McGinty, 1955)	––L	––L–	1	––	O–	1	–	–	–	–	–
	Limaria pellucida (C. B. Adams, 1846)	OML	UMLT	158	SD	OB	56	–	x	x	x	x
	Limatula confusa (E. A. Smith, 1885)	––L	––––	0	––	––	0	–	–	x	–	–
	Limatula setifera Dall, 1886	––L	––––	0	––	––	0	–	x	–	–	–
	Limatula subauriculata (Montagu, 1808)	–ML	–––T	1	–D	––	0	–	x	–	–	–
	Limea bronniana Dall, 1886	–ML	–––T	1	–D	––	0	–	–	–	–	–
Limopsidae	*Limopsis aurita* (Brocchi, 1814)	–ML	–––T	1	–D	––	0	–	x	–	–	x
	Limopsis cristata Jeffreys, 1876	OML	U–LT	4	–D	O–	0	–	x	–	–	x
	Limopsis minuta Philippi, 1836	–ML	U––T	3	–D	O–	0	–	x	–	–	x
	Limopsis sulcata A. E. Verrill & Bush, 1898	OM–	U–LT	6	–D	O–	3	–	–	–	–	x
Lucinidae	*Anodontia alba* Link, 1807	OML	UMLT	70	SD	OB	7	–	x	x	–	x
	Anodontia schrammi (Crosse, 1876)	–ML	–ML–	8	SD	–B	0	–	–	x	–	x

(Continues)

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Callucina keenae (Chavan, in Cox et al., 1971)	OML	UMLT	23	SD	OB	17	–	–	–	–	x
	Cavilinga blanda (Dall & Simpson, 1901)	OML	UMLT	42	SD	OB	5	–	x	x	x	x
	Codakia orbicularis (Linnaeus, 1758)	OML	UMLT	352	SD	OB	50	x	x	–	x	x
	Ctena orbiculata (Montagu, 1808)	OML	UMLT	287	SD	OB	44	x	x	x	x	x
	Ctena pectinella (C. B. Adams, 1852)	O–L	–––T	11	SD	––	0	–	x	x	x	x
	Divalinga quadrisulcata (d'Orbigny, 1842)	OML	UMLT	97	SD	OB	1	x	x	–	x	x
	Divaricella dentata (Wood, 1815)	OML	UMLT	46	S–	OB	0	–	–	x	x	x
	Lucina pensylvanica (Linnaeus, 1758)	OML	UMLT	244	SD	OB	24	x	x	x	x	x
	Lucinisca muricata (Spengler, 1798)	–ML	U–LT	7	S–	O–	4	x	x	x	x	x
	Lucinisca nassula (Conrad, 1846)	OML	UMLT	146	SD	OB	21	x	x	–	x	x
	Lucinoma filosa (Stimpson, 1851)	–ML	U––T	17	–D	O–	0	–	x	–	–	x
	Myrtea sagrinata (Dall, 1886)	––L	––––	0	––	––	0	–	x	–	–	x
	Myrteopsis lens (A. E. Verrill & Smith, 1880)	–ML	––L–	1	–D	––	0	–	x	–	–	–
	Parvilucina costata (d'Orbigny, 1842)	–ML	UMLT	10	SD	O–	2	x	–	x	x	x
	Parvilucina crenella (Dall, 1901)	OML	UMLT	55	SD	OB	11	–	x	x	x	x
	Phacoides pectinata (Gmelin, 1791)	–ML	UML–	10	SD	OB	2	–	–	x	x	x
	Pleurolucina leucocyma (Dall, 1886)	OML	U–LT	34	SD	O–	0	–	x	–	x	x
	Pleurolucina sombrerensis (Dall, 1886)	OML	UMLT	31	SD	OB	0	–	x	–	–	x
	Radiolucina amianta (Dall, 1901)	OML	UMLT	42	SD	OB	6	–	x	x	x	x
	Stewartia floridana (Conrad, 1833)	OML	UML–	5	–D	O–	0	–	x	–	–	x
Lyonsiidae	*Entodesma beana* (d'Orbigny, 1842)	OML	UMLT	14	SD	OB	5	–	x	x	x	x
	Lyonsia floridana Conrad, 1849	OML	UMLT	9	S–	OB	7	–	–	–	–	x
Mactridae	*Anatina anatina* (Spengler, 1802)	–ML	–M––	1	––	––	0	–	–	x	–	x
	Mactrotoma fragilis (Gmelin, 1791)	OML	UML–	57	S–	OB	3	–	x	x	x	x
	Mulinia lateralis (Say, 1822)	–ML	U–––	1	––	––	1	–	x	x	–	–

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Raeta plicatella (Lamarck, 1818)	–ML	U–L–	2	––	––	0	–	x	x	–	x
	Spisula raveneli (Conrad, 1831)	–ML	U–––	1	S–	–B	1	–	x	x	–	x
Malleidae	*Malleus candeanus* (d'Orbigny, 1842)	OML	UMLT	18	SD	O–	10	–	–	–	x	x
Myidae	*Sphenia fragilis* (H. Adams & A. Adams, 1854)	–M–	U–––	1	S–	–B	1	–	–	–	–	x
Mytilidae	*Amygdalum papyrium* (Conrad, 1846)	–ML	UM––	4	S–	OB	1	–	–	x	–	x
	Amygdalum politum (A. E. Verrill & Smith, 1880)	O–L	––LT	2	SD	OB	1	–	–	–	–	x
	Amygdalum sagittatum Rehder, 1934	–ML	U–LT	5	–D	OB	4	–	x	–	–	x
	Botula fusca (Gmelin, 1791)	OML	UMLT	47	SD	OB	12	x	x	x	x	x
	Brachidontes exustus (Linnaeus, 1758)	OML	UML–	334	S–	OB	167	x	x	x	x	x
	Brachidontes modiolus (Linnaeus, 1767)	OML	UML–	72	S–	OB	5	–	x	x	x	x
	Crenella decussata (Montagu, 1808)	OML	UMLT	36	SD	OB	12	–	x	x	x	x
	Dacrydium elegantulum hendersoni Salas & Gofas, 1997	OML	––L–	8	–D	O–	0	–	x	x	–	x
	Geukensia granosissima (G. B. Sowerby III, 1914)	–ML	–ML–	3	––	––	0	–	–	x	–	x
	Gregariella coralliophaga (Gmelin, 1791)	O–L	UMLT	4	S–	O–	1	x	x	x	x	x
	Ischadium recurvum (Rafinesque, 1820)	–ML	U–L–	3	S–	OB	1	–	x	x	–	x
	Lioberus castaneus (Say, 1822)	OML	UMLT	14	S–	OB	4	x	x	x	x	x
	Lithophaga antillarum (d'Orbigny, 1842)	OML	UMLT	53	SD	OB	5	–	x	x	x	x
	Lithophaga aristata (Dillwyn, 1817)	OML	UMLT	12	SD	OB	2	x	x	x	x	x
	Lithophaga bisulcata (d'Orbigny, 1842)	OML	UMLT	27	SD	OB	7	x	x	x	x	x
	Lithophaga nigra (d'Orbigny, 1842)	OML	UMLT	35	S–	OB	1	x	x	x	x	x
	Modiolus americanus (Leach, in Leach & Nodder, 1815)	OML	UMLT	143	SD	OB	13	–	–	x	x	x
	Modiolus squamosus Beauperthuy, 1967	OML	UMLT	55	SD	OB	20	–	–	–	x	x
	Musculus lateralis (Say, 1822)	OML	UMLT	43	SD	OB	24	–	x	x	x	x
Noetiidae	*Arcopsis adamsi* (Dall, 1886)	OML	UMLT	220	SD	OB	82	–	x	x	x	x
	Noetia ponderosa (Say, 1822)	–ML	UML–	9	––	––	0	–	x	x	–	x

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
Nuculanidae	*Ledella sublevis* A. E. Verrill & Bush, 1898	–ML	U–––	0	––	––	0	–	x	–	–	–
	Nuculana acuta (Conrad, 1832)	OML	UMLT	23	SD	OB	9	–	x	–	–	x
	Nuculana concentrica (Say, 1824)	O–L	–MLT	10	SD	–B	3	–	–	–	–	x
	Nuculana jamaicensis (d'Orbigny, 1842)	––L	––L–	1	–D	O–	0	–	–	–	–	–
	Nuculana solidifacta (Dall, 1886)	OML	––L–	2	–D	O–	0	–	–	–	–	–
	Nuculana verrilliana (Dall, 1886)	––L	––––	0	––	––	0	–	–	x	–	x
	Nuculana vitrea (d'Orbigny, 1842)	––L	––––	0	––	––	0	–	x	–	–	–
	Propeleda carpenteri (Dall, 1881)	OML	U–L–	8	SD	O–	1	–	x	x	–	–
Nuculidae	*Ennucula aegeensis* (Jeffreys, 1879)	––L	UMLT	10	S–	OB	10	–	x	x	–	x
	Ennucula tenuis (Montagu, 1808)	O––	UML–	5	S–	OB	0	–	–	–	–	x
	Nucula calcicola Moore, 1977	O–L	UML–	7	S–	OB	8	–	–	–	–	x
	Nucula crenulata A. Adams, 1856	–ML	U–L–	3	SD	O–	0	–	–	–	–	x
	Nucula proxima Say, 1822	OML	UMLT	55	SD	OB	0	–	–	–	–	x
Ostreidae	*Crassostrea rhizophorae* (Guilding, 1828)	––L	––LT	2	S–	––	0	x	–	–	–	x
	Crassostrea virginica (Gmelin, 1791)	OML	UMLT	10	SD	OB	3	–	x	x	–	x
	Dendostrea frons (Linnaeus, 1758)	OML	UMLT	119	SD	OB	32	–	x	x	x	x
	Ostreola equestris (Say, 1834)	OML	UML–	31	S–	OB	18	–	x	x	x	x
	Teskeyostrea weberi (Olsson, 1951)	OML	UML–	17	SD	OB	7	–	–	–	–	x
Pandoridae	*Pandora arenosa* Conrad, 1834	––L	––LT	2	––	O–	2	–	–	–	–	–
	Pandora bushiana Dall, 1886	–ML	U––T	3	SD	O–	2	–	–	–	–	x
	Pandora glacialis Leach, 1819	––L	––––	0	––	––	0	–	x	–	–	–
	Pandora inflata Boss & Merrill, 1965	OML	UMLT	14	SD	OB	3	–	–	–	–	x
Pectinidae	*Aequipecten glyptus* (A. E. Verrill, 1882)	–ML	––LT	13	–D	O–	0	–	–	–	–	x
	Aequipecten heliacus (Dall, 1925)	––L	––––	0	––	––	0	–	–	x	–	–
	Aequipecten lineolaris (Lamarck, 1819)	–ML	UMLT	17	SD	O–	1	–	–	–	–	x

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Argopecten gibbus (Linnaeus, 1758)	OML	UMLT	72	SD	OB	4	x	x	x	x	x
	Argopecten irradians (Lamarck, 1819)	OML	UML–	115	SD	OB	54	–	–	–	x	x
	Argopecten nucleus (Born, 1778)	OML	UMLT	57	S–	OB	2	–	x	x	x	x
	Brachtechlamys antillarum (Récluz, 1853)	OML	UMLT	74	SD	OB	8	x	x	x	x	x
	Caribachlamys imbricata (Gmelin, 1791)	OML	UMLT	51	SD	O–	0	x	x	x	x	x
	Caribachlamys mildredae (Bayer, 1941)	–ML	UMLT	9	S–	O–	0	–	–	–	x	x
	Caribachlamys ornata (Lamarck, 1819)	OML	UMLT	23	S–	OB	0	x	x	x	x	x
	Caribachlamys sentis (Reeve, 1853)	OML	UMLT	174	SD	OB	23	–	–	x	x	x
	Cryptopecten phrygium (Dall, 1886)	–ML	UMLT	16	–D	O–	0	–	x	–	–	x
	Euvola chazaliei (Dautzenberg, 1900)	–ML	UMLT	24	SD	O–	1	–	x	x	x	x
	Euvola laurentii (Gmelin, 1791)	–ML	––LT	4	–D	––	0	–	–	–	–	x
	Euvola cf. *papyracea* (Gabb, 1873)	–ML	–MLT	12	SD	O–	0	–	–	–	–	x
	Euvola raveneli (Dall, 1898)	OML	UMLT	38	SD	OB	1	x	x	x	–	x
	Euvola ziczac (Linnaeus, 1758)	OML	UMLT	42	SD	OB	5	–	x	x	x	x
	Laevichlamys multisquamata (Dunker, 1864)	––L	––––	0	––	––	0	–	x	–	x	x
	Lindapecten muscosus (Wood, 1828)	OML	UMLT	69	SD	OB	5	–	x	x	x	x
	Lyropecten kallinubilosus (Bayer, 1943)	–M–	––L–	1	S–	––	0	–	–	–	–	x
	Nodipecten fragosus (Conrad, 1849)	OML	UMLT	46	SD	OB	0	–	x	x	–	–
	Spathochlamys benedicti (A. E. Verrill & Bush, 1897)	OML	UMLT	18	SD	OB	2	–	–	–	x	x
Periplomatidae	*Cochlodesma pyramidatum* Stimpson, 1860	––L	––––	0	––	––	0	–	–	–	–	–
	Periploma margaritaceum (Lamarck, 1801)	–ML	––LT	2	––	––	0	x	x	x	–	x
	Periploma tenerum Fischer, 1882	O–L	–M––	1	S–	–B	0	–	x	x	–	x
Petricolidae	*Choristodon robustum* (G. B. Sowerby I, 1834)	OML	UMLT	41	S–	OB	11	x	x	–	x	x
	Cooperella atlantica Rehder, 1943	–ML	–ML–	2	––	––	0	–	–	–	–	–
	Petricola lapicida (Gmelin, 1791)	OML	UMLT	40	S–	OB	7	x	x	x	x	x

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Petricolaria pholadiformis (Lamarck, 1818)	–ML	––L–	1	––	––	0	–	x	x	–	x
Pharidae	*Ensis minor* Dall, 1900	–ML	U–L–	2	––	O–	0	–	x	–	–	x
Philobryidae	*Cratis antillensis* (Dall, 1881)	–ML	–––T	2	–D	––	1	–	x	–	–	–
Pholadidae	*Barnea truncata* (Say, 1822)	–ML	–M––	1	––	–B	1	–	x	x	–	x
	Cyrtopleura costata (Linnaeus, 1758)	–ML	UML–	6	S–	OB	1	–	x	x	–	x
	Martesia cuneiformis (Say, 1822)	––L	–MLT	3	––	––	0	x	x	x	–	x
	Martesia striata (Linnaeus, 1758)	OML	UMLT	7	S–	–B	0	–	x	x	–	x
	Pholas campechiensis Gmelin, 1791	––L	––––	0	––	––	0	–	x	x	–	–
Pinnidae	*Atrina rigida* (Lightfoot, 1786)	OML	UMLT	22	S–	OB	6	–	–	x	x	x
	Atrina seminuda (Lamarck, 1819)	OML	UML–	4	S–	OB	4	–	x	–	x	x
	Atrina serrata (G. B. Sowerby I, 1825)	OML	UMLT	10	SD	OB	1	x	x	x	–	x
	Pinna carnea Gmelin, 1791	OML	UMLT	93	SD	OB	18	x	x	x	x	x
Plicatulidae	*Plicatula gibbosa* Lamarck, 1801	OML	UMLT	84	SD	OB	4	–	x	x	x	x
Poromyidae	*Poromya albida* Dall, 1886	––L	––––	0	––	––	0	–	x	–	–	–
	Poromya granulata (Nyst & Westendorp, 1839)	OML	––LT	4	SD	O–	1	–	x	x	–	x
	Poromya rostrata Rehder, 1943	–M–	–M––	1	–D	O–	0	–	–	–	–	x
Propeamussiidae	*Cyclopecten nanus* A. E. Verrill & Bush, 1897	OM–	UMLT	10	SD	OB	0	–	–	–	–	–
	Cyclopecten strigillatus (Dall, 1889)	––L	––––	0	––	––	0	–	x	–	–	–
	Parvamussium cancellatum (E. A. Smith, 1885)	––L	––––	0	––	––	0	–	x	–	–	–
	Parvamussium thalassinum (Dall, 1886)	––L	––––	0	––	––	0	–	x	–	–	–
	Propeamussium pourtalesianum (Dall, 1886)	–ML	U–LT	5	–D	O–	1	–	x	–	–	x
	Propeamussium sayanum (Dall, 1886)	–ML	–––T	1	–D	––	0	–	x	–	–	x
Psammobiidae	*Asaphis deflorata* (Linnaeus, 1758)	OML	UMLT	26	S–	OB	4	x	x	x	x	x
	Gari circe (Mörch, 1876)	O––	UML–	3	S–	O–	0	x	–	–	–	–
	Heterodonax bimaculatus (Linnaeus, 1758)	–ML	–––T	1	––	––	0	x	x	x	–	x

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Sanguinolaria sanquinolenta (Gmelin, 1791)	–ML	UM–T	3	– –	– –	0	–	–	–	–	–
Pteriidae	*Pinctada imbricata* Röding, 1798	OML	UMLT	200	SD	OB	59	x	x	x	x	x
	Pinctada longisquamosa (Dunker, 1852)	OML	UMLT	256	SD	OB	137	–	–	–	–	x
	Pinctada margaritifera (Linnaeus, 1758)	– –L	– – –T	1	– –	– –	0	–	–	–	–	–
	Pteria colymbus (Röding, 1798)	OML	UMLT	98	SD	OB	18	–	x	x	x	x
	Pteria vitrea (Reeve, 1857)	–ML	U– –T	5	–D	O–	0	–	x	–	–	–
Semelidae	*Abra aequalis* (Say, 1822)	OML	U–LT	16	SD	OB	5	–	–	x	x	x
	Abra lioica (Dall, 1881)	–ML	UML–	14	SD	OB	3	–	x	x	–	x
	Abra longicallis americana A E. Verrill & Bush, 1898	– –L	– – – –	0	– –	– –	0	–	x	–	–	–
	Cumingia coarctata G. B. Sowerby I, 1833	OML	UMLT	47	S–	OB	9	–	–	x	x	x
	Cumingia vanhyningi Rehder, 1939	OML	UMLT	105	S–	OB	10	x	x	x	–	x
	Ervilia concentrica (Holmes, 1860)	OML	UMLT	53	SD	OB	7	x	x	x	x	x
	Ervilia nitens (Montagu, 1806)	OML	UMLT	13	SD	OB	6	x	x	x	x	x
	Ervilia subcancellata E. A. Smith, 1885	– –L	UMLT	7	– –	– –	0	–	–	–	–	x
	Semele bellastriata (Conrad, 1837)	OML	UMLT	30	SD	OB	7	–	x	x	x	x
	Semele proficua (Pulteney, 1799)	OML	UMLT	78	SD	OB	14	x	x	x	x	x
	Semele purpurascens (Gmelin, 1791)	OML	UMLT	42	SD	OB	0	x	x	x	x	x
	Semelina nuculoides (Conrad, in Hodge, 1841)	– –L	UMLT	17	SD	OB	11	–	–	x	x	x
Solecurtidae	*Solecurtus cumingianus* (Dunker, 1861)	OM–	UMLT	12	SD	O–	0	–	–	–	–	x
	Tagelus divisus (Spengler, 1794)	OML	UML–	20	S–	OB	6	–	x	x	–	x
	Tagelus plebeius (Lightfoot, 1786)	–ML	U– – –	1	S–	–B	1	–	–	–	–	x
Solemyidae	*Solemya occidentalis* Deshayes, 1857	OML	UMLT	14	S–	–B	13	–	x	x	x	x
	Solemya velum Say, 1822	–M–	–M– –	1	–D	O–	1	–	–	–	–	–
Spondylidae	*Spondylus americanus* Hermann, 1781	OML	UMLT	29	SD	O–	5	–	–	x	x	x
	Spondylus ictericus Reeve, 1856	OML	UMLT	96	SD	OB	12	x	x	–	x	x

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
Sportellidae	*Basterotia elliptica* (Récluz, 1850)	–ML	U–L–	2	S–	OB	0	–	–	–	x	x
	Basterotia quadrata (Hanley, 1843)	––L	––––	0	––	––	0	–	x	x	x	x
	Ensitellops protexta (Conrad, 1841)	––L	U–––	1	––	––	0	–	–	x	–	–
Tellinidae	*Acorylus gouldii* (Hanley, 1846)	OML	UMLT	43	SD	OB	5	x	x	x	x	x
	Angulus agilis (Stimpson, 1857)	–ML	––L–	3	S–	–B	1	–	x	x	–	x
	Angulus merus (Say, 1834)	OML	UMLT	170	SD	OB	29	x	x	x	x	x
	Angulus paramerus (Boss, 1964)	–ML	UMLT	5	S–	O–	0	–	–	–	x	x
	Angulus probrinus (Boss, 1964)	O–L	–MLT	17	SD	OB	1	–	–	–	x	x
	Angulus sybariticus (Dall, 1881)	OML	U–LT	15	S–	OB	6	–	–	–	x	x
	Angulus tampaensis (Conrad, 1866)	OML	U–L–	22	S–	OB	2	–	–	–	x	x
	Angulus tenellus (A. E. Verrill, 1874)	––L	–M––	1	S–	O–	1	–	x	x	–	–
	Angulus texanus (Dall, 1900)	OML	UMLT	53	S–	OB	9	–	–	x	x	x
	Angulus versicolor (DeKay, 1843)	OML	UMLT	30	SD	OB	2	–	–	x	x	x
	Arcopagia fausta (Pulteney, 1799)	OML	UMLT	150	SD	OB	2	x	x	x	x	x
	Cymatoica orientalis forma *hendersoni* Rehder, 1939	OML	––LT	5	SD	––	0	–	–	–	–	x
	Elliptotellina americana (Dall, 1900)	–ML	––L–	2	–D	O–	0	–	–	–	x	x
	Eurytellina alternata (Say, 1822)	OML	UMLT	12	SD	OB	1	x	x	x	x	x
	Eurytellina angulosa (Gmelin, 1791)	OML	U–L–	3	S–	––	0	–	x	x	x	x
	Eurytellina lineata (Turton, 1819)	–ML	UMLT	15	S–	–B	2	x	x	x	x	x
	Eurytellina nitens (C. B. Adams, 1845)	–ML	––LT	4	–D	O–	0	–	–	x	x	x
	Eurytellina punicea (Born, 1778)	–ML	––––	1	––	––	0	–	–	–	–	x
	Laciolina laevigata (Linnaeus, 1758)	OML	UMLT	11	S–	O–	1	–	–	–	x	x
	Laciolina magna (Spengler, 1798)	OML	UMLT	8	S–	O–	0	–	x	–	x	x
	Leporimetis intastriata (Say, 1827)	OML	UMLT	21	SD	O–	0	x	x	x	x	x
	Macoma brevifrons (Say, 1834)	–ML	U–LT	4	SD	–B	2	–	x	x	x	x

(Continues)

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Macoma cerina (C. B. Adams, 1845)	OML	UMLT	40	S–	OB	4	–	x	x	–	x
	Macoma constricta (Bruguière, 1792)	–ML	U–L–	3	––	––	0	–	–	x	–	x
	Macoma extenuata Dall, 1900	–ML	–ML–	3	–D	O–	0	–	–	–	–	–
	Macoma limula Dall, 1895	–ML	–MLT	3	SD	O–	0	–	–	x	–	–
	Macoma mitchelli Dall, 1895	–M–	U–––	1	S–	–B	1	–	–	–	–	x
	Macoma pseudomera Dall & Simpson, 1901	–ML	–M–T	2	S–	O–	0	–	–	–	–	–
	Macoma tageliformis Dall, 1900	–M–	––LT	3	–D	––	0	–	–	–	–	x
	Macoma tenta (Say, 1834)	OML	U–LT	11	SD	–B	2	–	x	x	–	x
	Merisca aequistriata (Say, 1824)	–ML	UMLT	10	–D	OB	2	–	–	x	x	x
	Merisca cristallina (Spengler, 1798)	––L	––––	0	––	––	0	–	–	x	–	–
	Merisca martinicensis (d'Orbigny, 1842)	O–L	––LT	8	SD	O–	0	–	–	x	x	x
	Scissula candeana (d'Orbigny, 1842)	–ML	–ML–	13	S–	OB	0	–	–	x	x	x
	Scissula consobrina (d'Orbigny, 1842)	–ML	UMLT	9	SD	O–	0	–	–	–	x	x
	Scissula iris (Say, 1822)	OML	UMLT	33	S–	OB	9	–	–	x	–	x
	Scissula similis (J. Sowerby, 1806)	OML	UMLT	224	SD	OB	42	x	x	x	x	x
	Strigilla carnaria (Linnaeus, 1758)	OML	–ML–	6	S–	O–	0	–	x	x	x	x
	Strigilla gabbi Olsson & McGinty, 1958	––L	––L–	4	––	––	0	–	–	–	x	x
	Strigilla mirabilis (Philippi, 1841)	OML	UMLT	26	S–	OB	0	–	x	x	x	x
	Strigilla pisiformis (Linnaeus, 1758)	–ML	––LT	6	––	––	0	x	x	x	–	x
	Tellidora cristata (Récluz, 1842)	–ML	UML–	5	S–	–B	2	–	x	x	x	x
	Tellina persica Dall & Simpson, 1901	–M–	––L–	1	–D	O–	0	–	–	–	–	x
	Tellina radiata Linnaeus, 1758	OML	UMLT	56	S–	O–	1	x	x	x	x	x
	Tellina squamifera Deshayes, 1855	OML	UMLT	12	–D	O–	0	–	x	x	x	x
	Tellinella listeri (Röding, 1798	OML	UMLT	69	SD	OB	2	x	x	x	x	x
Teredinidae	*Bankia carinata* (Gray, 1827)	–M–	–M––	1	––	––	1	–	–	–	–	x

(Continues)

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Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Bankia fimbriatula (Moll & Roch, 1931)	––L	––L–	1	––	––	0	–	x	x	–	–
	Lyrodus pedicellatus (de Quatrefages, 1849)	––L	––L–	1	––	––	0	–	–	–	–	–
	Nototeredo knoxi (Bartsch, 1917)	–M–	U–––	1	S–	––	0	–	–	–	–	x
	Teredo bartschi Clapp, 1923	––L	––––	0	––	––	0	–	–	–	–	–
	Teredo clappi Bartsch, 1923	–ML	U–L–	2	S–	––	2	–	–	x	–	x
	Teredora malleolus (Turton, 1822)	––L	––––	0	––	––	0	–	x	x	–	–
Thraciidae	*Asthenothaerus hemphilli* Dall, 1886	–ML	UMLT	18	S–	OB	15	–	x	x	x	x
	Bushia elegans (Dall, 1886)	–ML	U–––	3	S–	O–	3	–	x	–	–	–
	Thracia distorta (Montagu, 1803)	–ML	–M––	1	––	––	0	x	–	–	–	–
	Thracia morrisoni Petit, 1964	–ML	––L–	1	––	––	1	–	x	x	–	x
	"*Thracia phaseolina* Lamarck, 1822"	––L	––––	0	––	––	0	–	x	–	–	x
	Thracia stimpsoni Dall, 1886	––L	––L–	2	––	–B	2	–	–	–	–	x
Thyasiridae	*Thyasira grandis* (A. E. Verrill & Smith, in A. E. Verrill, 1885)	––L	––––	0	––	––	0	–	x	–	–	–
	Thyasira trisinuata (d'Orbigny, 1842)	OM–	U––T	2	–D	O–	0	–	–	–	–	x
Trapezidae	*Coralliophaga coralliophaga* (Gmelin, 1791)	OML	–MLT	18	S–	O–	1	x	–	x	x	x
Ungulinidae	*Diplodonta notata* Dall & Simpson, 1901	––L	––L–	1	––	––	0	–	–	x	–	–
	Diplodonta nucleiformis Wagner, 1838	OML	–M––	2	S–	OB	0	–	–	x	–	–
	Diplodonta punctata (Say, 1822)	OML	UML–	21	S–	OB	9	–	x	x	x	x
	Felaniella candeana (d'Orbigny, 1842)	–ML	–––T	1	––	––	0	x	–	–	–	–
	Phlyctiderma semiaspera (Philippi, 1836)	OML	UMLT	10	S–	OB	5	x	x	–	x	x
	Phlyctiderma soror (C. B. Adams, 1852)	––L	–––T	2	––	––	0	x	x	x	–	–
Veneridae	*Anomalocardia auberiana* (d'Orbigny, 1842)	OML	UMLT	114	SD	OB	31	–	x	x	x	x
	Callista eucymata (Dall, 1890)	–ML	UMLT	15	–D	O–	0	–	–	x	–	x
	Chione elevata (Say, 1822)	OML	UMLT	372	SD	OB	168	x	x	x	x	x
	Chione mazyckii Dall, 1902	OML	UMLT	86	SD	OB	19	–	–	x	–	x

(Continues)

(Continued)

Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Circomphalus strigillinus (Dall, 1902)	–ML	–MLT	6	–D	O–	1	–	–	x	–	x
	Cyclinella tenuis (Récluz, 1852)	OML	UMLT	12	S–	OB	1	–	x	x	x	x
	Dosinia discus (Reeve, 1850)	–ML	UMLT	7	S–	O–	5	–	–	x	–	x
	Dosinia elegans (Conrad, 1846)	OML	UMLT	12	SD	OB	2	–	x	x	–	x
	Gemma gemma (Totten, 1834)	–ML	–M––	1	S–	––	0	–	–	x	–	–
	Globivenus rigida (Dillwyn, 1817)	OML	U–LT	4	SD	O–	0	–	x	x	x	x
	Globivenus rugatina (Heilprin, 1886)	OML	––LT	4	SD	O–	0	–	x	–	–	x
	Gouldia cerina (C. B. Adams, 1845)	OML	UMLT	78	SD	OB	14	–	x	x	x	x
	Lirophora clenchi (Pulley, 1952)	–M–	–––T	1	–D	––	0	–	–	–	–	–
	Lirophora latilirata (Conrad, 1841)	OML	U–LT	20	SD	OB	0	–	–	x	x	x
	Lirophora paphia (Linnaeus, 1767)	–ML	U–LT	12	SD	O–	2	x	–	x	–	x
	Macrocallista maculata (Linnaeus, 1758)	OML	UMLT	31	SD	OB	3	–	x	x	x	x
	Macrocallista nimbosa (Lightfoot, 1786)	–ML	UMLT	7	––	––	1	–	x	x	–	x
	Mercenaria campechiensis (Gmelin, 1791)	–ML	––L–	4	––	––	1	x	–	x	–	x
	Mercenaria mercenaria (Linnaeus, 1758)	–ML	–M––	4	S–	O–	1	–	x	x	–	x
	Parastarte triquetra (Conrad, 1846)	OML	UMLT	45	SD	OB	10	–	–	x	–	x
	Periglypta listeri (Gray, 1838)	OML	UMLT	161	SD	OB	24	x	–	x	x	x
	Pitar albidus (Gmelin, 1791)	––L	––––	0	––	––	0	–	x	x	–	–
	Pitar circinatus (Born, 1778)	––L	–––T	1	––	––	0	x	–	–	–	–
	Pitar cordatus (Schwengel, 1951)	OML	––LT	18	SD	–B	2	–	–	–	–	x
	Pitar dione (Linnaeus, 1758)	––L	–––T	2	––	––	0	x	x	x	–	–
	Pitar fulminatus (Menke, 1828)	OML	UMLT	59	SD	OB	9	x	x	x	x	x
	Pitar simpsoni (Dall, 1895)	OML	UMLT	123	SD	OB	34	–	x	x	x	x
	Puberella intapurpurea (Conrad, 1849)	OML	UMLT	27	SD	OB	1	–	–	–	x	x
	Puberella pubera (Bory Saint-Vincent, 1827)	––L	––––	0	––	––	0	–	–	x	x	x

(Continues)

(Continued)

Family	Species	Data Sources*	Fla. Keys Distrib.†	Recs**	Depth‡	Side§	Live††	Simpson, 1887-1889	Dall, 1889a, 1903	Lermond, 1936	L&Q, 1995‡‡	M&B, 2000§§
	Timoclea grus (Holmes, 1858)	OML	UMLT	25	SD	OB	5	–	–	x	–	x
	Timoclea pygmaea (Lamarck, 1818)	OML	UMLT	41	S–	OB	4	x	x	x	x	x
	Tivela abaconis Dall, 1902	–M–	–ML–	3	––	––	1	–	–	–	–	–
	Tivela floridana Rehder, 1939	O––	U–L–	2	S–	O–	0	–	–	–	–	x
	Tivela mactroides Born, 1778	––L	–––T	1	––	––	0	–	x	x	–	–
	Tivela trigonella (Lamarck, 1818)	––L	–––T	0	––	––	0	x	–	–	–	–
	Transennella conradina (Dall, 1884)	OML	UMLT	40	SD	OB	8	x	x	x	x	x
	Transennella cubaniana (d'Orbigny, 1842)	OML	UMLT	7	SD	OB	0	–	x	x	x	x
	Transennella culebrana (Dall & Simpson, 1901)	––L	––L–	1	–D	––	0	–	–	–	–	x
	Transennella stimpsoni Dall, 1902	OML	UMLT	9	SD	OB	2	–	–	x	x	x
Verticordiidae	*Euciroa elegantissima* (Dall, 1881)	––L	––L–	1	–D	O–	0	–	–	–	–	–
	Haliris fischeriana (Dall, 1881)	–ML	–––T	1	––	––	0	–	x	–	–	x
	Spinosipella acuticostata (Philippi, 1844)	–ML	––L–	5	–D	O–	0	–	x	–	–	x
	Trigonulina ornata d'Orbigny, 1842	OML	U–LT	4	–D	O–	0	–	x	x	–	x
Vesicomyidae	*Vesicomya vesica* (Dall, 1886)	––L	––––	0	––	––	0	–	x	–	–	–
Yoldiidae	*Yoldia liorhina* Dall, 1881	––L	––––	0	––	––	0	–	x	–	–	–
Totals:	389			12,382			2,797	86	225	214	163	304

*Data sources: O = original collection, M = museum specimen, L = literature record.

†Florida Keys Distribution: U = Upper Keys, M = Middle Keys, L = Lower Keys, T = Dry Tortugas.

**Records: number of records in database.

‡Depth (database only): S = shallow, D = deep.

§Side (database only): O = oceanside, B = bayside.

††Live: number of live-collected records in database.

‡‡Lyons & Quinn, 1995

§§Mikkelsen & Bieler, 2000. Although 325 species were originally listed by this survey, 16 species have been eliminated through synonymy, exclusion of less-than-fully-identified species, and restriction by depth.

known cases, the records were entered as "dead" in the database.

To maintain a measure of relative abundance in our data in the face of the obviously mixed sampling effort in this heterogeneous dataset, our analyses employed standardized data, that is, data converted from raw abundances into percentage abundances. In addition, we repeated analyses as (a) untransformed (thus allowing common species, i.e., those with greater inferred abundance [= more database records], greater influence) and (b) presence/absence-transformed (thus giving rare and common species identical levels of influence). Results of these multiple runs are reported where relevant.

All statistical calculations and resulting graphs were generated with the software package PRIMER 5 (ver. 5.2.8) for Microsoft Windows® (Clarke & Warwick, 2001). Each species-by-location matrix was initially converted into a triangular location-by-location array of similarities by calculating the Bray-Curtis Similarity Index between location pairs, based on joint species abundances or presences. Further analyses employed hierarchical clustering into sample groups (CLUSTER; e.g., Everitt, 1980), as well as ordination by non-metric Multi-Dimensional Scaling (MDS; Kruskal & Wish, 1978), which constructs a rank-similarity-matrix-based sample configuration (or "map") in a specified number of dimensions. The inter-point distances in this map have the same rank order as the corresponding dissimilarities between samples. Stress values of the two-dimensional MDS plots indicate the difficulty involved in compressing the sample relationships into low-dimensional space (a perfect fit has stress = 0, whereas stress > 0.3 approaches arbitrary placement in two-dimensional ordination space). Permutation-based hypothesis testing was performed by non-metric, one-way, pair-wise analyses of similarity (ANOSIM, an analogue of univariate ANOVA; Clarke & Green, 1988), which tests between groups of multivariate samples and was here used to determine significant differences between regional samples (with R values given for standardized data unless otherwise stated). When such differences were encountered, exploratory analyses of similarity/dissimilarity of percentages (SIMPER; Clarke, 1993) were performed to determine which species were principally responsible for within-group similarity and between-group dissimilarity. The SIMPER routine implemented in PRIMER examines the contribution each species makes to the *average similarity within a group* (e.g., which species "typify" the bayside samples) as well as its contribution to the *average dissimilarity between two groups* (e.g., which species are good "discriminators" between bayside and oceanside samples).

Faunal Comparisons

As in the previous analysis (Mikkelsen & Bieler, 2000), other western Atlantic regions for which comprehensive species lists could be compiled were used for comparison with the Florida Keys fauna. These regions were selected as those having similar ecological complexity, including estuarine/mangrove habitats, coral reefs, and shallow-to-deep water components. Their selection and delineation was admittedly arbitrary and depends greatly on available published and unpublished data. We revised the taxonomic listings of the four previously used comparative areas; those for two areas were substantially modified from the previous analysis, and so a full list of sources is given here: *Gulf of Mexico* (compiled from Steger, 1962, West Florida; Haas, 1940 and Gundersen, 1998, Sanibel Island; Lipe, 1984, Tampa Bay; Lee, 1999, Cedar Key; Lipka, 1974, Flower Garden Bank; Shelton, 1997, Alabama; García & Lee, 2002, 2003, Louisiana; articles in *Texas Conchologist*, 1964–1999, Texas; Garcia-Cubas, 1968 [which includes records from Parker, 1959], Mexico just south of Texas), *Cuba* (from Aguayo & Jaume 1947–1948; Espinosa et al., 1994), *Yucatan* (from Jaume, 1946; Rice & Kornicker, 1962, 1965; Ekdale 1974; Garcia-Cubas, 1981; H. E. Vokes & E. H. Vokes 1984; Cruz-Abrego & Flores-Andolais, 1994), and *eastern peninsular Florida* (from Voss et al., 1969, Biscayne National Monument; McGinty & Nelson, 1972, Pompano Beach; Reed & Mikkelsen, 1987, eastern Florida *Oculina* coral reefs; Lyons, 1989, Hutchinson Island; Mikkelsen et al., 1995, Indian River Lagoon). Two new listings were compiled for this study: *Bahamas* (from Dall, 1896; Clench & McLean, 1936; Lawson, 1993; Redfern, 2001 [plus full species list provided by that author]; and unpublished data (PMM) from the island of Andros), and *Bermuda* (from an unpublished species list compiled by the late Russell H. Jensen, Delaware Museum of Natural History). Incompletely identified taxa (e.g., to genus- or family-level only) were excluded from these analyses.

RESULTS AND DISCUSSION

Characterization of the Fauna

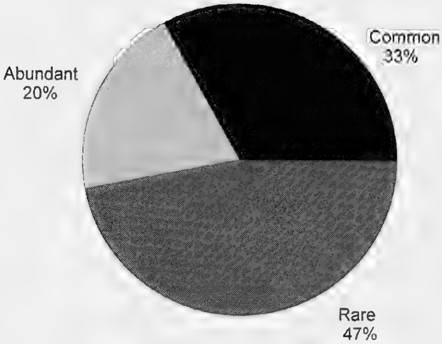
A total of 389 bivalve species are now recorded from the Florida Keys (Table 1), an increase of 28% over the previously recorded total (Mikkelsen & Bieler, 2000; as adjusted; Table 1), and a 139% increase over the previous FKNMS checklist (Lyons & Quinn, 1995). The Florida Keys bivalve fauna presents wide taxonomic diversity, including 61 families and 212 genera. The most diverse families are Tellinidae (47 species), Veneridae (39), Lucinidae (22), Pectinidae (22), and Mytilidae (19). The fauna includes 86% (279 species, plus six now regarded as synonyms) of the 331 shallow-water (< 37 m) bivalves of Florida (Lyons, 1997), plus 24 additional species recorded from shallow water. It also includes 62% (347 of 557) of North American, Atlantic coast marine bivalve species from < 200 m depth, plus an additional 42 species not included on the Turgeon et al. (1998) checklist.

355 (91%) of the 389 "ever-recorded" bivalve species were represented in the database. Of these, 71 species (20%) were abundant, 116 species (33%) were common, and 168 species (47%) were rare, as defined in Materials and Methods: Analyses (Fig. 4). The most frequently collected species were *Chione elevata* (372 records), *Codakia orbicularis* (352), *Brachidontes exustus* (334), and *Barbatia cancellaria* (297). For comments on extremely rarely encountered species (singletons and doubletons), see below. To eliminate possible artifact in the database caused by sampling bias by other collectors, we considered these same statistics for our original collection records only (212 species; Fig. 5), and found them comparable in scale: 39 species (18%) abundant, 72 species (34%) common, and 101 species (48%) rare. The frequency distribution of occurrences appears in Fig. 6.

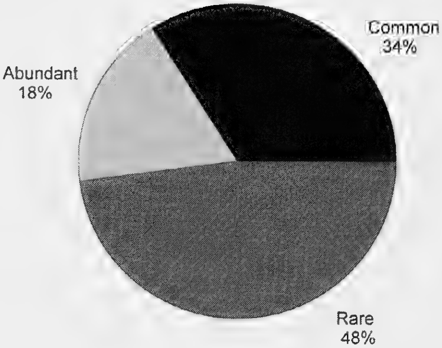
Of the 389 ever-recorded species, 163 species (43%) have never been recorded as live-collected (Table 1). This exceeds the already high percentage of the total fauna recorded by Bouchet et al. (2002; 28.5%) and Kidwell (2002; 25%).

The data were insufficient to reveal strong indications of species losses or gains throughout the Florida Keys or at specific localities (largely due to the paucity of dated collection data). Our previous analysis (Mikkelsen & Bieler, 2000) noted loose correlation of records of the Lions' Paw scallop (*Nodipecten frago-*

4



5



FIGS. 4–5. Percent of records in the database categorized as abundant (> 50 records), common (10–49 records), and rare (< 10 records). FIG. 4: For all collections; FIG. 5: For original collections only.

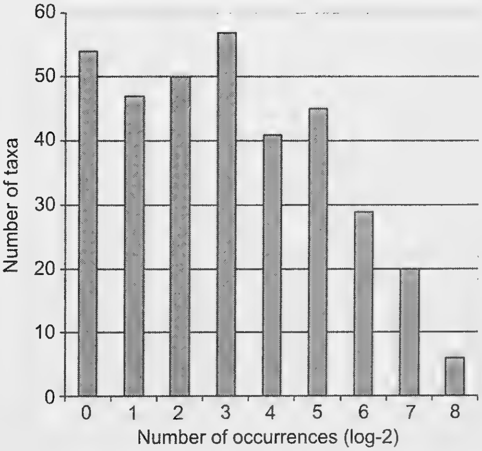


FIG. 6. Histogram of the frequency distribution of occurrences, plotting number of taxa versus number of occurrences ($\log_2$) binned to full integers.

sus) with the popularization of scuba diving (especially on artificial reefs), and of two species of false mussels (*Mytilopsis* spp.) with increased recreational boat traffic and/or freshwater input into Florida Bay. Three additional notes can now be made. (A) An initially suspicious record of the Indo-Pacific black-lipped pearl mussel, *Pinctada margaritifera*, in the Dry Tortugas in 1893 (Nutting, 1895) has been reinforced by recent, irrefutable records along the eastern coast of Florida (Chesler, 1994; Carlton, 1996), and could thus be the first, considerably earlier, record of this introduction. (B) The discovery of a living, large-bodied, Indo-Pacific gryphaeid oyster on a shipwreck off the Middle Florida Keys strongly indicates a recent introduction (Bieler et al., in press). (C) A predicted invasion by the green mussel, *Perna viridis* (Linnaeus, 1758), from now-ubiquitous populations in western Florida (Benson et al., 2001), has not yet been discovered but must be anticipated in sheltered, reduced-salinity habitats of Florida Bay similar to those colonized by *P. viridis* in western Florida.

Faunistic Relationships – Within Subregions of the Keys

Overall Regional Comparison: Within the database of 12,382 records, 99% could be assigned to one of the Florida Keys subregions. 354 species (91%) were recorded for at least one subregion (the remainder included 34 species coded only as Florida Keys, plus two species in the database solely for other parameters). 163 of the regionally assigned species (46%) were recorded from all Florida Keys subregions, that is are ubiquitous at this spatial scale ("UMLT" in Table 1). 74 species (19%) were restricted to a single subregion (Upper Keys 14; Middle Keys 12; Lower Keys 27; Dry Tortugas 21). The remaining 116 species (30%) were recorded from two or more subregions.

None of the MDS and CLUSTER analyses of untransformed (raw numbers of occurrences/records), standardized (converted to percentage abundances), or presence/absence data demonstrated any serial pattern of community similarities along the island archipelago. Likewise, CLUSTER and MDS analyses of all records showed no clear clustering of Upper, Middle, Lower, or Dry Tortugas records, and the ANOSIM analysis confirmed this impression (global R = 0.036, p = 0.2). The strongest R-values under any data transformation were generated in pair-wise tests between the westernmost records (Dry Tortugas) and the other groups. To explore this as a potential artifact of the comparatively low number of Dry Tortugas records, the analyses were rerun using only Upper, Middle, Lower, and Western Keys subregions (see Materials and Methods). While the MDS analysis indicated a relatively well-defined Western Keys group, the ANOSIM analysis again resulted in a low global R-value (0.17, p = 0.001), although significant differences (R > 0.53, p = 0.001) were evident between the Upper Keys and the Western Keys, as well as the Middle Keys and the Western Keys.

To test for the effect of deepwater species (by omitting all deep stations, and again using the Western Keys subregion), MDS plots showed no distinct subregional-shallow groups along the Keys, with the exception of the Western Keys localities. The ANOSIM analysis showed low global values (R = 0.144, p = 0.004), and non-significant differences between the neighboring Upper-Middle and Middle-Lower regions. We can conclude that the lack of significant differences found in pairwise comparisons of the subregions was not due to the inclusion of the deep stations, which led to the depth-related analysis discussed below.

Bayside Versus Oceanside: 288 (74%) of the 389 species could be coded as to whether they occur either on oceanside or bayside of the Keys axis. Because of the exposed position of the Dry Tortugas, records from this region were never coded for ocean- or bayside. Most Florida Keys bivalve species (169 species or 59%) occur on both sides of the island chain. 95 species (33%) were recorded as oceanside only, and 24 species (8%) were bayside only.

An MDS analysis of all records (coded for position, i.e., bayside, shallow-oceanside, deep-oceanside, and shallow Dry Tortugas; Fig. 7) showed three groups of stations, with bayside and shallow-oceanside groups overlapping. The single shallow Dry Tortugas station clustered with the shallow-oceanside group, which is not surprising considering its extreme position far removed from Florida Bay; in subsequent analyses it was coded as such. Three outlier stations (circled in Fig. 7) are likewise readily explained. The Marquesas/bayside station, located between Key West and the Dry Tortugas, is also far removed from the influence of Florida Bay and groups with the oceanic stations (and was recoded accord-

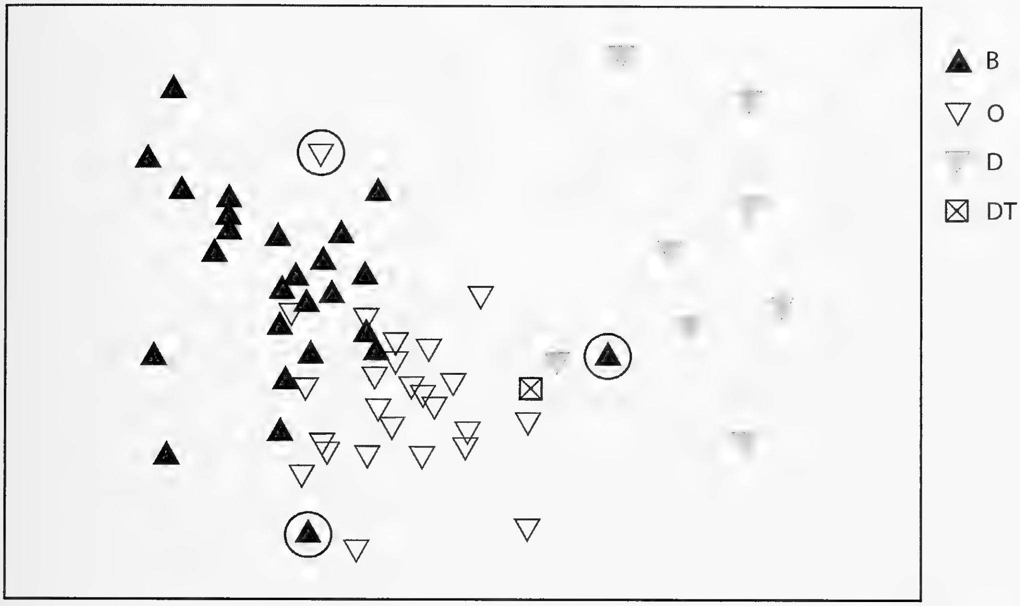


FIG. 7. Two-dimensional MDS ordination of *all station* data, coded as bayside (B), shallow-oceanside (O), deep-oceanside (D), and shallow Dry Tortugas (DT), based on standardized (percentage-transformed) data and Bray-Curtis similarities (stress = 0.16). Circled outlier stations, top to bottom, representing Big-Pine-Key/oceanside, Marquesas/bayside, and Pigeon-Key/bayside, are discussed in the text.

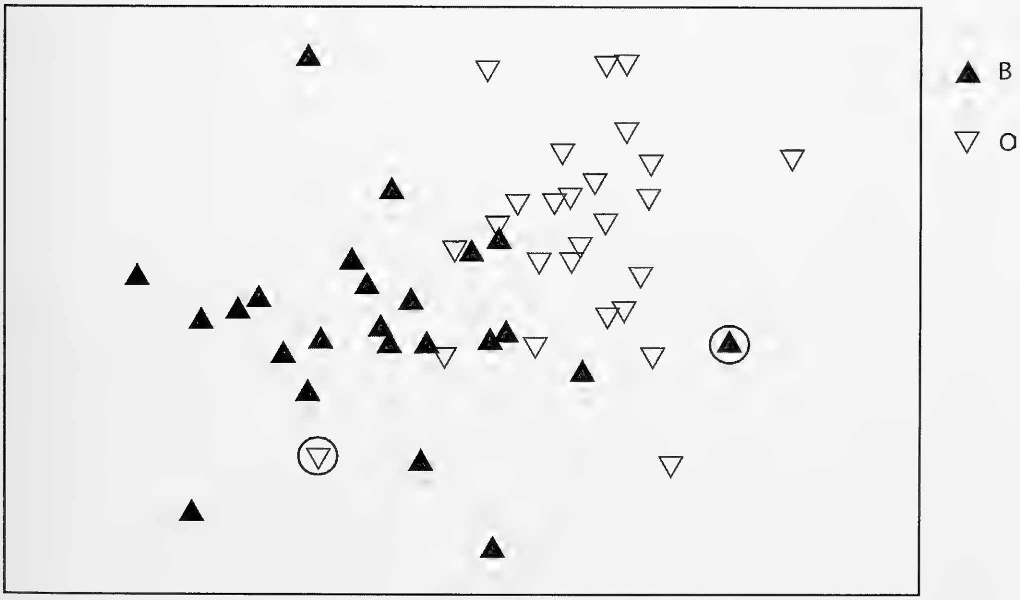


FIG. 8. Two-dimensional MDS ordination of *shallow station* data that were coded as bayside (B) or oceanside (O). Based on standardized (percentage-transformed) data and Bray-Curtis similarities (stress = 0.17). The two circled outliers are again Pigeon-Key/bayside, and Big-Pine-Key/oceanside.

ingly for subsequent analyses). Pigeon-Key/bayside, although farther east in the island chain in the center of the Seven-Mile Bridge, is in a relatively exposed position and subject to massive tidal changes that apparently bring shallow-oceanside elements into this part of the bay; it also groups with shallow-oceanside stations. In contrast, the Big-Pine-Key/oceanside location is technically on the oceanside of the island chain, but includes a number of smaller islands and mudflats that provide bay-like habitats. The ANOSIM analysis (global R = 0.516, p = 0.001) showed significant differences between the shallow-oceanside and bayside communities (R = 0.356, p = 0.001), between shallow-oceanside and deep-oceanside communities (R = 0.874, p = 0.001), and between bayside and deep-

TABLE 2a. Comparisons of *similarity*. Breakdown of average *within-group* similarities between bayside, shallow-oceanside (as in Fig. 7), and deep-oceanside stations into contributions from each species. Bold-font numbers indicate the percent contributions to within-group similarities within the top 55% of total similarity. Numbers in parentheses are values contributing to the remaining 45%, here provided for comparison. Compare to *between-group dissimilarities* given in Tables 2b, c.

Species	Bayside	Oceanside	Deep
Chione elevata	**9.97%**	**3.74%**	(0.23)
Codakia orbicularis	**7.18%**	**7.12%**	-
Ctena orbiculata	**6.13%**	**3.32%**	(1.27)
Brachidontes exustus	**5.33%**	(0.44)	-
Carditamera floridana	**4.93%**	(0.61)	-
Angulus merus	**4.76%**	(0.75)	-
Scissula similis	**4.47%**	**2.55%**	(0.91)
Laevicardium mortoni	**4.46%**	(0.95)	-
Arcopsis adamsi	**4.06%**	(0.86)	(1.00)
Pinctada longisquamosa	**4.01%**	(0.88)	-
Barbatia cancellaria	(2.93)	**6.23%**	-
Lucina pensylvanica	(1.82)	**4.20%**	-
Arca imbricata	(2.41)	**4.10%**	**3.90%**
Arca zebra	(0.97)	**3.42%**	(0.84)
Laevicardium laevigatum	(1.91)	**3.10%**	(0.89)
Tucetona pectinata	(2.77)	**2.88%**	(0.84)
Arcopagia fausta	(0.50)	**2.65%**	-
Pinctada imbricata	(0.44)	**2.56%**	-
Dendostrea frons	(0.07)	**2.36%**	(0.81)
Lima caribaea	(0.04)	**2.49%**	-
Anadara notabilis	(0.88)	**2.12%**	(0.13)
Chama congregata	(0.28)	**2.12%**	(0.84)
Nemocardium peramabile	-	-	**8.96%**
Plicatula gibbosa	(0.01)	(0.51)	**5.83%**
Pleurolucina leucocyma	-	-	**5.37%**
Pleurolucina sombrerensis	-	-	**3.96%**
Spondylus ictericus	-	(1.42)	**3.82%**
Lucinisca nassula	(3.54)	(0.92)	**3.72%**
Pandora inflata	-	-	**3.27%**
Spondylus americanus	-	-	**2.97%**
Cryptopecten phrygium	-	-	**2.88%**
Argopecten gibbus	-	(0.21)	**2.19%**
Lucinoma filosa	-	-	**2.14%**
Callista eucymata	-	-	**1.97%**
Semele bellastriata	-	(0.07)	**1.96%**
Nodipecten fragosus	-	(0.12)	**1.80%**
Cumulative percent contribution (bold font numbers only)	**55.31%**	**54.97%**	**54.73%**

oceanside communities (R = 0.897, p = 0.001) – pairwise tests with Dry Tortugas data, represented by only two stations, have low significance levels. It is thus evident that Florida Keys bivalve communities differ between bayside and oceanside, and that there is a very strong difference between the shallow (0–35 m) and deeper (> 35 m) oceanside communities.

A shallow-to-deep signal could also be detected *within* the near-shore oceanside communities when the faunas of inner patch reefs (in Hawk Channel) and outer bank reefs (at the edge of the Floridian Plateau) were compared. Analyzing only those records identifiable as having been collected in reef settings (1,659 records, 164 species, from 29 reefs along the Florida Keys), MDS plots show two distinct but overlapping groups (with a low R = 0.209, based on standardized data). The strong overlap is likely the result of disproportionately extensive sampling of the shallow-water back-reef rubble zones associated with the outer reefs.

TABLE 2b. Comparisons of *dissimilarity*. Breakdown of average *between-group* dissimilarities between shallow-oceanside and bayside stations into contributions from each species. Species are ordered in decreasing contribution within the top 55% of total dissimilarity. Average dissimilarity = 69.23.

Species	OCEANSIDE Average Abundance	BAYSIDE Average Abundance	Average Dissim.	Dissim./ SD	Contrib. %	Cum. %
Brachidontes exustus	1.19	10.24	2.31	0.89	3.34	3.34
Chione elevata	3.69	8.96	1.84	1.32	2.66	6.00
Pinctada longisquamosa	1.42	7.40	1.57	0.88	2.27	8.27
Carditamera floridana	1.38	5.08	1.51	1.35	2.19	10.46
Laevicardium mortoni	1.46	6.08	1.50	1.14	2.16	12.63
Ctena orbiculata	3.88	5.16	1.42	1.19	2.05	14.67
Codakia orbicularis	6.38	4.72	1.37	1.26	1.98	16.65
Angulus merus	1.65	4.04	1.36	1.28	1.97	18.62
Barbatia cancellaria	5.92	3.16	1.35	1.11	1.95	20.57
Arcopsis adamsi	1.85	5.24	1.33	1.21	1.92	22.49
Tucetona pectinata	4.46	2.92	1.30	0.91	1.88	24.36
Caribachlamys sentis	4.31	0.28	1.30	0.61	1.87	26.24
Lucina pensylvanica	5.00	1.40	1.08	1.36	1.56	27.80
Lucinisca nassula	1.58	2.76	1.05	1.17	1.52	29.32
Scissula similis	2.92	3.68	1.02	1.52	1.48	30.80
Arca zebra	4.00	1.08	0.93	1.41	1.34	32.13
Cumingia vanhyningi	0.42	3.16	0.91	0.99	1.32	33.45
Argopecten irradians	0.54	3.84	0.90	0.48	1.30	34.75
Periglypta listeri	3.08	1.32	0.88	1.04	1.27	36.02
Laevicardium laevigatum	4.35	1.88	0.88	1.33	1.27	37.28
Nucula proxima	0.19	1.88	0.87	0.88	1.26	38.54
Pinctada imbricata	3.69	0.76	0.86	1.28	1.24	39.79
Lima caribaea	3.46	0.20	0.85	1.47	1.22	41.01
Anomalocardia auberiana	0.54	3.00	0.84	0.85	1.21	42.22
Limaria pellucida	2.27	3.12	0.83	0.69	1.21	43.42
Anadara notabilis	2.73	1.04	0.83	1.16	1.21	44.63
Modiolus americanus	2.31	1.72	0.83	1.17	1.20	45.83
Arca imbricata	4.42	1.68	0.82	1.41	1.18	47.01
Dendostrea frons	3.23	0.24	0.80	1.46	1.16	48.17
Chione mazyckii	1.15	1.92	0.77	0.85	1.11	49.28
Pitar fulminatus	0.46	1.60	0.77	0.83	1.11	50.39
Chama macerophylla	3.12	0.92	0.76	1.16	1.10	51.49
Arcopagia fausta	3.12	0.72	0.75	1.48	1.09	52.58
Pitar simpsoni	1.54	2.80	0.73	1.08	1.06	53.64
Trachycardium muricatum	1.62	1.32	0.69	1.16	1.00	54.64

TABLE 2c. Comparisons of *dissimilarity*. Breakdown of average *between-group* dissimilarities between shallow-oceanside and deep-oceanside stations into contributions from each species. Species are ordered in decreasing contribution to the top 55% of total dissimilarity. Average dissimilarity = 83.47. (Average dissimilarity between bayside and deep-oceanside groups: 89.21; table not shown here.)

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In an analysis omitting all deep stations and coding all shallow stations west of Key West as oceanside (as described above), MDS plots (of both untransformed and transformed data) exhibit overlapping clusters (Fig. 8). These differences were confirmed as significant by an ANOSIM analysis (R = 0.404, p = 0.001). Within-group similarity analyses (SIMPER; Table 2a) revealed that *Brachidontes exustus, Carditamera floridana*, and *Angulus merus* contributed primarily to bayside similarities (i.e, they were "typical" bayside species), while *Barbatia cancellaria, Lucina pensylvanica*, and *Arca zebra* contributed primarily to shallow-oceanside percentages. Both of these top-three lists include species associated with hard and soft substrata. Four species (*Codakia orbicularis*, *Chione elevata, Ctena orbiculata*, and *Scissula similis,* all soft-substratum inhabitants) contributed substantially to both ocean- and baysides. The different character of bayside and shallow-oceanside communities is thus largely based on a different fractional combination of the same group of species. Most of the within-group similarity of the deep-oceanside stations, on the other hand, was a result of a different group of species (e.g., *Nemocardium peramabile*, *Plicatula gibbosa*, and *Pleurolucina* spp.) that hardly overlap with the shallow-water communities. *Arca imbricata* is an exception in that it is a more or less "typical" representative of all groups. Tables 2b–c list those species most responsible for the between-group dissimilarities. Of these, *Brachidontes exustus* leads the dissimilarity between bayside and shallow-oceanside groups, whereas *Nemocardium peramabile* leads that between shallow-oceanside and deep-oceanside groups).

Different Patterns of Shallow-Water Communities in Bay and Ocean: As shown above, analyses including all records (transformed or untransformed; with or without the deep-oceanside stations) revealed no clear clustering of Upper, Middle, and Lower Keys bivalve data. However, a pattern emerged when only bayside records were analyzed (bayside records from west of Key West here omitted, see above). An MDS analysis based on untransformed data showed clustering of each of the three groups, although with a fair amount of overlap. The ANOSIM analysis (global R = 0.326, p = 0.001) confirmed significant differences between Upper and Middle (R = 0.384, p = 0.002), Middle and Lower (R = 0.173, p = 0.008), and Upper and Lower (R = 0.41, p = 0.001) groups. A SIMPER analysis (Table 3a) showed that the ubiquitous venerid *Chione elevata* is an important (typical) member of all three subregions here analyzed. *Brachidontes exustus, Pinctada longisquamosa, Laevicardium mortoni*, and *Limaria pellucida* contributed most to the within-group similarity of the Upper Keys bayside communities, while other species, such as *Tucetona pectinata, Modiolus americanus*, and *Laevicardium laevigatum*, were strong contributors to the Middle Keys bayside percentage. Major components of the Lower Keys bayside included *Angulus merus, Lucinisca nassula,* and *Lucina pensylvanica*. Upper and Middle Keys share a strong component of *Arcopsis adamsi* in their faunas, while Middle and Lower Keys share a high contribution of *Codakia orbicularis.* Tables 3b-c list the species most responsible for the between-group dissimilarities (lead by *Brachidontes exustus* and *Pinctada longisquamosa* for the dissimilarity between Upper and Middle Keys groups, and *Tucetona pectinata* and *Ctena orbiculata* for the dissimilarity between Middle and Lower Keys groups).

