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VOL. 40, NO. 1–2 MALACOLOGIA 1998

CONTENTS

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THE DEEP-WATER SPECIES OF *DACRYDIUM* TORELL, 1859 (DACRYDIINAE: MYTILIDAE: BIVALVIA), OF THE ATLANTIC

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ABSTRACT

Species of the genus *Dacrydium* are ubiquitous, mostly at bathyal and abyssal depths within the world's oceans. Here, 11 species are described from the Atlantic at depths greater than 500 m, and of these six are described for the first time. In addition, a bibliography of the world's species described to date is appended. The Dacrydiinae are neotenous mytilids, many being associated with sponges to which they are byssally attached. Multiple fine byssal threads are produced, which may form a nest. The shells are small, rarely more than 4 mm total length, fragile, and transluscent, white or pale cream in colour. Ornamentation, when present, consists of fine concentric striae, sometimes with very fine radial lines and occasionally a scattering of tiny shell granules. The hinge is narrow, with fine, multiple, nepioconch teeth retained throughout life. The ligament is small, internal, and amphidetic. Ventral to the posterior hinge plate is a shell buttress parallel to the dorsal shell margin, which probably provides necessary strength to an extremely fragile shell at times subject to adduction. The viscera occupy the dorsal-most third of the mantle cavity, the organs within being arranged parallel to the dorsal shell margin. Sexes are separate. The palps and gills are reduced in size. The outer demibranch, if present, develops late in life at the time the gonads are begining to mature. At most, it occupies a third of the gill axis and acts as a repository for sperm or eggs when they are first released. At the same time, the fused inner folds of the posterior mantle edge, ventral to the point of the attachment of the gill axis, enlarge and form an aperture that is probably related to the release of sperm or eggs, or spat in the case of those species that brood.

Key words: *Dacrydium*, Mytilidae, Bivalvia, deep-sea, Atlantic.

INTRODUCTION

Of the mytilids present in the deep sea (>500 m), the vast majority belong to the genus *Dacrydium* Torell, 1859. The first species to be described was *Dacrydium vitreum* (Møller, 1842) from off West Greenland and which is now known to occur in relatively shallow water at shelf and upper slope depths in northern seas (Appendix 2). Although a shallow-water species, *D. hyalinum,* was described by Monterosato (1870, 1875, 1878) from the Recent of Sicily and another, *D. occidentale,* by Smith (1885) from the Caribbean, and six varieties of *D. vitreum* were recognized by Locard (1898), until 1959 all records from the North Atlantic were referred to *D. vitreum.* Then, Ockelmann (1959), recognizing differences in shell shape and shell characters in specimens from northern seas, tentatively identified three species that he referred to as species a, b, and c, one of which (b) he was later to describe as *D. viviparum* (Ockelmann, 1983). In the years between Ockelmann's two papers, others also recognized that species other than *D. vitreum* occurred in the North Atlantic (Soot-Ryen, 1966; Allen, 1979). One of these, *D. ockelmanni,* was described by Mattson & Warén (1977).

Elsewhere, species of *Dacrydium* had been described from Australasian waters (Hedley, 1904, 1906), from the Southern Ocean (Pelseneer, 1903; Theile, 1912), and the Pacific (Dall, 1916).

With the upsurge of deep-sea exploration in the last 25 years, a number of new species have been described from the world oceans (Okutani, 1975; Bernard, 1978; Knudsen, 1970; Poutiers, 1989; Okutani & Izumidate, 1992; Hayami & Kase, 1993; Salas & Gofas, 1997), bringing the total, prior to this paper, to 28 known species in the world oceans. This total includes five species that have not yet been given specific names and may yet prove to be synonymous with other species. A list of all the above species and a bibliography to

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them is given in Appendix 2. Unknown until shortly before publication, Salas & Gofas (1997) and the present author had been working simultaneously on Atlantic species of the genus. This paper takes account of their work.

Apart from *D. ockelmanni* (Mattson & Warén, 1977), *D. angulare* and, to a lesser degree *D. viviparum* (Ockelmann, 1983), and a note on their nephridia by Odhner (1912), the species of *Dacrydium* are known from their shell features alone. Here are added details of their internal morphology.

MATERIAL AND METHODS

The species described here were present in the deep-sea samples taken by the research vessels of the Natural Environment Research Council, U.K.; of the Woods Hole Oceanographic Institution, U.S.A.; and of the Centre National pour l'Exploration des Oceans, France. These ships and the names of the various expeditions are included in the list of material in Appendix 1. For the most part, the specimens were collected with a Sanders epibenthic sledge (ES) or some variant of it (Oban - OS; Wormley - WS), and a few were collected by other means, namely, Anchor Dredges (AD, DP), Beam Trawls (CP, CLG), Agassiz Trawl (CV), Reineck Box Corer (KR), large Boillet Trawls (GBO, GBS), small Boillet Trawl (PBS).

The samples were elutriated on board, using sieves (mesh 0.42 mm USA and UK; 0.25 mm and 0.50 mm France), fixed in 4% or 10% formal saline and then after 24 h, washed and transferred to 70% or 95% ethanol. Internal morphology was studied using whole mounts stained lightly in Ehrlich's haematoxylin and sections cut at 10 µm and stained with Meyer's haemotoxylin and eosin and with Azan.

DESCRIPTIONS

Family Mytilidae Rafinesque, 1815

Subfamily Dacrydiinae Ockelmann, 1983

Adult shell eqivalve, markedly inequilateral, small, rarely more than 4 mm total length, homologous to nepioconch of other mytilids; sculpture of fine concentric lines, marked in some species; fine radial lines present in some species; colour white or, occasionally, cream, frequently hyaline; umbo far anterior and somewhat dorsal to anterior limit of shell; highest part of shell varying in position from anterior to posterior to the mid-vertical axis; hinge may have derivatives of provincular teeth adjacent to primary ligament, a dorsal series of fine, transverse nepioconch teeth persist, the posterior series usually much more numerous than anterior; "subligamental ridge" (Ockelmann, 1983), or dorsal buttress shelf, ventral to and more or less parallel to posterior hinge plate; antero-ventral ridge, in-

Abbreviations Used in Figures

AA	anterior adductor
AF	axial muscle fibres
AL	ascending lamella
AN	anus
AP	anterior (upper) palp
AR	anterior pedal retractor
BC	basiphyllic gland cells
BG	byssal groove
CG	cerebral ganglion
DD	digestive duct
DG	digestive diverticula
DL	descending lamella
EC	eosinophyllic gland cells
FM	posterior fused inner mantle fold
FT	foot
HG	hindgut
GA	gill axis
GF	gill filament
GS	gastric shield
GV	ventral margin of inner demibranch
HB	hinge buttress
ID	inner demibranch
LI	ligament
LP	lip
MI	mantle isthmus
MT	mouth
OD	outer demibranch
OE	oesophagus
OR	rudiment of outer demibranch
OV	ovary
PA	posterior adductor muscle
PG	pedal ganglion
PM	longitudinal pallial muscle
PP	posterior (lower) palp
PR	posterior pedal retractor muscle
RA	reproductive aperture
SB	suprabranchial cavity
SP	sperm
ST	stomach
TE	testis
UC	umbonal cavity
VE	ventricle
VG	visceral ganglion

ternal to anterior hinge plate, variously developed; primary ligament small, internal and amphidetic; if present, secondary ligament very small, slender, opisthodetic. Viscera occupying dorsal third of shell space, digestive glands and gonads elongate, following line of dorsal margin; mantle margins simple, unfused, except where gill axis attaches to mantle margin; adductor muscles sometimes subequal in size, but usually heteromyarian, with the posterior muscle the larger; labial palps minute, few, if any, palp ridges; inner demibranch of gill extending length of mantle cavity, but with relatively few filibranch filaments; when present, outer demibranch developing late in life as a small posterior triangular flap; foot relatively small, with functional byssus, producing many fine threads.

Genus *Dacrydium* Torell, 1859

Type species by monotypy, *Modiola? vitrea* Møller, 1842:92.

Description as for subfamily. Occurs from shelf to abyssal depths, most species being found from mid-slope to lower slope depths.

The genus *Quendreda* was proposed by Iredale (1936:271) but without diagnosis. He designated *D. fabale* Hedley, 1904, as the type species, remarking that it "differs in shape, form and sculpture from the Spitzbergen shell, the type of Torell's genus." There is debate as to whether this distinction is justified (Soot-Ryen, 1955; Bernard, 1978; Ockelmann, 1983).

Dacrydium sandersi, new species

Figs. 1–3

Type Locality: Atlantis II, Sta. 66, North America Basin, 38°46.7'N 70°08.8'W, 2802 m.

Type Material: Holotype, BMNH 1996136; paratypes, BMNH 1996137.

Material: North America Basin: Atlantis II, sta. 62, 69 spec.; sta. 64, 175 spec.; sta. 66, 12 spec.; sta. 72, 132 spec.; sta. 118, 5 spec;

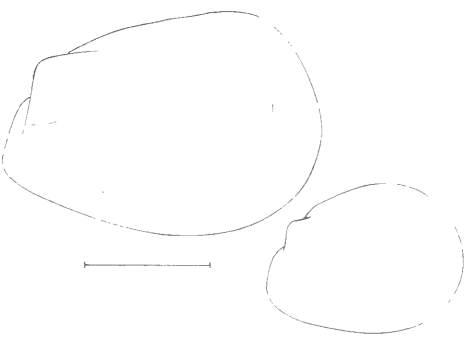

FIG. 1. *Dacrydium sandersi.* Lateral views from the left side of two specimens from Atlantis II sta. 72, North America Basin, 2864 m. Scale = 1 mm.

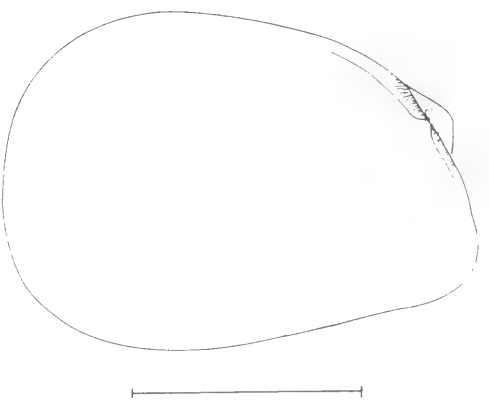

FIG. 2. *Dacrydium sandersi.* Lateral internal view of right valve from Biogas III sta. DS41, Bay of Biscay, 3548 m. Scale = 1 mm.

Abbreviations of Museums

AHF	Allan Hancock Foundation (see LACMNH)
AMS	Australian Museum, Sydney
BMNH	Natural History Museum, London
IRSNB	Institut Royal des Sciences Naturelles, Belgique
LACMNH	Los Angeles County Museum of Natural History
MNHNP	Muséum National d'Histoire Naturelle, Paris
NMNZ	National Museum of New Zealand
NSMT	National Science Museum, Tokyo
SBMNH	Santa Barbara Museum of Natural History
SMNH	Naturhistoriska Riksmuseet, Stockholm
TRFRL	Tokai Regional Fisheries Research Laboratory
UMUT	University Museum, University of Tokyo
USNM	United States National Museum
ZMHU	Zoologisches Museum Humbolt-Universitat, Berlin
ZMUB	Zoological Museum, University of Bergen
ZMUC	Zoological Museum, University of Copenhagen

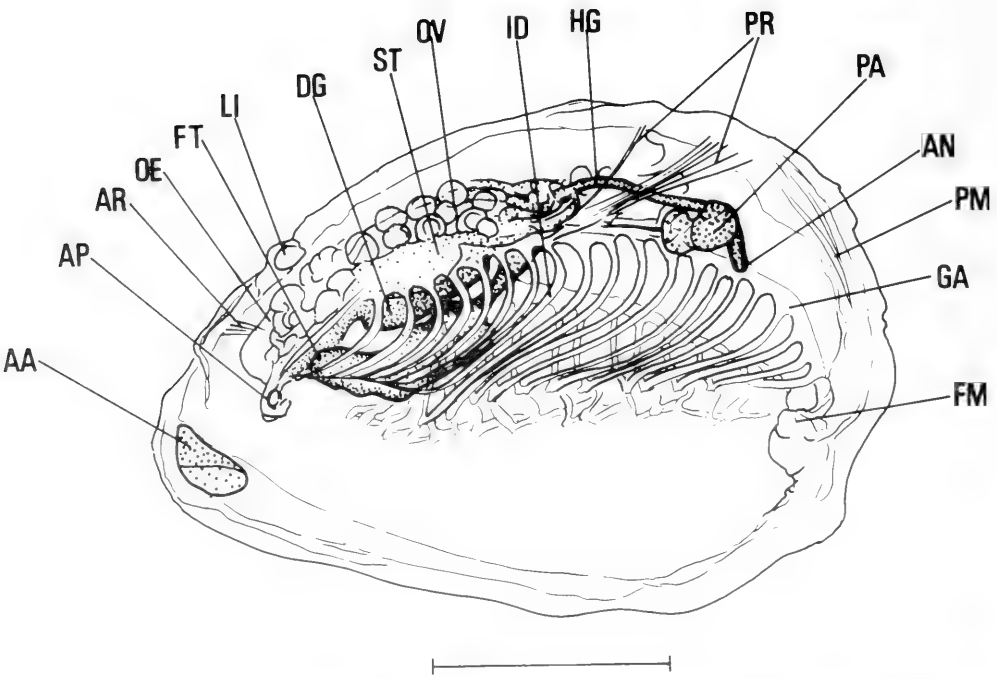

FIG. 3. *Dacrydium sandersi*. Semidiagrammatic view of the internal morphology of a specimen from the left side from Atlantis II sta. 72. North America Basin. 2864 m. Scale = 0.5 mm. Refer to Materials & Methods for list of abbreviations.

sta. 119, 32 spec.; Chain, sta. 76, 133 spec. Brazil Basin: Atlantis II, sta. 155, 90 spec.; sta. 156, 396 spec.; sta. 167, 39 spec.; sta. 169, 17 spec. West European Basin: Biogas II, sta. DS31, 10 spec.; Biogas III, sta. DS41, 61 spec.; Biogas IV, sta. DS58, 6 spec.; sta. DS59, 2 spec.; Biogas VI, sta. 74, 17 spec.; sta. CV38, 7 spec. Azores Mid Atlantic Ridge: Biacores, sta. 126, 19 spec.

Distribution: Occurs most commonly at lower slope depths (2500–3000 m), although the overall range is much wider (587–3783 m). It occurs across the Atlantic, predominantly at boreal latitudes in the North America and West European basins, although in the West Atlantic it has been taken from the northern part of the Brazil Basin.

Shell Description (Figs. 1, 2). Shell small (<4 mm), fragile, modioliform, greatest shell height posterior to mid-vertical axis, relatively wide, transluscent white, occasional growth lines and faint concentric striations, otherwise smooth; umbones large, distant from anteroventral limit of shell margin; ventral margin convex in small specimens, with slight sinuosity anteriorly in larger specimens; posterior margin broadly curved; dorsal margin very slightly concave, slightly angled where posterior limit of hinge meets margin; anterior margin relatively long and straight, except close to umbo where it curves inwards; hinge plate interrupted by ligament pit; anterior hinge plate moderately elongate, with 13–15 nepioconch teeth; posterior hinge plate approximately the same length as anterior but broader, with 10–12 nepioconch teeth; narrow buttress shelf extending from anterior limit of posterior hinge plate along the dorsal margin to the highest point of the shell; a narrower buttress shelf extending from posterior limit of the anterior hinge plate along the anterior margin to a point where the margin starts to curve to the ventral margin; ligament small, internal, amphidetic, separating anterior and posterior hinge plates. Prodissoconch length: 123 μm.

Internal Morphology (Fig. 3). The mantle margin has outer, middle sensory and inner muscular folds. Posteriorly, there is fusion of the latter to form an extensive exhalent aperture. The area of fusion is relatively broad and is much more prominant in large than small specimens. The gill axes attach to the dorsal

edge of the fused tissue. In large specimens, the area of fusion might be mistaken for an inturned and contracted inhalent siphon (Fig. 3), but in the present specimens neither whole mounts nor sections reveal a clear lumen from the exterior to the mantle cavity, although sections show that there is an inner cavity. It will be seen that in fully mature specimens of other species a lumen does connect the mantle cavity to the exterior, and it would appear that the aperture when formed is used for the discharge of eggs and sperm. Neither Mattson & Warén (1977) nor Ockelmann (1983) mention this, despite its presence in the species that they describe.

The adductor muscles are small and equal in size. The gills consist of only the inner demibranchs. No rudiment of an outer demibranch is present, even in specimens with maturing ova. The inner demibranchs comprise of a relatively broad descending lamella and an ascending lamella about half the length of the descending. The filaments are typically filibranch without interlamellar and interfilamentar junctions. The main axes are attached dorsally to the body wall and to the mantle posterior to the foot.

The palps are very small, slight enlargements to the lateral limits of the lips. The mouth opens to an oesophagus that has a lumen with six longitudinal grooves. The course of the oesophagus is straight, opening to the anterior part of the stomach. The latter is also elongate and tubular, lying along the antero-posterior axis. There is an extensive gastric shield that extends over much of the dorsal and left lateral walls of the stomach. The ciliation on the remaining wall appears to be relatively simple; however, there is a major typhlosole that extends the length of the combined style sac and mid gut. The hind gut turns immediately dorsal to the style sac, first taking an anterior course as far as the mid point of the stomach, and then turns sharply on itself and continues directly and mid-dorsally over the posterior adductor muscle to the anus. There is a very short digestive duct opening from what appears to be a simple caecum on the left side of the stomach. The duct connects with a digestive diverticulum that forms a longidinal tube on the left ventral side of the viscera. There is also a second duct opening anteriorly on the right side of the stomach. This branches, one branch connecting with a longitudinal diverticulum on the right side that parallels the one on the left, the other branch connecting with a smaller diverticulum ventral to the stomach. The right and left diverticula are finger-like and extend one each side of the oesophagus and terminate a short distance anterior to the mouth.

Dorsal to the paired diverticula are a pair of tubular gonads dorso-lateral to the digestive system. Sexes are separate; 30–35 ova (68 µm diameter) were present in a specimen 2 mm in length.

The kidneys are a pair of simple sacs posterior to the posterior adductor. The nervous system is of the typical bivalve design; however, all the ganglia are small in size.

Diagnosis: *D. sandersi* is characterized by the greatest shell height being posterior to the mid-vertical axis, the posterior hinge being short and of similar length to the anterior, the umbo being relatively distant from the antero-ventral point of the shell, and the adductor muscles being small and dimyarian.

Other species of similar shell shape are *D. rostriferum*. *D. occidentale* and *Dacrydium* sp. of Poitiers (1989), but these differ from the present species in that the posterior hinge is significantly longer than the anterior. The position of the umbo in *D. occidentale* and *Dacrydium* sp. is much closer to the antero-ventral limit of the shell (see Poitiers, 1989: fig. 3)

Dacrydium vitreum (Møller, 1842)
Figs. 4–7

Type Locality: West Greenland.

Type Material: originally ZMUC; appears to be lost (Warén, 1991).

Original description: Møller, 1842: 92 (for other references, see Appendix 2).

Cited specimen (figured in text): BMNH 1996144

Material: North America Basin: Atlantis, sta. D, 3 spec.; Chain, sta. 88, 34 spec.; sta. 105, 43 spec.; Knorr, sta. 346, 3 spec.

Also, specimens from off East Greenland identified and donated by Kurt Ockelmann to Howard Sanders of the Woods Hole Oceanographic Institution, have been examined.

Distribution: In the past, *D. vitreum* has been recorded widely from the North Atlantic south to the Azores and Florida (Ockelmann, 1959; Abbott, 1974), but it is now clear that southern specimens have been misidentified. It is a cold-water, panarctic species (Ockelmann, 1959; Mattson & Warén, 1977; Warén, 1991) and possibly circumglobal (Bernard, 1983; Salas & Gofas, 1997). Although the present specimens come from the shelf edge off Cape Cod at a boreal latitude, these relate to the southward extension of the Labrador Current.

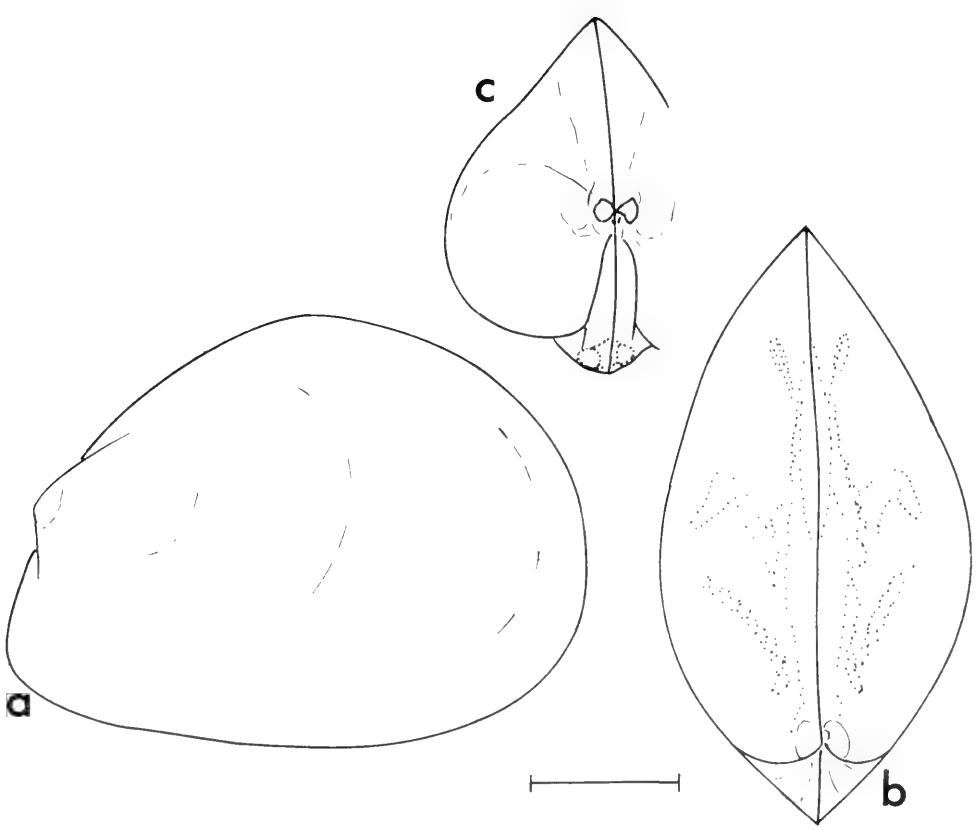

FIG. 4. *Dacrydium vitreum.* Three views of a shell from Knorr sta. 346, North America Basin. 475 m. (a) lateral from left side; (b) dorsal; (c) anterior. Scale = 1 mm.

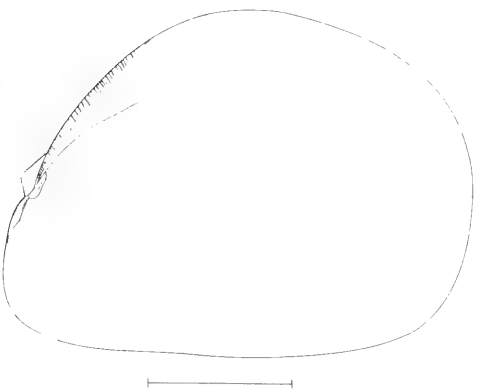

FIG. 5. *Dacrydium vitreum.* Lateral internal view of right valve from Atlantis 227 sta. D, 466–508 m. Scale = 1 mm.

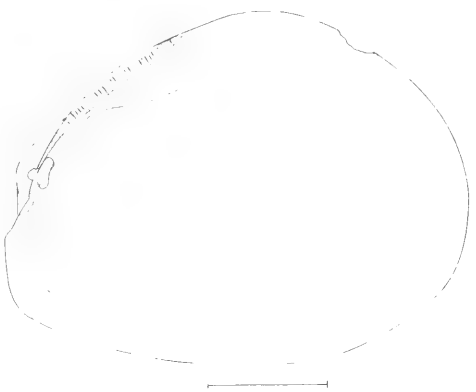

FIG. 6. *Dacrydium vitreum.* Lateral internal view of right valve of a specimen from off East Greenland (Ockelmann, 1953: 175). Scale = 1 mm.

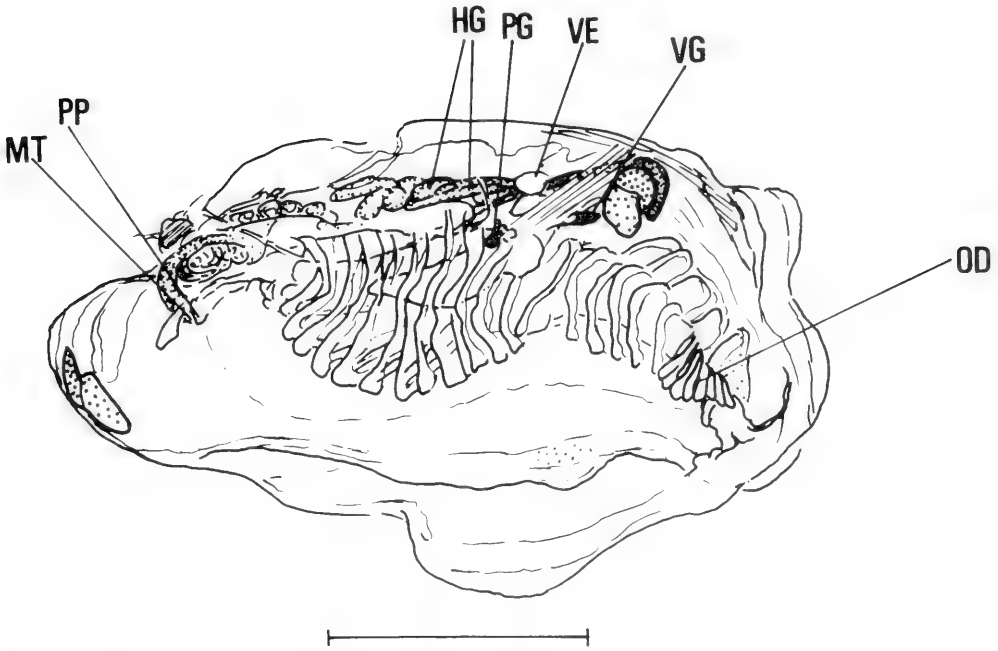

FIG. 7. *Dacrydium vitreum*. Semidiagrammatic view of the internal morphology of a specimen from the left side from Chain 58 sta. 105, North America Basin, 530 m. Scale = 1 mm. Refer to Materials & Methods for list of abbreviations and Fig. 3 for identification of other parts.

other species of Arctic bivalves are found at the same stations (Allen et al., 1995). Depth range: 5–698 m, deeper records down to 2258 m need to be confirmed (Ockelmann, 1959).

Shell Description (Figs. 4–6). Sars (1878) gave good descriptions and figures of the shell (Mattson & Warén, 1977), and since then other good figures and photographs have been provided by Ockelmann (1959, 1983), Mattson & Warén (1977), Warén (1991), and Salas & Gofas (1997). For completeness and for comparative purposes, shells from the North America Basin and from East Greenland are figured and described and, for the first time, the internal anatomy is described.

Shell small (<6 mm total length), semi-transparent or opaque, white, periostracum cream in larger specimens, semi-ovate, equivalve; shell relatively high, maximum height measurement immediately posterior to mid-vertical axis; umbo prominant, dorsal, slightly posterior to the anterior limit of the shell; ventral margin a shallow convex curve; posterior margin smoothly rounded; postero-dorsal margin broadly convex; antero-dorsal margin a shallow convex curve indented at juxtaposition of umbo and internal ligament; posterior hinge plate elongate, occupying 1/3 posterior dorsal margin, present specimens with 55–65 nepioconch teeth (number increasing with size); posterior hinge plate strengthened by broad buttress shelf thickened along ventral edge ("subligamental ridge" of Ockelmann, 1983); shelf extending just posterior to summit of dorsal shell margin, thereafter merging with pallial line of shell; anterior hinge plate short, with 5–8 nepioconch teeth; antero-ventral corner of shell somewhat thickened where anterior adductor muscle inserts; insertion of posterior adductor close to postero-dorsal pallial line posterior to buttress shelf; ligament internal, amphidetic, with very short fine external extensions not usually visible unless shell is dissolved. Prodissoconch length: 120–136 μm (Ockelmann, 1983; Salas & Gofas, 1997).

Internal Morphology (Fig. 7). The morphology is similar to that described for *D. sandersi*. The mantle margins are relatively unmodified, with three simple folds that are unfused, except posteriorly where the gill axes meet the

margin and where the inner muscular folds are fused and thickened over a short distance. No papillae are present on the middle sensory lobe, and there is no extension of sensory and inner folds to form siphons. Very fine scattered radial pallial muscle fibres are present as a band internal to the inner muscular fold. The adductor muscles are relatively well developed, the anterior being of a similar size to the posterior, except that it is crescent-shaped in cross section as opposed to oval. The gill axes are attached latero-ventrally to the body and to the mantle posterior to the body. The inner demibranch, with approximately 25 filaments in a specimen 3 mm total length, is well developed, with the descending and ascending lamellae of similar size. The outer demibranch is restricted to a small, posterior, triangular structure close to where the axis meets the mantle margin, and it has up to nine short filaments. The anterior filament of the inner demibranch is situated somewhat distant from the minute palps, there being a long distal oral groove between gill and mouth.

The viscera are confined to a narrow band in the dorsal third of the shell cavity. This restriction is reminiscent of the condition in the deep-sea limopsids, in which the viscera occupy less than a third of the available mantle space (Oliver & Allen, 1980). Thus, in *D. vitreum,* the oesophagus, stomach, style sac and intestine are arranged in a longitudinal fashion within the body. The oesophagus is relatively elongate, joining the stomach anteriorly, the midgut is combined with the style sac; the hind gut is first reflected anteriorly, along the dorsal 2/3rds of the length of the stomach, and then posteriorly, passing through the heart and dorsal to the posterior adductor, to the anus. The major portion of the digestive diverticula comprise a pair of parallel tubules, one each side of the stomach and oesophagus. In addition, there are a few short tubules ventral to the stomach. The gonads are paired elongate tubes lying dorsal to the oesophagus and stomach. The sexes are separate. The kidney lies ventral to the hindgut, anterior to the posterior adductor. The foot joins the viscera posterior to the style sac. In preserved specimens, it is small and cylindrical enclosed by the gill lamellae. There is a functional byssus gland at the postero-ventral limit of the foot, and clearly in life the latter must be capable of considerable extension. Two paired posterior pedal retractor muscles insert immediately anterior to the posterior adductor, and a pair of fine anterior pedal retractors attach to the shell immediately dorsal to the umbones.

Dacrydium ockelmanni
Mattson & Warén, 1977
Figs. 8–15

Type Locality: Korsfjorden, W. Norway, 60°08.58′N 05°00.67′W, 260–290 m.

Type Material: Holotype ZMUB 58 633; paratypes ZMUB 58 634.

Original Description: Mattsen & Warén, 1977: 2, figs. 4–6, 10–13 (for other references, see Appendix 2).

Cited Specimens: BMNH 1996138 and 1996139.

Material: North America Basin: Atlantis II, sta. 73, 90 spec.; sta. 115, 50 spec.; sta. 119, 24 spec.; sta. 128, 37 spec.; Chain, sta. 87, 16 spec.; sta. 103, 1 spec.; sta. 210, 77 spec. Brazil Basin: Atlantis II, sta. 142, 89 spec.; sta. 144, 2 spec.; sta. 147, 9 spec. Argentine Basin: Atlantis II, sta. 239, 9 spec.; sta. 240, 2 spec.; sta. 245, 21 spec. West European Basin: Sarsia, sta. S33/2, 1 spec.; sta. S44, 19 spec.; sta. S50, 52 spec.; sta. S66; 1 spec.; Discovery, sta. 7601, 1 spec.; Challenger, sta. E80–73, 24 spec.; Biogas I, sta. DS11, 1 spec.; Polygas, sta. DS15, 9 spec.; sta. DS17, 2 spec.; DS18, 5 spec.; sta. DS25, 1 spec.; sta. DS31, 4 spec.; Biogas II, sta. DS32, 3 spec.; Biogas III, sta. DS36, 1 spec.; sta. DS37, 3 spec.; sta. DS38, 1 spec.; sta. DS50, 7 spec.; Thalassa, sta. Z397, 5 spec.; sta. Z400, 13 spec.; sta. Z413, 2 spec.; sta. Z417, 4 spec.; sta. Z427, 1 spec.; sta. Z447, 1 spec.; Biogas IV, sta. DS52, 13 spec.; sta. DS61, 4 spec.; sta CP01, 2 spec.; sta. DS62, 8 spec.; sta. DS63, 6 spec.; sta. DS64, 14 spec.; Biogas VI, sta. CP08, 3 spec.; sta. CP09, 7 spec.; sta. DS71, 3 spec.; sta. DS86, 36 spec.; sta. CP23, 1 spec.; sta. DS87, 30 spec.; Incal, sta. DS01, 12 spec.; sta. CP01, 41 spec.; sta. DS02, 31 spec.; sta. CP08, 1 spec.; Chain, sta. 313, 7 spec.; sta. 318, 1 spec.; sta. 321, 24 spec. Canary Basin: Discovery, sta. 6701, 13 spec.; sta. 6704, 5 spec. Azores Mid Atlantic Ridge: Biacores, sta. 105, 2 spec.; sta. 120, 1 spec.

Distribution: Ockelmann (1958), Mattson & Warén (1977) and Warén (1991) reported *D. ockelmanni* as occurring WSW and SE of Iceland, SW of the Faroes, NW of Ireland and probably Bay of Biscay. The species is confirmed as common in the Bay of Biscay and, further, as being present throughout most of the Atlantic, with the possible exception of the Angola and Cape basins. It is also reported as

FIG. 8. *Dacrydium ockelmanni.* Lateral views of six shells from the left side to show variation in shell outline with increasing size. Specimens taken from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 0.5 mm.

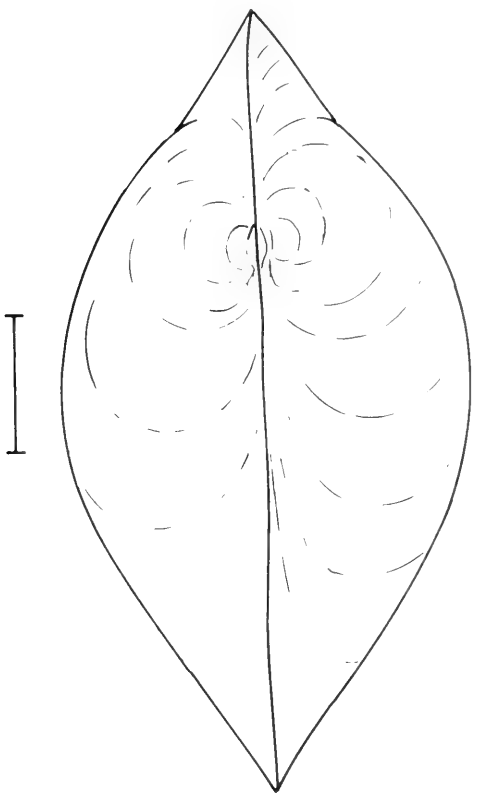

FIG. 9. *Dacrydium ockelmanni.* Dorsal view of shell from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 0.5 mm.

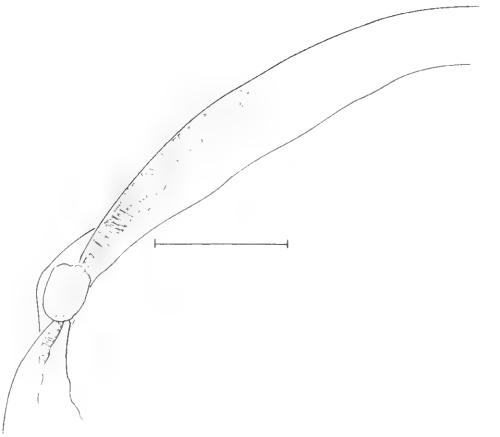

FIG. 10. *Dacrydium ockelmanni.* Detail of the hinge of a right valve from Atlantis II sta. 240, Argentine Basin, 2195–2323 m. Scale = 0.5 mm.

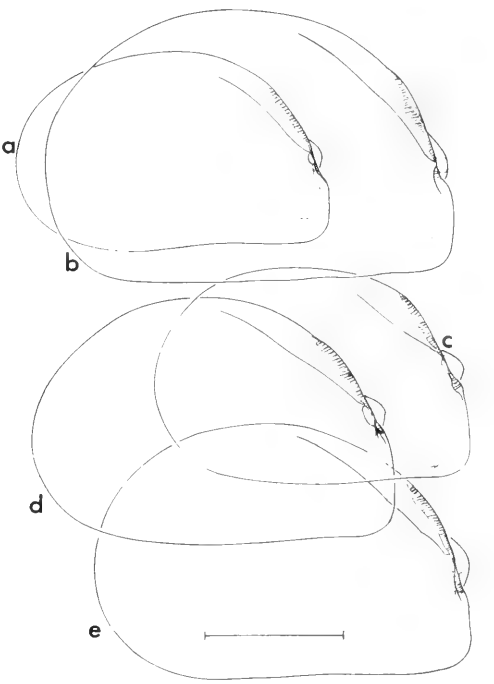

FIG. 11. *Dacrydium ockelmanni.* Lateral internal views of five right valves to show variation in form. (a) Discovery sta. 6704, Canary Basin, 2129 m; (b) Sarsia sta. S44, Bay of Biscay, 1739 m; (c) Atlantis II sta. 142, Brazil Basin, 1624–1796 m; (d) Atlantis II sta. 239, Argentine Basin, 1661–1669 m; (e) Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 1 mm.

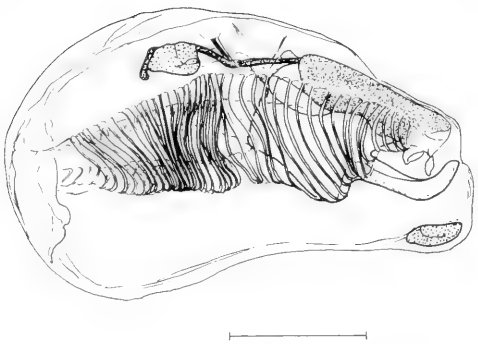

FIG. 12. *Dacrydium ockelmanni.* Semidiagrammatic view of the internal morphology of a male specimen from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 1 mm. See Fig. 3 for identification of the parts.

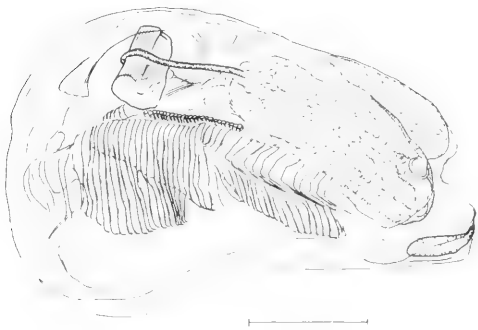

FIG. 13. *Dacrydium ockelmanni.* Semidiagrammatic view of the internal morphology of a female specimen from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 1 mm. See Fig. 3 for identification of the parts.

a Pleistocene fossil from the Mediterranean (Salas & Gofas, 1997). It occurs at lower shelf to lower slope depths with an extreme range of 100–3100 m, but most of the above records are from mid to lower slope depths (1000–2500 m).

Shell Description (Figs. 8–11). The shell is described and figured by Mattson & Warén (1977), Warén (1991), and Salas & Gofas (1997). Here further detail is added.

Shell small (<6.0 mm), semi-transparent, white or tinged with yellow/green, semi-ovate, greatest height coincident with mid-vertical axis or, in largest specimens, posterior to it; umbo moderate in size; ventral shell margin slightly concave in smallest specimens, as length increases ventral margin first becomes

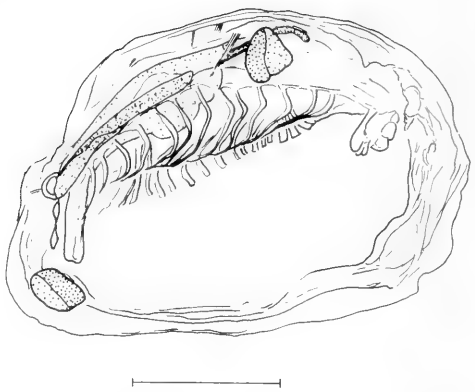

FIG. 14. *Dacrydium ockelmanni.* Semidiagrammatic view of the internal morphology of an immature specimen from Atlantis II sta. 142, Brazil Basin, 1624–1796 m. Scale = 0.5 mm. See Fig. 3 for the identification of the parts.

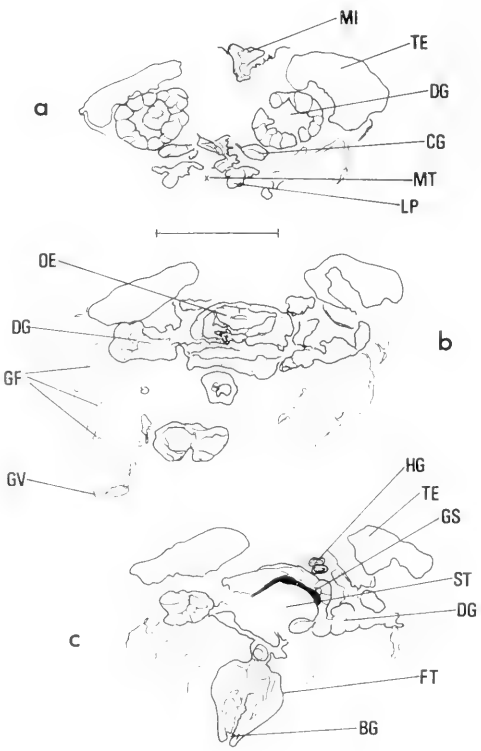

FIG. 15. *Dacrydium ockelmanni.* Transverse vertical 10 μm sections through a specimen from Atlantis II sta. 73, North America Basin, 1330–1470 m. (a) through region of mouth; (b) through oesophagus; (c) through stomach and gastric shield. Scale = 0.5 mm. Refer to Materials & Methods for list of abbreviations.

straight and then slightly convex; posterior and dorsal margins forming smooth, broad, convex curve; antero-dorsal margin dorsal to umbo almost straight, ventral to umbo slightly sinuate, then straight for short distance before curving sharply to meet ventral margin; posterior hinge plate occupying <1/4 dorsal shell margin, with 33–38 nepioconch teeth in present specimens (larger numbers are present in larger specimens, e.g. Salas & Gofas, 1997: fig. 8), supported by relatively wide buttress shelf that extends beyond hinge for a similar distance but short of the highest point of the shell; in intact specimens, ventral edge of buttress usually visible through shell; posterior limit of hinge plate frequently marked by slight angulation of shell margin; anterior hinge plate short with 5–7 nepioconch teeth, very small provincular tooth at proximal limit of anterior hinge plate; antero-ventral part of shell slightly thickened, with inner ventral ridge originating at anterior limit of anterior hinge plate; ligament internal, amphidetic, seated in pit between hinge plates. Prodissoconch length: 141–150 μm (Ockelmann, 1983).

Dacrydium ockelmanni (height/length 0.72–0.77) differs from *D. vitreum* (height/length 0.63–0.71) in being slightly more elongate and less high, with the ventral margin concave in larger specimens. The posterior hinge plate is shorter in *D. ockelmanni* with fewer nepioconch teeth, and the buttress shelf is somewhat less wide. The antero-dorsal margin is straighter and the umbo smaller and less distant from the antero-ventral limit of shell.

Ockelmann (1959) reported on a number of possible species, including one later described as *D. ockelmanni,* within a relatively small area of the North Atlantic off Iceland. The species described here, including *D. ockelmanni,* have fairly wide distributions. Because it is known that shell shape and internal morphology changes with increasing size, internal shell characters from specimens from different basins have been figured (Fig. 11), as well as differences in shell outline with increasing size from a large sample (Fig. 8). This confirms the variation, with that seen in a single sample being as great as the interbasinal differences. The variation is not consistant enough to warrent naming subspecies or varieties.

Internal Morphology (Figs. 12–15). Although their figures are diagrammatic, the morphology of *D. ockelmanni* is well described by Mattson & Warén (1977). Immature and mature whole mounts are illustrated here, and additional information given. Thus, the anterior adductor muscle is more round in cross-section and smaller than the posterior adductor. The gill filaments on the inner demibranch are more widely spaced compared with those of the outer demibranch, and specimens 1.6 mm in length have only a rudiment of the outer demibranch (Fig. 14). Ventral to the attachment of the gill axis with the mantle margin, the inner muscular mantle fold is fused and thickened over some distance and extended inwards to form an internal "collar." This structure is much more developed in larger specimens, particularly so in specimens that have mature gonads. The posterior pedal retractor muscles are not particularly well developed. The presence of a longitudinal pallial muscle is confirmed, and is perhaps better developed than the diagrammatic drawing of Mattson & Warén (1977) might indicate. Sexes are separate, and large female specimens from Station 73 were mature, with approximately 400 eggs (75 μm diameter) in specimens >4 mm total length (Figs. 13, 14).

Dacrydium abyssorum, new species
Figs. 16–19

Type Locality: Knorr 25, Station 287, Guyana Basin, 13°16.0′N 54°52.2′W 13°15.8′N 54°53.1′W, 4980–4934 m.

Type Material: Holotype BMNH 1996140; paratype BMNH 1996141.

Material: Newfoundland Basin: Chain, sta. 331, 2 spec.; North America Basin: Atlantis II, sta. 70, 3 spec.; sta. 93, 1 spec.; Chain, sta. 80, 1 spec.; sta. 83, 2 spec.; sta. 84, 5 spec.; sta. 84, 8 spec. Guyana Basin: Knorr, sta. 287, 27 spec.; sta. 288, 14 spec.; sta. 306, 2 spec.; Vema, sta. CP02, 2 spec.; sta. DS05, 2 spec. West European Basin: Biacores, sta. 245, 11 spec.; Polygas, sta. DS20, 89 spec.; sta. DS21, 26 spec.; sta. CV13, 17 spec.; sta. DS22, 59 spec.; sta. DS23, 21 spec.; sta. DS26, 9 spec.; Biogas II, sta. DS30, 12 spec.; Biogas III, sta. DS42, 1 spec.; sta. DS44, 4 spec.; sta. DS45, 8 spec.; sta. DS46, 3 spec.; sta. DS48, 2 spec.; Biogas IV, sta. 54, 4 spec.; sta. DS55, 264 spec.; sta. KR31, 1 spec.; sta. DS56, 15 spec.; sta. KR35, 2 spec.; Biogas V, sta. DS67, 23 spec.; sta. DS68, 10 spec.; sta. DS69, 4 spec.; sta. CP07, 1 spec.; Biogas VI, sta. DS75, 1 spec.; sta. DS76, 579 spec.; sta. CP13, 32 spec.; sta. CP14, 53 spec.; sta. KR60, 5 spec.; sta. KR64, 2 spec.; sta. DS77. 148 spec.; sta. DS78, 21 spec.; sta. CP16, 13 spec.; sta. DS79, 9 spec.; sta. CP17, 17 spec.; sta. CP18, 1 spec.; sta. DS80, 2 spec.; sta. DS81, 1 spec.; sta. CP21, 2 spec.; sta. DS87,

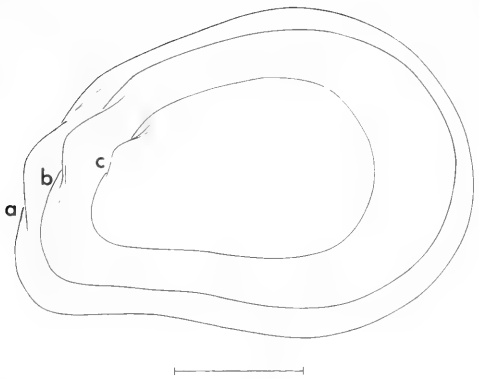

FIG. 16. *Dacrydium abyssorum.* Lateral views of three shells from the right side. (a & c) Chain 50 sta. 85, North America Basin, 3834 m; (b) Knorr sta. 287, Guyana Basin, 4980–4934 m. Scale = 0.5 mm.

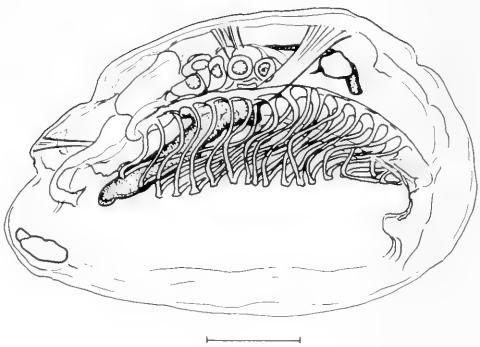

FIG. 18. *Dacrydium abyssorum.* Semidiagrammatic view from the left side of the internal morphology of a mature female from Knorr sta. 287, Guyana Basin, 4980–4934 m. Scale = 0.5 mm. See Fig. 3 for the identification of the parts.

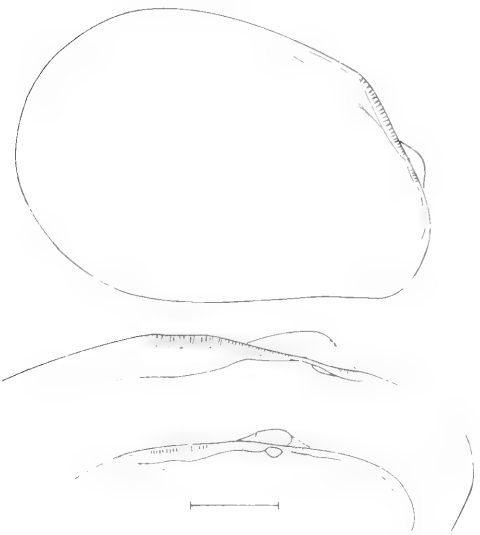

FIG. 17. *Dacrydium abyssorum.* Lateral internal view of right valve of a specimen from Knorr sta. 288, Guyana Basin, 4417–4429 m, and the detail of the hinge of two right valves from Chain 50 sta. 85, North America Basin, 3834 m. Scale = 0.5 mm.

13 spec.; Incal, sta. CP10, 6 spec.; sta. DS11, 5 spec.; sta. CP11, 30 spec.; sta. WS02, 64 spec.; sta. OS03, 19 spec.; sta. OS05, 26 spec.; sta. KR14, 3 spec.; sta. WS07, 388 spec.; sta. DS14, 73 spec.; sta. DS15, 42 spec.; sta. DS16, 123 spec.; sta. WS08, 274 spec.; sta. OS06, 63 spec.; sta. OS07, 515 spec.; sta. WS09, 111 spec.; sta. WS10, 280 spec.; sta. OS08, 145 spec. Sierra Leone Basin: Atlantis II, sta. 148, 1 spec.; sta. 149, 13 spec. Cape Basin: Walvis, sta. DS02, 2 spec.; sta. KG14, 1 spec.; sta. DS05, 39 spec.; sta. DS06, 43 spec.; sta. DS07, 2 spec.

Distribution: *Dacrydium abyssorum* is widespread at abyssal depths throughout the Atlantic. It occurs at depths from 1913–5280 m, but predominantly at depths >4000 m.

Shell Description (Figs. 16, 17). Shell small, modioliform, fragile, transluscent, white, greatest height posterior to mid-vertical transverse axis; umbo relatively large, distant from the antero-ventral limit of shell; antero-ventral margin broadly rounded; ventral margin sinuous; posterior margin a smooth, broad curve; postero-dorsal margin a smooth convex curve; antero-dorsal margin much less convex, angulate at posterior limit of hinge plate; antero-dorsal margin almost straight; anterior margin dipping slightly where umbo meets margin; anterior and posterior hinge plates continuous, although edentulous section below umbo narrow; anterior hinge-plate short, but relatively broad, with 5–9 nepioconch teeth; posterior hinge-plate elongate, broadening distally, with approximately 42 nepioconch teeth in specimen 4.5 mm total length; buttress shelf broad, except ventral to the anterior half of the posterior hinge plate, where it narrows, usually making a sinuous curve with the broader posterior part; internal ridge from anterior limit of hinge plate curving postero-ventrally, forming margin of antero-

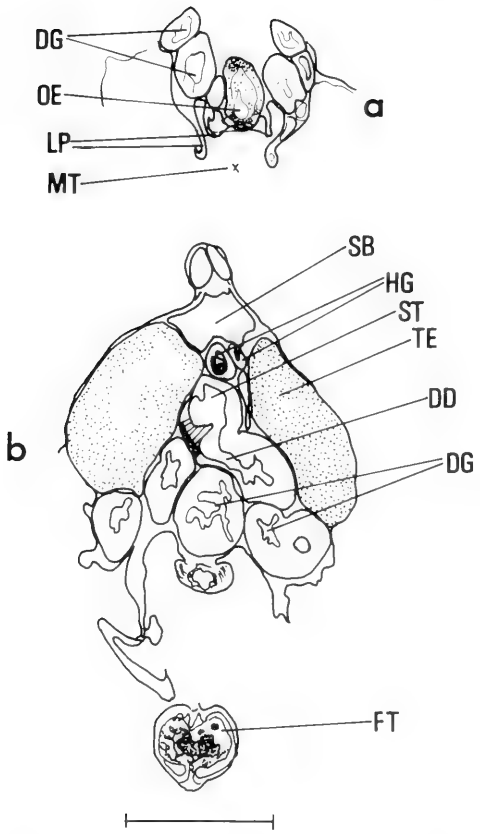

FIG. 19. *Dacrydium abyssorum.* Transverse vertical 10 μm sections through a mature male specimen from Knorr sta. 287, Guyana Basin, 4980–4934 m, (a) through the mouth; (b) through the stomach. Scale = 0.5 mm. Refer to Materials & Methods for list of abbreviations.

ventral triangular area to which anterior adductor muscle attaches; ligament small, internal, amphidetic. Prodissoconch length: 191–204 μm.

Internal Morphology (Figs. 18, 19). The internal morphology is similar to that of *D. sandersi.* The adductor muscles are small, the anterior slightly larger in size. The gill is without an outer demibranch, and the inner demibranch comprises both ascending and descending lamellae. There are relatively few filaments, 17 and 27 in the demibranchs of specimens 1.8 mm and 3.0 mm total length, respectively. There are no interfilamentar connectives and no interlamellar connectives. The posterior mantle margin is thickened at the point where the gill axes attach to it and also ventral and dorsal to the point of attachment. Fusion of the inner mantle folds occurs at the point where the gill axes meet the mantle margin and ventral to this. In mature specimens, through this is a channel from mantle cavity to the exterior, homologous to an inhalent aperture, which is probably used for the passage of sexual products. Inhalent repiratory and feeding currents pass through the extensive pedal gape. Internally, the margin of this reproductive aperture is characteristically curved, forming a funnel. Anteriorly, the lips and mouth also form a wide buccal funnel; this is directed postero-ventrally and so placed to receive material traveling the length of the gill margin. The palps are reduced to slight thickenings at the extremities of the lips, and it would appear that little or no sorting of incoming material can occur. The oesophagus is wide and the stomach relatively voluminous. The digestive diverticula are more branched than in *D. sandersi,* but similar in their distribution. The pedal musculature is relatively stout compared with that of *D. sandersi.* Mature specimens were present in the samples, 10 and 24 large eggs (115 μm max. dimension) were present in specimens 1.8 mm and 3.0 mm total length, respectively.

Diagnosis: *Dacrydium abyssorum* is a species in which the maximum shell height is posterior to the vertical mid-line and thus is similar to *D. sandersi.* It differs from the latter in the more pronounced angulation of the shell margin opposite the posterior limit of the hinge, the more sinusoidally curved ventral margin of the shell, and in the difference in length of the hinge plates and the numbers of nepioconch teeth.

Dacrydium wareni Salas & Gofas, 1997
Figs. 20–25

Type Locality: Off northwestern Morocco, 35°31′N 07°42′W, 1510 m.

Type Material: Holotype and paratypes MNHNP; paratypes SMNH.

Description: Salas & Gofas 1997: 271, figs. 94–96, 97–99 (for other references, see Appendix 2). Cited specimen: BMNH 1996146.

Material: North America Basin: Atlantis II, sta. 73, 2 spec.; sta. 118, 1 spec. West European Basin: Sarsia, sta. S61, 1 spec.; sta. S63, 4 spec.; Thalassa, sta. Z400, 1 spec.; sta. 435, 2 spec.; Biogas IV, sta. DS51, 1 spec. Canary Basin: Discovery, sta. 6696, 1 spec.

Distribution: This species occurs at mid-

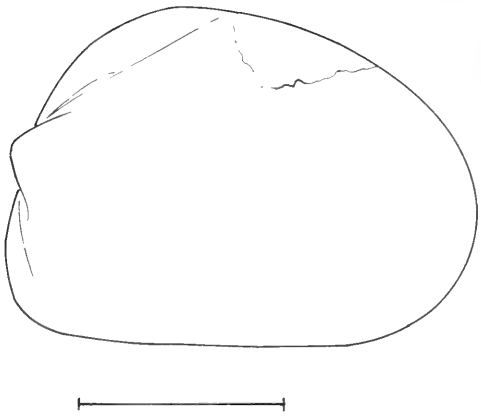

FIG. 20. *Dacrydium viviparum.* Lateral view from the left side of the shell of the paratype BMNH 1983035. Scale = 1 mm.

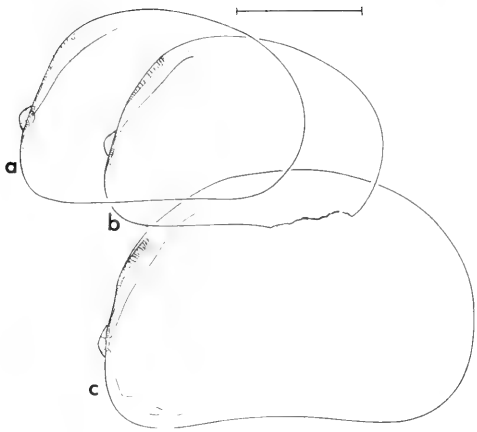

FIG. 22. *Dacrydium wareni.* Lateral internal views of right valves from (a) Sarsia sta. S63, Bay of Biscay, 1336 m; (b) Thalassa sta. Z400, West European Basin, 1175 m and (c) Atlantis II sta. 118, North America Basin, 1135–1153 m. Scale = 1 mm.

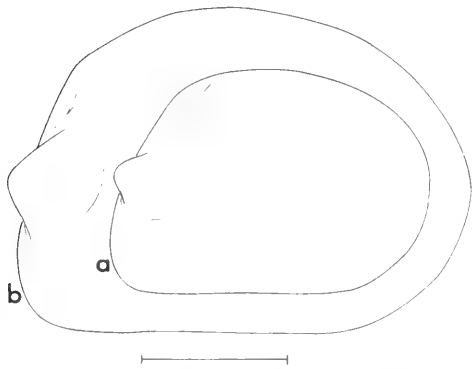

FIG. 21. *Dacrydium wareni.* Lateral view from the left side of two shells from (a) Sarsia sta. S63, Bay of Biscay, 1336 m and (b) from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 1.0 mm.

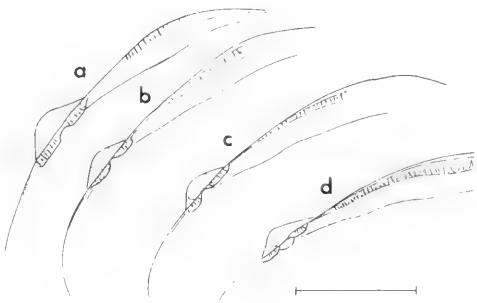

FIG. 23. *Dacrydium.* Comparative detail of the hinges of four left valves. (a) *Dacrydium viviparum.* Paratype, BMNH 1983035, Ingolf sta. 78, Reykjanes Ridge, 1505 m; (b) *Dacrydium wareni.* Thalassa sta. Z400, West European Basin, 1175 m, (c) Sarsia sta. S63, Bay of Biscay, 1336 m and (d) Atlantis II sta. 118, North America Basin, 1135–1153 m. Scale = 0.5 mm.

slope depths in the temperate North Atlantic and western Mediterranean (depth range: 952–2340 m). Maximum length of present specimens, 4.4 mm.

Shell Description (Figs. 20–23). Salas & Gofas (1997) give a description *D. wareni,* which is extended here. The present specimens were recognized as belonging to a new species before the description by the latter authors was published. The present specimens correspond in every respect with their excellent description. Salas & Gofas (1997) do not describe the internal morphology.