The bayside stations thus show a northeast-to-southwest pattern of Upper, Middle, and Lower Keys groups that appears to be driven by the relative abundances of certain species. This is not surprising because the northeastern part of Florida Bay is largely separated from open ocean waters by the island of Key Largo, undergoes substantial temperature and salinity fluctuation, and is strongly influenced by freshwater runoffs from the Everglades (Schomer & Drew, 1982), whereas the Middle and Lower Keys are (east to west) increasingly exposed to the open waters of the Gulf of Mexico and, through the interrupted island chain, to the open Atlantic. In contrast to the confirmed bayside pattern, an analysis of the shallow-oceanside stations showed no erlying

Species	SHALLOW Average Abundance	DEEP Average Abundance	Average Dissim.	Dissim./ SD	Contrib. %	Cum. %
Nemocardium peramabile	0.00	3.14	2.38	1.10	2.86	2.86
Codakia orbicularis	6.38	0.14	1.98	1.84	2.37	5.23
Pleurolucina leucocyma	0.12	3.71	1.78	0.96	2.13	7.36
Barbatia cancellaria	5.92	0.14	1.72	1.79	2.06	9.42
Lucina pensylvanica	5.00	0.14	1.38	1.50	1.65	11.07
Pleurolucina sombrerensis	0.12	3.29	1.33	0.90	1.60	12.66
Caribachlamys sentis	4.31	0.14	1.25	0.58	1.50	14.16
Chione elevata	3.69	0.86	1.14	1.31	1.36	15.52
Ctena orbiculata	3.88	1.00	1.13	1.27	1.36	16.88
Lucinoma filosa	0.00	2.29	0.98	0.72	1.17	18.05
Lucinisca nassula	1.58	2.57	0.95	1.25	1.14	19.18
Callista eucymata	0.04	1.57	0.93	0.68	1.12	20.30
Pinctada imbricata	3.69	0.14	0.90	1.27	1.08	21.38
Tucetona pectinata	4.46	0.86	0.89	1.23	1.07	22.46
Arca zebra	4.00	0.71	0.89	1.49	1.06	23.52
Laevicardium laevigatum	4.35	0.71	0.88	1.43	1.05	24.57
Lima caribaea	3.46	0.00	0.86	1.46	1.03	25.60
Arcopagia fausta	3.12	0.00	0.85	1.62	1.02	26.62
Plicatula gibbosa	2.35	1.86	0.85	1.12	1.01	27.64
Scissula similis	2.92	0.57	0.83	1.28	0.99	28.63
Divalinga quadrisulcata	1.69	2.14	0.81	0.81	0.97	29.59
Anadara notabilis	2.73	0.43	0.79	1.11	0.94	30.54
Gouldia cerina	1.27	2.00	0.76	0.88	0.91	31.44
Abra lioica	0.08	0.86	0.76	0.79	0.91	32.35
Spondylus americanus	0.31	1.29	0.76	1.14	0.91	33.26
Arca imbricata	4.42	1.14	0.72	1.30	0.86	34.12
Pandora inflata	0.08	1.29	0.71	1.35	0.85	34.97
Chama macerophylla	3.12	0.71	0.70	1.12	0.84	35.81
Periglypta listeri	3.08	0.14	0.70	1.29	0.83	36.64
Dendostrea frons	3.23	0.43	0.67	1.29	0.80	37.45
Cryptopecten phrygium	0.12	1.29	0.64	1.32	0.77	38.21
Modiolus americanus	2.31	0.43	0.62	1.22	0.75	38.96
Acar domingensis	2.73	0.86	0.62	1.36	0.74	39.70
Isognomon bicolor	2.08	0.14	0.62	0.99	0.74	40.44
Papyridea soleniformis	1.38	0.43	0.62	0.72	0.74	41.18
Dacrydium elegantulum hendersoni	0.00	1.14	0.61	0.51	0.73	41.91
Nodipecten fragosus	0.73	1.71	0.61	1.01	0.73	42.64
Argopecten gibbus	1.42	2.00	0.60	1.15	0.72	43.36
Pteria colymbus	2.12	0.29	0.59	0.99	0.70	44.07
Chama congregata	3.15	0.71	0.59	1.34	0.70	44.77
Puberella intapurpurea	0.73	0.71	0.58	0.64	0.69	45.46
Spondylus ictericus	2.88	1.43	0.58	1.36	0.69	46.16
Cardiomya striata	0.00	1.00	0.57	0.48	0.68	46.84
Arcopsis adamsi	1.85	0.57	0.57	1.11	0.68	47.52
Radiolucina amianta	0.50	1.57	0.57	0.60	0.68	48.20
Aequipecten lineolaris	0.12	1.29	0.56	0.69	0.67	48.86
Trachycardium muricatum	1.62	0.14	0.55	0.98	0.66	49.52
Ctenoides mitis	2.62	0.57	0.55	1.17	0.66	50.18
Lindapecten muscosus	1.12	1.71	0.54	1.07	0.65	50.83
Eucrassatella speciosa	0.00	1.57	0.53	1.02	0.64	51.47
Tellina squamifera	0.15	1.00	0.52	0.74	0.62	52.10
Carditamera floridana	1.38	0.00	0.52	0.63	0.62	52.72
Laevicardium mortoni	1.46	0.00	0.52	0.88	0.62	53.34
Americardia media	2.27	0.71	0.51	1.04	0.62	53.95
Cucullaearca candida	1.65	0.43	0.50	1.07	0.60	54.56

TABLE 3a. Comparisons of *similarity*. Breakdown of average *within-group* similarities into contributions from each species. Bold-font numbers indicate the percentage contribution to within-group similarities of Upper, Middle, and Lower *bayside* stations within the top 55% of total similarity. Numbers in parentheses are values contributing to the remaining 45%, here provided for comparison. Compare to *between-group dissimilarities* given in Tables 3b, c.

Species	Upper	Middle	Lower
Brachidontes exustus	**15.75%**	(3.20)	(1.32)
Chione elevata	**11.29%**	**4.86%**	**13.61%**
Pinctada longisquamosa	**9.10%**	(2.66)	(1.51)
Laevicardium mortoni	**8.20%**	(3.31)	(1.67)
Arcopsis adamsi	**6.11%**	**5.08%**	(0.33)
Limaria pellucida	**4.24%**	(0.87)	(0.38)
Codakia orbicularis	(3.30)	**8.80%**	**7.56%**
Tucetona pectinata	(0.42)	**7.60%**	(1.75)
Scissula similis	(2.68)	**5.72%**	**3.28%**
Ctena orbiculata	(3.46)	**4.98%**	**9.22%**
Barbatia cancellaria	(0.75)	**4.94%**	(3.16)
Modiolus americanus	(0.55)	**4.41%**	(0.88)
Laevicardium laevigatum	(0.53)	**3.89%**	(1.31)
Arca imbricata	(0.50)	**3.82%**	(2.44)
Angulus merus	(3.55)	(3.46)	**5.44%**
Lucinisca nassula	(1.76)	(2.67)	**5.27%**
Carditamera floridana	(4.24)	(2.15)	**7.53%**
Lucina pensylvanica	(0.17)	(1.87)	**4.53%**
Cumulative percent contribution (bold font numbers only)	**54.68%**	**54.10%**	**56.45%**

TABLE 3b. Comparisons of *dissimilarity*. Breakdown of average *between-group* dissimilarities between Upper and Middle Keys *bayside* stations into contributions from each species. Species are ordered in decreasing contribution within the top 55% of total dissimilarity. Average dissimilarity = 62.07.

Species	UPPER Average Abundance	MIDDLE Average Abundance	Average Dissim.	Dissim./ SD	Contrib. %	Cum. %
Brachidontes exustus	26.38	3.22	4.44	1.62	7.15	7.15
Pinctada longisquamosa	20.38	1.67	2.90	1.42	4.67	11.82
Tucetona pectinata	1.25	5.11	2.56	1.25	4.13	15.95
Chione elevata	17.88	4.67	2.48	1.54	4.00	19.95
Argopecten irradians	10.25	1.56	2.21	0.82	3.57	23.51
Laevicardium mortoni	14.38	2.78	2.15	1.62	3.47	26.98
Codakia orbicularis	5.13	5.11	1.79	1.30	2.88	29.87
Barbatia cancellaria	1.75	4.78	1.74	0.96	2.81	32.67
Limaria pellucida	7.13	1.33	1.51	0.81	2.43	35.10
Carditamera floridana	8.88	2.67	1.49	1.39	2.39	37.50
Anomalocardia auberiana	7.88	0.78	1.35	1.23	2.18	39.67
Cumingia vanhyningi	7.13	1.89	1.30	1.48	2.09	41.77
Arcopsis adamsi	10.00	4.11	1.28	1.31	2.06	43.83
Laevicardium laevigatum	1.38	3.00	1.22	1.42	1.97	45.79
Modiolus americanus	1.75	2.44	1.20	1.59	1.93	47.72
Angulus merus	6.25	3.33	1.12	1.41	1.80	49.51
Ctena orbiculata	6.38	4.00	1.08	1.09	1.75	51.26
Trachycardium muricatum	0.38	2.44	1.06	1.49	1.71	52.97
Scissula similis	4.00	4.22	1.02	1.46	1.64	54.61

TABLE 3c. Comparisons of *dissimilarity*. Breakdown of average *between-group* dissimilarities between Upper and Middle Keys *bayside* stations into contributions from each species. Species are ordered in decreasing contribution within the top 55% of total dissimilarity. Average dissimilarity = 62.60. (Average dissimilarity between Upper and Lower Keys groups: 68.61; table not shown here.)

Species	MIDDLE Average Abundance	LOWER Average Abundance	Average Dissim.	Dissim./ SD	Contrib. %	Cum. %
Tucetona pectinata	5.11	2.13	2.18	1.07	3.48	3.48
Ctena orbiculata	4.00	5.25	1.85	1.33	2.95	6.43
Arcopsis adamsi	4.11	1.75	1.69	1.27	2.70	9.13
Codakia orbicularis	5.11	3.88	1.67	1.36	2.67	11.80
Barbatia cancellaria	4.78	2.75	1.65	1.00	2.64	14.44
Carditamera floridana	2.67	4.00	1.51	1.35	2.40	16.85
Angulus merus	3.33	2.63	1.47	1.35	2.34	19.19
Chione elevata	4.67	4.88	1.34	1.49	2.14	21.33
Periglypta listeri	2.11	1.50	1.19	0.95	1.91	23.24
Lucinisca nassula	2.44	2.38	1.19	1.11	1.91	25.14
Nucula proxima	1.89	1.00	1.19	1.03	1.90	27.04
Modiolus americanus	2.44	0.88	1.14	1.60	1.83	28.87
Scissula similis	4.22	2.75	1.14	1.36	1.82	30.69
Laevicardium laevigatum	3.00	1.13	1.13	1.36	1.80	32.50
Chione mazyckii	1.44	2.75	1.11	1.00	1.78	34.27
Laevicardium mortoni	2.78	1.50	1.08	1.49	1.73	36.00
Brachidontes exustus	3.22	2.00	0.96	1.37	1.53	37.53
Arca zebra	1.22	1.50	0.95	1.24	1.53	39.06
Pitar fulminatus	1.33	0.50	0.92	1.01	1.46	40.52
Anadara notabilis	1.44	0.88	0.91	1.09	1.46	41.98
Trachycardium muricatum	2.44	1.00	0.90	1.34	1.43	43.41
Pinctada longisquamosa	1.67	0.88	0.88	1.47	1.40	44.81
Lucina pensylvanica	1.67	1.88	0.83	1.44	1.32	46.14
Cumingia vanhyningi	1.89	0.63	0.78	1.06	1.25	47.38
Arca imbricata	2.11	1.63	0.76	1.60	1.22	48.60
Anomalocardia auberiana	0.78	0.63	0.76	0.81	1.21	49.81
Isognomon alatus	0.89	2.00	0.73	0.79	1.17	50.98
Pitar simpsoni	1.78	0.88	0.72	1.30	1.14	52.12
Polymesoda maritima	0.11	0.63	0.71	0.68	1.14	53.25
Modiolus squamosus	1.11	1.00	0.70	1.10	1.12	54.37
Arcopagia fausta	0.67	1.13	0.70	1.14	1.12	55.49

significant clustering into Upper/Middle/Lower groups; many species occur in similar percentage proportions along the Keys. The northeast-to-southwest pattern of bivalve community similarity inferred in the earlier study (Mikkelsen & Bieler, 2000) thus appears to be a reflection of differences on the bayside alone.

Faunistic Relationships – Between the Florida Keys and Other Regions

The bivalve species composition of the Florida Keys was compared with those of other well-documented western Atlantic locations (eastern Florida, Gulf of Mexico, Yucatan, Cuba, Bahamas, Bermuda) via a Bray-Curtis CLUSTER similarity analysis. The non-Keys localities formed two groups (Fig. 9): Cuba with the Gulf of Mexico (72.9% similarity), and Yucatan with eastern Florida (74.9%). In the earlier analysis (Mikkelsen & Bieler, 2000), the Florida Keys grouped with the latter group. Here, the Florida Keys has switched affinities, now appearing closer to the Gulf of Mexico within the Cuba-GOM group. The change can be largely attributed to the expanded datasets for Florida Keys, Gulf of Mexico, and Yucatan, which added species to each list, plus the revision of taxonomies, which reduced each list through synonymy. All localities except Bermuda showed a strong underlying similarity to each other (64.3% of shared taxa) that is essentially Caribbean in nature. Bermuda, although an extreme outlier and based on far fewer species than the other localities, is not considered artifactual in this analysis because it is based on the unquestionably thorough, multi-decadal compilation of Bermuda malacofauna by R. H. Jensen, compiled from a similarly wide range of data sources.

Our study shows a comparatively high bivalve species richness in the context of the entire Florida Keys malacofauna, which differs from the finding of the most diverse molluscan fauna studied so far. Bouchet et al. (2002), exploring a much smaller study area in New Caledonia (295 km^2), reported 2,738 molluscan species, of which 519 were bivalves (19%). Our study yielded proportionally more bivalve taxa: 1,684 molluscan species (current tally, in prep.), of which 389 are bivalves (23%). This could be a result of greater gastropod diversity in the tropical reef environments of the Indo-Pacific, or a reflection of the inclusion of more soft-bottom samples in our study.

Relative Efficacy of Data Sources

Museum and Literature-Based Data: In the expanded database analyzed here, our original collections account for approximately half of the total records, while literature and museum records each comprise approximately one-quarter of the total (Fig. 2). Despite these proportions, original collections were the least successful of the three data sources in capturing the total species list (Fig. 10); this is in close agreement with results of our previous analysis (Mikkelsen & Bieler, 2000).

The new results differ from the previous, however, in the proportions of species recovered by museum collections versus the literature. In the previous analysis, data derived from museum collections captured the greatest percentage of known species (77%), followed by published literature (73%). In the current analysis, we increased our coverage of bivalve-relevant literature by a factor of 4.4 (despite our prior assessment of having been "exhaustive"), and as a result, literature has

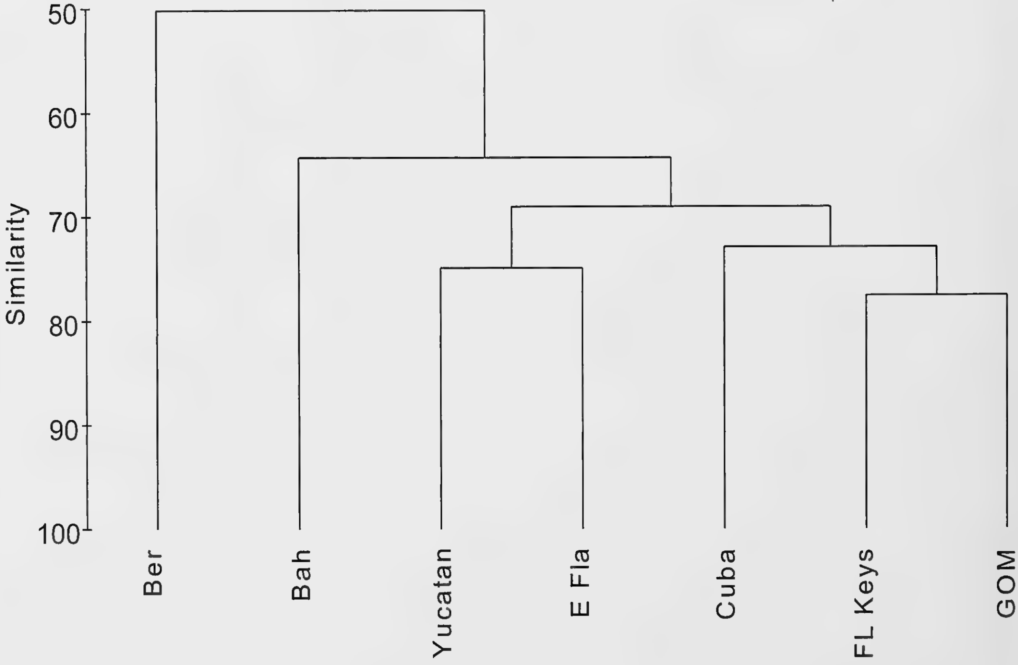

FIG. 9. Bray-Curtis similarity CLUSTER dendrogram of bivalve species presence/absence in the Florida Keys (389 species, 67% of total list), eastern Florida (243 species, 42%), Gulf of Mexico (398 species, 68%), Yucatan (261 species, 45%), Cuba (356 species, 61%), Bahamas (244 species, 42%), and Bermuda (167 species, 29%). Total species list comprised 582 species.

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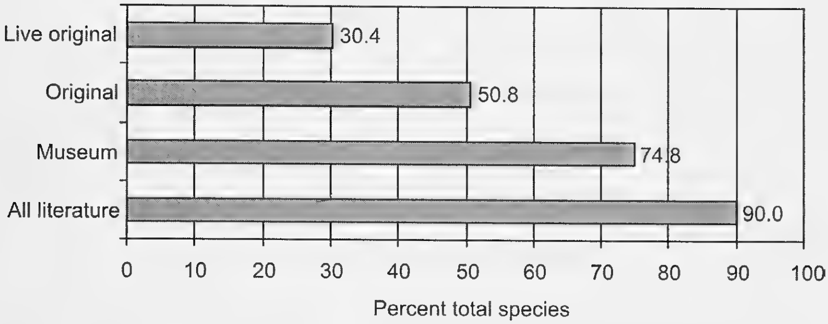

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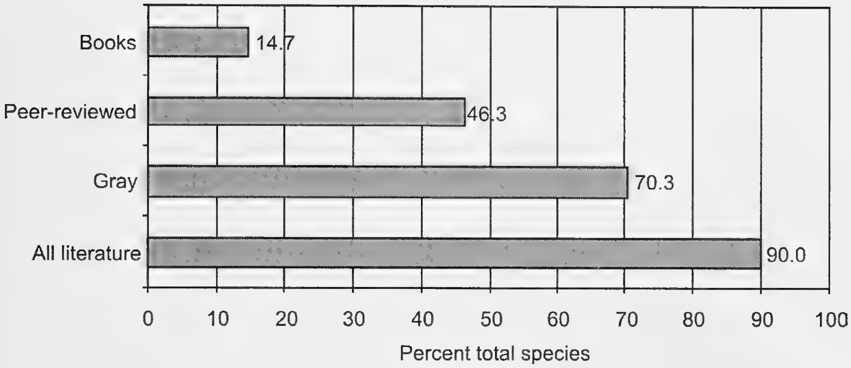

FIGS. 10, 11. Percent of total species list recovered. FIG. 10: By each of three main data sources (original collections, museum holdings, literature) and by live-only original collections in the present analysis; FIG. 11: By the various categories of literature: books, peer-reviewed literature, gray literature, and all literature categories combined.

risen to the rank of most successful source (90%). Although we are confident in this result, we are aware of a lingering conundrum involving literature-only records. In theory, if any literature-only records were based on error (i.e., misidentifications, unsound locality data, etc.), then non-literature sources would not encounter those species. The success rate of literature data to capture the highest number of "ever recorded" species could then be interpreted as the result of its own poor quality. Nevertheless, most of these published records are here considered "reasonable" because (a) they represent western Atlantic species that are known from neighboring waters (see below), (b) the volume of literature on south Florida mollusks is particularly extensive and relatively well studied (evidenced by the paucity of new species discovered by this study), and (c) the literature survey for this project can (again, but now more confidently) claim to be "exhaustive", having canvassed relevant as well as spurious publications for more than a decade. While additional fieldwork and collections-based research are, theoretically, open-ended, there is a finite number of published works with available data, and we believe we are fast approaching that limit. We therefore expect the relative species-list-recovery success of literature data to decline in the future, as fieldwork and collections studies continue to validate otherwise literature-only records.

To interpret the rise of literature over museum data, we analyzed the composition of literature in the previous and present analyses. We have continued to use the category "gray literature" to encompass unpublished theses and dissertations, shell club and other newsletters, agency reports, and other informal checklists. The previously used category "traditional literature" is now divided into books (which usually provided Florida Keys records only as part of species ranges) and peer-reviewed (or, for the older literature, mainstream-journal) articles. We examined both the number of works within each category and the number of records generated by the works in each category.

While gray literature contributed a substantial proportion of the records in the previous analysis (Mikkelsen & Bieler, 2000: fig. 1b), its contribution to the present, expanded dataset is dramatically greater. In this analysis, the proportion of gray literature to total works was nearly equal to that of peer-reviewed literature (Fig. 12), yet it recovered 24% more of the total species list than did peer-reviewed literature (Fig. 11), and contributed almost three-quarters of the total literature-based records (Fig. 13). The importance of such "non-traditional" literature for regional biodiversity research thus cannot be overstated, although these data can be difficult to vet. As production costs and editorial attitudes have driven the wealth of raw data out of mainstream publications, these "gray" means of data deposition have become vital. The recent trend of providing data-rich electronic supplements (see, for example, Brewster-Wingard et al., 2001), *if permanently archived*, promises to help the peer-reviewed body of literature regain its information content.

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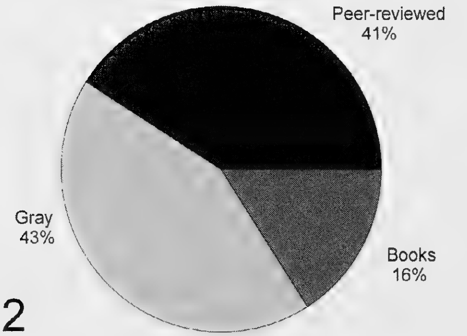

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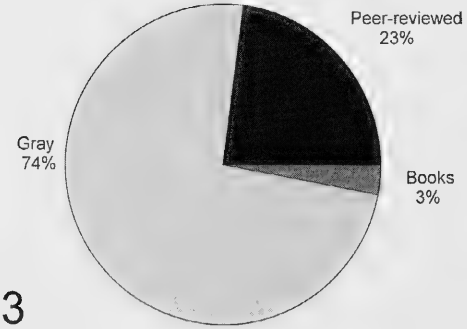

FIGS. 12, 13. Percent of records. FIG.12: From peer-reviewed, book, and gray literature as part of the total works examined; FIG. 13: Total database records generated in this analysis.

In view of the strength of literature-derived data, the question is posed whether the Florida Keys bivalve species list could have been accurately built through literature search alone. In general, the answer is positive but qualified; such a search can only be effective if gray literature is included and *can be adequately interpreted*. Gray literature remains the most problematic to access and often is taxonomically outdated, and could not have been adequately interpreted without a sound foundation in bivalve taxonomy and specimen-based knowledge of the fauna in question.

187 (48%) of the 389 species were found by all three data sources (museum, literature, and original collecting; "UML" in Table 1). Five species remain unique to our original collections and are thus new records for the Keys as a result of this survey: *Mytilopsis leucophaeata, Ennucula tenuis, Cardiomya ornatissima, Gari circe,* and *Tivela floridana.* Reflecting the source proportions, 17 species (4%) were unique to museum collections and 59 species (15%) were unique to literature data.

Original Collection Data: There are at least two approaches to evaluate how close an original field study comes to capturing all available species. One method is to examine the number of singletons and doubletons (in this case, species recorded only once or twice in our database). Coddington et al. (1996, analyzing spiders) have argued that the number of such extremely rare taxa should decrease as sampling effort increases (although this could be argued against because original mollusk collecting, especially including empty shells, often increases the taxon list with time; pers. obs.). 84 species (21%) appear as singletons (56) or doubletons (28) in this database (Table 1). Of these, 35 are not true singletons or doubletons, because they are represented by additional data sources (e.g., records indicating "Florida Keys" only), although only one or two, respectively, was sufficiently robust to score for the database. 49 true singletons and doubletons (12.5%) thus remain, and although no "threshhold of sufficient sampling" was suggested by Coddington et al. (1996), this can be interpreted as a relatively low percentage of the fauna. This is considerably less than the 20% singletons found by Bouchet et al.'s (2002) New Caledonia field study. A closer look at the singletons revealed that in some cases, their collection records clearly explain the lack of re-collection. Of the 28 singleton lots, 13 (9 museum, 4 literature) are from offshore dredge samples and are thus not routinely captured by shallow-water collecting; this undersampled faunal component is being addressed by an ongoing deeper-water soft-bottom transect study (in prep.). Four are from a highly specialized habitat (wood) that is rarely sampled; these are shipworms (Teredinidae), all of which are represented by fewer than three records in our database, which clearly is an artifact of sampling.

An alternate approach to evaluating how well an original field study captures all available species is to look at species-accumulation or collectors curves. In this method, the assumption is that a curve approaching zero slope indicates that most "possible" taxa have been captured. This has been demonstrated to work well with standardized collecting efforts in reasonably homogenous areas of habitat (e.g., Colwell & Coddington, 1994). However, such standardization is not feasible when exploring, as in our case, an entire marine molluscan fauna and its great range of inhabited ecological niches. Here, species accumulation strongly reflects changes in effort and technique over time (see below). In addition in this case, these curves are a useful tool because of the unusual circumstance that we "know" the potential total fauna from the composite dataset drawn from archived collections and 160 years of literature data. The difference between the observed endpoint of the curve and its expected ceiling (= all "ever recorded" species) could be indicative of undersampling, loss of species over time (which could mean a small- or large scale change of occurrence), or taxonomic problems/other errors in the ceiling records. For example, 17 species are known solely from Dall (1889a), listed as "FK, archibenthal, 50–800 fms" with unknown supporting source data: *Abra longicallis americana, Bentharca sagrinata, Cyclopecten thalassinus, Juliacorbula cubaniana, Limatula setifera, Limatula subauriculata, Limea bronniana, Cratis antillensis, Myonera lamellifera, Nuculana vitrea, Pandora glacialis, Pectinella sigsbeei, Poromya albida, Propeamussium cancellatum, Thyasira grandis, Varicorbula krebsiana,* and *Yoldia liorhina*. These species could actually originate from depths beyond our project depth limit (300 m or 164 fms), and can thus be considered in most need of verification.

Our flattened species accumulation curve points to a relative completeness of the collecting efforts. Accordingly, a log-normal frequency distribution of occurrences could be expected. However, the abundance frequency of Florida Keys bivalve species is not log-normal (Fig. 6), but strongly right-skewed, with a median occurrence of 10 and rare taxa very numerous.

To analyze our original collecting efforts versus the total known species list, species accumulation curves were generated for all four Keys subregions as well as the entire study region; only those for the entire region (all-original, live-original, dead-original) are presented here (Fig. 14). After ten years of sampling, only 207 species (53% of total) have been collected in our original samples of all-original material. The dead-original curve closely emulates the all-original curve, indicating, as do the raw numbers [5768 records, 4582 (79.4%) dead, 1186 (20.5%) live], that these two datasets are essentially identical; only seven species were never collected dead. Three abrupt increases (Fig. 14, arrows) can each be attributed to a new collecting method or new location: scuba operations (July 1995), the first Dry Tortugas cruise (April 1997) and the first samples on the Pourtales Terrace (July 2001); the reduced expression of these three events in the live species accumulation curve (Fig. 14) emphasizes the paucity of live-collected records. These past records predict that additional jumps in the curve will accompany each new data source as long as we can identify new ways or places to sample. Two gaps to be filled have already been mentioned: floating wood (for shipworms) and deep-water soft substrata. The transect study mentioned above (in prep.) has already proven its worth in this regard: even in its early stages of data processing, 29 bivalve species have been added to the Florida Keys checklist.

Examination of the species accumulation curve begs the question: could we have stopped collecting sooner and still accomplished our goal to understand the bivalves of the Florida Keys? This depends on the percent "completeness" that one considers adequate, but is in fact a circular question, dependent on hindsight applied to the ten-year results. Fig. 14 shows that the curve leveled off substantially after the first Dry Tortugas cruise in April 1997, approximately three years into our study, when 75% of the total collected

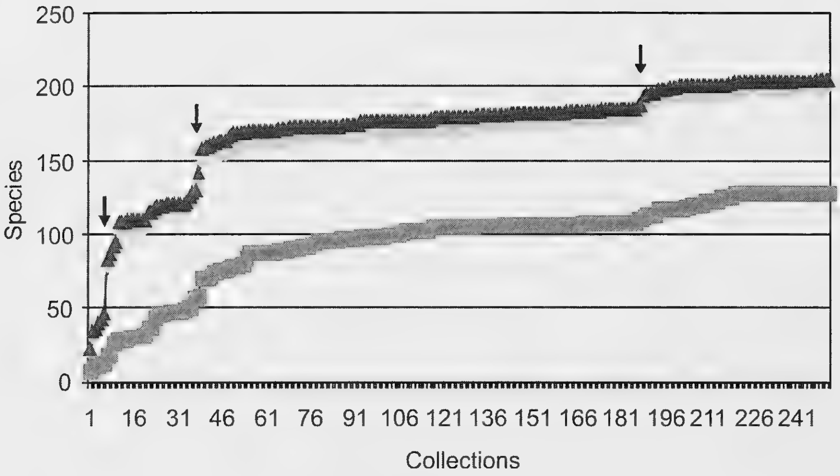

FIG. 14. Florida Keys bivalve species accumulation curves (recorded species list versus original collecting events for Florida Keys) for all-original (—▲—), live-original (—■—), and dead-original (— —) records.

fauna had been captured; note that this is less than 40% of the expected total. 90% of the collected total was not achieved until April 2001, and 95% was not reached until one year later (April 2002) after a second Dry Tortugas cruise that included sampling Pourtales Terrace.

Ecological studies most often only consider live-collected records, although we and others have argued earlier in strong support of including empty mollusk shells in biotic surveys. To press this point further, if we consider live original records only in this analysis (which comprise 20.5% of the total original records), the percent recovery of the total species list is reduced by nearly 20% to only 34% of the total (131 species) – even despite the ten-year sampling period (Fig. 14). Nevertheless, analyses of these live-only records reproduce the same general pattern in bayside, shallow-oceanside, and deep-oceanside groups found in the full-data analysis (Fig. 15; compare to Fig. 7), giving further credence to use of empty shells in such analyses.

A final advantage of the ten-year results is the ability to judge the effectiveness of Rapid Assessment (RAP) methods, such as have become standard and in fact critical to the speedy generation of diversity data necessary for environmental decision-making (Wells, 2002). Embedded in the dataset are four samples of live and dead specimens (FK-260, 261, 262, 264), taken during a four-day period (10–11 and 13 August 1999) from Looe Key Reef (Lower Florida Keys, ca. 24°32.809'N, 81°24.158'W). These samples came from diverse habitats, including spur-and-groove reef formation, rubble zone, and *Thalassia* seagrass beds, all in waters of 2–8 m depth, and include three components: visually located specimens, a sample of dead coral rock to be cracked for boring bivalves, and a sediment sample to be sorted for sand dwellers and smaller species. Together they can thus be considered a Rapid Assessment sample in terms of temporal and spatial dimensions, but are robust in covering a wide range of habitats and collecting methods. Looe Key has been historically well-sampled, and the database indicates a total expected species richness of 104 species from 267 records (excluding those from the four RAP samples). Bivalves recorded from our four "rapid" Looe Key samples in August 1999 captured a total of 96 records and 62 species, or 60% of the expected total (Fig. 16); 11 of these species had not been previously recorded from Looe Key. Contrasted with the results of the ten-year study for the entire Florida Keys, this four-day study at Looe Key captured a higher percentage of its expected fauna; we therefore consider these RAP samples as effective. In contrast, live-collected specimens in these four RAP samples recovered only 20 species (none of which were new records), or 19% of the expected fauna, which cannot be considered effective in representing bivalve diversity at this site. With regard to judging the success of RAP

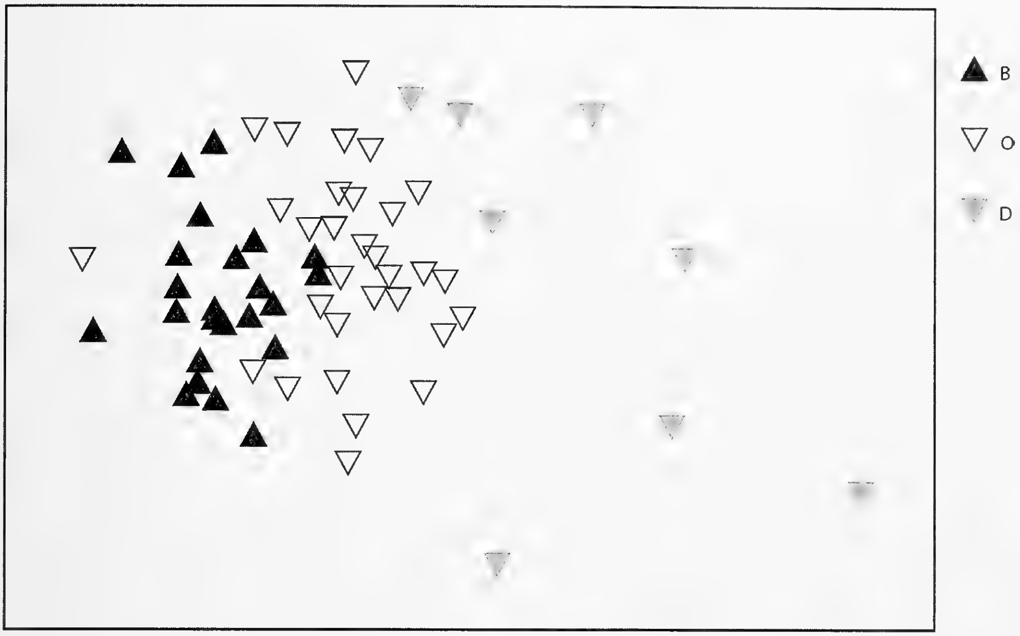

FIG. 15. Two-dimensional MDS ordination of all *live-collected station data*, coded as bayside (B), shallow-oceanside (O), and deep-oceanside (D). Based on standardized (percentage-transformed) data and Bray-Curtis similarities (stress = 0.17). ANOSIM: global R = 0.443, p = 0.001. Compare to Fig. 7.

sampling of marine bivalves, these results underscore the great value of including empty shells in generating statements of species richness. In such studies, we further stress the necessity of physical samples taken from multiple habitat types, despite the substantial commitment in processing time that they require.

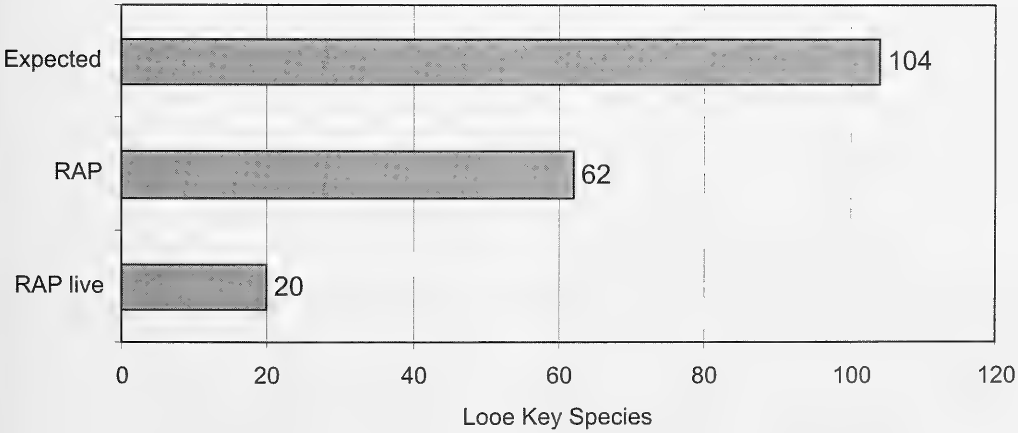

FIG. 16. Species richness of marine bivalves at Looe Key Reef, including total recorded (= expected) species based on the total ten-year database, total species recovered by RAP samples (FK-260, 261, 262, 264) taken over a four-day period in 1999, and live-collected species from the same RAP samples.

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CRITICAL CATALOG AND ANNOTATED BIBLIOGRAPHY OF MARINE BIVALVE RECORDS FOR THE FLORIDA KEYS

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ABSTRACT

Literature data contributing to a biodiversity survey of bivalve species of the Florida Keys are presented in the form of 361 annotated references and a documented species list. 389 species are recorded as identified to at least the species level; all except ten species can be traced to at least one literature citation. Thirty-one nominal species-level taxa were originally described from Florida Keys material or had their type localites designated as such. Annotations on synonyms, confirmed or suspected misidentifications, and a discussion of problematic geographic information are included, as tools for accessing and interpreting the full body of literature, including 19th century works and 91 entries of "gray" literature (i.e., non-peer-reviewed reports, newsletters, unpublished dissertations, websites, etc.). This paper provides supporting data for an analysis of the bivalve fauna of the Florida Keys, based on a new database of over 12,000 original, museum, and literature records, included elsewhere in this volume.

INTRODUCTION

Biodiversity surveys rely on thorough reviews of pertinent literature, in the context of original field observations and studies of existing collections. As in the case of historic collections, literature data can provide temporal depth (e.g., showing the appearance or disappearance of taxa in a given region), taxonomic insight, and distributional information. However, literature data must be reviewed and interpreted (especially when not accompanied by verifiable illustrations or actual voucher specimens), because its information can be suspect due to the variable taxonomic expertise of authors as well as changes in nomenclature over time.

The Florida Keys is a highly diverse region, heavily impacted by human-induced change. For most of its invertebrate fauna, few if any baseline studies of species-level diversity exist. However, for more than a century, the Keys have served as a source region for numerous academic studies of mollusks and have been extremely popular with the shell-collecting community. This has led to a steady but extremely scattered outflow of formal and informal publications containing distributional and natural history data for the bivalved mollusks of this region. The current catalog provides access to this wealth of information, which cumulatively can contribute to our understanding of past and present diversity. We have captured and critically reviewed the species records in each work, fully documenting any taxonomic interpretations of synonymy and/or potential misidentification; each species record and its interpretation, if any, are thus open to subsequent corroboration or falsification. Our goals for this literature review of molluscan diversity data are thus (1) to compile the literature in an accessible format, (2) to interpret, and if necessary correct, the taxonomic information, (3) to interpret, and if necessary correct, the geographic information, and (4) to cross-reference the data, allowing taxonomic/geographic access by species.

Most works, by design or necessity, take a cumulative approach in reporting distributional data and combine individual records into broad distibutional statements. In the case of western Atlantic taxa, the given distribution often indicates the northern- and southernmost extremes of occurrence, with little or no indication whether this reflects merely two collecting events, spans a continuous area of distribu-

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tion, or is based on extreme chance occurrences of an otherwise more restricted range (the latter case an example of how summarizing accumulated information can dilute meaningful biogeographic data). The current work takes the opposite approach, where possible "deconstructing" literature data into occurrence information for concrete smaller subregions within the Florida Keys (i.e., Upper, Middle, and Lower Florida Keys, and Dry Tortugas).

In an earlier analysis (Mikkelsen & Bieler, 2000), we evaluated the relative contribution of the different types of source data (original collections, museum records, and literature) toward capturing species-level Florida Keys bivalve diversity. The literature review included book publications (e.g., Johnson, 1934; Abbott, 1974), entire runs of scientific serials (e.g., *American Malacological Bulletin, Bulletin of Marine Science, Journal of Molluscan Studies, The Nautilus, The Veliger*), shell club newsletters (e.g., *American Conchologist, Texas Conchologist*), the published papers of malacologists known to have worked in the Keys (e.g., Pilsbry, McGinty, Houbrick), and relevant agency reports (e.g., Lyons & Quinn, 1995; Vittor & Associates, 1998). Of all the bivalve species ever recorded from the Keys, literature data documented 73% of the total known species list, including 38 species not otherwise reported. "Gray" literature (non-peer-reviewed reports, newsletters, unpublished dissertations, websites, etc.) played a significant role in this contribution; traditional literature (books and peer-reviewed journals) recovered only 44% of the list, that is, effectively missing 56% of the known diversity. We concluded that multiple sources (including literature) are most effective in producing a biotic inventory, although traditional literature was viewed as the least effective single resource.

Since completion of the earlier survey, we have continued our research toward a complete faunistic analysis of Florida Keys bivalves. Results of this expanded study, based on a new database of more than 12,000 original, museum, and literature records, is included elsewhere in this volume (Bieler & Mikkelsen, 2004). This catalog represents an annotated bibliography of the literature sources included in this and the earlier survey, now expanded four-fold to comprise 361 bivalve literature sources, with special focus on gray literature data. Significant additions include one of the earliest surveys of Florida Keys bivalves (22 fully-identified species; Calkins, 1878), the earliest comprehensive survey (87 species [by today's taxonomic criteria]; Simpson, 1887–1889), and Lermond's (1936) checklist with 216 species, which although fraught with outdated nomenclature, surpasses the only other, much more recent, extensive compilation (163 species; Lyons & Quinn, 1995). It is noteworthy that both of these last two extensive compilations are gray literature; the present database includes 1886 records from 91 separate pieces of gray literature [marked below by superscript "G"].

For the purpose of this study, we have included references to species only if specifically listed from the Florida Keys (i.e., excluding those with broadly stated distributions, for example, from Georgia to Venezuela, which theoretically could also include the Florida Keys). We define the Florida Keys as the waters surrounding the entire island chain from Broad Creek (about 25°21'N, 80°15'W) at the northern end of Key Largo (including Card Sound but not Biscayne Bay, southwest of but not including Old Rhodes Key) to slightly west of the Dry Tortugas (83°30'W). The borders between Keys regions are here defined as between Craig Key and Fiesta Key (Upper Keys/Middle Keys), between the Seven-Mile Bridge and Little Duck Key (Middle Keys/Lower Keys), and between Rebecca Shoal and the Dry Tortugas (Lower Keys/Dry Tortugas), with Dry Tortugas standing alone as a fourth region. A tangential east-west line was drawn through Florida Bay in the Upper and Middle Keys (at the levels of, from east to west, the Nest Keys, Russell Key, and the northern limit of Rabbit Key Basin), eliminating what is more properly considered the southern end of the Florida Everglades. Oceanward, the depth limit was set at the 300 m (= 164 fms or 984 ft) isobath, which includes the historically and biologically important Pourtales Terrace. Our study area thus encompasses (and exceeds) the Florida Keys National Marine Sanctuary, as well as all state and county parks, reserves, and management areas of this region, with the excpetion of the Biscayne Bay area and the northern parts of the Everglades National Park.

Most of the 19th century records and the majority of deepwater collections off the Florida Keys stem from U.S. government surveys. The U.S. Coast Survey Steamers *Corwin* (1867, collections by L. F. Pourtales), *Bibb* (1868–1869, Pourtales; 1872, W. Stimpson), *Bache* (1872, Stimpson), and *Blake* (1877–1878, A. Agassiz), and the U.S. Fish Commission

Steamer *Albatross* (1885) all sounded and dredged/trawled off the Keys. Their station records are generally well documented (e.g., S. Smith, 1889; Townsend, 1901). Most named localites (e.g., Key West, Looe Key Reef, Carysfort Reef, etc.), even if unaccompanied by geodetic coordinates, are likewise clearly part of the Florida Keys record. However, the identities of certain named localities remain problematic:

First, Gordon Key (a single unnumbered site sampled at 68 fathoms (124 m) by the U. S. Coast Steamer *Bache* in the 1870s; Dall, 1881, 1886; repeated from Dall by four subsequent authors, see below) is by all accounts part of the Florida Keys (Dall, 1903b; Johnson, 1934). However, no locality of that name exists to our knowledge on any chart or in any gazetteer, so its relative location within the Keys is unclear. It is quite possible that the name is a corruption of Garden Key, the site of the U. S. Civil War era Fort Jefferson (and a popular ship anchorage at the time) in the Dry Tortugas (J. Clupper, pers. comm., August 2003). According to our records, W. H. Dall never specifically mentioned Garden Key in his molluscan reports until 1889 (original description of *Lippistes acrilla* Dall 1889: 391), so it is plausible that he earlier miswrote the island's name. S. Smith's (1889) official compilation of dredging stations by the U.S. Coast Survey steamers during this period shows the *Bache* operating off the Dry Tortugas in 1872, however, no 68 fathom station is evident; the *Blake* (the primary source of mollusks described in Dall's 1881 and 1886 reports) likewise is not recorded to have sampled any stations at this specific depth. S. Smith (1889) indicated a single 68 fathom station sampled by the *Bibb* in 1869, but this is charted near Alligator Reef in the Upper Keys. Without more definite data on the vessel and date of the expedition during which this deepwater station was collected, its location remains enigmatic. "Gordon Key" is the type locality of *Corbula cymella*.

Another issue involves the confusion of the often-cited locality "off Sombrero", which might refer to Sombrero Key/Reef in the Middle Florida Keys. "Off Sombrero, 54 fms" reported by W. H. Dall (1881, 1886) as a station collected by the *Blake* (or *Bache*?) sometime during 1877–1879 has been interpreted as pertaining to the island of Sombrero in the western Caribbean, east of the Virgin Islands (E. V. Coan, in Turgeon et al., 1998: 189). (The situation is further complicated by the fact that the station was unnumbered, and no 54-fm station, from either Sombrero locality, appears in S. Smith's (1889) compilation of stations dredged by the *Blake*.) The 54-fm Sombrero station was never called "Key" by Dall, although it was later and probably erroneously called Sombrero Key by Clench & Smith (1944) and Pulley (1952). In six bivalve accounts by Dall, the 54-fm station is combined with one at 72 fms (as "off Sombrero, 54–72 fms"), lending support to their co-identity if not their exact location. The uncertainties of these data and their source vessel led us to compare other contemporary expedition accounts, but these provided little additional understanding: Nine *Bibb* stations (sta. 5P–13P) were definitely sampled off Sombrero Reef in April-May 1868, but depths ranged from 111–517 fms (Pourtales, 1871: 169; Peirce & Patterson, 1880: 1; S. Smith, 1889: 958; with several of these stations on the official 1868 survey chart [No. 10] of the Straits of Florida). All 1872 expedition stations of the British Steamer *Challenger* from "off Sombrero" are referable to the Caribbean island (S. Smith, 1889: 973). In January of 1879, the *Blake* operated in the vicinity of the island of Sombrero (sta. 140–141), listed by S. Smith (1889: 967) as "off Virgin Gorda," and again at much deeper depths of 861 and 1,097 fms. In November of 1887, the *Albatross* sampled a single station (2750) south of Sombrero Island in 496 fms (Townsend, 1901: 403). For purposes of this study, both 54 and 72 fm stations listed by Dall as "off Sombrero" (the type locality of *Lucina sombrerensis, L. leucocyma, Nemocardium peramabile,* and *Myrtea compressa*), have been excluded from Florida Keys records.

Three other localities hint at potential locality confusion but have been retained in this survey for lack of more conclusive data. (1) Turtle Harbor is a 8–9 m (25–30 ft) anchorage just inside Carysfort Reef in the Upper Florida Keys, yet Turtle Harbor at 40–50 fms (73–91 m) was listed by Hayes (1972) and Boss (1972) for two species (*Pteria colymbus, Semele bellastriata*). Although this could refer to a station offshore of the Upper Florida Keys (as in the case of *Eolis* sta. 58; Bieler & Mikkelsen, 2003), there are at least two other Turtle Harbors in the Caribbean: in the Bahamas (Dall, 1886; Pulley, 1952), and off Isla de Utila, Honduras (a popular scuba diving site, with a wall to 300 m). (2) Long Key is a large island in the Middle Florida Keys, between Fiesta Key and Duck Key, but also refers to part of Bush Key in the Dry Tortugas (Clupper, 2003), and to the island on which the city of

St. Petersburg Beach, Florida, lies, adjacent to Boca Ciega Bay. (3) Three Sand Keys are recorded for the Florida Keys: as the site of an historical lighthouse seven miles southwest of Key West, as a former name for Hospital Key in the Dry Tortugas, and as one of the Molasses Keys oceanside of the Seven-Mile Bridge (Clupper, 2003). At least one additional Sand Key exists in Florida, off Clearwater Beach in Pinellas County.

In total, 389 bivalve species are included in this diversity survey, all but ten of which can be traced to at least one literature citation (those ten known to occur in the Florida Keys, but not previously recorded as such, are included in the catalog without following references). An additional 57 taxa are recorded from literature identified to the genus level, plus an additional 25 to family level; most of these probably represent previously listed species, although a few (e.g., *Cymatioa* sp., *Semierycina* sp.) are probably otherwise unrepresented. An additional four species remain of uncertain taxonomic status.

Thirty-one nominal species-level taxa were originally described from Florida Keys material or had their type localites designated as such:

Amphidesma laeta "Adams" Reeve, 1853 [now regarded as a synonym of *Semele purpurascens* (Gmelin, 1791)], had Key West designated as its type locality by Boss (1972).

Amphidesma variegata Lamarck, 1818 [now regarded as a synonym of *Semele purpurascens* (Gmelin, 1791)], had Key West designated as its type locality by Boss (1972).

Anadara springeri Rehder & Abbott, 1951 (now regarded as a synonym of *A. baughmani* Hertlein, 1951), from off the Dry Tortugas.

Arca (*Barbatia*) *balesi* Pilsbry & McLean, 1939 [now regarded as a synonym of *Fugleria tenera* (C. B. Adams, 1845)], holotype from Missouri Key (paratypes from Key West).

Argopecten irradians taylorae Petuch, 1987 [now regarded as a synonym of *A. irradians concentricus* (Say, 1822)], from Rabbit Key Basin [Florida Bay, off Long Key].

Asthenothaerus balesi Rehder, 1943a, from Missouri Key.

Cardium (*Fulvia*) *peramabilis* Dall, 1881 (now *Nemocardium*), from various localities including *Blake* station 9 (111 fms) off Sand Key, and station 26 (110 fms), west of the Dry Tortugas. Subsequent lectotype selection (Clench & Smith, 1944) restricted the type locality to off Yucatan, *Blake* station 36.

Ctenoides sanctipauli Stuardo, 1982, with original (but not type) material including a specimen from an *R/V Eolis* station at Sand Key Reef.

Condylocardia floridensis Pilsbry & Olsson, 1946 [now regarded as a synonym of *Carditopsis smithii* (Dall, 1896)], from Ohio Key.

Corbula cymella Dall, 1881, a Florida Keys endemic species, known only from 68 fms off "Gordon Key".

Cumingia tellinoides vanhyningi Rehder, 1939, from Lower Matecumbe Key.

Cytherea (*Ventricola*) *strigillinus* Dall, 1902 (now *Circomphalus*), from off Key West.

Dosinia floridana Conrad, 1866 [now regarded as a synonym of *D. elegans* (Conrad, 1846)] from "Florida Keys, Gulf of Mexico".

Jagonia orbiculata var. *filiata* Dall, 1901 [a named form of *Ctena orbiculata* (Montagu, 1808)], from Florida Keys, deep water.

Jagonia orbiculata var. *recurvata* Dall, 1901 [a named form of *Ctena orbiculata* (Montagu, 1808)], from Florida Keys, deep water.

Modiola tulipa var. *nigra* Calkins, 1878 [now regarded as a synonym of *Modiolus americanus* (Leach in Leach & Nodder, 1815)], an unrayed form from Key Vaccas (*sic*).

Nucula calcicola Moore, 1977, from Key Largo.

Ostrea weberi Olsson, 1951 (now *Teskeyostrea*), from Key West (type locality) and Grassy Key.

Pecten (*Plagioctenium*) *gibbus* var. *amplicostatus* Dall, 1898 (now regarded as a subspecies or variety of *Argopecten irradians*), Pliocene to Recent, ranging from west of the Mississippi River, on the Texas coast, and south to Cartagena, Colombia; no type locality nor type specimen was specified. Schuchert et al. (1905) subsequently listed cotypes (USNM 154186) from Pliocene deposits of Monroe County, Florida (only part of which lies in the Florida Keys); USNM label data more specifically places the material from the Caloosahatchie (*sic*, Caloosahatchee) beds of Monroe County (T. Waller, pers. comm., July 2003). Waller (1969) explained the complicated history of type material for this species, selecting a lectotype from another type lot, USNM 106990, from Texas; he considered the Monroe County fossil lot (USNM 154186) as an unnecessary subsequent designation without nomenclatural standing. Waller (1969) furthermore rejected all evidence of this species from the Pliocene of Florida [claiming all examined specimens from this locality were *P. irradians concentricus* (Say, 1822), effectively removing this taxon from this list of those originally described from the Florida Keys.

Pecten (*Chlamys*) *imbricatus mildredae* F. M. "T." Bayer, 1941 (now *Caribachlamys*), ranging from Biscayne Bay to Dry Tortugas and Bahamas; no type locality was originally specified. Although the author (Bayer, 1942) subsequently designated Biscayne Bay as the type locality, the holotype (USNM 598977) is from Long Key Reef, Dry Tortugas (Waller, 1993: fig. 9d, e).

Pecten (*Euvola*) *tereinus* Dall, 1925 [now regarded as a synonym of *Euvola chazaliei* (Dautzenberg, 1900)], from off Key West.

Pitaria cordatus Schwengel, 1951 (now *Pitar*), from Key West.

Pseudamusium strigillatum Dall, 1889b (now *Palliolum*), from "the Antilles and Florida Reefs".

Pseudochama inezae F. M. Bayer, 1943 (now *Chama*), from Carysfort Reef.

Syndosmya lioica Dall, 1881 (now *Abra*), from various localities including *Blake* station 9 (111 fms) off Sand Key, station 5 (229 fms) south of the Marquesas Keys, and off Sand Key (30 fms). Boss et al. (1968: 188) subsequently gave "20 miles W of Florida; and others" as the type locality.

Tellina obliqua Wood, 1815 (*non* J. Sowerby, 1817) [now regarded as a synonym of *Semele purpurascens* (Gmelin, 1791)], had Key West designated as its type locality by Boss (1972).

Tellina (*Angulus*) *paramera* Boss, 1964 (now *Angulus*), from various localities, including from off American Shoals (45 fms), Key West, Dry Tortugas (15 fms); type locality is Miami Beach, Florida.

Tellina (*Angulus*) *probrina* Boss, 1964 (now *Angulus*), from various localities, including from off Sombrero Key, off Sand Key, Key West, and Dry Tortugas; type locality is off Fowey Light, Dade County, Florida.

Teredo (*Zopoteredo*) *clappi* Bartsch, 1923, from off Key West, from timber.

Transennella stimpsoni Dall, 1902, from Cape Hatteras, Egmont Key, and south to Key West. Boss et al. (1968) subsequently gave Egmont Key (at the mouth of Tampa Bay, Hillsborough County, western Florida) as the type locality, based on USNM 54100.

Venus purpurascens Gmelin, 1791 (now *Semele*), had Key West designated as its type locality by Boss (1972).

Names listed in the annotations are as used in the referenced work. Abbreviations used include: ANSP, Academy of Natural Sciences of Philadelphia; DT, Dry Tortugas; ^{G}, "gray" literature; LFK, Lower Florida Keys; MCZ, Museum of Comparative Zoology; MFK, Middle Florida Keys; UFK, Upper Florida Keys; USNM, National Museum of Natural History [United States National Museum]; *, literature included in earlier analysis (Mikkelsen & Bieler, 2000); |, "Florida Keys" literature or taxa excluded from this analysis (for geographical reasons) or former taxonomic names with reference to epithet in present use.

ANNOTATED BIBLIOGRAPHY OF WORKS CONTAINING REFERENCES TO FLORIDA KEYS BIVALVES

ABBOTT, R. T., 1954, *American seashells*. Van Nostrand, New York. xiv + 541 pp., 40 pls.
With distributions including Florida Keys (or specific localities): *Aequipecten (Plagioctenium) gibbus nucleus, A. lineolaris, A. phrygius, Chione (Timoclea) grus, C. (Lirophora) paphia, Cumingia coarctata, Isognomon bicolor, Noetia (Eontia) ponderosa, Nucula crenulata, Pitar (Pitarenus) cordata, Pseudocyrena floridana, Strigilla pisiformis, Tellina (Eurytellina) angulosa, T. (Scissula) candeana, T. (Eurytellina) punicea, Trachycardium magnum.*

ABBOTT, R. T., 1958, The marine mollusks of Grand Cayman Island, British West Indies. *Monographs of the Academy of Natural Sciences of Philadelphia*, 11: 138 pp., 5 pls. [second printing, October 1967, also contains 16 unnumbered pages of common names]
Specifically occurring in the Florida Keys: *Americardia guppyi, Barbatia tenera, Cumingia coarctata, Trachycardium magnum.*

ABBOTT, R. T., 1961, *How to know the American marine shells*, rev. ed. A Signet Book, New American Library, New York. 222 pp., 12 color pls.
With distributions including Florida Keys (or specific localities): *Antigona listeri, Pseudocyrena floridana, Trachycardium magnum*. An index list for the common species for "Miami to Key West" also includes *Noetia ponderosa, Macrocallista nimbosa* [*Mytilus californianus* and *Macoma calcarea* are also included here, obviously incorrectly].

ABBOTT, R. T., 1968, *Seashells of North America: a guide to field identification*. Golden Press, New York. 280 pp.

Map of North America (p. 35) showing faunal provinces includes Florida Keys in Caribbean Province; text (p. 37) refers specifically only to Lower Keys. With distributions including Florida Keys: *Noetia ponderosa, Strigilla pisiformis, Tellina candeana.*

ABBOTT, R. T., 1970, *How to know the American marine shells*, rev. ed. A Signet Book, New American Library, Bergenfield, New Jersey. 222 pp., 12 color pls.

Specifically occurring in the Florida Keys: *Antigona listeri, Pseudocyrena floridana.* This book also has an interesting zoogeographic section, listing "Shells by Localities". Also, with distributions including Key West: *Macrocallista nimbosa, Noetia ponderosa* (also indicated as occurring in this region, obviously in error, are *Mytilus californianus* and the northern *Macoma calcarea*).

*ABBOTT, R. T., 1974, *American seashells: the marine Mollusca of the Atlantic and Pacific coasts of North America, 2nd ed.* Van Nostrand Reinhold, New York. 663 pp., 24 pls.

With distributions including Florida Keys (or specific localities): *Aequipecten phrygium, Americardia guppyi, Argopecten irradians, Asthenothaerus balesi, Chama sarda, Chione* (*Chione*) *pubera, Codakia* (*Ctena*) *pectinella, Isognomon bicolor, Lima albicoma, Lucina* (*Lucinisca*) *muricata, Myrtea* (*Eulopia*) *sagrinata, Nuculana pusio, N. verrilliana, Ostrea weberi, Periploma anguliferum, P. tenerum, Pitar* (*Pitarenus*) *cordatus, Plectodon granulatus, Pteria longisquamosa, P. vitrea, Strigilla* (*Strigilla*) *gabbi, Tellina* (*Angulus*) *versicolor, Thracia corbuloides, Trachycardium* (*Acrosterigma*) *magnum, Transennella cubaniana, Ventricolaria rigida.*

ABBOTT, R. T. & P. A. MORRIS, 1995, *A field guide to shells, Atlantic and Gulf coasts and the West Indies.* Peterson Field Guide 3. Houghton Mifflin Company, Boston & New York. 350 pp., 74 pls.

With distributions including Florida Keys (or specific localities): *Aequipecten acanthodes, Periploma anguliferum, Pitar cordatus, Trachycardium magnum.*

AGUAYO, C. G. & M. L. JAUME, 1947a, Pelecypoda – Thracidae (*sic*). *Catalogo Moluscos de Cuba*, no. 126, 1 p.

Asthenothaerus (*Asthenothaerus*) *balesi* with Missouri Key as type locality.

AGUAYO, C. G. & M. L. JAUME, 1947b, Pelecypoda – Arcidae. *Catalogo Moluscos de Cuba*, no. 143, 1 p.

Arca (*Barbatia*) *balesi* with Missouri Key as type locality.

AGUAYO, C. G. & M. L. JAUME, 1948a, Pelecypoda – Semelidae. *Catalogo Moluscos de Cuba*, no. 336, 1 p.

Cumingia vanhyningi with Lower Matecumbe Key as type locality.

*AGUAYO, C. G. & M. L. JAUME, 1948b, Pelecypoda – Veneridae. *Catalogo Moluscos de Cuba*, no. 525, 1 p.

Transennella culebrana from Key West, deep water.

AGUAYO, C. G. & M. L. JAUME, 1948c, Pelecypoda – Veneridae. *Catalogo Moluscos de Cuba*, no. 526, 1 p.

Tivela mactroides from "Cayos de la Florida".

*AGUAYO, C. G. & M. L. JAUME, 1949a, Pelecypoda – Erycinidae. Catalogo Moluscos de Cuba, no. 567, 1 p.

Lasaea rubra from Tortugas.

AGUAYO, C. G. & M. L. JAUME, 1949b, Pelecypoda – Lucinidae. *Catalogo Moluscos de Cuba*, no. 564, 1 p.

Ctena orbiculata forma *recurvata* from "Cayos de la Florida".

AGUAYO, C. G. & M. L. JAUME, 1949c, Pelecypoda – Veneridae. *Catalogo Moluscos de Cuba*, no. 566, 1 p.

Antigona strigillina from Key West.

AGUAYO, C. G. & M. L. JAUME, 1949d, Pelecypoda – Periplomatidae. *Catalogo Moluscos de Cuba*, no. 580, 1 p.

Cochlodesma pyramidatum from "Cayos de la Florida".

AGUAYO, C. G. & M. L. JAUME, 1949e, Pelecypoda – Lucinidae. *Catalogo Moluscos de Cuba*, no. 587, 1 p.

Phacoides muricatus from "Cayos de la Florida".

AGUAYO, C. G. & M. L. JAUME, 1950a, Pelecypoda – Corbulidae. *Catalogo Moluscos de Cuba*, no. 664, 1 p.

Corbula cymella with "Gordon Key" as type locality.

AGUAYO, C. G. & M. L. JAUME, 1950b, Pelecypoda – Chamidae. *Catalogo Moluscos de Cuba*, no. 602, 1 p.

Pseudochama inezae with Carysfort Reef as type locality.

AGUAYO, C. G. & M. L. JAUME, 1950c, Pelecypoda – Condylocardiidae. *Catalogo Moluscos de Cuba*, no. 604, 1 p.

Condylocardia floridensis with Ohio Key as type locality.

AGUAYO, C. G. & M. L. JAUME, 1950d, Pelecypoda – Cuspidariidae. *Catalogo Moluscos de Cuba*, no. 606, 1 p.

Leiomya granulata forma *velvetina* from "Cayos de la Florida".

AGUAYO, C. G. & M. L. JAUME, 1950e, Pelecypoda – Thraciidae. *Catalogo Moluscos de Cuba*, no. 622, 1 p.

Thracia stimpsoni from "Cayos de la Florida".

AGUAYO, C. G. & M. L. JAUME, 1950f, Pelecypoda – Cuspidariidae. *Catalogo Moluscos de Cuba*, no. 626, 1 p.

Cuspidaria rostrata from Sand Key.

AGUAYO, C. G. & M. L. JAUME, 1950g, Pelecypoda – Teredidae. *Catalogo Moluscos de Cuba*, no. 648, 1 p.

Teredo clappi with Key West as type locality.

AGUAYO, C. G. & M. L. JAUME, 1950h, Pelecypoda – Pectinidae. *Catalogo Moluscos de Cuba*, no. 649, 1 p.

Pecten tereinus from Key West.

ALDRICH, B. & E. SNYDER, 1936, *Florida sea shells*. Houghton Mifflin Company, Boston & New York, and The Riverside Press, Cambridge, Massachusetts. ix + 126 pp., 11 pls.

With distributions including Florida Keys (or specific localities): *Arca transversa, Lithophaga bisulcata, Lucina floridana, Tellina radiata.*

*ALLEN, D. M., 1979, Biological aspects of the calico scallop, *Argopecten gibbus*, determined by spat monitoring. *The Nautilus*, 94(4): 107–119.

Key West listed among commercial fishing grounds for the calico scallop. Florida Keys populations postulated as source of larvae recruited to major commercial beds off Cape Canaveral.

ANDREWS, J., 1971, *Sea shells of the Texas Coast*. University of Texas Press, Austin & London. xvii + 298 pp.

With distributions including Florida Keys (or specific localities): *Aequipecten muscosus, Chione grus, Isognomon bicolor, Lioberis castaneus, Lyropecten* (*Nodipecten*) *nodosus, Polycyrena floridana, Noetia* (*Eontia*) *ponderosa, Rocellaria hians.*

ANDREWS, J., 1977, *Shells and shores of Texas*. University of Texas Press, Austin & London. xx + 365 pp.

With distributions including Florida Keys (or specific localities): *Aequipecten muscosus, Chione* (*Timoclea*) *grus, Isognomon bicolor, Lioberis castaneus, Lyropecten* (*Nodipecten*) *nodosus, Noetia* (*Eontia*) *ponderosa, Polymesoda* (*Pseudocyrena*) *maritima.*

ANDREWS, J., 1981a, *A field guide to Texas shells*. University of Texas Press, Austin & London. xxvi + 175 pp.

With distributions including Florida Keys (or specific localities): *Chione* (*Timoclea*) *grus, Isognomon bicolor, Lioberis castaneus, Lyropecten* (*Nodipecten*) *nodosus, Noetia* (*Eontia*) *ponderosa, Polymesoda* (*Pseudocyrena*) *maritima.*

ANDREWS, J., 1981b, *Texas shells: a field guide*. University of Texas Press, Austin. xxvi + 175 pp.

With distributions including Florida Keys (or specific localities): *Chione* (*Timoclea*) *grus, Isognomon bicolor, Lioberis castaneus, Lyropecten* (*Nodipecten*) *nodosus, Noetia* (*Eontia*) *ponderosa, Polymesoda* (*Pseudocyrena*) *maritima.*

ANDREWS, J., 1992, *A field guide to shells of the Texas coast*. Gulf Publishing Company, Houston, Texas. xxiv + 176 pp.

With distributions including Florida Keys (or specific localities): *Chione* (*Timoclea*) *grus, Isognomon bicolor, Lioberis castaneus, Lyropecten* (*Nodipecten*) *nodosus, Noetia* (*Eontia*) *ponderosa, Polymesoda* (*Pseudocyrena*) *maritima.*

ANDREWS, J., 1994, *A field guide to shells of the Florida coast*. Gulf Publishing Company, Houston, Texas. xxiii + 182 pp.

With distributions including Florida Keys (or specific localities): *Aequipecten muscosus, Arca* (*Arca*) *zebra, Chione* (*Timoclea*) *grus, Isognomon bicolor, Lioberis castaneus, Lyropecten* (*Nodipecten*) *nodosus, Noetia* (*Eontia*) *ponderosa, Polymesoda* (*Pseudocyrena*) *maritima, Semele bellastriata.*

^{G}ANTONIUS, A., A. H. WEINER, J. C. HALAS & E. DAVIDSON, 1978, *Looe Key Reef resource inventory*. Florida Reef Foundation, Homestead, Florida. [6 +] 63 pp. + unpag. figures.

Results of a biological inventory of Looe Key, in summer–fall 1977, by Florida Reef Foundation, in support of the proposal of Looe Key as a National Marine Sanctuary. Data collected by visual transect-diving, with some samples taken for subsequent identification. The molluscan species list includes: *Acropsis* (*sic*) *adamsi, Anadara notabilis, Arca imbricata, Arcopagia fausta, Atrina rigida* (one of the most commonly observed species on reef flat), *Barbatia cancellaria, B. candida, Brachiodontes* (*sic*) *exustus, Chama congregata, C. florida, C. sinosa* (*sic*), *Chione intapurpurea, Chlamys imbricata, C. sentis, Codakia orbicularis, Corbula swiftiana, Isognomon radiatus, Lima pellucida, L. scabra, Lioberus castaneus, Lithophaga aristata, L. bisulcata, L. nigra, Modiolus americanus, Phacoides pectinatus,* *Pinctada radiata, Plicatula spondyloidea, Pseudochama radians, Tellina laevigata, Trachycardium isocardia.* Includes a description of the origin of the Florida Keys, their geology, and a physical description of Looe Key.