Shell small, transluscent white, semi-ovate, greatest height dimension usually anterior to mid vertical axis, but may be coincident or slightly posterior to axis in larger specimens; umbo small, distant from the antero-ventral limit of shell; maybe one or two faint radial lines from umbo to mid-dorsal and postero-dorsal margin respectively, faint incremental lines present; anterior shell margin ventral to umbo a shallow, convex curve dorsal to umbo almost straight, steeply inclined, meeting broadly convex dorsal margin in slight break

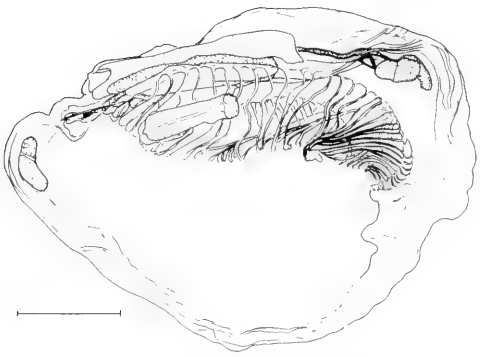

FIG. 24. *Dacrydium wareni.* Semidiagrammatic view from the left side of the internal morphology of a male specimen from Atlantis II sta. 73, North America Basin, 1330–1470 m. Scale = 0.5 mm. See Fig. 3 for the identification of parts.

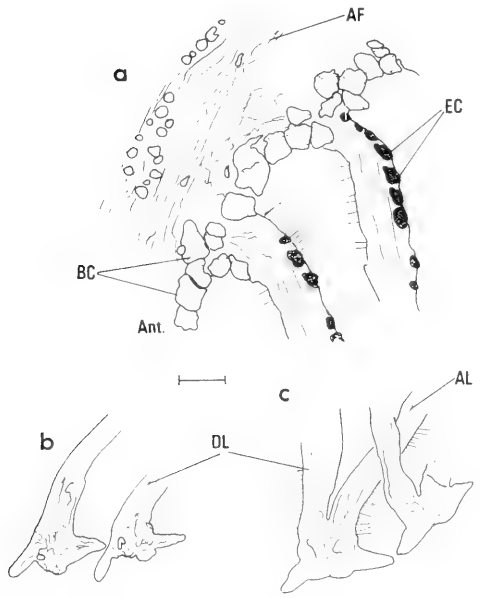

FIG. 25. *Dacrydium wareni.* Detail of (a) the distribution of gland cells at junction of the filaments of the inner demibranch with the gill axis; (b) ventral margin of two filaments of the outer demibranch and (c) of the inner demibranch. Scale = 50 µm. Refer to Materials & Methods for list of abbreviations.

opposite dorsal limit of hinge plate; dorsal and posterior margins forming a smooth curve; ventral margin almost straight or very slightly concave; hinge with short anterior plate with up to 8 teeth; posterior plate in two parts, that close to umbo is of similar length to anterior plate and with up to 8 teeth, narrow, edentulous posterior to this section, followed by elongate section with 16–34 nepioconch teeth (dependent on specimen size) similar to the posterior hinge plates of other species; relatively broad buttress extending from umbo to a point opposite highest point of shell; small ridge extending for short distance ventral to anterior hinge plate; internal ligament amphidetic, ventral to umbo; secondary external ligament, opisthodetic, slender, consisting of fused periostracum. Prodissoconch length: 121–130 µm.

Internal Morphology (Figs. 24, 25). The internal morphology is similar to that of *D. ockelmanni.* The adductor muscles are relatively small and similar in size. The anterior muscle is crescent-shaped in cross section, and the posterior adductor is oval. The gills have an inner demibranch comprising of descending and ascending lamellae and a short posterior outer demibranch comprising of a descending lamella. The size of the latter varies according to the length of the animal. In a specimen 2.4 mm total length, there are 16 closely arrayed filaments forming the outer demibranch. In the same specimen, there are 25 filaments in the inner demibranch, but these are much more widely separated than those of the outer demibranch. The latter occupies less than a fifth of the total gill area. The reflected ascending filament of the inner demibranch is approximately half the length of the descending. As in other species, at the tips of the filaments of the outer demibranch and at the point of reflection (ventral edge) of the inner demibranch, there are a pair of horn-like processes oriented along the horizontal axis and which bridge the interfilamentar gap. In addition, dorsally the gills are well supplied with gland cells (Fig. 25). These comprise 8–10 small eosinophilic cells on the outer posterior face of the filament close to where it joins the axis, and numerous large squamous basiphyllic cells lining the arch of axial tissue joining the filaments ventral to the axial muscle. The mouth is a particularly broad, shallow cone without palps on the lower lip and tiny palp rudiments on the upper lips, with traces of two or possibly three ridges. The viscera are similar to those of the previous species.

No mature specimens or specimens brooding eggs were present in the available samples.

Not mentioned by Salas & Gofas (1997) is the similarity in shell and hinge form to *D. vi-*

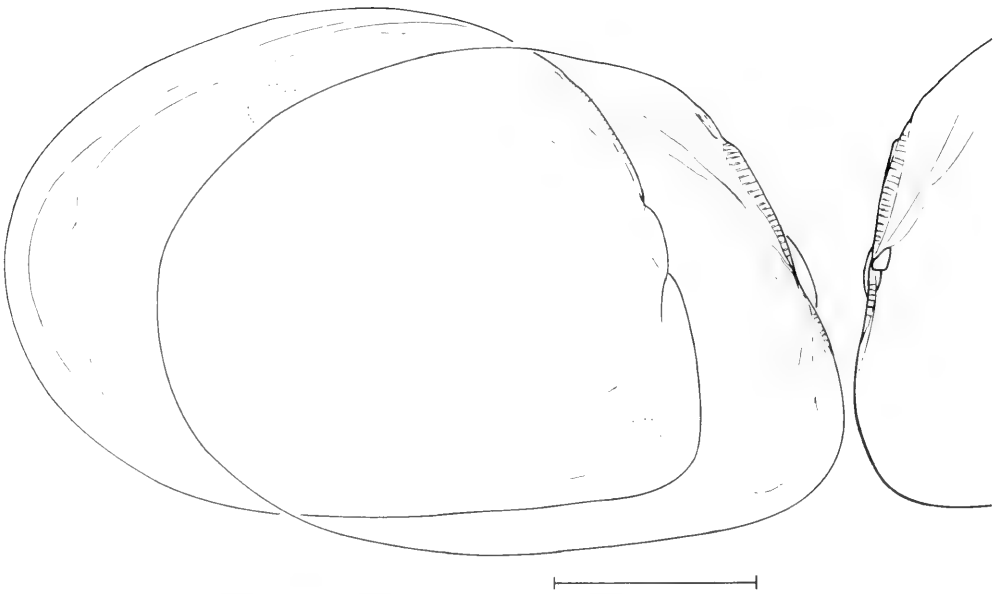

FIG. 26. *Dacrydium angulare*. Lateral view of a shell from the right side, an internal view of a left valve and detail of the hinge of a right valve from Atlantis II sta. 202, Angola Basin, 1427–1643 m. Scale = 0.5 mm.

viparum (Ockelmann, 1983) (Figs. 20–23). This might be within the range of variation to be expected within a species of *Dacrydium,* but, because of the great difference in size of the prodissoconch of specimens of *D. viviparum* described by Ockelmann (1983) (252–292 μm) and the lack of evidence of viviparity in the present specimens, the case for synonymy is doubtful. The Ockelmann material was taken from latitude 60°N–64N°, in comparison with 32°N–48°N for the present specimens, and it seems unlikely that there could be so much variation in egg size and development between northern and southern populations. Nevertheless, the prodissoconch length of *D. wareni* reported by Sales & Gofas (1997) is larger (approx. 170 μm) than that of the present specimens. This is the only difference in our respective descriptions.

Dacrydium angulare Ockelmann, 1983
Figs. 26–28

Type Locality: Vema Sta. 54, Cape Basin, 34°35′S 17°31′E, 1849 m.

Type Material: Holotype and paratypes ZMUC; paratypes USNM 822398.

Original Description: Ockelmann 1983: 114, figs. 46–48, 51 (for other references, see Appendix 2).

Cited specimen: BMNH 1996147.

FIG. 27. *Dacrydium angulare*. Lateral view of shell from the right side and detail of the hinge of a left valve from J. Charcot Walda sta. DS13, Angola Basin, 3985 m. Scale a = 1 mm; scale b = 0.5 mm.

Material: Angola Basin: Walda, sta. DS13, 10 spec.; Atlantis II, sta. 202, 7 spec.

Distribution: This species occurs at lower slope to abyssal depths in the Cape Verde, Angola and Cape basins. Depth range 1427–3985 m.

Shell Description (Figs. 26, 27). Shell small (<4.0 mm), fragile, semi-transluscent, moderately elongate, greatest height coinciding with

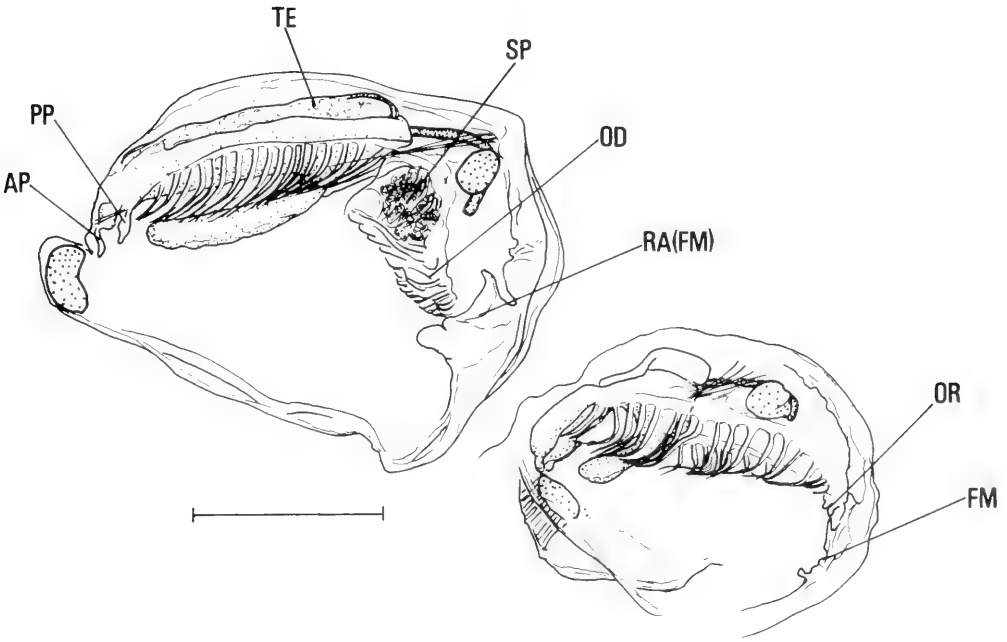

FIG. 28. *Dacrydium angulare*. Semidiagrammatic views from the left side of the internal morphology of a mature male and an immature specimen from J. Charcot Walda sta. DS13, Angola Basin. Scale = 1 mm. Refer to Materials & Methods for list of abbreviations and to Fig. 3 for identification of other parts.

the mid-vertical axis, extremely fine close concentric sculpture with faint growth lines; umbo moderately small, some distance from the antero-ventral limit of shell; ventral margin slightly sinuous in large specimens, otherwise broadly convex, joining posterior margin in smooth, deep curve; dorsal margin broadly convex, somewhat angulate at limit of posterior hinge plate; antero-dorsal margin slightly convex, high-angled in relation to ventral margin; anterior margin indented ventral to umbo particularly in large specimens, then slightly convex dorsal to antero-ventral margin; anterior hinge plate, narrow, short, with 3–7 indistinct nepioconch teeth, narrow edentulous subumbonal section joining relatively short posterior hinge plate, 20–28 nepiconch teeth; posterior buttress relatively broad, extending beyond dorsal limit of hinge plate to a point approximately twice the length of the posterior hinge plate; antero-ventral ridge short, extending to posterior limit of anterior adductor scar, less sharply deliniated than posterior buttress; ligament small, internal, amphidetic. Prodissoconch length: 159–165 μm (Ockelmann, 1983), 165–170 μm (Salas & Gofas, 1997), present specimens 170 μm.

The present specimens differ slightly from the excellent description given by Ockelmann (1983). The sinuous ventral shell margin of larger specimens is somewhat more pronounced than those described by Ockelmann (1983), but similar to those of Salas & Gofas (1997). The present specimens also have a more marked indentation ventral to the umbo and have a less extended anterior hinge plate with fewer teeth (see Ockelmann 1983: fig. 47). Such slight variation can be expected in specimens of differing size and from different basins.

Internal Morphology (Fig. 28). The internal morphology was described in detail by Ockelmann (1983), but, except for the oral field, not figured. Minor additions are given here. The adductor muscles are moderate and equal in size. Both inner and outer demibranchs are present in the largest specimens, and the filaments are relatively short. The first rudiments of the outer demibranch appear in specimens of approximately 2.0 mm length. The palps, although minute, are larger than other species examined. Ockelmann (1983) notes that "posterior fusion of the inner mantle folds large and muscular" and that "gills attach slightly below its upper border." He then further notes that the "inner mantle lobes sur-

rounding the inhalent and pedal opening" are well developed. He clearly believes that the pedal and and inhalent openings are combined, although he has noted the thickened muscular development ventral to the gill attachment. It has been possible, in the present samples, to demonstrate that the posterior inner mantle fold enlarges as the outer demibranch develops and the gonads mature. One mature male was found with sperm packed in the space enclosed by the outer demibranch (Fig. 28), and this specimen showed the greatest development of the posterior inner mantle fold and a channel to the exterior.

Dacrydium hedleyi, new species
Figs. 29–31

Type Locality: Knorr Cruise 25 sta. 287, 13°16.0′N 54°52.2′W–13°16.8′N 54° 53.1′W, 4980–4934 m.

Type Material: Holotype BMNH 1996143.

Material: Guyana Basin: Knorr, sta. 287, 2 spec.; sta. 288, 9 spec.; sta. 291, 23 spec.; Biovema, sta. DS11, 2 spec.

Distribution: This species appears to be restricted to abyssal depths in the Guyana Basin. Depth range: 3859–5867 m.

Shell description (Figs. 29, 30). Shell small, fragile, modioloid, transluscent when fresh, turning opaque white on death or preservation, growth lines faint, without other ornamentation, greatest height anterior to mid-vertical axis; umbo relatively large, distant from the antero-ventral shell margin; ventral margin concave in smallest specimens, with slight antero-ventral sinuosity in larger specimens, joining posterior and postero-dorsal margins in a broad curve; postero-dorsal margin slightly angulate at posterior limit of hinge plate; anterior margin almost straight, angled to meet ventral margin in acute curve; antero-ventral margin less acute in larger specimens; hinge plates extremely narrow, barely wider than shell thickness; both anterior and posterior plates with 10–15 extremely fine nepioconch teeth; posterior and anterior buttresses faint, barely extending beyond the limits of the hinge plate; ligament small, internal, amphidetic, more or less globular, supported by two very small nymphs ventral to umbo. Prodissoconch length: 167 μm.

Internal Morphology (Fig. 31). The internal morphology differs little from any of the described species above. The adductor muscles are relatively small. The posterior inner mantle folds are fused in the manner described above. The gills comprise the descending lamella of the inner demibranchs. These comprise 12–13 widely spaced gill filaments, the distal half of which are typically angled anteriorly. No outer demibranchs were developed in any of the specimens in the collection.

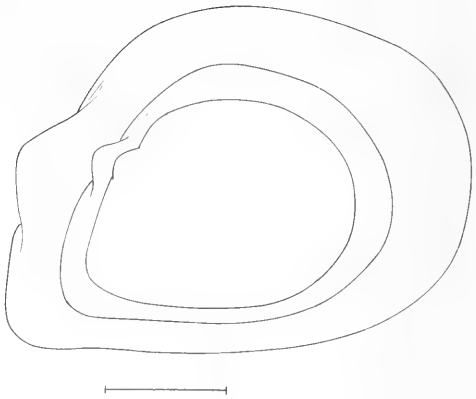

FIG. 29. *Dacrydium hedleyi.* Lateral views of three shells from left side from Knorr sta. 291, Guyana Basin, 3859–3868 m to show changes in shell outline with increasing size. Scale = 0.5 mm.

It is likely that the specimens are all juveniles. No maturing sperm or ova were seen.

The species is named after Dr. Charles Hedley who described Australiasian species of *Dacrydium.*

Diagnosis: This species is characterized by the slender hinge plates and that the greatest height measurement is anterior to the mid vertical shell axis. In shape, *D. hedleyi* resembles that of *D. nipponicum* (Okutani, 1975), but the ventral margin is less concave. The latter species also has stouter hinge plates and shell buttresses, and the adductor scars are much larger.

Dacrydium albidum Pelseneer, 1903
Figs. 32–34

Type Locality: S. Y. Belgica, Sta. 1046, 71°18′S 88°02′W, 400 m.

Type Material: IRSNB.

Cited Specimen: BMNH 1996145.

Material: Weddell Sea: IWSOE, sta. 001, 12 spec.; sta. 002, 3 spec.; sta. 004, 1 spec.; sta. 005, 1 spec.; sta. 007, 3 spec.; sta. 008, 2 spec.; sta. 010, 2 spec.

Distribution:Circum-Antarctic, occurring at outer shelf to mid-slope depths in the Ross, Davis and Weddall seas and off the South Shetland Islands (depth range: 122–1437 m).

Shell Description (Figs. 32, 33). The original description (Pelseneer 1903), although short, is accurate. The description was later extended by Nicol (1966).

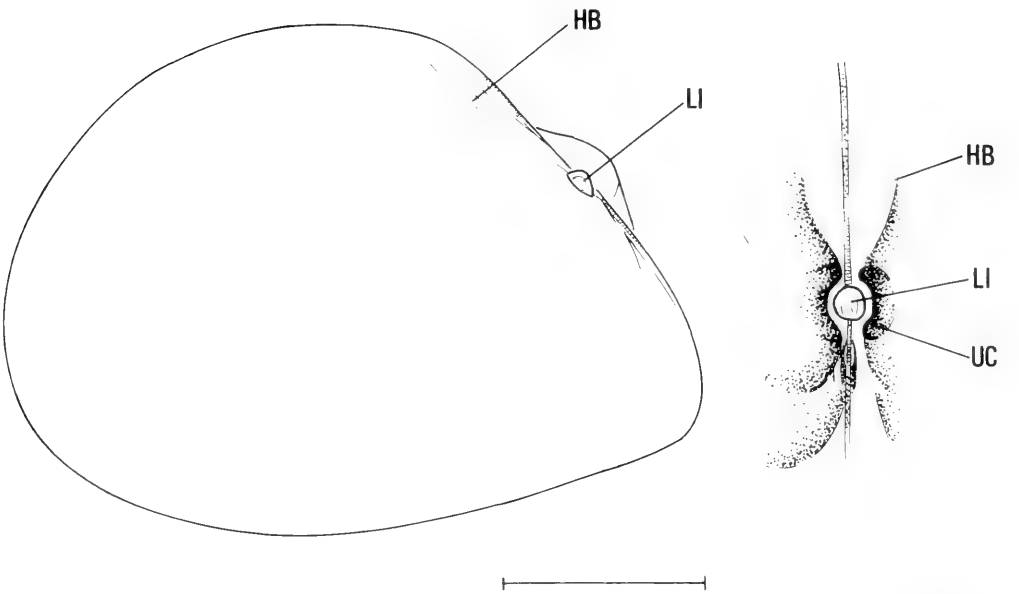

FIG. 30. *Dacrydium hedleyi.* Internal view of a left valve and internal view of an intact hinge and ligament of specimens from Knorr sta. 291, Guyana Basin, 3859–3868 m. Scale = 0.5 mm. Refer to Materials & Methods for list of abbreviations.

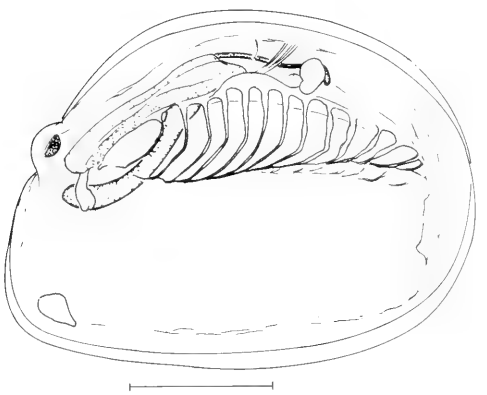

FIG. 31. *Dacrydium hedleyi.* Semidiagrammatic view of the internal morphology as seen through the transparent shell of a specimen from Knorr sta. 291, Guyana Basin, 3859–3868 m. Scale = 0.5 mm. See Fig. 3 for identification of parts.

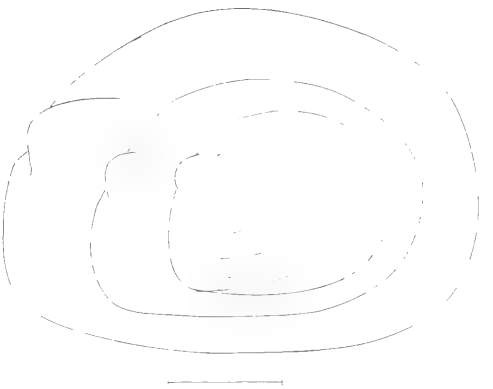

FIG. 32. *Dacrydium albidum.* Lateral views of three shells from the International Weddell Sea Oceanographic Expedition sta. 002, 412 m, to show differences in outline with increasing growth. Scale = 0.5 mm.

Shell small (<5 mm), fragile, greatest height varies from slightly anterior to mid-vertical axis to slightly posterior, opaque white or hyaline, with faint growth lines, periostracum very pale brown; umbo moderately large, relatively distant from antero-ventral limit of shell; ventral margin almost straight, in large specimens sometimes very slightly sinuous; posterior margin broadly rounded, joining postero-dorsal margin in a smooth curve; anterior margin ventral to umbo relatively elongate, convex, slightly incurved at umbo; antero-ventral margin smoothly rounded; anterior hinge plate short, slightly expanded internally, with 7–8

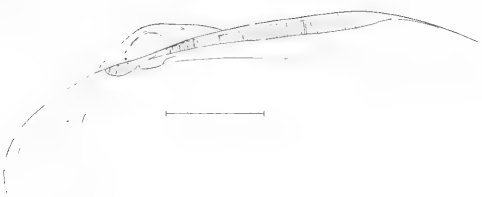

FIG. 33. *Dacrydium albidum.* Detail of hinge of right valve of a specimen from the International Weddell Sea Oceanographic Expedition sta. 001, 728 m. Scale = 0.5 mm.

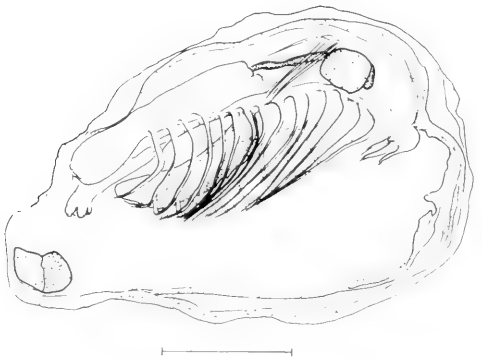

FIG. 34. *Dacrydium albidum.* Semidiagrammatic view from the left side of the internal morphology of a specimen from the International Weddell Sea Oceanographic Expedition sta. 004, 793 m. Scale = 0.5 mm. See Fig. 3 for identification of the parts.

nepioconch teeth; short edentulous section dorsal to ligament connecting with long posterior plate, terminating just short of the highest point of shell, with 50–55 nepioconch teeth; broad posterior buttress extending from ligament and slightly angled to hinge plate, terminating opposite highest point of shell; short, curved antero-ventral buttress terminating dorsal to anterior adductor muscle; ligament internal, ventral to umbo, amphidetic, elongate-oval. Prodissoconch length: 213 µm.

Nicol (1966) orientated the shell such that his dorsal margin equates with the anterior margin as described here and by others. He also overlooked the anterior nepioconch teeth.

Internal Morphology (Fig. 34). The internal morphology differs little from those described above. The adductor muscles are larger than in most other species. In addition, the outer palps, although still much reduced, are larger than in other species and have two well-defined ridges. The gills comprise of the inner demibranch, with descending and ascending lamellae and a rudiment of outer demibranch with a few unreflected filaments at the posterior end of the gill axis. In a specimen of 2.5 mm total length, the outer demibranch comprises two very short unreflected filaments.

Dell (1990) figure a specimen from the R. V. Eltanin collections from the Ross Sea which, although identical in other respects, has the highest point of the shell slightly posterior to the mid-vertical axis, and he refered to shell variation, though without definition, when he stated that "valves varying to such a degree" that he, like Nicol (1966), could not separate *D. albidum* from *D. modioliforme* Theile (1912). Poitiers (1989) also remarked on the confusion and refers to a bathyal complex of forms involving *D. albidum* and *D. modioliforme*.

The original description of *D. modioliforme* (Theile, 1912) does differ little from the description of *D. albidum,* and the type specimen came from a depth (385 m) within the range of the latter species. Specimens identified as *D. modioliforme* from abyssal depths (e.g., Theile & Jaeckel, 1931) do differ from *D. albidum* (Knudsen, 1970) (see below).

Dacrydium knudseni, new species
Figs. 35–37

Type Locality: International Weddell Sea Oceanographic Expedition sta. 023, 72°47.6′S 30°29.7′W, 3697 m.

Type Material: Holotype BMNH 1996142.

Material:Weddell Sea: IWSOE, sta. 022, 3 spec.; sta. 023, 6 spec.; sta. 027, 10 spec.

Distribution: This species is distributed at abyssal depths in the Weddell Sea. Depth range: 3111–4636 m.

Shell Description (Figs. 35, 36). Shell small, fragile, relatively short, maximum height more or less coincident with mid-vertical axis, opaque white, with fine concentric growth lines; umbo moderately large, distant from antero-ventral limit of shell; ventral margin a shallow convex curve in small specimens, straight and sometimes faintly concave in larger specimens; postero-ventral and posterior margins forming a smooth, broad curve; postero-dorsal margin slightly flattened in most specimens; anterior margin slightly indented ventral to umbo, forming a relatively long convex curve, making a characteristic

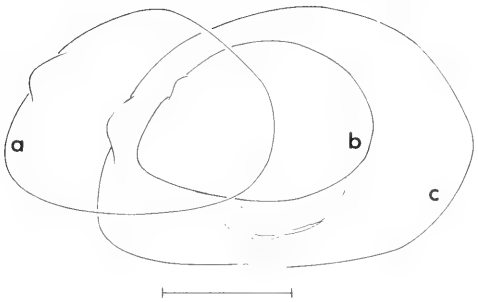

FIG. 35. *Dacrydium knudseni.* Lateral views of three shells from the International Weddell Sea Oceanographic Expedition sta. (a) 022, 3111 m; (b & c) 023, 3697 m, to show variation in outline. Scale = 1 mm.

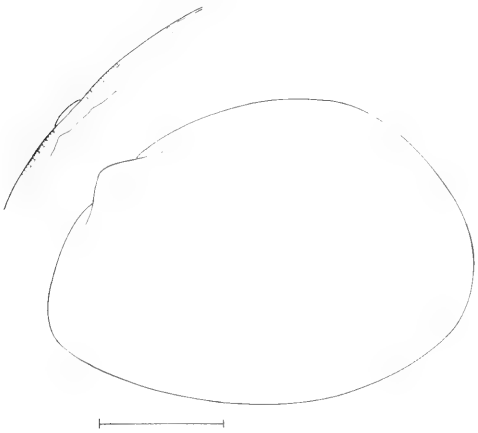

FIG. 36. *Dacrydium knudseni.* Lateral view of a shell from the left side and detail of the hinge of a right valve. Specimens taken by the International Weddell Sea Oceanographic Expedition sta. 023, 3697 m. Scale = 0.5 mm.

acutely rounded antero-ventral shell margin; anterior and posterior hinge plates narrow, each with 15–17 nepioconch teeth, moderately long, narrow edentulous section ventral to umbo joining the toothed parts; posterior hinge plate short; posterior buttress moderately narrow, extending from anterior limit of posterior hinge plate to a short distance posterior to the posterior plate buttress, continuing ventral to umbo and accommodating the resilifer; ligament ventral to umbo, amphidetic, oval. Prodissoconch length: 195 µm.

Internal morphology (Fig. 37). The internal morphology is similar to that of *D. albidum.* Differences include smaller adductor muscles, gills that comprise only the descending

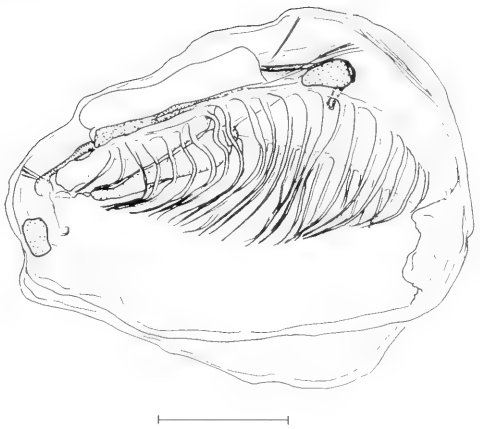

FIG. 37. *Dacrydium knudseni.* Semidiagrammatic view of the internal morphology of a specimen from the International Weddell Sea Oceanographic Expedition sta. 027, 4575 m. Scale = 0.5 mm. See Fig. 3 for the identification of parts.

lamellae of the inner demibranchs and no outer demibranchs. The dorsal lip is characteristically elongate and with a minute palp rudiment.

Dacrydium knudseni is named after Dr. Jørgen Knudsen, distinguished deep-sea malacologist who first recognized that there was a clear difference between the deep-water Antarctic specimen collected by the R. V. Valdivia and the more shallow water species *D. albidum.*

Diagnosis: *Dacrydium knudseni* is characterized by an acutely angled antero-ventral shell margin and approximately equal numbers of nepioconch teeth on the anterior and posterior hinge plates. It most closely resembles *D. panamensis* Knudsen, 1970, the latter differing in having a more foreshortened antero-ventral shell margin, a shorter anterior hinge plate with fewer teeth, a shorter edentulous section, and a more extensive inner buttress.

Dacrydium sp. a
Figs. 38, 39

Specimen: MNHNP

Material: Cape Basin: Walvis, sta. DS05, 2 spec.

Distribution: These are juveniles of an abyssal species that has only been recorded from one locality at abyssal depth (4560 m) immediately south of the south west extremity of the Walvis Ridge.

Shell Description (Figs. 38, 39). Shell tiny,

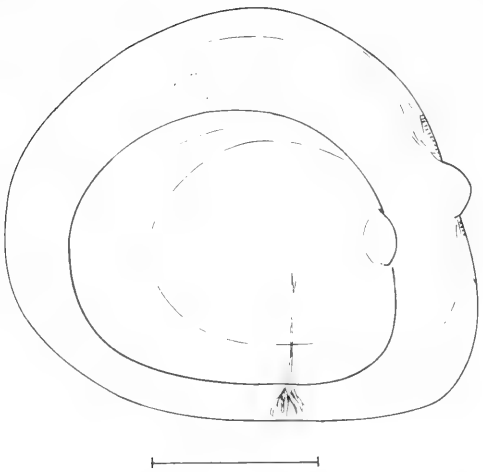

FIG. 38. *Dacrydium* sp. a. Lateral views of two shells from the left side from J. Charcot Walvis Expedition sta. DS05, Cape Basin, 4560 m. Scale = 0.5 mm.

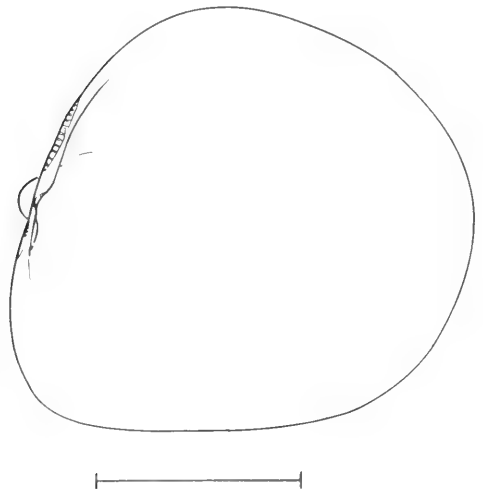

FIG. 39. *Dacrydium* sp. a. Internal view of a right valve from J. Charcot Walvis Expedition sta. DS05, Cape Basin, 4560 m. Scale = 0.5 mm.

broadly ovate, semitranslucent, with a few faint growth lines; greatest shell height very slightly anterior to the mid-vertical axis, only slightly longer than high; umbo moderately large, prominent, distant from the antero-ventral margin; ventral margin almost straight, at most slightly convex; posterior and dorsal margins broadly rounded; anterior margin in hinge region almost straight, antero-ventrally meeting ventral margin in a broad curve; hinge plates short, narrow; posterior plate with 12–14 nepioconch teeth; anterior plate with 2–4 teeth; plates reinforced by narrow buttresses that parallel the shell margin rather than deviating from it; ligament internal, amphidetic, rounded. Prodissoconch length 185 μm.

Internal Morphology. The internal morphology, as seen through the transparent shell, appears to be similar to that of *D. hedleyi.* The adductor muscles are moderately large, and only the inner demibranch is present. The foot is particularly slender and secretes a byssus composed of many extremely fine strands.

Although the shell shape with its great height is so distinctive, because only two tiny, fragile, juvenile specimens (1 mm and 1.5 mm total length) were taken, it was decided not to name a new species at this stage.

Dacrydium sp. b
Fig. 40

Specimen: BMNH 1996148.

Material: Brazil Basin: Atlantis II, sta. 167, 20 spec.

Distribution: This species was taken at one mid-slope station in the Brazil Basin, 943–1007 m.

Shell Description (Fig. 40). Shell, tiny, extremely fragile, broadly ovate, with very fine, close, concentric lines, opaque white, greatest height coincident with or slightly anterior to mid-vertical axis; umbo relatively large, distant from antero-ventral shell margin; ventral shell margin straight or slightly convex; posterior margin broad, rounded, joining dorsal margin in a smooth curve; antero-dorsal margin angulate at limit of posterior hinge plate; anterior margin straight, almost vertical to rounded antero-ventral margin; ventral margin varies from slightly convex in smallest specimens, through straight, to slightly concave in largest specimens; hinge plates relatively short, narrow; posterior plate with 15–16 nepioconch teeth; anterior plate slightly shorter with 9–10 teeth; posterior shell buttress, narrow, not extending far beyond limit of hinge faint anterior buttress extending short distance towards anterior adductor; ligament internal, amphidetic, relatively large, globular. Prodissoconch length: 122–129 μm.

Internal Morphology (Fig. 40). The internal morphology is similar to that of the preceeding species. The adductor muscles are small and round, the anterior somewhat smaller than the posterior. Mantle fusion is similar to that in other species but little thickened, suggesting

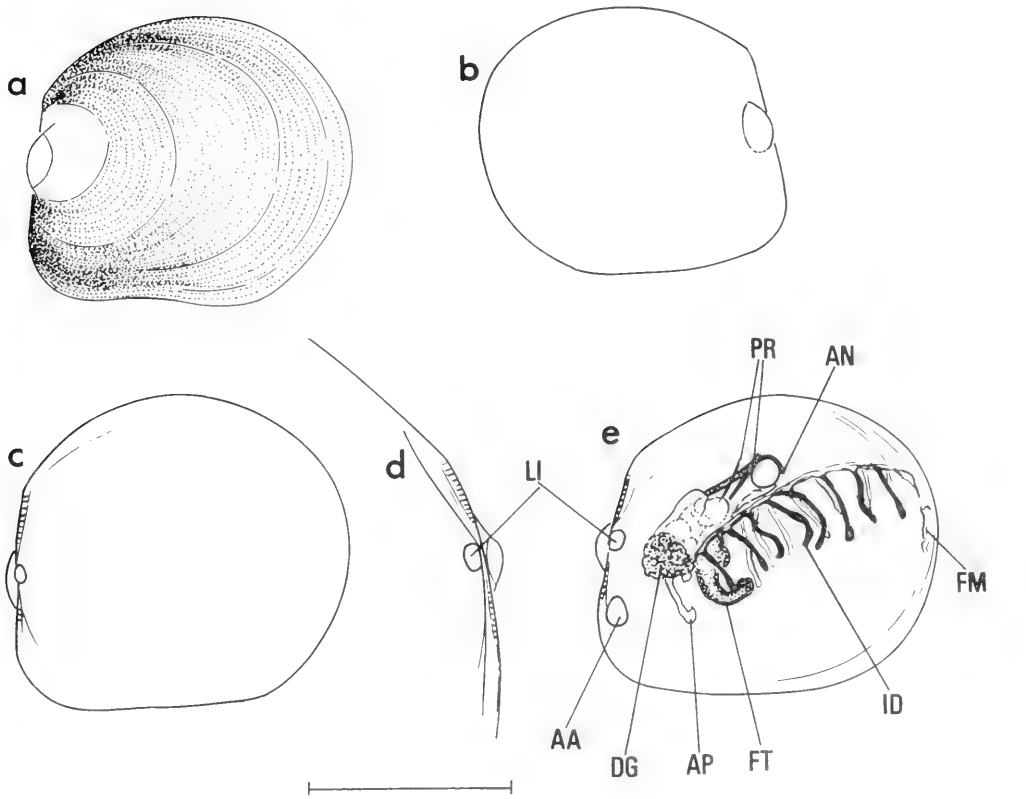

FIG. 40. *Dacrydium* sp. b. Lateral view of (a) shell from the right side; (b) outline of shell from left side; (c) internal view of right valve; (d) detail of hinge of left valve; (e) semidiagrammatic view of the internal morphology as seen through a transparent shell from the left side. Specimens from Atlantis II sta. 167, Brazil Basin, 943–1007 m. Scale = 1 mm a, b, c and e; = 0.5 mm d. Refer to Materials & Methods for list of abbreviations.

that these are juvenile specimens. There is no outer demibranch, and the inner demibranchs consists of 10–12 unreflected descending filaments in a specimen of 1.7 mm total length. Unlike other species, in which the foot extends anteriorly within the canopy of the gill filaments, here the foot is recurved so that the tip is facing posteriorly, but this is is likely to be an artifact of preservation. The palps are small, distal enlargements of the lips, the upper of which are extended. The course of the gut is similar to that of other species, but the digestive diverticula comprise of a pair of sacs lateral to the stomach. In this, they resemble the post-larval gut of other bivalves.

The internal features all suggest that these specimens are the juveniles of a larger species rather than neotenous adults of a miniature species. In addition, the shell shape is reminiscent of the nepioconch stage in mytilid development. It is for these reasons, and the fact that the shells of all but two or three of the specimens have disintegrated, that this species is not named, even though it has characters unlike those any other described species.

DISCUSSION

The species of the genus *Dacrydium* are present throughout the world's oceans and, for the most part, in deep waters (>500 m). They are anchored by a fine tuft of byssus threads and may form nesting congregations incorporating fine sediment, without the shell fragments and sediment particles that form the nests of *Lima hians,* as described by

Gilmour (1967). In many cases, there is clear evidence in the form of attached tissue and spicules that they are associated with sponges. It is not known whether this is a universal association. Other mytilids are known to occur with sponges, tunicates and, even, skulls of whales, although not necessarily all the species of a genus are associated with a particular phylum.

All species are small (<6 mm and the majority approximately 3 mm) and fragile, with unpigmented shells that are either translucent or opaque and with little or no ornamentation. Some species may have faint radial and/or concentric lines. The species can be distinguished by the shell outline and hinge morphology. This includes the position of the greatest height of the shell in relation to the mid-vertical axis of the shell, the extent of the anterior and posterior hinge plates, the number of nepioconch teeth on the hinge plates, and the degree of development of a shell buttress associated with the hinge plate. Ockelmann (1983) points out that the dacrydines have shells that are homologous to the nepioconch stage of other mytilids, sometimes with provincular teeth present, and always with a series of anterior and posterior teeth homologous with nepioconch teeth.

There is a degree of variation in the shape of the shell outline and hinge features in all species, and this has been noted by other authors (e.g., Nicol, 1966; Poitiers, 1989). This involves variation irrespective and respective of size. The curvature of the ventral margin changes with growth, becoming straighter or more concave or more sinuous. In addition, the position of maximum shell height tends to shift posteriorly with growth.

The internal morphology displays a number of features characteristic of the genus. While the adductor muscles vary in size and, as in the case of other mytilids, the anterior may be smaller than the posterior, the latter is always relatively well-developed. The posterior adductor muscle is not excessively enlarged. There must be a balance between the size and strength of the muscle and the strength of such a thin, fragile, shell. It is clear that the buttresses play a part in the balance of adductor forces and shell strength. The mantle margins are specialized in only one respect, namely the development of an aperture coincident with gonad maturity. It is homologous with the inhalent aperture of other lamellibranchs. It would appear that it develops as a channel for the release of sexual products and is probably not concerned with the inhalent flow, which is through the extensive pedal gape. The "inhalent" aperture is formed from the inner mantle folds, which are developed inwards. There no development of tentacles or papillae from the middle sensory mantle fold, and the structure has never been seen extended beyond the shell margins. It is more developed in the larger specimens of each species and only in specimens with maturing gonads has a lumen to the exterior been clearly identified. Prior to discharge, the eggs and sperm appear to be shed into the space enclosed by the outer demibranchs of species that develop them. Like the aperture, the full development of the outer demibranchs coincides with maturity.

The gills are unusual. In the juveniles, and in some species the mature adult, only the inner demibranchs are present. Species in which the outer demibranchs are absent in the adult are among those that occur at abyssal depths. The inner demibranchs consist of a relatively few widely spaced filaments (approx. 10–20). There are no interlamellar or interfilamentar connectives. Although the gill filaments in a few of the smallest specimens hang vertically within the mantle cavity, in most others the filaments are characteristically bent in an anterior direction at a point half way along their length. The outer demibranchs develop from gill rudiments at the posterior limit of the axes. The outer demibranchs at maximum extend anteriorly to about a third of the axial length. Their filaments are more closely set together and are not bent forward. It is hypothesized that the aperture and, when present, the outer demibranch combine to form a reproductive mechanism that canalizes the movement of eggs and sperm to ensure successful fertilization and the release of eggs or larvae. Sexes are separate. Although Ockelmann (1983) and Salas & Gofas (1997) showed that in *D. viviparum, D. hyalinum* and *D. balgimi* the eggs are incubated in the suprabranchial chamber, none of the species described here had embryos developing within the mantle cavity. Egg and prodissoconch size varies considerably among species, but it appears in general that those of abyssal and high latitude species are significantly larger than those of bathyal or shelf species in lower latitudes.

Other features characteristic of the genus include the dorsal position of the viscera. The oesophagus, stomach and combined style sac, and midgut are elongate and lie parallel

to the antero-posterior axis close to the shell buttress. Similarly, the foot is elongate and tubular and in the contracted state also lies parallel with this axis within the space enclosed by the inner demibranchs. The shell buttress provides the attachment surface for the pedal retractors.

Another unusual feature involves the palps and lips. The palps are extremely small, with no more than the rudiments of two small ridges being present. However, the upper lips tend to be elongate and attached vertically to the mantle such that they form a collecting area immediately ventral to the mouth, at the point where food particles from the filaments accumulate. The ventral margin of the filaments of the inner demibranch, which is construed as the main food collector, are laterally extended so that the lateral cilia interlock with those of the adjacent filaments. It is likely that there is little sorting of food particles on gills and palps.

The combination of these features gives a unique functional design, which fully supports Ockelmann (1983) in his decision to erect a new subfamily. Ockelmann (1983) argues that the dacrydines are probably derived from the crenellines rather than the modiolines as suggested by Soot-Ryen (1969), and the present study supports this view.

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APPENDIX 1.
Stations from which material was collected

Cruise	Station	Depth (m)	Latitude	Longitude	Date	Gear
			NEWFOUNDLAND BASIN			
Chain 106	331	4793	41°13.0′N	41°36.7′W	29.8.72	ES
			NORTH AMERICA BASIN			
Atlantis 277	D	466–508	39°54.5′N	70°35.0′W	23.5.62	AD
Atlantis II 12	62	2496	39°26.0′N	70°33.0′W	21.8.64	ES
	64	2886	38°46.0′N	70°06.0′W	21.8.64	ES
	66	2802	38°46.7′N	70°08.8′W	21.8.64	ES
	70	4680	36°23.0′N	67°58.0′W	23.8.64	ES
	72	2864	38°16.0′N	71°14.0′W	24.8.64	ES
	73	1330–1470	39°46.5′N	70°43.3′W	25.8.64	ES
Atlantis II 17	93	4926–5007	34°39.0′N	66°26.0′W	14.12.65	ES
Chain 50	76	2862	39°38.3′N	67°57.8′W	29.6.65	ES
	80	4970	34°49.8′N	66°34.0′W	2.7.65	ES
	83	5000	34°46.5′N	66°30.0′W	3.7.65	ES
	84	4749	36°24.4′N	67°56.0′W	4.7.65	ES
	85	3834	37°59.2′N	69°26.2′W	5.7.65	ES
Chain 50	87	110	39°48.7′N	70°40.8′W	6.7.65	ES
	88	478	39°54.1′N	70°37.0′W	6.7.65	ES
Chain 58	103	2022	39°43.6′N	70°37.4′W	4.5.66	ES
	105	530	39°56.6′N	71°03.6′W	5.5.66	ES
Atlantis II 24	115	2030–2050	39°39.2′N	70°24.5′W	18.8.66	ES
	118	1135–1153	32°19.4′N	64°34.9′W	18.8.66	ES
	119	2095–2223	34°15.8′N	64°31.6′W-	19.8.66	ES
			32°16.1′N	64°32.6′W		
Atlantis II 30	128	1254	39°46.5′N	70°45.2′W	16.12.66	ES
Chain 88	210	2024–2064	39°43.0′N	70°46.0′W-	22.2.69	ES
			39°43.2′N	70°49.5′W		
Knorr 35	346	475	39°54.1′N	70°10.7′W	3.12.73	ES
			GUYANA BASIN			
Knorr 25	287	4980–4934	13°16.0′N	54°52.2′W-	24.2.72	ES
			13°16.8′N	54°53.1′W		
	288	4417–4429	11°02.2′N	55°05.5′W-	25.2.72	ES
			11°03.8′N	55°04.8′W		
	291	3859–3868	10°06.6′N	55°15.4′W	26.2.72	ES
	306	3392–5073	09°31.1′N	56°24.4′W	2.3.72	ES
J. Charcot	CP02	5073	10°59.0′N	45°15.0′W	14.11.77	CP
Biovema	DS05	5100	10°46.0′N	42°40.3′W	18.11.77	ES
(Vema)	DS11	5867	11°37.5′N	32°53.8′W-	26.11.77	ES
			11°37.6′N	32°52.8′W		

			BRAZIL BASIN			
Atlantis II 31	142	1624–1796	10°30.0′N	17°51.5′W	5.2.67	ES
	144	2051–2357	10°36.0′N	17°49.0′W	6.2.67	ES
	147	2934	10°38.0′N	17°52.0′W	6.2.67	ES
	155	3730–3783	00°03.0′S	27°48.0′W	13.2.67	ES
	156	3459	00°46.0′S	29°28.0′W	14.2.67	ES
	167	943–1007	07°58.0′S	34°17.0′W	20.2.67	ES
	169	587	08°38.0′S	34°23.0′W	21.2.67	ES
			ARGENTINE BASIN			
Atlantis II 60	239	1661–1669	36°49.0′S	53°15.4′W	11.3.71	ES
	240	2195–2323	36°53.4′S	53°10.2′W	12.3.71	ES
	245	2707	36°55.7′S	53°01.4′W	14.3.71	ES
			WEST EUROPEAN BASIN			
Sarsia	S33/2	1537–183	43°41.0′N	03°36.0′W	13.7.67	ES
	S44	1739	43°40.8′N	03°35.2′W	16.7.67	ES
	S50	1102	43°46.7′N	03°38.0′W	18.7.67	ES
	S61	952	46°20.5′N	04°36.0′W	24.7.67	ES
	S63	1336	46°17.5′N	04°45.2′W	24.7.67	ES
	S66	1472	40°16.3′N	04°44.0′W	25.7.67	ES
Discovery	7601	3100	43°51.8′N	03°43.4′W	4.9.76	AD
Challenger E	80–73	900–2300	'off Rockall'		-.-.73	ES
Chain 106	313	1491–1500	51°32.2′N	12°35.9′W	17.8.72	ES
	318	2560	50°27.3′N	13°20.9′W	19.8.72	ES
	321	2868–2890	50°12.3′N	13°35.8′W	20.8.72	ES
J. Charcot Biacores	245	4270	40°57.0′N	22°16.0′W	14.11.71	CLG
La Perle Biogas I	DS11	2205	47°35.5′N	08°33.7′W	8.8.72	ES
J. Charcot Polygas	DS15	2246	47°35.2′N	08°40.1′W	21.10.72	ES
	DS17	2103	47°32.0′N	08°45.5′W	22.10.72	ES
	DS18	2138	47°32.2′N	08°′N.9′W	22.10.72	ES
	DS20	4226	47°33.0′N	09°36.7′ W	24.10.72	ES
	DS21	4190	47°31.5′N	09°40.7′W	24.10.72	ES
	CV13	4252	47°31.8′N	09°34.2′W	25.10.72	CV
	DS22	4144	47°34.1′N	09°38.4′W	25.10.72	ES
	DS23	4734	46°32.8′N	10°21.0′W	26.10.72	ES
	DS25	2096	44°08.2′N	04°15.7′W	1.11.72	ES
	DS26	2076	44°08.2′N	04°15.0′W	1.11.72	ES
	DS31	2813	47°32.5′N	09°04.2′W	19.4.73	ES
Biogas II	DS32	2138	47°32.2′N	08°05.3′W	19.4.73	ES
Biogas III	DS36	2147	47°32.7′N	08°36.5′W	24.8.73	ES
	DS37	2110	47°31.8′N	08°34.6′W	25.8.73	ES
	DS38	2138	47°32.5′N	08°35.8′W	25.8.73	ES
	DS41	3548	47°28.3′N	09°07.2′W	26.8.73	ES
	DS42	4104	47°32.′N4	09°35.6′W	27.8.73	ES
	DS44	3992	47°33.2′N	09°42.0′W	27.8.73	ES
	DS45	4260	47°33.9′N	09°38.4′W	27.8.73	ES
	DS46	4521	46°28.6′N	10°23.0′W	29.8.74	ES
	DS48	4203	44°29.0′N	04°54.0′W	31.8.73	ES
	DS50	2124	44°08.9′N	04°15.9′W	1.9.73	ES
J. Charcot Biogas IV	DS51	2430	44°11.3′N	04°15.4′W	18.2.74	ES
	DS52	2006	44°06.3′N	04°22.4′W	18.2.74	ES
	DS54	4659	46°31.3′N	10°29.2′W	21.2.74	ES
	DS55	4125	47°34.9′N	09°40.9′W	22.2.74	ES
	KR31	4097	47°37.0′N	09°41.′W6	22.2.74	ES
	DS56	4050	47°32.7′N	09°28.2′W	23.2.74	ES
	DS58	2775	47°34.1′N	09°08.2′W	23.2.74	ES
	DS59	2790	47°31.7′N	09°06.2′W	24.2.74	ES
	DS61	2250	47°34.7′N	08°38.8′W	25.2.74	ES
	CP01	2245	47°34.6′N	08°38.8′W	25.2.74	ES
	DS62	2175	47°32.8′N	08°40.0′W	26.2.74	ES
	DS63	2126	47°32.8′N	08°35.0′W	26.2.74	ES

	DS64	2156	47°29.2′N	08°30.7′W	26.2.74	ES
Biogas V	CP07	2170	′N°09.8′N	04°16.4′W	21.6.74	ES
	DS67	4150	47°31.0′N	09°35.0′W	17.6.74	ES
	DS68	4550	46°26.7′N	10°23.9′W	19.6.74	ES
	DS69	4510	′N°21.9′N	04°52.4′W	20.6.74	ES
Biogas VI	CP08	2177	′N°33.2′N	08°38.5′W	20.10.74	CP
	CP09	2171	47°33.0′N	08°′N.1′W	20.10.74	CP
	DS71	2194	47°34.3′N	08°33.8′W	20.10.74	ES
	DS75	3250	47°28.1′N	09°07.8′W	22.10.74	ES
	DS76	4228	47°34.8′N	09°33.3′W	23.10.74	ES
	CP13	4134	47°34.4′N	09°38.0′W	23.10.74	CP
	CP14	4237	47°32.0′N	09°35.9′W	23.10.74	CP
	KR60	4220	47°32.3′N	09°37.2′W	24.10.74	KR
	KR64	4700	46°30.8′N	10°20.8′W	24.10.74	KR
	DS74	2777	47°33.0′N	09°07.8′W	21.10.74	ES
	DS77	4240	47°31.8′N	09°34.6′W	24.10.74	ES
	DS78	4706	46°31.2′N	10°23.8′W	25.10.74	ES
	CP16	4825	46°27.6′N	10°26.8′W	25.10.74	CP
	DS79	4715	46°30.4′N	10°27.1′W	26.10.74	ES
	CP17	4706	46°30.8′N	10°19.5′W	26.10.74	CP
	CP18	4721	46°30.0′N	10°26.0′W	26.10.74	CP
	DS80	4720	46°29.5′N	10°29.5′W	27.10.74	ES
	DS81	4715	46°28.3′N	10°24.6′W	27.10.74	ES
	CP21	4453	44°21.2′N	04°49.3′W	30.10.74	CP
	DS86	1950	44°04.8′N	04°18.7′W	31.10.74	ES
	CP23	1980	44°04.6′N	04°21.4′W	31.10.74	CP
	DS87	1913	44°05.2′N	04°19.4′W	1.11.74	ES
	CV38	2690	47°30.9′N	08°59.5′W	24.2.74	CV
Thalassa	Z397	511	47°33.8′N	07°12.′W6	22.10.73	GBO
	Z400	1175	47°33.4′N	07°18.1′ W	22.10.73	GBS
	Z413	805	48°03.1′N	08°29.4′W	24.10.73	PBS
	Z417	865	48°12.0′N	09°09.5′W	24.10.73	PBS
	Z427	330	48°27.0′N	09°48.4′W	25.10.73	PBS
	Z435	1050	48°39.7′N	09°53.2′W	26.10.73	PBS
	Z447	1430–1530	48°47.3′N 48°47.4′N	11°12.0′W- 11°14.3′W	27.10.73	CP
Incal	DS01	2091	57°59.7′N	10°39.8′W	15.7.76	ES
	CP01	2041	57 57.7′N	10 55.0′W	16.7.76	CP
	DS02	2081	57°58.8′N	10°48.5′W	16.7.76	ES
	CP08	2644	50°14.7′N	13°13.5′W	27.7.76	CP
	CP10	4823	48°25.5′N	15°10.7′W	31.7.76	CP
	DS11	4823	48°18.6′N	15°12.0′W	1.8.76	ES
	CP11	4823	48°20.4′N	15°14.6′W	1.8.76	CP
	WS02	4829	48°19.2′N	15°23.3′W	1.8.76	WS
	OS03	4829	48°19.2′N	15°15.9′W	2.8.76	OS
	OS05	4296	47°31.3′N	09°34.6′W	7.8.76	OS
	KR14	4299	47°29.8′N	09°37.4′W	7.8.76	KR
	WS07	4281	47°30.6′N	09°37.1′W	7.8.76	WS
	DS14	4254	47°32.6′N	09°35.7′W	7.8.76	ES
	DS15	4211	47°33.4′N	09°39.1′W	8.8.76	ES
	DS16	4268	47°29.8′N	09°36.2 ′W	9.8.76	ES
	WS08	4287	47°30.5′N	09°33.7′W	9.8.76	WS
	OS06	4316	46°27.3′N	09°36.2′W	9.8.76	OS
	OS07	4249	47°31.8′N	09°34.3′W	10.8.76	OS
	WS09	4277	47°28.8′N	39°34.0′W	10.8.76	WS
	WS10	4354	47°27.3′N	09°39.9′W	11.8.76	WS
	OS08	4327	47°29.8′N	09°39.2′W	11.8.76	OS
			CANARY BASIN			
Discovery	6696	1564	27°57.0′N	13°36.2′W	15.3.68	ES
	6701	1934	27°45.2′N	14°13.0′W	16.3.68	ES
	6704	2129	27°44.9′N	14°25.0′W	17.3.68	ES

			AZORES MID-ATLANTIC RIDGE			
J. Charcot Bioacores	105	1675	39°35.0′ N	31°23.0′W	20.10.71	DP
	120	2100	39°03.5′N	32°43.5′W	22.10.71	ES
	126	3360	39°19.5′N	33°47.0′W	23.10.71	ES
			SIERRA LEONE BASIN			
Atlantis II	148	3828	10°37.0′N	18°14.0′W	7.2.67	ES
	149	3861	10°30.0′N	18°18.0′W	7.2.67	ES
			ANGOLA BASIN			
J. Charcot Walda	DS13	3985	14°21.5′S	09°46.2′E	? 8.71	ES
Atlantis II42	202	1427–1643	08°56.0′S	12°15.0′E-	23.5.68	ES
		1643	08°46.0′S	12°47.0′E		
			CAPE BASIN			
J. Charcot	DS02	5280	33°54.7′S	05°08.3′E	26.12.78	ES
Walvis	KG14	4610	33°20.9′S	02°38.0′E	29.12.78	KG
	DS05	4560	33°20.5′S	02°34.9′E	30.12.78	ES
	DS06	4585	33°24.5′S	02°32.9′E	31.12.78	ES
	DS07	5100	26°59.7′S	01°07.1′E	3.1.79	ES
			WEDDELL SEA			
IWSOE	001	728	74°07.0′S	39°38.0′W	6.2.68	ES
	002	412	75°31.5′S	30°08.0′W	25.2.69	AD
	004	793	77°05.5′S	35°04.0′W	26.2.69	AD
	005	1079	77°19.8′S	36°41.3′W	27.2.69	AD
	007	512	77°16.0′S	42°38.0′W	1.3.69	AD
	008	585	77°36.2′S	40°30.0′W	2.3.69	AD
	010	659	77°50.0′S	42°05.2′W	4.3.69	AD
	022	3111	73°28.4′S	30°26.9′W	13.3.69	ES
	023	3697	72°47.6′S	30°29.7′W	14.3.69	AD
	027	4575	64°46.2′S	41°30.1′W	19.3.69	ES

APPENDIX 2. DESCRIBED SPECIES OF THE GENUS *DACRYDIUM*

?Dacrydium sp. Pelseneer, 1911. Probably a juvenile *Amygdalum* (Mattson & Warén, 1977; Ockelmann, 1983).

Dacrydium sp. Salas, 1996
Location of specimens: MNHNP
Dacrydium sp. Salas, 1996: 53, figs, 97–99.
Distribution: Western Mediterranean, 890–2035 m.

Dacrydium sp. a Ockelmann, 1959
Location of specimen: ZMUC.
Dacrydium sp. a Ockelmann, 1959: 50, 195.
Dacydium sp. a Okutani, 1968: 15.
Distribution: Restricted to "depths of Norwegian Sea."

Dacrydium sp. c Ockelmann, 1959
Location of specimen: ZMUC.
Dacrydium sp. c Ockelmann, 1959: 50, 195.
Dacrydium sp. c Okutani, 1968: 15.
Distribution: North Atlantic, WSW and SE Iceland, SW Faroes and W. Norway. Depth range: "intermediate depths."

Dacrydium sp. Poutiers, 1989
Location of specimen: MNHNP.
Dacrydium sp. Poutiers, 1989: 214, 215, fig. 3d.
Distribution: Benthedi Sta. 87, SE Glorieuse Is. 11°44′S 47°35′E. Depth range: 3716 m.

Dacrydium albidum Pelseneer, 1903
Type locality: Southern Ocean, 71°18′S 88°02′W, 200 fm.
Type specimen: IRSNB.
Dacrydium albidum Pelseneer, 1903: 26, pl. VIII, fig. 100.
Dacrydium albidum, Hedley, 1906: 72.
Dacrydium albidum, Thiele, 1912: 21, pl. 17, figs. 10, 10a.
?Dacrydium albidum, Theile, 1912: 226, pl. 17, figs. 9, 9a.
Dacrydium albidum, Lamy, 1937: 70.
Dacrydium albidum, Soot-Ryen, 1951: 20.

Dacrydium albidum, Powell, 1958: 175.
Dacrydium albidum, Powell, 1960: 174.
?Dacrydium albidum, Clarke, 1961: 378.
Dacrydium albidum, Nicol, 1966: 25, pl. 3, figs. 2, 8.
Dacrydium albidum, Okutani, 1968: 15, fig. 1g.
Dacrydium albidum, Egorova, 1982: 64, figs. 271, 272.
Dacrydium albidum, Bernard, 1983: 19.
Dacrydium modioliforme, Bernard, 1983: 19.
Dacrydium albidum, Ockelmann, 1983: 112, 118.
Dacrydium albidum, Poutiers, 1989: 214, 215, fig. 3i.
Dacrydium albidum, Muhlenhardt-Siegal, 1989: 161, pl. 2, fig. 20.
?Dacrydium albidum, Dell, 1990: 33, figs. 55–57.
?Dacrydium modioliforme, Dell, 1990: 34.
Distribution: Southern Ocean, Davis and Ross seas, South Shetland Isles. Depth range: 122–1473 m (possibly to 4758 m–ee Dell (1990) and *D. knudseni* above).