^{G}ARTMAN, L. P., JR., 1974, *Key West giant map: guide to shells.* Privately published, 1 map.

Figured along with a map of Key West: *Spondylus americanus.*

BALES, B. R., 1940, The rock dwellers of the Florida Keys. *The Nautilus*, 54(2): 39–42.

With occurrence in Florida Keys, and characteristics of burrows: *Botula fusca, Lithophaga antillarum, L. bisulcata, L. nigra, Petricola lapicida, Rocellaria ovata, Rupellaria typica, Spengleria rostrata.* A brief summary (without mention of species names) of Bales' presentation "The Rock Dwellers of the Florida Keys" can be found on p. 5 of: H. R. ROBERTSON, 1940. *Tenth Annual Meeting of The American Malacological Union 1940.* [*Report of the*] *Tenth Annual Meeting, Academy of Natural Sciences, Philadelphia, Pennsylvania, June 17–21, 1940*: 1–11.

^{G}BALES, B. R., 1944, Florida rock dwellers. *Shell Notes*, 1(7): 47–48.

During several winters spent in shell collecting along the Florida Keys, that author has taken alive: *Lithophaga antillarum, L. bisulcata, L. nigra, L. aristata, Botula fusca, Gastrochaena ovata, G. cueniformis* (*sic*), *Rupellaria typica, Petricola lapicida, Coralliophaga coralliophaga, Fundella candeana. B. fusca, Gastrochaena rostrata, C. coralliophaga* are called "decidedly rarer" than others. *F. candeana* is found at only one [unspecified] locality. F. Lyman (ed.) notes immediately following the article that "*Botula Fusca* (*sic*) Gmelin, has long been considered the finest shells to be obtained from the Florida Keys".

^{G*}BARFIELD, B., 1990, Cognate bivalve species of the western Atlantic and eastern Pacific Oceans. *American Conchologist*, 18(2): 20–22.

Papyridea soleniformis figured from Key West.

BARRETT, R. & D. PATTERSON, eds., with technical assistance by the Shell Factory, Ft. Myers, Florida, 1967, *Shells and shelling.* Post Publications, Miami. 64 pp.

Figured in color, with distributions including Florida Keys: *Trachycardium magnum, Aequipecten lineolaris, Tivela mactroides, Chione paphia.*

BARTSCH, P., 1923, Additions to our knowledge of shipworms. *Proceedings of the Biological Society of Washington*, 36: 95–102.

Teredo (*Zopoteredo*) *clappi* n. sp., with the type from "a piece of oak timber, probably an old ship's keel ... at Key West".

^{G}BARTSCH, P., 1937, *An ecological cross-section of the lower part of Florida based largely upon its molluscan fauna.* Pp. 11–25, in: Report of the Committee on Paleontology 1936–1937, Washington Research Council, Division of Geology and Geography. Also available at http://www.aoml.noaa.gov/general/lib/cedardoc.html; last accessed 4 April 2003.

Characterizes ecological units from the Everglades to plankton. Bartsch "purposely avoided mentioning the numerous minute species ... selected those mollusks which force their attention upon the observer in each habitat ... represent the striking element of each association". From mangrove fringe of the Keys on the bay side: *Melina alata, Ostrea floridensis.* From shallow-water sandy stretches beyond the Keys: *Donax variabilis, Dosinia discus, Laevicardium mortoni, Strigilla flexuosa, Tellina alternata.* From shallow water (hard pan) beyond the Keys: *Chama sarda, Glycymeris americana.* From shallow water (mud flats) beyond the Keys: *Cardita floridana, Tagelus gibbus.* From coral reef walls (Miami to Key West, past the Marquesas and Dry Tortugas): *Chama congregata, Lima scabra.* From sandy stretches between the coral walls: *Anodontia alba, Dosinia elegans.* From the continental shelf, 5–100 fms: *Tellina lintea.* From Pourtales Plateau, 90–300 fms: *Arca glomerula, Euciroa elegantissima, Modiola polita, Protocardia peramabilis.* Also includes a listing from the Florida Straits.

*BAYER, [F. M.] "T.", 1941, Notes on Florida Mollusca, with descriptions of two new varieties. *The Nautilus*, 55(2): 43–46, pl. 3 (in part).

Pecten (*Chlamys*) *imbricatus mildredae* nov. var., with distribution to the Dry Tortugas.

*BAYER, F. M., 1942, The type locality and dates of *Pecten imbricatus mildredae* Bayer. *The Nautilus*, 55(3): 106.

Supplement to original description lists Sand Key, Carysfort Reef, and Dry Tortugas. [Biscayne Bay is designated the type locality.]

*BAYER, F. M., 1943, The Florida species of the family Chamidae. *The Nautilus*, 56(4): 116–124, pls. 12–15.

Chama florida, C. macerophylla, C. sarda, C. sinuosa bermudensis, C. s. firma, Pseudochama inezae n. sp.

BEAUPERTHUY, I., 1967, Los mitilidos de Venezuela (Mollusca: Bivalvia). *Boletin del Instituto Oceanografico de la Universidad de Oriente, Cumana*, 6(1): 7–115.
Original material of *Modiolus squamosus* n. sp. includes MCZ specimens from Lower Florida Keys.

^{G}*BENDER, J. F., 1965, Vacation shelling 1965. *Texas Conchologist*, 2(3): 6.
Collected from Pigeon Key to Key West: *Arca* spp., *Arcopagia fausta, Codakia orbicularis.*

^{G}*BENDER, J. F., 1968, Shelling in Florida – 1966. *Keppel Bay Tidings*, 6(4): 1, 4, 7; 7(1): 3–5.
Describes shelling at Bahia Honda, Little Duck Key, Boca Chica, Walkers Island, Shell Island, Pigeon Key, and Key West. Species included are: *Arcopagia fausta, Argopecten nucleus, Caribachlamys sentis, Rangia flexuosa, Spondylus americanus.*

BENSON, A. J., D. C. MARELLI, M. E. FRISCHER, J. M. DANFORTH & J. D. WILLIAMS, 2001, Establishment of the green mussel, *Perna viridis* (Linnaeus, 1758) (Mollusca: Mytilidae) on the west coast of Florida. *Journal of Shellfish Research*, 20(1): 21–29.
Perna viridis is predicted to invade the Florida Keys from its introduction point in Tampa Bay.

BIELER, R., I. KAPPNER & P. M. MIKKELSEN, 2004, *Periglypta listeri* (Gray, 1838) (Bivalvia: Veneridae) in the western Atlantic: taxonomy, anatomy, life habits, and distribution. In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 427–458.
Periglypta listeri from Florida Keys localities [material from this study].

BIELSA, L. M. & R. F. LABISKY, 1987, Food habits of blueline tilefish *Caulolatilus microps*, and snowy grouper, *Epinephelus niveatus*, from the Lower Florida Keys. *Northeast Gulf Science*, 9(2): 77–87.
Gut contents of blueline tilefish (*Caulolatilus microps*) taken off the Lower Keys included: *Laevicardium* sp., *Nuculana* sp.

BIGATTI, G., M. PEHARDA & J. TAYLOR, 2004, Size at first maturity, oocyte envelopes and external morphology of sperm in three species of Lucinidae (Mollusca: Bivalvia) from Florida Keys, U.S.A. In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 417–426.
Codakia orbicularis, Ctena orbiculata, Lucina pensylvanica [material from this study].

^{G}BIPPUS, A. C., JR., 1950, Real shells – real thrills – real fun. *Shell Notes*, 2(1012): 166–173.
Collecting in the Upper Keys by dip net, rock turner, etc., with Frank Lyman aboard the *Junonia*. From the outer reefs off Key Largo, 26 June 1950: *Pecten imbricatus.* From a reef off Tavernier, 29 June 1950: *Pecten sentis.* A partial species list also includes *Arca barbata, A. umbonata, Chione cancellata, Donax* sp., *Laevicardium mortoni, L. serratum, Pteria radiata* (variety?).

^{G}*BOONE, C., 1986, Search and seizure: *Dendostrea frons* found on mangrove roots. *Texas Conchologist*, 22(2): 41–45.
From off Marathon: *Dendostrea frons, Spondylus* sp.

*BOSS, K. J., 1964, New species of *Tellina* from the western Atlantic. *Occasional Papers on Mollusks, Department of Mollusks, Museum of Comparative Zoology, Harvard University*, 2(29): 309–324, pls. 54, 55.
Tellina paramera and *T. probrina* n. spp. from Florida Keys localities.

*BOSS, K. J., 1966, The subfamily Tellininae in the western Atlantic. The genus *Tellina* (part I). *Johnsonia*, 4(45): 217–272.
Museum lots (ANSP, MCZ, USNM) from the Florida Keys cited for: *Tellina* (*Merisca*) *aequistriata, T.* (*Elliptotellina*) *americana, T.* (*Arcopagia*) *fausta, T.* (*Acorylus*) *gouldii, T.* (*Laciolina*) *laevigata, T.* (*Tellinella*) *listeri, T.* (*Laciolina*) *magna, T.* (*Merisca*) *martinicensis, T.* (*T.*) *radiata, T.* (*Phyllodina*) *squamifera.*

^{G}BOSS, K. J., 1967, Evolutionary sequence in *Phyllodina* (Bivalvia: Tellinidae) [abstract]. *American Malacological Union, Annual Reports for 1966*, 33: 21–23.
Tellina (*Phyllodina*) *squamifera* from the Florida Keys.

^{G}BOSS, K. J., 1968a, On the evolution of *Spengleria* (Gastrochaenidae: Bivalvia) [abstract]. *American Malacological Union, Annual Reports for 1967*, 34: 1517.
Spengleria rostrata with its main distribution in the Florida Keys.

*BOSS, K. J., 1968b, The subfamily Tellininae in the western Atlantic. The genera *Tellina* (part II) and *Tellidora. Johnsonia*, 4(46): 273–344.
Museum lots (ANSP, MCZ, USNM) and private collection records (ex Schmidt) from the

Florida Keys cited for: *Tellidora cristata, Tellina* (*Eurytellina*) *alternata, T.* (*Eurytellina*) *angulosa, T.* (*Scissula*) *candeana, T.* (*Scissula*) *consobrina, T.* (*Scissula*) *iris, T.* (*Angulus*) *mera, T.* (*Eurytellina*) *nitens, T.* (*Angulus*) *probrina, T.* (*Scissula*) *similis, T.* (*Angulus*) *sybaritica, T.* (*Angulus*) *tampaensis, T.* (*Angulus*) *texana, T.* (*Angulus*) *versicolor.*

*BOSS, K. J., 1969, The subfamily Tellininae in the western Atlantic. The genus *Strigilla*. *Johnsonia*, 4(47): 345–366.

Museum lots (ANSP, MCZ, USNM) from the Florida Keys cited for: *Strigilla carnaria, S. gabbi, S. mirabilis.*

BOSS, K. J., 1972, The genus *Semele* in the western Atlantic (Semelidae; Bivalvia). *Johnsonia*, 5(49): 1–32.

Material examined includes lots from Florida Keys localities for *Semele bellestriata* (*sic*), *Semele* (*Semelina*) *nuculoides, Semele proficua,* and *Semele purpurascens*. The last species has Key West designated as its type locality (as well as for those of its synonyms *obliqua* Wood, *variegata* Lamarck, and *laeta* Reeve).

*BOSS, K. J. & A. S. MERRILL, 1965, The family Pandoridae in the western Atlantic. *Johnsonia*, 4(44): 181–216.

Museum lots (MCZ, USNM) from the Florida Keys cited for: *Pandora bushiana, P. inflata.*

*BOSS, K. J. & D. R. MOORE, 1967, Notes on *Malleus* (*Parimalleus*) *candeanus* (d'Orbigny) (Mollusca: Bivalvia). *Bulletin of Marine Science*, 17(1): 85–94.

Malleus candeanus listed and figured from several Florida Keys localities.

BOSS, K. J., J. ROSEWATER & F. A. RUHOFF, 1968, The zoological taxa of William Healey Dall. *United States National Museum Bulletin*, no. 287, 427 pp.

In a catalog of Dall's taxa, from type localities in the Florida Keys: *Corbula cymella, Thracia stimpsoni, Cytherea* (*Ventricola*) *strigillina, Pecten* (*Euvola*) *tereinus.*

*BOSS, K. J. & M. L. WASS, 1970, Northward range extension of *Cyclinella tenuis* Recluz. *The Nautilus*, 83(3): 112–113.

Localities cited from Middle, Lower Keys and Dry Tortugas.

BREWSTER-WINGARD, G. L. & S. E. ISHMAN, 1999, Historical trends in salinity and substrate in central Florida Bay: a paleoecological reconstruction using modern analogue data. *Estuaries*, 22(2B): 369–383.

Summary of data on Florida Bay mollusks from earlier reports by Wingard et al. (1995) and Brewster-Wingard et al. (1996, 1997). Living taxa (from Brewster-Wingard et al., 1996) are *Anomalocardia* sp., *Arcopsis adamsi, Brachiodontes* (*sic*) sp., *Chione cancellata, Laevicardium* spp., *Nucula proxima, Parastarte triquetra, Pinctada radiata, Polymesoda* sp., *Transennella* spp. Core 19B taxa (from Brewster-Wingard et al., 1997) are: *Brachiodontes* (*sic*) sp., *Chione cancellata, Transennella* sp. Core 6A taxa (from Wingard et al., 1995) are: *Transennella* spp., *Brachiodontes* (*sic*) sp.

^{G}BREWSTER-WINGARD, G. L., S. E. ISHMAN, L. E. EDWARDS & D. A. WILLARD, 1996, Preliminary report on the distribution of modern fauna and flora at selected sites in north-central and north-eastern Florida Bay. *United States Geological Survey Open-File Report* 96-732, 34 pp. Electronic version available at http://pubs.usgs.gov/pdf/of/ofr96732.html; last accessed 12 September 2003.

Of the 14 numbered stations sampled, 9 are within our definition of the Florida Keys [excluding the approximate northern half of Florida Bay, i.e., stations 1, 2, 3, 8, and 9]. Living mollusks were collected in February and July of 1995 using push cores, and abundances are compared among stations and between the two collections. For the entire study, *Transenella* (*sic*) spp. and *Brachiodontes* (*sic*) sp. are considered "ubiquitous" taxa; *Anomalocardia* sp. and *Parastarte triquetra* are present in significant numbers. *Cyrenoida floridana, Polymesoda* sp., and *Mytilopsis leucophaeata* are among indicator species for oligohaline-mesohaline conditions. No obvious seasonal trends were observed from the overall molluscan data. *Anomalocardia* sp., *Chione cancellata,* and *Lima* sp. showed seasonal differences, perhaps related to "seasonal spawning". Molluscan data are presented for stations 11–13 only (these correspond to Turney & Perkins' (1972) "interior subenvironment"): *Anomalocardia* sp., *Arcopsis adamsi, Brachiodontes* (*sic*) sp., *Chione cancellata, Codakia* sp., *Cumingia tellinoidea* (*sic*), *Laevicardium* spp., *Lima* sp., *Nucula proxima, Parastarte triquetra, Pinctada radiata, Polymesoda* sp., *Tellina* spp., *Transenella* (*sic*) spp., rare pelecypods, unidentified pelecypod fragments. A summary of these data was published by Brewster-Wingard & Ishman (1999).

BREWSTER-WINGARD, G. L., S. E. ISHMAN & C. W. HOLMES, 1998, Environmental impacts on the southern Florida coastal waters: a history of change in Florida Bay.

Journal of Coastal Research, Special issue 26: 162–172.

Summary of data on Florida Bay mollusks from earlier reports by Wingard et al. (1995) and Brewster-Wingard et al. (1997), derived from living communities and death assemblages in sediment cores (from cores 6A and 19B). From Bob Allen Core 6A: *Brachiodontes* (*sic*) sp. From Russell Bank Core 19B: *Brachiodontes* (*sic*) sp. Modern studies (living mollusks) at monitoring sites indicate probable habitats through time in the sediment cores. *Anomalocardia* sp. is relatively abundant in mesohaline-polyhaline sites. *Pinctada radiata*, *Transennella* spp., *Laevicardium* sp., and *Chione cancellata* prefer polyhaline to euhaline conditions. *Brachiodontes* (*sic*) sp. is predominantly found on macroalgae associated with *Thalssia* grassbeds. *Pinctada radiata* is found on both *Thalassia* and macroalgal mats.

|BREWSTER-WINGARD, G. L., S. E. ISHMAN, N. J. WAIBEL, D. A. WILLARD, L. E. EDWARDS & C. W. HOLMES, 1998, Preliminary paleontologic report on Core 37, from Pass Key, Everglades National Park, Florida Bay. *United States Geological Survey Open-File Report* 98-122, 22 pp. Electronic version available at http://pubs.usgs.gov/pdf/of/ofr98122.html; last accessed 12 September 2003.

This work is here excluded as outside our defined area, which extends roughly half-way between the Florida Keys island chain and the tip of peninsular Florida. Pass Key is north of this limit.

ᴳBREWSTER-WINGARD, G. L., S. E. ISHMAN, D. A. WILLARD, L. E. EDWARDS & C. W. HOLMES, 1997, Preliminary paleontologic report on Cores 19A and 19B, from Russell Bank, Everglades National Park, Florida Bay. *United States Geological Survey Open-File Report* 97-460, 29 pp. Electronic version available at http://131.247.143.93/publications/ofr/97-460/; last accessed 12 September 2003.

Study of core samples from Russell Bank, Florida Bay, dating to 115–118 yrs at the core bottom, included shells of *Anomalocardia* sp., *Arcopsis adamsi*, *Brachiodontes* (*sic*) sp., *Chione cancellata*, *Cumingia tellinoidea* (*sic*), *Laevicardium* spp., *Nucula proxima*, pectinid, *Pinctada radiata*, *Tellina* spp., *Transenella* (*sic*) spp., rare pelecypods, unidentified pelecypod fragments. A summary of these data was published by Brewster-Wingard et al. (1998) and Brewster-Wingard & Ishman (1999).

BREWSTER-WINGARD, G. L., J. R. STONE & C. W. HOLMES, 2001, Molluscan faunal distribution in Florida Bay, past and present: an integration of down-core and modern data. Pp. 199–231, in: B. R. WARDLOW, ed., Paleoecological Studies of South Florida, *Bulletins of American Paleontology*, no. 361. See full data matrix at http://flaecohist/database/Reference/synthesis; and core data at http://sofia.usgs.gov/flaecohist.

A summary and update of living and dead molluscan assemblages in Florida Bay (previously published in part by Brewster-Wingard et al. (1996, 1997), Brewster-Wingard & Ishman (1999), and Wingard et al. (1995); taxonomy is much updated, acknowledging W. G. Lyons. Analysis of core versus living data suggests changes in Florida Bay marine environments during the past 200 years. Most mollusks are generally present throughout the study period, however the study documents fluctuations in dominance and diversity. Modern assemblages are defined and include: *Brachidontes* assemblage (most dominant), *Pteria* assemblage (on sides of mudbanks in dense *Thalassia*), and three "western" assemblages (near channels, indicative of euhaline conditions). Considered as important biological indicators of conditions in Florida Bay during mandated restoration efforts: *Anomalocardia auberiana, Brachidontes exustus*, *Pteria longisquamosa*. *Brachidontes exustus* is the dominant mollusk in Florida Bay, due to its tolerance of varying salinity and substrate, and poor water quality.

Live-mollusk data previously presented by Brewster-Wingard et al. (1996) include *Anomalocardia auberiana, Arcopsis adamsi, Brachidontes exustus, Chione cancellata, Laevicardium mortoni, Parastarte triquetra, Pteria longisquamosa*, tellinid, *Transennella* sp. Push core data previously published by Brewster-Wingard et al. (1997), Brewster-Wingard & Ishman (1999), and Wingard et al. (1995): include *Anomalocardia auberiana, Arcopsis adamsi, Argopecten irradians, Brachidontes exustus, Chione cancellata, Codakia spp., Cumingia tellinoides, Laevicardium mortoni, Limaria cf. pellucida, Lucinisca nassula, Mysella planulata, Nucula proxima, Parastarte triquetra, Parvilucina multilineata, Pitar simpsoni, Pteria longisquamosa, Semele bellastriata, Tellina spp., Transennella* sp.

ᴳBRITTON, J. C., 1970, The Lucinidae (Mollusca: Bivalvia) of the western Atlantic

Ocean. Ph.D. dissertation, George Washington University, Washington, DC. v + 567 pp., including 23 pls.

Recorded in materials examined sections from Florida Keys localities: *Anodontia (Anodontia) alba, A. (Anodontia) schrammi, Callucina (Callucina) radians, Cavilinga blanda, Codakia (Codakia) orbicularis, C. (Ctena) orbiculata, Divaricella (Divaricella) dentata, D. (Divalinga) quadrisulcata, Lucina (Pleurolucina) leucocyma, L. (Lucina) pensylvanica, L. (Pleurolucina) sombrerensis, Megaxinus floridanus, Parvilucina (Bellucina) amiantus, P. (Parvilucina) costata, P. (Parvilucina) multilineata, P. (Lucinisca) nassula, P. (Parvilucina) pectinella, Phacoides (Lucinoma) filosus, P. (Phacoides) pectinatus.*

GBROOKS, J., 1968a, Keys after “Abby”. *Seafari* [*Palm Beach County Shell Club Newsletter*], 10(7): 8.

Results from collecting in the Middle Keys after Hurricane Abby passed between the Dry Tortugas and Key West in early June 1968 include *Antigona listeri, Arcopagia fausta, Lima lima, Lithophaga antillarum, Tellina similis*, tellins, many other dead bivalves. Continued by Brooks (1968b).

GBROOKS, J., 1968b, Further report on Marathon and vicinity in June 1968. *Seafari* [*Palm Beach County Shell Club Newsletter*], 10(10): 8.

Continuing notes from Brooks (1968a). Collected from Marathon and vicinity: *Americardium media, Chama* spp., *Chlamys sentis, Codakia orbicularis, Glycymeris pectinata, Laevicardium laevigatum, Lima pellucida, Lima scabra* form *tenera, Lucina pensylvanica, Papyridea soleniformis, Tellina fausta, T. similis*, several other tellins, *Trachycardium egmontianum, T. muricatum.*

GBROOKS, J., 1969, The Keys in August. *Seafari* [*Palm Beach County Shell Club Newsletter*], 11(11): 7.

Collected in early August [1969] from the Marathon area: *Botula fusca, Chlamys sentis.*

GBURGGRAF, P., 1969, Broward member in the Keys. *Seafari* [*Palm Beach County Shell Club Newsletter*], 11(10): 6–7.

From Lower Keys localities, June 28–29 [1969]: *Chlamys sentis, Glycymeris pectinata, Tellina radiata.*

CALKINS, W. W., 1878, Catalogue of the marine shells of Florida, with notes and descriptions of several new species. *Proceedings of the Davenport Academy of Natural Sciences*, 2: 232–252, pl. 8.

“The material for the following monograph has been mainly derived from my own collections, and observations made during two winters spent in Florida in 1875 and 1877. The first time as member of an expedition in the interest of the Chicago Academy of Sciences, and in 1877 on my own account. In addition to my personal collections, I have received since my return valuable accessions from my collectors living in Florida. In the determination of species I have been assisted in many instances by Mr. George W. Tryon, Jr., of Philadelphia, to whom, and also to Mr. Thomas Bland, I desire to express my acknowledgments for kindly aid. [...] The largest part of the species enumerated are in my cabinet. A number are in the Museum of the Chicago Academy and in that of the Davenport Academy of Sciences. Other species will be deposited from time to time.” [pp. 232–233]. From Florida Keys localities are: *Avicula atlantica, A.* sp., *Chama arcinella, C. macrophylla, Cytherea dione, Lima scabra, L. squamosa, Lithodomus antillarum, L. lithophagus, Modiola sulcata, M. tulipa, M. t.* var. *nigra* n. var., *Pectunculus pennaceus, Perna perna, Sanguinolaria sanguinolenta, Spondylus gaederopus, Strigilla flexuosa, S. pisiformis, Tellina braziliana, T. decora, T. iris, T. radiata, T. tenera, Xylotrya fimbiata* (*sic*).

*CAMPBELL, D. C., K. J. HOEKSTRA & J. G. CARTER, 1998, 18S Ribosomal DNA and evolutionary relationships within the Bivalvia. Pp. 75–85, in: P. A. JOHNSTON & J. W. HAGGART, eds., *Bivalves: an eon of evolution – paleobiological studies honoring Norman D. Newell.* University of Calgary Press, Calgary, Alberta, Canada. 461 pp.

Molecular sequences from *Barbatia cancellaria, Pinctada imbricata, Isognomon alatus* from West Summerland Key; *Ostrea equestris* from Marathon.

CAMPBELL, M. R., G. STEINER, L. D. CAMPBELL & H. Dreyer, 2004, Recent Chamidae (Bivalvia) from the western Atlantic Ocean. In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 381–415.

From Florida Keys localities: *Arcinella cornuta, Chama congregata, C. florida, C. inezae, C. lactuca, C. macerophylla, C. radians, C. sarda, C. sinuosa* [some material from this study].

CANTILLO, A. Y., G. G. LAUENSTEIN & T. P. O’CONNOR, 1997, Mollusc and sediment

contaminant levels and trends in South Florida coastal waters. *Marine Pollution Bulletin*, 34(7): 511–521.

The NOAA National Status and Trends (NS&T) Program includes one station in its Mussel Watch Project at Bahia Honda Key (24°39.52'N, 81°16.43'W, three years of data through 1995). *Chama sinuosa* from this site was collected for analysis of organic and inorganic contaminants, although this paper does not present the results on that species. Two other Mussel Watch Project stations in Florida Bay (Flamingo Bay and Joe Bay) are too far north to be included in this survey.

CARTER, J. G., 1978, Ecology and evolution of the Gastrochaenacea (Mollusca, Bivalvia) with notes on the evolution of the endolithic habitat. *Peabody Museum of Natural History, Yale University, Bulletin* 41, 92 pp.

The "three more common gastrochaenids of the Florida Keys" are *Spengleria rostrata*, *Gastrochaena* (*G.*) *hians*, and *G.* (*Rocellaria*) *ovata*. *G. hians* dominates the Keys gastrochaenid fauna in terms of population density, whereas *S. rostrata* is generally rare.

^{G}CHAN, E. I., 1977a, *The ecology of the seagrasses of South Florida: a community profile*. United States Fish and Wildlife Services, FWS/OBS - 82/25, 158 pp. Reprinted September 1985.

Cited by Zieman, 1982; reporting on the effects of a 1975 tanker discharge SW of the Marqueses, attributed mass mortalities of the pearl oyster (*Pinctada radiata*) a grass bed inhabitant, to some soluble fraction of petroleum.

^{G}CHAN, E. I., 1977b, Oil pollution and tropical littoral communities: biological effects of the 1975 Florida Keys oil spill. Pp. 539–542, in: *Proceedings 1977 Oil Spill Conference* (*Prevention, Behavior, Control, Cleanup*), March 8–10, 1977, New Orleans, Louisiana.

Reports on impact of crude oil discharge 26 mi SSW of the Marquesas, affecting the lower Florida Keys from Little Pine Key to Boca Chica Key. Molluscan species discussed: *Crassostrea virginica*, *Isognomen* (*sic*) *alatus*, *Pinctada radiata* (with mass mortality attributed to oil spill).

^{G}*CLAMPIT, L., 1987, Florida Keys. *Texas Conchologist*, 24(1): 8–11.

From Missouri Key, Grassy Key, Little Duck Key, and Ohio Key in July 1987: Arcidae, Chamidae, *Codakia orbicularis*, *Linga pensylvanica*, Pinnidae, Tellinidae.

^{G}*CLAMPIT, L., 1988, Florida Keys revisited. *Texas Conchologist*, 25(1): 28.

From Missouri Key: *Chama macerophylla*.

CLENCH, W. J., 1942, The genera *Dosinia*, *Macrocallista* and *Amiantis* in the western Atlantic. *Johnsonia*, 1(3): 1–8.

Museum lots (ANSP) from the Florida Keys cited for: *Dosinia floridana*.

*CLENCH, W. J. & L. C. SMITH, 1944, The family Cardiidae in the western Atlantic. *Johnsonia*, 1(13): 1–32.

Museum lots (MCZ) and private collections (ex Van Hyning) from the Florida Keys cited for: *Laevicardium laevigatum*, *L. mortoni*, *Microcardium peramabile*, *Papyridea semisulcata*, *P. hiatus*, *Trachycardium egmontianum*, *T. magnum*, *T. muricatum*, *Trigoniocardia* (*Americardia*) *media*.

^{G}CLOSE, H. T., 1974, Shelling in the Florida Keys?? *Of Sea & Shore*, 5(4): 183, 200.

Account of a 1973 trip to the lower Keys includes *Chama macerophylla* from Sand Key.

COHEN, S. & R. COHEN, 1991, *Florida Keys divers guide — The Upper Keys*. Seapen, Key Largo & Tel Aviv. 156 pp.

Includes a photo (unnamed) of a living *Ctenoides floridanus* (with light-orange tentacles).

COLIN, P. L., 1978, *Caribbean reef invertebrates and plants*. T. F. H. Publications, Neptune City, New Jersey. 512 pp.

With Florida Keys specifically cited in species distribution: *Spondylus americanus*.

CONRAD, T. A., 1866, Descriptions of new marine bivalve Mollusca. *American Journal of Conchology*, 2(3): 280–281, pl. 15.

Dosinia floridana n. sp., from Florida Keys, Gulf of Mexico.

^{G}CROVO, M. E., 1970, *Gastrochaena hians* Gmelin 1791. *Seafari* [*Palm Beach County Shell Club Newsletter*], 12(11): 6–7.

Study includes shells examined from the Lower Florida Keys.

*DALL, W. H., 1881, Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877–79, by the United States Coast Survey steamer "Blake", Lieutenant-Commander C. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U.S.N., commanding. XV. Preliminary report on the Mollusca. *Bulletin of the Museum of Comparative Zoology*, 9(2): 33–144.

Station information in this paper is insufficient to place all localities. Decisions were made on the basis of S. Smith (1889). Eighteen

Blake stations are mentioned with reference to localities in or off the Florida Keys or Dry Tortugas; these are stations 5, 6, 9, 10, 11, 12, 26, 27, 28, 29, 30, 31, 43, 44, 45, 46, 70, and 72. Of these, stations 44, 45, and 46 are here excluded because they are located too far northwest into the Gulf of Mexico (north of the latitude of Cape Sable); stations 29, 30, and 31 are here excluded because they are too far west (beyond 83°30'N), which is also where the 1,000 fm isobath is located (stations 29–31 are very deep); 28 and 43 are also excluded as too deep (863 and 339 fms, respectively). All remaining stations (5, 6, 9, 10, 11, 12, 26, 27, 70, 72) are less than 300 m (164 fms). "Off Sombrero, 54 fms" is in the Virgin Islands, not the Florida Keys (see Introduction). Identified by S. R. Roberts for Dall, and from the Florida Keys, are *Amussium lucidum, Avicula* sp., *Cardium* (*Fulvia*) *peramabilis* n. sp., *C.* (*F.*) *p.* var. *tinctum* n. var., *Corbula cymella, C. disparilis, Gouldia cubaniana, Leda carpenteri* n. sp., *L. jamaicensis, Neaera alternata, N. rostrata, Poromya granulata, Syndosmya lioica* n. sp., *Verticordia acuticostata* n. sp.

DALL, W. H., 1883, On a collection of shells sent from Florida by Mr. Henry Hemphill. *Proceedings of the United States National Museum*, 6(21): 318–342, pl. 10.

"In the absence of a good collection of named specimens from the region, it is difficult and tedious work identifying specimens connected, as the South Florida shells are, with the West Indian fauna. Consequently it is with a certain diffidence that I attempted, at Mr. Hemphill's request, to work up the extremely interesting collection he has given to the National Museum. The only catalogues relating to South Florida are extremely imperfect though praiseworthy attempts. Conrad's work was never complete and is antiquated; the paper of Mr. Melvill is marred by the inaccuracies of identification for which the present Mr. Sowerby is famous; Mr. Calkins' work is the best of all, but would have been more useful if the specimens actually collected by him had been discriminated in some way from those quoted from other authors, whose localities or identifications may not have been accurate, or at least may not have been confirmed. It is known to most persons interested that the Smithsonian collection of East American shells, especially those belonging south of New York, was in the hands of Dr. Stimpson, and with his own matchless collection was destroyed totally by the fire at Chicago in 1871.

Under these circumstances, believing it better to make some sort of start at cataloging the shells of our southern coast (even at the risk some erroneous identifications) than to wait for opportunities which not seem likely to be soon offered, the present list has been prepared in the hope that its deficiencies may stimulate others to correct and enlarge it from specimens actually obtained on the spot." (pp. 319–320).

Discussed from Key West: *Anomalocardia flexuosa, Arca* (*Barbatia*) *dominguensis, A.* (*Barbatia*) *gradata, Cyrena carolinensis* (*sic*), *Lucina tigerina, Mytilus exustus, Perna ephippium, Tellina mera.* The list was continued by Dall (1885).

DALL, W. H., 1885, List of marine Mollusca comprising the Quaternary and Recent forms from American localities between Cape Hatteras and Cape Roque including the Bermudas. *Bulletin of the United States Geological Survey*, 24: 1–336.

Cited from Key West (all specifically referring to Dall, 1883): *Anomalocardia flexuosa, Arca* (*Barbatia*) *dominguensis, A.* (*B.*) *gradata, Cyrena carolinensis* (*sic*), *Lucina tigerina, Mytilus exustus, Perna ephippium, Tellina mera.*

*DALL, W. H., 1886, Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer "Blake", Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XXIX. Report on the Mollusca. Part I. Brachiopoda and Pelecypoda. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 12: 171–318, pls. 1–9.

Abra lioica, Cardium laevigatum, C. (*Fulvia*) *peramabilis, Corbula dietziana, C. disparilis, Cuspidaria rostrata, Cytherea hebraea, Leda acuta, Lima inflata, Pecten antillarum, P. dislocatus, Petricola divaricata, Semele obliqua, Tellina tenera, Thracia corbuloidea,* and *Venus cancellata* are included from Keys localities collected by the *Blake* Expedition (1877–1880) or noted from other Keys localities. "Off Sombrero, 54 fms" is in the Virgin Islands, not the Florida Keys (see Introduction).

DALL, W. H., 1889a, A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States, with illustrations of many of

the species. *Bulletin of the United States National Museum*, no. 37: 1–121, 74 pls.

The Florida Keys, “very intimately connected, faunally, with the northern shores of Cuba opposite, and with the Bahamas, includes the region south of Biscayne Bay on the east, and south of the southern entrance to Charlotte Harbor on the west side of the Peninsula, to and including the Keys and Tortugas reefs and islands” (p. 10).

A table of species distributions includes the Florida Keys as a single column, plus northern and southern extreme distributional points. Marked as “*” [known from shores, either picked up on beach or found living between high water and 50 fms]: *Anomia simplex, Arca* (*Byssoarca*) *adamsi, A.* (*Argina*) *americana, A.* (*Scapharca*) *auriculata, A.* (*Barbatia*) *barbata, A.* (*Arca*) *imbricata, A.* (*Scapharca*) *incongrua, A.* (*S.*) *lienosa, A.* (*Arca*) *noae, A.* (*Noetia*) *orbignyi, A.* (*N.*) *ponderosa, A.* (*Byssoarca*) *reticulata, A.* (*Scapharca*) *transversa, Asaphis deflorata, Astarte nana, Asthenothaerus hemphillii, Avicula nitida, Basterotia quadrata, Cardita conradii, C. floridana, Cardium antillarum, Chama arcinella, C. macerophylla, Cardium isocardia, C. magnum, C. medium, C. muricatum, Circe* (*Gouldia*) *cerina, Corbula barrattiana, C. nasuta, Crassatella floridana, C.* (*Eriphyla*) *lunulata, Crenella divaricata, Cumingia tellinoides, Cyrena* (*Leptosiphon*) *carolinensis* (sic), *Cyrenoidea floridana* [*nomen nudum*], *Cytherea albida, C.* (*Transennella*) *conradina, C.* (*T.*) *cubaniana, C.* (*Dione*) *dione, C.* (*Callista*) *gigantea, C.* (*Tivela*) *mactroides, C.* (*Callista*) *maculata, C. simpsoni, Dacrydium vitreum, Diplodonta semiaspera, D. soror, D. subglobosa, Donax denticulatus, D. fossor, D. variabilis, Dosinia elegans, Ensis americana, Ervilia concentrica, E. nitens, Gastrochaena cuneiformis, G. ovata, G.* (*Spengleria*) *rostrata, Heterodonax bimaculata, Iphigenia braziliana, Labiosa canaliculata, Lima hians, L. inflata, L. scabra, L. squamosa, L. tenera, Lithophagus antillarum, L. bisulcatus, L. caribaeus, L. forficatus, Loripes edentula, L. e.* var. *chrysostoma, Lucina* (*Lucina*) *costata, L.* (*L.*) *crenulata, L.* (*L.*) *floridana, L.* (*L.*) *multilineata, L.* (*L.*) *pecten, L.* (*L.*) *pennsylvanica* (sic), *L.* (*L.*) *squamosa, L.* (*L.*) *tigrina, L.* (*L.*) *trisulcata, Lucinopsis tenuis, Lutricola interstriata, Lyonsia beana, Macoma brevifrons, M. cerina, M. tenta, M. t.* var. *souleyetiana, Mactra brasiliana, M. lateralis, M. solidissima* var. *similis, Margaritiphora radiata, Martesia corticaria, M. cuneiformis, M. striata, Modiola* (*Botula*) *cinnamomea, M.* (*Amygdalum*) *lignea, M.* (*Botulina*) *opifex, M.* (*Brachydontes*) *sulcata, Modiolaria lateralis, Mytilus exustus, M. hamatus, Ostrea cristata, O. frons, O. virginica, Papyridea bullata, P. petitiana, P.* (*Liocardium*) *serratum, Pecten* (*Pecten*) *antillarum, P.* (*P.*) *exasperatus, P.* (*P.*) *imbricatus, P.* (*P.*) *irradians* var. *dislocatus, P.* (*P.*) *nodosus, P.* (*P.*) *nucleus, P.* (*P.*) *ornatus, P.* (*Janira*) *ziczac, Pectunculus pectinatus, P. undatus, Periploma angulifera, Perna ephippium, P. obliqua, Petricola pholadiformis, P.* (*Choristodon*) *robusta, P.* sp., *Pholas campechiensis, P.* (*Barnea*) *costata, P.* (*B.*) *truncata, Pinna carnea, P. muricata, P. seminuda, Placunanomia rudis, Plicatula ramosa, Saxicava arctica, S. azaria, Semele cancellata, S. obliqua, S. reticulata, Solenomya occidentalis, Spondylus spathuliferus, Strigilla carnaria, S. flexuosa, S. pisiformis, Tagelus divisus, Tellidora cristata, Tellina alternata, T. decora, T. fausta, T. gouldii, T. interrupta, T. lineata, T. magna, T. mera, T. modesta, T. radiata, T. squamifera, T. striata, T. tenera, T.* sp., *Teredo thomsoni, Thracia corbuloidea, T. phaseolina, T. stimpsoni, Venus beaui, V. cancellata, V. crispata, V. mercenaria, V. m.* var. *mortoni, V. pygmaea, V.* (*Anomalocardia*) *rostrata, Verticordia* (*Trigonulina*) *ornata, Xylotrya fimbriata.*

Marked as “dagger” [archibenthal, 50–800 fms]: *Abra longicallus, Arca* (*Byssoarca*) *glomerula, A.* (*Macrodon*) *sagrinata, A.* (*M.*) sp., *Asthenothaerus* (*Bushia*) *elegans, Astarte lens, A. smithii, Cardita domingensis, Cardium peramabilis, Corbula cubaniana, C. cymella, C. dietziana, C. krebsiana, Crassatella* (*Eriphyla*) *lunulata* var. *parva, Cryptodon obesus, C. pyriformis, Cuspidaria* (*Liomya, Plectodon*) *granulata, C.* (*L., P.*) *g.* var. *velvetina, C.* (*Cuspidaria*) *obesa, C.* (*Cardiomya*) *perrostrata, C.* (*Cuspidaria*) *rostrata, C.* (*Cardiomya*) *striata, Cytherea* (*Veneriglossa*) *vesica, C.* sp., *Leda* (*Leda*) *acuta, L.* (*L.*) *messanensis, L.* (*L.*) *vitrea, L.* (*Y.*) *liorhina, Lima albicoma, L.* (*Limatula*) *setifera, L.* (*L.*) *subauriculata, Limopsis antillensis, L. aurita, L. cristata, L. minuta, Loripes lens, Lucina* (*Lucina*) *filosa, L.* (*L.*) *lenticula, L.* (*L.*) *leucocyma, L.* (*L.*) *pectinella, L.* (*Divaricella*) *quadrisulcata, L.* (*Lucina*) *sagrinata, L.* (*L.*) *scabra, L.* (*L.*) *sombrerensis, Modiola* (*Amygdalum*) *polita, M.* (*A.*) *p.* var. *sagittata, Myonera lamellifera, Nucula*

aegeënsis, Periploma tenera, Pandora (*Kennerlia*) *glacialis, Pecten* (*Amusium, Propeamussium*) *cancellatum, P.* (*A., P.*) *pourtalesianum, P.* (*A., P.*) *P.* var. *marmoratum, P.* (*A., P.*) *sayanum, P.* (*Pecten*) *effluens, P.* (*P.*) *phrygium, P.* (*Pecten, Pseudamusium*) *sigsbeei, P.* (*P., P.*) *thalassinus, Poromya* (*Cetomya*) *albida, P. granulata, Venus granulata, V. lamarckii, V. pilula, V. rugosa, V. r.* var. *rugatina, Verticordia acuticostata, V.* (*Haliris*) *fischeriana.*

Marked as "* + dagger" [both shallow (known from shores, either picked up on beach or found living between high water and 50 fms) and deep (archibenthal, 50–800 fms)]: *Avicula atlantica, Arca* (*Byssoarca*) *nodulosa, Leda* (*Leda*) *carpenteri, Lucina* (*Lucina*) *lintea, Chama sarda, Cardium peramabilis* var. *tinctum, Papyridea* (*Liocardium*) *laevigatum, Pecten* (*Janira*) *hemicyclica, Cytherea hebraea, Petricola* (*Naranaio*) *lapicida, Abra lioica, Cuspidaria* (*Cardiomya*) *costellata, Corbula swiftiana.*

DALL, W. H., 1889b, Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer "Blake", Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R Bartlett, U.S.N., commanding. XXIX. Report on the Mollusca. Part II. Gastropoda and Scaphopoda [with "Addenda and Corrigenda to Part I, 1886", pp. 433–452]. *Bulletin of the Museum of Comparative Zoology*, 18: 1–492, pls. 10–40.

Additions and Corrigenda to Part I (Dall, 1886) includes *Pseudamusium strigillatum* n. sp., from the Antilles and Florida Reefs.

DALL, W. H., 1890, Scientific results of explorations by the U.S. Fish Commission Steamer *Albatross*. No. VII. – Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887–88. *Proceedings of the United States National Museum*, 12(773): 219–362, pls. 5–14 [07 March 1890].

With distribution including Florida Keys: *Crassatella floridana.*

DALL, W. H., 1896a, The mollusks and brachiopods of the Bahama Expedition of the State University of Iowa. *Bulletin from the Laboratories of Natural History of the State University of Iowa*, 4(1): 12–27, pl. 1.

From Florida Keys localities, some general, others from stations of the May–July 1893 S.U. I. Bahama Biological Expedition aboard the 95-foot schooner *Emily E. Johnson*, led by Charles C. Nutting: *Arca noae, A. umbonata, Avicula atlantica, A. crocata, A. radiata, Cardium medium, C. serratum, Chama* (*Echinochama*) *arcinella, Lithophagus antillarum, Macoma* sp., *Pecten ornatus, Perna oblique* (*sic*), *Pinna pernula, Tagelus divisus, Tellina* sp., *Venus* (*Chione*) *cancellata, Venus* sp. A full narrative of the expedition and station data were published by Nutting (1895).

DALL, W. H., 1896b, On the American species of *Ervilia. The Nautilus*, 10(3): 25–27.

With distributions including Florida Keys: *Ervilia concentrica, E. nitens.*

DALL, W. H., 1897, Synopsis of the Pinnidae of the United States and West Indies. *The Nautilus*, 11(3): 25–26.

With distribution including Florida Keys: *Pinna carnea.*

DALL, W. H., 1898, Contributions to the Tertiary fauna of Florida, with especial reference to the silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Part. IV. 1. Prionodesmacea: *Nucula* to *Julia*. 2. Telodesmacea: *Teredo* to *Ervilia. Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(4): 571–947; pls. 23–35.

As Recent or Pleistocene from the Florida Keys: Arca *(Lunarca) occidentalis, A. (L.) umbonata, Pecten (Chlamys, section Nodipecten) antillarum, P. (C., section C.) ornatus, P. (C., section Plagioctenium) gibbus* var. *nucleus, Pinna carnea, Scapharca (S., section S.) transversa, S. (S., section S.) auriculata.*

DALL, W. H., 1899a, Synopsis of the American species of the family Diplodontidae. *Journal of Conchology*, 9(8): 244–246.

Diplodonta soror, with distribution to the Florida Keys.

DALL, W. H., 1899b, Synopsis of the Solenidae of North America and the Antilles. *Proceedings of the United States National Museum*, 22(1185): 107–112.

Ensis directus, with distribution to Indian Key.

DALL, W. H., 1900a, Contributions to the Tertiary fauna of Florida, with especial reference to the silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Part V. Teleodesmacea: *Solen* to *Diplodonta. Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(5): 949–1218, pls. 36–47.

With Recent Florida Keys included in species distributions: *Cardium (Papyridea) semisulcatum, Cumingia coarctata, Donax fossor, Ensis directus, Metis intastriata.*

DALL, W. H., 1900b, Synopsis of the family Cardiidae and of the North American species. *Proceedings of the United States National Museum*, 23(1214): 381–392.

Protocardia tincta, from Key West.

DALL, W. H., 1900c, Synopsis of the family Tellinidae and of the North American species. *Proceedings of the United States National Museum*, 23(1210): 285–326, pls. 2–4.

With distributions including Florida Keys (or specific localities): *Strigilla pisiformis, S. rombergii, Tellina* (*Eurytellina*) *angulosa, T.* (*Scissula*) *candeana, T.* (*S.*) *exilis, T.* (*S.*) *iris.*

DALL, W. H., 1901, Synopsis of the Lucinacea and of the North American species. *Proceedings of the United States National Museum*, 23(1237): 779–833, pls. 39–42.

With distributions including Florida Keys (or specific localities): *Codakia orbicularis, Jagonia orbiculata* var. *filiata* n. var., *J. o.* var. *recurvata* n. var., *Myrtaea* (*Eulopia*) *sagrinata, Phacoides* (*Lucinisca*) *muricatus.*

DALL, W. H., 1902a, Illustrations and descriptions of new, unfigured, or imperfectly known shells, chiefly American, in the U.S. National Museum. *Proceedings of the United States National Museum*, 24(1264): 499–566, pls. 27–40.

Listed and figured from the Florida Keys: *Meretrix* (*Transennella*) *conradina.*

*DALL, W. H., 1902b, Synopsis of the family Veneridae and of the North American Recent species. *Proceedings of the United States National Museum,* 26(1312): 335–412, pls. 12–16.

With distributions including Florida Keys (or specific localities): *Chione* (*Chione*) *intapurpurea, C.* (*C.*) *subrostrata, C.* (*Timoclea*) *pygmaea, Cytherea* (*Cytherea*) *listeri, C.* (*Ventricola*) *rigida, Cytherea* (*Ventricola*) *strigillina* n. sp., *Dosinia* (*Dosinidia*) *concentrica, D. elegans, Macrocallista* (*Chionella*) *maculata, Parastarte triquetra, Transennella stimpsoni* n. sp., *Venus mercenaria.*

DALL, W. H., 1903a, Contributions to the Tertiary fauna of Florida with especial reference to the silex beds of Tampa and the Pliocene beds of the Caloosahatchie River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species. Part VI. Concluding the work. *Transactions of the Wagner Free Institute of Science of Philadelphia*, 3(6): 1219–1654, pls. 48–60.

As Recent or fossil from Florida Keys localities: *Cardita* (*Carditamera*) *floridana, Codakia orbicularis, Cyrena* (*Pseudocyrena*) *floridana, Cytherea* (*Cytherea,* section *Ventricola*) *rugatina, Dosinia* (*Dosinidia*) *concentrica, Dosinia* (*Dosinidia*) *elegans, Lucina chrysostoma, Macrocallista nimbosa, Parastarte triquetra, Periploma angulifera, Phacoides* (*Lucinisca*) *muricatus, Venus mercenaria* var. *notata.*

DALL, W. H., 1903b, A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States, with illustrations of many of the species. Reprint to which are added twenty-one plates not in the edition of 1889. *Bulletin of the United States National Museum*, no. 37: 1–232, 95 pls.

With the same text entries as the original version (Dall, 1889a), with the following additional Florida Keys reference in the added plates (pls. 75–95): *Cytherea* (*Ventricola*) *strigillina.*

DALL, W. H., 1903c, Synopsis of the family Astartidae, with a review of the American species. *Proceedings of the United States National Museum*, 26(1342): 933–951, pls. 62–63.

Astarte nana, with "Florida reefs" within its distribution.

*DALL, W. H., 1925, Notes on the nomenclature of some of our east American species of *Pecten* with descriptions of new species. *The Nautilus*, 38(4): 112–120.

With distributions including Florida Keys (or specific localities): *Pecten* (*Plagioctenium*) *nucleus, Pecten* (*Euvola*) *tereinus* n. sp. from Key West.

DALL, W. H., 1927, Small shells from dredgings off the southeast coast of the United States by the United States Fisheries Steamer "Albatross" in 1885 and 1886. *Proceedings of the United States National Museum*, 70 (Art. 18): 1–134.

With distributions including Florida Keys: *Poromya granulata.*

^GDALTON, I., 1991, Shelling Marquesas Keys. *Of Sea & Shore*, 13(4): 165–166, 190.

Arcinella arcinella collected July 2–4? [1991] at Marquesas Keys, with Metal Detector's Club.

*DAVIS, J. D., 1973, Systematics and distribution of western Atlantic *Ervilia* (Pelecypoda: Mesodesmatidae) with notes

on living *Ervilia subcancellata*. *The Veliger*, 15(4): 307–313, 3 pls.
Ervilia concentrica, *E. nitens* and *E. subcancellata* contrasted, including Florida Keys material.

^{G}DEMARIA, K., 1996, *Changes in the Florida Keys ecosystem based upon interviews with experienced residents*. The Nature Conservancy, Key West; and Center for Marine Conservation, Washington, D.C. [iii +] iii + 105 + 5 + 21 + 3 pp.
An interesting interview-based compilation giving the historical perspective on many topics, including the impact of landfills on water circulation, freshwater runoff from the Everglades, the C-111 canal opened in the mid-1960s, etc. "Scallops" (probably *Argopecten irradians*) are discussed as components of the Florida Bay fauna off the Upper and Middle Keys in the 1950s and 1960s.

^{G}DENT, S. R., 1998, Recent mollusk shell encrustation patterns on the South Florida shelf: indicators of environmental conditions? [abstract] *Geological Society of America Abstracts with Program* (*32nd Annual Meeting, North-Central Section and associated societies*), 30(2): 14.
Epibiont coverage compared on Chamidae and *Tellina* spp. from the Florida Keys.

DÍAZ MERLANO, J. M. & M. PUYANA HEGEDUS, 1994, *Moluscos del Caribe Colombiano, un catálogo ilustrado*. Colciencias y Fundación Natura Colombia, INVEMAR, Santefe de Bogota, Colombia. 291 pp., 74 pls.
Caribbean Colombian mollusks with "cayos de La Florida" in species distributions: *Chama sarda, Divarilima albicoma, Lucina* (*Lucinisca*) *muricata, Nucula calcicola, Transenella* (*sic*) *cubaniana, Ventricolaria rigida*.

DOMANESCHI, O. & C. MANTOVANI MARTINS, 2002, *Isognomon bicolor* (C. B. Adams (Bivalvia, Isognomonidae): primeiro registro para o Brasil, redescrição da espécie e considerações sobre a ocorrência e distribuição de *Isognomon* na costa brasileira. *Revista Brasileira de Zoologia*, 19(2): 611–627.
From Florida Keys localities: *Isognomon alatus, I. bicolor*.

DOMANESCHI, O. & E. K. SHEA, 2004, Shell morphometry of western Atlantic and Indo-West Pacific *Asaphis*; functional morphology and ecological aspects of *A. deflorata* from Florida Keys, U.S.A. (Bivalvia: Psammobiidae). In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 249–275.
Asaphis deflorata cited from West Summerland Key [material from this study].

^{G}EDWARDS, C. E., 1968a, Looe Key have everything, almost. *Seafari* [*Palm Beach County Shell Club Newsletter*], 10(12): 1–4.
79 species were collected in two trips to Looe Key in November 1968 (plus a short stop at American Shoals) including *Chama florida*, *Chlamys sentis*, *Pinna carnea*, *Spondylus ictericus*, and from cracking rocks: *Botula fusca*, *Cummingia* (*sic*) *antillarum*, *Gastrochaena hians*, *Lithophagis* (*sic*) *nigra*, *Petricola lapicida*.

^{G}EDWARDS, C. E., 1968b, Snorkeling at Bahia Honda. *Miami Malacological Society Quarterly*, 2(2): 2–5.
From a collecting trip off oceanside of Bahia Honda State Park in summer 1969: *Arca imbricata, A. zebra, Arcopsis adamsi, Barbatia domingensis, Chlamys sentis, Codakia orbicularis, Isognomon radiatus, Lima pellucida*. Reprinted with minor modifications in *Of Sea & Shore*, 7(3): 167–168.

^{G}EDWARDS, C. E., 1969, Off Tavernier on the reefs. *Seafari* [*Palm Beach County Shell Club Newsletter*], 11(7): 2–4.
From the south end of Molasses Reef in May 1969: *Chama florida, Chlamys imbricata, C. ornata, C. sentis*.

^{G}EDWARDS, C. E., 1970, Off Key West's Key Wester [Motel]. *Seafari* [*Palm Beach County Shell Club Newsletter*], 12(8–9): 6–7.
Collected near Key West during the 1970 American Malacological Union annual meeting: *Arca imbricata*, 5 spp. of ark shells, and large and small *Chama* spp.

^{G*}EDWARDS, C. [E.], 1980, Convention shelling and other thoughts ... *Conchologists of America Bulletin*, (21): 3, 8, 13.
From the Keys during the Conchologists of America Convention in Key West, shortly after Hurricane Allen, on Geiger Key: *Arca cancellaria, A. zebra, Brachidontes modiolus, Codakia orbicularis, Periglypta listeri, Tellina fausta, T. radiata*. A small unidentified Pectinidae was also mentioned, as specimens presented to banquet attendees.

^{G}EDWARDS, C. E., 1987, Key West/Marquesas Keys trip. *The Busycon* [*Broward Shell Club, Ft. Lauderdale, Florida*], 22(8): 5.
Account of shelling trip on 16 May 1987, listing identifiable species by common names

only: Mytilidae, and "pearly-inside Oyster Shells".

EMERSON, W. K. & M. K. JACOBSON, 1976, *The American Museum of Natural History guide to shells; land, freshwater, and marine, from Nova Scotia to Florida*. Alfred A. Knopf, New York. 482 + xviii pp., 47 pls.
With distributions including Florida Keys (or specific localities): *Botula fusca, Chione grus, Cumingia antillarum, Isognomon bicolor, Lithophaga antillarum, L. aristata, L. nigra, Noetia ponderosa, Pseudocyrena floridana, Tellina fausta, Transennella cubaniana. Atrina seminuda* is "strangely absent" from the Keys.

G*EUBANKS, L., 1964, A shell collector's vacation in the Florida Keys. *Texas Conchologist*, 1(1): 3–4.
From a shelling trip, at unspecified localities in the Keys: *Anadara nobilis* (*sic*), *Arcopagia fausta, Barbatia cancellaria, Chama congregata, C. macerophylla, Chlamys sentis, Codakia orbicularis, Glycymeris pectinata, Lima lima, L. pellucida, Lucina pensylvanica, Papyridea soleniformis, Pseudochama radians, Pteria colymbus.*

FORBES, M. L., 1964, Distribution of the commensal oyster, *Ostrea permollis*, and its host sponge. *Bulletin of Marine Science of the Gulf and Caribbean*, 14(3): 453–464.
Ostrea permollis from off Molasses Reef in UMML collection (based on G. L. Voss, pers. comm.).

GFOSTER, R. W., 1945, The Museum of Comparative Zoology – Burry Marine Museum Expedition of 1944. *The American Malacological Union, News Bulletin and Annual Report, 1944–1945*: 5.
An account of dredging operations off the "Lower Florida Keys" including 40 stations from Carysfort Light to Molasses Reef, and from Sombrero Light to Looe Key, depths 21–117 fms, July–Aug. 1944, *M/M L. A. Burry* [Pompano, Florida], yielded 4,500 lots and ~350 species, including: *Modiolus politus sagittatus, Pecten tereinus.* Conspicuous for the number of species and abundance of specimens were Pectinidae, Cardiidae, Aloididae.

GFRUMAR, F., 2000, *Treasures from South Florida*. The Greater St. Louis Shell Club web site, http://www.stlshell.com/members/FrankFumar/dredging_off_the_florida keys.htm; last modified June 14, 2000; last accessed April 12, 2001, 2 pp.
From deep water off the Florida Keys, illustrated by color photographs: *Amusium laurenti, Chlamys benedicti.*

GGAERTNER, N. J., 1978, Florida shelling adventure. *Of Sea & Shore*, 9(2): 86.
From Bahia Honda Key, 1948: "40 different species", including egg cockles, mussels, sunrise clams, turkey wings. Also gives a description of shells collected at Bahia Honda and shown to the author by a shop owner in Cocoa, Florida, including Lion's Paws.

*GILMOUR, T. H. J., 1990, The adaptive significance of foot reversal in the Limoida. Pp. 249–263, in: B. S. MORTON, ed., *Proceedings of a memorial symposium in honor of Sir Charles Maurice Yonge (1899–1986), Edinburgh, 1986*. Hong Kong University Press, Hong Kong. viii + 355 pp.
Material includes *Ctenoides scabra* from Big Pine Key.

*GINSBURG, R. N., 1953, Intertidal erosion on the Florida Keys. *Bulletin of Marine Science of the Gulf and Caribbean*, 3(1): 55–58.
Key Largo Limestone erosion is described from Indian Key, Key Largo Sound, and the bay side of Key Vaca. *Arca barbata, Mytilus* (*Brachidontes*) *exustus*, and *Acanthopleura granulata* are attributed to the "generally shallow burrows". *Arca* is stated to "almost buried in the rock". No regional differences among the three localities are provided.

GGODCHARLES, M. F. & W. C. JAAP, 1973, Fauna and flora in hydraulic clam dredge collections from Florida west and southeast coasts. *Florida Department of Natural Resources, Marine Research Laboratory, Special Scientific Report*, 40: 89 pp.
Report of taxa collected during an exploratory clam survey, including stations in Hawk Channel from Indian Key to Fowey Rocks. Raw data are presented for stations and taxa but no analysis is offered. Area III, charts 1249 (3.1–5.2 m) and 1250 (4.0–4.6 m) include 13 box dredges by the *R/V Hernan Cortez,* oceanside along the Upper Florida Keys, in 1971. Chart 1249 shows stations 619 through 625, off Key Largo, between shore and the 10 m isobar. Chart 1250 shows stations 617–619, off the Matecumbes, also within the 10 m isobar. W. G. Lyons identified the mollusks; "all live specimens". Bivalves include: *Anadara notabilis, Antigona listeri, Arca zebra, Argopecten gibbus, A. nucleus, Barbatia domingensis, Chama congregata, Chione cancellata, C. intapurpurea, Codakia orbicularis, Glycymeris pectinata, Laevicardium laevigatum, Lima lima, Lucina pensylvanica,*

Modiolus americanus, Pecten ziczac, Pseudochama radians, Trachycardium egmontianum, T. muricatum.

^{G}GOLDBERG, R., 1978, Shelling in the Florida Keys. *Of Sea & Shore*, 9(2): 109–110.
From a compilation of three shelling trips to the Florida Keys between January 1977 and January 1978: *Arca zebra, Chama macerophylla, Isognomon alatus, Laevicardium laevigatum, Spondylus ictericus, Tellina fausta, Ventricolaria rugatina.* A change in molluscan fauna was noted between January 1977 and January 1978 at Indian Key Fill, attributed to a widening project for the Overseas Highway. Ohio Key oceanside is described as one of the best collecting sites in the Keys.

GRAU, G., 1955, A rectification of *Pecten* nomenclature. *The Nautilus*, 68(4): 113–115.
The holotype of *Pecten tereinus* Dall [= *P. chazaliei* Dautzenberg] is cited as from off Key West.

^{G}GUNDERSEN, R., 1997, Blinded by the color. *American Conchologist*, 25(4): 19.
Distinguishing characters of *Caribachlamys sentis* and *C. ornata*, from the Florida Keys.

HARRY, H. W., 1985, Synopsis of the supraspecific classification of living oysters (Bivalvia: Graphaeidae and Ostreidae). *The Veliger*, 28(2): 121–158.
Teskeyostrea weberi.

^{G}HAVILAND, E., 1994, Tellin' it like it is. *Of Sea & Shore*, 17(1): 21–22.
From Keys localities: *Tellina radiata*, "candy stripe tellin" (later called *T. similis*).

HAYAMI, I., 1984, *Natural history and evolution of Cryptopecten (a Cenozoic-Recent pectinid genus).* University of Tokyo Press, Tokyo. ix + 149 pp., 13 pls.
Cryptopecten phrygium from off Lower Keys, from AMNH collection lots.

^{G}HAYES, H. L., 1972, *The Recent Pteriidae (Mollusca) of the western Atlantic and eastern Pacific Oceans.* Ph.D. Dissertation, Georgetown University, Washington, D.C. 202 pp., 14 pls.
Material examined (with localities and repositories) includes *Pinctada imbricata, Pteria colymbus, P. hirundo vitrea, P. longisquamosa.*

HEMMEN, J. & C. HEMMEN, 1979, Beiträge zur Kenntnis der Meeresmollusken-Fauna der Karibischen See. Grenada. *Jahrbuch, Nassauischer Verein für Naturkunde*, 104: 137–172.
Annotated species list, based on own collecting and literature. Those with specific reference to Florida Keys occurrence include *Codakia (Ctena) pectinella.*

HENDERSON, J. B., 1911, Extracts from the log of the *Eolis*. *The Nautilus*, 25(6): 71–72; 25(7): 81–82.
From Sand Key, 1910: *Avicula, Lima, Lithodomus, Pecten.* From off Key West, 1911: pectens. From Tortugas Islands, 1911: Limas, Pectens.

*HENDERSON, J. B., 1913, Marine shells from drift on Upper Matecumbe Key, Florida. *The Nautilus*, 27(5): 59–60.
From shore-drift collecting during *Eolis* cruises in May 1913: *Chione grus, Codakia orbiculata, Pleuromeris tridentata, Transenella (sic) stimpsoni.*

HENDLER, G., J. E. MILLER, D. L. PAWSON & P. M. KIER, 1995, *Sea stars, sea urchins, and allies: Echinoderms of Florida and the Caribbean.* Smithsonian Institution Press, Washington, DC. 390 pp.
Molluscan associations with Florida Keys echinoderms [based on literature and original research at Looe Key] include: commensal bivalve on *Ophiophragmus septus* (figured); juvenile Leptonacea symbiotic on *Amphioplus sepultus*; *Mysella* sp. C symbiotic on arm spines of *Amphipholis gracillima*; *Neaeromya* sp. commensal on *Meoma ventricosa.*

^{G}HERTWECK, V., 1977, The Sarasota Shell Show – 1977. *Of Sea & Shore*, 8(1): 36–38.
Shell of the show, *Xenophora conchyliophora* with a perfect *Glycymeris pectinata* attached, was found by Mr. & Mrs. Ernest Bradley [Bradenton, Florida] at Key West.

HOWARD, J. F., D. L. KISSLING & J. A. LINEBACK, 1970, Sedimentary facies and distribution of biota in Coupon Bight, Lower Florida Keys. *Geological Society of America Bulletin*, 81: 1929–1946.
An excellent description of Coupon Bight. Whole or fragmented molluscan shells form 22–87% of sediments in all parts of Coupon Bight. "From approximately six liters of unconsolidated sediment from each station sieved through a screen, 4,200 specimens assigned to 94 species of small mollusks were gathered and identified. Of these, 57 percent were bivalves and the remainder gastropods." No overall species list is provided, and no mention is made of voucher specimens. Identifications as per Abbott (1954) and Perry (1940). An open bay assemblage is dominated by bivalves, especially *Chione cancellata*, *Laevicardium*

mortoni, *Nucula proxima*, and *Pitar* cf. *fulminata*. Restricted bay includes *Anomalocardia cuneimeris*, *Parastarte triquetra*, and *Polymesoda floridana*. Baymouth Bank includes *Tellina* cf. *mera*. Tidal channel fauna includes *Codakia orbiculata*, *Lucina nassula*, and *Tellina candeana*. Specifically mentioned as absent (while present in comparable Inner Reef Tract waters) are *Arca umbonata, A. zebra, Atrina rigida, Barbatia cancellaria*, and *Codakia orbicularis*.

^{G}HUDSON, J. H., D. M. ALLEN & T. J. COSTELLO, 1970, The flora and fauna of a basin in Central Florida Bay. *United States Fish and Wildlife Service Special Scientific Report – Fisheries*, 604, iii + 14 pp.

Sampling sites, 1965–1968, were mudbanks surrounding Porpoise Lake (triangular depression, surrounded by mudbanks, bordered by Foxtrot Keys, Panhandle Key and Bob Allen Key; bayside of Indian Key Fill, next row of keys bayside of Shell Key) in the southern part of central Florida Bay. The authors used a wide variety of techniques (sled-mounted suction sampler, slednet, pushnet, beach seine, castnet, hand collecting, roller-frame trawl from bait-shrimp trawler, snorkeling, hook and line); maximum depth of "lake" 2.1 m; "… we did not attempt to retain plants and animals less than 5 mm long or wide." (p. 4). Robert C. Work is given as the specialist who identified the mollusks. Included are *Anomalocardia cuneimeris, Arcopsis adamsi, Argopecten irradians concentricus, Brachidontes exustus, Cardita floridana, Chione cancellata, Codakia orbiculata, Laevicardium mortoni, Lima pellucida, Lyonsia hyalina floridana, Pinctada radiata, Tellina lineata, T. similis, T. tampaensis, Transennella cubaniana, T. stimpsoni.*

^{G}*HUGHES, M., 1976, Field trip to the Keys. *Conchologists of America Bulletin*, (6): 4–5.

From the Keys, June 1975, by Palm Beach and Broward Shell Clubs: *Chlamys sentis*.

HUMFREY, M., 1975, *Seashells of the West Indies – A guide to the marine molluscs of the Caribbean*. Taplinger Publishing Company, New York. 351 pp., 32 color pls.

With distributions including Florida Keys (or specific localities): *Aequipecten lineolaris, Antigona* (*Ventricolaria*) *rigida, Chama sarda, Chione paphia, Isognomon bicolor, Phacoides muricatus, Tellina punicea, Trachycardium magnum.*

HUTSELL, K. C., L. L. HUTSELL & D. L. PISOR, 1997, *Registry of world record size shells*. Snail's Pace Productions, San Diego, California. ii + 101 pp.

Florida Keys specimens among world size records: *Arca zebra, Caribachlamys sentis, Isognomon alatus, Lyropecten antillarum, Mercenaria campechiensis, Pteria colymbus, Tellina magna.*

*INGHAM, R. E. & J. A. ZISCHKE, 1977, Prey preferences of carnivorous intertidal snails in the Florida Keys. *The Veliger*, 20(1): 49–51.

Included as molluscan prey species: *Brachidontes exustus, Isognomon bicolor,* and *I. radiatus.*

|ISHMAN, S. E., G. L. BREWSTER-WINGARD, D. A. WILLARD, T. M. CRONIN, L. E. EDWARDS & C. W. HOLMES, 1996, Preliminary paleontologic report on Core T-24, Little Madeira Bay, Florida. *United States Geological Survey Open-File Report* 96–543, 47 pp. Electronic version available at http://pubs.usgs.gov/pdf/of/ofr96543.html; last accessed 12 September 2003.

This work is here excluded as outside our defined area, which extends roughly half-way between the Florida Keys island chain and the tip of peninsular Florida. Little Madeira Bay is north of this limit.

^{G}IVERSEN, E. S. & M. A. ROESSLER, 1969, *Survey of the biota of Card Sound*. Report to the Florida Power and Light Company. Institute of Marine and Atmospheric Sciences, University of Miami, Miami, Florida. 51 pp. Also available at: http://www.aoml.noaa.gov/general/lib/cedardoc.html; last accessed 4 April 2003.

A biotic survey of Card Sound in March–May 1969 included otter-trawl and plankton samples to assess various ecological zones, including mangroves, shallows and deep basins of the Sound. *Aequipecten muscosus, Americardia media, Arca imbricata, A. umbonata, A. zebra, Argopecten irradians* [an exploited species; also as *Aequipecten* or *Aeguipecten* (*sic*)], *Atrina rigida*, *Barbatia cancellaria*, bivalve unid., *Brachidontes exustus* [also as *Trachidontes* (*sic*)], *Chione cancellata, Codakia orbiculata, Lima pellucida, Lyropecten antillarum, Modiolus americanus, Pinctada imbricata, Pteria colymbus, Trachycardium* sp.

^{G}JAAP, W. C., 1984, *The ecology of the South Florida coral reefs: a community profile*. United States Fish and Wildlife Services, FWS/OBS – 82/08, 138 pp.

Describes the impact by divers and aquarium collectors in the Florida Keys as "quite heavy

on colorful and distinctive species such as ... thorny oyster (*Spondylus* spp.)".

JACOBSON, M. K. & L. HERNANDEZ, 1973, An unusual habitat for the rough file shell, *Lima scabra* (Born, 1780). *The Veliger*, 16(1): 85–86, 1 pl.
Lima scabra cited from the Dry Tortugas.

JINDRICH, V., 1969, Recent carbonate sedimentation by tidal channels in the Lower Florida Keys. *Journal of Sedimentary Petrology*, 39(2): 531–553.
Molluscan shells form a major constituent of the sediments in Bluefish Channel, north of Key West, carbonate bank on Pleistocene bedrock: *Arca umbonata, Chione cancellata, Codakia orbicularis.*

*JOHNSON, C. W., 1934, List of marine Mollusca of the Atlantic coast from Labrador to Texas. *Proceedings of the Boston Society of Natural History*, 40(1): 1–204.
From Florida Keys localities: *Antigona* (*Circomphalus, Ventricola*) *rigida, A.* (*C., V.*) *strigillina, Arca auriculata, Chama sarda, Chione* (*Timoclea*) *granulata, C. pubera, C.* (*T.*) *pygmaea, Codakia* (*Jagonia*) *orbiculata filiata, C.* (*J.*) *orbiculata recurvata, C.* (*J.*) *pectinella, Cochliolepis parasitica, Congeria rossmässleri, Corbula* (*Caryocorbula*) *cymella, Donax denticulata, Dosinia concentrica, Ervilia concentrica, E. nitens, Gouldia parva, Kellia rubra, Leiomya* (*Plectodon*) *granulata granulata, L.* (*P.*) *g. velvetina, Lucina* (*Lucinisca*) *muricata, Myrtea* (*Eulopia*) *sagrinata, Nuculana verrilliana, Pecten* (*Chlamys*) *imbricatus, P.* (*Lyropecten*) *antillarum, P.* (*Plagioctenium*) *nucleus, P.* (*Euvola*) *tereinus, Pedalion listeri, P. semiaurita, Periploma angulifera, P. tenera, Petricola lapicida, Poromya granulata granulata, Protocardia tincta, Pteria hirundo vitrea, Strigilla pisiformis, Tellina* (*Arcopagia, Eurytellina*) *angulosa, T.* (*Angulus, Scissula*) *candeana, T.* (*A., S.*) *iris, Thracia corbuloides, T. stimpsoni, Tivela mactroides, Transenella* (*sic*) *conradina, T. cubaniana, T. stimpsoni.*

JOZEFOWICZ, C. J. & D. Ó FOIGHIL, 1998, Phylogenetic analysis of Southern Hemisphere flat oysters based on partial mitochondrial 16S rDNA gene sequences. *Molecular Phylogenetics and Evolution*, 10: 426–435.
Includes *Ostreola equestris* (as *Teskeyostrea weberi*, misidentification indicated by P. Baker, unpub., in Kirkendale et al., 2004) from Big Pine Key.

KIRKENDALE, L., T. LEE, P. BAKER & D. Ó FOIGHIL, 2004, Oysters of the Conch Republic (Florida Keys); a molecular phylogenetic study of *Parahyotissa mcgintyi, Teskeyostrea weberi* and *Ostreola equestris*. In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 309–326.
From Florida Keys localities: *Dendostrea frons, Ostreola equestris, Hyotissa mcgintyi, Pinna* sp., *Teskeyostrea weberi* [material from this study].

KISSLING, D. L., 1965, Coral distribution on a shoal in Spanish Harbor, Florida Keys. *Bulletin of Marine Science*, 15(3): 599–611.
The most common bivalves in Spanish Harbor Channel are *Arca umbonata, Atrina rigida*, and *Codakia orbicularis*.

KISSLING, D. L., 1977a, [Partial list of organisms ... from examination of patch reefs south of Boca Chica, Newfound Harbor Keys and at Mosquito Banks]. Pp. 181–182, in: H. G. MULTER, *Field guide to some carbonate rock environments – Florida Keys and western Bahamas,* new ed. Kendall/Hunt Publishing Company, Dubuque, Iowa. 415 pp. + 10 maps.
Arca umbonata, A. zebra, Barbatia sp., *Brachiodontes recurvus, Codakia orbicularis, Isognomen* (*sic*) *alatus, Lithophaga antillarum.*

KISSLING, D. L., 1977b, [A partial list of organisms that inhabit the surfaces and margins of Rodriguez Bank]. P. 176, in: H. G. MULTER, *Field guide to some carbonate rock environments – Florida Keys and western Bahamas,* new ed. Kendall/Hunt Publishing Company, Dubuque, Iowa. 415 pp. + 10 maps.
Arca umbonata, Atrina rigida, Barbatia cancellaria, Chlamys sentis, Codakia orbicularis, Pinctada radiata, Tellina lineata.

KLEEMANN, K. H., 1983, Catalogue of Recent and fossil *Lithophaga* (Bivalvia). *Journal of Molluscan Studies*, Suppl. 12: 1–46.
With distribution including Florida Keys: *Lithophaga nigra*.

KNUDSEN, J. W., 1982, Anomalodesmata (Mollusca, Bivalvia) from Saba Bank, the Caribbean region. *Proceedings, Koninklijke Nederlandse Akademie van Wetenschappen*, Ser. C, 85(1): 121–146.
Cardiomya alternata is included, citing Dall's (1881) Florida Keys record.

*KRAEUTER, J. N., 1973, Notes on mollusks *Ostrea* and *Siphonaria* from Georgia (U.S.A.). *The Nautilus*, 87(3): 75–77.
Ostrea permollis from Molasses Reef.

KRAUSE, M. K., W. S. ARNOLD & W. G. AMBROSE, JR., 1994, Morphological and genetic variation among three populations of calico scallops, *Argopecten gibbus*. *Journal of Shellfish Research*, 13(2): 529–537.

Argopecten gibbus, from the vicinity of the Marquesas Keys, is compared to populations from Cape Canaveral and North Carolina.

^{G}KRISBERG, M. F., 1993, A holiday observation trip to the Keys. *New York Shell Club Notes*, no. 327: 11.

From the Lower Florida Keys: *Chione cancellata, Chlamys sentis, Lima lima, Papyridea soleniformis, Tagelus divisus, Tellina fausta, T. lineata, T. listeri, T. radiata*.

LAWSON, B., 1993, *Shelling San Sal*. Bahamian Field Station, San Salvador, Bahamas. ix + 63 pp.

With distribution including Florida Keys [accompanied by black-and-white sketch]: *Trachycardium magnum*.

^{G}LEE, V., 1969, After the Lower Keys show. *Seafari* [*Palm Beach County Shell Club Newsletter*], 11(5): 8–9.

Collected from various localities in the Lower Florida Keys: *Anomalocardia brasiliensis* (*sic*), *Arca imbricata, Brachidontes citrinus, Chama macerophylla, Codakia orbicularis, Codakia orbiculata, C. o.* ?form *filiata, Glycymeris pectinatus, Lima pellucida, Pinctada radiata, Pseudochama radians variegata, Tellina similis*.

^{G}LERMOND, N. W., 1936, *Check list of Florida marine shells*. Privately published, Gulfport, Florida. 56 pp.

247 Florida Keys bivalve names (= 216 species here considered valid), compiled from personal collections (1913–14 through date of publication) and records from various collectors (A. G. Reynolds, C. B. Lungren, C. C. Allen, D. L. Emery), professionals (H. Van Hyning, Florida State Museum, Gainesville; W. J. Clench, MCZ; C. T. Stimpson, "veteran naturalist" of Little River, Florida; H. A. Pilsbry and E. G. Vanatta, ANSP; W. H. Dall and W. B. Marshall, USNM). From "beaches, reefs, and in the bays" of the Florida Keys, excluding deep water forms seldom encountered by collectors [covered by Dall, 1889a, 1903b; Johnson, 1934]: *Abra aequalis, A. lioica, Anatina lineata, A.* (*Raeta*) *canaliculata, Animalocardia* (*sic*) *brasilana* (*sic*), *A. cuneimeris, Anomia simplex, Antigona listeri, A. rigida, A. strigillina, Apolymetis intasriata* (*sic*), *Arca admsi* (*sic*), *A. auriculata, A. barbata, A. campechiensis americana, A. candida, A. chemnitzi, A. imbricata, A. incongrua, A. occidentalis, A. ponderosa, A. reticulata, A. secticostata, A. transversa, A. umbonata, Asaphis deflorata, Astarte nana, Asthenothaerus hemphillii, Avicula atlantica, Basterotia quadrata, B. q. granatina, Botula castanea, B. fusca, Cardita floridana, Cardium arcinella* [but corrected to *Chama* in this copy, signed by Lermond], *C. isocardia, C. magnum, C. muricatum, C.* (*Hemicardium*) *medium, C.* (*Laevicardium*) *laevigatum, C.* (*L.*) *serratum, C.* (*Papyridea*) *semisulcatum, C.* (*P.*) *spinosum, C.* (*Protocardia*) *peramabilis, C.* (*Trigoniocardia*) *antillarum, Chama congregata, C. macerophylla, C. sarda, Circe cerina, Congeria rossmassleri, Coralliophaga coralliophaga, Corbula barrattiana, C. contracta, C. cymella, C. dietziana, C. disparillis* (*sic*), *C. nasuta, C. swiftiana, Crassatellites gibbsii, Crenella divaricata, Cumingia coarctata, C. tellinoides, Cuspidaria* (*Cardiomya*) *costellata, Cyclinella tenuis, Cytherea albida, C. hebraea, C. simpsoni, C.* (*Dione*) *dione, C.* (*Tivela*) *mactroides, C.* (*Transennella*) *conradiana* (*sic*), *C.* (*T.*) *cubaniana, Dacrydium vitreum, Donax denticulata, D. fossor, D. f. protractus, D. roemeri, D. tumidus, D. variabilis, Dosinia concentrica, D. discus, D. elegans, Egeta protexta, Ervilia concentrica, E. nitens, Gastrochaena cuneiformis, G. ovata, G. rostrata, Gemma purpurea, Glycymeris americana, G. lineata, G. pectinata, G. pennacea, Gouldia cerina, G. mactracea, G. parva, Heterodonax bimaculata, Iphigenia brasiliana, Lima hians, L. inflata, L. lima, L. scabra, L. tenera, Limatula confusa, Lithodomus antillarum, L. aristata, L. bisulcatus, L. nigra, Lucina pennsylvanica* (*sic*), *L.* (*Anodontia*) *jamaicensis, L.* (*A.*) *trisulcata, L.* (*Bellucina*) *amiantus, L.* (*Divaricella*) *dentata, L.* (*Jagonia*) *costata, L.* (*J.*) *orbiculata, L.* (*J.*) *o. filiata, L.* (*J.*) *o. recurvata, L.* (*J.*) *pectinella, L.* (*Loripinus*) *edentula, L.* (*L.*) *e. chrysostoma, L.* (*L.*) *schrammi, L.* (*Lucinisca*) *muricata, L.* (*Parvilucina*) *crenella, Lyonsia beana, Macoma brevifrons, M. cerina, M. constricta, M. leptonoides* (*sic*), *M. cimula* (*sic*), *M. tenta, M. t. souleyetiana, Macrocallista maculata, M.* (*Callista*) *gigantea, Mactra fragilis, Margaritifera radiata, Martesia caribaea, M. cuneiformis, M. striata, Modiolaria lateralis, M. arborescens, M. demissus, M. d. granosissimus, M. opifex, M. sulcatus, M. tulipus, Mulinia lateralis, Mytilus exustus, M. recurvus, Nucula*

aegeensis, Nuculana carpenteri, N. solidula, N. verrilliana, Ostrea cristata, O. frons, O. verginica (*sic*), *Pecten acanthodes, P. antillarum, P. exasperatus, P. gibbus, P. heliacus, P. imbricatus, P. nodosus, P. n. fragosus, P. nucleus, P. ornatus, P. raveneli, P. sentis, P. tereinus, P. ziczac, Pedalion bicolor, P. listeri, P. semiaurita, P.* (*Perna*) *alata, Periploma angulifera, P. tenera, Petricola pholadiformis, P. lapicida, Pholas campechiensis, P.* (*Barnea*) *costata, P.* (*B.*) *truncata, Pinna carnea, P. rigida, P. serrata, Plicatula gibbosa, Pitar encymata* (*sic*), *P. fulminata, Polodesmus* (*sic*) *decipiens, Poromya granulata, Semele bellastriata, S. nuculoides, S. proficua, S. purpurascens, Solemya occidentalis, Spisula solidissima similis, Spondylus americanus, S. echinatus, Strigilla carnaria, S. flexuosa, S. pisiformis, S. rombergii, Tagelus divisus, Taras notata, T. nucleiformis, T. punctata, T. soror, Tellidora cristata, Tellina aequistriata, T. alternata, T. angulosa, T. candeana, T. crystallina, T. decora, T. fausta, T. georgiana, T. gouldi, T. interrupta, T. iris, T. lintea, T. lineata, T. martinicensis, T. mera, T. modesta, T. radiata, T. sayi, T. squamifera, T. striata, T. tenera, T. versicolor, Teredo clappi, T. thomsoni, Thracia corbuloides, Tivela mactroides, Transenella* (*sic*) *conradina, T. cubaniana, T. stimpsoni, Venus campechiensis, V. mercenaria, V.* (*Chione*) *cancellatus, V.* (*C.*) *granulatus, V.* (*C.*) *grus, V.* (*C.*) *latiliratus, V.* (*C.*) *mazyckii, V.* (*C.*) *paphia, V.* (*C.*) *pubera, V.* (*C.*) *pygmaeus, V.* (*C.*) *subrostrata, Verticordia ornata, Xylotrya fimbriata.*

LEVY, J. M., M. CHIAPPONE & K. M. SULLIVAN, 1996, Invertebrate infauna and epifauna of the Florida Keys and Florida Bay. Pp. 1–166, in: *Site characterization for the Florida Keys National Marine Sanctuary and environs*, Vol. 5. The Nature Conservancy, Florida and Caribbean Marine Conservation Science Center, University of Miami & The Preserver, Zenda, Wisconsin.

Initially lists 5 classes, 26 orders, 31 families, and 712 species of mollusks in the Florida Keys, based on "24" uncited and unacknowledged references. Claims that (p. 24) "Previous studies have shown that mollusks are well-represented and serve important roles in benthic communities of the Florida Keys and Florida Bay (Appendices 7–8). Except for a few ecological inventories that include mollusks, there is a lack of comprehensive, ecosystem-wide species inventories for species in the Florida Keys." Appendix 7 gives a systematic list of mollusks "from southern Florida" [not restricted to Florida Keys], listing 359 species of gastropods, 174 bivalves, 13 cephalopods, 17 polyplacophorans, and 8 scaphopods, or a total of 571 species (not 712 species as cited earlier). Appendix 8 gives an alphabetical listing of molluscan species "recorded in southern Florida".

LINEBACK, J. A., 1977, Macrofaunal and floral distributions and controls in Coupon Bight, Lower Florida. P. 96, in: H. G. MULTER, *Field guide to some carbonate rock environments – Florida Keys and western Bahamas,* new ed. Kendall/Hunt Publishing Company, Dubuque, Iowa. 415 pp. + 10 maps.

From Coupon Bight: *Anomalocardia cuneimeris, Chione cancellata, Codakia orbiculata, Laevicardium mortoni, Lucina nassula, Nucula proxima, Parastarte triquetra, Pinctada radiata, Pitar* cf. *fulminata, Polymesoda floridana, Tellina candeana, T.* cf. *mera.*

LONG ISLAND SHELL CLUB, 1988, *Seashells of Long Island, New York: a guide to their identification and local status.* Long Island Shell Club, New York. 209 pp.

With distributions including Florida Keys: *Noetia ponderosa.*

GLYMAN, F., 1943, About finding shells. *Shell Notes*, 1(4): 20.

Pecten sentis and other *Pecten* (*Chlamys*) in Florida Keys, usually under stones, corals, inside rotten rock and coral. Also *Lima, Lithophaga* while turning large slabs of stone or plate coral. *Pedalion listeri* on underside of flat stones between high and low water marks in Lower Keys, especially near "the long bridge" [presumably the Seven-Mile Bridge].

GLYMAN, F., 1944a, Expect to find these shells living as stated. *Shell Notes*, 1(7): 49.

Illustrated (for purchase) from the Florida Keys: *Pecten imbricatus, P. nucleus, P. ornatus, P. sentis.*

GLYMAN, F., 1944b, Shell collector's paradise. *Shell Notes*, 1(8): 57–58, 1 map.

A map of Indian Key includes a map of shallow habitats as a guide to sampling methods and expected species. On the northern side is sandy bottom and boggy flats (*Codakia*, etc.). On the northeastern side is grassy bottom. On the eastern side are small loose rock (pectens, etc.) and grassy bottom. On the southeastern side is jagged rock (*Arca*, etc.). On the southern side is rock

bottom (many shelled species). On the western side are grassy bottom and boggy flats (*Codakia*, etc.).

GLYMAN, F., 1944c, Pearls are sometimes found in the *Pinna* shells ... *Shell Notes*, 1(9): 67.
Pinna carnea, almost unknown in America, except the Florida Keys, on soft mud banks.

GLYMAN, F., 1945, A report of a trip to the Florida Keys. *Shell Notes*, 1(14): 120–125.
Off Key Largo, 26 July 1945, at a known reef that sticks out of the water at low tide, *Pecten* (*Chlamys*) *Mildredaea* (*sic*) [measuring 40 x 35 mm, from an additional paragraph on p. 126].

GLYMAN, F., 1946, *Pinna carnea*. *Shell Notes*, 1(17): 151.
Giant 10–12 inch specimens sometimes occur on certain flats in the Florida Keys.

GLYMAN, F., 1947a, A trip to the Florida Keys from the log book of the boat *Junonia*. *Shell Notes*, 1(19): 170–175.
Modiolus tulipus on the beach at Duck Key, January 1, 1947.

GLYMAN, F., 1947b, A report of our second shell hunting trip to the Florida Keys in 1947 ... from the log book of the *Junonia*. *Shell Notes*, 1(20): 187–194.
By dredging in February 1947: *Arca occidentalis* at Rodriguez Key, *Glycimerus* (*sic*) *pectinatus* in Key Largo Sound.

GLYMAN, F., 1948a, *Pecten imbricatus* ... *Shell Notes*, 2(2–3): 36.
Pecten imbricatus categorized as the rarest species of *Pecten* in shallow waters in Florida, often found on the outer reefs of the Florida Keys.

GLYMAN, F., 1948b, Barrier reef list. *Shell Notes*, 2(5): 72–74.
An incomplete list of mollusks taken during a four-day cruise aboard the *Junonia*, on the "barrier reef" off the Florida Keys: *Pecten sentis, P. imbricatus, Lima lima, Lithophaga antillarum*.

GLYMAN, F., 1949a, As to plate, outer reef shells (Fla. Keys). 1. *Shell Notes*, 2(7–9): 110–111.
Illustrated (for purchase) from the Florida Keys: *Pecten sentis* red form and purplish form.

GLYMAN, F., 1949b, As to plate, outer reef shells (Fla. Keys). 2. *Shell Notes*, 2(7–9): 122–123.
Illustrated (for purchase) from the Florida Keys: *Arca barbata* outer reef form and inshore form.

GLYMAN, F., 1949c, As to plate, outer reef shells (Fla. Keys). 4. *Shell Notes*, 2(7–9): 128–129.
Illustrated (for purchase) from the Florida Keys: *Semele bellastriata, S. proficua, S. purpurascens, S. radiata*.

GLYMAN, F., 1950, Reef shell collecting. *Shell Notes*, 2(10–12): 128–129.
Further comments about Bippus collecting trip [off Upper Keys, June 1950; see Bippus, 1950]: red *Pecten sentis*.

GLYMAN, F., 1951, Dredging for shells out from Key Largo. *Shell Notes*, 2(13–15): 128–129.
Dredging at 50+ ft., 5 April 1951: black pecten.

GLYONS, W. G., 1999, Responses of benthic fauna to salinity shifts in Florida Bay: evidence from a more robust sample of the molluscan community. Pp. 47–49, in: *Programs and Abstracts, 1999 Florida Bay and Adjacent Marine Systems Science Conference*, Key Largo, Florida.
From sampling in Florida Bay, 1994 and 1996: *Brachidontes exustus*, dominating in 1994.

GLYONS, W. "S" (err. pro G.), 1998, Changes in benthic molluscan assemblages in Florida Bay, 1994–1996. Pp. 177–187, in: T. V. ARMENTANO, ed., *Proceedings, Conference on Ecological and Hydrological Assessment of the 1994–95 High Water Conditions in the Southern Everglades*, Miami, Florida, 22–23 August 1996.
From sampling in Florida Bay, 1994 and 1996: *Anomalocardia auberiana, Brachidontes exustus, Chione cancellata, Tellina tampaensis*.

G*LYONS, W. G. & J. F. QUINN, JR., 1995, Appendix J. Marine and terrestrial species and algae: Phylum Mollusca. Pp. J-10–J-26, in: *Florida Keys National Marine Sanctuary Draft Management Plan / Environmental Impact Statement, Vol. III. Appendices*. National Oceanographic and Atmospheric Administration, Silver Spring, Maryland.
630 species of marine mollusks are listed (undocumented) from the Florida Keys, including Florida Bay to Cape Sable (W. G. Lyons, pers. comm.); 423 species are gastropods. 207 species are bivalves: *Abra aequalis, Aequipecten acanthodes, Americardia guppyi, A. media, Anadara notabilis, Anomalocardia auberiana, Arca imbricata, A. zebra, Arcinella cornuta, Arcopsis adamsi, Argopecten gibbus, A. irradians, A. nucleus, Asaphis deflorata, Asthenothaerus balesi, Atrina rigida, A. seminuda, Barbatia cancellaria, B. domingensis, B. tenera, Basterotia elliptica, B. quadrata, Botula fusca, Brachidontes domingensis, B. modiolus, Bractechlamys*

antillarum, Carditamera floridana, Carditopsis smithii, Chama congregata, C. lactuca, C. macerophylla, C. sarda, C. sinuosa, Chione cancellata, C. intapurpurea, C. latilirata, C. puber, C. pygmaea, Chlamys beneditcti, C. imbricata, C. mildredae, C. multisquamata, C. ornata, C. sentis, Codakia costata, C. orbicularis, C. orbiculata, C. pectinella, Coralliophaga coralliophaga, Crassinella lunulata, C. martinicensis, Crenella divaricata, Cumingia coarctata, Cyclinella tenuis, Dendostrea frons, Diplodonta punctata, D. semiaspera, Divaricella dentata, D. quadrisulcata, Entodesma beana, Ervilia concentrica, E. nitens, Gastrochaena hians, G. ovata, Glans dominguensis, Glycymeris decussata, G. pectinata, G. undata, Gouldia cerina, Gregariella coralliophaga, Isognomon alatus, I. bicolor, I radiatus, Laevicardium laevigatum, L. mortoni, L. sybariticum, Leporimetis intastriata, Lima lima, L. pellucida, L. scabra scabra, L. s. tenera, Linga amiantus, L. leucocyma, L. pensylvanica, Lioberus castaneus, Lithophaga antillarum, L. aristata, L. bisulcata, L. nigra, Lucina muricata, L. nassula, L. pectinata, Macoma brevifrons, Macrocallista maculata, Mactra fragilis, Malleus candeanus, Modiolus americanus, M. modiolus squamosus, Musculus lateralis, Nodipecten nodosus, Ostreola equestris, Papyridea semisulcata, P. soleniformis, Parvilucina blanda, P. multilineata, Pecten chazaliei, P. ziczac, Periglypta listeri, Petricola lapicida, Pinctada imbricata, Pinna carnea, Pitar fulminatus, P. simpsoni, Pleuromeris tridentata, Plicatula gibbosa, Polymesoda maritima, Pseudochama radians, Pteria colymbus, Pteromeris perplana, Rupellaria typica, Semele bellastriata, S. proficua, S. purpurascens, Semelina nuculoides, Solemya occidentalis, Spengleria rostrata, Spondylus americanus, S. ictericus, Strigilla carnaria, S. gabbi, S. mirabilis, Tellidora cristata, Tellina aequistriata, T. alternata, T. americana, T. angulosa, T. candeana, T. consorbrina (sic), *T. fausta, T. gouldii, T. laevigata, T. lineata, T. listeri, T. magna, T. martinicensis, T. mera, T. nitens, T. paramera, T. probina* (sic), *T. radiata, T. similis, T. squamifera, T. sybaritica, T. tampaensis, T. texana, T. versicolor, Trachycardium egmontianum, T. magnum, T. muricatum, Transennella conradina, T. cubaniana, T. stimpsoni, Ventricolaria rigida.*

MAGNOTTE, G., 1970–1979 (various versions, all undated), *Shelling & beachcombing in southern & Caribbean waters.* International Graphics, Hollywood, Florida. 96 pp. With distributions including Florida Keys (or specific localities): *Aequipecten gibbus, A. irradians, A. lineolaris, A. muscosus, Americardia media, Anadara lienosa floridana, A. notabilis, Anatina plicatella, Anodontia alba, Anomalocardia cuneimeris, Anomia simplex, Antigona listeri, Arca imbricata, A. zebra, Arcinella cornuta, Asaphis deflorata, Atrina rigida, Barbatia cancellaria, B. candida, B. tenera, Barnea truncata, Brachidontes exustus, B. recurvus, Chama congregata, C. macerophylla, C. sardo* (sic), *Chione cancellata, C. grus, C. paphia, Chlamys imbricatus, C. mildredae, C. sentis, Codakia orbicularis, Cyrtopleura costata, Dinocardium robustum, Diplodonta punctata, Dosinia discus, D. elegans, Eucrassatella speciosa, Glycymeris americana, G. decussata, G. pectinata, Iphigenia brasiliana, Isognomon alatus, I. radiatus, Laevicardium laevigatum, L. mortoni, Lima lima, L. scabra, Lithophaga antillarum, Lucina pensylvanica, Lyropecten antillarum, Macrocallista maculata, Mercenaria campechiensis, Modiolus americanus, Mulinia lateralis, Noetia ponderosa, Ostrea equestris, O. frons, Pecten ziczac, Petricola pholadiformis, Phacoides pectinata, Pinctada radiata, Pinna carnea, Pitar fulminatus, Plicatula gibbosa, Pteria colymbus, Spondylus americanus, S. gussoni, Strigilla romgergi* (sic), *Tagelus divisus, T. plebeius, Tellidora cristata, Tellina alternata, T. laevigata, T. lineata, T. listeri, T. magna, T. mera, T. radiata, T. similis, T. tampaensis, Trachycardium egmontianum, T. muricatum.* More specifically distributed is *Lyropecten nodosus* (to Dry Tortugas). According to the text, the illustrated specimens are deposited at Burry's Shell Museum, Pompano Beach, Florida.

*MARELLI, D. C., M. K. KRAUSE, W. S. ARNOLD & W. G. LYONS, 1997, Systematic relationships among Florida populations of *Argopecten irradians* (Lamarck, 1819) (Bivalvia: Pectinidae). *The Nautilus*, 110(2): 31–41.

Neither morphometric nor genetic evidence supports the distinction of *A. irradians taylorae* from *A. irradians concentricus* in Florida Bay.

^{G}MASON, L., 1969, AMU report – excerpts. *Seafari* [*Palm Beach County Shell Club Newsletter*], 11(11): 12–13.

On display during the conference at the Uni-

versity of Wisconsin – Green Bay in Marinette, Wisconsin, is *Spondylus americanus*, collected from the sides and deck of a salvaged vessel that sank near Key West.

MAURY, C. J., 1920, Recent molluscs of the Gulf of Mexico and Pleistocene and Pliocene species from the Gulf states. Part I: Pelecypoda. *Bulletins of American Paleontology*, 8(34): 35–147, pl. 1.
With distributions including Florida Keys (or specific localities): *Donax fossor, Ensis directus, Pteria vitrea, Scapharca auriculata, Thracia stimpsoni.*

MAURY, C. J., 1925, A further contribution to the paleontology of Trinidad (Miocene horizons). *Bulletins of American Paleontology*, 10(42): 153–402, pls. 12–54.
Scapharca (*Scapharca*) *auriculata*, with distribution including Key West.

*McGINTY, P. L. & T. L. McGINTY, 1957, Dredging for deep water shells in southern Florida. *The Nautilus*, 71(2): 37–47.
An account of dredging operations from the cabin-cruiser *Triton*, off Palm Beach, Sombrero Key, and Key West. Keys mollusks include: *Aequipecten lineolaris, Antigona strigillina, Aurinia schmitti, Chama lactuca, Pecten chazaliei* (*tereinus*), *Pecten phrygium.*

McGINTY, T. L., 1939, Collecting on a coral reef in Florida. *The Nautilus*, 53(2): 37–39.
From Middle Sambo Shoal, 8 mi SE of Key West: *Arca, Chama, Spondylus.*

GMcGINTY, T. L., 1942, Diving as applied to shell collecting. Pp. 32–36, in: *The American Malacological Union, The Eleventh Annual Meeting, Rockland and Thomaston, Maine, August 26–29, 1941* [*with*] *Papers Presented at the Symposium on Methods of Collecting and Preserving Mollusks,* Wednesday, August 27, 1941.
An account of "an imaginary diving trip" [but based on the author's experience?] on "a wreck of an old schooner which lies in thirty feet of water along the edge of a Florida coral reef". Using a diving helmet, the diver finds *Arca* sp., *Chama* sp., *Pecten nodosus* "hanging like a pendant, byssus attached to a bit of old spar", *Spondylus* sp.

McGINTY, T. L., 1955, New marine mollusks from Florida. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 107: 75–85.
Describes material from the cruiser yacht *Triton* [see Thompson et al., 1951]: *Semele bellastriata.*

*MELVILL, J. C., 1880, List of Mollusca obtained in South Carolina and Florida (principally at the island of Key West in 1871–1872). *Journal of Conchology*, 3: 155–173.
Anomalocardia impressa, Arca noae, Asaphis dichotoma, Barbatia sp., *Callista* (*Dione*) *gigantea, Cardita* (*Mytilicardia*) *floridana, Cardium muricatum, Chama macerophylla, Chione cancellata, Hemicardium medium, Laevicardium laevigatum, L. serratum, Lima scabra, Loripes chrysostoma, L. edentula, Lucina jamaicensis, L. tigerina, Modiola plicatula, Mytilus cubitus, Ostrea frons, O. rhizophorae, Pectunculus pectiniformis, Pholas costata, Ricinula nodulosa, Scalaria venosa, Scapharca inaequivalvis, S. occidentalis, Spondylus ramosus, Strigilla carnaria, S. pisiformis, Tellina fausta, T. interrupta, T. lineata, T. radiata, T. r.* var. *unimaculata, T. robusta, T. similis, T. sol, T. tenera.* Dall (1889a: 21) stated: "This catalog contains many erroneous identifications."

GMIKKELSEN, P. M., 1981, Mollusks. Pp. 45–48, in: S. C. JAMESON, ed., *Key Largo Coral Reef National Marine Sanctuary Deep Water Resource Survey*, NOAA Technical Report CZ/SP-1, 144 pp.
From *Johnson-Sea-Link* submersible dives as part of Key Largo Coral Reef National Marine Sanctuary Deep Water Resource Survey: *Arca imbricata, Arcopsis adamsi, Barbatia* (*Acar*) *domingensis, Chama* sp., *Diplodonta* (*Diplodonta*) *?punctata, Isognomon radiatus.* Voucher specimens referenced in Harbor Branch Oceanographic Museum, Ft. Pierce, Florida.

MIKKELSEN, P. M. & R. BIELER, 2000, Marine bivalves of the Florida Keys: discovered biodiversity. Pp. 367–387, in: E. M. HARPER, J. D. TAYLOR & J. A. CRAME, eds., *The evolutionary biology of the Bivalvia* [Proceedings of "Biology & Evolution of the Bivalvia", an international symposium organized by the Malacological Society of London, 14–17 September 1999, Cambridge, UK]. Geological Society, London, Special Publication 177.
325 bivalve species reported for the Florida Keys: *Abra aequalis, A. lioica, Aequipecten glyptus, Americardia guppyi, A. media, Amusium laurentii, A. papyraceum, Amygdalum papyrium, A. politum, A. sagittatum, Anadara baughmani, A. floridana, A. notabilis, A. ovalis, A. transversa, Anatina anatina, Anodontia alba,*

A. philippiana, Anomalocardia auberiana, Anomia simplex, Arca imbricata, A. zebra, Arcinella cornuta, Arcopsis adamsi, Argopecten gibbus, A. irradians, A. lineolaris, A. nucleus, Asaphis deflorata, Astarte nana, Asthenothaerus balesi, A. hemphilli, Atrina rigida, A. seminuda, A. serrata, Bankia carinata, Barbatia cancellaria, B. candida, B. domingensis, Barnea truncata, Basterotia elliptica, B. quadrata, Bathyarca glomerula, Botula fusca, Brachidontes domingensis, B. exustus, B. modiolus, Brachtechlamys antillarum, Callista eucymata, Cardiomya costellata, C. glypta, C. ornatissima, C. perrostrata, Carditamera floridana, Carditopsis smithii, Caribachlamys imbricata, C. mildredae, C. ornata, C. sentis, Chama congregata, C. florida, C. lactuca, C. macerophylla, C. sarda, C. sinuosa, Chione cancellata, C. mazyckii, C. paphia, Choristodon robustum, Circomphalus strigillinus, Codakia costata, C. orbicularis, C. orbiculata, C. pectinella, Coralliophaga coralliophaga, Corbula barrattiana, C. caribaea, C. contracta, C. dietziana, C. swiftiana, Crassinella dupliniana, C. lunulata, C. martinicensis, Crassostrea rhizophorae, C. virginica, Crenella decussata, Cryptopecten phrygium, Cryptostrea permollis, Ctenoides floridanus, C. planulatatus (sic), *C. sanctipauli, C. scaber, Cumingia coarctata, C. tellinoides vanhyningi, Cuspidaria gigantea, C. rostrata, Cyclinella tenuis, Cyclopecten* sp., *Cymatioa* sp., *Cymatoica orientalis hendersoni, Cyrenoida floridana, Cyrtopleura costata, Dacrydium elegantulum hendersoni, Dendostrea frons, Diplodonta punctata, D. semiaspera, Divalinga quadrisulcata, Divaricella dentata, Divarilima albicoma, Donax variabilis, Dosinia discus, D. elegans, Ennucula tenuis, Ensis minor, Entodesma beana, Ervilia concentrica, E. nitens, E. subcancellata, Eucrassatella speciosa, Euvola chazaliei, E. raveneli, E. ziczac, Gastrochaena hians, G. ovata, Geukensia granosissima, Glans dominguensis, Globivenus rigida, G. rugatina, Glycymeris americana, G. decussata, G. pectinata, G. undata, Gouldia cerina, Gregariella coralliophaga, Halirus fischeriana, Heterodonax bimaculatus, Hiatella arctica, Iphigenia brasiliana, Ischadium recurvum, Isognomon alatus, I. bicolor, I. radiatus, Kellia suborbicularis, Laevicardium laevigatum, L. mortoni, L. pictum, L. sybariticum, Laevichlamys multisquamata, Lasaea adansoni, Leporimetis intastriata, Lima caribaea, Limaria pellucida, Limopsis aurita, L. cristata, L. minuta, L. sulcata, Lindapecten exasperatus, L. muscosus, Lioberus castaneus, Lirophora latilirata, Lithophaga antillarum, L. aristata, L. bisulcata, L. nigra, Lucina amianta, L. floridana, L. leucocyma, L. pectinata, L. pensylvanica, L. radians, L. sombrerensis, L. trisulcata, Lucinisca muricata, L. nassula, Lucinoma filosum, Lyonsia floridana, Lyropecten kallinubilosus, Macoma brevifrons, M. cerina, M. constricta, M. mitchelli, M. tageliformis, M. tenta, Macrocallista maculata, M. nimbosa, Mactrotoma fragilis, Malleus candeanus, Martesia cuneiformis, M. striata, Mercenaria campechiensis, M. mercenaria* forma *notata, Modiolus americanus, M. modiolus squamosus, Musculus lateralis, Myrtea sagrinata, Mysella planulata, Mytilopsis leucophaeata, M. sallei, Nemocardium peramabile, N. tinctum, Neopycnodonte cochlear, Nodipecten nodosus, Noetia ponderosa, Nototeredo knoxi, Nucula aegeensis, N. calcicola, N. crenulata, N. proxima, Nuculana acuta, N. concentrica, N. pusio, N. solidula, N. verrilliana, Orobitella floridana, Ostreola equestris, Pandora bushiana, P. inflata, Papyridea semisulcata, P. soleniformis, Parastarte triquetra, Parvilucina multilineata, Periglypta listeri, Periploma anguliferum, P. tenerum, Petricola lapicida, Petricolaria pholadiformis, Pinctada imbricata, P. longisquamosa, Pinna carnea, P. rudis, Pitar cordatus, P. fulminatus, P. simpsoni, Plectodon granulatus, Pleuromeris tridentata, Plicatula gibbosa, Polymesoda maritima, Poromya granulata, P. rostrata, Propeamussium pourtalesianum, P. sayanum, Protothaca granulata, Pseudochama inezae, P. radians, Pteria colymbus, Pteromeris perplana, Puberella intapurpurea, P. pubera, Raeta plicatella, Rangia flexuosa, Semele bellastriata, S. proficua, S. purpurascens, Semelina nuculoides, Semierycina* sp., *Solecurtus cumingianus, Solemya occidentalis, Spathochlamys benedicti, Spengleria rostrata, Sphenia antillensis, Spisula raveneli, Spondylus americanus, S. gussoni, S. ictericus, Strigilla gabbi, S. mirabilis, S. pisiformis, Tagelus divisus, T. plebeius, Tellidora cristata, Tellina aequistriata, T. agilis, T. alternata, T. americana, T. angulosa, T. candeana, T. consobrina, T. fausta, T.*

gouldii, T. iris, T. laevigata, T. lineata, T. listeri, T. magna, T. martinicensis, T. mera, T. nitens, T. paramera, T. persica, T. probrina, T. punicea, T. radiata, T. similis, T. squamifera, T. sybaritica, T. tampaensis, T. texana, T. versicolor, Teredo clappi, Thracia corbuloides, T. phaseolina, T. stimpsoni, Thyasira trisinuata, Timoclea grus, T. pygmaea, Tivela floridana, Trachycardium egmontianum, T. magnum, T. muricatum, Transenella (*sic*) *conradina, T.* (*sic*) *cubaniana, T.* (*sic*) *culebrana, T.* (*sic*) *stimpsoni, Trigonulina ornata, Varicorbula limatula, V. philippii, Verticordia acuticostata.*

MIKKELSEN, P. M. & R. BIELER, 2001, *Varicorbula* (Bivalvia: Corbulidae) of the western Atlantic: taxonomy, anatomy, life habits, and distribution. *The Veliger*, 44(3): 271–293.

With Florida Keys specimens cited [including material from this study]: *Varicorbula disparilis, V. philippii.*

MIKKELSEN, P. M. & R. BIELER, 2003, Systematic revision of the western Atlantic file clams, *Lima* and *Ctenoides* (Bivalvia: Limoida: Limidae). *Invertebrate Systematics*, 17: 667–710, cover.

With Florida Keys specimens cited [including material from this study]: *Ctenoides mitis, C. planulatus, C. sanctipauli, C. scaber, C. miamiensis* sp. nov., *Lima caribaea*.

MIKKELSEN, P. M., I. TËMKIN, R. BIELER & W. G. LYONS, 2004, *Pinctada longisquamosa* (Dunker, 1852) (Bivalvia: Pteriidae), an unrecognized pearl oyster in the western Atlantic. In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 473–501.

Pinctada longisquamosa is redescribed based on living populations from the Florida Keys [material from this study]; *Pinctada imbricata* and *Pteria colymbus* also listed.

^{G}MILLER, J., 2001, *Euvola ziczac* (Linnaeus, 1758). *American Conchologist*, 29(1): back cover.

Euvola ziczac figured from Key West.

*MOORE, D. R., 1977, Small species of Nuculidae (Bivalvia) from the tropical western Atlantic. *The Nautilus*, 91(4): 119–128.

Nucula calcicola n. sp., from Key Largo.

MOORE, H. B. & B. N. LÓPEZ, 1970, A contribution to the ecology of the lamellibranch *Tellina alternata*. *Bulletin of Marine Science*, 20(4): 971–979.

With distributions including Florida Keys (or specific localities): *Tellina alternata, T. radiata.*

MORRIS, P. A., 1947, *A field guide to the shells of our Atlantic coast.* Houghton Mifflin Company, Boston. xvii + 190 pp., 40 pls.

With distributions including Florida Keys: *Chama sarda, Codakia orbicularis.*

MORRIS, P. A., 1951, *A field guide to the shells of our Atlantic and Gulf coasts*, rev. and enlarged ed. Houghton Mifflin Company, Boston. xix + 236 pp., 45 pls.

With distributions including Florida Keys: *Chama sarda, Codakia orbicularis, Tellina anguilosa (sic).*

MORRIS, P. A., 1973, *A field guide to shells of the Atlantic and Gulf coasts and the West Indies*, 3rd ed. Houghton Mifflin Company, Boston. xxviii + 330 pp., 76 pls.

With distributions including Florida Keys: *Nuculana verrilliana, Pitar cordata.*

*MORRISON, J. P. E., 1958, Ellobiid and other ecology in Florida. *The Nautilus*, 71(4): 118–124.

Account of collecting at Bahia Honda Key and Plantation Key, Nov. 1955: *Brachidontes* sp., *Crenella* sp., *Laemodonta cubensis, Pseudocyrena maritima.*

^{G}MORRISON, J. P. E., 1970, East Florida *Donax*. *Seafari* [*Palm Beach County Shell Club Newsletter*], 12(7): 1–2, 5.

"Unsolved problems" are noted regarding Key West *Donax*.

MORTON, B., 2000, The pallial eyes of *Ctenoides floridanus* (Bivalvia: Limoidea). *Journal of Molluscan Studies*, 66(4): 449–455.

Using specimens from Stirrup Key [material from this study].

MORTON, B. & M. KNAPP, 2004, Predator-prey interactions between *Chione elevata* (Bivalvia: Chioninae) and *Naticarius canrena* (Gastropoda: Naticidae) in the Florida Keys, U.S.A. In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 295–307.

From Long Key and Lower Matecumbe Key [material from this study]: *Pleuromeris tridentata, Chione elevata, Ctena orbiculata, Laevicardium mortoni, Lucinisca nassula, Pitar simpsoni, Tellina iris, T. mera, T. similis, Tucetona pectinata.*

MPITSOS, G. J., 1973, Physiology of vision in the mollusk *Lima scabra*. *Journal of Neurophysiology*, 36(2): 371–383.

Lima scabra and *L. s. tenera* collected from the Florida Keys for visual physiological studies.

NUTTING, C. C., 1895, Narrative and preliminary report of Bahama Expedition. *Bulletin from the Laboratories of Natural History of the State University of Iowa*, 3(1–2): i–vi + 1–252.
The 1893 S. U. I. Bahama Biological Expedition narrative contains reference to mollusks collected from the Dry Tortugas and Pourtales Plateau off Key West: *Arca velata, Arca* sp., *Avicula margaritifera, Cardium isocardium, Chione cigenda, Lucina tigrina, Pecten ornatus*. The author noted that "There is no place, probably, on our Atlantic coast where Mollusca are more abundant and more conspicuous than at the Tortugas" (p. 127). The mollusks were reported on more completely by Dall (1896a).

$^{\mathrm{G}}$*ODÉ, H., 1975, Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph). Part I. *Texas Conchologist*, 12(2): 40–56.
With distribution including Key West (citing earlier literature): *Strigilla gabbi*.

$^{\mathrm{G}}$*ODÉ, H., 1976a, Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph). Part I. *Texas Conchologist*, 12(3): 79–94.
With distributions including Florida Keys (citing earlier literature): *Pseudocyrena maritima, Ventricolaria rigida*.

$^{\mathrm{G}}$ODÉ, H., 1976b, Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph). *Texas Conchologist*, 12(4): 108–124.
With distributions including Florida Keys (citing earlier literature): *Pitar cordatus, Transennella cubaniana*.

$^{\mathrm{G}}$ODÉ, H., 1977a, Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph). *Texas Conchologist*, 13(3): 74–81, 84–88.
With distribution including Florida Keys (or specific localities): *Plectodon granulatus*.

$^{\mathrm{G}}$ODÉ, H., 1977b, Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph). *Texas Conchologist*, 13(4): 106–107, 114–122.
With distribution including Florida Keys (citing earlier literature): *Myrtea sagrinata*.

$^{\mathrm{G}}$ODÉ, H., 1979a, Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph). *Texas Conchologist*, 15(3): 69–80.
With distribution including Florida Keys (citing earlier literature): *Isognomon bicolor*.

$^{\mathrm{G}}$ODÉ, H., 1979b, Distribution and records of the marine Mollusca in the northwest Gulf of Mexico (a continuing monograph). *Texas Conchologist*, 16(1): 14–32.
With distribution including Florida Keys (citing earlier literature): *Divarilima albicoma*.

$^{\mathrm{G}}$ODÉ, H., 1984, Additions to monographic list of bivalves of the northwest Gulf of Mexico. *Texas Conchologist*, 20(3): 76–83.
With distributions including Florida Keys (citing earlier literature): *Cymatioa* sp. D.

OLIVER, P. G. & J. JÄRNEGREN, 2004, How reliable is morphology based species taxonomy in the Bivalvia? A case study on *Arcopsis adamsi* (Bivalvia: Arcoidea) from the Florida Keys. In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 327–338.
Acar domingensis, Arca imbricata, Arca sp., *Arcopsis adamsi, Brachidontes* sp., *Chama* sp., *Isognomon* sp., oysters [material from this study].

*OLSSON, A. A., 1951, New Floridan species of *Ostrea* and *Vermicularia*. *The Nautilus*, 65(1): 6–8, pl. 1.
Ostrea weberi n. sp. described from Grassy Key and Key West.

OLSSON, A. A. & A. HARBISON, 1952 [reprint 1979], *Pliocene Mollusca of southern Florida with special reference to those from North Saint Petersburg*. Academy of Natural Sciences of Philadelphia Monograph 8. v + 457 pp., 65 pls.
With Recent distributions including Florida Keys (or specific localities): *Cumingia coarctata, Hemimetis* (*Florimetis*) *intastriata, Papyridea semisulcatum, Tellina* (*Scissula*) *candeana, T.* (*S.*) *similis*.

$^{\mathrm{G}}$ORLIN, Z., 2003, A shelling trip to Florida and the Bahamas. *La Conchiglia*, 34(305): 36–40.
While based at Grassy Key, the author collected on the Atlantic beaches of Key Vaca, Missouri Key, Ohio Key, and Boca Chica. The largest number of species (44) was found on Ohio Key; 34 species were not found on the Gulf coast of Florida. An additional 28 species were collected as microshells. On Boca Chica beach, Atlantic side: *Codakia orbicularis, Lucina pensylvanica*. Also from unclear localities: *Arca zebra, Chama macerophylla, Pinctada imbricata, Pteria*

colymbus. In all, 45 species were found that were not found the weeks before on Florida's Gulf coast.

PALMER, K. V. W., 1927–1929, The Veneridae of eastern America, Cenozoic and Recent. *Palaeontographica Americana*, 1(5): 209–522 (1927), pls. 32–76 (1929).

From Florida Keys: *Antigona* (*Dosina*) *listeri.*

*PALMER, K. V. W., 1947, Notes on *Costacallista eucymata* (Dall). *The Nautilus*, 61(2): 44–47, pl. 4.

Stations cited from off Key Largo to Looe Key.

PARKER, R. H. & J. R. CURRAY, 1956, Fauna and bathymetry of banks on continental shelf, northwest Gulf of Mexico. *Bulletin of the American Association of Petroleum Geologists*, 40(10): 2428–2439.

With distributions including Florida Keys (or specific localities): *Corbula cymella, Trachycardium magnum.*

PEARSE, A. S., 1929, Observations on certain littoral and terrestrial animals at Tortugas, Florida, with special reference to migrations from marine to terrestrial habitats. *Papers from Tortugas Laboratory of the Carnegie Institution of Washington*, 26(6) (Carnegie Institution of Washington Publication 391): 205–223.

From Loggerhead Key and Garden Key, Dry Tortugas: *Arca saccharina, Pteria vitrea.*

^{G}*PEASE, R., 1980, Don't underestimate tourist spots. *Conchologists of America Bulletin*, (20): 14.

Account of diving at Sand Key in May 1979: *Chlamys sentis.*

PETERSEN, D. W., 1989, Assessing environmental parameters and transport from the spatial distribution of a mollusc-dominated modern shell concentration in a restricted subtropical lagoon, Long Key Lake, Florida Keys, USA. *The Compass* [*Earth Science Journal of Sigma Gamma Epsilon*], 67(1): 15–29.

An assessment of the malacofauna of an oceanside lagoon on Long Key includes *Acropsi* (*sic*) *adamsi, Anomalocardia auberiana, Argopectin* (*sic*) *nucleus, Brachiodonta* (*sic*) *exustus* [listed under Gastropoda], *Carditamera floridana, Chione cancellata, Codakia costata, Laevicardium mortoni, Ostrea frons, Pseudocyrena maritima, Tellina mera, T. texana.* This is a published version of a Master's thesis (Petersen, 1988).

*PETUCH, E. J., 1987, *New Caribbean molluscan faunas.* Coastal Education & Research Foundation (CERF), Carlottesville, Virginia. 154 + 4 pp., incl. 29 pls.

Argopecten irradians taylorae n. ssp. from Rabbit Key Basin, Upper Florida Keys.

*PETUCH, E. J., 1988, *Neogene history of tropical American mollusks.* Coastal Estuarine & Research Foundation, Charlottesville, Virginia. 217 pp.

From Florida Keys localities: *Brachidontes modiolus.* Holotype of *Argopecten irradians taylorae* mentioned and refigured.

*PILSBRY, H. A., ed., 1890a, American Association of Conchologists, December 10, 1890. *The Nautilus*, 4(8): 91–95.

Among donations to the collection of the society is *Pinna carnea* from Key West.

*PILSBRY, H. A., ed., 1890b, American Association of Conchologists, December 31, 1890. *The Nautilus*, 4(9): 104–107.

Among donations to the collection of the society is *Cardium magnum* from Key West and *Asaphis deflorata* from Elbow Key [= Reef].

PILSBRY, H. A. & T. L. MCGINTY, 1938, Review of Florida Chamidae. *The Nautilus*, 51(3): 73–79, pl. 7.

Chama sarda not observed but earlier reported from Florida Keys by earlier authors.

*PILSBRY, H. A. & R. A. MCLEAN, 1939, A new *Arca* from the West Indian region. *Notula Naturae,* no. 39: 1–2.

Arca (*Barbatia*) *balesi* n. sp., from Missouri Key and Key West.

*PILSBRY, H. A. & A. A. OLSSON, 1946, *Condylocardia* in Florida and middle America. *The Nautilus*, 60(1): 6–7, pl. 1.

Condylocardia floridensis n. sp., from Ohio Key.

^{G}PLOCKELMAN, C., 1968a, *Chione pygmaea. Seafari* [*Palm Beach County Shell Club Newsletter*], 10(12): 5.

Chione pygmaea as uncommonly found in the Florida Keys.

^{G}PLOCKELMAN, C., 1968b, Do you collect chiones? *Seafari* [*Palm Beach County Shell Club Newsletter*], 10(8): 8–10.

Chione pygmaea occurs uncommonly under rocks and on old conchs, in generally silty spots in the Florida Keys.

^{G}PLOCKELMAN, C. H., ed., 1968c, Entries for the Whopper Club. *Seafari* [*Palm Beach County Shell Club Newsletter*], 10(9): 7.

Among large specimens collected by club members is *Papyridea soleniformis* (50 mm) from Molasses Keys.

^{G}PLOCKELMAN, C., 1968d, Mid-summer review of shelling. *Seafari* [*Palm Beach County Shell Club Newsletter*], 10(8): 1–3.
From the Florida Keys, June–July 1968: *Americardia* sp., *Codakia orbicularis, Tellina* sp., *Trachycardium* sp.

^{G}PLOCKELMAN, C. H., 1968e, Tiny chiton on *Codakia*. *Seafari* [*Palm Beach County Shell Club Newsletter*], 10(9): 3.
Codakia orbicularis abundant on Little Duck Key.

^{G}PLOCKELMAN, C. [H.], 1969a, A Florida prize. *Seafari* [*Palm Beach County Shell Club Newsletter*], 11(11): 5–6.
With type locality of *Pseudochama inezae* given as Carysfort Reef.

^{G}PLOCKELMAN, C. [H.], 1969b, November in the Keys. *Seafari* [*Palm Beach County Shell Club Newsletter*], 11(1): 12.
From Key West, mid-November 1969: *Chlamys sentis* among very little variety in bivalves. From Grassy Key: *Barbatia cancellaria, Lima scabra tenera*. Of special note on south Key West beach: large-sized *Brachidontes citrinus*.

^{G}PLOCKELMAN, C. H., ed., 1969c, Whopper Club. *Seafari* [*Palm Beach County Shell Club Newsletter*], 11(2): 3.
From Crawl Key: *Rupellaria typica* (35.7 mm).

^{G}PLOCKELMAN, C. H., ed., 1970a, Eleventh annual shell show. *Seafari* [*Palm Beach County Shell Club Newsletter*], 12(3): 1–3.
An award winning display by Corinne Edwards featured a *Strombus gigas* from the Florida Keys with a juvenile *Spondylus ictericus* lodged in the suture of the body whorl.

^{G}PLOCKELMAN, C. [H.], 1970b, Maybe you have one? *Seafari* [*Palm Beach County Shell Club Newsletter*], 12(5): 5–6.
Aequipecten acanthodes from west of Sombrero Light is noted in a display of deep water species at Elsie Malone's shell shop (Sanibel Island).

^{G}PLOCKELMAN, C. [H.], 1970c, Re: *Brachidontes citrinus* Roding (*sic*). *Seafari* [*Palm Beach County Shell Club Newsletter*], 12(3): 14.
Brachidontes citrinus is found on beaches in the Florida Keys, also living embedded in silt among seagrass and algae (patchy in distribution).

^{G}PLOCKELMAN, C. [H.], 1970d, Shells of Palm Beach County #23. *Seafari* [*Palm Beach County Shell Club Newsletter*], 12(6): 2–3.
Cooperella atlantica from Little Duck Key.

^{G}POLAND, P., 2001, Reef encounters of the first kind. *Shell-o-Gram* (*Jacksonville* [*Florida*] *Shell Club*), 42(3): 1, 6. Reproduced at http://www.jaxshells.org/looe.htm; last accessed May 29, 2001.
Caribachlamys sentis from Looe Key in the early 1970s.

^{G}POMPEY, S. L., 1974, Introducing the pretty pecten. *Of Sea & Shore*, 5(4): 161–164, 166.
With distribution including Florida Keys: *Aequipecten lineolaris*.

^{G}PULLEY, T. E., 1952, *A zoogeographic study based on the Bivalves of the Gulf of Mexico*. Ph.D. Dissertation, Harvard University, Cambridge, Massachusetts. 215 pp., 19 pls.
With distributions or figure captions including Florida Keys (or specific localities): *Aequipecten gibbus nucleus, Aloidis aequivalvis, A. operculata, Amusium papyraceum, Amygdalum arborescens, A. papyrium, Anadara baughmani, A. transversa, Antigona listeri, Astarte nana, Botula castanea, B. fusca, Brachidontes citrinus, Cardiomya perrostrata, Cardita domingensis* (*sic*), *C. floridana, Chlamys imbricatus, C. muscosus, C. phrygius, C. sentis, Codakia orbicularis, Coralliophaga coralliophaga, Costacallista eucymata, Cumingia antillarum, Cyrenoida floridana, Diplodonta simiaspera* (*sic*), *Eucrassatella speciosa, Euvola raveneli, Glycymeris decussata, G. pectinata, G. undata, Isognomon alata, I. bicolor, I. listeri, Lima caribaea, L. scabra, L. tenera, Lithophaga antillarum, Lucina amiantus, L. leucocyma, L. sombrerensis, Lyrodus pedicellata, Lyropecten antillarum, L. nodosus, Macoma cerina, M. extenuata, M. limula, M. pseudomera, Musculus lateralis, Nucula proxima, Nuculana carpenteri* (cotype figured), *Papyridea semisulcata, Pinctada radiata, Pseudocyrena floridana, Tellina candeana, T. lintea, T. mera, T. squamifera, T. versicolor, Teredo bartschi, Venericardia tridentata.*

^{G}*PURTYMUN, B., 1997, Echoes of the past. *American Conchologist*, 25(4): 28.
From vicinity of Key West, 1944: *Chama macerophylla*.

^{G}*REDLA, N. T., 1990, An excursion to the fabled land of Florida. *Texas Conchologist*, 26(2): 60–61.
Codakia orbicularis and *Linga pensylvanica* from Keys localities.

*REHDER, H. A., 1939, New marine mollusks from the west Atlantic. *The Nautilus*, 53(1): 16–21, pl. 6.

New species from Keys localities: *Cymatoica orientalis hendersoni, Cumingia tellinoides vanhyningi.*

*REHDER, H. A.,1943a, New marine mollusks from the Antillean region. *Proceedings of the United States National Museum*, 93(3161): 187–203, pls. 19–20.

Asthenothaerus balesi n. sp., from Missouri Key.

REHDER, H. A., 1943b, Corrections and ecological notes on some recently described Florida marine shells. *The Nautilus*, 57: 32–33.

From Missouri Key: *Asthenothaerus balesi.*

REHDER, H. A., 1981, *The Audubon Society field guide to North American seashells.* Alfred A. Knopf, New York. 894 pp., 705 figs.

With distributions including Florida Keys (or specific localities): *Chama sarda, Chlamys sentis, Glans dominguensis, Isognomon bicolor, Lucina dentata, L. leucocyma, Parvilucina amianta, P. multilineata, Phacoides muricata, Pleuromeris tridentata.*

*REHDER, H. A. & R. T. ABBOTT, 1951, Some new and interesting mollusks from the deeper waters of the Gulf of Mexico. *Revista de la Sociedad Malacologica "Carlos de la Torre"*, 8(2): 53–66, pls. 8–9.

Anadara springeri n. sp., from the Dry Tortugas. Also cited from Florida Keys localities are *Aequipecten glyptus, Amusium papyraceum, Pitar* (*Pitarenus*) *cordata.*

RICHARDS, H. G., 1936, Some shells from the North Carolina "banks". *The Nautilus*, 49(4): 130–134.

Arca auriculata from the Keys.

^{G}RING, F. M., 1980, Of coral reefs, intertidal shores and sand flats in the Florida Keys. *Of Sea & Shore*, 11(2): 129–135.

An ecological account of the marine habitats of the Keys, based on a March [presumably 1980] vacation trip. Specific localities visited were Sand Key Light, bridge channel between Boca Chica Key and Key West, and seaward sand flats off Bahia Honda Key, Marathon and Key Largo. Among the few mollusks specifically mentioned or figured are: *Lima scabra, Ostrea frons*, mussels.

RIOS, E. DE C., 1994, *Seashells of Brazil*, 2nd ed. Museu Oceanográfico, Rio Grande, Brazil. 368 pp., 113 pls.

With distributions including Florida Keys (or specific localities): *Chama sarda, Corbula* (*Caryocorbula*) *cymella, Limaria albicoma, Lucina* (*Lucinisca*) *muricata, Nuculana* (*Jupitaria*) *solidula, Pitar* (*Pitarenus*) *cordatus, Strigilla* (*Strigilla*) *gabbi, Trachycardium* (*Acrosterigma*) *magnum, Ventricolaria* (*Ventricolaria*) *rigida.*

RIPPLE, J. [with photographs by B. KEOGH & J. RIPPLE], 1995, *The Florida Keys – the natural wonders of an island paradise.* Voyageur Press, Stillwater, Minnesota. 128 pp.

Includes a photograph of a living *Ctenoides scaber* (as "rough fileclam") from an unspecified locality.

ROGERS, G. F., 1941, Wreck of the *Janthina janthina. The Nautilus*, 54(3): 75–77.

Janthina janthina washed ashore on Key Largo; also "a good Venus clam, two nice live cowries and several live discus clams".

ROGERS, J. E., 1908, *The shell book, a popular guide to a knowledge of the families of living mollusks, and an aid to the identification of shells native and foreign.* Doubleday, Page & Company, New York. xxi + 485 pp.

With distributions including Florida Keys (or specific localities): *Arca transversa, Lithodomus lithophagus, Lucina floridana.*

*ROMBOUTS, A., 1991, *Guidebook to pecten shells; Recent Pectinidae and Propeamussiidae of the world.* Universal Book Services/Dr. W. Backhuys, Oegstgeest. 157 pp.