Dacrydium angulare Ockelmann, 1983
Type locality: Cape Basin, Vema Sta. 54, 34°35′S 17°31′E, 1849 m.
Type specimen: Holotype ZMUC; paratypes ZMUC, USNM 822398.
?Dacrydium albidum, Clarke, 1961: 378.
Dacrydium angulare Ockelmann, 1983: 114, figs. 46–48, 51.
Dacrydium angulare, Poutiers, 1989: 214, 215, fig. 3j.
Dacrydium angulare, Salas &: Gofas, 1997: 266, figs. 15–19.
Distribution: South Atlantic. Depth range: 1849 m.

Dacrydium balgimi Salas & Gofas, 1997
Type locality: Off northwestern Morocco, 35°12′N 07°53′W, 2035 m.
Type specimen: Holotype and paratypes MNHNP.
Dacrydium balgimi Salas & Gofas, 1997: 275, figs. 52–57.
Distribution: North Canary Basin. Depth range: 2035 m.

Dacrydium dauvini Salas & Gofas, 1997
Type locality: Atlantis Bank, 34°05.1′N 30°13.6′W, 260 m.
Type specimen: Holotype and paratypes MNHNP; paratypes SMNH.
Dacrydium dauvini Salas & Gofas, 1997: 273, figs. 44–48.
Distribution: Atlantis Bank, Canaries Basin. Depth range: 280–330 m.

Dacrydium filiferum Salas & Gofas, 1997
Type locality: Atlantis Bank, 34°04.8′N 30°14.9W, 330 m.
Type specimen: Holotype and paratypes MNHNP.
Dacrydium filiferum Salas & Gofas, 1997: 275, figs. 49–51.
Distribution: Atlantis Bank, Canaries Basin. Depth range: 330–340 m.

Dacrydium elegantulum elegantulum Soot-Ryen, 1955
Type locality: Bahía de Gardner, Islas Galapagos, Sta. BS 453, 35 fms.
Type specimen: Holotype AHF.
Dacrydium (Quendreda) elegantulum Soot-Ryen, 1955: 87, pl. 8, fig. 41.
Dacrydium elegantulum, Bernard, 1978: 62.
Dacrydium (Quendreda) elegantulum, Bernard, 1983: 19.
Dacrydium elegantulum Ockelmann, 1983: 112, 113.
Distribution Bahía de Gardner, Islas Galapagos; Baja California; off Redondo Beach, California. Depth range: 45–64 m.

Dacrydium elegantulum hendersoni Salas & Gofas, 1997
Type locality: Florida, off Sand Key, 100 fm.
Type specimen: Holotype and paratypes. USNM 459094; paratypes USNM 459098.
Dacrydium elegantulum hendersoni Salas & Gofas, 1997: 278, figs. 61–65.
Distribution: off Sand Key, Florida. Depth range: 155–200 m.

Dacrydium fabale Hedley, 1904
Type locality: 16 m. E of Wollongong, New South Wales, 100 fm. Type specimen: Holotype AMS.
Dacrydium fabale Hedley, 1904: 199, pl. X, fig. 39.
Ouendreda fabale, Iredale, 1936: 271.
Dacrydium fabale, Lamy, 1937: 70.
Dacrydium (Quendreda) fabale, Soot-Ryen, 1955: 87, pl. 8, fig. 41.
Dacrydium fabale, Ockelmann, 1983: 112, 113.
Distribution: off New South Wales. Depth range: 182 m.

Dacrydium gloriosense Poutiers, 1989
Type locality: Benthidi Sta. 87, 11° 44′S 47°35′E, 3716 m.
Type specimen: Holotype MNHNP.

Dacrydium gloriosense Poutiers, 1989: 210, 212, 215, figs. 2a–c, 3g.
Distribution: SE of the Glorieuse Isles. Depth range: 3700–3718 m.

Dacrydium hyalinum (Monterosato, 1875)
Type locality: Off Palermo, Sicily.
Type specimen: Lectotype USNM 199198, paralectotypes from the same lot USNM.
Dacrydium sp. Monterosato, 1870: 43–46.
Dacrydium hyalinum Hidalgo, 1870: 128, *nomen nudum.*
Mytilus vitreus, Jeffreys, 1870: 68.
Dacrydium vitreum, Monterosato, 1872: 18.
Mytilus (Dacrydium) hyalinus Monterosato, 1875: 10.
Dacrydium hyalinum, Monterosato, 1878: 66.
Dacrydium vitreum, Jeffreys, 1883: 394.
Dacrydium hyalinum, Clessin, 1889: 156.
Dacrydium hyalinum, Locard, 1891: 342.
Dacrydium hyalinum, Locard, 1896: 205.
Dacrydium vitreum var. *hyalina,* Lamy, 1937: 68.
?Dacrydium sp. Soot-Ryen, 1966: 8. See Okutani (1968: fig. 1f) and Mattson & Warén (1977).
Dacrydium hyalinum, Okutani, 1968: 15.
Dacrydium hyalinum, Mattson & Waren, 1977: p. 1, figs. 3, 9.
Dacrydium hyalinum, Ockelmann, 1983: 112, 113, 120.
Dacrydium hyalinum, Nordsieck, 1989: 30.
Dacrydium hyalinum, Salas, 1996: 53, figs. 91–93.
Dacrydium hyalinum, Salas & Gofas, 1997: 266, figs. 20–24.
Distribution: Off Palermo and possibly lusitanean (35°34′N 07°35′W. See Soot-Ryen (1966) and Mattson & Warén (1977). Depth range: 76–1615 m.

?Dacrydium meridionale Smith, 1885. Probably a phylobryid. See Bernard (1897), Melville & Standen (1907), Lamy (1937), Powell (1960), Okutani (1968), and Poutiers (1989).

Dacrydium minimum Okutani & Izumidate, 1992
Type locality: Yamatotai Bank, Sea of Japan, 39°45.77′N 135°00.00′E, 1200 m.
Type specimen: Holotype NSMT Mo-69662; paratype NSTM Mo-69663.
Dacrydium minimum Okutani & Izumidate, 1992: 149, figs 1–3.
Distribution: Sea of Japan. Depth range: 394–1200 m.

?Dacrydium modioliforme Theile, 1912
Type locality: Gauss Station, Davis Sea, 400 m.
Type specimen: ?ZMHU
Dacrydium modioliforme Theile, 1912: 226–227, fig. 10, 10a. But see Nicol (1966), Knudsen (1970), Poutiers (1989), and Dell (1990). Probably synonymous with *D. albidum* See also *D. knudseni.*
?Dacrydium modioliforme, Thiele & Jaeckel, 1931: 170.
Dacrydium modioliforme, Lamy, 1937: 70.
Dacrydium modioliforme, Soot-Ryen, 1951: 20.
Dacrydium modioliforme, Powell, 1960: 174.
Dacrydium modioliforme, Nicol, 1966: 26.
Dacrydium modioliforme, Okutani, 1968: 15.
Dacrydium modioliforme, Knudsen, 1970: 92, 178.
Dacrydium modioliforme, Bernard, 1978: 63.
Dacrydium modioliforme, Poitiers, 1989: 214.
?Dacrydium modioliforme, Dell, 1990: 34.
Distribution: Southern Ocean. Depth range: 400–?4758 m.

Dacrydium nipponicum Okutani, 1975
Type locality: Soyo-Maru Sta. B2 (11-XII-1967) 34°22.2′N 139°41.9′E. 1080–1205 m.
Type specimen: Holotype and paratypes TRFRL.
Dacrydium pacificum (*non* Dall 1916), Okutani, 1968: 14, fig. 1a.
Dacrydium nipponicum Okutani, 1975: 68, fig. 1, pl. III, fig. 2.
Dacrydium nipponicum, Bernard, 1978: 62.
Dacrydium nipponicum, Ockelmann, 1983: 112.
Dacrydium nipponicum, Poutiers, 1989: 214, 215, fig. 3k.
Dacrydium nipponicum, Hayami & Kase, 1993: 47.
Dacrydium nipponicum, Salas & Gofas, 1997: 263.
Distribution: Off Miyake Isle, Sea of Japan. Depth range: 1000–1250 m.

Dacrydium occidentale Smith, 1885
Type locality: Challenger Sta. 24, off Culebra Isle, 18°38.5′N 65°05.5′W, 390 fm.
Type specimen: Syntype, BMNH: type material completely destroyed by Bynes' disease; no other material exists.
Dacrydium occidentale Smith, 1885: 282, pl. XVII, fig. 1, 1a.
Dacrydium occidentale, Lamy, 1937: 69.

Dacrydium occidentale, Okutani, 1968: 15 fig. 1b.
Dacrydium occidentale, Nordsieck, 1969: 30, pl. IV, figs. 20. 12.
Dacrydium occidentale, Bernard, 1978: 63.
Dacrydium occidentale, Ockelmann, 1983: 112.
Dacrydium occidentale, Poutiers, 1989: 214, 215, fig. 3e.
Dacrydium occidentale, Kayami & Kase, 1993: 47.
?Dacrydium occidentale, Salas & Gofas, 1997: 270, figs. 33–35.
Distribution: West Indies. Depth range: 702 m.

Dacrydium ockelmanni Mattson & Warén, 1977
Type locality: W. Norway, Korsfjorden, 60°08.35′N 05°00.40′E, 260–290 m.
Type material: Holotype ZMUB 58633, paratypes 58634. Other paratypes MNHN and USNM.
?Dacrydium sp. Lande, 1975: 10, 12.
Dacrydium ockelmanni Mattson & Warén, 1977: 2, figs. 4–6, 10–13.
Dacrydium ockelmanni, Ockelmann, 1983: 112, 113, 116.
Dacrydium ockelmanni, Høisaeter, 1986: 115.
Dacrydium ockelmanni, Smith & Heppell, 1991: 60.
Dacrydium ockelmanni, Warén, 1991: 114, 115, fig. 40A–C.
Dacrydium ockelmanni, Salas & Gofas, 1997: 264, figs. 7–14.
Distribution: Bay of Biscay, NW of Ireland, WSW and SE of Iceland, SW of Faroes, off W Norway. Depth range: 145–600 m.

Dacrydium pacificum Dall, 1916
Type locality: Albatross Sta. 3604, 54°54′N 168°59′W, 1401 fm.
Type material: Syntypes USNM 214092, SBMNH 34061, paratypes ZMUC.
Dacrydium pacificum Dall, 1916: 405.
Dacrydium pacificum, Dall, 1921: 22.
Dacrydium pacificum, Oldroyd, 1924: 72.
Dacrydium pacificum, Lamy, 1937: 69.
Dacrydium pacificum, Clarke, 1962: 58.
Dacrydium pacificum, Boss et al., 1968, p. 335.
Dacrydium pacificum, Knudsen, 1970: 89, fig. 52C–E.
Dacrydium pacificum, La Rocque, 1973: 38.
Dacrydium pacificum, Abbott, 1974: 437.
Dacrydium pacificum, Okutani, 1975: 69.
Dacrydium pacificum, Bernard, 1978: 62.
Dacrydium pacificum, Bernard, 1983: 19.
Dacrydium pacificum, Ockelmann, 1983: 112.
Dacrydium pacificum, Poutiers, 1989: 212, 215, fig. 3b.
Dacrydium pacificum, Scott et al., 1990: 11.
Distribution NE Pacific and SE Bering Sea. Depth range: 2562 m.

Dacrydium panamensis Knudsen, 1970
Type locality: Galathea Sta. 726, 05°49′N 78°52′W, 3270–3670 m.
Type specimen: Holotype ZMUC.
Dacrydium sp. Wolff, 1961: 150, fig. 19.
Dacrydium sp. Okutani, 1968: 15, fig. 1e.
Dacrydium panamensis Knudsen, 1970: 91, figs. 53, 54.
Dacrydium panamensis, Abbott, 1974: 437.
Dacrydium panamensis, Bernard, 1978: 62, 63.
Dacrydium panamensis, Bernard, 1983: 19.
Dacrydium panamensis, Ockelmann, 1983: 112.
Dacrydium panamensis, Poutiers, 1989: 212, 215, fig. 3h.
Dacrydium panamensis, Dell, 1990: 34.
Distribution: East Pacific, Gulf of Panama. Depth range: 3270–3670 m.

Dacrydium pelseneeri Hedley, 1906
Type locality: 'continental shelf', New Zealand. Type specimen: ?NMNZ.
Dacrydium pelseneeri Hedley, 1906: 72, pl. II, fig. 8.
Dacrydium pelseneeri, Lamy, 1937: 70.
Dacrydium pelseneeri, Soot-Ryen, 1955: 87.
Dacrydium pelseneeri, Ockelmann, 1983: 112.
Distribution: Depth range, shelf depths.

Dacrydium radians Suter, 1908. Gatliff & Gabriell (1916) and Lamy (1937–71), indicate probably a senior synonym of *Modiolaria rhyllensis* Gatliff & Gabriell, 1912.

Dacrydium rostriferum Bernard, 1978
Type locality: West of Cape Flattery, 48°26.6′N 126°54.5′W, 2532 m.
Type specimen: Holotype LACMNH 1880, Paratypes USNM 771804, NSMT .55441, California Academy of Sciences 59409, Oregon State University Biological Institution 01501.
Dacrydium (Dacrydium) rostriferum Bernard, 1978: 62, figs. 1, 12.
Dacrydium rostriferum, Bernard, 1983: 19.
Dacrydium rostriferum, Ockelmann, 1983: 112.
Dacrydium rostriferum, Poutiers, 1989: 214, 215, fig. 3f.
Dacrydium rostriferum, Hayami & Kase, 1993: 47.

Distribution: Off the coast of Washington, USA, between 44°38′N 125°35′W and 48°22′N 126°54′W. Depth range: 2530–2865 m.

Dacrydium speculum Poutiers, 1989
Type locality: off SW Sri Lanka, Safari II Sta. 2 SIPAN 19, SW of Sri Lanka, 05°37′N 78°24′E, 3660 m.
Type specimen: Holotype MNHNP.
Dacrydium speculum Poutiers, 1989: 210, 212, 214, 215, figs. 1a–c, 3a.
?*Dacrydium* cf. *speculum* Salas & Gofas, 1997: 277, figs. 58–60.
Distribution SW of Sri Lanka; ?Cape Verde Basin (Salas & Gofas, 1997). Depth range: 3660 m, (4580 m if present in Cape Verde Basin).

Dacrydium vitreum (Møller, 1842)
Type locality: Sukkertoppen, West Greenland, 73 m.
Type specimen: originally ZMUC, probably lost (Warén, 1991).
Modiola? vitrea Holböll MS, in Møller, 1842: 92
Dacrydium vitreum, Torell, 1859: 138, pl. i, fig. 2a, b.
?*Dacrydium vitreum,* Hidalgo, 1870: 128.
Modiolaria (Dacrydium) vitrea, Mörch, in Jones, 1875: 133
Dacrydium vitreum, Jeffreys, 1876: 429.
Dacrydium vitreum, Friele, 1878: 222.
Dacrydium vitreum, Sars, 1878 (in part): 28, pl. 3, fig. 2a, b.
Dacrydium vitreum, Jeffreys, 1879: 569.
Dacrydium vitreum, Verrill, 1882: 579, pl. 44, fig. 8.
Dacrydium vitreum, Verrill, 1884: 281.
?*Dacrydium vitreum,* Smith, 1885: 282.
?*Dacrydium vitreum,* Dautzenberg, 1889: 77.
Dacrydium vitreum, Clessin, 1889: 155, pl. 6, figs. 16, 17.
Dacrydium vitreum, Dall, 1889: 38.
Dacrydium vitreum, Posselt, 1895 (in part): 66.
Dacrydium vitreum, Locard, 1896: 205.
Dacrydium vitreum, Dautzenberg, 1897: 199.
?*Dacrydium vitreum,* Bernard, 1898: 71.
Dacrydium vitreum, Locard, 1898: 364.
Dacrydium vitreum, Posselt & Jensen (in part), 1898: 21.
Dacrydium vitreum, Locard, 1899: 170.
Dacrydium vitreum, Friele & Grieg, 1901: 24.
Dacrydium vitreum, Whiteaves, 1901: 121.
Dacrydium vitreum, Jensen, 1905: 325.
?*Dacrydium vitreum,* Dautzenberg & Fisher, 1912: 373.
Dacrydium vitreum, Jensen (in part), 1912: 54.
Dacrydium vitreum, Johnson, 1915: 34.
Dacrydium vitreum, Odhner, 1915: 82.
Dacrydium vitreum, Grieg, 1916: 8.
?*Dacrydium vitreum,* Dautzenberg, 1927: 275.
Dacrydium vitreum, Thorson, 1934: 6.
Dacrydium vitreum, Johnson, 1934: 28.
Dacrydium vitreum, Theile, 1935: 798.
Dacrydium vitreum, Lamy, 1937: 66.
Dacrydium vitreum, La Rocque, 1953: 38.
Dacrydium vitreum, Ockelmann, 1959: 48, pl. 1, fig. 19.
Dacrydium vitreum, Scarlato, 1960: 61, pl. 1, fig. 3.
Dacrydium vitreum, Soot-Ryen, 1966: 8.
Dacrydium vitreum, Okutani, 1968: 14, 15, fig. 1d.
Dacrydium vitreum, Knudsen, 1970: 90, 92, fig. 52A, B.
Dacrydium vitreum, Abbott, 1974: 436, fig. 5102.
Dacrydium vitreum, Mattson & Warén, 1977: 1–3, figs. 1, 2, 7.
Dacrydium vitreum, Bernard, 1978: 62.
Dacrydium vitreum, Scarlato, 1981: 242, fig. 141.
Dacrydium vitreum, Bernard, 1983: 19.
Dacrydium vitreum, Ockelmann, 1983: 112, 113, 115, fig. 49.
Dacrydium vitreum, Høisaeter, 1986: 115.
Dacrydium vitreum, Nordsieck, 1989: 29, pl. IV, fig. 20.10.
Dacrydium vitreum, Poutiers, 1989: 212, 215, fig. 3c.
Dacrydium vitreum, Smith & Heppell, 1991: 60.
Dacrydium vitreum, Warén, 1991: 114, 115, fig. 40D–F.
Mytilus vitrea (= Dacrydium vitreum), Schiøtte & Warén, 1992: 14.
Dacrydium vitreum, Salas & Gofas, 1997: 263, figs. 2–6.
Distribution: W and E Greenland, Baffinland, off Nova Scotia, N and E of Iceland, Jan Mayen, Spitsbergen, W. Norway south to Lofoten Isles, Barents, White and Kara Seas, Bering Sea, North of Gulf of Alaska, Kamchatka, Sea of Okhotsk. Depth range: 5-2258 m, but most frequently found 5-200 m.

Dacrydium viviparum Ockelmann, 1983
Type locality: Ingolf Stas 78, 80, 90, 64°45′N 29°06′W south to 60°37′N 27°52′W, 1070–1505 m.

Type specimen: Holotype MZUC, paratypes BMNH 198335, USNM 822399.
?*Dacrydium vitreum* var. *elongata* Locard, 1898: 364.
Dacrydium vitreum, Jensen, 1912 (in part): 56–65.
Dacrydium sp. b Ockelmann, 1959: 50.
Dacrydium sp. b Okutani, 1968: 15.
Dacrydium viviparum Ockelmann, 1983: 118, 120, figs. 52–54, 56, 57.
Dacrydium viviparum, Warén, 1991: 115.
Dacrydium viviparum, Hayami & Kase, 1993: 48.
?*Dacrydium* cf. *hyalinum,* Salas & Gofas, 1997: 269, figs. 27–32.
Dacrydium viviparum, Salas & Gofas, 1997: 269.
Distribution: West European, Canary and North America Basins and possibly the Mediterranean. Depth range: 952–2430 m.

Dacrydium wareni Salas & Gofas 1997
Type locality: Off northwestern Morocco, 35°31′N 07°42′W, 1510m.
Type specimen: Holotype MNHMP; paratypes SMNH.
Dacrydium cf. *hyalinum,* Salas 1996: 53, figs. 94–96.
Dacrydium wareni Salas & Gofas 1997: 271, figs. 36–43.
Distribution: Mediterranean off Morocco, Gulf of Sirte (JAA pers. obs.); off northwestern Spain, West European and Canary Basin. Depth range: 395–2018 m.

Dacrydium zebra Hayami & Kase, 1993
Type locality: "Devil's Palace," Shimoji Islet, Miyako Islands, 24°49.6′N 125°08.2E, 25 m.
Type specimen: Holotype UMUT, RM19432a; paratypes UMUT RM19432–41.
Dacrydium sp. Kase & Hayami, 1992: 448.
Dacridium sp. Hayami & Kase, 1993a: 3, fig. 7.
Dacrydium Zebra Hayami & Kase, 1993b: 46, figs. 148–158.
Distribution: Submarine caves, Sea of Japan. Depth range: 12–40 m.

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PHYLOGENY OF STEM-GROUP EUCARDIIDS (BIVALVIA: CARDIIDAE) AND THE SIGNIFICANCE OF THE TRANSITIONAL FOSSIL *PERUCARDIA*.

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ABSTRACT

A cladistic analysis of stem-group eucardiids produces a phylogenetic hypothesis in which the subfamily Profraginae (Aptian [late Early Cretaceous] – Maastrichtian [latest Cretaceous]) is the sister taxon to *Perucardia* (Maastrichtian) + Cenozoic eucardiids. Character analysis of the radial ribs and external ornamentation of cardiids indicates that the morphology of the ribs and ornament on Cenozoic eucardiids is the result of fusion of two adjacent ribs. Furthermore, the radial ribs and ornament on *Perucardia* is a mosaic of Cretaceous profragine and Cenozoic eucardiid ribbing and ornament. *Perucardia* may be considered a "transitional fossil," because it is morphologically and stratigraphically (Maastrichtian) "intermediate" between profragines and Cenozoic eucardiids.

Key words: cardiids, phylogenetics, paleontology, evolution, homology, *Perucardia*, Profraginae, *Profragum*.

INTRODUCTION

In a preliminary phylogenetic analysis of the Late Triassic to Recent bivalve family Cardiidae (Schneider, 1992), it was found that the subfamilies Cardiinae, Clinocardiinae, Lymnocardiinae, Fraginae and Tridacninae formed a monophyletic group, informally dubbed the "eucardiids" (Schneider, 1995). *Nemocardium* + Laevicardiinae formed the sister taxon to eucardiids (Schneider, 1992). In a detailed analysis of basal cardiids (Tulongocardiinae, Protocardiinae, Lahilliinae, Pleuriocardiinae and Laevicardiinae [which therein included *Nemocardium*]; Schneider, 1995), it was found that the Pleuriocardiinae and eucardiids are sister taxa, and together are in turn the sister taxon to Laevicardiinae. As part of an ongoing study of the evolutionary history of the bivalve family Cardiidae, the aim of the present study is to gain an understanding of the morphological evolution of the stem-group eucardiids. (Smith, 1994: 94–95, provides a lucid discussion of the concepts of stem-group and crown-group). For this goal to be realized, a robust phylogenetic hypothesis for these cardiids must be proposed.

MATERIALS AND METHODS

To gain an understanding of the phylogenetic relationships, homologies and morphological evolution of stem-group eucardiids, a cladistic analysis of 20 taxa with 16 characters comprising 52 character states (Table 1) was performed using PAUP 3.1.1 (Swofford, 1993) on a Macintosh Quadra 650 computer. The heuristic branch-swapping routine with random addition and tree-bisection-reconnection options was used. The accelerated transformation option (ACCTRAN) was used, and steps were not added to taxa with polymorphisms (Schneider [1995] discusses these options). One character, shell shape (character 2) is ordered on the basis of ontogeny. All other characters are unordered. There is no ordering of characters based on stratigraphic occurrence or morphoclines. Unless otherwise indicated (Appendix 1, material examined), all coding of characters came from examination of specimens. Missing data are coded by a question mark ("?"). The results are presented in Figures 1 and 2.

The following abbreviations are used for repositories: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; DSIRGS, New Zealand Department of Scientific and Industrial Research, Geology and Geophysics; GSI, Geological Survey of India; IRSNB, Institut Royal des Sciences Naturelles de Belgique; MACS-RI, Maharashtra Association for the Cultivation of Science Research Institute; MNHN, Muséum National d'Histoire Naturelle;

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TABLE 1. Data matrix for Cretaceous to Eocene cladistic analysis. Missing data indicated by "?". "X" indicates taxon polymorphic for states 0 and 1.

Pleuriocardia	XF00000001300110
Granocardium	0A00101110101200
Criocardium	0B00101110101200
Ethmocardium	0A00101000100000
Profragum	0G00001000100000
Indocardium	0B00100200100020
Austrocardium	0D00000200000220
Perucardia	?C01102300100100
Hedecardium	0K11100001400100
Agnocardia	0D11010101400100
Orthocardium	0D11110101400100
Loxocardium	0E11000001400130
Schedocardia	1L11100101100100
Sawkinsia	1?01100101?0??00
Plagiocardium	1H11000001100040
Papillicardium	1I11000001000040
Parvicardium	1I11000001000040
Goniocardium	1J11000001210050
Avicularium	1J1100000021?051
Byssocardium	1J1100000021?0?1

Key to Abbreviations

ac	anterior cardinal
al	anterior length
als	anterior lateral socket
bg	byssal gape
cl	crossed-lamellae
cs	cross-striae
dh	dorsal height
fp	fibrous prisms
h	height
i	interspace
is	intercalary spine
isp	irregular simple prisms
l	length
ml	midline (line connecting midpoints of anterior and posterior adductor muscles)
pc	posterior cardinal tooth
pcs	posterior cardinal socket
phl	post-hinge length
pl	posterior length
pls	posterior lateral socket
plt	posterior lateral tooth
prt	primary radial threads
ps	primary spine
r	rib
s	spine
sc	scute
srt	secondary radial threads
ss	secondary spine
u	umbo
vm	ventral margin

NHM, The Natural History Museum London; NMB, Naturhistorisches Museum in Basel; PRI, Paleontological Research Institution; PUDG, Purdue University Department of Geology; UNC, University of North Carolina-Chapel Hill, Department of Geology; USNM, United States National Museum; UWIGM, University of the West Indies Geological Museum; YPMIP, Yale Peabody Museum, Invertebrate Paleontology Collection.

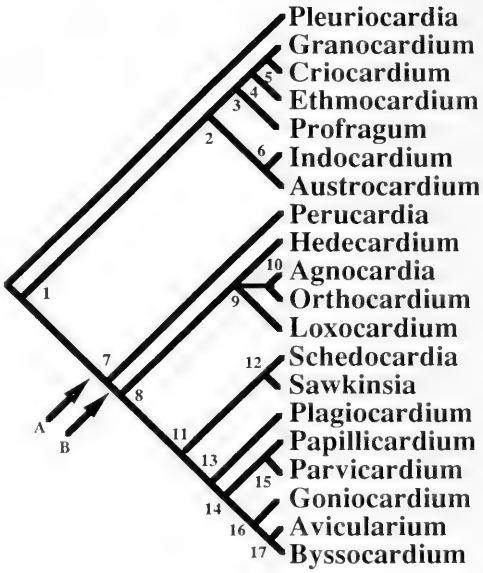


FIG. 1. One of six most parsimonious trees. Synapomorphies for each node are given in Table 2.

(1) *Selection of ingroup taxa:* All genera and subgenera of eucardiids that have any members that are known to have lived at anytime from the beginning of the Cretaceous to the end of the Eocene are represented in the analysis (Appendix 2). If the type species of the genus or subgenus occurs during the Cretaceous to Eocene interval, then the type species is used to represent the taxon in the cladistic analysis (*Criocardium* is the one exception). The method of representation of other cardiid (sub) genera is given in Appendix 2.

(2) *Selection of outgroup:* Schneider (1995) found that the subfamily Pleuriocardiinae is the sister-group to eucardiids. The Pleuriocardiinae is therefore used as the outgroup in the present analysis, represented by *Pleuriocardia eufaulense* (Conrad, 1860).

Description of Characters and Character States.

1. Posterior margin (Schneider, 1995: fig. 5): (0) digitate, (1) crenulate.

2. Shell shape (Fig. 3–5). Cardiids, like

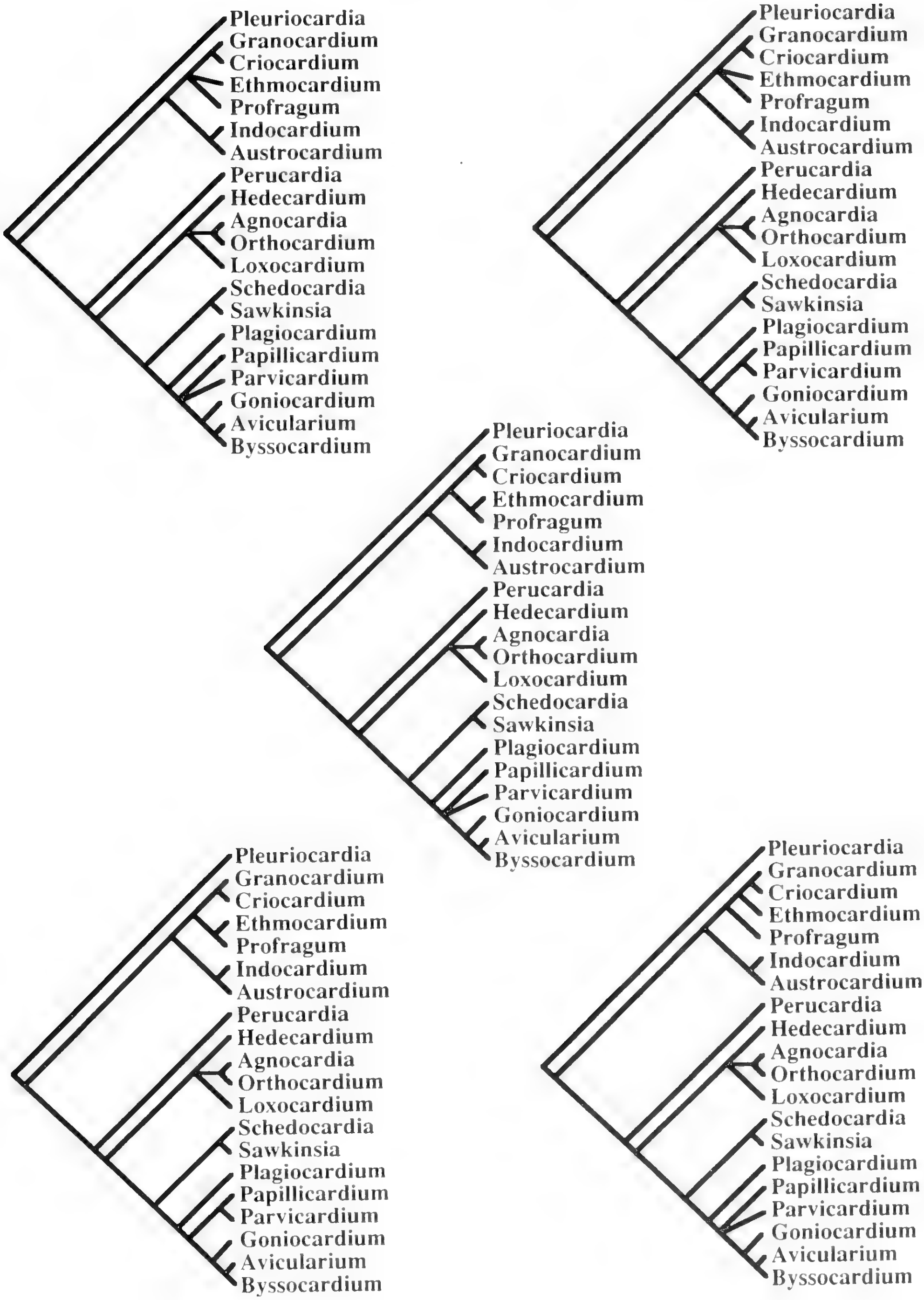


FIG. 2. Remaining five most parsimonious trees.

most bivalves, change the shape of their shell during ontogeny (Schneider, 1995). The structure of a mollusc shell is completely determined by the temporal process of its development (Wagner, 1994), and therefore the molluscan shell can be seen as a record of its own growth (Jones, 1983). The ontogenetic history of the shell shape of a single specimen can usually be traced by examining the growth lines. I have found that virtually all cardiids pass through at least two discernible "states" of shell shape during ontogeny, and that the sequence of these shape changes is orderly, predictable, and consistent (Table 2). Because of accretionary growth of bivalve shells, the shape of the shell at time 1 depends upon the shape of the shell at time 0. This is a causal sequence and can be order under Alberch's (1985) criterion (Schneider, 1998).

Various methods have been proposed to describe the ontogeny of bivalve shell shape (Raup, 1966; Løvtrup & Løvtrup, 1988; Checa, 1991; Johnston et al., 1991; Ackerly 1992a, b). However, a rigorous method of converting morphometric information on bivalve ontogeny into cladistic character states has yet to be invented. In fact, Bookstein (1994) adamantly argues that any attempt to link morphometrics and systematics would be "futile"; that "morphometrics cannot supply homologous shape characters" (p. 198); that biometrics and cladistics are logically, algebraically, and geometrically incompatible; and, finally, that "the languages of homology and of morphometrics are mutually incomprehensible" (p. 224).

However, shell shape is obviously a heritable attribute of bivalves, and to exclude shell shape in any cladistic analysis of bivalves would be at best using an incomplete data set in an attempt to propose a phylogenetic hypothesis and at worst a nihilistic exercise in purposeful ignorance. Therefore, as in Schneider (1995), shell shape is considered a character, the states of which can be determined by using a key. This key is meant to be used on adult shells that have attained their terminal shape state. However, shell shape character states are not solely defined by the adult shell shape, but by the *ontogenetic pathway* taken to that terminal (i.e., adult) shell shape (Jones, 1983; Wagner, 1994; Mabee & Humphries, 1993). For this reason, *Profragum*'s (Fig. 3B) terminal shell shape (trigonal) is not considered a homologue to other trigonal terminal shell shapes, for the latter group arrive at this shell shape via a different ontogenetic pathway. A detailed analysis of the ontogeny of *Profragum* will be published elsewhere.

TABLE 2. Shell shape character states detected during ontogeny of species considered in the present analysis. Shell shapes are listed in their order of ontogenetic appearance. All character analyses conducted with specimens in hand, except for *Granocardium* (*Granocardium*) *carolinum* and *Parvicardium* (*Parvicardium*) *triangulatum,* for which illustrations were examined. No shell shape character states recognized in any other cardiids were detected in *Sawkinsia matleyi;* therefore this species is not listed.

Pleuriocardia eufaulense: ovate, oblique-ovate
Granocardium (*Granocardium*) *carolinum:* quadrate
Granocardium (*Granocardium*) *kuemmeli:* quadrate, ovate
Granocardium (*Ethmocardium*) *whitei:* quadrate
Profragum praecurrens: quadrate, ovate, pseudotrigonal
Indocardium blanfordi: quadrate, ovate
Austrocardium acuticostatum: circular-ovate, circular
Perucardia brueggeni: ovate, circular-ovate
Loxocardium obliquum: circular, loxoform
Hedecardium waitakiense: circular, hedeform
Agnocardia dissidepictum: circular-ovate, circular
Orthocardium porulosum: circular-ovate, circular
Schedocardia hatchetigbeense: circular, schediform
Plagiocardium granulosum: circular, oval
Parvicardium (*Papillicardium*) *etheridgei:* oval, trigonal
Parvicardium (*Parvicardium*) *triangulatum:* oval, trigonal
Goniocardium rachitis: oval, trigonal, triangular
Avicularium aviculare: oval, trigonal, triangular
Byssocardium emarginatum: oval, trigonal, triangular

Sawkinsia (Fig. 4E), with its double keel and concave ventral margin, has a unique shell shape in the Cardiidae. I have been unable to discern any of the other cardiid shell shape states during its ontogeny. Therefore, *Sawkinsia*'s shell shape character cannot fit into the character state tree, and is coded as missing (?) for this character.

There are numerous terms that exist to describe bivalve shell shape. Many of these shell shapes have been figured and given verbal definitions by Cox (1969). However, there has been no attempt to define bivalve shell shape in an objective quantitative or semi-quantitative manner. Therefore, as in Schneider

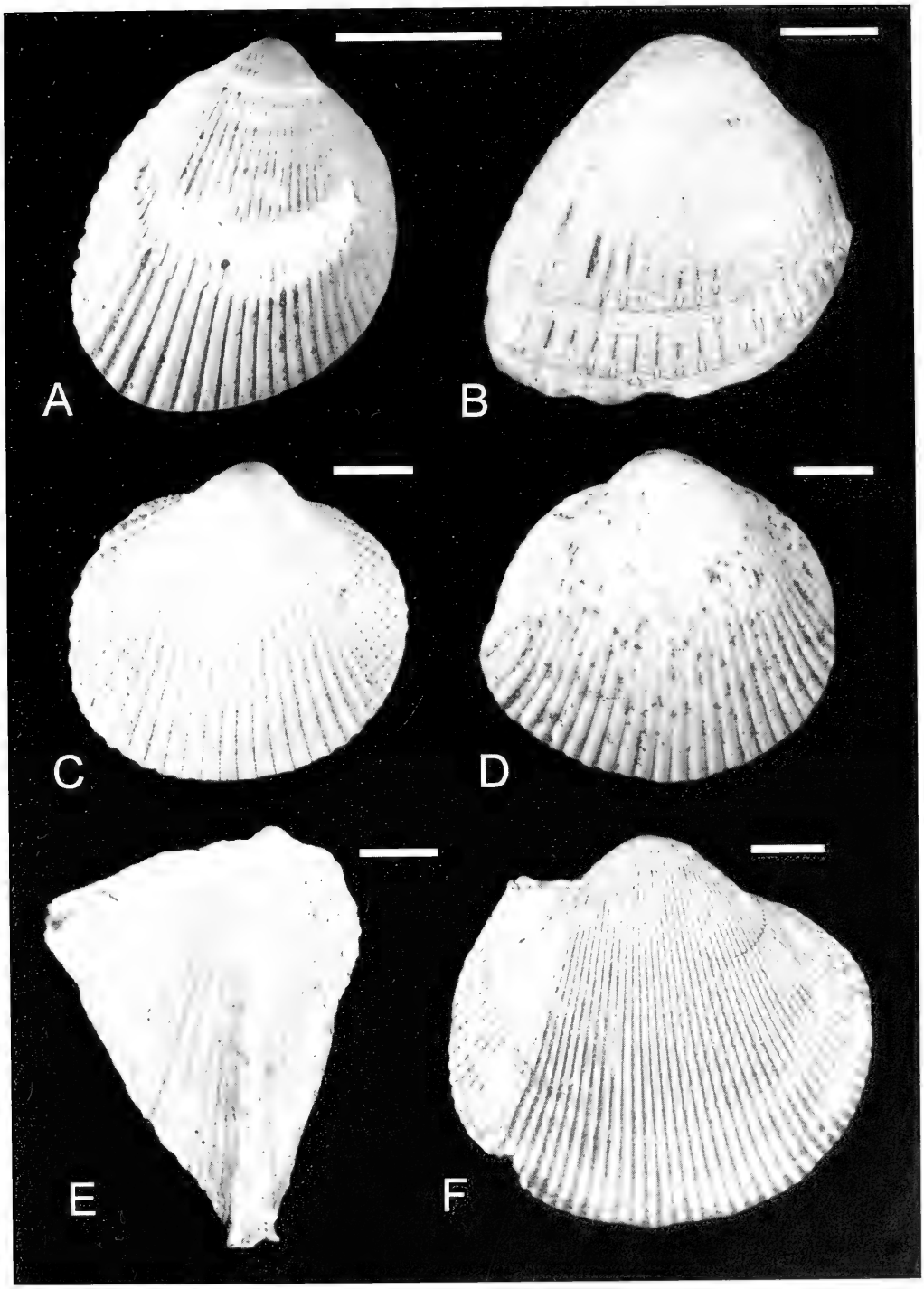


FIG. 3. Shell shapes. All figures display external views of right valves. A, *Pleuriocardia eufaulense* (ANSP 36491; scale bar = 10 mm); oblique/ovate. B, *Profragum praecurrens* (GSI 1061 [plaster cast of cotype], scale bar = 10mm); pseudotrigonal. C, *Plagiocardium granulosum* (ANSP 6268; scale bar = 5 mm); oval. D, *Loxocardium obliquum* (FMNH PE 3642; scale bar = 5 mm); loxoform. E, *Avicularium aviculare* (ANSP 6279; scale bar = 5 mm); triangular. F, *Hedecardium waitakiense* (DSIRGS 10837; scale bar = 10 mm); hedeform.

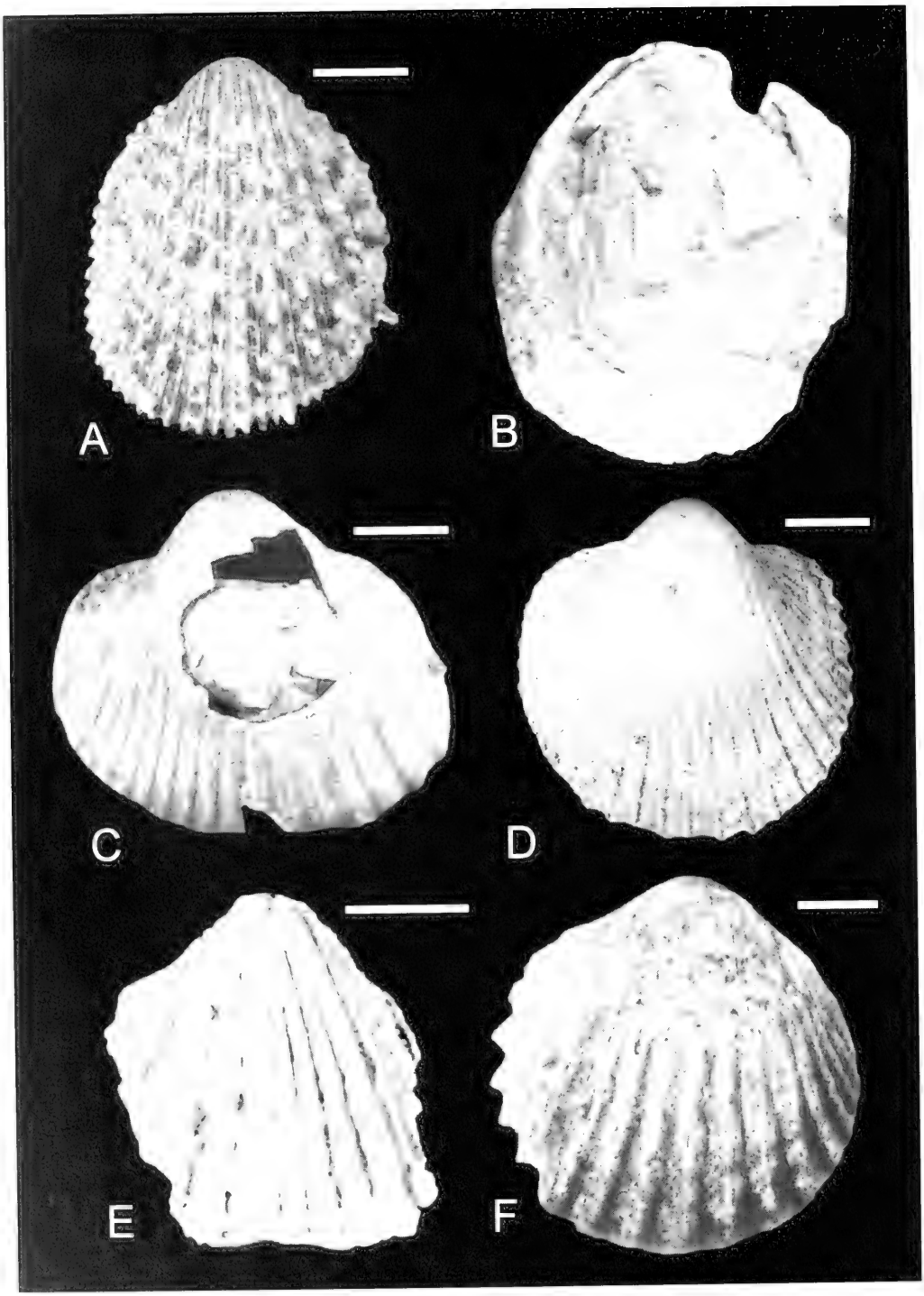


FIG. 4. Shell shapes. A, external view of right valve of *Granocardium kuemmeli* (AMNH 45042; scale bar = 10 mm); quadrate. B, external view of left valve of *Perucardia brueggeni* (PRI 4827 [holotype]; scale in mm indicated in figure); circular-ovate. C, external view of left valve of *Schedocardia hatchetigbeense* (USNM 645087 [syntype]; scale bar = 10 mm); schediform. D, external view of left valve of *Orthocardium porulosum* (ANSP 6266; scale bar = 10 mm); circular. E, external view of left valve of *Sawkinsia matleyi* (NMB G 14096; scale bar = 20 mm). F, external view of right valve of *Austrocardium acuticostatum* (PUDG 162; scale bar = 10 mm); circular.

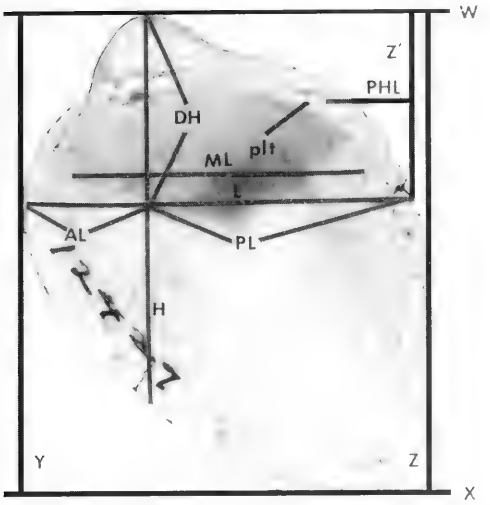


FIG. 5. Determination of shell shape. *Goniocardium rachitis* (ANSP 12429), length (L) = 31 mm. In this example, *G. rachitis* has a carina and PL > (0.6) × L, so it has a triangular shell shape. Z′ is a line parallel to Z which begins at the posteriormost point along line L and ends at line W. Post-hinge length (PHL) is the distance from the posteriormost point of the posterior lateral tooth (plt) to Z′.

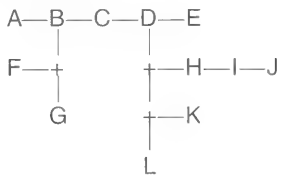
(1995), shell shape is determined using a shell shape character key (Fig. 5). Length (L) is defined as a line parallel to the line connecting the midpoint of the adductor muscles (the midline, ML) which starts at the anteriormost point of the shell margin (AL). Height (H) is defined as the line perpendicular to L which results in the greatest value of dorsal height (DH). Lines W and X are the two furthest possible lines (dorsal and ventral) parallel to L which contact the shell. Apparent height (AH) is the distance between W and X. On most shells, AH = H. Lines Y and Z are the two furthest possible lines (anterior and posterior) parallel to H which contact the shell. Apparent length (ApL) is the distance between lines Y and Z. In many shells, the greatest values of both ApL and L will occur along the same line, in which case ApL = L. Anterior length (AL) is that portion of line L which is anterior of line H; posterior length (PL) is that portion of line L which is posterior of line H; AL + PL = L. In this paper, "quadrate" = "quadrate-short" of Schneider (1995). Also, "quadrate-long" of Schneider (1995) is subdivided into "schediform" and "loxoform", based on "post-hinge length" (PHL), which the length of the shell posterior of the posterior lateral teeth of the hinge.

SHELL SHAPE CHARACTER KEY

1. Carina present 9
   Carina absent 2
2. Posterior length < anterior length . . . . . oblique-ovate
   Posterior length > anterior length 3
3. H/L > 1.2 . . . . . ovate
   1.1 < H/L < 1.2 . . . . . circular-ovate
   H/L < 1.1 4
4. Apparent height > true height . . . . . oval
   Apparent height = true height 5
5. H/L > 1.0 6
   H/L < 1.0 7
6. ApL > L . . . . . quadrate (= quadrate-short of Schneider, 1995)
   ApL = L . . . . . circular
7. ApL > L . . . . . 8 (= quadrate-long of Schneider, 1995)
   ApL = L . . . . . hedeform
8. PHL < (0.2) × L . . . . . schediform
   PHL > (0.2) × L . . . . . loxoform
9. PL > (0.6) × L . . . . . triangular
   PL < (0.6) × L 10
10. Juveniles/early growth stages oval . . . . . trigonal

Juveniles/early growth stages ovate pseudotrigonal States: (A) quadrate, (B) ovate, (C) circular-ovate, (D) circular, (E) loxoform, (F) oblique-ovate, (G) pseudotrigonal, (H) oval, (I) trigonal, (J) triangular, (K) hedeform, (L) schediform.

Character state tree:



3. Underside of anterior and posterior ribs (Fig. 6): (0) solid, (1) grooved.

4. Underside of central ribs (Fig. 6): (0) solid, (1) grooved.

5. Primary radial threads (prt; Fig. 6): (0) absent, (1) present. These are raised threads that run from the umbo to the ventral margin, either along rib tops or in rib interspaces, connecting rows of primary (large) spines.

6. Rib shape (Fig. 7B): (0) flat/convex, (1) concave.

7. Secondary spines (ss; Fig. 6): (0) absent, (1) present over entire shell, (2) present only on anterior and posterior slopes of shell. (Keen [1980: 13, fig. 6] provides a diagrammatic representation of anterior, central and

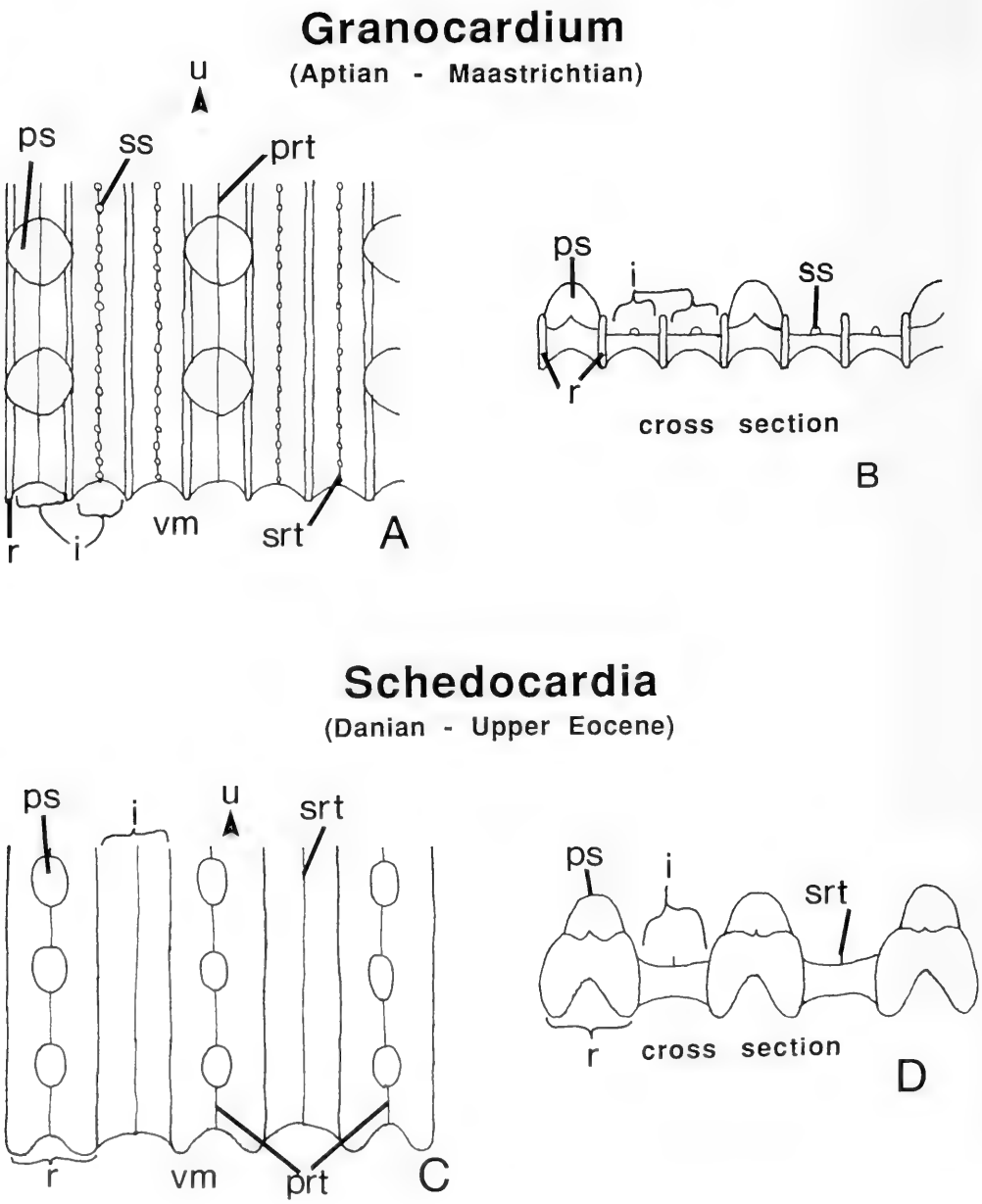


FIG. 6. Schematic diagrams of ribbing and ornamentation, illustrating how the *Granocardium*-type morphology can give rise to the Cenozoic eucardiid-type morphology by fusion of adjacent ribs. A, B, *Granocardium;* C, D, Cenozoic eucardiids, represented by *Schedocardia.* External views of shell margins on left, corresponding cross-sectional views on right.

posterior slopes.) These are small spines which are found in rib interspaces.

8. Secondary radial threads (srt; Fig. 6): (0) absent, (1) present over entire shell, (2) present on posterior slope only, (3) present on anterior and posterior slopes. These are raised threads which run from the umbo to the ventral margin, always in rib interspaces, often connecting rows of small (secondary) spines.

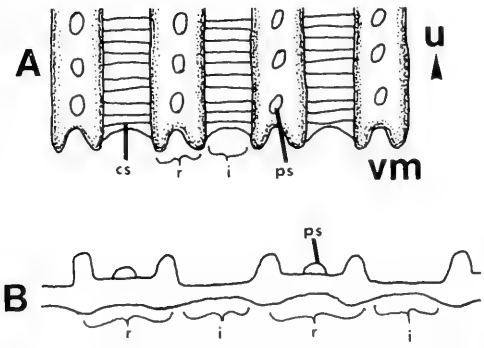


FIG. 7. A, schematic diagram of the ventral margin of a shell of a hypothetical eucardiid. Primary spines are on top of ribs. Cross-striae are in interspaces. B, Cross-section of a eucardiid with "concave" ribs. The ribs are wide and the rib tops are low, only slightly higher than the interspaces. Compare with Fig. 6D.

9. Intercalary ribs (Fig. 6): (0) absent, (1) present. These are radial ribs that occur between two rows of secondary spines.

10. Cross-striae (cs) are concentric raised threads in rib interspaces (Fig. 7A): (0) cross-striae absent, (1) cross-striae present.

11. Primary spines.

(0) Absent (Fig. 4F).
(1) Simple. External morphology: circular to subcircular knobs (Figs. 4A, 8). Microstructure: crossed-lamellar structure at base grading upward to fibrous prismatic structure with crossed lamellar structure distally; microstructurally continuous with shell (Fig. 9).
(2) Scutes (sc): External morphology: curved plates, width several times greater than height (Fig. 10).
Microstructure: predominantly branching crossed lamellar structure at base, with local inclined complex crossed lamellar to fibrous prismatic structure distally (towards tip of scute); microstructurally continuous with shell (Schneider, 1998: fig. 17).
(3) Non-imbricated concave-down triangles. External morphology: see Schneider (1995: fig. 8C, D, F, G). Microstructure: unknown (Schneider, 1995: 334).
(4) Complex. External morphology: knobs or imbricated concave-down triangles (Fig. 11A). Microstructure: predominantly fibrous prisms, microstructurally separated from shell by basal layer of irregular simple prisms (ISP) (Fig. 11B, C).
(5) Composite (Schneider, 1998): External morphology: small circular knobs. Microstructure: outer portion of spine like state 1), inner portion of formed entirely of fibrous prisms, microstructurally separate from rest of shell, but basal irregular simple prismatic layer lacking (Schneider, 1998: fig. 21).
(6) Fibrous prisms: External morphology: subcircular, wider than high (Schneider, 1998: figs. 19, 20).
Microstructure: spine entirely of fibrous prisms which are microstructurally separate from shell, no basal layer of irregular simple prisms (Schneider, 1998: fig. 18).

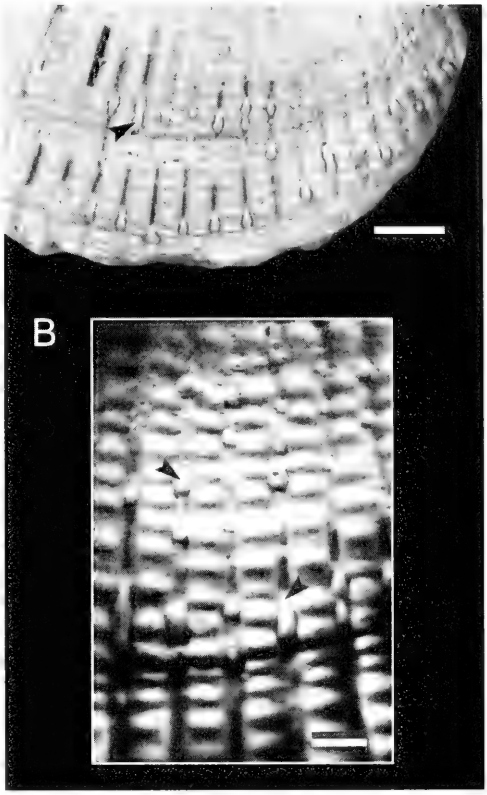


FIG. 8. External ornamentation of right valve of *Profragum praecurrens* (GSI 1061). A, ventral margin. Scale bar = 5 mm. B, central slope. Scale bar = 1.88 mm. Note presence of secondary spines (example indicated by arrow) and absence of cross-striae.

Because all body fossils of all species of *Sawkinsia* are recrystallized, the microstructure of the spines is unknown. Therefore, *Sawkinsia* is coded missing (?) for character 11.

12. Adductor muscle scar shape and location (Fig. 12): (0) anterior and posterior ad-

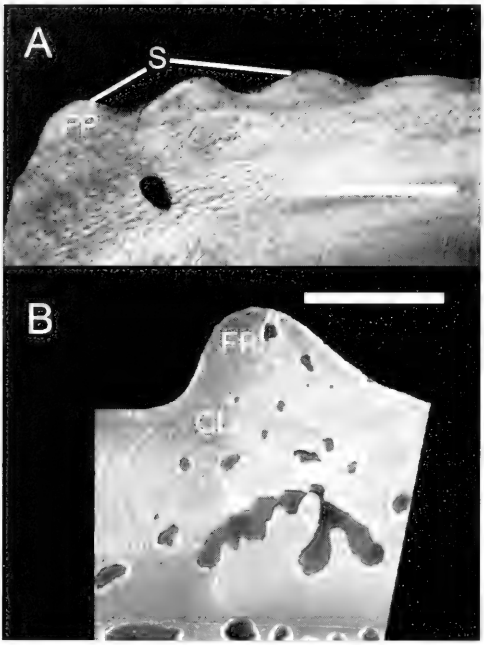


FIG. 9. Radial sections through shells of profragines. A, section through a portion of the middle of a rib of a *Profragum praecurrens* (UNC 15564, right valve). Ventral margin is at left, the direction of the umbo would be to the right. Note microstructural continuity of ornament with underlying shell. Scale bar = 1 mm. B, section through a portion of the middle of a rib of a *Granocardium kuemmeli* (AMNH 45043, right valve), displaying microstructural relationships of primary spine to underlying shell. Direction of the ventral margin would be to the left, direction of the umbo would be to the right. Scale bar = 1 mm.

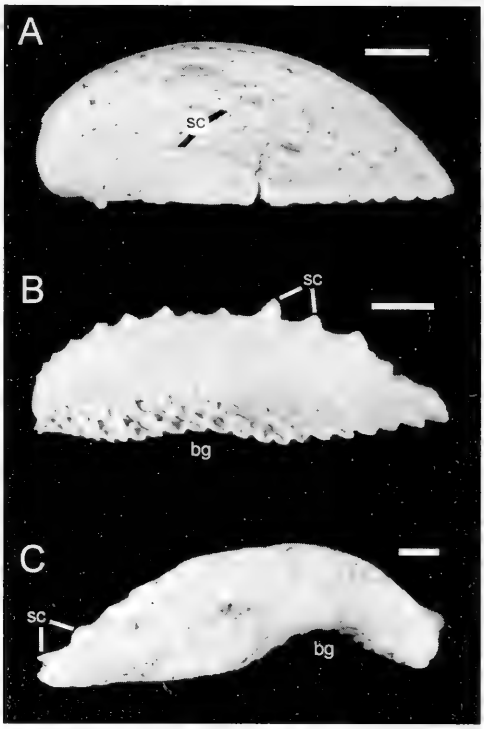


FIG. 10. Byssal gapes and scutes. A, Posterior of right valve of *Goniocardium rachitis* (ANSP 12429; scale bar = 5 mm.). Byssal gape absent. B, posterior of right valve of *Avicularium aviculare* (ANSP 6279; scale bar = 5 mm.). Byssal gape present. C, posterior of left valve of *Byssocardium emarginatum* (IRSNB I.G. 10591; scale bar = 5 mm.). Byssal gape present.

ductor muscle scars equal in size, equally distant from shell margin, (1) posterior adductor muscle scar larger and located further from shell margin.