Figured from Keys localities: *Aequipecten glyptus, A. muscosus, Euvola ziczac, Nodipecten nodosus.*

ROMASHKO, S., 1984, *The complete collector's guide to shells & shelling.* Windward Publishing Company, Miami, Florida. 112 pp.

With distributions including Florida Keys (or specific localities): *Aequipecten lineolaris, Chlamys sentis, Trachycardium magnum.*

ROOPNARINE, P. D. & G. J. VERMEIJ, 2000, One species becomes two: the case of *Chione cancellata*, the resurrected *C. elevata*, and a phylogenetic analysis of *Chione. Journal of Molluscan Studies*, 66(4): 517–534.

Among the material used to distinguish the two species is *Chione elevata* from Key Largo (ANSP 264071).

^{G}ROSS, B., 1969, Field trip to the Keys. *Seafari* [*Palm Beach County Shell Club Newsletter*], 11(7): 8–10.

Collected in the Marathon area, during Memorial Day weekend 1969: *Anadara notabilis, Anomalocardia cuneimeris, Antigona listeri, Arca imbricata, A. zebra, Arcopagia fausta, Barbatia cancellaria, B. domingensis, Brachidontes citrinus, B. exustus, Chama congregata, C. macerophylla,Chione cancellata, Chlamys sentis, Codakia obicularis* (*sic*), *C. orbiculata,* *Glycymeris pectinata, Isognomon alatus, I. radiatus, Laevicardium laevigatum, L. mortoni, Lima pellucida, L. scabra, L. s. tenera, Lima* sp., *Lucina pensylvanica, Mactra fragilis, Modiolus americanus, Papyridea soleniformis, Pinctada radiata, Pinna carnea, Tellina mera, T. paramera, T. similis, Trachycardium egmontianum, T. muricatum.*

^{G}ROSS, B., 1971, The Keys – what's become of *Melongena bicolor*? *Seafari* [*Palm Beach County Shell Club Newsletter*], 13(5): 14–15.

Collecting out of Marathon, May [1971]. A few bivalves in mud at East Sister Rock; *Chlamys sentis* and *Lyropecten antillarum* at Looe Key; *Botula fusca* and *Tellina similis* from Little Duck/Ohio/Missouri Keys; several *Tellina* from further north up the Keys. From the more productive gulf side [locale unspecified], Mr. Bennett (at Palm's Motel) found *Lima scabra tenera* by snorkeling. "While shelling in the Keys is not what it used to be, it is still better than any other place in Florida, on a day-to-day basis."

^{G}*SAGE, W., 1987, A day's collecting in the Florida Keys. *American Conchologist*, 15(3): 12.

Collecting by scuba near Boca Grande off Key West at 15–18 ft deep: *Chlamys imbricata, C. sentis, Lima scabra.* A second station 5 miles off Key West, less than 6 ft deep: *Chlamys imbricata, C. sentis.*

*SALAS, C. & S. GOFAS, 1997, Brooding and non-brooding *Dacrydium* (Bivalvia: Mytilidae): a review of the Atlantic species. *Journal of Molluscan Studies*, 63(2): 261–283.

Dacrydium elegantulum hendersoni n. ssp. described from *Eolis* specimens from Sand Key; other specimens from Key West and Western Dry Rocks. Reports of *D. vitreum* (Holbøll in Møller, 1842) are attributed to this species.

SALISBURY, A. E., 1952, Mollusca of the University of Oxford Expedition to the Cayman Islands in 1938. *Proceedings of the Malacological Society of London*, 30(1–2): 39–54, pls. 7, 8.

With distribution including Florida Keys (citing previous authors): *Chlamys nucleus.*

^{G}SCHOMER, N. S. & R. D. DREW, 1982, *An ecological characterization of the lower Everglades, Florida Bay and the Florida Keys.* United States Fish and Wildlife Service, Office of Biological Services, Washington, D.C., FWS/OBS-82/58.1, xv + 246 pp.

Chapter 9 lists Florida Keys mollusks, in great detail, by habitat (presumably based on Stephensen & Stephensen, 1950): *Anadara* sp., *Anomalocardia cuneiveis* (*sic*), *Arca* sp., *Atrina rigida, A. seminuda, Barbatia* sp., *Chione cancellata, Codakia orbicularis, C. orbiculata, Crassostrea virginica, Isognomon alatus, Laevicardium laevigatum, Lithophaga* sp., *Mytilus exustus, Tellina* sp.

^{G}SCHROEDER, R. E., 1964, Photographing the night creatures of Alligator Reef. *National Geographic*, 125(1): 128–154.

Color photographs of living *Dendostrea frons* [as "coon oysters ... on dead gorgonian"], and *Ctenoides floridanus* [as "flame scallop"].

*SCHWENGEL, J. S., 1951, New marine mollusks from British West Indies and Florida Keys. *The Nautilus*, 64(4): 116–119, pl. 8.

Pitaria cordata n. sp. from Key West.

^{G}*SEDLAK, R., 1986, A perfect "10". *The Busycon* [*Broward Shell Club, Ft. Lauderdale, Florida*], 21(9): 5–7.

From Money Key [near Little Duck Key at 7-Mile bridge, from a boat out of mile marker 50], August 1986: *Barbatia cancellaria, Codakia orbicularis, Papyridea soleniformis, Pinctada imbricata, Pinna carnea.*

*SHIRAI, S., 1994, *Pearls and pearl oysters of the world.* Marine Planning Company, Okinawa, Japan. 108 pp.

Pinctada imbricata figured from Key West, as Akoya Pearl Oyster.

SHOEMAKER, A. H., 1973, Thermal and salinity effects on ciliary activity of excised gill tissue from bivalves of North and South Carolina. *The Veliger*, 15(3): 215–222.

Arca zebra shells litter beaches of the Florida Keys after storms, attributed to preferred shallow depths in this part of its distribution.

SIEKMAN [as SEIKMAN (*sic*)], L. [with color illustrations by E. MALONE], 1965, *The great outdoors book of shells, 1st ed.* Great Outdoors Publishing Company, St. Petersburg, Florida. 99 pp.

With distributions including Florida Keys (illustrated by poor black-and-white line drawings and color photos): *Anomia simplex, Chione latilirata, Noetia ponderosa, Pseudocyrena floridana.*

*SIEKMAN, L., 1981, *Handbook of shells,* rev. ed. Great Outdoors Publishing Company, St. Petersburg, Florida. 46 [+ ii] pp.

With distribution including Key West: *Noetia ponderosa.*

SIEKMAN, L. [with color photographs by R. VAN DE GOHM], 1982, *Handbook of shells – sea shells of the Gulf and Atlantic Coast,* rev. ed. Great Outdoors Publishing Company, St. Petersburg, Florida. 48 pp., 16 color pls.

With distribution including Key West: *Noetia ponderosa*.

SIMONE, L. R. L. & A. CHICHVARKHIN, 2004, Comparative morphological study of four species of *Barbatia* occurring on the southern Florida coast (Arcoidea, Arcidae). In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 355–379.

From Florida Keys localities: *Arca zebra, Barbatia candida, B. cancellaria, B. domingensis, B. tenera* [material from this study].

SIMONE, L. R. L. & J. DOUGHERTY, 2004, Anatomy and systematics of northwestern Atlantic *Donax* (Bivalvia, Veneroidea, Donacidae). In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 459–472.

Donax variabilis from the Florida Keys.

SIMPSON, C. T., 1887–1889, Contributions to the Mollusca of Florida. *Proceedings of the Davenport Academy of Natural Sciences*, 5: 45–72, 63–72 ["read 31 December 1986"; exact dates of pages unclear: p. 49 dated 04 November 1887; p. 57 dated 04 February 1889; p. 65 dated 19 February 1889; second p. 63 dated 01 March 1889].

98 Florida Keys bivalve names (= 86 species here considered valid) are listed with specific localities: *Arca barbadensis* var., *A. candida, A. deshayesii, A. domingensis, A. fusca, A. gradata, A. imbricata, A. incongrua, A. noae* var. *americana, A. transversa, Asaphis deflorata, Avicula ala-perdicis, A. radiata, Botula semen, Cardita floridana, Cardium medium, C. petitianum, Chama macerophylla, Choristodon typicum, Coralliophaga hornbeckiana, Corbula swiftiana, Cumingia tellinoides, Cypricardia coralliophaga, Cyrenoida floridana, Cytherea circinata, C. conradina, C. convexa, C. dione, C. hebraea, C.* (*Trigona*) *incerta, Diplodonta candeana, D. semiaspera, D. soror, Donax denticulatus, Ervilia concentrica, E. nitens, Heterodonax bimaculatus, Laevicardium serratum, Lasea* (*sic*) *rubra, Lepton bowmani, Lima scabra, L. squamosa, L. tenera, Lithodomus bisulcatus, L. forficatus, L. niger, Lucina costata, L. lintea, L. muricata, L. pecten* yellow var., *L. pennsylvanica* (*sic*), *L. quadrisulcata, L. squamosa, L. tigrina, Lutricola gruneri, Macoma anomala, M. fausta, Martesia cuneiformis, Modiolaria cinnamomea, Mytilus exustus, M. lavalleanus, Ostrea parasitica, Pecten antillarum, P. dislocates* (*sic*), *P. hemicyclica, P. imbricatus, P. ornatus, P. ornatus* purplish var., *Pectunculus castaneus, Periploma angulifera, Perna ephippium, P. obliqua, Petricola divaricata, Pinna carnea, P. muricata, Rocellaria ovata, R. rostrata, Semele obliqua, S. reticulata, Spondylus croceus, S. spathuliferus, Strigilla pisum* (*sic*), *Tellina decora, T. decora* white var., *T. gouldii, T. interrupta, T. lineata, T lineata* var. *albida, T. mera, T. radiata* var., *T. tayloriana, Thracia rugosa, Venus beaui, V. granulata, V. listeri, V. mortoni, V. paphia, V. pygmaea, V. pygmaea* var. *inaequivalvia*. "Strigillas, *Mytilus exustas*, the pernas" are among species considered characteristic of the Florida Keys, scarcely ever found on Florida west coast, largely due to the trajectory of the Gulf Stream. The author further noted (p. 47) that "The molluscan fauna of the Bermudas, though these islands lie north of the northern limit of Florida, is much more like that of the lower Keys than that of the west coast."

SIMPSON, C. T., 1897, The ianthinas. *The Nautilus*, 10(12): 133–134.

From Key West, January 1893: An account of "untold millions of lanthina, which had washed up in the night". Also collected "bright Tellinas ... along the south shore".

SMITH, J. T., 1991, Cenozoic giant pectinids from California and the Tertiary Caribbean Province: *Lyropecten*, "*Macrochlamis*", *Vertipecten*, and *Nodipecten* species. *United States Geological Survey Professional Paper* 1391, vi + 155 pp., 38 pls.

Nodipecten fragosus common in the Florida Keys; this paper distinguishes continental *N. fragosus* from Caribbean *N. nodosus*.

SMITH, M., 1937, *East coast marine shells – descriptions of shore mollusks together with many living below tide mark, from Maine to Texas inclusive, especially Florida*. Edwards Brothers, Ann Arbor, Michigan. vii + 308 pp., 74 pls.

From Florida Keys localities: *Antigona listeri, Arca* (*Acar*) *adamsi, A. auriculata, A.* (*Barbatia*) *barbata, A.* (*Acar*) *reticulata, A. transversa, A.* (*Navicula*) *umbonata, Barnea truncata, Chama sarda, Chione* (*Timoclea*) *granulata, C. intapurpurea, C. pubera, C.* (*Timoclea*) *pygmaea, Corbula cymella, Cumingia coarctata, Donax denticulata, D. fossor, Dosinia concentrica, Ensis directus, Ervilia concentrica, E. nitens, Glycymeris*

pectinatus, Lucina (*Cavilucina, Lucinisca*) *muricata, Parastarte triquetra, Pecten* (*Lyropecten*) *antillarum, P.* (*Chlamys*) *imbricatus, P.* (*Aequipecten, Plagioctenium*) *nucleus, Pedalion alata, P. listeri, Periploma angulifera, Petricola lapicida, Pinna carnea, Polymesoda floridana, Semele bellastriata, Spondylus americanus, Strigilla flexuosa, S. pisiformis, Tellina* (*Acropagia, Eurytellina*) *angulosa, T.* (*Angulus, Scissula*) *candeana, T.* (*Acropagia, Cyclotellina*) *fausta, T.* (*Angulus, Scissula*) *iris, Tivela mactroides, Transennella conradina, Trigonocardia* (*Americardia*) *medium.*

SMITH, M. [together with two articles by Dr. JOSHUA L. BAILY], 1940, *World-wide sea shells – illustrations, geographical range and other data covering more than sixteen hundred species and sub-species of molluscs.* Tropical Photographic Laboratory, Lantana, Florida. xviii + 139 pp.

With distributions including Florida Keys (or specific localities): *Arca auriculata, Barnea truncata, Donax fossor, Ensis directus, Lucina muricatus, Tivela mactroides.*

SMITH, M., 1945, *East coast marine shells – descriptions of shore mollusks together with many living below tide mark, from Maine to Texas inclusive, especially Florida,* 3rd ed. Edwards Brothers, Ann Arbor, Michigan. vii + 314 pp., 77 pls.

From Florida Keys localities: *Arca* (*Acar*) *adamsi, A. auriculata, A.* (*Barbatia*) *barbata, A.* (*Acar*) *reticulata, A. transversa, A.* (*Navicula*) *umbonata, Barnea truncata, Chama sarda, Chione* (*Timoclea*) *granulata, C. intapurpurea, C. pubera, C.* (*Timoclea*) *pygmaea, Corbula cymella, Cumingia coarctata, Donax denticulatus, D. fossor, Dosinia concentrica, Ensis directus, Ervilia concentrica, E. nitens, Glycymeris pectinatus, Lucina* (*Cavilucina, Lucinisca*) *muricata, Parastarte triquetra, Pecten* (*Lyropecten*) *antillarum, P.* (*Chlamys*) *imbricatus, P. mildredae, P.* (*Aquipecten, Plagioctenium*) *nucleus, Pedalion alata, P. listeri, Periploma angulifera, Petricola lapicida, Pinna carnea, Polymesoda floridana, Pseudochama inezae, Semele bellastriata, Spondylus americanus, Strigilla pisiformis, Tellina* (*Acropagia, Eurytellina*) *angulosa, T.* (*Angulus, Scissula*) *candeana, T.* (*Acropagia, Cyclotellina*) *fausta, T.* (*Angulus, Scissula*) *iris, Tivela mactroides, Transennella conradina, Trigonocardia* (*Americardia*) *medium.*

SMITH, M., 1961, *Universal shells – marine-fresh water-land.* Alpine Press, Asheville, North Carolina. 254 pp. + unnumbered color pls.

From Florida Keys: *Eucrassatella floridana.*

*SOLEM, A., 1955, Living species of the pelecypod family Trapeziidae. *Proceedings of the Malacological Society of London*, 31 (2 "1954"): 64–84, pls. 5–7.

Coralliophaga coralliophaga, with an extensive synonymy and a distribution map showing records in the Lower Keys and Dry Tortugas. Plate 6, figs. 14–15, shows a photograph of a specimen from "Solem Coll. Garden Keys, Dry Tortugas" (verified as FMNH 99831).

STEPHENSON, T. A. & A. STEPHENSON, 1950, Life between tide-marks in North America. I. The Florida Keys. *The Journal of Ecology*, 38: 354–402, pls. 9–15.

Clearly datable, well-identified material, based on fieldwork in 1947-48. Mostly covering region from Key Largo to Key West ("North of Key Largo we visited two keys which can only be reached by boat"; p. 362). Areas visited/collected: Plantation Key, Crawl Key, Vaca Key, West Summerland Key, sea-wall at Key West, Little Duck Key, points of the coast of Key Largo, Knights Key, Pigeon Key, Missouri Key, Ohio Key, East Summerland Key and Big Pine Key. Detailed locality informantion given on p. 362. Mollusks were identified by Clench, Keen, Test, Salisbury, Hubendick, A.G. Smith, Hertlein, and F.M. Bayer. Includes detailed discussion of zonation patterns and individual habitats. From the Florida Keys (some with specific localities): *Arca barbata, A. occidentalis, A. umbonata, Isognomon* (*Pedalion*) *alata, I. chemnitziana, Mytilus* (*Brachidontes*) *exustus.*

STEVENSON, G. B., 1970, *Keyguide to Key West and the Florida Keys*. Banyan Books, Miami, Florida. 64 pp.

Identifiable species from line drawings are labelled with common names only: *Anadara notabilis* (ark shell), *Arca zebra* (turkey wing), *Chama* sp. (jewelbox), *Codakia orbicularis* (lucine), *Dinocardium* sp. (great heart cockle), Mytilidae (mussel), Pinnidae (pen shell), *Pteria colymbus* (Atlantic wing oyster), Teredinidae (shipworm).

STEVENSON, G. B., 1993, *Keyguide to the Florida Keys and Key West*. Blue Water Publishing, Key Largo, Florida. 64 pp.

Identifiable species from line drawings labelled with common names only: *Anadara notabilis* (ark shell), *Arca zebra* (turkey wing), *Chama* sp. (jewelbox), *Codakia orbicularis*

(lucine), *Dinocardium* sp. (great heart cockle), Mytilidae (mussel), Pinnidae (pen shell), *Pteria colymbus* (Atlantic wing oyster), Teredinidae (shipworm).

^{G}STUARDO, J. R., 1968, On the phylogeny, taxonomy and distribution of the Limidae (Mollusca: Bivalvia). Ph.D. dissertation, Harvard University, Cambridge, Massachusetts. 327 pp., 37 pls., 24 maps, 44 figs.

Two new species are described from the Florida Keys, although never formally published: *Limaria* (*Limatulella*) sp., *Limea* (*Limea*) sp.

STUARDO, J. [R.], 1982, A new species of *Ctenoides* from the central Atlantic (Bivalvia: Limidae). *Boletin de la Sociedad de Biologia de Concepción, Chile*, 53: 145–149.

Ctenoides sanctipauli n.sp., described in part from Sand Key Reef.

^{G}*SUNDERLAND, K., 1988, Exploring Pickles Reef. *American Conchologist*, 16(3): 12–13.

From south end of Key Largo (with black-and-white photographs): *Nodipecten nodosus, Spondylus americanus.*

^{G}*SUNDERLAND, K. & M. CAHILL, 1990, Caribbean Pectinidae and Propeamussidae. *American Conchologist*, 18(2): 14–15.

From the Keys (with black-and-white photograph): *Aequipecten acanthodes.*

SUTTY, L., 1990, *Seashells of the Caribbean.* MacMillan Press Ltd., London, etc. vi + 106 pp.

With distribution including Florida Keys (or specific localities): *Chione paphia.*

SWEENEY, M. J. & M. G. HARASEWYCH, 1999, Harald A. Rehder (1907–1996): biographical sketch and malacological contributions. *The Nautilus*, 113(4): 127–150.

Rehder's taxa originally described from Florida Keys localities: *Anadara springeri, Asthenothaerus balesi, Cumingia tellinoides vanhyningi.*

|TABB, D. C. & R. B. MANNING, 1961, A checklist of the flora and fauna of northern Florida Bay and adjacent brackish waters of the Florida mainland collected during the period July, 1957 through September, 1960. *Bulletin of Marine Science of the Gulf and Caribbean*, 11(4): 552–649.

Although frequently cited as a source of Florida Keys biotic records, it is here excluded as outside our defined area, which extends roughly half-way between the Florida Keys island chain and the tip of peninsular Florida. The southernmost sampling site, Sandy Key Basin, is north of this limit. The list includes species more typical of the brackish Everglades fringe [e. g., *Tagelus plebeius, Crassostrea virginica*] than of the more saline, yet still estuarine, Florida Bay.

TAYLOR, J. D., E. GLOVER, M. PEHARDA, G. BIGATTI & A. BALL, 2004, Extraordinary flexible shell sculpture: the structure and formation of calcified periostracal lamellae in *Lucina pensylvanica* (Bivalvia: Lucinidae). In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve studies in the Florida Keys*, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 277–294.

Lucina pensylvanica [material from this study].

^{G}TEARE, M. M., 1949, The Key Largo trip. *The American Malacological Union, News Bulletin and Annual Report 1949*, pp. 16–17.

Field trip "near an inlet" [called "a shoal at the north end of Key Largo" in annual meeting report on p. 15] during 1949 annual meeting in Miami, 19 June 1949: *Arca barbata.*

^{G}TESKEY, M. C., ed., 1969, American Malacological Union thirty-fifth annual meeting. *The American Malacological Union, Inc., Annual Reports for 1969, Bulletin* 36: 1–2.

On display throughout the meeting were a dozen specimens of *Spondylus americanus* from the steel hull of an experimental Navy ship, sunk off Key West in 165 ft of water.

^{G}THEROUX, R. B. & R. L. WIGLEY, 1983, *Distribution and abundance of east coast bivalve mollusks based on specimens in the National Marine Fisheries Service Woods Hole Collection.* NOAA Technical Report NMFS SSRF-768, 174 pp.

From distribution maps of the east coast of the US (extending to 82°W, approximately midway between Key West and Marquesas Keys): *Abra* sp., *Astarte crenata subequilatera*, Cuspidariidae, *Cyclocardia borealis, Glycymeris pectinata, Glycymeris* sp., Limopsidae, *Nemocardium peramabile, Nuculana carpenteri, Nuculana* sp., Nuculanidae, Pectinidae, *Periglypta listeri, Pitar* sp., *Pleuromeris tridentata, Tellina* sp.

THIELE, J., 1910, Molluskenfauna Westindiens. *Zoologische Jahrbücher*, Suppl. 11: 109–132, pl. 9.

Pre-1910 data for mollusks from the Dry Tortugas: *Arca listeri, A. plicata, A. umbonata, Cardium mortoni, Chama macrophylla, Glycymeris pectinatus, Lima lima, L. scabra, Lithophaga nigra, Melina lata, M. listeri, Modiolaria lateralis, Pecten* (*Chlamys*) *imbricatus, P.* (*C.*) *pusio, Pinna carnea, Pteria radiata.*

^{G}THOMAS, R. D. K., 1970, *Functional morphology, ecology and evolution in the genus Glycymeris*. Ph.D. Dissertation, Harvard University, Cambridge, Massachusetts. xxii + 397 pp., 11 pls.

Locality data are provided for living and dead *Glycymeris pectinata* (supplementing those provided in the published version; Thomas 1975) and *G. decussata* from the Middle and Lower Florida Keys.

THOMAS, R. D. K., 1975, Functional morphology, ecology, and evolutionary conservatism in the Glycymerididae (Bivalvia). *Paleontology*, 18(2): 217–254, pl. 38. [published version of Thomas, 1970]

The distribution of living and dead *Glycymeris pectinata* [assumed 1960s] is indicated on a map of the Lower and Middle Keys, with symbols indicating relative abundance. Occasional specimens were widely distributed on offshore, unstable, poorly sorted, skeletal sands in 2–5 m; the species was more common on very shallow subtidal gravel banks and most abundant in sheltered bayside bays, in quiet water at 1–4 m.

THOMPSON, A. R., P. L. MCTINTY & T. L. MCTINTY, 1951, Dredging from the cruiser *Triton*. *The Nautilus*, 65(2): 37–43.

General account of dredging for mollusks from the *Triton* which included the Florida Keys.

|TRAPPE, C. A. & G. L. BREWSTER-WINGARD, 2001, Molluscan fauna from Core 25B, Whipray Basin, Central Florida Bay, Everglades National Park. *United States Geological Survey Open-File Report* 01-143, 21 pp. Electronic version available at http://pubs.usgs.gov/of/of01-143/; last accessed 12 September 2003.

This work is here excluded as outside our defined area, which extends roughly half-way between the Florida Keys island chain and the tip of peninsular Florida. Whipray Basin is north of this limit.

^{G}*TREMOR, M. E., JR., 1998, A shelling trip to Key West. *Shell-o-gram* [*Jacksonville Shell Club, Jacksonville, Florida*], 39(5): 7–9.

An account of a shelling trip with Peggy Williams. From snorkeling at 3 ft in the back country, north of Key West: *Codakia orbicularis, Linga pensylvanica, Lithopoma americanum, Periglypta listeri*. West of Key West: *Tellina fausta, T. radiala* (*sic*). Originally published in *Tidelines* [*St. Petersburg Shell Club*], September 1998 [not seen].

TRYON, G. W., JR., 1873, *American marine conchology: descriptions of the shells of the Atlantic coast of the United States from Maine to Florida*. G. W. Tryon Jr., Philadelphia, Pennsylvania. 208 pp., 44 pls.

From Florida Keys localities: *Cardita* (*Carditamera*) *floridana*.

TURGEON, D. D., J. F. QUINN, JR., A. E. BOGAN, E. V. COAN, F. G. HOCHBERG, W. G. LYONS, P. M. MIKKELSEN, R. J. NEVES, C. F. E. ROPER, G. ROSENBERG, B. ROTH, A. SCHELTEMA, F. G. THOMPSON, M. VECCHIONE & J. D. WILLIAMS, 1998, *Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks*, 2nd ed. American Fisheries Society, Special Publication 26, Bethesda, Maryland. 526 pp. + CD.

From the Florida Keys: *Argopecten irradians taylorae*.

*TURNER, R. D., 1955, The family Pholadidae in the western Atlantic and the eastern Pacific. Part II – Martesiinae, Jouannetiinae and Xylophaginae. *Johnsonia*, 3(34): 65–160.

Museum lots (ANSP, Charleston Museum, USNM) from the Florida Keys cited for: *Martesia cuneiformis, M. striata.*

TURNER, R. D., 1966, *A survey and illustrated catalogue of the Teredinidae* (*Mollusca: Bivalvia*). Museum of Comparative Zoology, Harvard University, Cambridge, Massachusettes. 265 pp., 64 pls.

Reiteration of original description of *Teredo* (*Zopoteredo*) *clappi* Bartsch, from Key West.

*TURNER, R. D. & K. J. BOSS, 1962, The genus *Lithophaga* in the western Atlantic. *Johnsonia*, 4(41): 81–116.

Museum lots (MCZ, USNM) from the Florida Keys cited for: *Lithophaga antillarum, L. aristata, L. bisulcata, L. nigra.*

*TURNER, R. D. & J. ROSEWATER, 1958, The family Pinnidae in the western Atlantic. *Johnsonia*, 3(38): 285–326.

Museum lots (ANSP, CAS, MCZ, USNM, collections of Flipse, Kline, Merrill, Schwengel, Schmidt, Yale) from the Florida Keys cited for: *Atrina rigida, A. serrata, Pinna carnea.*

TURNEY, W. J., 1977, Molluscan distribution in Florida Bay. P. 85, in: H. G. MULTER, *Field guide to some carbonate rock environments – Florida Keys and western Bahamas*, new ed. Kendall/Hunt Publishing Company, Dubuque, Iowa. 415 pp., 10 maps.

No specific molluscan taxa are mentioned, but four subenvironments are described in Florida Bay. “The fauna of Florida Bay is predominantly molluscan, principally gastropods and bivalves which are represented by ap-

proximately 100 genera and 140 recognized species. [...] Molluscan debris comprises 58 to 95 percent of the sediment particles greater than 1/8 mm."

^G^TURNEY, W. J. & B. F. PERKINS, 1972, Molluscan distribution in Florida Bay. *Sedimentia III*: 37 pp. Comparative Sedimentology Laboratory, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida.

These results first appeared as a Shell Development Company report in 1958. Each station included a 2-gallon sample of sediment down to an average depth of seven inches [estimate age of deposition = 300–400 yrs]; 100 genera and 140 species are tabulated, "based chiefly on death assemblages". Identifications were verified using the collections and type specimens at USNM.

Florida Bay was divided into four hydrological "subenvironments": Northern (freshwater from mainland/Everglades), Interior (restricted circulation – includes shoreline of Upper Keys above Snake Creek on Plantation Key), Atlantic (tidal flow through Florida Keys – the border meets the Keys chain at Plantation Key), and Gulf (continuous with Gulf of Mexico). To assimilate these data into this survey, we drew our mid-line through Florida Bay (as described above), and found that all stations of the Northern subenvironment, and part of the stations of the Interior and Gulf subenvironments were outside of our Florida Keys definition; all included stations fell either within our Upper or Middle Keys zones. Collections from each station were qualitatively recorded by the authors as abundant, common, few, or rare, and as including living specimens or dead only.

Recorded from Florida Keys stations: *Abra lioica, Anadara notabilis, Anodontia alba, A. philippiana, Anomalocardia auberiana, A. cuneimeris, Arca umbonata, A. zebra, Arcopagia fausta, Arcopsis adamsi, Atrina* sp., *Barbatia cancellaria, Barnea costata, Brachidontes exustus, Cardiomya costellata, Cardita floridana, Chione cancellata, C. pygmaea, Codakia orbicularis, C. orbiculata, Corbula* sp., *Crenella divaricata, Cumingia tellinoides, Diplodonta punctata, Divaricella quadrisulcata, Glycymeris pectinata, Laevicardium laevigatum, L. mortoni, Lima pellucida, Linga trisulcata, Lucina multilineata, L. pensylvanica, Mactra fragilis, Noetia ponderosa, Nucula proxima, Nuculana acuta, Parastarte triquetra, P.* sp., Pectinidae, *Phacoides nassula, Pinctada radiata, Pitar fulminata, Plicatula gibbosa, Pseudochama radians, Pseudocyrena maritima, Semele proficua, Strigilla mirabilis, Tagelus divisus, Tellidora cristata, Tellina alternata, T. mera, T. similis, T. texana, Trachycardium muricatum, Transennela* (*sic*) sp., *Trigonocardia medium, Venericardia tridentata, Volsella americana.*

^G^UNITED STATES GEOLOGICAL SURVEY [USGS], 2003 [ver. 24 January 2003], South Florida Ecosystem History Project: Florida Bay. http://sofia.usgs.gov/flaecohist/floridabay.html; last accessed 12 September 2003.

Twenty-eight of 39 USGS field sites in Florida Bay lie within our definition of the Florida Keys; to our knowledge only sites 1–25 have had data published in some form. The online database includes living molluscan species occurrences from 160 specific USGS stations sampled between 1994 and 2001 in Florida Bay: *Anodontia alba, Anomalocardia auberiana, Anomia simplex*, Arcoidea, *Arcopsis adamsi, Argopecten irradians, Brachidontes exustus, Carditamera floridana, Chione cancellata, Codakia* spp., *Cumingia* sp. or spp., *Cyrenoida floridana, Diplodonta* spp., *Laevicardium mortoni, Limaria* sp. cf. *L. pellucida, Lucina pectinata*, Lucinidae, Mactridae, *Mercenaria* spp., *Modiolus squamosus, Nucula proxima*, Ostreidae, *Parastarte triquetra*, Pinnidae, *Pitar simpsoni, Polymesoda maritima, Pteria longisquamosa, Tagelus* spp., *Tellina* sp. or spp., *Trachycardium muricatum, Transennella* spp., and unknown pelecypod. Empty shell records dated to the mid-1800s are derived from six sediment cores: *Anodontia ?alba, Anomalocardia auberiana, Arcopsis adamsi, Argopecten irradians, Brachidontes exustus, Chione cancellata, Codakia orbicularis, Codakia* spp., *Cumingia tellinoides, Cyrenoida floridana, Laevicardium laevigatum, L. mortoni, L.* spp., *Lima* spp., *Limaria* sp. cf. *L. pellucida, Lucinisca nassula, Mysella planulata, Nucula proxima, Ostreea equestris, Parastarte triquetra, Parvilucina multilineata*, pectinid, *Pitar simpsoni, Pteria longisquamosa, Semele bellastriata, Tellina* spp., *Transennella* spp., and unidentified pelecypod.

VALENTICH-SCOTT, P. & G. E. DINESEN, 2004, Rock and coral boring Bivalvia (Mollusca) of the Middle Florida Keys, U.S.A. In: R. BIELER & P. M. MIKKELSEN, eds., *Bivalve stud-*

ies in the Florida Keys, Proceedings of the International Marine Bivalve Workshop, Long Key, Florida, July 2002. *Malacologia*, 46(2): 339–354.
From Florida Keys localities: *Botula fusca, Choristodon robustum, C.* sp. A, *Gastrochaena hians, Lithophaga antillarum, L. aristata, L. bisulcata, Petricola lapicida* [material from this study].

VERRILL, A. E., 1882, Catalogue of marine Mollusca added to the fauna of the New England region, during the past ten years. *Transactions of the Connecticut Academy*, 5: 447–587, pls. 42–44, 57, 58.
Neaera rostrata from Sand Key as per Dall's *Blake* report (Dall, 1881).

*VILAS, C. N. & N. R. VILAS, 1945, *Florida marine shells – a guide to* [*sic*] *amateur collectors of Florida marine shells which is completely illustrated with colored photoengravings.* Aberdeen Press, Chicago. iv + 152 pp., incl. 12 color pls.
With distribution including Florida Keys (or specific localities): *Barnea truncata, Codakia orbicularis, Pecten muscosus, Pedalion alata, Pinctada radiata, Semele bellastriata, Spondylus americanus, Tellina radiata, T. r. unimaculata.*

VILAS, C. N. & N. R. VILAS, 1970, *Florida marine shells*. Charles E. Tuttle, Rutland, Vermont. 170 pp., 14 pls.
With distribution including Florida Keys (or specific localities): *Aequipecten muscosus, Barnea truncata, Codakia orbicularis, Pedalion alata, Pinctada imbricata, Semele bellastriata, Spondylus americanus, Tellina radiata, T. r.* var. *unimaculata.*

^{G}*[BARRY A.] VITTOR & ASSOCIATES, INC., 1997a [March], *Florida Bay Benthic Community Assessment*. Report to NOAA, Silver Spring, Maryland, 42 pp.
From bayside localities in Upper, Middle and Lower Florida Keys: Lucinidae, *Nucula aegeenis, Solemya occidentalis,* Tellinidae.

^{G}*[BARRY A.] VITTOR & ASSOCIATES, INC., 1997b [June], *Florida Bay and adjacent waters benthic community assessment*. Report to NOAA, Silver Spring, Maryland, unpaginated.
From bayside localities in Lower Florida Keys: *Crassinella martinicensis, Diplodonta semiaspera, Tellina* sp.

^{G}*[BARRY A.] VITTOR & ASSOCIATES, INC., 1997c [August], *Biscayne Bay, Florida benthic community assessment*. Report to NOAA, Silver Spring, Maryland, unpaginated.
From Card Sound: *Americardia media, Arcopsis adamsi, Brachidontes exustus, Chione cancellata, Diplodonta semiaspera, Laevicardium mortoni, Lucina multilineata, L. radians, L.* sp., Lucinidae, *Modiolus modiolus squamosus, Musculus lateralis, Mysella planulata,* Mytilidae, *Nucula aegensis,* Pelecypoda, *Pitar* sp., Semelidae, *Tellina similis, T. sybaritica, T.* sp., Tellinidae, *Transennella conradina,* Veneridae.

^{G}*[BARRY A.] VITTOR & ASSOCIATES, INC., 1998 [April], *Florida Keys to Dry Tortugas benthic community assessment*. Report to NOAA, Silver Spring, Maryland, unpaginated.
From localities from Lower Florida Keys to Dry Tortugas: *Abra aequalis, Amygdalum sagittatum, Anadara* sp., *Anomalocardia auberiana, Arca zebra,* Arcidae, *Arcinella cornuta, Argopecten gibbus, Asthenothaerus hemphilli,* Bivalvia, *Bushia* sp., Carditidae, *Cardiomya perrostrata, Cardiomya* sp., *Chama congregata, Chione cancellata, C. grus, C.* sp., *Codakia orbicularis, C.* sp., *Corbula contracta,* Corbulidae, Crassatellidae, *Crassinella lunulata, C. martinicensis, C.* sp., *Crenella divaricata, Cumingia coarctata, C. tellinoides, Diplodonta semiaspera, D.* sp., *Dosinia discus, Ervilia concentrica, Gastrochaena hians, Glans dominguensis,* Glycymerididae, *Glycymeris pectinata, G.* sp., *Gouldia cerina, Hiatella arctica, Lima pellucida, Linga amiantus, L. pensylvanica, L.* sp., *Lioberus castaneus, Lucina blanda, L. multilineata, L. nassula, L.* sp., Lucinidae, *Lyonsia beana, L. hyalina floridana, Macoma brevifrons, M.* sp., *Macrocallista maculata,* Mactridae, *Modiolus modiolus squamosus,* Montacutidae, *Musculus lateralis,* Mytilidae, *Naeromya floridana, Nucula aegeenis, Nuculana acuta, N. concentrica, N.* sp., *Pandora* sp., Pectinidae, *Pitar fulminatus, P. simpsoni, P.* sp., *Pleuromeris tridentata, Semele bellastriata, S. nuculoides, S. proficua,* Semelidae, *Solemya occidentalis, S.* sp., *Tellidora cristata, Tellina aequistriata, T. iris, T. listeri, T. mera, T. similis, T. sybaritica, T. texana, T. versicolor, T.* sp., Tellinidae, Thraciidae, *Trachycardium egmontianum, Transennella stimpsoni,* Ungulinidae, *Varicorbula operculata,* Veneridae.

^{G}[BARRY A.] VITTOR & ASSOCIATES, INC., 1999a [June], *Florida Keys (including outer Florida Keys National Marine Sanctuary Boundary) – Dry Tortugas benthic commu-*

nity assessment, July 1998. Report to NOAA, Silver Spring, Maryland, unpaginated.

Twenty stations from off the oceanside of the Upper and Lower Keys and Dry Tortugas include collections of: *Abra aequalis, Amygdalum sagittatum, A.* sp., *Anadara notabilis, Arca zebra, Argopecten* sp., *Asthenothaerus hemphilli,* Bivalvia, Cardiidae, *Cardiomya perrostrata,* Carditidae, *Chione grus, Corbula contracta, Crassinella lunulata, C. martinicensis,Crenella divaricata, Dosinia discus, Ervilia concentrica, Gastrochaena hians, Glans dominguensis, Glycymeris decussata, Gouldia cerina, Hiatella arctica, Laevicardium laevigatum, Lima locklini, L. pellucida, L.* sp., *Lucina multilineata, L. muricata, L. nassula, L. pectinata, L. radians, L.* sp., Lucinidae, *Lyonsia hyalina floridana, Macoma tenta, Macrocallista maculata, M. nimbosa,* Montacutidae, *Musculus lateralis, Musculus* sp., *Mysella* sp., *Nucula aegeenis* (*sic*), *Nuculana acuta, N. concentrica, Pandora arenosa, P.* sp., *Pitar simpsoni, P.* sp., *Pleuromeris tridentata, Semele bellastriata, S. nuculoides, S. proficua, S. purpurascens, S.* sp., Semelidae, *Tellina sybaritica, T. texana, T.* sp., Tellinidae, Thraciidae, *Varicorbula operculata*, Veneridae.

G[BARRY A.] VITTOR & ASSOCIATES, INC., 1999b [November], *Florida Keys National Marine Sanctuary benthic community assessment, August–September 1998.* Report to NOAA, Silver Spring, Maryland, unpaginated.

Thirteen stations from off the oceanside of the Upper, Middle and Lower Keys include collections of: *Abra lioica, A.* sp., *Anadara notabilis, Arca zebra,* Arcidae, *Asthenothaerus hemphilli, A.* sp., Bivalvia, *Bushia elegans,* Cardiidae, Carditidae, *Chione cancellata, C. grus, C.* sp., *Codakia orbicularis, Crassinella lunulata, C.* sp., *Crenella divaricata, Cumingia tellinoides, Diplodonta punctata, D.* sp., *Dosinia discus, Ervilia concentrica, E. nitens, E.* sp., *Glans dominguensis,* Glycymerididae, *Gouldia cerina, Hiatella arctica, Laevicardium laevigatum, L. sybariticum, L.* sp., *Lima pellucida, L.* sp., Limidae, *Lioberus castaneus, Lucina muricata, L. nassula, L. radians, L.* sp., Lucinidae, *Macoma* sp., *Modiolus modiolus squamosus,* Montacutidae, *Musculus lateralis*, Mytilidae, *Neaeromya floridana, Nucula aegeenis* (*sic*), Pectinidae, *Pitar fulminatus, P. simpsoni, P.* sp., *Pleuromeris tridentata,* Pteriidae, *Semele bellastriata, S. nuculoides, S.* sp., Semelidae, *Tagelus divisus, Tellina gouldii, T. iris, T. mera, T. similis, T. tampaensis, T. tenella, T.* sp., Tellinidae, *Trachycardium muricatum, T.* sp., Veneridae. Five stations (98FKNMS09, -10, -13, -14, -15) had no mollusks listed; two additional stations (98FKNMS01, -02) lie north of Keys northeastern boundary, as defined by this study.

*VOKES, H. E., 1969, The anadarid subgenus *Caloosarca* in the western Atlantic region. *Tulane Studies in Geology and Paleontology*, 7(1): 1–40, incl. pls. 1–6.

Anadara (*Caloosarca*) *notabilis* from Long Key.

GVOSS, G. L., 1948, A trip to the outer reef. *Shell Notes*, 2(5): 58–72.

Collecting with Frank Lyman and Don Moore, from reefs out of Garden Cove [Key Largo]: *Pecten imbricatus, P. sentis.*

GVOSS, G. L., 1949, Notes from the log of the *Junonia*. *Shell Notes*, 2(7–9): 112–120.

From reefs out of Garden Cove [Key Largo]: *Arca* sp., *Glycimeris americana lineata, Lima* spp., *Pecten antillarum, P. sentis.* The authors notes of Conch Reef: "We had very little luck here ... as the reef in this section is dead as far as molluscan life is concerned."

GVOSS, G. L., 1983, *Final report: an environmental assessment of the Key Largo National Marine Sanctuary.* Rosenstiel School of Marine and Atmospheric Science, University of Miami. 517 pp.

Requested by the U.S. Office of Coastal Zone Management, "to provide a base-line study of the fauna and flora for use in management, planning and future studies". Surveying 10 reef sites and 7 shallow grass and hard-bottom sites shoreward of 18 m isobath, using rotenone, visual transect lines, and collection of unknown organisms. Identifications of mollusks were achieved using Voss (1980). In sand areas, the sand was removed to a depth of 10 cm in 4 m^2 quadrats, then screened; all specimens 1 cm or longer in length were retained for identification. Voucher specimens are deposited at the Rosenstiel School of Marine and Atmospheric Sciences. The molluscan species list includes *Americardia media, Anadara notabilis, Arca imbricata, A. zebra, Argopecten gibbus, Barbatia cancellaria, B. candida, B. domingensis, Chama macerophylla, Chione cancellata, C. paphia, Codakia orbicularis, Diplodonta* punctata, *Glycimeris*

(*sic*) *pectinata, Laevicardium laevigatum, Lima lima, L. pellucida, Linga pensylvanica, Lithophaga* sp., *Lopha frons, Lyropecten antillarum, Modiolus americanus, M. modiolus squamosus, Musculus lateralis, Ostrea frons, Papyridea semisulcata, Pecten* sp., *Periglypta listeri, Pinctada radiata, Plicatula gibbosa, Tagelus* sp., *Tellina listeri.*

[G]VOSS, G. L., N. A. VOSS, A. Y. CANTILLO & M. J. BELLO, 1983, *An environmental assessment of the John Pennekamp Coral Reef State Park and the Key Largo Coral Reef Marine Sanctuary.* Joint NOAA/University of Miami Report. NOAA Technical Memorandum NOS NCCOS CCMA 161. NOAA LISD Current References 2002-6. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, Florida. 452 pp. 2002 edited version available at http://www.aoml.noaa.gov/general/lib/cedardoc.html; last accessed 04 April 2003.

Qualitative and quantitative studies were conducted to determine the state of marine communities after approximately 10 years post-establishment of John Pennekamp Coral Reef State Park and Key Largo Coral Reef Marine Sanctuary. Transects of 400 m length (3 per site) perpendicular to the reef or shoreline were surveyed by scuba divers. Some voucher specimens were located by PMM in February 2003 in the Invertebrate Museum, Rosenstiel School of Marine and Atmospheric Science. *Americardia media, Anadara floridana, A. notabilis, Arca imbricata, A. zebra, Arca* sp., ark shells, *Argopecten gibbus, Barbatia cancellaria, B. candida, B. domingensis,* bivalve, *Chama congregata, C. macerophylla, Chione cancellata, C. paphia, Codakia orbicular* (*sic*), *C. orbicularis, Diplodonta punctata, Glycymeris pectinata, Glycymeris* sp., *Isognomon* sp., *Laevicardium laevigatum, Lima lima, L. pellucida, L. scabra, Lima* spp. (with "red and yellow tentacles"), *Linga pensylvanica, Lithophaga antillarum, L. nigra, Lithophaga* spp., *Lopha frons, Lyropecten antillarum, Modiolus americanus, M. modiolus squamosus, Musculus lateralis, Ostrea frons, O.* (*Lopha*) *frons, Papyridea semisulcata, Pecten antillarum, P.* sp., *Periglyphus* (*sic*) *listeri, Periglypta listeri, Pinctada radiata, Plicatula gibbosa, Tagelus* sp., *Tellina listeri.*

|VOSS, G. L. & N. A. VOSS, 1955, An ecological survey of Soldier Key, Biscayne Bay, Florida. *Bulletin of Marine Science of the Gulf and Caribbean*, 5(3): 203–229.

Although cited as a source of Florida Keys biotic records (Levy et al., 1996), this work is here excluded as being outside our defined area, which extends south of Broad Creek at the northern end of Key Largo. Soldier Key is north of this point, at the eastern extent of Biscayne Bay.

WAGNER, R. J. L. & R. T. ABBOTT, 1990, *Wagner and Abbott's world size records.* Standard Catalog of Shells, Suppl. 4. American Malacologists, Melbourne, Florida. ii + 80-001–80-080.

World size records from Florida Keys: *Aequipecten acanthodes, A. muscosus, Arca zebra, Chlamys sentis, Isognomon alatus, Lyropecten antillarum, Mercenaria campechiensis, Psammotreta intastriata, Tellina fausta, T. listeri, T. magna, T. radiata, T. r. unimaculata.*

WALLER, T. R., 1969, The evolution of the *Argopecten gibbus* stock (Mollusca: Bivalvia), with emphasis on the Tertiary and Quaternary species of eastern North America. The Paleontological Society, Memoir 3. *Journal of Paleontology*, 43(Suppl. to no. 5): v + 125 pp., 3 fold-outs.

From Florida Keys or Keys localities: *Argopecten gibbus, A. irradians concentricus, A. nucleus.*

*WALLER, T. R., 1993, The evolution of "*Chlamys*" (Mollusca: Bivalvia: Pectinidae) in the tropical western Atlantic and eastern Pacific. *American Malacological Bulletin*, 10(2): 195–249.

From Florida Keys localities: *Caribachlamys imbricata, C. mildredae, C. ornata, C. sentis.*

*WALLER, T. R. & I. G. MACINTYRE, 1982, Larval settlement behavior and shell morphology of *Malleus candeanus* (d'Orbigny) (Mollusca: Bivalvia). Pp. 489–497, in: K. RUTZLER & I. G. MACINTYRE, eds., *The Atlantic barrier reef ecosystem at Carrie Bow Cay, Belize, 1. Structure & Communities*, Smithsonian Contributions to Marine Science 12, 539 pp.

Malleus candeanus from the Dry Tortugas.

*WARMKE, G. L. & R. T. ABBOTT, 1961, *Caribbean seashells.* Dover Publications, New York. 348 pp., 44 pls.

With distribution including Florida Keys (or specific localities): *Aequipecten lineolaris, Antigona rigida, Chama sarda, Chione paphia, Cumingia antillarum, Isognomon bicolor, Phacoides muricata, Strigilla pisiformis, Tellina punicea, Trachycardium magnum, Transennella cubaniana.*

WATTERS, G. T., 2002, The status and identity of *Papyridea soleniformis* (Bruguière,

1789) (Bivalvia: Cardiidae). *The Nautilus*, 116(4): 118–128.
A systematic study of *Papyridea soleniformis* reveals involvement of a second species, *P. lata*. Florida Keys localities are cited for each, from University of Florida, University of Michigan, ANSP, and H. G. Lee collections.

WEBB, W. F., 1937, *Shells and other invertebrates of the United States*. Privately published, Rochester, New York. xiv + 80 pp.
From Florida Keys (or specific localities): *Cytherea hebraea, Dosinia discus, Mytilus perna, Ostrea foliata, Transenella* (*sic*) *conradina.*

WEBB, W. F., 1939, *A Catalogue of Recent Mollusca for sale by Walter F. Webb*. W. F. Webb, Rochester, New York. [iv] + 148 pp. incl. 34 pls.
From Florida Keys (or specific localities): *Cytherea hebraea, Mytilus perna, Transenella* (*sic*) *conradina.*

WEBB, W. F., 1942, *United States Mollusca: a descriptive manual of many of the marine, land and fresh water shells of North America, north of Mexico*, 1st ed. Privately published, Rochester, New York. 220 pp., 63 pls.
"The Pourtales Plateau which lies just off the S. E. Florida coast at the Tropic of Cancer fairly swarms with oceanic life. The Gulf Stream sweeps over it constantly, bringing warm water literally swarming with minute life. The larger Pelagic life like *Janthina*s and the smaller *Hyalaea*s, *Creseis*, *Cuveria*s and others sweep along by the millions. The minute pelagic animals are constantly dying, and there is always a gengle rain of food falling over the bottom of the ocean. A veritable free soup kitchen for the myriads of shell life. The food literally drops into their mouth without any effort to obtain same. It is no wonder that the dredge bridge brings up unbelievable quantities of shells which are seldom found on the shore lines." (p. 37).
From Florida Keys (or specific localities): *Chama variegata, Chione latilirata, C. paphia, Cytherea hebraea, Dosinia discus, Glycimeris* (*sic*) *americana, Lima fragilis, L. tenera, Lithophaga antillarum, Lucina pensylvanica, Macoma constricta, Modiola duplicata, Mytilus perna, Ostrea foliata, Paphridea* (*sic*) *spinosum, Pecten antillarum, P. sentis, Pitar fulminata, Plicatula mantilla, Strigilla pisiformis, Tellina candeana, Transenella* (*sic*) *conradina.*

WEBB, W. F., 1951, *United States Mollusca – a descriptive manual of many of the marine, land and fresh water shells of North America, north of Mexico*. Privately published, St. Petersburg, Florida. 224 pp., incl. 67 pls.
With distribution including Florida Keys (or specific localities): *Arca candida, Chama variegata, Chione latilirata, C. paphia, Cyrena floridana, Cytherea hebraea, Dosinia discus, Glycimeris americana, Lima fragilis, L. tenera, Lithophaga antilarum* (*sic*), *Lucina pensylvanica, Macoma constricta, Modiola duplicata, Mytilus perna, Ostrea foliata, Paphridea spinosum, Pecten antillarum, P. imbricatus, P. muscosus, P. nucleus, P. ornatus, P. sentis, Pitar fulminata, Plicatula mantilla, Strigilla pisiformis, Tellina braziliana, T. candeana, T. crystallina, T. laevigata, Transenella* (*sic*) *conradina.*

WEBSTER, R., 1978, *Gems: their sources, descriptions and identification*, 3rd ed. Archon Books, Handon, Connecticut. 931 pp.
Reference to pearling (undoubtedly from *Pinctada imbricata*) is made: "The Gulf of Mexico is often mentioned as an area for pearl fishery, and admittedly there is an unimportant fishery off the Marquesas ...".

WHEATLEY, C. M., 1845, *Catalogue of the shells of the United States, with their localities*, 2nd ed. John Towers, New York. 35 pp.
Chama lazerus from Key West.

^{G}WIENER, J., 1988b, More Mystery Island ... *The Busycon* [*Broward Shell Club, Ft. Lauderdale, Florida*], 23(10): 2–4.
Account of a July 1988 shelling trip to Sawyer Island, out of Little Torch Key lists only "assorted bi-valves".

^{G}WILLIAMS, P., 1990, Scallops I have known. *American Conchologist*, 18(2): 3–4.
Chlamys sentis, common in shallow reefs in the Keys.

*WILLIAMS, W., 1988, *Florida's fabulous seashells and other seashore life*, 2nd ed. World Publications, Tampa, Florida. 112 pp.
From Florida Keys (with color photographs labelled by common names): *Chlamys imbricatus, C. sentis, Codakia orbicularis, Ctenoides floridana* [photographed, as "file clam"], *Lima lima, Lyropecten nodosus, Spondylus americanus*. Also notes on commercial use of bivalve species.

^{G}WINGARD, G. L., S. ISHMAN, T. CRONIN, L. E. EDWARDS, D. A. WILLARD & R. B. HALLEY, 1995, Preliminary analysis of downcore biotic assemblages: Bob Allen Keys, Everglades National Park, Florida Bay. *United States Geological Survey Open-File Report* 95-628, 35 pp. Electronic version available at http://131.247.143.93/publications/ofr/95-628/; last accessed 12 September 2003.

From Core 6A, a sediment core dated to the mid-1800s, at the Bob Allen Keys, Florida Bay: *Anomalocardia cuneimeris*, *Arcopsis adamsi*, *Brachiodontes* (*sic*) sp., *Chione cancellata*, *Cumingia tellinoidea*, *Laevicardium* spp., *Lima* sp., *Mysella* sp., *Nucula proxima*, *Parastarte triquetra*, pectinid, *Pinctada radiata*, *Pitar* sp., *Semele bellastriata*, *Tellina* spp., *Transenella* (*sic*) spp., unidentified pelecypod fragments. A summary of these data was published by Brewster-Wingard et al. (1998) and Brewster-Wingard & Ishman (1999).

^{G}WOODS, E., 1970, June Keys field trip. *Seafari* [*Palm Beach County Shell Club Newsletter*], 12(10): 2–4.

From Missouri Key [June 1970], among rubble, seagrass, and mud: *Antigona listeri, Arca imbricata, A. zebra, Arcopagia fausta,* arks, *Codakia orbicularis, Glycymeris pectinata, Laevicardium laevigatum, Lucina pensylvanica, Modiolus americanus, Pinctada radiata*; from along shore: *Pecten antillarum*; from an evening trip to an unspecified area: *Arcopsis adamsi, Lima scabra tenera.*

^{G}WOODS, E., 1971, Grassy Key enclosure – gone! *Seafari* [*Palm Beach County Shell Club Newsletter*], 13(1): 1–2.

The author is lamenting closure of a "man-made pool" on the Gulf side of Grassy Key that was formerly a popular shelling site. From among rocks at that site are *Barbatia cancellaria, Lima pellucida, Lima scabra tenera,* and "little mussels and oysters".

WORK, R. C., 1969, Systematics, ecology, and distribution of the mollusks of Los Roques, Venezuela. *Bulletin of Marine Science*, 19(3): 614–711.

From Florida Keys localities (citing literature and author's personal records): *Americardia media, Arca imbricata, Arca zebra, Barbatia cancellaria, Barbatia candida, Brachidontes exustus, Chama congregata, C. macerophylla, Chlamys imbricata, C. ornata, Codakia orbicularis, Isognomon alatus, I. radiatus, Laevicardium laevigatum, Lima lima, L. pellucida, L. scabra, L. scabra* form *tenera, Modiolus americanus, Pinctada imbricata, Pinna carnea, Pteria colymbus, Spondylus americanus, S. ictericus, Tellina fausta, T. laevigata, T. listeri, T. radiata.*

^{G}ZIEMAN, J. C., 1982, *The ecology of the seagrasses of south Florida: a community profile.* United States Fish and Wildlife Services, FWS/OBS - 82/25, 158 pp. Reprinted September 1985.

Referring to a paper by Chan (1977), reporting on the effects of a 1975 tanker discharge SW of the Marqueses: "The author attributed mass mortalities of the pearl oyster (*Pinctada radiata*) a grass bed inhabitant, to some soluble fraction of petroleum" (p. 88).

^{G}ZISCHKE, J. A., 1973, *An ecological guide to the shallow-water marine communities of Pigeon Key, Florida.* St. Olaf College, Northfield, Minnesota. [vi +] 44 pp.

The text refers to some molluscan species' particular zones and habitats. "This list does not include all species present, nor does it include species that are exclusively found in mangrove and coral communities or forms generally restricted to deeper water" (p. 26). The listing indicates habitats for each species [intertidal, *Echinometra* zone, loose rock, Alcyonaria-sponge zone, grass beds]. Included are: *Americardia media, Anadara notabilis, Antigona listeri, Arca imbricata, A. zebra, Arcopsis adamsi, Atrina rigida, Barbatia cancellaria, Brachidontes exustus, Chione cancellata, Chlamys sentis, Codakia orbicularis, Isognomon alatus, I. bicolor, I. radiatus, Lima scabra, Lithophaga antillarum, L. nigra, Lucina pensylvanica, Modiolus americanus, Ostrea equestris, Petricola lapicida, Pinctada imbricata, Sanguinolaria sanquinolenta.*

ZISCHKE, J. A., 1977a, Checklist of macroflora, invertebrates and fishes of Pigeon Key. Pp. 27–30, in: H. G. MULTER, *Field guide to some carbonate rock environments – Florida Keys and western Bahamas,* new ed. Kendall/Hunt Publishing Company, Dubuque, Iowa. 415 pp., 10 maps.

From Pigeon Key: *Americardia media, Anadara notabilis, Antigona listeri, Arca imbricata, A. zebra, Arcopsis adamsi. Atrina rigida, Barbatia cancellaria, Brachidontes exustus, Chione cancellata, Chlamys sentis, Codakia orbicularis, Isognomon alatus, I. bicolor, I. radiatus, Laevicardium laevigatum, Lima scabra, Lithophaga antillarum, L. nigra, Lucina pensylvanica, Modiolus americanus, Ostrea equestris, Petricola lapicida, Pinctada imbricata, Pteria colymbus, Sanguinolaria sanguinolenta.*

ZISCHKE, J. A., 1977b, An ecological guide to the shallow-water marine communities of Pigeon Key, Florida. Pp. 23–27, in: H. G. MULTER, *Field guide to some carbonate rock environments – Florida Keys and western Bahamas,* new ed. Kendall/Hunt Publishing Company, Dubuque, Iowa. 415 pp., 10 maps.

Mentions mollusks (some with sketched fig-

ures) and other organisms and their occurrence in the various ecological zones of Pigeon Key, including: *Anadara* sp., *Arca* sp., *Arcopsis adamsi, Atrina rigida, Barbatia* sp., *Brachidontes exustus, Chione cancellata, Isognomon alatus, I. bicolor, Ostrea equestris.*

ZISCHKE, J. A., 1977c, Some common invertebrates of Pigeon Key. Figure A.14, in: H. G. MULTER, *Field guide to some carbonate rock environments – Florida Keys and western Bahamas*, new ed. Kendall/Hunt Publishing Company, Dubuque, Iowa. 415 pp. + 10 maps.
Illustrated from Pigeon Key: *Anadara notabilis, Antigona listeri, Arca zebra, Arcopsis adamsi, Atrina rigida, Barbatia cancellaria, Brachidontes exustus, Chione cancellata, Chlamys sentis, Codakia orbicularis, Isognomon alatus, Lima scabra.*

CRITICAL CATALOG OF FLORIDA KEYS BIVALVES

(Those species listed without references occur in the Florida Keys according to our survey of original and museum collections, but have not been previously recorded as such in the literature.)

Anomiidae

Anomia simplex Orbigny, 1842: Dall, 1889a, 1903b; Lermond, 1936; Siekman, 1965; Magnotte, 1970–1979; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK, MFK].

Pododesmus rudis (Broderip, 1834): Dall, 1889a [as *Placunanomia*]; Lermond, 1936 [as *Polodesmus* (*sic*) *decipiens* Philippi, 1837].

Arcidae

Edwards, 1970 [LFK; as ark shells]; Woods, 1970 [LFK; as arks]; Voss et al., 1983 [UFK; as ark shells]; Clampit, 1987 [LFK; as ark shells]; Vittor & Associates, 1998 [DT], 1999b [MFK, LFK].

Acar domingensis (Lamarck, 1819): Dall, 1883 [LFK; as *Arca* (*Barbatia*) *dominguensis* and misidentified as *Arca* (*Barbatia*) *gradata* Broderip & G. B. Sowerby I, 1829, a recognized eastern Pacific species], 1885 [LFK; as *Arca* (*Barbatia*) *dominguensis* and as *Arca* (*Barbatia*) *gradata*], 1889a [as *Arca* (*Byssoarca*) *reticulata* auctt. *non* Gmelin, 1792; also misidentified as *Arca* (*Byssoarca*) *nodulosa* Müller, 1776, a synonym of *Barbatia scabra* (Poli, 1795), a recognized European species], 1903b [as *Arca* (*Byssoarca*) *reticulata*]; Simpson, 1887–1889 [DT; as *Arca domingensis* and as *Arca gradata*]; Thiele, 1910 [DT; misidentified as *Arca plicata* Dillwyn, 1817, a recognized Indo-Pacific species]; Lermond, 1936 [as *Arca reticulata*]; M. Smith, 1937, 1945 [as *Arca* (*Acar*) *reticulata*]; Edwards, 1968b [LFK; as *Barbatia*]; Ross, 1969 [MFK; as *Barbatia*]; Godcharles & Jaap, 1973 [UFK; as *Barbatia*]; Mikkelsen, 1981 [UFK; as *Barbatia* (*Acar*)]; Voss, 1983 [UFK; as *Barbatia*]; Voss et al., 1983 [UFK; as *Barbatia*]; Lyons & Quinn, 1995 [as *Barbatia*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Barbatia*]; Oliver & Järnegren, 2004 [LFK]; Simone & Chichvarkhin, 2004 [MFK, LFK; as *Barbatia*].

Anadara baughmani Hertlein, 1951: Rehder & Abbott, 1951 [DT; as *A. springeri* Rehder & Abbott, 1951]; Pulley, 1952 [DT]; Sweeney & Harasewych, 1999 [DT; as *A. springeri*]; Mikkelsen & Bieler, 2000 [DT].

|*Anadara brasiliana* (Lamarck, 1819) – see under *Scapharca.*

|*Anadara chemnitzii* (Philippi, 1851) – see under *Scapharca.*

Anadara floridana (Conrad, 1869): Dall, 1889a [misidentified as *Arca* (*Scapharca*) *lienosa* Say, 1832, which is fossil]; Pearse, 1929 [DT; as *Arca* "*saccharina*", probably a misspelling for *Arca* (*Anadara*) *floridana* var. *secernenda* Lamy, 1907]; Lermond, 1936 [misidentified as *Arca secticostata* Reeve, 1844, from indeterminate locality]; Magnotte, 1970–1979 [as *A. lienosa floridana*]; Voss et al., 1983 [UFK]; Mikkelsen & Bieler, 2000 [LFK].

Anadara notabilis (Röding, 1798): Simpson, 1887–1889 [LFK; as *Arca deshayesii* Hanley, 1843]; Dall, 1889a, 1903b [LFK; misidentified as *Arca* (*Scapharca*) *auriculata* Lamarck, 1819, a recognized Red Sea species], 1898 [LFK; as *Scapharca* (*Scapharca*, section *Scapharca*) *auriculata*]; Maury, 1920 [LFK; as *S.* (*S.*) *auriculata*], 1925 [as *S.* (*S.*) *auriculata*]; Johnson, 1934 [as *Arca auriculata* and *A. deshayesii*]; Lermond, 1936 [as *Arca auriculata*]; Richards, 1936; M. Smith, 1937, 1940, 1945 [as *Arca auriculata*]; Eubanks, 1964 [as *A. nobilis*]; Ross, 1969 [MFK]; Vokes, 1969 [MFK];

Magnotte, 1970–1979; Stevenson, 1970, 1993 [both as ark shell]; Turney & Perkins, 1972 [UFK, MFK]; Godcharles & Jaap, 1973 [UFK]; Zischke, 1973, 1977a, c [MFK]; Antonius et al., 1978 [LFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Vittor & Associates, 1999a [UFK], b [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

|*Anadara ovalis* (Bruguière, 1789) – see under *Lunarca*.

Anadara transversa (Say, 1822): Simpson, 1887–1889 [LFK; as *Arca*]; Dall, 1889a, 1903b [LFK; as *Arca* (*Scapharca*)], 1898 [LFK; as *Scapharca* (*Scapharca*, section *Scapharca*)]; Rogers, 1908 [as *Arca*]; Aldrich & Snyder, 1936 [as *Arca*]; Lermond, 1936 [as *Arca*]; M. Smith, 1937, 1945 [LFK; as *Arca*]; Pulley, 1952 [DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Anadara sp.: Zischke, 1977b [MFK]; Schomer & Drew, 1982; Vittor & Associates, 1998 [LFK].

Arca imbricata Bruguière, 1789: Simpson, 1887–1889 [DT; also as *Arca noae* var. *americana* Orbigny, 1846]; Nutting, 1895 [DT; as *Arca velata* "Sowerby", [date unknown]. Although the taxonomic status of Sowerby's name could not be verified, Nutting's Tortugas material was later identified as the recognized synonym, *A. umbonata* Lamarck, 1819, by Dall, 1896a]; Dall, 1889a [as *A.* (*Arca*)], 1896a [DT; as *A. umbonata*], 1903b [as *A.* (*Arca*)], 1898 [Pleistocene; as *A.* (*Lunarca*) *umbonata*]; Thiele, 1910 [DT; as *A. umbonata*]; Lermond, 1936 [also as *A. umbonata*]; M. Smith, 1937 [as *A.* (*Navicula*) *umbonata*], 1945 [as *A.* (*Navicula*) *umbonata*]; Bippus, 1950 [UFK; as *A. umbonata*]; T. A. Stephenson & A. Stephenson, 1950 [LFK; as *A. umbonata*]; Kissling, 1965 [LFK], 1977a [UFK, LFK], 1977b [UFK; all as *A. umbonata*]; Edwards, 1968b [LFK]; Iversen & Roessler, 1969 [UFK; also as *A. umbonata*]; Jindrich, 1969 [LFK; as *A. umbonata*]; Lee, 1969 [LFK]; Ross, 1969 [MFK]; Work, 1969 [LFK]; Edwards, 1970 [LFK]; Magnotte, 1970–1979; Woods, 1970 [LFK]; Turney & Perkins, 1972 [UFK, MFK; as *A. umbonata*]; Zischke, 1973, 1977a [MFK]; Antonius et al., 1978 [LFK]; Mikkelsen, 1981 [UFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Oliver & Järnegren, 2004 [LFK].