See Figures 13–16 for characters 13–15.

13. Left anterior lateral socket (als): (0) absent/weak, (1) moderate.

14. Left posterior lateral socket (pls): (0) absent/weak, (1) moderate, (2) large.

15. Right anterior cardinal (ac) shape. States 0 to 5. (In Schneider 1995, figs. 17B and 17C were erroneously reversed. fig. 17B is *Pleuriocardia eufaulense;* fig 17C is *Granocardium kuemmeli.*)

16. Byssal gape (bg; Fig. 10): (0) absent, (1) present.

RESULTS

PAUP 3.1.1 found 6 most parsimonious trees with a length of 54 steps (Figs. 1, 2). The consistency index (CI) = 0.741 and the retention index (RI) = 0.851. Synapomorphies for the internal nodes for one of the six trees are indicated in Table 3.

The subfamily Profraginae, members of which are known only from the Cretaceous (Table 4), is the sister taxon to *Perucardia* + Cenozoic eucardiids. Profraginae is united by the presence of secondary spines (7:1) and an absent or weak left posterior lateral socket (15:0).

Granocardium and *Criocardium* are sister taxa and differ only in shell shape (character 2). For this and other reasons it is recommended that *Criocardium* be considered a

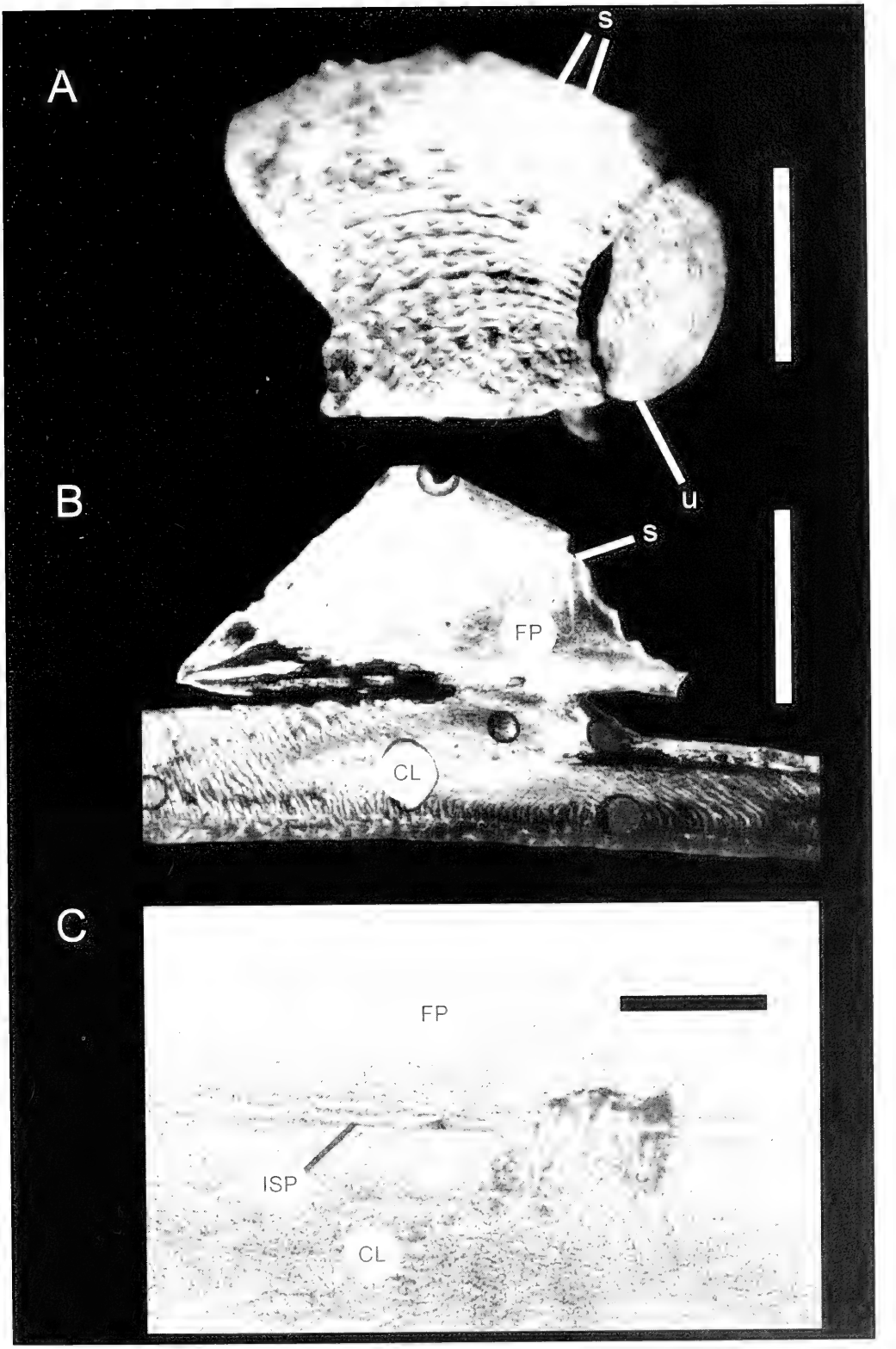


FIG. 11. Ornamentation of *Agnocardia dissidepictum* (ANSP 11035). A, external view of posterior of left valve. Note rows of imbricated concave-down triangular spines (s). Scale bar = 10 mm. B, radial section through a portion of a rib and spine, scale bar = 0.1 mm. Direction of umbo to the right; direction of ventral margin to the left. C, close-up of ISP layer between fibrous prismatic (FP) spine and crossed lamellae (CL) CL of underlying shell, scale bar = 0.01 mm.

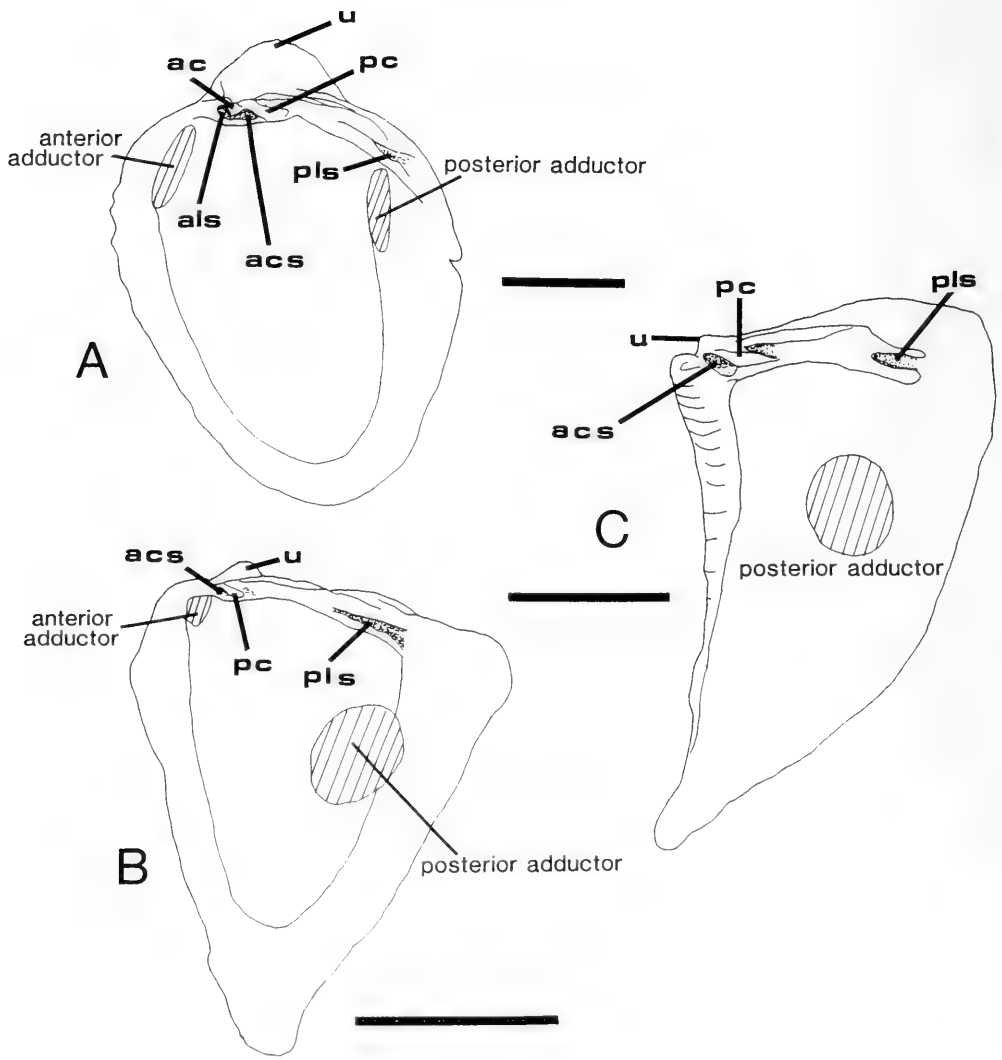


FIG. 12. Camera lucida drawings of interior of right valves. Scale bars equal 10 mm. A, *Goniocardium rachitis* (ANSP 12429); B, *Avicularium aviculare* (ANSP 6279); C, *Byssocardium emarginatum* (IRSNB I.G. 10591).

subjective junior synonym of *Granocardium* (Appendix 3 for a discussion of the *Granocardium*/*Criocardium* taxonomic problem).

The two characters that unite *Perucardia* with Cenozoic eucardiids are shell shape (2:2) and the presence of central ribs with grooved undersides (4:1). Cenozoic eucardiids (united at node 8) share shell shape (2:3), presence of cross-striae (10:1), and anterior and posterior ribs that have grooved undersides (3:1). *Loxocardium, Orthocardium, Agnocardia,* and *Hedecardium* (the *Orthocardium*-group) are united by the possession of ornament with a basal ISP layer (11:4) and *Orthocardium* and *Agnocardia* are united by concave ribs (6:1) and presence of striations across the entire shell (8:1). The *Orthocardium*-group is the sister taxon to other Cenozoic eucardiids, which are united (node 11) by a crenulate posterior margin (1:1).

Plagiocardium and *Parvicardium* were considered to be members of the Fraginae by Kafanov & Popov (1977) and Schneider (1992). In the present study, *Plagiocardium* is

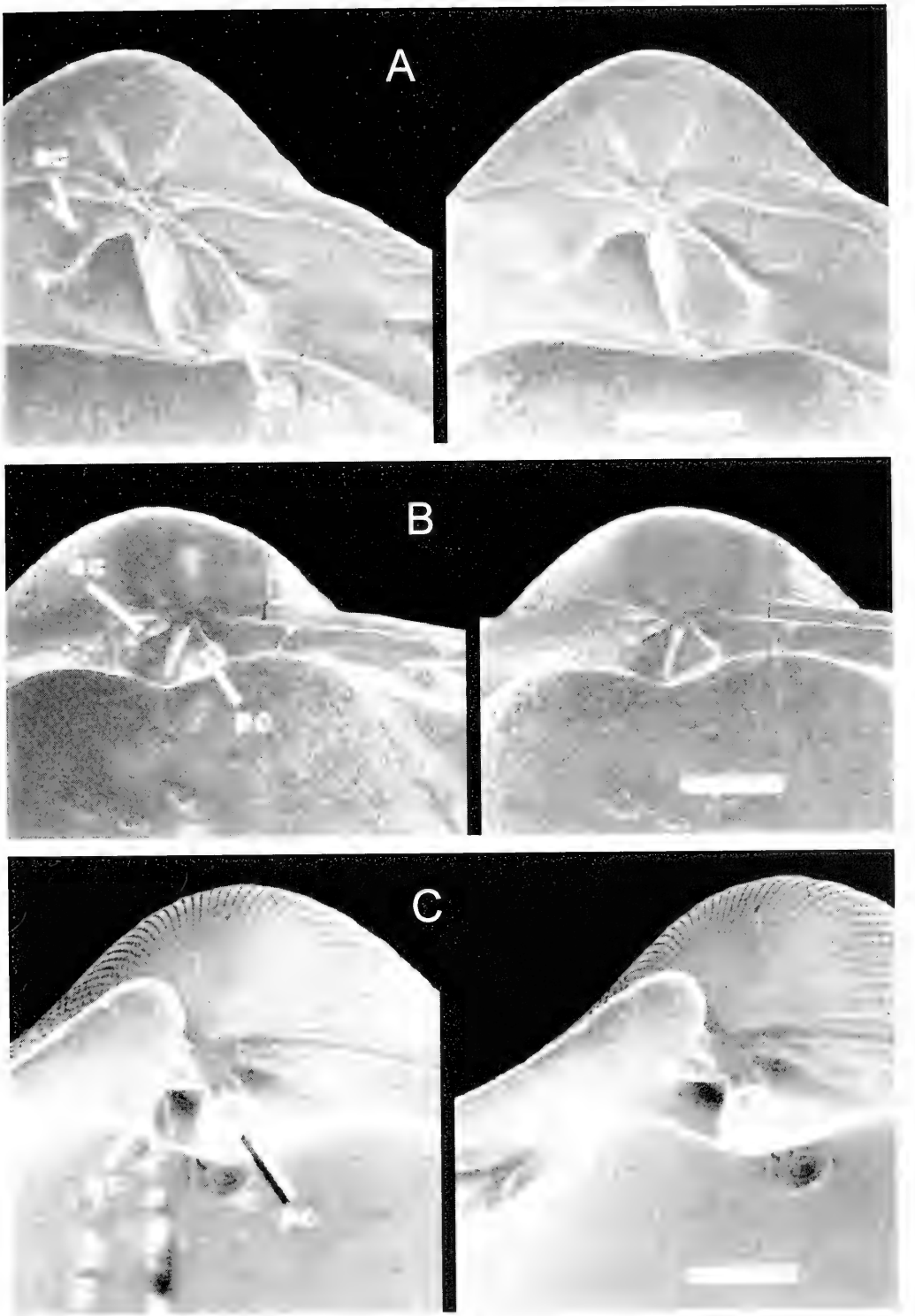


FIG. 13. Stereo electron micrographs of cardinal area of right hinges. A, *Pleuriocardia eufaulense* (ANSP 36491; scale bar = 2 mm.). Same as Fig. 17B (NOT 17C) in Schneider (1995). Anterior cardinal shape 1. B, *Loxocardium obliquum* (FMNH PE 3642; scale bar = 2 mm.), anterior cardinal shape 3. C, *Plagiocardium granulosum* (ANSP 6268; scale bar = 2 mm.), anterior cardinal shape 4.

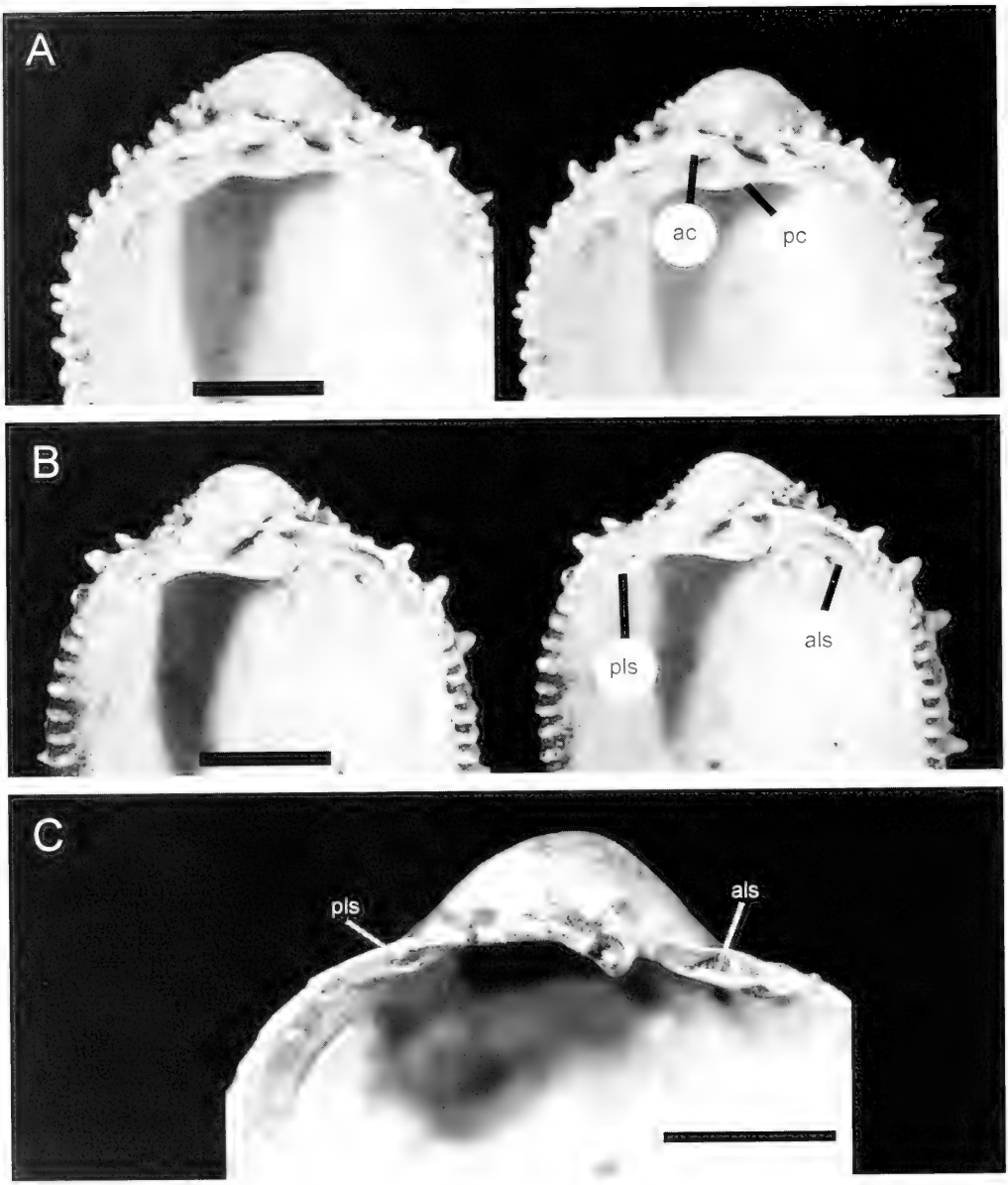


FIG. 14. Hinges. A, B. Stereo photographs of hinge of *Granocardium kuemmelli.* A, right valve (AMNH 45046); B, left valve (AMNH 45048); als moderate, pls large. Scale bars = 10 mm. C, left hinge of *Schedocardia hatchetigbeense* (USNM 645087 [syntype]; scale bar = 10 mm); als weak, pls moderate.

found to be the basal member of a clade consisting of *Papillicardium, Parvicardium,* and the three tridacnines (*Goniocardium, Aviculariumand Byssocardium*). This clade is united by shell shape (2:H), loss of rib thread (5:0), primary spine structure (11:2), an absent or weak left posterior lateral socket (14:0) and shape of right anterior cardinal (15:4).

Papillicardium has usually been considered a subgenus of *Parvicardium* (Keen, 1969, 1980; Voskuil & Onverwagt, 1989) or a close relative thereof (Kafanov & Popov, 1977). These two taxa are sister taxa in three of the six most parsimonious trees; in the other three trees they form a trichotomy with the tridacnines.

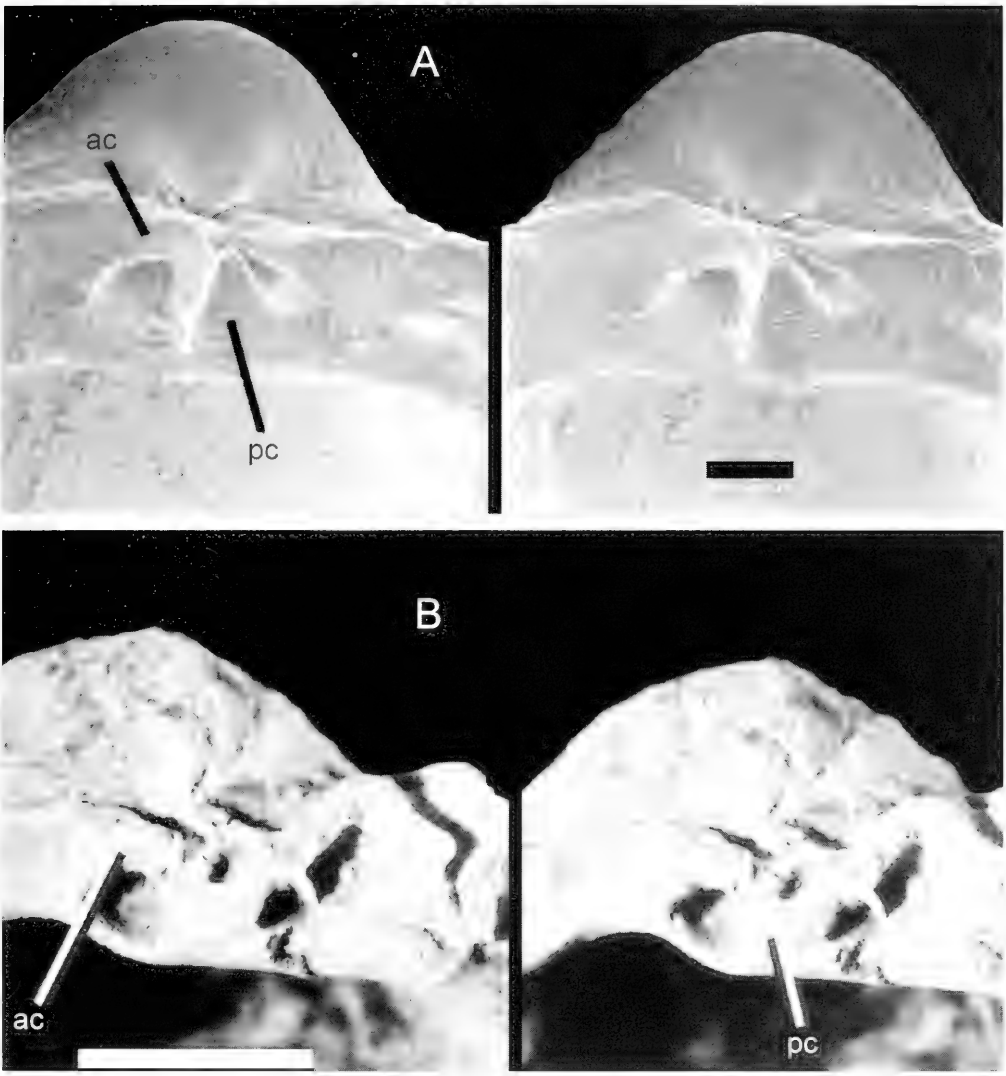


FIG. 15. Hinge stereo photographs and electron micrographs. A, right valve of *Granocardium kuemmeli* (AMNH 45046, scale bar = 2 mm.). Same as Fig. 17C (NOT 17B) in Schneider (1995), anterior cardinal shape 0. B, right valve of *Austrocardium acuticostatum* (PUDG 162, scale bar = 12 mm.), anterior cardinal shape 2.

DISCUSSION

From their appearance in the Norian (Late Triassic) through the Neocomian (Early Cretaceous), cardiids either have simple, unornamented ribs or have lost the ribs entirely (Schneider, 1995; figs. 7, 11). In the Early Cretaceous, cardiids with spines upon their ribs appear in the fossil record. *Nemocardium* has round spines atop its posterior radial ribs (Schneider, 1995: figs. 8A, 9C, D). On the profragine *Granocardium* (Figs. 4A, 6A, B), there is a row of large spines with a rib on either side of the large spine. These rows of large spines are followed by one to three rows (variable not only within a species, but within an individual [Stephenson, 1941, 1955; Scott, 1978; personal obs.]) of small spines, which are also between ribs. The two size classes of spines are herein termed primary (for the larger spines) and secondary (for the smaller spines). The space between ribs is called the interspace. Running down the middle of the rows of both the primary and secondary spines

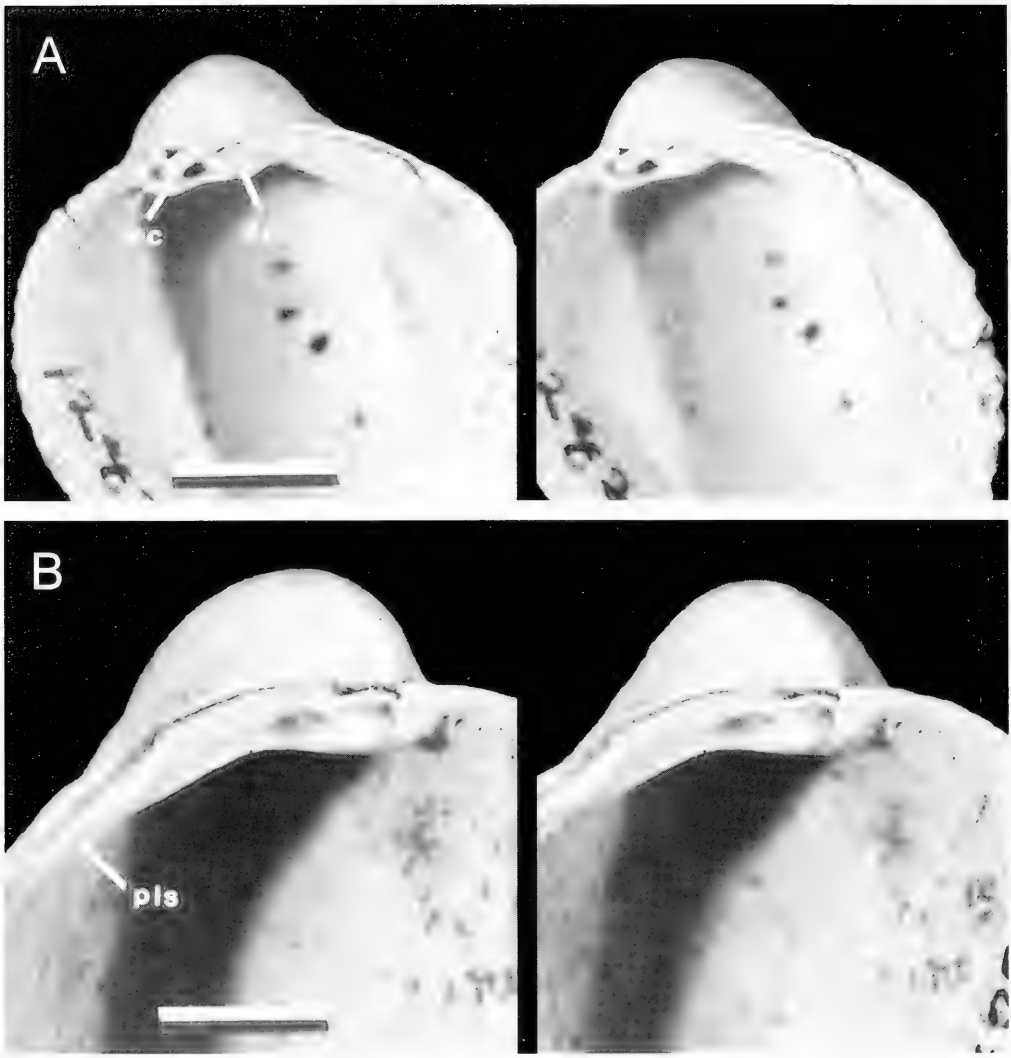


FIG. 16. Hinge stereo photographs of *Goniocardium rachitis* (ANSP 12429). A, right valve, scale bar = 4 mm. Anterior cardinal shape 5. B, left valve, scale bar = 2 mm; als absent, pls weak.

are fine raised threads, herein called radial threads. The ribs are narrow and solid underneath; this is also the condition found in all Protocardiinae, Laevicardiinae, and the outgroup taxon *Pleuriocardia.* On *Granocardium,* interspaces bearing rows of primary spines are raised slightly higher than the interspaces bearing rows of secondary spines. At the ventral margin, ribs extend further than the interspaces. The rows of secondary spines are not manifested by marginal serrations at the commisure.

When the character states of the primary and secondary spines, their respective threads, ribs, and interspaces are analyzed throughout the Cardiidae, it becomes apparent that in the evolution of Cenozoic eucardiids, two adjacent radial ribs have fused into a single radial rib. On Cenozoic cardiids (Fig. 6C, D), the primary spines and their radial threads are not between ribs, but on top of them. The ribs are wide and flat-topped. The primary spines and radial threads are on top of wide ribs that are grooved underneath. On some forms, there are threads, not associated with any spines, in the interspaces. Appar-

TABLE 3. Synapomorphies for interior nodes. Nodes numbered as in Figure 1.

Node	Synapomorphies (character:state)
1	2:B, 5:1, 10:0, 11:1, 15:0
2	14:0
3	7:1
4	2:A
5	8:1, 9:1, 13:1, 14:2
6	8:2, 15:2
7	2:C, 4:1
8	2:D, 3:1, 10:1
9	11:4
10	6:1, 8:1
11	1:1
12	2:L, 8:1
13	2:H, 5:0, 11:2, 14:0, 15:4
14	2:I
15	11:5
16	2:J, 12:1, 15:5
17	10:0, 16:1

TABLE 4. Stratigraphic ranges of cardiid genera and subgenera represented in the present analysis. Except where noted, stratigraphic ranges from J. J. Sepkoski Jr.'s unpublished compendium of marine invertebrate stratigraphic ranges. Abbreviations of stratigraphic units from Harland et al. (1990).