Arca zebra (Swainson, 1833): Melvill, 1880 [LFK; as *Scapharca occidentalis* (Philippi, 1847) and misidentified as *Arca noae* (Linnaeus, 1758), a recognized eastern Atlantic species]; Simpson, 1887–1889 [DT; as var. of *A. barbadensis* "Petiver" Orbigny, 1846]; Dall, 1889a [as *A.* (*A.*) *noae*], 1896a [LFK; as *A. noae*], 1898 [Pleistocene; as *A.* (*Lunarca*) *occidentalis*], 1903b [as *A.* (*A.*) *noae*]; Lermond, 1936 [as *A. occidentalis*]; Lyman, 1947b [UFK; as *A. occidentalis*]; T. A. Stephenson & A. Stephenson, 1950 [LFK; as *A. occidentalis*]; Edwards, 1968b [LFK]; Iversen & Roessler, 1969 [UFK]; Ross, 1969 [MFK]; Work, 1969 [LFK]; Magnotte, 1970–1979; Stevenson, 1970, 1993 [both as turkey wing]; Woods, 1970 [LFK]; Turney & Perkins, 1972 [UFK, MFK]; Godcharles & Jaap, 1973 [UFK]; Shoemaker, 1973; Zischke, 1973, 1977a, c [MFK]; Kissling, 1977a; Goldberg, 1978 [LFK]; Edwards, 1980 [LFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Wagner & Abbott, 1990; Andrews, 1994: Lyons & Quinn, 1995; Hutsell et al., 1997; Vittor & Associates, 1998 [DT], 1999a [UFK], b [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Orlin, 2003; Simone & Chichvarkhin, 2004 [LFK].

Arca (s. l.) sp.: Nutting, 1895 [LFK]; T. L. McGinty, 1939 [LFK], 1942; Lyman, 1944b [UFK]; Voss, 1949 [UFK; as "some Arcas"]; Bender, 1965 [MFK, LFK; as *Arcas*]; Zischke, 1977b [MFK]; Gaertner, 1978 [LFK, as turkey wings]; Schomer & Drew, 1982; Voss et al., 1983 [UFK]; Oliver & Järnegren, 2004 [LFK].

Barbatia cancellaria (Lamarck, 1819): Simpson, 1887–1889 [DT; misidentified as *Arca fusca* Bruguière, 1789, synonym of *Barbatia amygdalumtostum* (Röding, 1798) a recognized Indian Ocean species]; Dall, 1889a, 1903b [misidentified as *Arca* (*Barbatia*) *barbata* Linnaeus, 1758, a recognized Mediterranean species]; Thiele, 1910 [DT; as *Arca listeri* Philippi, 1849, newly synonymized herein]; Lermond, 1936 [as *Arca barbata*]; M. Smith, 1937, 1945 [UFK; as *Arca* (*B.*) *barbata*]; Lyman, 1949b [as *A. barbata*]; Teare, 1949 [UFK; as *A. barbata*]; Bippus, 1950 [UFK; as *A. barbata*]; T. A. Stephenson & A. Stephenson, 1950 [LFK; as *A. barbata*]; Ginsburg, 1952 [UFK, MFK; as *A. barbata*]; Eubanks, 1964; Iversen & Roessler, 1969 [UFK]; Plockelman, 1969b [MFK]; Ross, 1969 [MFK]; Work, 1969 [LFK]; Magnotte, 1970–1979; Woods, 1971 [MFK]; Turney & Perkins, 1972 [UFK, MFK]; Zischke, 1973, 1977a, c [MFK]; Kissling, 1977b [UFK]; Antonius et al., 1978 [LFK]; Edwards, 1980 [LFK; as *Arca*]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Sedlak, 1986

[LFK]; Lyons & Quinn, 1995; Campbell et al., 1998 [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Simone & Chichvarkhin, 2004 [UFK, MFK, LFK].

|*Barbatia candida* (Helbling, 1779) – see under *Cucullaearca.*

|*Barbatia domingensis* (Lamarck, 1819) – see under *Acar.*

|*Barbatia tenera* (C. B. Adams, 1845) – see under *Fugleria.*

Barbatia sp.: Melvill, 1880 [LFK]; Kissling, 1977a; Zischke, 1977b [MFK]; Schomer & Drew, 1982.

Bathyarca glomerula (Dall, 1881): Dall, 1889a, 1903b [as *Arca* (*Byssoarca*)]; Bartsch, 1937 [LFK; as *Arca*]; Mikkelsen & Bieler, 2000 [DT].

Bathyarca inaequalis (Dall, 1927).

Bentharca sagrinata (Dall, 1886): Dall, 1889a [as *Arca* (*Macrodon*)].

Bentharca sp.: Dall, 1889a [as *Arca* (*Macrodon*)].

Cucullaearca candida (Helbling, 1779): Simpson, 1887–1889 [DT; as *Arca*]; Lermond, 1936 [as *Arca*]; Webb, 1951 [as *Arca*]; Work, 1969 [LFK; as *Barbatia*]; Magnotte, 1970–1979 [as *Barbatia*]; Antonius et al., 1978 [LFK; as *Barbatia*]; Voss, 1983 [UFK; as *Barbatia*]; Voss et al., 1983 [UFK; as *Barbatia*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Barbatia*]; Simone & Chichvarkhin, 2004 [UFK, MFK, LFK; as *Barbatia*].

Fugleria tenera (C. B. Adams, 1845): Pilsbry & McLean, 1939 [LFK; as *Arca* (*Barbatia*) *balesi* Pilsbry & McLean, 1939]; Aguayo & Jaume, 1947b [LFK; as *Arca* (*B.*) *balesi*]; Abbott, 1958 [LFK; as *Barbatia* and as *Arca balesi*]; Magnotte, 1970–1979 [as *Barbatia*]; Lyons & Quinn, 1995 [as *Barbatia*]; Simone & Chichvarkhin, 2004 [MFK, LFK; as *Barbatia*].

Lunarca ovalis (Bruguière, 1789): Dall, 1889a [as *Arca* (*Argina*) *Americana* "Gray" Wood, 1828]; Lermond, 1936 [as *Arca campechiensis americana*]; Mikkelsen & Bieler, 2000 [MFK].

Scapharca brasiliana (Lamarck, 1819): Melvill, 1880 [LFK; misidentified as *S. inaequivalvis* (Bruguière, 1789), a recognized Indian Ocean species]; Simpson, 1887–1889 [as *A. incongrua* Say, 1822]; Dall, 1889a, 1903b [both as *A.* (*S.*) *incongrua*]; Lermond, 1936 [as *A. incongrua*].

Scapharca chemnitzii (Philippi, 1851): Dall, 1889a [as *Arca* (*Noetia*) *Orbignyi* (err. pro *d'orbignyi*) Kobelt, 1891]; Lermond, 1936 [as *Arca*].

Astartidae

Astarte crenata subequilatera G. B. Sowerby II, 1854: Dall, 1889a [as *A. lens* "Stimpson" Verrill, 1872]; Theroux & Wigley, 1983 [UFK, LFK].

Astarte globula Dall, 1886.

Astarte nana Jeffreys in Dall, 1886: Dall, 1889a, 1903b, c; Lermond, 1936; Pulley, 1952 [UFK]; Mikkelsen & Bieler, 2000 [UFK, DT].

Astarte smithii Dall, 1886: Dall, 1889a, 1903b [as *A. Smithii*].

Cardiidae

Foster, 1945; Vittor & Associates, 1999a [UFK], 1999b [UFK, MFK].

Acrosterigma magnum (Linnaeus, 1758): Dall, 1889a, 1903b [as *Cardium*]; Pilsbry, 1890b [LFK; as *Cardium*]; Lermond, 1936 [as *Cardium*]; Clench & Smith, 1944 [DT; as *Trachycardium*]; Abbott, 1954 [LFK; as *Trachycardium*], 1958 [LFK; as *Trachycardium*], 1961 [LFK; as *Trachycardium*], 1974 [as *Trachycardium* (*Acrosterigma*)]; Parker & Curray, 1956 [LFK; as *Trachycardium*]; Warmke & Abbott, 1961 [LFK; as *Trachycardium*]; Barrett & Patterson, 1967 [LFK; as *Trachycardium*]; Humfrey, 1975 [LFK; as *Trachycardium*]; Romashko, 1984 [LFK; as *Trachycardium*]; Lawson, 1993 [as *Trachycardium*]; Rios, 1994 [as *T.* (*Acrosterigma*)]; Abbott & Morris, 1995 [LFK; as *Trachycardium*]; Lyons & Quinn, 1995 [as *Trachycardium*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Trachycardium*].

Americardia guppyi (Thiele, 1910): Abbott, 1958 (MFK, LFK], 1974; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Americardia media (Linnaeus, 1758): Melvill, 1880 [LFK; as *Hemicardium medium*]; Simpson, 1887–1889 [LFK; as *Cardium*]; Dall, 1889a [as *C. medium*], 1896a [LFK; as *C. medium*], 1903b [as *C. medium*]; Lermond, 1936 [as *C.* (*Hemicardium*) *medium*]; M. Smith, 1937, 1945 [both UFK; as *Trigoniocardia* (*A.*) *medium*]; Clench & Smith, 1944 [UFK, MFK, LFK; as *Trigoniocardia* (*A.*)]; Brooks, 1968b [MFK]; Iversen & Roessler, 1969 [UFK]; Work, 1969 [LFK]; Magnotte, 1970–1979; Turney & Perkins, 1972 [UFK, MFK; as *T. medium*]; Zischke, 1973, 1977a [both MFK]; Voss, 1983 [UFK];

Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Vittor & Associates, 1997c [UFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Americardia sp.: Plockelman, 1968d.

Dinocardium robustum (Lightfoot, 1786): Magnotte, 1970–1979.

Dinocardium sp.: Stevenson, 1970, 1993 [both as great heart cockle].

Laevicardium laevigatum (Linnaeus, 1758): Melvill, 1880 [LFK; as *L. laevigatum* and misidentified as *L. serratum* (Linnaeus, 1758), a recognized Indo-Pacific species]; Dall, 1886 [LFK; as *Cardium*], 1889a [as *Papyridea* (*Liocardium*) *laevigatum* and *P.* (*L.*) *serratum*], 1896a [LFK; as *C. serratum*], 1903b [as *P.* (*Liocardium*) *laevigatum* and *P.* (*L.*) *serratum*]; Simpson, 18871889 [LFK; as *L. serratum*]; Lermond, 1936 [as *Cardium* (*Laevicardium*) *laevigatum* and *C.* (*L.*) *serratum*]; Clench & Smith, 1944 [LFK, DT]; Bippus, 1950 [UFK; as *L. serratum*]; Brooks, 1968b [MFK]; Ross, 1969 [MFK]; Work, 1969 [LFK]; Magnotte, 1970–1979; Woods, 1970 [LFK]; Turney & Perkins, 1972 [UFK, MFK]; Godcharles & Jaap, 1973 [UFK]; Zischke, 1977a [MFK]; Goldberg, 1978c [LFK]; Schomer & Drew, 1982; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Vittor & Associates, 1999a [DT], b [MFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2002 [UFK].

Laevicardium mortoni (Conrad, 1830): Thiele, 1910 [DT; as *Cardium*]; Bartsch, 1937; Clench & Smith, 1944 [UFK, MFK]; Bippus, 1950 [UFK]; Ross, 1969 [MFK]; Howard et al., 1970 [LFK]; Hudson et al., 1970 [UFK]; Magnotte, 1970–1979; Turney & Perkins, 1972 [UFK, MFK]; Lineback, 1977 [LFK]; Petersen, 1989 [MFK]; Lyons & Quinn, 1995; Wingard et al., 1995 [UFK; as *L.* spp.]; Brewster-Wingard et al., 1996, 1997 [both as *L.* spp.], 1998 [as *L.* sp.] 2001 [also as *L.* spp.] [all UFK]; Vittor & Associates, 1997c [UFK]; Brewster-Wingard & Ishman, 1999 [UFK; as *L.* spp.]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK, MFK]; Morton & Knapp, 2004 [UFK, MFK].

Laevicardium pictum (Ravenel, 1861): Mikkelsen & Bieler, 2000 [UFK, LFK, DT].

Laevicardium sybariticum (Dall, 1886): Lyons & Quinn, 1995; Vittor & Associates, 1999b [LFK]; Mikkelsen & Bieler, 2000.

Laevicardium sp.: Gaertner, 1978 [LFK; as egg cockles]; Bielsa & Labisky, 1987 [LFK]; Vittor & Associates, 1999b [LFK]; USGS, 2003 [UFK; as *L.* spp.].

Nemocardium peramabile (Dall, 1881): Dall, 1881 [DT; as *Cardium* (*Fulvia*) *peramabilis*], 1886 [LFK; as *C.* (*F.*) *peramabilis*], 1889a, 1903b [as *C. peramabilis*]; Lermond, 1936 [as *C.* (*Protocardia*) *peramabilis*]; Bartsch, 1937 [LFK; as *P. peramabilis*]; Clench & Smith, 1944 [LFK; as *Microcardium*]; Theroux & Wigley, 1983 [LFK]; Mikkelsen & Bieler, 2000 [UFK, LFK].

Nemocardium tinctum (Dall, 1881): Dall, 1881 [DT; as *Cardium* (*Fulvia*) *peramabilis* var. *tinctum*], 1889a [LFK; as *C. peramabilis* var. *tinctum*], 1903b [LFK; as *C. peramabilis* var. *tinctum*], 1900b [LFK; as *Protocardia tincta* Dall, 1886]; Johnson, 1934 [LFK; as *P. tincta*]; Mikkelsen & Bieler, 2000 [LFK, DT].

Papyridea lata (Born, 1778): Webb, 1942, 1951 [in part, figured as *Paphridea spinosum* (Meuschen, 1787)]; Clench & Smith, 1944 [in part, as *P. hiatus* (Meuschen, 1787)]; Barfield, 1990 [LFK; as *P. soleniformis* (Bruguière, 1789)]; Watters, 2002 [LFK].

Papyridea semisulcata (Gray, 1825): Simpson, 1887–1889 [DT; as *Cardium petitianum* Orbigny, 1842]; Dall, 1889a [as *P. Petitiana*], 1900a [UFK; as *Cardium* (*Papyridea*) *semisulcatum*]; Lermond, 1936 [as *Cardium* (*Papyridea*) *semisulcatum*]; Clench & Smith, 1944 [LFK]; Olsson & Harbison, 1952 [LFK; as *P. semisulcatum*]; Pulley, 1952 [LFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Papyridea soleniformis (Bruguière, 1789): Dall, 1889a [misidentified as *P. bullata* (Linnaeus, 1758)]; Lermond, 1936 [as *Cardium* (*Papyridea*) *spinosum*]; Webb, 1942, 1951 [in part, figured as *Paphridea spinosum* (Meuschen, 1787)]; Clench & Smith, 1944 [MFK, LFK; in part, as *P. hiatus* (Meuschen, 1787)]; Brooks, 1968b [MFK]; Plockelman, 1968c [MFK]; Ross, 1969 [MFK]; Sedlak, 1986 [LFK]; Krisberg, 1993 [LFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Watters, 2002 [LFK, DT].

Trachycardium egmontianum (Shuttleworth, 1856): Dall, 1889a [misidentified as *Cardium isocardia* Linnaeus, 1758, a recognized southern Caribbean species]; Nutting, 1895 [DT; as *C. isocardium*]; Lermond, 1936 [as *C. isocardia*]; Clench & Smith, 1944 [DT]; Brooks, 1968b [MFK]; Ross, 1969 [MFK]; Magnotte, 1970–1979; Godcharles & Jaap, 1973 [UFK]; Antonius et al., 1978 [LFK; as *T. isocardia*]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

|*Trachycardium magnum* (Linnaeus, 1758) – see under *Acrosterigma*.

Trachycardium muricatum (Linnaeus, 1758): Melvill, 1880 [LFK]; Dall, 1889a, 1903b [as *Cardium*]; Lermond, 1936 [as *Cardium*]; Clench & Smith, 1944 [MFK, LFK]; Brooks, 1968b [MFK]; Ross, 1969 [MFK]; Magnotte, 1970–1979; Turney & Perkins, 1972 [UFK, MFK]; Godcharles & Jaap, 1973 [UFK]; Lyons & Quinn, 1995; Vittor & Associates, 1999b [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK]; USGS, 2003 [MFK].

Trachycardium sp.: Plockelman, 1968d; Iversen & Roessler, 1969 [UFK]; Vittor & Associates, 1999b [LFK].

Trigoniocardia antillarum (Orbigny, 1842): Dall, 1889a [as *Cardium*]; Lermond, 1936 [as *Cardium* (*Trigoniocardia*)].

Carditidae

Vittor & Associates, 1998 [LFK, DT], 1999a [DT], 1999b [UFK].

Carditamera floridana Conrad, 1838: Tryon, 1873 [LFK; as *Cardita* (*Carditamera*)]; Melvill, 1880 [LFK; *Cardita* (*Mytilicardia*) *floridana* "(Sowerby)"]; Simpson, 1887–1889 [MFK; as *Cardita*]; Dall, 1889a [LFK; also as "?" *Cardita Conradii* (err. pro *conradi*) Shuttleworth, 1856], 1903b [LFK; as *Cardita*], 1903a [as *C.* (*Carditamera*)]; Lermond, 1936 [as *Cardita*]; Bartsch, 1937 [as *Cardita*]; Pulley, 1952 [as *Cardita*]; Hudson et al., 1970 [UFK; as *Cardita*]; Turney & Perkins, 1972 [UFK, MFK; as *Cardita*]; Petersen, 1989 [MFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK, MFK; also as *Cardita*].

Glans dominguensis (Orbigny, 1842): Dall, 1889a [as *Cardita domingensis* (*sic*)]; Pulley, 1952 [UFK; as *Cardita domingensis* (*sic*)]; Rehder, 1981; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK, DT], 1999a [UFK], b [MFK, LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Pleuromeris tridentata (Say, 1826): Henderson, 1913 [UFK]; Pulley, 1952 [as *Venericardia*]; Turney & Perkins, 1972 [UFK; as *Venericardia*]; Rehder, 1981; Theroux & Wigley, 1983 [UFK]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK, DT], 1999a [UFK, LFK, DT], b [UFK, MFK, LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Morton & Knapp, 2004 [UFK, MFK].

Pteromeris perplana (Conrad, 1841): Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Chamidae

Dent, 1998.

Arcinella cornuta Conrad, 1866: Calkins, 1878 [DT; misidentified as *Chama arcinella* Linnaeus, 1767, a recognized Caribbean species of *Arcinella*]; Dall, 1889a [as *C. arcinella*], 1896a [as *C.* (*Echinochama*) *arcinella*], 1903b [as *C. arcinella*]; Lermond, 1936 [as *Cardium arcinella*, but corrected to *Chama arcinella* in copy signed by Lermond]; Magnotte, 1970–1979; Dalton, 1991 [LFK; as *A. arcinella*]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT]; Campbell et al., 2004.

Chama congregata Conrad, 1833: Lermond, 1936; Bartsch, 1937 [LFK, DT]; Eubanks, 1964; Ross, 1969 [MFK]; Work, 1969 [LFK]; Magnotte, 1970–1979; Godcharles & Jaap, 1973 [UFK]; Antonius et al., 1978 [LFK]; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Campbell et al., 2004 [MFK, LFK].

Chama florida Lamarck, 1819: Bayer, 1943b [UFK, DT]; Edwards, 1968a [LFK], 1969 [UFK]; Antonius et al., 1978 [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Campbell et al., 2004 [MFK].

Chama inezae (F. M. Bayer, 1943): Bayer, 1943b [UFK; as *Pseudochama*]; M. Smith, 1945 [UFK; as *Pseudochama*]; Aguayo & Jaume, 1950b [UFK; as *Pseudochama*]; Plockelman, 1969a [UFK; as *Pseudochama*]; Mikkelsen & Bieler, 2000 [UFK; as *Pseudochama*]; Campbell et al., 2004 [MFK].

Chama lactuca Dall, 1886: P. L. McGinty & T. L. McGinty, 1957 [MFK, LFK]; Mikkelsen, 1981 [UFK; as *C.* sp.]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK]; Campbell et al., 2004.

Chama macerophylla Gmelin, 1791: Wheatley, 1845 [misidentified as *C. lazarus* Linnaeus, 1758, a recognized Indo-Pacific species]; Calkins, 1878; Melvill, 1880 [LFK]; Simpson, 1887–1889 [DT]; Dall, 1889a, 1903b; Thiele, 1910 [DT]; Lermond, 1936; Bayer, 1943b [LFK, DT]; Eubanks, 1964; Lee, 1969 [LFK]; Ross, 1969 [MFK]; Work, 1969 [LFK]; Magnotte, 1970–1979; Close, 1974 [LFK]; Goldberg, 1978 [MFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Clampit, 1987 [LFK]; Clampit 1988 [LFK]; Lyons & Quinn, 1995; Purtymun, 1997 [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Orlin 2003; Campbell et al., 2004 [MFK, LFK].

Chama radians Lamarck, 1819: Webb, 1942, 1951 [as *Chama variegata* Reeve, 1847, a small corrugated growth form from eastern Florida]; Eubanks, 1964 [as *Pseudochama*]; Lee, 1969 [LFK; as *Pseudochama radians variegata*]; Turney & Perkins, 1972 [MFK; as *Pseudochama*]; Godcharles & Jaap, 1973 [UFK; as *Pseudochama*]; Antonius et al., 1978 [LFK; as *Pseudochama*]; Lyons & Quinn, 1995 [as *Pseudochama*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Pseudochama*]; Campbell et al., 2004 [MFK, LFK].

Chama sarda Reeve, 1847: Dall, 1889a, 1903b; Johnson 1934; Lermond, 1936; Bartsch, 1937; M. Smith, 1937, 1945; Pilsbry & McGinty, 1938; Bayer, 1943b [UFK]; Morris, 1947, 1951; Warmke & Abbott, 1961; Magnotte, 1970–1979 [as *C. sardo* (*sic*)]; Abbott, 1974; Humfrey, 1975; Rehder, 1981; Díaz Merlano & Puyana Hegedus, 1994; Rios, 1994; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Campbell et al., 2004 [UFK, MFK, LFK].

Chama sinuosa Broderip, 1835: Bayer, 1943b [DT; as *C. sinuosa bermudensis* Heilprin, 1889, & as *C. sinuosa firma* Pilsbry & McGinty, 1938]; Antonius et al., 1978 [LFK; as *C. sinosa* (*sic*)]; Lyons & Quinn, 1995; Cantillo et al., 1997 [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Campbell et al., 2004 [MFK].

Chama sp.: T. L. McGinty, 1939 [LFK], 1942; Brooks, 1968b [MFK]; Edwards, 1970 [LFK, as large and small *Chama*]; Stevenson, 1970, 1993 [both as Jewelbox]; Oliver & Järnegren, 2004 [LFK].

|*Pseudochama inezae* F. M. Bayer, 1943 – see under *Chama*.

|*Pseudochama radians* (Lamarck, 1819) – see under *Chama*.

Condylocardiidae

Carditopsis smithii (Dall, 1896): Pilsbry & Olsson, 1946 [LFK; as *Condylocardia floridensis* Pilsbry & Olsson, 1946]; Aguayo & Jaume, 1950c [LFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Corbiculidae

Polymesoda maritima (Orbigny, 1842): Dall, 1883, 1885 [LFK; misidentified as *Cyrena carolinensis*; err. pro *caroliniana* Bosc, 1801, a recognized western Atlantic species], 1889a, 1903b [as *Cyrena* (*Leptosiphon*) *carolinensis* (*sic*)], 1903a [as *C.* (*Pseudocyrena*) *floridana* Conrad, 1846]; M. Smith, 1937, 1945 [LFK; as *Polymesoda floridana*]; Webb, 1951 [as *Cyrena floridana*]; Pulley, 1952 [as *Pseudocyrena floridana*]; Abbott, 1954, 1961 [LFK, as *Pseudocyrena*], 1970 [LFK; as *Pseudocyrena floridana*]; Morrison, 1958 [UFK, LFK; as *Pseudocyrena*]; Siekman, 1965 [as *Pseudocyrena floridana*]; Bender, 1968 [probably misidentified as *Rangia flexuosa* (Conrad, 1840), a recognized species of *Rangianella* from Gulf of Mexico marshes]; Howard et al., 1970 [LFK; as *Polymesoda floridana*]; Andrews, 1971 [LFK; as *Polycyrena floridana*]; Turney & Perkins, 1972 [MFK]; Emerson & Jacobson, 1976 [LFK; as *Pseudocyrena floridana*]; Odé, 1976a [LFK; as *Pseudocyrena*]; Andrews, 1977, 1981a, b, 1992, 1994 [LFK; as *P.* (*Pseudocyrena*)]; Lineback, 1977 [LFK; as *P. floridana*]; Petersen, 1989 [MFK; as *Pseudocyrena*]; Lyons & Quinn, 1995; Brewster-Wingard et al., 1996 [UFK; as *Polymesoda* sp.]; Brewster-Wingard & Ishman, 1999 [UFK; as *Polymesoda* sp.]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK; also as *Rangia flexuosa*, based on Bender, 1968 (see previous)]; USGS, 2003 [UFK, MFK].

Corbulidae

Foster, 1945 [as Aloididae]; Vittor & Associates, 1998 [LFK, DT].

Caryocorbula caribaea Orbigny, 1842: Simpson, 1887–1889 [DT; as *Corbula swiftiana* (C. B. Adams, 1852)]; Dall, 1889a [as *Corbula barrattiana* (C. B. Adams, 1852) and *Corbula swiftiana*], 1903b [as *Corbula Barrattiana* and *Corbula Swiftiana*]; Lermond, 1936 [as *Corbula barrattiana* and *Corbula swiftiana*]; Antonius et al., 1978 [LFK; as *Corbula swiftiana*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Corbula*, also as *Corbula barrattiana* and *Corbula swiftiana*].

Caryocorbula chittyana (C. B. Adams, 1852): Dall, 1889a [as *Corbula nasuta* Say, 1833]; Lermond, 1936 [as *Corbula nasuta*].

Caryocorbula contracta (Say, 1822): Lermond, 1936 [as *Corbula*]; Vittor & Associates, 1998 [DT; as *Corbula*], 1999a [LFK, DT; as *Corbula*]; Mikkelsen & Bieler, 2000 [DT; as *Corbula*].

Caryocorbula cymella (Dall, 1881): Dall, 1881, 1889a, 1903b [all Gordon Key; as *Corbula*]; Johnson, 1934 [Gordon Key; as *Corbula* (*Caryocorbula*)]; Lermond, 1936 [as *Corbula*]; M. Smith, 1937, 1945 [both Gordon Key; as *Corbula*]; Aguayo & Jaume, 1950a [Gordon Key; as *Corbula*]; Parker & Curray, 1956 [Gordon Key; as *Corbula*]; Boss et al., 1968 [Gordon Key; as *Corbula*]; Abbott, 1974 [Gordon Key; as *Corbula* (*Caryocorbula*)]; Rios, 1994 [as *Corbula* (*Caryocorbula*)].

Caryocorbula dietziana (C. B. Adams, 1852): Dall, 1886 [Gordon Key; as *Corbula*], 1889a [as *Corbula*], 1903b [as *Corbula Dietziana*]; Lermond, 1936 [as *Corbula*]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT; as *Corbula*].

Corbula (s. l.) sp.: Turney & Perkins, 1972 [UFK, MFK].

Juliacorbula aequivalvis Philippi, 1836: Dall, 1889a [as *Corbula Cubaniana* (Orbigny, 1842)]; Pulley, 1952 [as *Aloidis*].

Varicorbula disparilis (Orbigny, 1842): Dall, 1881 [DT]; Lermond, 1936 [as *Corbula disparillis* (*sic*)]; Pulley, 1952 [as *Aloidis operculata* (Philippi, 1848)]; Vittor & Associates, 1998 [LFK, DT; as *V. operculata*], 1999a [LFK, DT; as *V. operculata*]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT; as *V. limatula* (Conrad, 1846)], 2001 [UFK, LFK, DT].

Varicorbula krebsiana (C. B. Adams, 1852): Dall, 1889a [as *Corbula Krebsiana*].

Varicorbula philippii (E. A. Smith, 1885): Mikkelsen & Bieler, 2000 [LFK, DT], 2001 [LFK, DT].

Crassatellidae

Vittor & Associates, 1998 [LFK].

Crassinella dupliniana (Dall, 1903): Mikkelsen & Bieler, 2000 [MFK].

Crassinella lunulata (Conrad, 1834): Dall, 1889a [as *Crassatella* (*Eriphyla*), also as *Crassatella* (*Eriphyla*) *lunulata* var. *parva* (C. B. Adams, 1845)], 1903b [as *Crassatella* (*Eriphyla*)]; Johnson, 1934 [as *Gouldia parva* (C. B. Adams, 1845)]; Lermond, 1936 [as *Gouldia mactracea* (Linsley, 1845) and as *G. parva*]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK, DT], 1999a [LFK, DT], b [UFK, MFK, LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Crassinella martinicensis (Orbigny, 1842): Lyons & Quinn, 1995; Vittor & Associates, 1997b [LFK], 1998 [LFK, DT], 1999a [LFK, DT]; Mikkelsen & Bieler, 2000 [LFK, DT].

Crassinella sp.: Vittor & Associates, 1998 [LFK, DT], 1999b [MFK].

Eucrassatella speciosa (A. Adams, 1852): Dall, 1889a [as *Crassatella floridana* Dall, 1881], 1890 [as *Crassatella floridana*], 1903b [as *Crassaella floridana*]; Lermond, 1936 [as *Crassatellites gibbsii* err. pro *gibbesii* (Tuomey & Holmes, 1856)]; Pulley, 1952; M. Smith, 1961 [as *Eucrassatella floridana*]; Magnotte, 1970–1979; Mikkelsen & Bieler, 2000 [UFK, LFK, DT].

Cuspidariidae

Theroux & Wigley, 1983 [UFK, LFK].

Cardiomya alternata (Orbigny, 1842): Dall, 1881 [LFK; as *Neaera*]; Knudsen, 1982 [LFK].

Cardiomya costellata (Deshayes, 1830): Dall, 1889a, 1903b [as *Cuspidaria* (*Cardiomya*)]; Lermond, 1936 [as *Cuspidaria* (*Cardiomya*)]; Turney & Perkins, 1972 [MFK]; Mikkelsen & Bieler, 2000 [LFK].

Cardiomya glypta (Bush, 1885): Mikkelsen & Bieler, 2000 [DT].

Cardiomya ornatissima (Orbigny, 1842): Mikkelsen & Bieler, 2000 [DT].

Cardiomya perrostrata (Dall, 1881): Dall, 1886 [DT; as *Cuspidaria* (*Cardiomya*)], 1889a, 1903b [DT; as *Cuspidaria* (*Cardiomya*)]; Pulley, 1952 [DT]; Vittor & Associates, 1998 [LFK, DT], 1999a [LFK]; Mikkelsen & Bieler, 2000 [LFK, DT].

Cardiomya striata (Jeffreys, 1876): Dall, 1889a [as *Cuspidaria* (*Cardiomya*)].

Cardiomya sp.: Vittor & Associates, 1998 [DT].

Cuspidaria gigantea (A. E. Verrill, 1884): Mikkelsen & Bieler, 2000 [LFK].

Cuspidaria obesa (Lovén, 1846): Dall, 1889a [as *Cuspidaria* (*Cuspidaria*)].

Cuspidaria rostrata (Spengler, 1793): Dall, 1881 [LFK; as *Neaera*], 1889a, 1903b [as *C.* (*Cuspidaria*)]; A. E. Verrill, 1882 [LFK; as *Neara*]; Aguayo & Jaume, 1950f [LFK]; Mikkelsen & Bieler, 2000 [DT].

|*Leiomya claviculata* (Dall, 1881) – all records based on *Blake* sta. 44 (here excluded; see entry for Dall, 1881).

Myonera lamellifera (Dall, 1881): Dall, 1889a.

|*Myonera limatula* (Dall, 1881) – all records based on *Blake* sta. 44 (here excluded; see entry for Dall, 1881).

Myonera paucistriata Dall, 1886.

Plectodon granulatus (Dall, 1881): Dall, 1889a, 1903b [as both *Cuspidaria* (*Liomya*, *Plectodon*) *granulata* and *C.* (*L.*, *P.*) *g.* var.

velvetina Dall, 1881]; Johnson, 1934 [as both *Leiomya* (*P.*) *granulata granulata* and *L.* (*P.*) *granulata velvetina*]; Aguayo & Jaume, 1950d [as *Leiomya* (*P.*) *granulata* f. *velvetina*]; Abbott, 1974; Odé, 1977a; Mikkelsen & Bieler, 2000 [UFK].

Cyrenoididae

Cyrenoida floridana (Dall, 1896): Simpson, 1887–1889 [MFK; *nomen nudum*]; Dall, 1889a [*nomen nudum,* as *Cyrenoidea*], 1903b [as *Cyrenoidea*]; Pulley, 1952; Mikkelsen & Bieler, 2000 [UFK, LFK]; USGS, 2003 [MFK].

Donacidae

Donax variabilis Say, 1822: Simpson, 1887–1889 [LFK; misidentified as *D. denticulatus* Linnaeus, 1758, a recognized Caribbean species]; Dall, 1889a, 1903b [also misidentified as *D. denticulatus* and *D. fossor* Say, 1822, a recognized Atlantic U.S. species], 1900a [as *D. fossor*]; Maury, 1920 [as *D. fossor*]; Johnson, 1934 [as *D. denticulata*]; Lermond, 1936 [also as *D. roemeri* Philippi, 1849, and *D. fossor protractus* Conrad, 1849, and misidentified as *D. denticulata, D. fossor,* and *D. tumidus* Philippi, 1848, a synonym of *D. texasianus* Philippi, 1847, a recognized Gulf of Mexico species]; Bartsch, 1937; M. Smith, 1937, 1945 [as *D. denticulata* and *D. fossor*], 1940 [as *D. fossor*]; Mikkelsen & Bieler, 2000 [UFK, MFK]; Simone & Dougherty, 2004 [UFK].

Donax sp.: Bippus, 1950 [UFK]; Morrison, 1970 [LFK].

Iphigenia brasiliana (Lamarck, 1818): Dall, 1889a [as *I. braziliana*], 1903b; Lermond, 1936; Magnotte, 1970–1979; Mikkelsen & Bieler, 2000 [UFK].

Dreissenidae

Mytilopsis leucophaeata (Conrad, 1831): Mikkelsen & Bieler, 2000 [UFK].

Mytilopsis sallei (Récluz, 1849): Johnson, 1934 [as *Congeria rossmässleri* Dunker, 1853]; Lermond, 1936 [as *C. rossmassleri*]; Mikkelsen & Bieler, 2000 [UFK].

Entoliidae

Pectinella sigsbeei (Dall, 1886): Dall, 1889a [as *Pecten* (*Pecten, Pseudamusium*) *Sigsbeei*].

Galeommatoidea

Hendler et al., 1995 [as "commensal bivalve"]; Vittor & Associates, 1998 [LFK, DT; as Montacutidae], 1999a [LFK; as Montacutidae], b [LFK; as Montacutidae].

Cymatioa sp.: Odé, 1984; Mikkelsen & Bieler, 2000 [UFK].

Kellia suborbicularis (Montagu, 1803): Mikkelsen, 1981 [UFK; misidentified as *Diplodonta* (*Diplodonta*) *?punctata* (Say, 1822); reidentification of voucher specimen]; Mikkelsen & Bieler, 2000 [UFK].

Lasaea adansoni (Gmelin, 1791): Simpson, 1887–1889 [DT; as *Lasea* (*sic*) *rubra* (Montagu, 1803)]; Johnson, 1934 [DT; as *Kellia rubra*]; Aguayo & Jaume, 1949a [DT]; Mikkelsen & Bieler, 2000 [MFK, DT].

Mysella planulata (Krause, 1885): Wingard et al., 1995 [UFK; as *M.* sp.]; Vittor & Associates, 1997c [UFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Brewster-Wingard et al., 2001 [UFK]; USGS, 2003 [UFK].

Mysella sp.: Hendler et al., 1995 [as *M.* sp. C]; Vittor & Associates, 1999a [DT].

Orobitella floridana (Dall, 1899): Hendler et al., 1995 [LFK; as *Naeromya* sp.]; Vittor & Associates, 1998 [DT; as *Naeromya*], 1999b [UFK, LFK; as *Naeromya*]; Mikkelsen & Bieler, 2000 [MFK, LFK, DT].

Semierycina sp.: Mikkelsen & Bieler, 2000 [UFK, MFK].

Gastrochaenidae

Gastrochaena hians (Gmelin, 1791): Dall, 1889a [misidentified as *G. cuneiformis* Spengler, 1783], a recognized Indo-Pacific species; Bales, 1944 [as *G. cueniformis* (*sic*)]; Lermond, 1936 [as *G. cuneiformis*]; Edwards, 1968a [LFK]; Crovo, 1970 [LFK]; Andrews, 1971 [as *Rocellaria*]; Carter, 1978 [as *G.* (*Gastrochaena*)]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK], 1999a [UFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Valentich-Scott & Dinesen, 2004 [MFK, LFK].

Gastrochaena ovata G. B. Sowerby I, 1834: Simpson, 1887–1889 [LFK; as *Rocellaria*]; Dall, 1889a, 1903b; Lermond, 1936; Bales, 1940, 1944; Carter, 1978 [as *G.* (*Rocellaria*)]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

|*Rocellaria ovata* (G. B. Sowerby I, 1834) – see under *Gastrochaena*.

Spengleria rostrata (Spengler, 1783): Dall, 1886 [LFK; as *Cuspidaria*], Dall, 1889a, 1903b [as *Gastrochaena* (*Spengleria*)]; Simpson, 1887–1889 [LFK; as *Rocellaria*]; Lermond, 1936 [as *Gastrochaena*]; Bales, 1940, 1944 [as *Gastrochaena*]; Boss, 1968a; Carter, 1978; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Glycymerididae

Vittor & Associates, 1998 [LFK], 1999b [UFK].

Glycymeris americana (DeFrance, 1829): Lermond, 1936; Bartsch, 1937; Webb, 1942, 1951 [as *Glycimeris*]; Magnotte, 1970–1979; Mikkelsen & Bieler, 2000 [UFK, DT].

Glycymeris decussata (Linnaeus, 1758): Calkins, 1878 [as *Pectunculus pennaceus* Lamarck, 1819]; Lermond, 1936 [as *G. pennacea*]; Pulley, 1952 [LFK]; Magnotte, 1970–1979; Thomas, 1970 [MFK]; Lyons & Quinn, 1995; Vittor & Associates, 1999a [UFK, LFK, DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

|*Glycymeris pectinata* (Gmelin, 1791) – see under *Tucetona*.

Glycymeris spectralis (Nicol, 1952).

Glycymeris undata (Linnaeus, 1758): Dall, 1889a, 1903b [as *Pectunculus undatus*]; Lermond, 1936 [as *G. lineata* Reeve, 1847]; Voss, 1949 [UFK; as *Glycimeris americana lineata*]; Pulley, 1952; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000.

Glycymeris (s. l.) sp.: Theroux & Wigley, 1983 [UFK, MFK]; Voss et al., 1983 [UFK]; Vittor & Associates, 1998 [LFK, DT].

Tucetona pectinata (Gmelin, 1791): Melvill, 1880 [LFK; misidentified as *Pectunculus pectiniformis* Lamarck, 1819, a junior synonym of *Tucetona pectunculus* (Linnaeus, 1758), a recognized Indo-Pacific species]; Dall, 1889a, 1903b [as *Pectunculus pectinatus*]; Thiele, 1910 [DT; as *Glycymeris pectinatus*]; Lermond, 1936 [as *Glycymeris*]; M. Smith, 1937, 1945 [as *G. pectinatus*]; Lyman, 1947b [UFK; as *Glycimeris* (*sic*) *pectinatus*]; Pulley, 1952 [as *Glycymeris*]; Eubanks, 1964 [as *Glycymeris*]; Brooks, 1968b [MFK; as *Glycymeris*]; Burggraf, 1969 [LFK; as *Glycymeris*]; Ross, 1969 [MFK; as *Glycymeris*]; Magnotte, 1970–1979 [as *Glycymeris*]; Thomas, 1970 [MFK, LFK; as *Glycymeris*]; Woods, 1970 [LFK; as *Glycymeris*]; Turney & Perkins, 1972 [UFK, MFK; as *Glycymeris*]; Godcharles & Jaap, 1973 [UFK; as *Glycymeris*]; Thomas, 1975 [MFK, LFK; as *Glycymeris*]; Hertweck, 1977 [LFK; as *Glycymeris*]; Theroux & Wigley, 1983 [UFK; as *Glycymeris*]; Voss, 1983 [UFK; as *Glycimeris* (*sic*)]; Voss et al., 1983 [UFK; as *Glycymeris*]; Lyons & Quinn, 1995 [as *Glycymeris*]; Vittor & Associates, 1998 [LFK, DT; as *Glycymeris*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Glycymeris*]; Morton & Knapp, 2004 [UFK, MFK].

Gryphaeidae

Hyotissa mcgintyi (Harry, 1985): Kirkendale et al., 2004 [MFK].

Neopycnodonte cochlear (Poli, 1795): Mikkelsen & Bieler, 2000 [UFK, LFK].

Hiatellidae

Hiatella arctica (Linnaeus, 1767): Dall, 1889a, 1903b [as *Saxicava*]; Vittor & Associates, 1998 [LFK, DT], 1999a [DT], b [UFK, MFK]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT].

Hiatella azaria (Dall, 1881): Dall, 1889a [as *Saxicava*].

Isognomonidae

Isognomon alatus (Gmelin, 1791): Calkins, 1878 [DT; misidentified as *Perna perna* “Wood”, err. pro (Linnaeus, 1767) (*non* Linnaeus, 1758 = Mytilidae) with synonym *Perna ephippium* “Sowerby” err. pro (Linnaeus, 1758), a recognized Indo-Pacific species of *Isognomon*]; Dall, 1883, 1885 [LFK; misidentified as *P. ephippium*], 1889a [as *P. ephippium* “Lamarck” and *P. obliqua* Lamarck, 1819], 1896a [as *Perna oblique* (*sic*)]; 1903b [as *P. ephippium* “Lamarck”]; Simpson, 1887–1889 [LFK, DT, as *Perna obliqua*; also DT, as *P. ephippium*]; Thiele, 1910 [DT; as *Melina lata* (*sic*)]; Lermond, 1936 [as *Pedalion* (*Perna*)]; Bartsch, 1937 [as *Melina*]; M. Smith, 1937 [UFK; as *Pedalion alata*], 1945 [UFK; as *Pedalion alata*]; C. N. Vilas & N. R. Vilas, 1945, 1970 [as *Pedalion alata*]; T. A. Stephenson & A. Stephenson, 1950 [LFK; as *I.* (*Pedalion*) *alata*]; Pulley, 1952 [UFK; as *I. alata*]; Ross, 1969 [MFK]; Work, 1969 [LFK]; Magnotte, 1970–1979; Zischke, 1973, 1977a, b, c [MFK]; Chan, 1977b [LFK]; Kissling, 1977a [as *Isognomen* (*sic*)]; Goldberg, 1978c [MFK]; Schomer & Drew, 1982; Wagner & Abbott, 1990; Lyons & Quinn, 1995; Hutsell et al., 1997; Campbell et al., 1998 [LFK];

Mikkelsen & Bieler, 2000 [UFK, MFK, LFK]; Domaneschi & Mantovani, 2002 [MFK, LFK].

Isognomon bicolor (C. B. Adams, 1845): Johnson, 1934 [as *Pedalion semiaurita* (Linnaeus, 1758)]; Lermond, 1936 [as *Pedalion,* also as *P. semiaurita*]; T. A. Stephenson & A. Stephenson, 1950 [LFK; as *I. chemnitziana* (Orbigny, 1846)]; Pulley, 1952; Abbott, 1954 [LFK]; Warmke & Abbott, 1961; Andrews, 1971, 1977, 1981a, b, 1992, 1994; Zischke, 1973, 1977a, b [MFK]; Abbott, 1974; Humfrey, 1975; Emerson & Jacobson, 1976; Ingham & Zischke, 1977 [MFK]; Odé, 1979a; Rehder, 1981; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Domaneschi & Mantovani, 2002.

Isognomon radiatus (Anton, 1839): Thiele, 1910 [DT; as *Melina listeri* Hanley, 1846]; Johnson 1934 [as *Pedalion listeri*]; Lermond, 1936 [as *P. listeri*]; M. Smith, 1937, 1945 [as *P. listeri*]; Lyman, 1943 [LFK; as *P. listeri*]; Pulley, 1952 [as *Isognomon listeri*]; Edwards, 1968b [LFK]; Ross, 1969 [MFK]; Work, 1969 [LFK]; Magnotte, 1970–1979; Zischke, 1973, 1977a [MFK]; Ingham & Zischke, 1977 [MFK]; Antonius et al., 1978 [LFK]; Mikkelsen, 1981 [UFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; also as *Neopycnodonte cochlear* from MFK, based on misidentified specimen].

Isognomon sp.: Voss et al., 1983 [UFK]; Oliver & Järnegren, 2004 [LFK].

Limidae

Henderson, 1911 [DT; as Limas]; Vittor & Associates, 1999b [UFK].

|*Ctenoides floridanus* (Olsson & Harbison, 1953) – see *Ctenoides mitis.*

Ctenoides miamiensis Mikkelsen & Bieler, 2003: Mikkelsen & Bieler, 2003 [LFK, DT].

Ctenoides mitis (Lamarck, 1807): Simpson, 1887–1889 [DT; as *Lima tenera* "Chemnitz" G. B. Sowerby II, 1843]; Dall, 1889a, 1903b [both as *L. tenera*]; Lermond, 1936 [as *L. tenera*]; Webb, 1942, 1951 [both as *L. tenera*]; Pulley, 1952 [as *L. tenera*]; Schroeder, 1964 [UFK; as flame scallop]; Brooks, 1968b [MFK; as *L. scabra* form *tenera*]; Plockelman, 1969b [MFK; as *L. scabra tenera*]; Ross, 1969 [MFK; as *L. scabra tenera*], 1971 [MFK; as *L. scabra tenera*]; Work, 1969 [LFK; as *L. scabra* form *tenera*]; Woods, 1970, 1971 [MFK] [both as *L. scabra tenera*]; Mpitsos, 1973 [as *L. scabra tenera*]; Voss et al., 1983 [UFK; as *Lima* sp. with "red and yellow tentacles"]; Williams, 1988 [as "file clam"]; Cohen & Cohen, 1991 [UFK; unnamed, with light-orange tentacles]; Lyons & Quinn, 1995 [as *L. scabra tenera*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *C. floridanus* (Olsson & Harbison, 1953)], 2003 [UFK, MFK, LFK, DT]; Morton, 2000 [MFK; as *C. floridanus*].

Ctenoides planulatus (Dall, 1886): Mikkelsen & Bieler, 2000 [LFK; as *C. planulatatus* (*sic*)]; 2003 [LFK].

Ctenoides sanctipauli Stuardo, 1982: Stuardo, 1982 [LFK]; Mikkelsen & Bieler, 2000 [MFK, LFK, DT], 2003 [MFK, LFK, DT].

Ctenoides scaber (Born, 1778): Calkins, 1878 [DT; as *Lima scabra*]; Melvill, 1880 [LFK; as *L. scabra*]; Simpson, 1887–1889 [DT; as *L. scabra*]; Dall, 1889a, 1903b [as *L. scabra*]; Thiele, 1910 [DT; as *L. scabra*]; Lermond, 1936 [as *L. scabra*]; Bartsch, 1937 [LFK, DT; as *L. scabra*]; Webb, 1942 [misidentified as *L. tenera*, synonym of *Ctenoides floridanus* (see above)]; Pulley, 1952 [as *L. scabra*]; Ross, 1969 [MFK; as *L. scabra*]; Work, 1969 [LFK; as *L. scabra*]; Magnotte, 1970–1979 [as *L. scabra*]; Jacobson & Hernandez, 1973 [DT; as *L. scabra*]; Mpitsos, 1973 [as *L. scabra*]; Zischke, 1973, 1977a, c [MFK; as *L. scabra*]; Antonius et al., 1978 [LFK; as *L. scabra*]; Ring, 1980 [LFK; as *L. scabra*]; Voss et al., 1983 [UFK; as *L. scabra* and as *L.* sp. with "red and yellow tentacles"]; Sage, 1987 [LFK; as *L. scabra*]; Gilmour, 1990 [LFK; as *C. scabra*]; Lyons & Quinn, 1995 [as *L. scabra scabra*]; Ripple, 1995 [as rough fileclam]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT], 2003 [UFK, MFK, LFK, DT].

Divarilima albicoma (Dall, 1886): Dall, 1889a, 1903b [as *Lima*]; Abbott, 1974 [as *Lima*]; Odé, 1979b; Díaz Merlano & Puyana Hegedus, 1994; Rios, 1994 [as *Limaria*]; Mikkelsen & Bieler, 2000.

Lima caribaea Orbigny, 1842: Calkins, 1878 [DT; misidentified as *Lima squamosa* Lamarck, 1801, a synonym of *L. lima* Linnaeus, 1758, a recognized eastern Atlantic species]; Simpson, 1887–1889 [DT; as *L. squamosa*]; Dall, 1889a [as *L. squamosa*], 1903b [as *L. squamosa*]; Thiele, 1910 [DT; as *L. lima* (Linnaeus, 1758)]; Lermond, 1936 [as *L. lima*]; Lyman, 1948b [as *L. lima*]; Pulley, 1952; Eubanks, 1964 [as *L. lima*]; Brooks, 1968a [MFK; as *L. lima*]; Work, 1969 [LFK; as *L. lima*]; Magnotte, 1970–1979 [as *L. lima*]; Godcharles & Jaap, 1973 [UFK; as *L. lima*]; Voss, 1983 [UFK; as *L. lima*]; Voss et al., 1983 [UFK; as *L. lima*]; Williams, 1988 [as "spiny lima *Lima lima*"]; Krisberg, 1993 [LFK; as *L. lima*]; Lyons & Quinn, 1995 [as *L. lima*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT], 2003 [UFK, MFK, LFK, DT].

|*Lima lima* Linnaeus, 1758 – see *Lima caribaea*.

|*Lima scabra* (Born, 1778) – see *Ctenoides scaber*.

|*Lima tenera* "Chemnitz" G. B. Sowerby II, 1843 – see *Ctenoides floridanus*.

Lima (s. l.) sp.: Henderson, 1911 [LFK]; Lyman, 1943; Voss, 1949 [UFK]; Ross, 1969 [MFK]; Wingard et al., 1995 [UFK]; Brewster-Wingard et al., 1996 [UFK]; Vittor & Associates, 1999a [UFK], b [UFK, MFK]; USGS, 2003 [UFK; as *Lima* spp.].

Limaria locklini (T. L. McGinty, 1955): Vittor & Associates, 1999a [LFK; as *Lima*].

Limaria pellucida (C. B. Adams, 1846): Dall, 1886 [LFK; misidentified as *Lima inflata* Link, 1807, a recognized eastern Atlantic species], 1889a [misidentified as *Lima inflata* and *Lima hians* (Gmelin, 1791), a recognized eastern Atlantic species], 1903b [as *Lima inflata*]; Lermond, 1936 [as *Lima inflata* and *Lima hians*]; Webb, 1942, 1951 [both misidentified as *Lima fragilis* "Conrad" (?)]; Eubanks, 1964; Brooks, 1968b [MFK; as *Lima*]; Edwards, 1968b [LFK; as *Lima*]; Iversen & Roessler, 1969 [UFK; as *Lima*]; Lee, 1969 [LFK; as *Lima*]; Ross, 1969 [MFK; as *Lima*]; Work, 1969 [LFK; as *Lima*]; Hudson et al., 1970 [UFK; as *Lima*]; Woods, 1971 [MFK; as *Lima*]; Turney & Perkins, 1972 [UFK, MFK]; Antonius et al., 1978 [LFK; as *Lima*]; Voss, 1983 [UFK; as *Lima*]; Voss et al., 1983 [UFK; as *Lima*]; Lyons & Quinn, 1995 [as *Lima*]; Vittor & Associates, 1998 [LFK; as *Lima*], 1999a [UFK, DT; as *Lima*], b [UFK, MFK, LFK; as *Lima*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK, MFK; as *Limaria* sp. cf. *L. pellucida*]; Brewster-Wingard et al., 2001 [UFK; as *Limaria* cf. *pellucida*].

Limaria sp.: Stuardo, 1968 [UFK; as *Limaria* (*Limatulella*) sp. nov., but never published].

Limatula confusa (E. A. Smith, 1885): Lermond, 1936.

Limatula setifera Dall, 1886: Dall, 1889a [as *Lima* (*Limatula*)].

Limatula subauriculata (Montagu, 1808): Dall, 1889a [as *Lima* (*Limatula*)].

Limea bronniana Dall, 1886.

Limea sp.: Stuardo, 1968 [LFK; as *Limea* (*Limea*) sp. nov., but never published].

Limopsidae

Theroux & Wigley, 1983 [LFK].

Limopsis aurita (Brocchi, 1814): Dall, 1889a, 1903b; Mikkelsen & Bieler, 2000 [DT].

Limopsis cristata Jeffreys, 1876: Dall, 1889a, 1903b; Mikkelsen & Bieler, 2000 [DT].

Limopsis minuta Philippi, 1836: Dall, 1889a, 1903b; Mikkelsen & Bieler, 2000 [DT].

Limopsis sulcata A. E. Verrill & Bush, 1898: Mikkelsen & Bieler, 2000 [UFK, DT].

|*Limopsis tenella* Jeffreys, 1876 – all records based on *Blake* sta. 44 (here excluded; see entry for Dall, 1881).

Lucinidae

Vittor & Associates, 1997a [UFK, MFK, LFK], 1997c [UFK], 1998 [LFK, DT], 1999a [UFK, LFK, DT], b [UFK, MFK, LFK]; USGS, 2003 [MFK].

Anodontia alba Link, 1807: Melvill, 1880 [LFK; as *Loripes chrysostoma* ("Meuschen" Philippi, 1847) and misidentified as *L. edentula* (Linnaeus, 1758), a recognized Micronesian species]; Dall, 1889a [as *Loripes edentula* and as *L. e.* var. *chrysostoma*]; 1903a [Pleistocene; as *Lucina chrysostoma*], b [as *Loripes edentula* and as *L. e.* var. *chrysostoma* "Mörch"]; Lermond, 1936 [as *Lucina* (*Loripinus*) *edentula* and as *L.* (*L.*) *e. chrysostoma*]; Bartsch, 1937; Britton, 1970 [MFK, LFK, DT; as *A.* (*Anodontia*)]; Magnotte, 1970–1979; Turney & Perkins, 1972 [UFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK, MFK].

Anodontia schrammi (Crosse, 1876): Lermond, 1936 [as *Lucina* (*Loripinus*)]; Britton, 1975 [LFK, DT; as *A.* (*Anodontia*)]; Turney & Perkins, 1972 [MFK; as *A. philippiana* (Reeve, 1850), a recognized Indo-Pacific species]; Mikkelsen & Bieler, 2000 [LFK; as *A. philippiana*].

Callucina keenae Chavan in Cox et al., 1971: Britton, 1975 [LFK, DT; as *Callucina* (*Callucina*) *radians* Conrad, 1841, *non* Bory de St. Vincent, 1824]; Vittor & Associates, 1997c [UFK; as *Lucina radians*], 1999a [UFK, LFK, DT; as *L. radians*], b [UFK, MFK, LFK; as *L. radians*]; Mikkelsen & Bieler, 2000 [UFK, DT; as *L. radians*].

Cavilinga blanda (Dall & Simpson, 1901): Dall, 1889a [misidentified as *Lucina* (*Lucina*) *trisulcata* Conrad, 1841, and *L.* (*L.*) *crenulata* Conrad, 1845, two recognized Miocene-Pliocene fossil species from the eastern United States], 1903b [as *L.* (*Lucina*) *trisulcata*]; Lermond, 1936 [as *L.* (*Anodontia*) *trisulcata*]; Britton, 1975 [UFK, MFK, LFK, DT]; Turney & Perkins, 1972 [UFK, MFK; as *Linga trisulcata*]; Lyons & Quinn, 1995 [as *Parvilucina*]; Vittor & Associates, 1998 [LFK; as *Lucina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; *Lucina trisulcata*].

Codakia orbicularis (Linnaeus, 1758): Melvill, 1880 [LFK; as *Lucina tigerina* (Linnaeus, 1758)]; Dall, 1883, 1885 [LFK; as *L. tigrina* (*sic*)], 1889a, 1903b [as *L.* (*L.*) *tigrina* (*sic*)], 1901, 1903a [Pleistocene]; Simpson, 1887–1889 [LFK; as *L. tigrina* (*sic*)]; Nutting, 1895 [DT, as *L. tigrina* (*sic*)]; C. N. Vilas & N. R. Vilas, 1945, 1970; Morris, 1947, 1951; Pulley, 1952 [MFK]; Eubanks, 1964; Bender, 1965 [MFK, LFK]; Kissling, 1965 [LFK], 1977a [UFK], 1977b [UFK]; Brooks, 1968b [MFK]; Plockelman, 1968d, 1968e [MFK]; Edwards, 1968b, 1980 [both LFK]; Jindrich, 1969 [LFK]; Ross, 1969 [MFK; as *C. obicularis* (*sic*)]; Work, 1969 [LFK]; Britton, 1975 [UFK, MFK, LFK, DT; as *C.* (*Codakia*)]; Magnotte, 1970–1979; Stevenson, 1970, 1993 [both as lucine]; Woods, 1970 [LFK]; Turney & Perkins, 1972 [UFK, MFK]; Godcharles & Jaap, 1973 [UFK]; Zischke, 1973, 1977a, c [MFK]; Antonius et al., 1978 [LFK]; Schomer & Drew, 1982; Voss, 1983 [UFK]; Voss et al., 1983 [UFK; also as *C. orbicular* (*sic*)]; Sedlak, 1986 [LFK]; Clampit, 1987 [LFK]; Williams, 1988; Redla 1990 [UFK, LFK]; Lyons & Quinn, 1995; Tremor, 1998 [LFK]; Vittor & Associates, 1998 [LFK], 1999b [UFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK]; Orlin, 2003 [LFK]; Bigatti et al., 2004 [UFK, MFK, LFK].

Codakia (s. l.) sp.: Lyman, 1944b [UFK]; Brewster-Wingard et al., 1996, 2001 [as *Codakia* spp.] [both UFK]; Vittor & Associates, 1998 [LFK, DT]; USGS, 2003 [UFK, MFK; as *Codakia* spp.].

Ctena orbiculata (Montagu, 1808): Simpson, 1887–1889 [MFK, LFK; as *Lucina squamosa* Lamarck, 1806, and *L. pecten* Lamarck, 1818, yellow var.]; Dall, 1889a [as *L.* (*Lucina*) *pecten* and *L.* (*L.*) *squamosa*]; Dall, 1901 [as *Jagonia orbiculata* var. *filiata* n. var. and *J. o.* var. *recurvata* n. var.]; Henderson, 1913 [UFK; as *Codakia*]; Johnson 1934 [as *Codakia* (*Jagonia*) *orbiculata filiata* and *C.* (*Jagonia*) *orbiculata recurvata*]; Lermond, 1936 [as *Lucina* (*J.*), also as *L.* (*J.*) *o. filiata* and *L.* (*J.*) *o. recurvata*]; Aguayo & Jaume, 1949d [as *Codakia*]; Iversen & Roessler, 1969 [UFK; as *Codakia*]; Lee, 1969 [LFK; as *Codakia orbiculata* and as *C. o.* ?form *filiata*]; Ross, 1969 [MFK; as *Codakia*]; Britton, 1975 [UFK, MFK, LFK, DT; as *Codakia* (*Ctena*)]; Howard et al., 1970 [LFK; as *Codakia*]; Hudson et al., 1970 [UFK; as *Codakia*]; Turney & Perkins, 1972 [UFK, MFK; as *Codakia*]; Lineback, 1977 [LFK; as *Codakia*]; Schomer & Drew, 1982 [as *Codakia*]; Lyons & Quinn, 1995 [as *Codakia*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Codakia*]; Bigatti et al., 2004 [UFK, MFK, LFK]; Morton & Knapp, 2004 [UFK, MFK].

Ctena pectinella (C. B. Adams, 1852): Dall, 1889a [as *Lucina*], 1903b [as *Lucina* (*Lucina*)]; Johnson 1934 [as *Codakia* (*Jagonia*)]; Lermond, 1936 [as *L.* (*Jagonia*)]; Britton, 1975 [UFK, LFK, DT; as *Parvilucina* (*Parvilucina*)]; Abbott, 1974 [as *Codakia* (*Ctena*)]; Hemmen & Hemmen, 1979 [as *Codakia* (*Ctena*)]; Lyons & Quinn, 1995 [as *Codakia*]; Mikkelsen & Bieler, 2000 [DT; as *Codakia*].

Divalinga quadrisulcata (Orbigny, 1842): Simpson, 1887–1889 [DT; as *Lucina*]; Dall, 1889a, 1903b [as *Lucina* (*Divaricella*)]; Britton, 1975 [UFK, MFK, LFK, DT; as *Divaricella* (*Divalinga*)]; Turney & Perkins, 1972 [UFK; as *Divaricella*]; Lyons & Quinn, 1995 [as *Divaricella*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Divaricella dentata (Wood, 1815): Lermond, 1936 [as *Lucina* (*D.*)]; Britton, 1975 [UFK, MFK, LFK, DT; as *D.* (*Divaricella*)]; Rehder, 1981 [as *Lucina*]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Linga sp.: Vittor & Associates, 1998 [LFK].

|*Lucina leucocyma* (Dall, 1886) – see under *Pleurolucina*.

|*Lucina pectinata* (Gmelin, 1791) – see under *Phacoides*.

Lucina pensylvanica (Linnaeus, 1758): Melvill, 1880 [LFK; as *Lucina*]; Simpson, 1887–1889 [LFK; as *L. pennsylvanica* (*sic*)]; Dall, 1889a, 1903b [as *L.* (*L.*) *pennsylvanica* (*sic*)]; Lermond, 1936 [as *L. pennsylvanica* (*sic*)]; Webb, 1942, 1951 [MFK]; Eubanks, 1964; Brooks, 1968b [MFK]; Ross, 1969 [MFK]; Britton, 1975 [UFK, MFK, LFK, DT; as *Lucina* (*Lucina*)]; Magnotte, 1970–1979; Woods, 1970 [LFK]; Turney & Perkins, 1972 [UFK, MFK]; Godcharles & Jaap, 1973 [UFK]; Zischke, 1973, 1977a [MFK]; Voss, 1983 [UFK; as *Linga*]; Voss et al., 1983 [UFK; as

Linga]; Clampit, 1987 [LFK]; Redla 1990 [UFK, LFK]; Lyons & Quinn, 1995 [as *Linga*]; Tremor, 1998 [LFK]; Vittor & Associates, 1998 [LFK, DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Orlin, 2003 [LFK]; Bigatti et al., 2004 [UFK, MFK, LFK]; Taylor et al., 2004 [UFK, MFK].

|*Lucina radians* Conrad, 1841 – see *Callucina keenae*.

|*Lucina sombrerensis* (Dall, 1886) – see under *Pleurolucina*.

Lucina sp.: Vittor & Associates, 1997c [UFK], 1998 [LFK, DT], 1999a [UFK, LFK], b [MFK, LFK].

Lucinisca muricata (Spengler, 1798): Simpson, 1887–1889 [DT; as *Lucina*]; Dall, 1889a [as *Lucina* (*Lucina*) *scabra* Lamarck, 1819], 1901, 1903a [as *Phacoides* (*Lucinisca*) *muricatus*]; Johnson, 1934 [as *L.* (*Lucinisca*) *muricata* and *L. scabra*]; Lermond, 1936 [as *Lucina* (*Lucinisca*)]; M. Smith, 1937, 1945 [as *Lucina* (*Cavilucina, Lucinisca*)], 1940 [as *Lucina muricatus*]; Warmke & Abbott, 1961 [as *Phacoides*]; Aguayo & Jaume, 1949g; Abbott, 1974 [LFK; as *Lucina* (*Lucinisca*)]; Humfrey, 1975 [as *Phacoides*]; Rehder, 1981 [LFK; as *Phacoides*]; Díaz Merlano & Puyana Hegedus, 1994 [as *Lucina* (*Lucinisca*)]; Rios, 1994 [as *Lucina* (*Lucinisca*)]; Lyons & Quinn, 1995 [as *Lucina*]; Vittor & Associates, 1999a [LFK; as *Lucina*], b [UFK, LFK; as *Lucina*]; Mikkelsen & Bieler, 2000 [LFK].

Lucinisca nassula (Conrad, 1846): Simpson, 1887–1889 [MFK; as *Lucina lintea* Conrad, 1866]; Dall, 1889a [as *Lucina* (*Lucina*) *lintea*]; Howard et al., 1970 [LFK; as *Lucina*]; Britton, 1975 [UFK, MFK, LFK, DT; as *Parvilucina* (*Lucinisca*)]; Turney & Perkins, 1972 [UFK, MFK; as *Phacoides*]; Lineback, 1977 [LFK; as *Lucina*]; Lyons & Quinn, 1995 [as *Lucina*]; Vittor & Associates, 1998 [LFK, DT; as *Lucina*], 1999a [LFK; as *Lucina*], b [MFK, LFK; as *Lucina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Brewster-Wingard et al., 2001 [UFK]; USGS, 2003 [UFK]; Morton & Knapp, 2004 [UFK, MFK].

Lucinoma filosa (Stimpson, 1851): Dall, 1889a, 1903b [as *Lucina* (*Lucina*)]; Britton, 1975 [LFK, DT; as *Phacoides* (*Lucinoma*) *filosus*]; Mikkelsen & Bieler, 2000 [DT].

|*Myrtea lens* (A. E. Verrill & Smith, 1880) – see under *Myrteopsis*.

Myrtea sagrinata (Dall, 1886): Dall, 1889a, 1903b [as *Lucina* (*Lucina*)], 1901 [as *M.* (*Eulopia*)]; Johnson, 1934 [as *M.* (*Eulopia*)]; Abbott, 1974 [as *M.* (*Eulopia*)]; Odé, 1977b; Mikkelsen & Bieler, 2000.

Myrteopsis lens (A. E. Verrill & Smith, 1880): Dall, 1889a, 1903b [both as *Loripes*].

Parvilucina costata (Orbigny, 1842): Simpson, 1887–1889 [DT; as *Lucina*]; Lermond, 1936 [as *Lucina* (*Jagonia*)]; Britton, 1975 [UFK, LFK, DT; as *P.* (*Parvilucina*)]; Turney & Perkins, 1972 [UFK, MFK; as *Barnea*]; Petersen, 1989 [MFK; as *Codakia*]; Lyons & Quinn, 1995 [as *Codakia*]; Mikkelsen & Bieler, 2000 [as *Codakia*].

Parvilucina crenella (Dall, 1901): Dall, 1889a [as *Lucina* (*L.*) *multilineata* ("Conrad" Tuomey & Holmes, 1857)], 1903b [as *L.* (*L.*) *multilineata*]; Lermond, 1936 [as *L.* (*Parvilucina*)]; Britton, 1975 [UFK, MFK, LFK; as *P.* (*Parvilucina*) *multilineata*]; Turney & Perkins, 1972 [UFK; as *L. multilineata*]; Rehder, 1981 [as *P. multilineata*]; Lyons & Quinn, 1995 [as *P. multilineata*]; Vittor & Associates, 1997c [UFK; as *L. multilineata*], 1998 [LFK, DT; as *L. multilineata*], 1999a [LFK, DT; as *L. multilineata*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *P. multilineata*]; Brewster-Wingard et al., 2001 [UFK; as *P. multilineata*]; USGS, 2003 [UFK; as *P. multilineata*].

Phacoides pectinata (Gmelin, 1791): Melvill, 1880 [LFK; as *Lucina jamaicensis* (Lamarck, 1801)]; Lermond, 1936 [as *Lucina* (*Anodontia*) *jamaicensis*]; Britton, 1975 [LFK; as *Phacoides* (*Phacoides*) *pectinatus*]; Magnotte, 1970–1979; Antonius et al., 1978 [LFK; as *Phacoides pectinatus*]; Lyons & Quinn, 1995 [as *Lucina*]; Vittor & Associates, 1999a [LFK; as *Lucina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK; as *Lucina*]; USGS, 2003 [MFK; as *Lucina*].

Pleurolucina leucocyma (Dall, 1886): Dall, 1889a [as *Lucina*], 1903b [as *Lucina* (*Lucina*)]; Pulley, 1952 [UFK; as *Lucina*]; Britton, 1975 [UFK, MFK, LFK, DT; as *Lucina* (*Pleurolucina*)]; Rehder, 1981 [as *Lucina*]; Lyons & Quinn, 1995 [as *Linga*]; Mikkelsen & Bieler, 2000 [UFK, DT; as *Lucina*].

Pleurolucina sombrerensis (Dall, 1886): Dall, 1889a [as *Lucina*], 1903b [as *Lucina* (*Lucina*)]; Pulley, 1952 [MFK; as *Lucina*]; Britton, 1975 [UFK, MFK, LFK; as *Lucina* (*Pleurolucina*)]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Lucina*].

|*Pseudomiltha floridana* (Conrad, 1833) – see under *Stewartia*.

Radiolucina amianta (Dall, 1901): Dall, 1889a [as *Lucina* (*L.*) *costata* Tuomey & Holmes, 1857, *non* Orbigny, 1842]; Lermond, 1936 [as *Lucina* (*Bellucina*) *amiantus*]; Pulley, 1952 [LFK; as *Lucina amiantus*]; Britton, 1975 [UFK, LFK, DT; as *Parvilucina* (*Bellucina*) *amiantus*]; Rehder, 1981 [as *Parvilucina*]; Lyons & Quinn, 1995 [as *Linga amiantus*]; Vittor & Associates, 1998 [LFK, DT; as *Lucina amiantus*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Lucina amiantus*].

Stewartia floridana (Conrad, 1833): Dall, 1889a, 1903b [both LFK; as *Lucina* (*Lucina*)]; Rogers, 1908 [as *Lucina Floridana*]; Aldrich & Snyder, 1936 [as *Lucina*]; Britton, 1975 [LFK; as *Megaxinus floridanus*]; Mikkelsen & Bieler, 2000 [LFK; as *Lucina*].

Lyonsiidae

Entodesma beana (Orbigny, 1842): Dall, 1889a, 1903b [as *Lyonsia Beana*]; Lermond, 1936 [as *Lyonsia*]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [UFK; as *Lyonsia*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Lyonsia floridana Conrad, 1849: Hudson et al., 1970 [UFK; as *L. hyalina floridana*]; Vittor & Associates, 1998 [LFK, DT; as *L. hyalina floridana*], 1999a [LFK, DT; as *L. hyalina floridana*]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT].

Mactridae

Vittor & Associates, 1998 [LFK]; USGS, 2003 [UFK, MFK].

Anatina anatina (Spengler, 1802): Lermond, 1936 [as *A. lineata* (Say, 1822)]; Mikkelsen & Bieler, 2000 [MFK].

Mactrotoma fragilis (Gmelin, 1791): Dall, 1889a [as *Mactra brasiliana* Lamarck, 1818]; Lermond, 1936 [as *Mactra*]; Ross, 1969 [MFK; as *Mactra*]; Turney & Perkins, 1972 [MFK; as *Mactra*]; Lyons & Quinn, 1995 [as *Mactra*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Mulinia lateralis (Say, 1822): Dall, 1889a [as *Mactra*]; Lermond, 1936; Magnotte, 1970–1979.

Raeta plicatella (Lamarck, 1818): Dall, 1889a [as *Labiosa canaliculata* Say, 1822]; Lermond, 1936 [as *Anatina* (*Raeta*) *canaliculata*]; Magnotte, 1970–1979 [as *Anatina*]; Mikkelsen & Bieler, 2000 [UFK, LFK].

Spisula raveneli (Conrad, 1831): Dall, 1889a, 1903b [as *Mactra solidissima* var. *similis* Say, 1822]; Lermond, 1936 [as *Spisula solidissima similis*]; Mikkelsen & Bieler, 2000 [UFK, MFK].

Malleidae

Malleus candeanus (Orbigny, 1842): Bales, 1944 [as *Fundella candeana*]; Boss & Moore, 1967 [UFK, LFK, DT; as *M.* (*Parimalleus*)]; Waller & McIntyre, 1982 [DT]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Myidae

Sphenia fragilis (H. & A. Adams, 1854): Mikkelsen & Bieler, 2000 [UFK; as *Sphenia antillensis* Dall & Simpson, 1901].

Mytilidae

Stevenson, 1970, 1993 [both as mussel]; Woods, 1971 [MFK; as little mussels]; Gaertner, 1978 [LFK; as mussels]; Ring, 1980 [LFK; as mussels]; Edwards, 1987 [LFK; as Ribbed Mussel]; Vittor & Associates, 1997c [UFK], 1998 [DT], 1999b [MFK, LFK].

Amygdalum papyrium (Conrad, 1846): Lermond, 1936 [as *Modiolaria arborescens* (Dillwyn, 1817); this species name is variously considered as a synonym of *A. dendriticum* Muhlfeld, 1811, or (as *auctt.*, *non* Dillwyn) a synonym of *A. papyrium*; it is conservatively listed here]; Pulley, 1952 [also as *A. arborescens*]; Mikkelsen & Bieler, 2000 [UFK, MFK].

Amygdalum politum (A. E. Verrill & Smith, 1880): Dall, 1881, 1886 [DT; as *Modiola polita*], 1889a, 1903b [as *M.* (*Amygdalum*) *polita*]; Bartsch, 1937 [LFK; as *Modiola polita*]; Mikkelsen & Bieler, 2000 [DT].

Amygdalum sagittatum (Rehder, 1935): Dall, 1889a, 1903b [as *Modiola* (*Amygdalum*) *polita* var. *sagittata* (*nomen nudum*)]; Foster, 1945 [as *Modiolus politus sagittatus*]; Vittor & Associates, 1998 [LFK, DT], 1999a [LFK]; Mikkelsen & Bieler, 2000 [LFK, DT].

Amygdalum sp.: Vittor & Associates, 1999a [DT].

Botula fusca (Gmelin, 1791): Simpson, 1887–1889 [DT; as *Modiolaria cinnamomea* Lamarck, 1819]; Dall, 1889a [as *Modiola* (*Botula*) *cinnamomea*]; Bales, 1940, 1944; Lermond, 1936; Pulley, 1952; Edwards, 1968a [LFK]; Brooks, 1969 [MFK]; Ross, 1971 [LFK]; Emerson & Jacobson, 1976; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Valentich-Scott & Dinesen, 2004 [MFK, LFK].

|*Brachidontes domingensis* (Lamarck, 1819) – see *B. exustus*.

Brachidontes exustus (Linnaeus, 1758): Dall, 1883, 1885 [LFK; as *Mytilus*], 1889a, 1903b [as *Mytilus*]; Simpson, 1887–1889 [LFK; as *Mytilus*]; Simpson, 1887-1889 [LFK; as *Mytilus lavalleanus* Orbigny, 1842]; Lermond, 1936 [as *Mytilus*]; T. A. Stephenson & A. Stephenson, 1950 [MFK, LFK; as *M.* (*Brachidontes*)]; Ginsburg, 1952 [UFK, MFK]; Iversen & Roessler, 1969 [UFK; also as *Trachidontes* (*sic*)]; Ross, 1969 [MFK]; Work, 1969 [UFK]; Hudson et al., 1970 [UFK]; Magnotte, 1970–1979; Turney & Perkins, 1972 [UFK, MFK]; Zischke, 1973, 1977a, b, c [MFK]; Ingham & Zischke, 1977 [MFK]; Antonius et al., 1978 [LFK; as *Brachiodontes* (*sic*)]; Schomer & Drew, 1982 [as *Mytilus*]; Petersen, 1989 [MFK; as *Brachiodonta* (*sic*)]; Lyons & Quinn, 1995 [as *B. domingensis* (Lamarck, 1819)]; Wingard et al., 1995 [UFK; as *Brachiodontes* (*sic*) sp.]; Brewster-Wingard et al., 1996, 1997, 1998 [as *Brachiodontes* (*sic*) sp.], 2001 [all UFK]; Vittor & Associates, 1997c [UFK]; Lyons, 1998 [UFK, MFK]; Brewster-Wingard & Ishman, 1999 [as *Brachiodontes* (*sic*) sp.], 2001 [both UFK]; Lyons, 1999; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK; also as *B. domingensis*]; USGS, 2003 [UFK, MFK].

Brachidontes modiolus (Linnaeus, 1767): Calkins, 1878 [LFK; as *Modiola sulcata* Lamarck, 1819]; Melvill, 1880 [LFK; as *Mytilus cubitus* Say, 1822]; Dall, 1889a, 1903b [both as *Modiola* (*Brachydontes*) *sulcata*]; Lermond, 1936 [as *Modiolaria sulcatus*]; Webb, 1937, 1939, 1942, 1951 [LFK; figured, as *Mytilus perna* “Dall” (Linnaeus, 1758)] Pulley, 1952 [as *Brachidontes citrinus* (Röding, 1798)]; Lee, 1969 [LFK; as *B. citrinus*]; Plockelman, 1969b [LFK, as *B. citrinus*]; Ross, 1969 [MFK; as *B. citrinus*]; Plockelman, 1970c [as *B. citrinus*]; Edwards, 1980 [LFK; as *Brachidonta* (*sic*)]; Petuch, 1988 [UFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Brachidontes sp.: Morrison, 1958 [UFK]; Oliver & Järnegren, 2004 [LFK].

Crenella decussata (Montagu, 1808): Dall, 1889a, 1903b [as *C. divaricata* (Orbigny, 1845)]; Lermond, 1936 [as *C. divaricata*]; Turney & Perkins, 1972 [UFK, MFK; as *C. divaricata*]; Lyons & Quinn, 1995 [as *C. divaricata*]; Vittor & Associates, 1998 [LFK, DT; as *C. divaricata*], 1999a [LFK, DT; as *C. divaricata*], 1999b [UFK, MFK, LFK; as *C. divaricata*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Crenella sp.: Morrison, 1958 [UFK].

Dacrydium elegantulum hendersoni Salas and Gofas, 1997: Dall, 1889a, 1903b [misidentified as *D. vitreum* (Møller, 1842, *ex* Holbøll ms), a recognized North Atlantic species]; Lermond, 1936 [as *D. vitreum*]; Salas and Gofas, 1997 [LFK]; Mikkelsen & Bieler, 2000 [LFK].

Geukensia granosissima (G. B. Sowerby III, 1914): Melvill, 1880 [LFK; as *Modiola plicatula* Lamarck, 1819]; Lermond, 1936 [as *Modiolaria demissus* (Dillwyn, 1817) and *M. d. granosissimus*]; Mikkelsen & Bieler, 2000 [MFK].

Gregariella coralliophaga (Gmelin, 1791): Simpson, 1887–1889 [LFK, DT; as *Botula semen* (“Reeve” err. pro Lamarck, 1819)]; Dall, 1889a [as *Modiola* (*Botulina*) *opifex* Say, 1825]; Lermond, 1936 [as *Modiolaria opifex*]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Ischadium recurvum (Rafinesque, 1820): Dall, 1889a, 1903b [as *Mytilus hamatus* Say, 1822]; Lermond, 1936 [as *Mytilus recurvus*]; Magnotte, 1970–1979 [as *Brachidontes recurvus*]; Kissling, 1977a [as *Brachiodontes* (*sic*) *recurvus*]; Mikkelsen & Bieler, 2000 [UFK, LFK].

Lioberus castaneus (Say, 1822): Simpson, 1887–1889 [DT; as *Pectunculus*]; Dall, 1889a [as *Modiola* (*Amygdalum*) *lignea* Reeve, 1858]; Lermond, 1936 [as *Botula castanea*]; Pulley, 1952 [as *Botula*]; Andrews, 1971, 1977, 1981a, b, 1992, 1994 [as *Lioberis* (*sic*)]; Antonius et al., 1978 [LFK]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [DT], 1999b [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Lithophaga antillarum (Orbigny, 1842): Calkins, 1878 [DT; as *Lithodomus*]; Dall, 1889a [as *Lithophagus*], 1896a [DT; as *Lithophagus*], 1903b [as *Lithophagus*]; Lermond, 1936 [as *Lithodomus*]; Bales, 1940, 1944; Webb, 1942 [LFK], 1951 [LFK; as *L. antilarum* (*sic*)]; Lyman, 1948b; Pulley, 1952; Turner & Boss, 1962 [UFK, MFK, LFK]; Brooks, 1968a [MFK]; Magnotte, 1970–1979; Zischke, 1973, 1977a [MFK]; Emerson & Jacobson, 1976; Kissling, 1977a; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Valentich-Scott & Dinesen, 2004 [UFK, MFK, LFK].

Lithophaga aristata (Dillwyn, 1817): Melvill, 1880 [LFK; as *Lithodomus candigerus*, err. pro *L. caudigerus* (Lamarck, 1819)]; Simpson, 1887–1889 [DT; as *Lithodomus* *forficatus* Ravenel, 1861]; Dall, 1889a [as *Lithophagus forficatus*]; Lermond, 1936 [as *Lithodomus*]; Bales, 1944; Turner & Boss, 1962 [LFK, DT]; Emerson & Jacobson, 1976; Antonius et al., 1978 [LFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [LFK, DT]; Valentich-Scott & Dinesen, 2004 [LFK].

Lithophaga bisulcata (Orbigny, 1842): Simpson, 1887–1889 [MFK; as *Lithodomus bisulcatus*]; Dall, 1889a, 1903b [as *Lithophagus bisulcatus*]; Aldrich & Snyder, 1936; Lermond, 1936 [as *Lithodomus*]; Bales, 1940, 1944; Turner & Boss, 1962 [MFK]; Antonius et al., 1978 [LFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK]; Valentich-Scott & Dinesen, 2004 [MFK, LFK].

Lithophaga nigra (Orbigny, 1842): Calkins, 1878 [DT; misidentified as *Lithodomus lithophagus* (Linnaeus, 1758), a recognized eastern Atlantic species]; Simpson, 1887–1889 [DT; as *Lithodomus niger*]; Dall, 1889a [as *Lithophagus caribaeus* Philippi, 1847]; Rogers, 1908 [as *Lithodomus lithophagus*]; Thiele, 1910 [DT]; Lermond, 1936 [as *Lithodomus*]; Bales, 1940, 1944; Turner & Boss, 1962 [UFK, MFK, LFK, DT]; Edwards, 1968a [LFK; as *Lithophagis* (*sic*) *nigra*]; Zischke, 1973, 1977a [MFK]; Emerson & Jacobson, 1976; Antonius et al., 1978 [LFK]; Kleemann, 1983; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Lithophaga sp.: Henderson, 1911 [LFK; as *Lithodomus* sp.]; Lyman, 1943; Schomer & Drew, 1982; Voss, 1983 [UFK]; Voss et al., 1983 [UFK].

Modiolus americanus (Leach in Leach & Nodder, 1815): Calkins, 1878 [LFK, as *Modiola tulipa* Lamarck, 1819; MFK, as *M. t.* var. *nigra* n. var.]; Lermond, 1936 [as *Modiolaria tulipus*]; Lyman, 1947a [MFK; as *Modiolus tulipus*]; Iversen & Roessler, 1969 [UFK]; Ross, 1969 [MFK]; Work, 1969 [LFK]; Magnotte, 1970–1979; Woods, 1970 [LFK]; Turney & Perkins, 1972 [UFK, MFK; as *Volsella americana*]; Godcharles & Jaap, 1973 [UFK]; Zischke, 1973, 1977a [MFK]; Antonius et al., 1978 [LFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Modiolus squamosus Beauperthuy, 1967: Beauperthuy, 1967 [LFK]; Voss, 1983 [UFK; as *M. modiolus squamosus*]; Voss et al., 1983 [UFK; as *M. modiolus squamosus*]; Lyons & Quinn, 1995 [as *M. modiolus squamosus*]; Vittor & Associates, 1997c [UFK], 1998 [LFK], 1999b [LFK] [all as *M. modiolus squamosus*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *M. modiolus squamosus*]; USGS, 2003 [UFK, MFK].

Musculus lateralis (Say, 1822): Dall, 1889a [as *Modiolaria*], 1903b [as *Modiolaria*]; Thiele, 1910 [DT; as *Modiolaria*]; Lermond, 1936 [as *Modiolaria*]; Webb, 1942, 1951 [as *Modiola duplicata* (Say, [date unknown]); although this name has not been verified as a synonym and Webb's (1942: 74, pl. 25, fig. 30) figure is poor, the figure and brief text suggest *M. lateralis*]; Pulley, 1952; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Vittor & Associates, 1997c [UFK], 1998 [LFK, DT], 1999a [DT], b [UFK, MFK, LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Musculus sp.: Vittor & Associates, 1999a [UFK].

|*Mytilus californianus* Conrad, 1837: Abbott, 1961 [LFK; in error].

|*Mytilus perna* (Linnaeus, 1758) – see under *Brachidontes Modiolus*.

|*Perna viridis* (Linnaeus, 1758): Benson et al., 2001 (predicted introduction).

|Neilonellidae

|*Neilonella pusio* (Philippi, 1844) – Florida Keys records (Abbott, 1974 [LFK; as *Nuculana*]; Mikkelsen & Bieler, 2000 [LFK; as *Nuculana*]) based on Dall's (1889a, 1903b [as *Leda* (*Leda*)]) archibenthal category (50–800 fms); however species' minimum depth range given by Dall (1889a) is 856 [fms], and it is here excluded as beyond depth limit.

Noetiidae

Arcopsis adamsi ("Shuttleworth" Dall, 1886): Dall, 1889a [as *Arca* (*Byssoarca*) *Adamsi*]; Lermond, 1936 [as *Arca admsi* (*sic*)]; M. Smith, 1937, 1945 [as *Arca* (*Acar*)]; Edwards, 1968b [LFK]; Hudson et al., 1970 [UFK]; Woods, 1970; Turney & Perkins, 1972 [UFK, MFK]; Zischke, 1973, 1977a, b, c [MFK]; Antonius et al., 1978 [LFK; as *Acropsis* (*sic*)]; Mikkelsen, 1981 [UFK]; Petersen, 1989 [MFK; as *Acropsi* (*sic*)]; Lyons & Quinn, 1995; Wingard et al., 1995 [UFK]; Brewster-Wingard et al., 1996, 1997, 2001 [all UFK]; Vittor & Associates, 1997c [UFK]; Brewster-Wingard & Ishman, 1999, 2001 [UFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK, MFK]; Oliver & Järnegren, 2004 [MFK, LFK].

Noetia ponderosa (Say, 1822): Dall, 1889a, 1903b [as *Arca* (*Noetia*)]; Lermond, 1936 [as *Arca*]; Abbott, 1954 [LFK; as *N.* (*Eontia*)], 1961 [LFK], 1968, 1970 [LFK]; Siekman, 1965, 1981, 1982 [LFK]; Magnotte, 1970–1979; Andrews, 1971, 1977, 1981a, b, 1992, 1994 [LFK; as *N.* (*Eontia*)]; Turney & Perkins, 1972 [UFK, MFK]; Emerson & Jacobson, 1976 [LFK]; Long Island Shell Club, 1988; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Nuculanidae

Theroux & Wigley, 1983 [UFK]

|*Ledella solidula* (E. A. Smith, 1885): Florida Keys records (Lermond, 1936, as *Nuculana*]; Rios, 1994 [as *N.* (*Jupitaria*)]; Mikkelsen & Bieler, 2000 [as *Nuculana*]) probably based on Dall (1889a, 1903b [as *Leda* (*Leda*)]), categorized as archibenthal (50–800 fms) but with minimum species depth as 640 [fms]; here excluded as beyond depth limit.

Ledella sublevis A. E. Verrill & Bush, 1898: Dall, 1889a [misidentified as *Leda* (*Leda*) *messanensis* Seguenza, 1877, a recognized eastern Atlantic species of *Yoldiella*; some material identified as *Y. messanensis* was subsequently described as the new species *L. bushae* Warén, 1978, but all cited material is post-1889; *L. sublevis* was originally described as a western Atlantic variety of *Y. messanensis*].

Nuculana acuta (Conrad, 1832): Dall, 1886 [LFK; as *Leda*], 1889a, 1903b [as *Leda* (*Leda*)]; Turney & Perkins, 1972 [UFK, MFK]; Vittor & Associates, 1998 [LFK, DT], 1999a [LFK, DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Nuculana concentrica (Say, 1824): Vittor & Associates, 1998 [LFK, DT], 1999a [DT]; Mikkelsen & Bieler, 2000 [MFK, LFK, DT].

Nuculana jamaicensis (Orbigny, 1842): Dall, 1881 [LFK; as *Leda*].

Nuculana solidifacta (Dall, 1886).

Nuculana verrilliana (Dall, 1886): Johnson, 1934; Lermond, 1936; Morris, 1973; Abbott, 1974; Mikkelsen & Bieler, 2000.

Nuculana vitrea (Orbigny, 1842): Dall, 1889a [as *Leda* (*Leda*)].

Nuculana sp.: Theroux & Wigley, 1983 [MFK, LFK]; Bielsa & Labisky, 1987 [LFK]; Vittor & Associates, 1998 [LFK, DT].

Propeleda carpenteri (Dall, 1881): Dall, 1881 [LFK; as *Leda*], 1889a [as *L.* (*L.*) *Carpenteri*]; Lermond, 1936 [as *Nuculana*]; Pulley, 1952 [LFK; as *Nuculana*]; Theroux & Wigley, 1983 [UFK; as *Nuculana*].

Nuculidae

Ennucula aegeensis (Forbes, 1844): Dall, 1889a, 1903b [both as *Nucula aegeënsis*]; Lermond, 1936 [as *Nucula*]; Vittor & Associates, 1997a [UFK, MFK, LFK; as *N. aegeenis* (*sic*)], 1997c [UFK; as *N. aegensis* (*sic*)], 1998 [LFK, DT; as *N. aegeenis* (*sic*)], 1999a [DT; as *N. aegeenis* (*sic*)], 1999b [LFK; as *N. aegeenis* (*sic*)]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Nucula*].

Ennucula tenuis Montagu, 1808: Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Nucula calcicola Moore, 1977: Moore, 1977 [UFK]; Díaz Merlano & Puyana Hegedus, 1994; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Nucula crenulata A. Adams, 1856: Abbott, 1954 [LFK]; Mikkelsen & Bieler, 2000 [DT]; other "Tortugas" records are based on *Blake* sta. 44, here excluded (see entry for Dall, 1881).

Nucula proxima Say, 1822: Pulley, 1952; Howard et al., 1970 [LFK]; Turney & Perkins, 1972 [UFK, MFK]; Lineback, 1977 [LFK]; Wingard et al., 1995 [UFK]; Brewster-Wingard et al., 1996, 1997, 2001 [all UFK]; Brewster-Wingard & Ishman, 1999 [UFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK].

Ostreidae

Woods, 1971 [MFK; as little oysters]; USGS, 2003 [UFK, MFK]; Oliver & Järnegren, 2004 [LFK; as oysters].

Crassostrea rhizophorae (Guilding, 1828): Melvill, 1880 [LFK; as *Ostrea*]; Simpson, 1887–1889 [DT; misidentified as *O. parasitica* "Lamarck" err. pro Gmelin, 1791, a recognized Indo-Pacific species of *Striostrea*]; Mikkelsen & Bieler, 2000 [LFK].

Crassostrea virginica (Gmelin, 1791): Dall, 1889a, 1903b [as *Ostrea*]; Lermond, 1936 [as *O. verginica* (*sic*)]; Bartsch, 1937 [as *Ostrea floridensis* G. B. Sowerby II, 1871]; Chan, 1977b [LFK]; Schomer & Drew, 1982; Mikkelsen & Bieler, 2000 [UFK, LFK].

|*Cryptostrea permollis* (G. B. Sowerby II, 1871) – see *Teskeyostrea weberi*.

Dendostrea frons (Linnaeus, 1758): Melvill, 1880 [LFK; as *Ostrea*]; Dall, 1889a, 1903b [as *Ostrea*]; Lermond, 1936 [as *Ostrea*]; Webb, 1937, 1942, 1951 [all as *Ostrea foliata* Lamarck [date unknown]; although the taxonomic status of this name is unverified, Webb's illustrations strongly suggest *D. frons*; ?err. pro *Ostrea folium* Linnaeus, 1758, a recognized Indo-West Pacific species of *Dendostrea*; Schroeder, 1964 [UFK; as "coon oysters"]; Magnotte, 1970–1979 [as *Ostrea*]; Voss, 1983 [UFK; as *Lopha* and as *Ostrea*]; Voss et al., 1983 [UFK; as *Lopha*, *Ostrea* and as *Ostrea* (*Lopha*)]; Boone, 1986 [MFK]; Petersen, 1989 [MFK; as *Ostrea*]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Kirkendale et al., 2004.

Ostrea equestris (Say, 1834): Dall, 1889a [misidentified as *Ostrea cristata* Born, 1778, a recognized South American species]; Lermond, 1936 [as *Ostrea cristata*]; Magnotte, 1970–1979; Zischke, 1973, 1977a, b [MFK]; Lyons & Quinn, 1995 [as *Ostreola*]; Campbell et al., 1998 [MFK; as *Ostreola*]; Jozefowicz & Ó Foighil, 1998 [LFK; misidentied as *Teskeyostrea weberi*, fide Kirkendale et al., 2004]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK; as *Ostreola*]; USGS, 2002 [UFK]; Kirkendale et al., 2004 [MFK, LFK; as *Ostreola*].

Teskeyostrea weberi (Olsson, 1951): Olsson, 1951 [MFK, LFK; as *Ostrea*]; Forbes, 1964 [UFK; misidentified as *Ostrea permollis* G. B. Sowerby II, 1871, a recognized obligate sponge commensal of *Cryptostrea* from the western Atlantic]; Kraeuter, 1973 [UFK; as *Ostrea permollis*]; Harry, 1985 [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK; as *Ostrea permollis*]; Kirkendale et al., 2004 [MFK].

Pandoridae

Pandora arenosa Conrad, 1834: Vittor & Associates, 1999a [LFK, DT].

Pandora bushiana Dall, 1886: Boss & Merrill, 1965 [UFK, DT]; Mikkelsen & Bieler, 2000 [UFK, DT].

Pandora glacialis Leach, 1819: Dall, 1889a, 1903b [as *P.* (*Kennerlia*)].

Pandora inflata Boss & Merrill, 1965: Boss & Merrill, 1965 [UFK, MFK, LFK, DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Pandora sp.: Vittor & Associates, 1998 [LFK, DT], 1999a [UFK].

Pectinidae

Henderson, 1911 [LFK; as Pectens]; Lyman, 1944b [UFK; as pectens], 1951 [UFK, as black pecten]; Foster, 1945; Turney & Perkins, 1972 [UFK, MFK]; Edwards, 1980 [LFK; as Pecten pairs]; Theroux & Wigley, 1983 [MFK]; Wingard et al., 1995 [UFK; as pectinid]; Brewster-Wingard et al., 1997 [UFK; as pectinid]; Vittor & Associates, 1998 [DT], 1999b [MFK, LFK]; USGS, 2002 [UFK].

|*Aequipecten acanthodes* Dall, 1925 – see *Lindapecten muscosus.*

Aequipecten glyptus (A. E. Verrill, 1882): Rehder & Abbott, 1951 [DT]; Rombouts, 1991 [DT]; Mikkelsen & Bieler, 2000 [LFK, DT].

Aequipecten heliacus (Dall, 1925): Lermond, 1936 [as *Pecten*].

Aequipecten lineolaris (Lamarck, 1819): Abbott, 1954; P. L. McGinty & T. L. McGinty, 1957 [MFK, LFK]; Warmke & Abbott, 1961; Barrett & Patterson, 1967; Magnotte, 1970–1979; Pompey, 1974; Humfrey, 1975; Romashko, 1984; Mikkelsen & Bieler, 2000 [MFK, LFK, DT; as *Argopecten*].

|*Aequipecten exasperatus* (G. B. Sowerby II, 1847) – see *Lindapecten muscosus.*

|*Aequipecten muscosus* (Wood, 1828) – see under *Lindapecten.*

|*Aequipecten phrygius* (Dall, 1886) – see *Cryptopecten phrygium.*

|*Amusium laurentii* (Gmelin, 1791) – see under *Euvola.*

|*Amusium papyraceum* (Gabb, 1873) – see *Euvola* cf. *papyracea.*

Argopecten gibbus (Linnaeus, 1758): Dall, 1886 [LFK; as *Pecten dislocatus* Say, 1822], 1889a, 1903b [as *P.* (*Pecten*) *irradians* var. *dislocatus*]; Simpson, 1887–1889 [MFK; as *P. dislocates* (*sic*)]; Lermond, 1936 [as *Pecten*]; Waller, 1969; Magnotte, 1970–1979 [as *Aequipecten*]; Godcharles & Jaap, 1973 [UFK]; Allen, 1979 [LFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Krause et al., 1994 [LFK]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Argopecten irradians (Lamarck, 1819): Iversen & Roessler, 1969 [UFK; also as *Aequipecten* or *Aeguipecten* (*sic*)]; Waller, 1969 [MFK; as *A. i. concentricus* (Say, 1822)]; Hudson et al., 1970 [UFK; as *A. i. concentricus*]; Magnotte, 1970–1979 [as *Aequipecten*]; Petuch, 1987 [MFK; as *A. i. taylorae* Petuch, 1987], 1988 [MFK; as *A. i. taylorae*]; Marelli et al., 1997 [MFK; as *A. i. concentricus* and *A. i. taylorae*]; Turgeon et al., 1988; Abbott, 1974; Lyons & Quinn, 1995; DeMaria, 1996 [UFK, MFK; as scallops]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK]; Brewster-Wingard et al., 2001 [UFK]; USGS, 2003 [UFK, MFK].

Argopecten nucleus (Born, 1778): Dall, 1889a, 1903b [as *Pecten* (*Pecten*)], 1898 [as *P.* (*Chlamys,* section *Plagioctenium*) *gibbus* var. *nucleus*]; 1925 [as *P.* (*Plagioctenium*)]; Johnson 1934 [as *Pecten* (*Plagioctenium*)]; Lermond, 1936 [as *Pecten*]; M. Smith, 1937, 1945 [as *Pecten* (*Aequipecten, Plagioctenium*)]; Lyman, 1944a [as *Pecten*]; Webb, 1951 [as *Pecten*]; Salisbury, 1952 (as *Chlamys*); Abbott, 1954 [as *Aequipecten* (*Plagioctenium*) *gibbus nucleus*]; Bender, 1968 [LFK]; Waller, 1969; Godcharles & Jaap, 1973 [UFK]; Petersen, 1989 [MFK; as *Argopectin* (*sic*)]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Argopecten sp.: Vittor & Associates, 1999a [LFK].

Brachtechlamys antillarum (Récluz, 1853): Simpson, 1887–1889 [LFK, DT; as *Pecten*]; Dall, 1886 [as *Pecten*], 1889a, 1903b [LFK; as *Pecten* (*Pecten*)], 1898 [as *P.* (*Chlamys,* section *Nodipecten*)]; Johnson, 1934 [as *Pecten* (*L.*)]; Lermond, 1936 [as *Pecten*]; M. Smith, 1937, 1945 [as *Pecten* (*Lyropecten*)]; Webb, 1942, 1951 [LFK; as *Pecten*]; Voss, 1949 [UFK; as *Pecten*], 1983 [UFK; as *Lyropecten*]; Pulley, 1952 [as *Lyropecten*]; Iversen & Roessler, 1969 [UFK; as *Lyropecten*]; Magnotte, 1970–1979 [as *Lyropecten*]; Woods, 1970 [LFK; as *Pecten*]; Ross, 1971 [LFK; as *Lyropecten*]; Voss et al., 1983 [UFK; as *Lyropecten* and as *Pecten*]; Wagner & Abbott, 1990 [as *Lyropecten*]; Lyons & Quinn, 1995; Hutsell et al., 1997 [as *Lyropecten*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Caribachlamys imbricata (Gmelin, 1791): Simpson, 1887–1889 [DT; as *Pecten imbricatus*]; Dall, 1889a, 1903b [DT; as *P.* (*P.*) *imbricatus*]; Thiele, 1910 [DT; as *P.* (*Chlamys*) *imbricatus*]; Johnson 1934 [as *P.* (*Chlamys*) *imbricatus*]; Lermond, 1936 [as *P. imbricatus*]; M. Smith, 1937, 1945 [as *P.* (*Chlamys*)]; Lyman, 1944a, 1948a, b [as *P. imbricatus*]; Voss, 1948 [UFK; as *P. imbricatus*]; Bippus, 1950 [UFK; as *P. imbricatus*]; Webb, 1951 [as *P. imbricatus*]; Pulley, 1952 [as *Chlamys*]; Edwards, 1969 [UFK; as *Chlamys*]; Work, 1969 [UFK, LFK; as *Chlamys*]; Magnotte, 1970–1979 [as *Chlamys*]; Antonius et al., 1978 [LFK; as *Chlamys*]; Sage, 1987 [LFK; as *Chlamys*]; Williams, 1988; Waller, 1993 [UFK]; Lyons & Quinn, 1995 [as *Chlamys*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Caribachlamys mildredae (F. M. Bayer, 1941): Bayer, 1941 [DT, as *Pecten* (*Chlamys*) *imbricatus* var. *mildredae*], 1942 [UFK, LFK, DT; as *Pecten imbricatus mildredae*]; Lyman, 1945 [UFK; as *P.* (*Chlamys*) *Mildredaea* (*sic*)]; M. Smith, 1945 [as *Pecten*]; Magnotte, 1970–1979 [as *Chlamys*]; Waller, 1993 [DT]; Lyons & Quinn, 1995 [as *Chlamys*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Caribachlamys ornata (Lamarck, 1819): Simpson, 1887–1889 [LFK, DT; as *Pecten ornatus* and as purplish var.]; Dall, 1889a [as *P.* (*P.*) *ornatus*], 1896a [DT; as *P. ornatus*]; 1903b [as *P.* (*P.*) *ornatus*]; 1898 [Pleistocene; as *P.* (*Chlamys,* section *Chlamys*) *ornatus*]; Nutting, 1895 [DT; as *P. ornatus*]; Lermond, 1936 [as *P. ornatus*]; Lyman, 1944a [as *P. ornatus*]; Webb, 1951 [as *Pecten*]; Edwards, 1969 [UFK; as *Chlamys*]; Work, 1969 [UFK; as *Chlamys*]; Waller, 1993 [UFK]; Lyons & Quinn, 1995 [as *Chlamys*]; Gundersen, 1997; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Caribachlamys sentis (Reeve, 1853): Lermond, 1936 [LFK; as *Pecten*]; Webb, 1942 [LFK; as *Pecten*], 1951 [as *Pecten*]; Lyman, 1943 [as *Pecten*]; Lyman, 1944a, 1948b, 1949a [as *Pecten*], 1950 [UFK; as *Pecten*]; Voss, 1948, 1949 [UFK; as *Pecten*]; Bippus, 1950 [UFK; as *Pecten*]; Pulley, 1952 [as *Chlamys*]; Eubanks, 1964 [as *Chlamys*]; Bender, 1968 [LFK]; Brooks, 1968b [MFK; as *Chlamys*]; Edwards, 1968a, b [both LFK], 1969 [UFK] [all as *Chlamys*]; Brooks, 1969 [MFK; as *Chlamys*]; Burggraf, 1969 [LFK; as *Chlamys*]; Magnotte, 1970–1979 [as *Chlamys*]; Plockelman, 1969b [LFK, as *Chlamys*]; Ross, 1969 [MFK; as *Chlamys*], 1971 [LFK; as *Chlamys*]; Zischke, 1973, 1977a, c [MFK; as *Chlamys*]; Hughes, 1976 [LFK; as *Chlamys*]; Kissling, 1977b [UFK; as *Chlamys*]; Antonius et al., 1978 [LFK; as *Chlamys*]; Pease, 1980 [LFK; as *Chlamys*]; Rehder, 1981 [as *Chlamys*]; Romashko, 1984 [as *Chlamys*]; Sage, 1987 [LFK; as *Chlamys*]; Williams, 1988 [as *Chlamys*]; Wagner & Abbott, 1990 [as *Chlamys*]; Williams, 1990 [as *Chlamys*]; Krisberg, 1993 [LFK; as *Chlamys*]; Waller, 1993 [UFK]; Lyons & Quinn, 1995 [as *Chlamys*]; Gundersen, 1997; Hutsell et al., 1997; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Poland, 2001 [LFK].

|*Chlamys benedicti* A. E. Verrill & Bush, 1897 – see under *Spathochlamys.*

|*Chlamys imbricata* (Gmelin, 1791) – see under *Caribachlamys.*

|*Chlamys multisquamata* (Dunker, 1864) – see under *Laevichlamys.*

|*Chlamys mildredae* (F. M. Bayer, 1941) – see under *Caribachlamys.*

|*Chlamys ornata* (Lamarck, 1819) – see under *Caribachlamys.*

|*Chlamys sentis* (Reeve, 1853) – see under *Caribachlamys.*

Chlamys (s. l.) sp.: Lyman, 1943 [as *Pecten* (*Chlamys*)].

Cryptopecten phrygium (Dall, 1886): Dall, 1889a, 1903b [as *Pecten* (*Pecten*)]; Pulley, 1952 [UFK, DT; as *Chlamys phrygius*]; Abbott, 1954 [LFK; as *Aequipecten phrygius*]; P. L. McGinty & T. L. McGinty, 1957 [MFK, LFK; as *Pecten*]; Abbott, 1974 [as *Aequipecten*]; Hayami, 1984 [LFK]; Mikkelsen & Bieler, 2000 [MFK, LFK, DT].

Euvola chazaliei (Dautzenberg, 1900): Dall, 1925 [LFK; as *Pecten* (*E.*) *tereinus* Dall, 1925]; Johnson, 1934 [LFK; as *P.* (*E.*) *tereinus*]; Lermond, 1936 [LFK; as *P. tereinus*]; Foster, 1945 [as *Pecten tereinus*]; Aguayo & Jaume, 1950h [LFK; as *P.* (*E.*) *tereinus*]; Grau, 1955 [LFK; as *P.* (*E.*) *tereinus*]; P. L. McGinty & T. L. McGinty, 1957 [MFK,LFK; as *P. chazaliei* (*tereinus*)]; Boss et al., 1968 [LFK; as *P.* (*E.*) *tereinus*]; Lyons & Quinn, 1995 [as *Pecten*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Euvola laurentii (Gmelin, 1791): Frumar, 2000 [DT; as *Amusium*]; Mikkelsen & Bieler, 2000 [LFK, DT; as *Amusium*].

Euvola cf. *papyracea* (Gabb, 1873) [= *Euvola* sp. A of Waller (1991); *Amusium papyraceum*, a Dominican Republic fossil, is a true *Amusium* and not conspecific]: Rehder & Abbott, 1951 [DT; as *Amusium papyraceum*]; Pulley, 1952 [DT; as *A. papyraceum*]; Mikkelsen & Bieler, 2000 [LFK, DT; as *A. papyraceum*].

Euvola raveneli (Dall, 1898): Simpson, 1887–1889 [misidentified as *Pecten* "*hemicyclica*", err. pro *P. hemicyclicus* "Ravenel" Tuomey & Holmes, 1855, a recognized Pliocene *Euvola* from South Carolina]; Dall, 1889a [as *Pecten* (*Janira*) *hemicyclica*]; Lermond, 1936 [as *Pecten*]; Pulley, 1952; Mikkelsen & Bieler, 2000 [MFK, LFK, DT].

Euvola ziczac (Linnaeus, 1758): Dall, 1889a, 1903b [as *Pecten* (*Janira*)]; Lermond, 1936 [as *Pecten*]; Magnotte, 1970–1979 [as *Pecten*]; Godcharles & Jaap, 1973 [UFK; as *Pecten*]; Rombouts, 1991 [LFK]; Lyons & Quinn, 1995 [as *Pecten*]; Mikkelsen & Bieler, 2000 [LFK, DT]; Miller, 2001 [LFK].

Laevichlamys multisquamata (Dunker, 1864): Dall, 1889a [as *Pecten* (*Pecten*) *effluens* Dall, 1886]; Lyons & Quinn, 1995 [as *Chlamys*]; Mikkelsen & Bieler, 2000.

Lindapecten muscosus (Wood, 1828): Dall, 1889a, 1903b [both misidentified as *Pecten* (*Pecten*) *exasperatus* G. B. Sowerby II, 1847, a recognized Caribbean species of *Lindapecten*]; Lermond, 1936 [as *P. exasperatus* and *P. acanthodes* Dall, 1925]; C. N. Vilas & N. R. Vilas, 1945 [as *Pecten*], 1970 [as *Aequipecten*]; Webb, 1951 [as *Pecten*]; Pulley, 1952 [as *Chlamys*]; Iversen & Roessler, 1969 [UFK; as *Aequipecten*]; Magnotte, 1970–1979 [as *Aequipecten*]; Plockelman, 1970b [MFK; as *Aequipecten acanthodes*]; Andrews, 1971, 1977, 1994 [as *Aequipecten*]; Sunderland & Cahill, 1990 [MFK; as *A. acanthodes*]; Wagner & Abbott, 1990 [as *Aequipecten*, also as *A. acanthodes*]; Rombouts, 1991 [LFK; as *Aequipecten*]; Abbott & Morris, 1995 [as *A. acanthodes*]; Lyons & Quinn, 1995 [as *A. acanthodes exasperatus*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK; also as *L. exasperatus*].

|*Lyropecten antillarum* (Récluz, 1853) – see under *Brachtechlamys.*

Lyropecten kallinubilosus (F. M. Bayer, 1943): Mikkelsen & Bieler, 2000 [LFK].

Nodipecten fragosus (Conrad, 1849): Dall, 1889a, 1903b [both misidentified as *Pecten* (*Pecten*) *nodosus* (Linnaeus, 1758), a recognized Caribbean species of *Nodipecten*]; Lermond, 1936 [as *P. nodosus fragosus*, also as *P. nodosus*]; T. L. McGinty, 1942 [as *P. nodosus*]; Pulley, 1952 [as *Lyropecten nodosus*]; Magnotte, 1970–1979 [DT; as *Lyropecten nodosus*]; Andrews, 1971, 1977, 1981a, b, 1992, 1994 [all as *Lyropecten* (*Nodipecten*) *nodosus*]; Gaertner, 1978 [LFK, as Lion's Paws]; Sunderland, 1988 [UFK; as *N. nodosus*]; Williams, 1988 [as *N. nodosus*]; Rombouts, 1991 [DT; as *N. nodosus*]; Lyons & Quinn, 1995 [as *N. nodosus*]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT; as *N. nodosus*].

|*Nodipecten nodosus* (Linnaeus, 1758) – see *Nodipecten fragosus.*

|*Pecten chazaliei* (Dautzenberg, 1900) – see under *Euvola.*

|*Pecten raveneli* Dall, 1898 – see under *Euvola.*

|*Pecten ziczac* (Linnaeus, 1758) – see under *Euvola.*

Pecten (s. l.) sp.: Henderson, 1911 [LFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK].

Spathochlamys benedicti (A. E. Verrill & Bush, 1897): Lyons & Quinn, 1995 [as *Chlamys*]; Frumar, 2000 [DT; as *Chlamys*]; Mikkelsen & Bieler, 2000 [LFK, DT].

Periplomatidae

Cochlodesma pyramidatum Stimpson, 1860: Aguayo & Jaume, 1949 f.

Periploma margaritaceum (Lamarck, 1801): Simpson, 1887–1889 [DT; as *P. angulifera* (Philippi, 1847)]; Dall, 1889a, 1903a, b [as *P. angulifera*]; Johnson 1934 [as *anguliferum*]; Lermond, 1936 [as *P. angulifera* (*sic*)]; M. Smith, 1937, 1945 [both as *P. angulifera*]; Abbott, 1974 [as *P. anguliferum*]; Abbott & Morris, 1995 [as *P. anguliferum*]; Mikkelsen & Bieler, 2000 [LFK; as *P. anguliferum*].

Periploma tenerum P. Fischer, 1882: Dall, 1889a [as *P. tenera* "Jeffreys"]; Johnson 1934 [as *P. tenera*]; Lermond, 1936 [as *P. tenera*]; Mikkelsen & Bieler, 2000 [MFK].

Petricolidae

Choristodon robustum (G. B. Sowerby I, 1834): Simpson, 1887–1889 [LFK, DT; as *C. typicum* Jonas, 1844]; Dall, 1889a, 1903b [as *Petricola* (*Choristodon*) *robusta*]; Bales, 1940 [as *Rupellaria typica*], 1944 [as *R. typica*]; Plockelman, 1969c [MFK; as *R. typica*]; Lyons & Quinn, 1995 [as *R. typica*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Valentich-Scott & Dinesen, 2004 [LFK].

Choristodon sp.: Valentich-Scott & Dinesen, 2004 [LFK; as *C.* sp. A].

Cooperella atlantica Rehder, 1943: Plockelman, 1970d [LFK].

Petricola lapicida (Gmelin, 1791): Dall, 1886 [Gordon Key; as *P. divaricata* Chemnitz in Orbigny, 1842], 1889a, 1903b [as *P.* (*Naranaio*)]; Simpson, 1887–1889 [DT; as *P. divaricata*]; Johnson, 1934; Lermond, 1936; M. Smith, 1937, 1945; Bales, 1940, 1944; Edwards, 1968a [LFK]; Zischke, 1973, 1977a [MFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Valentich-Scott & Dinesen, 2004 [LFK].

Petricolaria pholadiformis (Lamarck, 1818): Dall, 1889a, 1903b [as *Petricola*]; Lermond, 1936 [as *Petricola*]; Magnotte, 1970–1979; Mikkelsen & Bieler, 2000 [LFK].

Petricolaria sp.: Dall, 1889a, 1903b [as *Petricola*].

|*Rupellaria typica* (Jonas, 1844) – see *Choristodon robustum*.

Pharidae

Ensis minor Dall, 1900: Dall, 1889a [misidentified as *E. americana* (Gould, 1870), a synonym of the recognized but much larger *E. directus* Conrad, 1843, from the eastern United States], 1899b [UFK; as *E. directus*], 1900a [UFK; as *E. directus*]; Maury, 1920 [as *E. directus*]; M. Smith, 1937, 1940, 1945 [as *E. directus*]; Mikkelsen & Bieler, 2000 [LFK].

Philobryidae

Cratis antillensis (Dall, 1881): Dall, 1889a, 1903b (both as *Limopsis*).

Pholadidae

Barnea truncata (Say, 1822): Dall, 1889a, 1903b [as *Pholas* (*Barnea*)]; Lermond, 1936 [as *Pholas* (*Barnea*)]; M. Smith, 1937, 1940, 1945; C. N. Vilas & N. R. Vilas, 1945, 1970; Magnotte, 1970–1979; Mikkelsen & Bieler, 2000.

Cyrtopleura costata (Linnaeus, 1758): Dall, 1889a, 1903b [as *Pholas* (*Barnea*)]; Lermond, 1936 [as *Pholas* (*Barnea*)]; Magnotte, 1970–1979; Mikkelsen & Bieler, 2000 [LFK].

Martesia cuneiformis (Say, 1822): Simpson, 1887–1889 [MFK, DT]; Dall, 1889a, 1903b; Lermond, 1936 [also as *M. caribaea* (Orbigny, 1842)]; Turner, 1955 [LFK]; Mikkelsen & Bieler, 2000 [LFK].

Martesia striata (Linnaeus, 1758): Simpson, 1887–1889 [DT; as *Coralliophaga hornbeckiana*, err. pro *Pholas hornbeckii* Orbigny, 1842]; Dall, 1889a [also as *M. corticata* Adams, err. pro *corticaria* "Gray" G. B. Sowerby II, 1849], 1903b; Lermond, 1936; Turner, 1955 [LFK]; Mikkelsen & Bieler, 2000 [UFK, LFK].

Pholas campechiensis Gmelin, 1791: Dall, 1889a, 1903b; Lermond, 1936.

|*Xylopholas altenai* Turner, 1972 – Florida Keys records (Abbott, 1974; Mikkelsen & Bieler, 2000 [as *X. altanai* (*sic*)]) based on original description, here excluded as beyond depth limit).

Pinnidae

Stevenson, 1970, 1993 [both as pen shell]; Clampit, 1987 [LFK; as "two types of Pen Shells"]; USGS, 2003 [UFK, MFK].

Atrina rigida (Lightfoot, 1786): Lermond, 1936 [as *Pinna*]; Turner & Rosewater, 1958 [MFK, LFK]; Kissling, 1965 [LFK], 1977b [UFK]; Iversen & Roessler, 1969 [UFK]; Magnotte, 1970–1979; Zischke, 1973, 1977a, b, c [MFK]; Antonius et al., 1978 [LFK]; Schomer & Drew, 1982; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Atrina seminuda (Lamarck, 1819): Dall, 1889a, 1903b [as *Pinna*]; Schomer & Drew, 1982; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK].

Atrina serrata (G. B. Sowerby I, 1825): Simpson, 1887–1889 [as *Pinna muricata* Linnaeus, 1758]; Dall, 1889a [as *P. muricata*]; Lermond, 1936 [as *Pinna*]; Turner & Rosewater, 1958 [UFK, MFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Atrina sp.: Turney & Perkins, 1972 [MFK].

Pinna carnea Gmelin, 1791: Simpson, 1887–1889 [LFK, DT]; Dall, 1889a, 1896a [DT; as *Pinna pernula* Chemnitz, 1785], 1898 [post-Pleistocene], 1903b; Pilsbry, 1890a [LFK]; Dall, 1897; Thiele, 1910 [DT]; Lermond, 1936; M. Smith, 1937, 1945 [DT]; Lyman, 1944c, 1946; Turner & Rosewater, 1958 [UFK, MFK, LFK, DT]; Edwards, 1968a [LFK]; Ross, 1969 [MFK]; Work, 1969 [LFK, DT]; Magnotte, 1970–1979; Sedlak, 1986 [LFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; also misidentified as *Pinna rudis* Linnaeus, 1758, a recognized Mediterranean species].

Pinna sp.: Kirkendale et al., 2004 [MFK].

Plicatulidae

Plicatula gibbosa Lamarck, 1801: Dall, 1889a [as *P. ramosa* Lamarck, 1819]; Lermond, 1936; Webb, 1942, 1951 [as *Plicatula mantilla* Conrad [date unknown]) (not verified as a synonym)]; Magnotte, 1970–1979; Turney & Perkins, 1972 [MFK]; Antonius et al., 1978 [LFK; as *P. spondyloidea* Meuschen, 1781]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Poromyidae

|*Cetoconcha margarita* (Dall, 1886) – all records based on *Blake* sta. 44 (here excluded; see entry for Dall, 1881), including Mikkelsen & Bieler, 2000.

Poromya albida Dall, 1886: Dall, 1889a [as *Poromya* (*Cetomya*)].

|*Poromya elongata* Dall, 1886 – only Florida Keys record (Dall, 1889a) probably based on Gulf of Mexico, 199 fms (Abbott, 1974; here excluded as beyond depth limit.

Poromya granulata (Nyst & Westendorp, 1839): Dall, 1881 [LFK], 1889a, 1903b, 1927; Johnson, 1934 [as *P. g. granulata*]; Lermond, 1936; Mikkelsen & Bieler, 2000 [DT].

Poromya rostrata Rehder, 1943: Mikkelsen & Bieler, 2000 [MFK].

Propeamussiidae

Cyclopecten nanus A. E. Verrill & Bush, 1897.

Cyclopecten strigillatus (Dall, 1889): Dall, 1889b [as *Pseudamusium*].

Cyclopecten sp.: Mikkelsen & Bieler, 2000 [DT].

Parvamussium cancellatum (E. A. Smith, 1885): Dall, 1889a [as *Pecten* (*Amusium, Propeamussium*)].

Parvamussium thalassinum (Dall, 1886): Dall, 1889a [as *Pecten* (*Pecten, Pseudamusium*)].

|*Propeamussium dalli* (E. A. Smith, 1885) – only Florida Keys record (Mikkelsen & Bieler, 2000) based on specimens beyond depth limit).

Propeamussium pourtalesianum (Dall, 1886): Dall, 1881 [LFK; as *Amussium lucidum* (Jeffreys in Thompson, 1873)], 1889a [as *Pecten* (*Amusium, Propeamussium*) *Pourtalesianum* and as var. *marmoratum* (Dall, 1881)], 1903b [as *Pecten* (*Amusium, Propeamussium*) *Pourtalesianum*]; Mikkelsen & Bieler, 2000 [DT].

Propeamussium sayanum (Dall, 1886): Dall, 1889a, 1903b [as *Pecten* (*Amusium, Propeamussium*) *Sayanum*]; Mikkelsen & Bieler, 2000 [DT].

Psammobiidae

Asaphis deflorata (Linnaeus, 1758): Melvill, 1880 [LFK; as *Asaphis dichotoma* (Anton, 1839), synonym of *A. violascens* (Forsskål, 1775), a recognized Indo-Pacific species]; Simpson, 1887–1889 [DT]; Dall, 1889a, 1903b; Pilsbry, 1890b [UFK]; Lermond, 1936; Magnotte, 1970–1979; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK]; Domaneschi & Shea, 2004 [LFK].

Gari circe (Mörch, 1876): Simpson, 1887–1889 [MFK; misidentified as *Macoma anomala* (Deshayes, 1855), a recognized Indo-Pacific species of *Gari*].

Heterodonax bimaculatus (Linnaeus, 1758): Simpson, 1887–1889 [DT]; Dall, 1889a, 1903b [as *H. bimaculata*]; Lermond, 1936 [as *H. bimaculata*]; Mikkelsen & Bieler, 2000.

Sanguinolaria sanquinolenta (Gmelin, 1791): Calkins, 1878 [DT]; Zischke, 1973, 1977a [MFK].

Pteriidae

Vittor & Associates, 1999b [UFK, MFK].

Pinctada imbricata Röding, 1798: Simpson, 1887–1889 [DT; as *Avicula radiata* Leach, 1814, also as *A. ala-perdicis* Reeve, 1857]; Dall, 1889a [as *Margaritiphora radiata*], 1896a [DT; as *A. radiata* and as *A. crocata* (Swainson, 1831), a possible synonym described from Ceylon], 1903b [as *Margaritiphora radiata*]; Thiele, 1910 [DT; as *Pteria radiata*]; Lermond, 1936 [as *Margaritifera radiata*]; Webb, 1937 [misidentified as *Pedalion alata* Gmelin, 1791, now *Isognomon alatus* (see above)]; C. N. Vilas & N. R. Vilas, 1945 [as *Pinctada radiata*], 1970; Bippus, 1950 [UFK; as *Pteria radiata* (variety?)]; Pulley, 1952 [as *Pinctada radiata*]; Iversen & Roessler, 1969 [UFK]; Ross, 1969 [MFK; as *Pinctada radiata*]; Work, 1969 [LFK]; Magnotte, 1970–1979 [as *Pinctada radiata*]; Woods, 1970 [LFK; as *Pinctada radiata*]; Hayes, 1972 [UFK, MFK, UFK, DT]; Zischke, 1973, 1977a [both MFK]; Chan, 1977a, b [LFK; as *Pinctada radiata*]; Kissling, 1977b [UFK; as *Pinctada radiata*]; Lineback, 1977 [LFK; as *P. radiata*]; Antonius et al., 1978 [LFK; as *Pinctada radiata*]; Webster, 1978 [LFK]; Voss, 1983 [UFK; as *Pinctada radiata*]; Voss et al., 1983 [UFK; as *Pinctada radiata*]; Sedlak, 1986 [LFK]; Shirai, 1994 [LFK]; Lyons & Quinn, 1995; Campbell et al., 1998 [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK]; Orlin 2003; Mikkelsen et al., 2004.

Pinctada longisquamosa (Dunker, 1852): Hudson et al., 1970 [UFK; misidentified as *Pinctada radiata* (Leach, 1814), a synonym of *P. imbricata* (above)]; Hayes, 1972 [UFK, MFK, LFK, DT; as *Pteria*]; Turney & Perkins, 1972 [UFK, MFK; misidentified as *Pinctada radiata*, fide Brewster-Wingard et al., 2001]; Abbott, 1974; Wingard et al., 1995 [UFK; as *Pinctada radiata*]; Brewster-Wingard et al., 1996, 1997, 1998 [all as *Pinctada radiata*], 2001 [as *Pteria*] [all UFK]; Brewster-Wingard & Ishman, 1999 [UFK; as *Pinctada radiata*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK, MFK; as *Pteria*]; Mikkelsen et al., 2004 [UFK, MFK, LFK, DT].

Pinctada margaritifera (Linnaeus, 1758): Nutting, 1895 [DT; as *Avicula*] [This distinctive Indo-Pacific species, widely appreciated for its natural and cultured pearls, has been recently and irrefutably recorded as introduced into the western Atlantic (Chesler, 1994; Carlton, 1996), but is not believed to have become established; if it can be believed, Nutting's record would establish a considerably earlier date of first introduction.].

Pteria colymbus (Röding, 1798): Calkins, 1878 [as *Avicula atlantica* Lamarck, 1819]; Dall, 1889a [as *A. atlantica*], 1896a [DT; as *A. atlantica*], 1903b [as *A. atlantica*]; Lermond, 1936 [as *A. atlantica*]; Eubanks, 1964; Iversen & Roessler, 1969 [UFK]; Work, 1969 [LFK]; Hayes, 1972 [UFK, MFK, LFK, DT]; Magnotte, 1970–1979; Stevenson, 1970, 1993 [as Atlantic wing oyster], 1993; Zischke, 1977a [MFK]; Lyons & Quinn, 1995; Hutsell et al., 1997; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Orlin, 2003; Mikkelsen et al., 2004.

|*Pteria longisquamosa* (Dunker, 1852) – see under *Pinctada*.

Pteria vitrea (Reeve, 1857): Dall, 1889a [as *Avicula nitida* A. E. Verrill, 1880]; Maury, 1920 [DT]; Pearse, 1929 [DT]; Johnson, 1934 [as *P. hirundo vitrea*]; Hayes, 1972 [UFK, DT; as *Pteria hirundo vitrea*]; Abbott, 1974.

Pteria (s. l.) sp.: Calkins, 1878 [DT; as *Avicula*]; Dall, 1881 [DT; as *Avicula*]; Henderson, 1911 [LFK; as *Avicula*].

Semelidae

Vittor & Associates, 1997c [UFK], 1998 [LFK, DT], 1999a [LFK, DT], 1999b [UFK, LFK].

Abra aequalis (Say, 1822): Lermond, 1936; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK, DT], 1999a [LFK]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT].

Abra lioica (Dall, 1881): Dall, 1881 [LFK; as *Syndosmya*], 1886 [LFK], 1889a, 1903b; Lermond, 1936; Turney & Perkins, 1972 [UFK, MFK]; Vittor & Associates, 1999b [LFK]; Mikkelsen & Bieler, 2000 [MFK, LFK].

Abra longicallis americana A. E. Verrill & Bush, 1898: Dall, 1889a [as *A. longicallus*, err. pro *A. longicallis* (Scacchi, 1836)].

Abra sp.: Theroux & Wigley, 1983 [UFK, MFK, LFK]; Vittor & Associates, 1999b [UFK].

Cumingia coarctata G. B. Sowerby I, 1833: Dall, 1900a; Lermond, 1936; M. Smith, 1937, 1945; Olsson & Harbison, 1952 [LFK]; Pulley, 1952 [LFK; as *C. antillarum* (Orbigny, 1842)]; Abbott, 1954 [LFK], 1958 [LFK]; Warmke & Abbott, 1961 [LFK; as *C. antillarum*]; Edwards, 1968a [LFK; as *Cummingia* (*sic*) *antillarum*]; Emerson & Jacobson, 1976 [as *C. antillarum*, a "form" of *C. tellinoides* (Conrad, 1831)]; Lyons &

Quinn, 1995; Vittor & Associates, 1998 [DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Cumingia vanhyningi Rehder, 1939: Simpson, 1887–1889 [MFK, DT; as *C. tellinoides* (Conrad, 1831)]; Dall, 1889a, 1903b [both as *C. tellinoides*]; Lermond, 1936 [as *C. tellinoides*]; Rehder, 1939 [UFK, LFK; as *C. tellinoides vanhyningi*]; Aguayo & Jaume, 1948a [UFK; as *C. vanhyningi*]; Turney & Perkins, 1972 [UFK, MFK; as *C. tellinoides*]; Wingard et al., 1995 [UFK; as *C. tellinoidea* (*sic*)]; Brewster-Wingard et al., 1996 [as *C. tellinoidea* (*sic*)], 1997, 2001 [both as *C. tellinoides*] [all UFK]; Vittor & Associates, 1998 [LFK; as *C. tellinoides*], 1999b [LFK; as *C. tellinoides*]; Sweeney & Harasewych, 1999 [UFK; as *C. tellinoides vanhyningi*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK; as *C. tellinoides vanhyningi*]; USGS, 2003 [UFK; as *C. tellinoides*].

Cumingia sp.: USGS, 2003 [UFK; as *Cumingia* sp. or spp.].

Ervilia concentrica (Holmes, 1860): Simpson, 1887–1889 [MFK, DT]; Dall, 1896b, 1889a, 1903b [LFK]; Johnson, 1934 [as Gould, 1862]; Lermond, 1936; M. Smith, 1937, 1945; Davis, 1973 [LFK, DT]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK, DT], 1999a [LFK, DT], b [UFK, MFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Ervilia nitens (Montagu, 1806): Simpson, 1887–1889 [DT]; Dall, 1896b, 1889a, 1903b [DT]; Johnson, 1934; Lermond, 1936; M. Smith, 1937, 1945; Davis, 1973 [MFK, LFK]; Lyons & Quinn, 1995; Vittor & Associates, 1999b [UFK, MFK, LFK]; Mikkelsen & Bieler, 2000 [MFK, LFK].

Ervilia subcancellata E. A. Smith, 1885: Davis, 1973 [UFK, MFK, LFK, DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Ervilia sp.: Vittor & Associates, 1999b [MFK].

Semele bellastriata (Conrad, 1837): Dall, 1889a [as *S. cancellata* (Orbigny, 1842)]; Lermond, 1936; M. Smith, 1937, 1945 [LFK]; C. N. Vilas & N. R. Vilas, 1945, 1970 [LFK]; Lyman, 1949c; T. L. McGinty, 1955; Boss, 1972 [UFK, LFK, DT; as *S. bellestriata* (*sic*)]; Andrews, 1994; Lyons & Quinn, 1995; Wingard et al., 1995 [UFK]; Vittor & Associates, 1998 [LFK], 1999a [UFK, DT], b [UFK, LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Brewster-Wingard et al., 2001 [UFK]; USGS, 2003 [UFK].

Semele proficua (Pulteney, 1799): Simpson, 1887–1889 [as *S. reticulata* "Lamarck" Spengler, 1798]; Dall, 1889a [as *S. reticulata* "Gmelin" Spengler, 1798]; Lermond, 1936; Lyman, 1949c [also as *S. radiata* (Say, 1826) and *S. radiata* "dark form"]; Boss, 1972 [UFK, MFK, LFK, DT]; Turney & Perkins, 1972 [MFK]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [DT], 1999a [LFK, DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Semele purpurascens (Gmelin, 1791): Dall, 1886 [DT], 1889a, 1903b [as *S. obliqua* (Wood, 1815, *non* J. Sowerby, 1817)]; Simpson, 1887–1889 [DT; as *S. obliqua*]; Lermond, 1936; Lyman, 1949c; Boss, 1972 [LFK, DT]; Lyons & Quinn, 1995; Vittor & Associates, 1999a [LFK, DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Semele sp.: Vittor & Associates, 1999a [UFK, LFK], b [UFK, MFK].

Semelina nuculoides (Conrad in Hodge, 1841): Lermond, 1936 [as *Semele*]; Boss, 1972 [LFK; as *Semele* (*Semelina*)]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK, DT; as *Semele*], 1999a [UFK, LFK, DT; as *Semele*], b [MFK, LFK; as *Semele*]; Mikkelsen & Bieler, 2000 [LFK, DT].

Solecurtidae

Solecurtus cumingianus (Dunker, 1861): Mikkelsen & Bieler, 2000 [MFK, LFK, DT].

Tagelus divisus (Spengler, 1794): Dall, 1889a, 1895a [LFK], 1903b; Lermond, 1936; Magnotte, 1970–1979; Turney & Perkins, 1972 [MFK]; Krisberg, 1993 [LFK]; Vittor & Associates, 1999b [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Tagelus plebeius (Lightfoot, 1786): Bartsch, 1937 [as *T. gibbus* (Spengler, 1794)]; Magnotte, 1970–1979; Mikkelsen & Bieler, 2000 [UFK].

Tagelus sp.: Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; USGS, 2003 [UFK, MFK; as *Tagelus* spp.].

Solemyidae

Solemya occidentalis Deshayes, 1857: Dall, 1889a, 1903b [as *Solenomya*]; Lermond, 1936; Lyons & Quinn, 1995; Vittor & Associates, 1997a [MFK, LFK], 1998 [LFK, DT]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Solemya velum Say, 1822.

Solemya sp.: Vittor & Associates, 1998 [DT].

Spondylidae

?Thiele, 1910 [DT; misidentified as *Pecten* (*Chlamys*) *pusio* Linnaeus, 1758, a recognized eastern Atlantic species of *Hinnites*; possibly a *Spondylus* sp.].

Spondylus americanus Hermann, 1781: Lermond, 1936 [also as *S. echinatus* Martyn, 1784]; M. Smith, 1937, 1945; C. N. Vilas & N. R. Vilas, 1945, 1970 [LFK]; Bender, 1968 [MFK]; Mason, 1969 [LFK]; Teskey, 1969 [LFK]; Work, 1969; Magnotte, 1970–1979; Artman, 1974 [LFK]; Colin, 1978; Sunderland, 1988 [UFK]; Williams, 1988; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; also as *S. gussoni* O. G. Costa, 1829, based on misidentified specimens].

Spondylus ictericus Reeve, 1856: Calkins, 1878 [DT; misidentified as *S. gaederopus* Linnaeus, 1758, a recognized Mediterranean species]; Simpson, 1887–1889 [misidentified as *S. croceus* "Chemnitz", err. pro Lamarck, 1819, a recognized Indo-Pacific species; and DT, misidentified as *S. spathuliferus* Lamarck, 1819, a recognized Indo-Pacific species]; Melvill, 1880 [LFK; as *S. ramosus* Reeve, 1856; Dall, 1889a [as *S. spathuliferus*]; Edwards, 1968a [LFK]; Work, 1969 [UFK, LFK]; Plockelman, 1970a; Goldberg, 1978c [LFK]; Magnotte, 1970–1979 [misidentified as *S. gussoni*]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Spondylus sp.: T. L. McGinty, 1939 [LFK], 1942; Jaap, 1984; Boone, 1986 [MFK].

Sportellidae

Basterotia elliptica (Récluz, 1850): Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000.

Basterotia quadrata (Hanley, 1843): Dall, 1889a, 1903b [as *B. quadrata* "Hinds"]; Lermond, 1936 [also as *B. q. granatina* (Dall, 1881)]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000.

Ensitellops protexta (Conrad, 1841): Lermond, 1936 [UFK; as *Egeta*].

Tellinidae

Brooks, 1968a [MFK; as tellins], b [MFK; as tellins]; Lee, 1969 [LFK]; Vittor & Associates, 1997a [UFK, MFK, LFK], 1997c [UFK], 1998 [LFK, DT], 1999a [LFK], b [UFK, MFK]; Brewster-Wingard et al., 2001 [UFK; as tellinid].

Acorylus gouldii (Hanley, 1846): Simpson, 1887–1889 [DT; as *Tellina*]; Dall, 1889a [as *Tellina*], 1903b [as *T. Gouldii*]; Lermond, 1936 [as *T. gouldi*]; Boss, 1966 [UFK, MFK, LFK, DT; as *Tellina* (*Acorylus*)]; Lyons & Quinn, 1995 [as *Tellina*]; Vittor & Associates, 1999b [UFK, MFK; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*].

Angulus agilis (Stimpson, 1857): Calkins, 1878 [as *Tellina tenera* Say, 1822]; Melvill, 1880 [LFK; as *T. tenera*]; Dall, 1886 [LFK; as *Tellina*], 1889a [as *Tellina*], 1903b [as *T. tenera*]; Lermond, 1936 [as *T. tenera*]; Mikkelsen & Bieler, 2000 [LFK; as *Tellina*].

Angulus merus (Say, 1834): Dall, 1883, 1885 [LFK; as *Tellina*], 1889a, 1903b [both as *Tellina*]; Simpson, 1887–1889 [LFK, DT; as *Tellina*]; Lermond, 1936 [as *Tellina*, also as *Macoma leptonoides*, err. pro *M. leptonoidea* Dall, 1895, a synonym of *Macoma carlottensis* Whiteaves, 1880, a recognized Californian species, superficially similar to *A. mera*]; Pulley, 1952 [MFK; as *Tellina*]; Boss, 1968b [UFK, MFK, LFK, DT; as *Tellina* (*Angulus*)]; Ross, 1969 [MFK; as *Tellina*]; Howard et al., 1970 [LFK; as *T.* cf. *mera*]; Magnotte, 1970–1979 [as *Tellina*]; Turney & Perkins, 1972 [UFK, MFK; as *Tellina*]; Lineback, 1977 [LFK; as *T.* cf. *mera*]; Petersen, 1989 [MFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Vittor & Associates, 1998 [LFK, DT; as *Tellina*], 1999b [LFK; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*]; Morton & Knapp, 2004 [UFK, MFK; as *Tellina*].

Angulus paramerus (Boss, 1964): Boss, 1964 [LFK, DT; as *Tellina* (*Angulus*)]; Ross, 1969 [MFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT; as *Tellina*].

Angulus probrinus (Boss, 1964): Boss, 1964 [MFK, LFK, DT; as *Tellina* (*Angulus*)]; Boss, 1968b [MFK, LFK, DT; as *Tellina* (*Angulus*)]; Lyons & Quinn, 1995 [as *T. probina* (*sic*)]; Mikkelsen & Bieler, 2000 [MFK, LFK, DT; as *Tellina*].

Angulus sybariticus (Dall, 1881): Boss, 1968b [UFK, LFK, DT; as *Tellina* (*Angulus*)]; Lyons & Quinn, 1995 [as *Tellina*]; Vittor & Associates, 1997c [UFK; as *Tellina*], 1998 [LFK, DT; as *Tellina*], 1999a [LFK, DT; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT; as *Tellina*].

Angulus tampaensis (Conrad, 1866): Henderson, 1913 [UFK]; Boss, 1968b [UFK, LFK; as *Tellina* (*Angulus*)]; Hudson et al., 1970 [UFK; as *Tellina*]; Magnotte, 1970–1979 [as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Lyons, 1998 [UFK, MFK; as *Tellina*];

Vittor & Associates, 1999b [UFK; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, LFK; as *Tellina*].

Angulus tenellus (A. E. Verrill, 1874): Dall, 1889a [as *Tellina modesta* A. E. Verrill, 1872, *non* Carpenter 1864]; Lermond, 1936 [as *T. modesta*]; Vittor & Associates, 1999b [MFK; as *Tellina*].

Angulus texanus (Dall, 1900): Lermond, 1936 [as *Tellina sayi* "Deshayes" Dall, 1900]; Boss, 1968b [UFK, MFK, LFK; as *Tellina* (*Angulus*)]; Turney & Perkins, 1972 [UFK, MFK; as *Tellina*]; Petersen, 1989 [MFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Vittor & Associates, 1998, 1999a [both DT, as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*].

Angulus versicolor ("Cozzens" DeKay, 1843): Lermond, 1936 [as *Tellina*]; Pulley, 1952 [MFK; as *Tellina*]; Boss, 1968b [UFK, MFK, LFK, DT; as *Tellina* (*Angulus*)]; Abbott, 1974 [LFK; as *Tellina* (*Angulus*)]; Lyons & Quinn, 1995 [as *Tellina*]; Vittor & Associates, 1998 [LFK; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*].

Arcopagia fausta (Pulteney, 1799): Melvill, 1880 [LFK; as *Tellina*, also as *Tellina robusta* Hanley, 1844, a recognized Indo-Pacific, possibly misidentified juvenile *T. fausta*; Simpson, 1887-1889 [LFK; as *Macoma fausta* "Dillwyn"]; Dall, 1889a, 1903b [as *Tellina*]; Lermond, 1936 [as *Tellina*]; M. Smith, 1937, 1945 [LFK; as *T.* (*Acropagia, Cyclotellina*)]; Eubanks, 1964; Bender, 1965 [MFK, LFK; as *Tellina*]; Boss, 1966 [UFK, MFK, LFK, DT; as *Tellina* (*Arcopagia*)]; Bender, 1968 [MFK, LFK]; Brooks, 1968a [MFK], b [MFK; as *Tellina*]; Ross, 1969 [MFK]; Work, 1969 [DT; as *Tellina*]; Woods, 1970 [LFK]; Turney & Perkins, 1972 [MFK]; Emerson & Jacobson, 1976 [as *Tellina*]; Goldberg, 1978c [LFK; as *Tellina*]; Antonius et al., 1978 [LFK]; Edwards, 1980 [LFK; as *Tellina*]; Wagner & Abbott, 1990 [as *Tellina*]; Krisberg, 1993 [LFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Tremor, 1998 [LFK; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*].

Cymatoica orientalis forma *hendersoni* Rehder, 1939: Rehder, 1939 [DT; as subspecies]; Mikkelsen & Bieler, 2000 [MFK, DT; as subspecies].

Elliptotellina americana (Dall, 1900): Boss, 1966 [LFK; as *Tellina* (*Elliptotellina*)]; Lyons & Quinn, 1995 [as *Tellina*]; Mikkelsen & Bieler, 2000 [LFK; as *Tellina*].

Eurytellina alternata (Say, 1822): Simpson, 1887–1889 [DT; as *Tellina tayloriana* G. B. Sowerby II, 1867]; Dall, 1889a [as *Tellina*], 1903b [as *Tellina*]; Bartsch, 1937 [as *Tellina*]; Lermond, 1936 [as *Tellina*]; Boss, 1968b [UFK, LFK, DT; as *Tellina* (*Eurytellina*)]; Magnotte, 1970–1979 [as *Tellina*]; Moore & Lopez, 1970 [as *Tellina*]; Turney & Perkins, 1972 [UFK, MFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*].

Eurytellina angulosa (Gmelin, 1791): Dall, 1889a [as *Tellina striata* "Hanley", err. pro Spengler, 1798, 1900c [as *T.* (*Eurytellina*)]; Johnson, 1934 [as *T.* (*Arcopagia, Eurytellina*)]; Lermond, 1936 [as *Tellina*; also as *T. striata*]; M. Smith, 1937, 1945 [as *T.* (*Acropagia* (*sic*), *Eurytellina*)]; Morris, 1951 [as *T. anguilosa* (*sic*)]; Abbott, 1954 [as *T.* (*Eurytellina*)]; Boss, 1968b [LFK; as *Tellina* (*Eurytellina*)]; Lyons & Quinn, 1995 [as *Tellina*]; Mikkelsen & Bieler, 2000 [LFK; as *Tellina*].

Eurytellina lineata (Turton, 1819): Calkins, 1878 [LFK; as *Tellina braziliana*, err. pro *brasiliana* Lamarck, 1819]; Melvill, 1880 [LFK; as *Tellina*]; Simpson, 1887–1889 [MFK, DT; also as *T. lineata* var. *albida* Hanley [date unknown]]; Dall, 1889a, 1903b [as *Tellina*]; Hudson et al., 1970 [UFK; as *Tellina*]; Lermond, 1936 [as *Tellina*]; Webb, 1951 [as *T. braziliana*, err. pro *brasiliana*]; Magnotte, 1970–1979 [as *Tellina*]; Kissling, 1977b [UFK; as *Tellina*]; Krisberg, 1993 [LFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, LFK; as *Tellina*].

Eurytellina nitens (C. B. Adams, 1845): Lermond, 1936 [as *Tellina georgiana* Dall, 1900]; Boss, 1968b [LFK; as *Tellina* (*Eurytellina*)]; Lyons & Quinn, 1995 [as *Tellina*]; Mikkelsen & Bieler, 2000 [LFK; as *Tellina*].

Eurytellina punicea (Born, 1778): Abbott, 1954 [as *Tellina* (*Eurytellina*)]; Warmke & Abbott, 1961 [as *Tellina*]; Humfrey, 1975 [as *Tellina*]; Mikkelsen & Bieler, 2000 [as *Tellina*].

Laciolina laevigata (Linnaeus, 1758): Webb, 1951 [as *Tellina*]; Boss, 1966 [UFK, LFK; as *Tellina* (*Laciolina*)]; Work, 1969 [as *Tellina*]; Magnotte, 1970–1979 [as *Tellina*]; Antonius et al., 1978 [LFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK; as *Tellina*].

Laciolina magna (Spengler, 1798): Melvill, 1880 [LFK; as *Tellina* (*Phylloda*) *sol* (Hanley, 1844)]; Dall, 1889a, 1903b [as *Tellina*]; Boss, 1966 [MFK, LFK, DT; as *Tellina* (*Laciolina*)]; Magnotte, 1970–1979 [as *Tellina*]; Wagner

& Abbott, 1990 [as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Hutsell et al., 1997 [as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*].

Leporimetis intastriata (Say, 1827): Simpson, 1887–1889 [LFK; as *Lutricola gruneri* (Philippi, 1845)]; Dall, 1889a [as *Lutricola interstriata* (*sic*)], 1900a [as *Metis*]; Lermond, 1936 [as *Apolymetis intasriata* (*sic*)]; Olsson & Harbison, 1952 [LFK; as *Hemimetis* (*Florimetis*)]; Wagner & Abbott, 1990 [as *Psammotreta*]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK].

Macoma brevifrons (Say, 1834): Dall, 1889a, 1903b; Lermond, 1936; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

|*Macoma calcarea* (Gmelin, 1791): Abbott, 1961 [LFK; in error].

Macoma cerina (C. B. Adams, 1845): Dall, 1889a, 1903b; Lermond, 1936; Pulley, 1952 [MFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Macoma constricta (Bruguière, 1792): Lermond, 1936; Webb, 1942, 1951 [LFK]; Mikkelsen & Bieler, 2000 [UFK].

Macoma extenuata Dall, 1900: Pulley, 1952 [MFK].

Macoma limula Dall, 1895: Lermond, 1936 [as *M. cimula* (*sic*)]; Pulley, 1952 [MFK].

Macoma mitchelli Dall, 1895: Mikkelsen & Bieler, 2000 [UFK].

Macoma pseudomera Dall & Simpson, 1901: Pulley, 1952 [MFK].

Macoma tageliformis Dall, 1900: Mikkelsen & Bieler, 2000 [LFK].

Macoma tenta (Say, 1834): Dall, 1889a [also as *M. t.* var. *Souleyetiana* Récluz, 1852], 1903b; Lermond, 1936 [also as *M. t. souleyetiana*]; Vittor & Associates, 1999a [DT]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT].

Macoma sp.: Dall, 1896a [LFK]; Vittor & Associates, 1998 [LFK, DT], 1999b [LFK].

Merisca aequistriata (Say, 1824): Lermond, 1936 [as *Tellina*; also as *T. lintea* Conrad, 1837]; Bartsch, 1937 [as *T. lintea*]; Pulley, 1952 [MFK; as *T. lintea*]; Boss, 1966 [UFK, LFK; as *Tellina* (*Merisca*)]; Lyons & Quinn, 1995 [as *Tellina*]; Vittor & Associates, 1998 [LFK, DT; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT; as *Tellina*].

Merisca cristallina (Spengler, 1798): Lermond, 1936 [as *Tellina crystallina* Wood, 1815]; Webb, 1951 [as *T. crystallina*].

Merisca martinicensis (Orbigny, 1842): Lermond, 1936 [LFK; as *Tellina*]; Boss, 1966 [LFK, DT; as *Tellina* (*Merisca*)]; Lyons & Quinn, 1995 [as *Tellina*]; Mikkelsen & Bieler, 2000 [LFK, DT; as *Tellina*].

|*Psammotreta intastriata* (Say, 1827) – see under *Leporimetis*.

Scissula candeana (Orbigny, 1842): Dall, 1900c [as *Tellina* (*Scissula*)]; Johnson, 1934 [as *T.* (*Angulus, Scissula*)]; Lermond, 1936 [as *Tellina*]; M. Smith, 1937, 1945 [as *T.* (*Angulus, Scissula*)]; Webb, 1942, 1951 [as *Tellina*]; Olsson & Harbison, 1952 [as *T.* (*Scissula*)]; Pulley, 1952 [MFK; as *Tellina*]; Abbott, 1954 [LFK; as *T.* (*Scissula*)], 1968 [LFK; as *Tellina*]; Boss, 1968b [MFK, LFK; as *Tellin* (*Scissula*)]; Howard et al., 1970 [LFK; as *Tellina*]; Lineback, 1977 [LFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Mikkelsen & Bieler, 2000 [MFK, LFK; as *Tellina*].

Scissula consobrina (Orbigny, 1842): Boss, 1968b [UFK, MFK, LFK, DT; as *Tellina* (*Scissula*)]; Lyons & Quinn, 1995 [as *T. consorbrina* (*sic*)]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*].

Scissula iris (Say, 1822): Calkins, 1878 [as *Tellina*]; Dall, 1900c [as *T.* (*Scissula*); also as *Tellina* (*Scissula*) *exilis* Lamarck, 1818, *non* Meuschen, 1787, nec Link, 1808] for which Boss (1968b) proposed *T.* (*S.*) *sandix* as a replacement name. *Scissula sandix* is Caribbean and South American in distribution and Floridian records were listed by Boss, who gave Jamaica as its northernmost record. Boss (1968b: 335) said *S. sandix* “has often been confused” and “is very closely allied” with *S. iris*]; Johnson, 1934 [as *T.* (*Angulus, Scissula*)]; Lermond, 1936 [as *Tellina*]; M. Smith, 1937, 1945 [as *T.* (*Angulus, Scissula*)]; Boss, 1968b [LFK, DT; as *Tellina* (*Scissula*)]; Vittor & Associates, 1998 [LFK, DT; as *Tellina*], 1999b [UFK, MFK, LFK; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*]; Morton & Knapp, 2004 [UFK, MFK; as *Tellina*].

Scissula similis (J. Sowerby, 1806): Calkins, 1878 [as *Tellina decora* Say, 1826]; Melvill, 1880 [LFK; as *Tellina*]; Simpson, 1887–1889 [MFK, LFK; as *T. decora* and *T. decora* white var.]; Dall, 1889a, 1903b [as *T. decora*]; Lermond, 1936 [as *T. decora*]; Olsson & Harbison, 1952 [as *T.* (*Scissula*)]; Boss, 1968b [UFK, MFK, LFK, DT; as *Tellina* (*Scissula*)]; Brooks, 1968a, b [MFK; as *Tellina*]; Ross, 1969 [MFK; as *Tellina*], 1971 [LFK; as *Tellina*]; Hudson et al., 1970 [UFK; as *Tellina*]; Magnotte, 1970–1979 [as *Tellina*]; Turney & Perkins, 1972 [UFK, MFK; as *Tellina*]; Clampit, 1987 [LFK; as “some small rose-striped tellin-like shells"]; Haviland, 1994 [LFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Vittor & Associates, 1997c [UFK; as *Tellina*], 1998 [LFK, DT; as *Tellina*], 1999b [LFK; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*]; Morton & Knapp, 2004 [UFK, MFK; as *Tellina*].

Strigilla carnaria (Linnaeus, 1758): Melvill, 1880 [LFK]; Dall, 1889a, 1900c [as *S. rombergii* Mörch, 1853]; 1903b; Lermond, 1936 [also as *S. rombergii*]; Boss, 1969 [LFK]; Magnotte, 1970–1979 [as *S. romgergi* (*sic*)]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [LFK].

Strigilla gabbi Olsson & McGinty, 1958: Boss, 1969 [LFK]; Abbott, 1974 [LFK; as *S.* (*Strigilla*)]; Odé, 1975 [LFK]; Rios, 1994 [LFK; as *S.* (*Strigilla*)]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [LFK].

Strigilla mirabilis (Philippi, 1841): Calkins, 1878 [DT; as *S. flexuosa* (Say, 1822), *non* Montagu, 1803]; Dall, 1889a, 1903b [as *S. flexuosa*]; Lermond, 1936 [as *S. flexuosa*]; Bartsch, 1937 [as *S. flexuosa*]; M. Smith, 1937 [LFK; as *S. flexuosa*]; Boss, 1969 [MFK, LFK]; Turney & Perkins, 1972 [UFK]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Strigilla pisiformis (Linnaeus, 1758): Simpson, 1887–1889 [LFK, DT; as *S. pisum* (*sic*)]; Calkins, 1878; Melvill, 1880 [LFK]; Dall, 1889a, 1903b [LFK], 1900c; Johnson, 1934; Lermond, 1936; M. Smith, 1937, 1945; Webb, 1942, 1951; Abbott, 1954, 1968; Warmke & Abbott, 1961; Mikkelsen & Bieler, 2000 [LFK].

Tellidora cristata (Récluz, 1842): Dall, 1889a, 1903b; Boss, 1968b [UFK]; Lermond, 1936; Magnotte, 1970–1979; Turney & Perkins, 1972 [MFK]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK]; Mikkelsen & Bieler, 2000 [UFK, LFK].

|*Tellina aequistriata* (Say, 1824) – see under *Merisca*.

|*Tellina agilis* (Stimpson, 1857) – see under *Angulus*.

|*Tellina alternata* (Say, 1822) – see under *Eurytellina*.

|*Tellina americana* (Dall, 1900) – see under *Elliptotellina*.

|*Tellina angulosa* (Gmelin, 1791) – see under *Eurytellina*.

|*Tellina candeana* (Orbigny, 1842) – see under *Scissula*.

|*Tellina consobrina* (Orbigny, 1842) – see under *Scissula*.

|*Tellina cristallina* (Spengler, 1798) – see under *Merisca*.

|*Tellina fausta* (Pulteney, 1799) – see under *Arcopagia*.

|*Tellina gouldii* (Hanley in G. B. Sowerby I, 1846) – see under *Acorylus*.

|*Tellina iris* (Say, 1822) – see under *Scissula*.

|*Tellina laevigata* (Linnaeus, 1758) – see under *Laciolina*.

|*Tellina lineata* (Turton, 1819) – see under *Eurytellina*.

|*Tellina listeri* (Röding, 1798) – see under *Tellinella*.

|*Tellina magna* (Spengler, 1798) – see under *Laciolina*.

|*Tellina martinicensis* (Orbigny, 1842) – see under *Merisca*.

|*Tellina mera* (Say, 1834) – see under *Angulus*.

|*Tellina nitens* (C. B. Adams, 1845) – see under *Eurytellina*.

|*Tellina paramera* (Boss, 1964) – see under *Angulus*.

Tellina persica Dall & Simpson, 1901: Mikkelsen & Bieler, 2000 [LFK].

|*Tellina probrina* (Boss, 1964) – see under *Angulus*.

|*Tellina punicea* (Born, 1778) – see under *Eurytellina*.

Tellina radiata Linnaeus, 1758: Calkins, 1878 [DT]; Melvill, 1880 [LFK; also *T. r.* var. *unimaculata* Lamarck, 1818]; Simpson, 1887–1889 [DT; as *T. radiata* var.]; Dall, 1889a, 1903b; Aldrich & Snyder, 1936 [LFK]; Lermond, 1936; C. N. Vilas & N. R. Vilas, 1945, 1970 [also as *T. r.* var. *unimaculata*; Boss, 1966 [UFK, MFK, LFK, DT; as *T.* (*Tellina*)]; Burggraf, 1969 [LFK]; Work, 1969 [UFK, DT]; Magnotte, 1970–1979; Moore & López, 1970; Gaertner, 1978 [LFK; as sunrise clams]; Edwards, 1980 [LFK]; Wagner & Abbott, 1990 [as *T. radiata* and *T. r. unimaculata*]; Krisberg, 1993 [LFK]; Haviland, 1994 [LFK]; Lyons & Quinn, 1995; Tremor, 1998 [LFK; as *radiala* (*sic*)]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

|*Tellina sandix* (Boss, 1968) – see under *Scissula iris*.

|*Tellina similis* (J. Sowerby, 1806) – see under *Scissula*.

Tellina squamifera Deshayes, 1855: Dall, 1889a, 1903b; Lermond, 1936; Pulley, 1952 [MFK]; Boss, 1967 [as *T.* (*Phyllodina*)]; Boss, 1966 [UFK, MFK, LFK, DT; as *T.* (*Phyllodina*)]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

|*Tellina sybaritica* (Dall, 1881) – see under *Angulus*.

|*Tellina tampaensis* (Conrad, 1866) – see under *Angulus*.

|*Tellina tenella* (A. E. Verrill, 1874) – see under *Angulus*.

|*Tellina texana* (Dall, 1900) – see under *Angulus*.

|*Tellina versicolor* ("Cozzens" DeKay, 1843) – see under *Angulus*.

Tellina (s. l.) sp.: Dall, 1889a [LFK], 1895a [LFK], 1903b [LFK]; Simpson, 1897 [LFK; as "bright Tellinas"]; Plockelman, 1968d; Ross, 1971 [UFK]; Schomer & Drew, 1982; Theroux & Wigley, 1983 [MFK, LFK]; Wingard et al., 1995 [UFK; as *T.* spp.]; Brewster-Wingard et al., 1996, 1997, 2001 [all UFK; as *T.* spp.]; Vittor & Associates, 1997b [LFK], 1997c [UFK], 1998 [LFK, DT], 1999a [UFK, LFK, DT], b [UFK, MFK, LFK]; Dent, 1998; USGS, 2003 [UFK, MFK; as *Tellina* sp. or spp.].

Tellinella listeri (Röding, 1798): Melvill, 1880 [LFK; as *Tellina interrupta* Wood, 1815]; Simpson, 1887–1889 [LFK, DT; as *T. interrupta*]; Dall, 1889a, 1903b [as *T. interrupta*]; Lermond, 1936 [as *T. interrupta*]; Boss, 1966 [UFK, MFK, LFK, DT; as *Tellina* (*Tellinella*)]; Work, 1969 [LFK; as *Tellina*]; Magnotte, 1970–1979 [as *Tellina*]; Voss, 1983 [UFK; as *Tellina*]; Voss et al., 1983 [UFK; as *Tellina*]; Wagner & Abbott, 1990 [as *Tellina*]; Krisberg, 1993 [LFK; as *Tellina*]; Lyons & Quinn, 1995 [as *Tellina*]; Vittor & Associates, 1998 [LFK; as *Tellina*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Tellina*].

Teredinidae

Stevenson, 1970, 1993 [both as shipworm].

Bankia carinata (Gray, 1827): Mikkelsen & Bieler, 2000 [MFK].

Bankia fimbriatula (Moll & Roch, 1931): Calkins, 1878 [LFK; as *Xylotrya fimbiata*, err. pro *X. fimbriata* (Jeffreys, 1860)]; Dall, 1889a [as *X. fimbriata*]; Lermond, 1936 [as *X. fimbriata*].

Lyrodus pedicellatus (de Quatrefages, 1849): Pulley, 1952 [LFK; as *L. pedicellata*].

Nototeredo knoxi (Bartsch, 1917): Mikkelsen & Bieler, 2000 [UFK].

Teredo bartschi Clapp, 1923: Pulley, 1952.

Teredo clappi Bartsch, 1923: Bartsch, 1923 [LFK; as *T.* (*Zopoteredo*)]; Johnson, 1934 [LFK; as *T.* (*Zopoteredo*)]; Lermond, 1936 [LFK]; Aguayo & Jaume, 1950g [LFK]; Turner, 1966 [LFK; as *T.* (*Zopoteredo*)]; Mikkelsen & Bieler, 2000 [UFK, LFK].

Teredora malleolus (Turton, 1822): Dall, 1889a [as *Teredo Thomsoni* Tryon, 1863]; Lermond, 1936 [as *T. thomsoni*].

Thraciidae

Vittor & Associates, 1998 [LFK, DT], 1999a [DT].

Asthenothaerus hemphillii Dall, 1886: Dall, 1889a, 1903b; Lermond, 1936 [as *A. hemphilli*]; Rehder, 1943a, b [LFK; as *A. balesi* Rehder, 1943]; Aguayo & Jaume, 1947a [LFK; as *A.* (*Asthenothaerus*) *balesi*]; Abbott, 1974 [LFK; as *A. balesi*]; Lyons & Quinn, 1995 [as *A. balesi*]; Vittor & Associates, 1998 [LFK, DT], 1999a [UFK, LFK, DT], b [MFK, LFK] [all as *A. hemphilli*]; Sweeney & Harasewych, 1999 [LFK; as *A. balesi*]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT; as *A. hemphilli* and *A. balesi*].

Asthenothaerus sp.: Vittor & Associates, 1999b [LFK].

Bushia elegans (Dall, 1886): Dall, 1889a [as *Asthenothaerus* (*Bushia*)]; Vittor & Associates, 1999b [UFK].

Bushia sp.: Vittor & Associates, 1998 [DT].

Thracia distorta (Montagu, 1803): Simpson, 1887–1889 [MFK; as *T. rugosa* Lamarck, 1818].

Thracia morrisoni Petit, 1964: Dall, 1886 [LFK; misidentified as *Thracia corbuloides* (*sic,* err. pro *corbuloidea*) Blainville, 1827, a recognized Mediterranean species], 1889a [LFK; as *T. corbuloidea*], 1903b [LFK; as *T. corbuloidea*]; Johnson 1934 [as *T. corbuloides* (*sic*)]; Lermond, 1936 [as *T. corbuloides* (*sic*)]; Abbott, 1974 [as *T. corbuloides* (*sic*)]; Mikkelsen & Bieler, 2000 [LFK; as *T. corbuloides* (*sic*)].

"*Thracia phaseolina* Lamarck, 1822" [a European species; western Atlantic specimens appear to represent a new species (Coan, 1990)]: Dall, 1889a, 1903b; Mikkelsen & Bieler, 2000.

Thracia stimpsoni Dall, 1886: Dall, 1889a, 1903b [DT]; Maury, 1920 [DT]; Johnson, 1934 [DT]; Aguayo & Jaume, 1950e [DT]; Boss et al., 1968 [DT]; Vittor & Associates, 1998 [LFK]; Mikkelsen & Bieler, 2000 [LFK, DT].

Thyasiridae

Thyasira grandis (A. E. Verrill & Smith, in: A. E. Verrill, 1885): Dall, 1889a [as *Cryptodon pyriformis* Dall, 1886, and misidentified as *C. obesus* A. E. Verrill, 1872 (fide Maury, 1920)].

Thyasira trisinuata (Orbigny, 1842): Mikkelsen & Bieler, 2000 [DT].

Trapezidae

Coralliophaga coralliophaga (Gmelin, 1791): Simpson, 1887–1889 [DT; as *Cypricardia*]; Lermond, 1936; Bales, 1944; Pulley, 1952; Solem, 1955 [LFK, DT]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [MFK, LFK, DT].

Ungulinidae

Vittor & Associates, 1998 [LFK].

Diplodonta notata Dall & Simpson, 1901: Lermond, 1936 [LFK; as *Taras*].

Diplodonta nucleiformis Wagner, 1838: Lermond, 1936 [as *Taras*].

|*Diplodonta pilula* Dall, 1881 – all records based on *Blake* sta. 43 (here excluded; see entry for Dall, 1881).

Diplodonta punctata (Say, 1822): Dall, 1889a [as *Diplodonta subglobosa* (C. B. Adams, 1852)]; Lermond, 1936 [as *Taras*]; Magnotte, 1970–1979; Turney & Perkins, 1972 [UFK, MFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK]; Lyons & Quinn, 1995; Vittor & Associates, 1999b [UFK, MFK, LFK]; Mikkelsen & Bieler, 2000 [MFK, LFK, DT].

Diplodonta sp.: Vittor & Associates, 1998 [LFK, DT], 1999b [UFK, MFK, LFK]; USGS, 2003 [MFK; as *Diplodonta* spp.].

Felaniella candeana (Orbigny, 1842): Simpson, 1887–1889 [DT; as *Diplodonta*].

Phlyctiderma semiaspera (Philippi, 1836): Simpson, 1887–1889 [DT; as *Diplodonta*]; Dall, 1889a, 1903b [both as *Diplodonta*]; Lyons & Quinn, 1995 [as *Diplodonta*]; Vittor & Associates, 1997c [UFK], 1997b [LFK], 1998 [LFK, DT] [all as *Diplodonta*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Diplodonta*].

Phlyctiderma soror (C. B. Adams, 1852): Simpson, 1887–1889 [DT; as *Diplodonta*]; Dall, 1889a [DT; as *Diplodonta*], 1899a [as *Diplodonta* (*Phlyctiderma*)]; Lermond, 1936 [as *Taras*].

Veneridae

Dall, 1889a [as *Cytherea* sp.; also as *Venus Lamarckii* Gray, 1838, synonym of *Antigona lamellaris* Schumacher, 1817, a recognized Indo-Pacific species, similar to several *Chione* s.l. spp. (so cannot be assigned to a recognized Florida Keys species)], 1896a [LFK; as *Venus* sp.]; Rogers, 1941 [UFK; as Venus clam]; Vittor & Associates, 1997c [UFK], 1998 [LFK, DT], 1999a [LFK], b [UFK, MFK].

Anomalocardia auberiana (Orbigny, 1842): Melvill, 1880 [LFK; misidentified as *Anomalocardia impressa* (Anton, 1837), synonym of *A. producta* Kuroda & Habe, 1951, a recognized Chinese/Japanese species]; Dall, 1883, 1885 [both LFK; as *A. flexuosa* (Linnaeus, 1767), a recognized Caribbean/South American species, probably misidentified *A. auberiana*], 1889a [as *Venus* (*Anomalocardia*) *rostrata* G. B. Sowerby II, 1853]; Lermond, 1936 [misidentified as *Animalocardia* (*sic*) *brasiliana*, err. pro *A. brasiliana* (Gmelin, 1791), a recognized species of the Caribbean, Central and South America, and as *A. cuneimeris* (Conrad, 1846)]; Lee, 1969 [LFK; as *A. brasiliensis* (*sic*)]; Ross, 1969 [MFK; as *A. cuneimeris*]; Howard et al., 1970 [LFK; as *A. cuneimeris*]; Hudson et al., 1970 [UFK; as *A. cuneimeris*]; Magnotte, 1970–1979 [as *A. cuneimeris*]; Turney & Perkins, 1972 [UFK, MFK; also as *A. cuneimeris*]; Lineback, 1977 [LFK; as *A. cuneimeris*]; Schomer & Drew, 1982 [as *A. cuneiveis* (*sic*)]; Petersen, 1989 [MFK]; Lyons & Quinn, 1995; Wingard et al., 1995 [UFK; as *A. cuneimeris*]; Brewster-Wingard et al., 1996, 1997, 1998 [all as *A.* sp.], 2001 [all UFK]; Lyons, 1998 [UFK, MFK]; Vittor & Associates, 1998 [LFK]; Brewster-Wingard & Ishman, 1999 [UFK; as *A.* sp.]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK, MFK].

Callista eucymata (Dall, 1890): Lermond, 1936 [as *Pitar encymata* (*sic*)]; Palmer, 1947 [UFK, MFK, LFK; as *Costacallista*]; Pulley, 1952 [UFK; as *Costacallista*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

|*Chione cancellata* (Linnaeus, 1767) – see *C. elevata*.

|*Chione clenchi* Pulley, 1952 – see under *Lirophora*.

Chione elevata (Say, 1822): Melvill, 1880 [LFK; as *C. cancellata* (Linnaeus, 1767)]; Dall, 1886 [Gordon Key; as *C. cancellata*], 1889a [as *Venus cancellata*; also LFK, as *V. Beaui* Récluz, 1852; also DT, misidentified as *V. granulata* Gmelin, 1791, a recognized Caribbean species of *Protothaca*], 1896a [LFK, DT; as *V.* (*C.*) *cancellata*], 1902b [misidentified as *C.* (*C.*) *subrostrata* (Lamarck, 1818), a recognized Brazilian species], 1903b [as *V. cancellata*; also DT, as *V. granulata*]; Simpson, 1887–1889 [DT, as *V. beaui*; also DT, as *V. granulata*]; Nutting, 1895 [LFK, DT; as *C. cigenda* (Dillwyn, 1817)]; Johnson, 1934 [as *C.* (*Timoclea*) *granulata*]; Lermond, 1936 [as *V.* (*C.*)

cancellatus, *V.* (*C.*) *subrostrata*, and *V.* (*C.*) *granulatus*]; M. Smith, 1937, 1945 [as *C.* (*Timoclea*) *granulata*]; Bippus, 1950 [UFK; as *C. cancellata*]; Iversen & Roessler, 1969 [UFK; as *C. cancellata*]; Jindrich, 1969 [LFK; as *C. cancellata*]; Ross, 1969 [MFK; as *C. cancellata*]; Howard et al., 1970 [LFK; as *C. cancellata*]; Hudson et al., 1970 [UFK; as *C. cancellata*]; Magnotte, 1970–1979 [as *C. cancellata*]; Turney & Perkins, 1972 [UFK, MFK; as *C. cancellata*]; Godcharles & Jaap, 1973 [UFK; as *C. cancellata*]; Zischke, 1973, 1977a, b, c [MFK; as *C. cancellata*]; Lineback, 1977 [LFK; as *C. cancellata*]; Schomer & Drew, 1982 [as as *C. cancellata*]; Voss, 1983 [UFK; as *C. cancellata*]; Voss et al., 1983 [UFK; as *C. cancellata*]; Petersen, 1989 [MFK; as *C. cancellata*]; Krisberg, 1993 [LFK; as *C. cancellata*]; Lyons & Quinn, 1995 [as *C. cancellata*]; Wingard et al., 1995 [UFK; as *C. cancellata*]; Brewster-Wingard et al., 1996, 1997, 1998 [all UFK; as *C. cancellata*]; Vittor & Associates, 1997c [UFK; as *C. cancellata*], 1998 [LFK, DT; as *C. cancellata*], 1999b [UFK, MFK, LFK; as *C. cancellata*]; Lyons, 1998 [UFK, MFK; as *C. cancellata*]; Brewster-Wingard & Ishman, 1999, 2001 [UFK; as *C. cancellata*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT, as *C. cancellata*; also as *Protothaca granulata*]; Roopnarine & Vermeij, 2000 [UFK]; USGS, 2003 [UFK, MFK; as *C. cancellata*]; Morton & Knapp, 2004 [UFK, MFK].

|*Chione grus* (Holmes, 1858) – see under *Timoclea*.

|*Chione intapurpurea* (Conrad, 1849) – see under *Puberella*.

|*Chione latilirata* (Conrad, 1841) – see under *Lirophora*.

Chione mazyckii Dall, 1902: Lermond, 1936 [as *Venus* (*Chione*)]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

|*Chione paphia* (Linnaeus, 1767) – see under *Lirophora*.

|*Chione pubera* (Bory Saint-Vincent, 1827) – see under *Puberella*.

|*Chione pygmaea* (Lamarck, 1818) – see under *Timoclea*.

Chione (s. l.) sp.: Vittor & Associates, 1998 [LFK, DT], 1999b [LFK].

Circomphalus strigillinus (Dall, 1902): Dall, 1902, 1903b [LFK; as *Cytherea* (*Ventricola*) *strigillina*]; Johnson, 1934 [as *Antigona* (*Circomphalus, Ventricola*)]; Lermond, 1936 [as *Antigona strigillina*]; Aguayo & Jaume, 1949e; P. L. McGinty & T. L. McGinty, 1957 [MFK, LFK; as *Antigona strigillina*]; Boss et al., 1968 [LFK; as *Cytherea* (*Ventricola*) *strigillina*]; Mikkelsen & Bieler, 2000 [MFK, LFK, DT].

Cyclinella tenuis (Récluz, 1852): Dall, 1889a, 1903b [as *Lucinopsis*]; Lermond, 1936; Boss & Wass, 1970 [MFK, LFK, DT]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Dosinia discus (Reeve, 1850): Lermond, 1936; Bartsch, 1937; Webb, 1937, 1942, 1951; Rogers, 1941 [UFK; as discus clam]; Magnotte, 1970–1979; Vittor & Associates, 1998 [DT], 1999a [LFK, DT], b [MFK]; Mikkelsen & Bieler, 2000 [MFK, LFK, DT].

Dosinia elegans (Conrad, 1846): Dall, 1889a, 1903b, 1902a, b [DT; as *Dosinia* (*Dosinidia*) and misidentified as *D.* (*Dosinidia*) *concentrica* (Born, 1780), a recognized Caribbean to South American species “not found in Florida” (Abbott, 1974: 533)]; Conrad, 1866 [as *D. floridana* Conrad, 1866]; Johnson 1934 [as *D. concentrica*]; Lermond, 1936 [also as *Dosinia concentrica*]; Bartsch, 1937; M. Smith, 1937, 1945 [as *D. concentrica*]; Clench, 1942a [as *D. floridana*]; Magnotte, 1970–1979; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Gemma gemma (Totten, 1834): Lermond, 1936 [as *Gemma purpurea* (H. C. Lea, 1842)].

Globivenus rigida (Dillwyn, 1817): Dall, 1889a [as *Venus rugosa* Gmelin, 1791, *non* Linnaeus, 1758], 1902b [as *Cytherea* (*Ventricola*)]; Johnson, 1934 [as *Antigona* (*Circomphalus, Ventricola*)]; Lermond, 1936 [as *Antigona*]; Abbott, 1974; Humfrey, 1975 [as *Antigona* (*Ventricolaria*)]; Odé, 1976a; Warmke & Abbott, 1961 [as *Antigona*]; Díaz Merlano & Puyana Hegedus, 1994 [as *Ventricolaria*]; Rios, 1994 [as *Ventricolaria* (*Ventricolaria*)]; Lyons & Quinn, 1995 [as *Ventricolaria*]; Mikkelsen & Bieler, 2000 [DT].

Globivenus rugatina (Heilprin, 1886): Dall, 1889a, 1903a [as *Cytherea* (*Cytherea*, section *Ventricola*)], 1903b [as *Venus rugosa* var. *rugatina*]; Goldberg, 1978c [LFK]; Mikkelsen & Bieler, 2000 [LFK, DT].

Globivenus sp.: Dall, 1889a [misidentified as *Venus pilula* Reeve, 1863, a recognized Okinawan species of *Globivenus*, similar to *G. rigida/rugatina*].

Gouldia cerina (C. B. Adams, 1845): Dall, 1889a, 1903b [as *Circe* (*Gouldia*)]; Lermond, 1936 [also as *Circe*]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK, DT], 1999a [LFK], b [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Lirophora clenchi (Pulley, 1952).

Lirophora latilirata (Conrad, 1841): Lermond, 1936 [as *Venus* (*Chione*) *latiliratus*]; Webb, 1942, 1951 [as *Chione*]; Siekman, 1965 [as *Chione*]; Lyons & Quinn, 1995 [as *Chione*]; Mikkelsen & Bieler, 2000 [LFK, DT].

Lirophora paphia (Linnaeus, 1767): Simpson, 1887–1889 [as *Chione*]; Lermond, 1936 [as *Venus* (*Chione*)]; Webb, 1942, 1951[as *Chione*]; Abbott, 1954 [LFK; as *Chione* (*Lirophora*)]; Warmke & Abbott, 1961 [LFK; as *Chione*]; Barrett & Patterson, 1967 [LFK; as *Chione*]; Magnotte, 1970–1979 [as *Chione*]; Humfrey, 1975 [LFK; as *Chione*]; Voss, 1983 [UFK; as *Chione*]; Voss et al., 1983 [UFK; as *Chione*]; Sutty, 1990 [LFK; as *Chione*]; Mikkelsen & Bieler, 2000 [LFK, DT; as *Chione*].

Macrocallista maculata (Linnaeus, 1758): Dall, 1889a, 1903b [as *Cytherea* (*Callista*)], 1902b [as *M.* (*Chionella*)]; Lermond, 1936; Magnotte, 1970–1979; Lyons & Quinn, 1995; Vittor & Associates, 1998 [DT], 1999a [DT]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT].

Macrocallista nimbosa (Lightfoot, 1786): Melvill, 1880 [LFK; as *Callista* (*Dione*) *gigantea* "(Chemnitz)" (Gmelin, 1790)]; Dall, 1889a [as *Cytherea* (*Callista*) *gigantea*], 1903a; Lermond, 1936 [as *M.* (*Callista*) *gigantea*]; Abbott, 1961 [LFK], 1970 [LFK]; Vittor & Associates, 1999a [DT]; Mikkelsen & Bieler, 2000 [UFK, LFK, DT].

Mercenaria campechiensis (Gmelin, 1791): Simpson, 1887–1889 [as *Venus mortoni* Conrad, 1837]; Dall, 1889a [as *V. mercenaria* var. *Mortoni*]; Lermond, 1936 [as *Venus*]; Magnotte, 1970–1979; Wagner & Abbott, 1990; Hutsell et al., 1997; Mikkelsen & Bieler, 2000 [LFK].

Mercenaria mercenaria (Linnaeus, 1758): Dall, 1889a [as *Venus*], 1903b [as *Venus* and as *V. m.* var. *notata* (Say, 1822)], 1902b [as *Venus*]; Lermond, 1936 [as *Venus*]; Mikkelsen & Bieler, 2000 [MFK; as *M. m.* forma *notata*].

Mercenaria sp.: USGS, 2003 [MFK; as *Mercenaria* spp.].

Parastarte triquetra (Conrad, 1846): Dall, 1902b, 1903a; M. Smith, 1937, 1945; Howard et al., 1970 [LFK]; Turney & Perkins, 1972 [UFK, MFK; also as *Parastarte* sp.]; Lineback, 1977 [LFK]; Wingard et al., 1995 [UFK]; Brewster-Wingard et al., 1996, 2001 [UFK]; Brewster-Wingard & Ishman, 1999 [UFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; USGS, 2003 [UFK].

Periglypta listeri (Gray, 1838): Simpson, 1887–1889 [LFK; as *Venus*]; Dall, 1889a, [misidentified as *Venus crispata* Deshayes, 1853, an Indo-Pacific form of unresolved status in *Periglypta*], 1902b [as *Cytherea* (*Cytherea*)]; Palmer, 1927–1929 [as *Antigona* (*Dosina*)]; Lermond, 1936 [as *Antigona*]; M. Smith, 1937 [LFK; as *Antigona*]; Pulley, 1952 [LFK; as *Antigona*]; Abbott, 1961, 1970 [both as *Antigona*]; Brooks, 1968a [MFK; as *Antigona*]; Ross, 1969 [MFK; as *Antigona*]; Magnotte, 1970–1979 [as *Antigona*]; Woods, 1970 [LFK; as *Antigona*]; Godcharles & Jaap, 1973 [UFK; as *Antigona*]; Zischke, 1973, 1977a, c [MFK; as *Antigona*]; Theroux & Wigley, 1983 [MFK]; Tremor, 1998 [LFK]; Edwards, 1980 [LFK]; Voss, 1983 [UFK]; Voss et al., 1983 [UFK; also as *Periglyphus* (*sic*)]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT]; Bieler et al., 2004 [UFK, MFK, LFK, DT].

Pitar albidus (Gmelin, 1791): Dall, 1889a [as *Cytherea albida*], 1896a [DT; as *C. albida*]; Lermond, 1936 [as *Cytherea*].

Pitar circinatus (Born, 1778): Simpson, 1887–1889 [DT; as *Cytherea circinata*].

Pitar cordatus (Schwengel, 1951): Schwengel, 1951 [DT; as *Pitaria cordata*]; Rehder & Abbott, 1951 [DT; as *P.* (*Pitarenus*) *cordata*], 1954 [as *P.* (*Pitarenus*) *cordata*], 1974 [as *P.* (*Pitarenus*)]; Morris, 1973 [LFK; as *Pitar cordata*]; Abbott & Morris, 1995 [LFK]; Odé, 1976b; Rios, 1994 [as *P.* (*Pitarenus*)]; Mikkelsen & Bieler, 2000 [LFK, DT].

Pitar dione (Linnaeus, 1758): Calkins, 1878 [DT; as *Cytherea dione*]; Simpson, 1887–1889 [DT; as *Cytherea*]; Dall, 1889a, 1903b [as *C.* (*Dione*) *Dione*]; Lermond, 1936 [as *C.* (*D.*)].

Pitar fulminatus (Menke, 1828): Simpson, 1887–1889 [DT; as *Cytherea hebraea* Lamarck, 1818]; Dall, 1886 [Gordon Key; as *C.* (*Dione*) *hebraea*], 1889a [as *C. hebraea*], 1903b [as *C. hebraea*]; Lermond, 1936 [also as *C. hebraea*]; Webb, 1937, 1939 [both as *C. hebraea*], 1942, 1951 [both as *P. fulminata* and *C. hebraea*]; Howard et al., 1970 [LFK; as *P.* cf. *fulminata*]; Magnotte, 1970–1979; Turney & Perkins, 1972 [UFK, MFK; as *P. fulminata*]; Lineback, 1977 [LFK; as *P.* cf. *fulminata*]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [DT], 1999b [UFK, LFK]; Mikkelsen & Bieler, 2000 [LFK, DT].

Pitar simpsoni (Dall, 1895): Dall, 1889a [as *Cytherea Simpsoni*]; Lermond, 1936 [as *Cytherea*]; Lyons & Quinn, 1995; Wingard et al., 1995 [UFK; as *P.* sp.]; Vittor & Associates, 1998 [LFK, DT], 1999a [UFK, LFK, DT], b [UFK, MFK, LFK]; Mikkelsen & Bieler, 2000

[UFK, MFK, LFK, DT]; Brewster-Wingard et al., 2001 [UFK]; USGS, 2003 [UFK, MFK]; Morton & Knapp, 2004 [UFK, MFK].

Pitar sp.: Theroux & Wigley, 1983 [MFK, LFK]; Vittor & Associates, 1997c [UFK], 1998 [LFK, DT], 1999a [LFK], b [UFK].

Puberella intapurpurea (Conrad, 1849): Dall, 1902b [as *Chione* (*Chione*)]; M. Smith, 1937, 1945 [as *Chione*]; Godcharles & Jaap, 1973 [UFK; as *Chione*]; Antonius et al., 1978 [LFK; as *Chione*]; Lyons & Quinn, 1995 [as *Chione*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Puberella pubera (Bory Saint-Vincent, 1827): Johnson, 1934 [as Valenciennes, 1827]; Lermond, 1936 [as *Venus* (*Chione*)]; M. Smith, 1937, 1945 [as *Chione*]; Abbott, 1974 [as *Chione* (*Chione*)]; Lyons & Quinn, 1995 [as *Chione puber*]; Mikkelsen & Bieler, 2000.

Timoclea grus (Holmes, 1858): Henderson, 1913 [UFK; as *Chione*]; Lermond, 1936 [as *Venus* (*Chione*)]; Abbott, 1954 [LFK; as *Chione* (*Tellina*)]; Magnotte, 1970–1979 [as *Chione*]; Andrews, 1971 [LFK; as *Chione*], 1977, 1981a, b, 1992, 1994 [LFK; as *Chione* (*Timoclea*)]; Emerson & Jacobson, 1976 [LFK; as *Chione*]; Vittor & Associates, 1998 [LFK, DT; as *Chione*], Vittor & Associates, 1999a [DT; as *Chione*], b [LFK; as *Chione*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Timoclea pygmaea (Lamarck, 1818): Simpson, 1887–1889 [DT; as *Venus*, also as *V. pygmaea* var. *inaequivalvia* Orbigny, 1846]; Dall, 1889a, 1903b [as *Venus*], 1902b [as *Chione* (*Timoclea*)]; Johnson, 1934 [as *Chione* (*Timoclea*)]; Lermond, 1936 [as *Venus* (*Chione*) *pygmaeus*]; M. Smith, 1937, 1945 [as *Chione* (*Timoclea*)]; Plockelman, 1968a, b [both as *Chione*]; Turney & Perkins, 1972 [UFK, MFK; as *Chione*]; Lyons & Quinn, 1995 [as *Chione*]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT].

Tivela abaconis Dall, 1902.

Tivela floridana Rehder, 1939: Mikkelsen & Bieler, 2000 [UFK].

Tivela mactroides Born, 1778: Dall, 1889a [as *Cytherea* (*T.*)]; Johnson, 1934; Lermond, 1936 [as *C.* (*T.*) *mactroides* and *T. mactroides*]; M. Smith, 1937, 1940, 1945; Aguayo & Jaume, 1948c; Barrett & Patterson, 1967.

Tivela trigonella (Lamarck, 1818): Simpson, 1887–1889 [DT; as *C.* (*Trigona*) *incerta* "Römer" err. pro G. B. Sowerby II, 1851].

Transennella conradina (Dall, 1884): Simpson, 1887–1889 [MFK; as *Cytherea*]; Dall, 1889a, 1903b [LFK; as *Cytherea* (*T.*) *Conradina*]; 1902a [LFK; as *Meretrix* (*T.*)]; Lermond, 1936 [as *C.* (*T.*) *conradiana* (*sic*) and *Transenella* (*sic*) *conradina*]; M. Smith, 1937, 1945; Webb, 1937, 1939, 1942, 1951 [all as *Transenella* (*sic*)]; Vittor & Associates, 1997c [UFK]; Johnson, 1934 [as *Transenella* (*sic*)]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK, DT; as *Transenella* (*sic*)].

Transennella cubaniana (Orbigny, 1842): Dall, 1881 [LFK; as *Gouldia*], 1889a, 1903b [as *Cytherea* (*T.*)]; Johnson, 1934 [as *Transenella* (*sic*)]; Lermond, 1936 [as *C.* (*T.*) *cubaniana* and *Transenella* (*sic*) *cubaniana*]; Hudson et al., 1970 [UFK]; Abbott, 1974; Emerson & Jacobson, 1976; Odé, 1976b; Warmke & Abbott, 1961; Díaz Merlano & Puyana Hegedus, 1994 [as *Transenella* (*sic*)]; Lyons & Quinn, 1995; Mikkelsen & Bieler, 2000 [MFK; as *Transenella* (*sic*)].

Transennella culebrana (Dall & Simpson, 1901): Aguayo & Jaume, 1948b [LFK]; Mikkelsen & Bieler, 2000 [as *Transenella* (*sic*)].

Transennella stimpsoni Dall, 1902: Dall, 1902b [LFK]; Henderson, 1913 [UFK; as *Transenella* (*sic*)]; Johnson, 1934 [LFK; as *Transenella* (*sic*)]; Lermond, 1936 [as *Transenella* (*sic*)]; Hudson et al., 1970 [UFK]; Lyons & Quinn, 1995; Vittor & Associates, 1998 [LFK]; Mikkelsen & Bieler, 2000 [UFK, MFK, LFK; as *Transenella* (*sic*)].

Transennella sp.: Turney & Perkins, 1972 [UFK, MFK; as *Transennela* (*sic*)]; Wingard et al., 1995 [UFK; as *Transenella* (*sic*) spp.]; Brewster-Wingard et al., 1996, 1997 [both as *Transenella* (*sic*) spp.], 1998 [as *T.* spp.], 2001 [all UFK]; Brewster-Wingard & Ishman, 1999 [UFK; as *T.* spp. and *T.* sp.]; USGS, 2003 [UFK, MFK; as *T.* spp.].

|*Ventricolaria* spp. – see *Globivenus* spp.

Verticordiidae

Euciroa elegantissima (Dall, 1881): Bartsch, 1937.

Haliris fischeriana (Dall, 1881): Dall, 1889a, 1903b [as *Verticordia* (*H.*) *Fischeriana*]; Mikkelsen & Bieler, 2000 [DT].

Spinosipella acuticostata (Philippi, 1844): Dall, 1881 [LFK], 1889a, 1903b; Mikkelsen & Bieler, 2000 [LFK] [all as *Verticordia*].

Trigonulina ornata Orbigny, 1842: Dall, 1889a, 1903b [as *Verticordia* (*Trigonulina*)]; Lermond, 1936 [as *Verticordia*]; Mikkelsen & Bieler, 2000 [UFK, DT].

|*Verticordia acuticostata* Philippi, 1844 – see under *Spinosipella*.

|*Verticordia elegantissima* (Dall, 1881) – see under *Euciroa*.

|*Verticordia fischeriana* (Dall, 1881) – see under *Haliris*.

|*Verticordia ornata* (Orbigny, 1842) – see under *Trigonulina*.

Vesicomyidae

|*Vesicomya venusta* (Dall, 1886) – only Florida Keys record (Dall, 1889a) probably based on Florida Straits, 801 fms (Abbott, 1974); here excluded as beyond depth limit.

Vesicomya vesica (Dall, 1886): Dall, 1889a [as *Cytherea* (*Veneriglossa*)].

Yoldiidae

Yoldia liorhina Dall, 1881: Dall, 1889a [as *Leda* (*Yoldia*)].

Species of Uncertain Taxonomic Status

Callucina bermudensis (Dall, 1901): Dall, 1889a [UFK; as *Lucina* (*Lucina*) *lenticula* Reeve, 1850, *non* Gould, 1850]. Dall (1889a) tabulated *L. lenticula* as a deep-water species from the Florida Keys, with Turtle Harbor (a problematic locality, see above) as its northern limit. However, Dall (1901: 810) stated in the original description of *C. bermudensis* that "it is not the species catalogued by me in 1889 as *L. lenticula*", without any indication of what the latter might be. Dall's (1889a) column listing might be suspected as derived from his *Blake* report material (Dall, 1886), all of which is deep water, but none from the Florida Keys. In his revision of western Atlantic Lucinidae, Britton (1970) did not include Dall (1889a) in his synonymy of *C. bermudensis*; neither did Britton list Turtle Harbor as the locality for any *L. lenticula* examined, stating that *C. bermudensis* occurs only in Bermuda. Dall (1886: 265) said that his *Blake* material (again, none from the Florida Keys) was "too poor and insufficient for a satisfactory determination"; Dall (1901) reidentified part of this material as *Codakia cubana* Dall, 1901, a species otherwise known from the Caribbean and Gulf of Mexico, but not from the Florida Keys [Dall's (1886) "*L. lenticula*" material also included specimens of *Myrtea pristiphora* Dall & Simpson, 1901 (Britton, 1970)]. Dall's (1889a) "Turtle Harbor" record must then derive from another source, possibly the USNM collections; Britton (1970) saw Turtle Harbor material in the USNM of *Cavilinga blanda, Codakia orbicularis, Ctena orbiculata, C. pectinella, Divalinga quadrisulcata, Lucinisca nassula, Pleurolucina leucocyma,* and *P. sombrerensis*, mainly from the *Eolis* expeditions (see Bieler & Mikkelsen, 2003).

Cyclocardia borealis (Conrad, 1831): Theroux & Wigley, 1983 [UFK]. This species' Florida Keys record is based on an unverified specimen lot at Woods Hole Oceanographic Institution; it is distributed from eastern Canada to North Carolina, and is thus probably misidentified.

Lepton bowmani (Holmes, 1860): Simpson, 1887–1889 [DT]. *Lepton bowmani* was originally described from the Pleistocene of South Carolina. To our knowledge, it does not appear in any current work on galeommatoidean bivalves, but it cannot be attributed to another species due to rampant taxonomic uncertainties in this group.

Pitar morrhuanus ("Linsley" Dall, 1902): Simpson, 1887–1889 [MFK; as *Cytherea convexa* "Say," err. pro Conrad, 1830]. *Pitar morrhuanus* is typically a cold-water species, ranging from eastern Canada to Cape Hatteras. Sometimes called the "false quahog", it is superficially similar to a cherrystone-sized *Mercenaria* spp., but it's true identity in the Florida Keys (from Long Key, a problematic locality, see above) cannot be determined with any degree of certainty. Both *P. fulminatus* and *Agriopoma texasiana* Dall, 1892, have been called similar to *P. morrhuanus*, but are distributed farther south.

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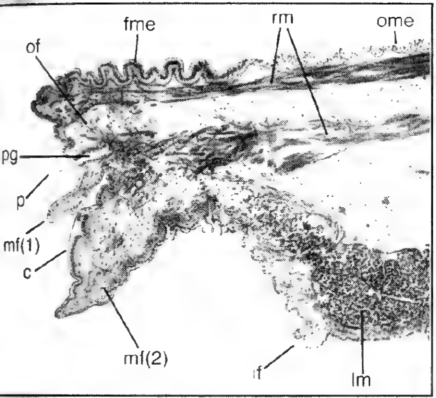

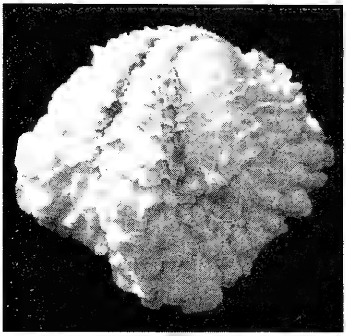

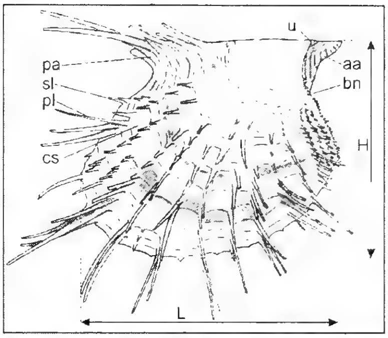

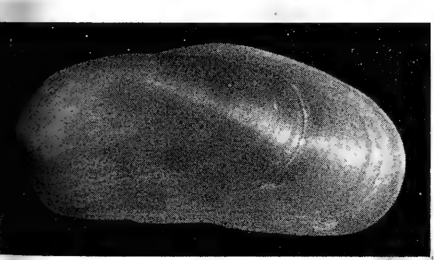

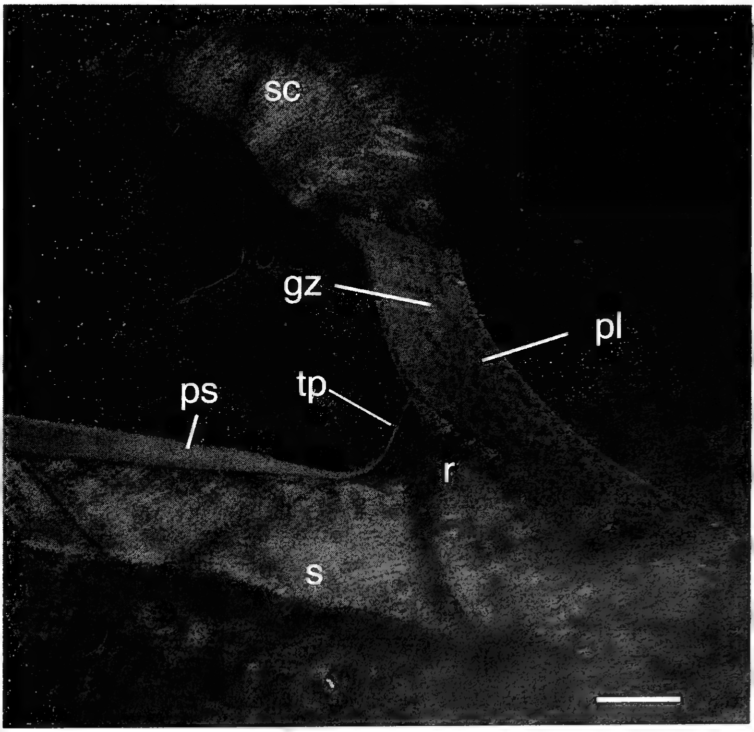

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