Paleuriocardia	Alb-Maa
Granocardium (*Granocardium*)	Alb-Maa
G. (*Ethmocardium*)	Cmp-Maa
Profragum	Alb-Maa (Badve, 1977; Schneider, unpubl.)
Indocardium	Alb-Cmp (Chiplonkar & Badve, 1976)
Austrocardium	Cmp-Maa (Schneider, unpubl.)
Perucardia	Maa
Hedecardium (*Hedecardium*)	Brt-Aqt (Schneider, unpubl.)
Agnocardia	Ypr-Zan
Orthocardium	Tha-Ypr
Loxocardium	Dan-Mio
Sawkinsia	Brt-Prb (Jung, 1976)
Schedocardia	Dan-Prb (Keen, 1980)
Plagiocardium	Dan-Mio
Papillicardium	Eoc-Hol
Parvicardium	Eoc-Hol
Goniocardium	Lut-Rup (Schneider, 1998)
Avicularium	M. Eoc.-Rup.
Byssocardium	M. Eoc.-L. Mio.

ently, the radial threads on the ribtops on Cenozoic cardiids are homologous to the primary radial threads of *Granocardium,* whereas the radial threads in the interspaces on Cenozoic cardiids are homologous to secondary radial threads of *Granocardium.* At the ventral margin, the rib sides extend further than both the rib tops and the interspaces.

If the rib pattern of the Cretaceous *Granocardium* is compared with those of Cenozoic eucardiids, it appears that the interspace bearing the primary spine on *Granocardium*—and this interspace is raised relative to other interspaces—is homologous to the rib top of Cenozoic eucardiids. On Cretaceous cardiids, the ribs are narrow and solid underneath, whereas on Cenozoic eucardiids, the ribs are wide and grooved underneath. Apparently, the individual ribs on *Granocardium* are homologous to the sides of the ribs on Cenozoic eucardiids. Some Cenozoic eucardiids even have a furrow running down the tops of the ribs, or have concave ribs. This

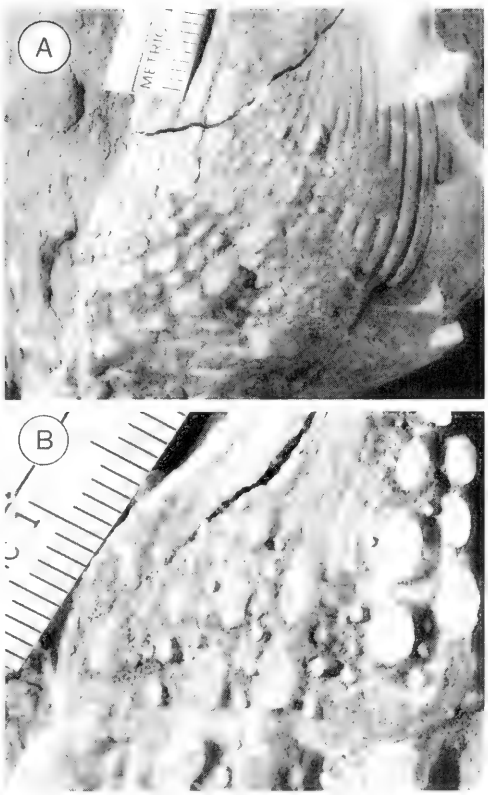


FIG. 17. Details of ribbing and ornamentation morphology of *Perucardia brueggeni* (PRI 4827 [cotype]). Scales indicated in mm in figures. A, anterior slope of left valve. B, posterior slope of left valve. On anterior and posterior slopes, rows of large spines are separated by one or two rows of small spines similar to the ornamentation pattern of the Cretaceous profragine *Granocardium* (Fig. 6A, B).

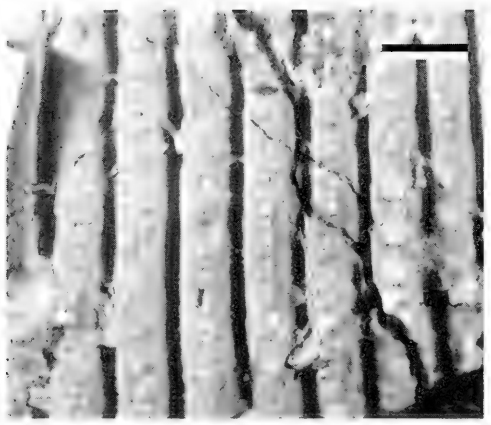


FIG. 18. *Perucardia brueggeni,* detail of ribbing and ornamentation morphology on ventral margin of central slope of right valve (PRI 4829 [paratype]; scale bar = 5 mm. Spines occur on top of wide ribs that are grooved underneath, as on Cenozoic eucardiids (Fig. 6C, D).

furrow is apparently homologous to the rib interspace, with the sides of the ribs being homologous to single ribs in Cretaceous cardiids.

Perucardia is intermediate in morphology between Cretaceous eucardiids and Cenozoic eucardiids. *Perucardia* is known from a few specimens from Maastrichtian sediments of Peru, Colombia, and Venezuela (Olsson, 1944). The ribs on the central slope of *Perucardia* (Fig. 18) are as in Cenozoic eucardiids, with spines on top of wide ribs, whereas the anterior and posterior slopes (Fig. 17) are as in Cretaceous eucardiids, with rows of secondary spines between rows of primary spines. These primary spines on the anterior and posterior slopes may be described as being on top of adjacent ribs with a very narrow interspace in between them; the two ribs have nearly "fused" into a single rib.

Perucardia is both morphologically and stratigraphically intermediate between Cretaceous and Cenozoic eucardiids (Fig. 19). Cladistically, rib fusion is manifested by the presence of ribs on the central slope that are grooved underneath (4:1), the character that unites *Perucardia* with Cenozoic cardiids. *Perucardia* shares the primitive state of anterior and posterior ribs that are solid underneath (3:0) with Cretaceous cardiids. One of the characters that unites Cenozoic cardiids is anterior and posterior ribs that are grooved underneath (3:1). This means that there were at least two episodes of rib fusion in the eucardiid lineage (Fig. 17 arrows). First, adjacent radial ribs on the central slope fused (*Perucardia;* arrow A). Subsequently, adjacent ribs on the distal slopes fused (Cenozoic eucardiids; arrow B). The lineage of cardiids with fusion of only the central ribs became extinct in the Maastrichtian with the demise of *Perucardia,* whilst the lineage that further underwent fusion of the more distal sets of ribs diversified (Fig. 19). A seemingly more complicated scenario would be that *Perucardia* represents one lineage that underwent rib fusion along on the distal slopes; whilst the Cenozoic eucardiids are a separate lineage that underwent rib fusion across the entire shell. In any event, the above statement that there were at least two episodes of rib fusion within the eucardiid lineage is accurate.

Gabb (1869), who erected *Granocardium,* and Weller (1907), are the only workers I know of who have previously recognized the similarity of the rows of primary spines in the interspaces of a species of *Granocardium* to the rib tops of most Cenozoic cardiids. Gabb described *Granocardium* as having two series of radial ribs, with the "larger" ribs bearing spines. However, Gabb did not recognize the homology between the sides of the "larger" ribs and a single "smaller" rib. Neither did Gabb perceive that the tops of the "larger" ribs were homologous to interspaces (Appendix 3). In describing *Granocardium kuemmeli* (Weller, 1907) (the representative of *Criocardium* in the present analysis), Weller (pp. 586–7) writes,

> Each third interspace is occupied by a row of strong and thick spines . . . their bases occupying the entire width of the furrow, in which case the two bounding costae with the row of spines rising from the intervening furrow, appear to form altogether, one broad rib supporting a row of strong spines . . . In some specimens the bases of the larger spines or nodes are confluent and appear to fill the interspace occupied by them, so that the two bounding costae with the row of spines together seem to constitute a single broad rib crowned with a rib of strong nodes . . .

Weller (p. 587) then goes on to write,

> . . . the surface of the shell is apparently marked by radiating rows of tubercles which apparently do not rise from interspaces between costae, but directly from the surface.

Weller recognized that at on least one species of Cretaceous cardiid, the ribbing pat-

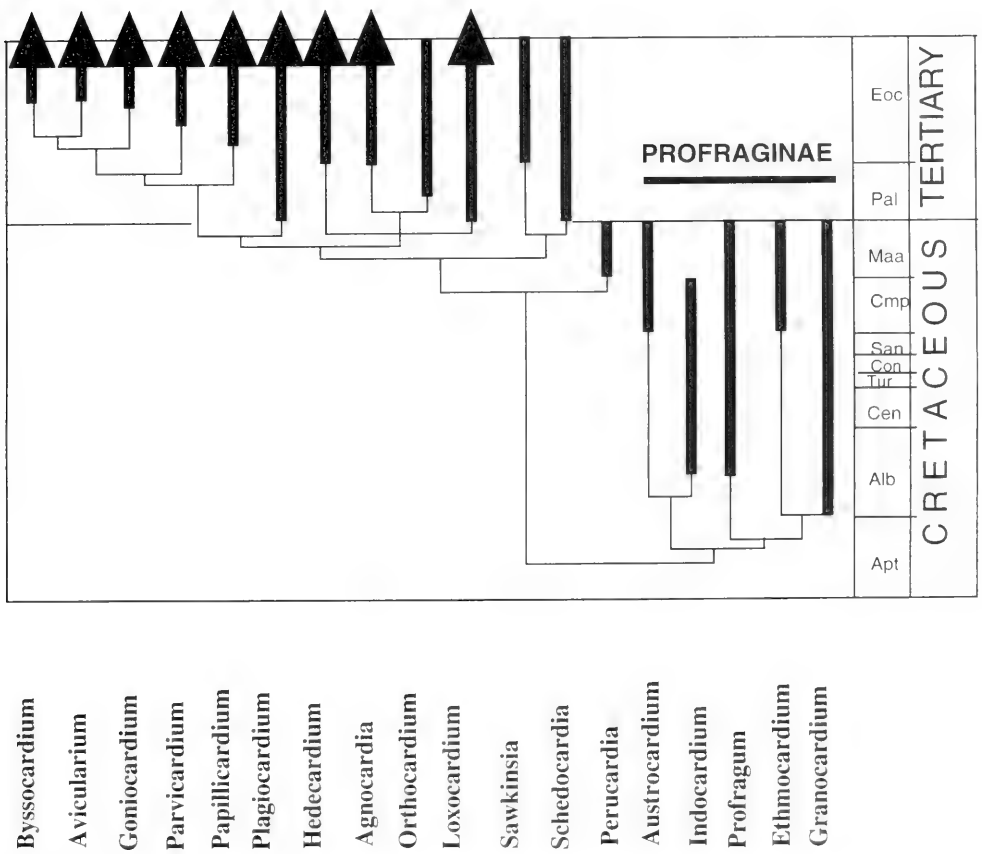


FIG. 19. Phylogenetic relationships of basal eucardiids plotted against geologic time. Time scale and abbreviations from Harland et al. (1990).

tern approached that of most Cenozoic cardiids. However, with *Perucardia* yet to be collected, Weller could not go further in recognizing the implications of *G. kuemmeli*'s morphology for determining homologies and reconstructing phylogenetic history of the Cardiidae.

Cardiid diversity and evolution during the Cretaceous to Eocene interval has been been misinterpreted not only by failing to recognize proper rib and ornamentation homologies, but by erroneously assigning numerous species of Cretaceous cardiids to genera otherwise known only from the Oligocene to Recent (Appendix 2). These generic assignments were based on superficial resemblances, usually shell shape. This situation is not dissimilar to that of flowering plants (angiosperms). For decades Cretaceous angiosperms were assigned to extant genera and families primarily on the basis of leaf outline, without taking into consideration any other characters, such as internal venation of the leaves (Doyle & Hickey, 1976; Hickey & Doyle, 1977). Therefore, the evolutionary history of flowering plants was erroneously interpreted as rapid diversification in the Cretaceous with little extinction and diversification since then (Doyle, 1978).

Cardiid evolution has likewise been misunderstood, although not to the degree as in angiosperms. Keen (1969, 1980) and Kafanov & Popov (1977) rejected all records of pre-Oligocene species of *Cardium s.s., Bucardium, Acanthocardia* (*Acanthocardia*), and *Fragum.* However, Keen (1969, 1980) considered (1) *Perucardia* to be a subgenus of *Vepricardium,* and (2) the Late Cretaceous pleuriocardiine *Incacardium* to be a subgenus of *Acanthocardia,* thus giving *Vepricardium* and *Acanthocardia* stratigraphic ranges of Late Cretaceous to Recent. Keen (1969,

1980) also considered all Cretaceous eucardiids, as well as the Norian (Late Triassic) anomalodesmatan *Septocardia* (Schneider, 1995: 322) as members of the subfamily Cardiinae.

The case of *Profragum* deserves special attention. Stoliczka (1871) erected the species *Fragum praecurrens* for some fossils from the Cretaceous of India. Badve (1977) erected the subfamily Profraginae and the genus *Profragum* for this one species. On the basis of its adult shell shape, strong carina, and alleged cross-striae, Badve thought that Profraginae was closely related to Fraginae. Badve discusses and figures strong cross-striae on the interspaces of the type specimen of *Fragum praecurrens.* Cross-striae are present in most fragines (Keen, 1951, 1969, 1980). However, examination of the type specimen of *Fragum praecurrens* shows that the sculpture on the interspaces is not cross-striae but secondary spines, as in the Cretaceous *Granocardium* (Figs. 4A, 9). The only Cretaceous cardiids that have cross-striae are the pleuriocardiines (Schneider, 1995); cross-striae are absent on the Cretaceous taxa *Granocardium, Indocardium,* and *Austrocardium.* Furthermore, *Profragum*'s ornamental microstructure is the same as that of *Granocardium* (Fig. 9) and not at all like that of *Fragum* (Schneider, 1998: fig. 18). Freneix (1956, 1957; Dartevelle & Freneix, 1957) assigned several other Cretaceous cardiids to *Fragum* (Table 5). Although microstructural work has yet to be done on these species, their hinge and ornamentation characters are clearly those of *Profragum,* and not *Fragum.*

Diversity of eucardiid subgenera using the taxonomy advocated in Table 4 is plotted in Figure 20.

TABLE 5. Species of Cretaceous cardiids referred to *Fragum* by Freneix. These species are herein considered members of the genus *Profragum,* except for *Cardium pulchrum,* which is considered a species of *Granocardium.* Unless otherwise indicated, assignments by Freneix were made in Dartevelle & Freneix (1957).

Cardium amotapense Olsson, 1934	
Cardium cerevicianum Pasic, 1951	
Cardium perobliquum Koenen, 1897	(Freneix, 1957)
Fragum praecurrens Stoliczka, 1871	
Cardium pulchrum Bruggen, 1910	
Cardium subperobliquum Riedel, 1932	(Freneix, 1956, 1957)

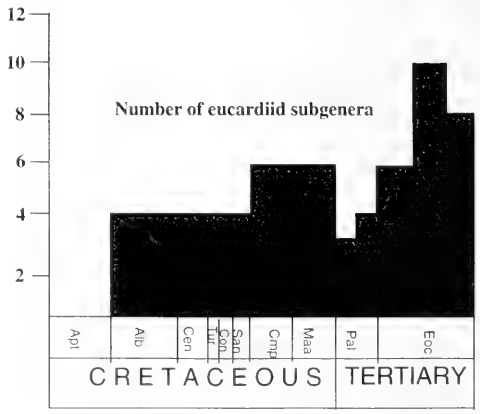


FIG. 20. Eucardiid diversity from the Lower Cretaceous Aptian stage through the Eocene.

CONCLUSIONS

A phylogenetic analysis of stem-group eucardiid bivalves produces a phylogenetic hypothesis that the Cretaceous subfamily Profraginae is the sister taxon to *Perucardia* + Cenozoic eucardiids. The Maastrichtian (latest Cretaceous) *Perucardia* displays a mosaic of profragine primitive characters and Cenozoic eucardiid derived characters.

The subfamily Cardiinae is a paraphyletic grade, not a monophyletic group. Cretaceous taxa belong to the Profraginae, which became extinct at the end of the Cretaceous. The *Orthocardium*-group is the sister taxon to the remaining eucardiids in the analysis, with *Schedocardia* + *Sawkinsia* the sister group to ((*Plagiocardium* (Fraginae + Tridacninae)).

The origin of Cenozoic eucardiids is marked by the evolutionary innovation of fusion of adjacent radial radial ribs into a single rib. The ribs on Cretaceous cardiids are homologous to the sides of ribs on Cenozoic eucardiids, and the interspaces of Cretaceous eucardiids are homologous to Cenozoic eucardiid rib tops. The Maastrichtian taxon *Perucardia* is morphologically and stratigraphically intermediate between Cretaceous eucardiids on one hand, and Cenozoic eucardiids on the other. There were at least two episodes of rib fusion in the eucardiid lineage.

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APPENDIX 1

Material examined. Numbers in parentheses indicates number of specimens examined.

Pleuriocardia eufaulense (Conrad, 1860): ANSP 19597 (1, holotype), 36491 (7); AMNH 45040 (1), 45041 (1), 45071 (1); FMNH 18647 (2); USNM 20847 (1).

Granocardium (*Granocardium*) *carolinum* (Orbigny, 1844): Data from Orbigny (1844).

Granocardium (*Granocardium*) *kuemmeli* (Weller, 1907): USNM 21126 (1, holotype); AMNH 45042 (1), 45043 (1), 45044 (1), 45045 (1), 45046 (1), 45047 (1), 45048 (1); ANSP 36475 (5); YPM IP.025574 (1).

Granocardium (*Ethmocardium*) *whitei* (Dall, 1900): USNM 315529 (1, holotype), USNM 28710 (1); AMNH 9402 (1), 27846 (1); ANSP 36948 (20); YPM IP.032009 (1), IP.032010 (50), IP.032636 (20), IP.032662 (20), IP.031422 (50).

Profragum praecurrens (Stoliczka, 1871): GSI 1060 (1, plaster cast of cotype), 1061 (1, plaster cast of cotype); UNC 15564 (20).

Indocardium blanfordi Chiplonkar & Badve, 1976: MNHN 9665 (2). Additional data from Chiplonkar & Badve (1976).

Austrocardium acuticostatum (Orbigny, 1842): PUDG 162 (7); MNHN 5697 (1, plaster cast of lectotype).

Perucardia brueggeni Olsson, 1944: PRI 3732 (1, hypotype), 4827 (1, cotype), 4827a (1, paratype), 4828 (1, paratype), 4829 (1, paratype), 4830 (1, cotype), 4831 (1, paratype).

Loxocardium obliquum (Lamarck, 1805): ANSP 6269 (1), 6970 (1), 7667 (5); FMNH PE3642 (144), PE3606 (2), PE17386 (7).

Hedecardium waitakiense (Suter, 1907): DSIRGS 10837 (3).

Agnocardia dissidepictum (Woodring, 1925): USNM 352819 (1, holotype); ANSP 11035 (1).

Orthocardium porulosum (Solander, 1766): ANSP 6266 (4); AMNH 3091 (1); FMNH UC 24932 (5); YPM IP.006880 (1).

Sawkinsia matleyi Cox, 1941:NHM L74121 (1, holotype), NHM L74764 (1, hypotype), L 74113 (1, hypotype), L 74763 (1, hypotype); NMB G 14089 (1, hypotype), NMB G 14091 (1, hypotype), NMB G 14093 (1, hypotype), NMB G 14094 (1, hypotype); UWIGM 1152 (3), 1154 (1).

Schedocardia hatchetigbeense (Aldrich, 1886): USNM 638802 (1, syntype), 645087 (1, syntype); ANSP 5420 (1), 8687 (1), 8756 (3).

Plagiocardium granulosum (Lamarck, 1805): ANSP 6268 (14), 7663 (1).

Parvicardium (*Papillicardium*) *etheridgei* (Tremlett, 1950): NHM L 80479 (1, holotype).

Parvicardium (*Parvicardium*) *triangulatum* (Laubrière, 1881): Data from Laubrière (1881).

Goniocardium rachitis (Deshayes, 1829): ANSP 12429 (6); FMNH PE3624 (2).

Avicularium aviculare (Lamarck, 1805): ANSP 6279 (3).

Byssocardium emarginatum (Deshayes, 1829): IRSNB I.G. 10591 (4).

APPENDIX 2

A. Taxa represented by a non-type species or a post-Eocene species.

(1) *Hedecardium.* The only Eocene species are *H. collinsi* Marwick, 1960, and *H. brunneri* (Hector, 1886). Although these two species are identifiable as *Hedecardium,* the material is fragmentary and the hinge is unknown (Marwick, 1944). The type species, the Oligocene *H. waitakiense* (Suter, 1907), is known from well-preserved specimens (Marwick, 1944; Beu & Maxwell, 1990) and is chosen to represent this taxon.

(2) *Papillicardium.* The type species is the Middle Miocene to Recent *Papillicardium papillosum* (Poli, 1791). The Eocene *P. etheridgei* (Tremlett, 1950) is chosen to represent *Papillicardium.*

(3) *Parvicardium.* The type species is the Recent *Parvicardium siculum* (Sowerby, 1841). The Eocene species *Parvicardium triangulatum* (Laubrière, 1881) is selected to represent this taxon.

(4) *Criocardium.* The type species is *Cardium* (*Criocardium*) *dumosum* Conrad, 1871. *Cardium kuemmeli* Weller, 1907, is used to represent *Criocardium,* because there is more and better preserved material. In erecting *C. kuemmeli,* Weller (p. 586) stated that "the species exhibits clearly the characteristics of the subgenus *Criocardium.*" Weller also stated that numerous specimens of this species were already in the collections of the USNM, labeled *Cardium dumosum,* the type species of *Criocardium.*

(5) *Pleuriocardia.* The type species is *Pleuriocardia kansasense* (Meek, 1871). *Pleuriocardia eufaulense* (Conrad, 1860) is used to represent *Pleuriocardia* because this is the most common species in the subfamily with an abundance of well-preserved material.

(6) *Austrocardium.* Freneix & Grant-Mackie (1978) erected *Austrocardium* as a monotypic genus, type species *A. acherontis* Freneix & Grant-Mackie, 1978. Schneider (1992) found that *Cardium acuticostatum* Orbigny, 1842, belonged in *Austrocardium. Austrocardium*

acuticostatum is chosen to represent *Austrocardium* because the material of *A. acuticostatum* is better preserved than that of *A. acherontis; A. acherontis* would be scored identically to *A. acuticostatum,* except that the states for its posterior margin and shape of anterior cardinal are unknown.

(7) *Loxocardium.* The type species is the Eocene *Loxocardium formosum* (Deshayes, 1858). This is a relatively rare species. By far the most common species of *Loxocardium* is *L. obliquum* (Lamarck, 1805), for which I was able to examine over 100 specimens.

(8) *Agnocardia.* The type species is the Eocene *Agnocardia claibornense* (Aldrich, 1911). This species is known from only a few broken valves. Vokes (1984, 1989) reported that the hinge of this species was unknown. After examination of specimens (including the types) of all the western hemisphere species of *Agnocardia* [*A. sorrentoensis* (Hanna, 1927), *A. glebosum* (Conrad, 1848), *A. acrocome* (Dall, 1900), *A. spinosifrons* Vokes, 1984, *A. dissidepictum* (Woodring, 1925), *A. cinderellae* (Maury, 1917) and *A. pessoae* (Maury, 1924); *A. rectispina* (Koenen, 1893) from the Early Oligocene of Germany is the only other species of *Agnocardia* that I know of] it was decided that the best material of *Agnocardia* is actually the youngest (Late Pliocene) species *A. dissidepictum.* All species of *Agnocardia* would be coded identically for the characters considered herein.

B. Reasons for not including taxa with alleged Cretaceous to Eocene members.

(1–3) *Cardium, Bucardium,* and *Acanthocardia* (*Acanthocardia*). Many authors have described species of Cretaceous cardiids as belonging to these taxa. However, Keen (1951, 1969, 1980) and Popov (1977) rejected all Cretaceous species of *Cardium, Bucardium,* and *A.* (*Acanthocardia*). Most of these species belong to *Austrocardium,* the rest to *Pleuriocardia.*

(4) *Vepricardium.* Keen (1969, 1980) gave the range of *Vepricardium* (*Vepricardium*) as Paleocene to Recent, and was followed by Popov (1977) and Kafanov & Popov (1977). I have found that alleged Paleogene species are either *Orthocardium, Agnocardia* or indeterminate.

(5) *Papyridea.* I have found that all alleged Eocene *Papyridea* are species of *Parvicardium.* Keen (1969, 1980) states that the stratigraphic range of *Papyridea* is Miocene to Recent.

(6) *Trigoniocardia.* A number of Eocene species have been variously classified as *Trigoniocardia. Cardium* (*Trigoniocardia?*) *colosseum* Cox, 1941, *Cardium* (*Anthocardia*) [sic] *avonum* Richards, in Richards & Palmer 1953, and *Cardium* (*Trigoniocardium*) [sic] *protoaliculum* Richards, in Richards & Palmer, 1953, are species of *Sawkinsia.* Palmer & Brann (1965) classified the latter two species as *Trigoniocardia* (*Americardia*). Keen (1969, 1980) and Kafanov & Popov (1977) reject pre-Oligocene records of *Trigoniocardia* and *Americardia.*

(7) *Fragum.* Many Cretaceous species have been classified as *Fragum.* Most of these species belong to *Profragum,* the rest to *Pleuriocardia.* Alleged Eocene species of *Fragum* are indeterminate or belong to one of the following: *Papillicardium, Parvicardium, Loxocardium,* or *Goniocardium.* Keen (1969, 1980) and Kafanov & Popov (1977) reject pre-Oligocene records of *Fragum.*

(8) *Europicardium.* The type species is the Miocene to Pliocene *Europicardium multicostatum* (Brocchi, 1814). Popov (1977) lists one Eocene species of *Europicardium, Cardium stilpnaulax* Cossmann, 1886. The type figures of *C. stilpnaulax* in Cossmann (1886) shows it to have the shell shape, wide concave ribs, hinge, and ornamentation of *Orthocardium.* However, the species figured as *C. stilpnaulax* in Cossmann & Pisarro (1906) has the shell shape and ornamentation of *Europicardium.* Given the unsettled taxonomic and stratigraphic status of this taxon, it was decided not to include it in the analysis.

(9) *Dinocardium. Laevicardium* (*Dinocardium*) *cubensis* Kojumdgieva & de la Torre, 1982, Late Eocene of Cuba, is indeterminate.

(10) *Tridacna.* Collignon (1949) described *Tridacna besairiei* as coming from the Maastrichtian (later redescribed as Danian [Collignon, 1968]) of Madagascar. However, the provenance of this specimen is dubious; it probably is no older than Miocene (Schneider, 1998).

APPENDIX 3

Synonymy of *Criocardium* Conrad, 1871, with *Granocardium* Gabb, 1869.

Gabb (1869) erected *Granocardium* for some Late Cretaceous species of cardiids. Gabb (p. 266) described *Granocardium* as follows:

Shell nearly equilateral, usually longer than wide; valves closed all round; surface ornamented by two series of radiating ribs; large ribs bearing spines, tubercles, or grains, and smaller ribs occupying the interspaces between the larger, and granulate.

As stated in the text, Gabb recognized the primary spines to be on top of ribs, not between them. However, he did not perceive that one side of these larger ribs was homologous with a single smaller rib, and that the spine-bearing tops of the larger rib were homologous with the interspaces. Gabb assigned the species *Cardium productum* Sowerby 1832, *C. moutonianum* Orbigny, 1844, *C. carolinum* Orbigny, 1844, *C. tippanum* Conrad, 1858, and *C. sabulosum* Gabb, 1869, to *Granocardium.* No type species was designated. In contrast to Gabb's definition of *Granocardium,* on all of these species the "smaller" ribs do not bear spines. Spines are present between the "smaller" ribs, or between the "smaller" ribs and the "larger" ribs.

Stoliczka (1871: 207–8) felt that *Granocardium* was a junior synonym of *Trachycardium:*

. . . the species forming the subgenus [*Granocardium*] are said to be characterized by the intermediate ribs being granulate. Such can be seen on both ends of the shell of *C. orbita* for instance, which is a *Trachycardium;* I don't see, therefore, the necessity for a new sub-genus.

Cardium orbita is considered a species of the Trachycardiine *Vasticardium* (Fischer-Piette, 1977; Vidal, 1997). No species of Trachycardiinae has "two series of radiating ribs" or "intermediate ribs." Stoliczka's statement above does not make sense in light of the morphology of either trachycardiines or Gabb's species of *Granocardium.* Stoliczka was at least consistent, classifying Gabb's *Granocardium* species as *Trachycardium.*

Apparently unaware of Gabb's (1869) erection of *Granocardium,* Conrad (1871) erected *Criocardium* as a subgenus of *Cardium,* and described *Criocardium* as "Multiradiate; interstices spinose, ribs smooth; anterior lateral tooth long and prominent." Although it is unclear what Conrad meant by "multiradiate" (numerous ribs?—this describes the vast majority of cardiids; or, multiple types of ribs, as in Gabb's [1869] description of *Granocardium?*), Conrad correctly noted ("interstices spinose, ribs smooth") that the spines are between ribs, not on top of them. Conrad placed *Cardium dumosum* Conrad, 1871, and *Cardium raulineanum* Orbigny, 1844, in *Criocardium.* A type species was not designated. Stoliczka (1871) thought that *Criocardium* was little different from *Granocardium,* and therefore also considered *Criocardium* a junior synonym of *Trachycardium.* Stoliczka did designate *C. dumosum* as the type species of *Criocardium.* Stewart (1930) designated *Cardium carolinum* as type species of *Granocardium.* Stewart did not discuss *Criocardium.*

Stephenson's (1941) descriptions of the ornamentation of *C. carolinum* and *C. dumosum* are accurate. Stephenson reached the same conclusions as I, regarding *Criocardium* as a junior synonym of *Granocardium.*

With *Granocardium* and *Criocardium* incorrectly described, and *Criocardium* erected without knowledge of *Granocardium,* these two genus-level names have since been used capriciously. Keen (1969, 1980) attempted to differentiate the two by defining *Granocardium* as having "intercalary ribs 2 to 3" and *Criocardium* as having "intercalary ribs tending to be single rows of small spines between ribs." However, *Cardium carolinum*'s ornamentation varies across the surface of the shell, as on many species that have been assigned to *Granocardium.* On the anterior and posterior slopes of the shell of *C. carolinum,* most rows of spines are of primary spines, with an occassional row of secondary spines. The central slope of the shell bears *only* rows of secondary spines. Therefore, the number of intercalary ribs on *Granocardium* varies from 0 or 1 on the anterior and posterior slopes to 30 consecutive "intercalary" ribs across the central slope of the shell. *Cardium carolinum* has rows of secondary spines between ribs, which Keen used to define *Criocardium.* On *Cardium dumosum,* there are both intercalary ribs *and* rows of secondary spines.

Given the foregoing taxonomic and morphologic confusion, I recommend that all cardiids with the following morphologic features be considered *Granocardium,* with *Criocardium* considered a subjective junior synonym:

Shell quadrate to ovate. Ribbing consists entirely of regularly spaced ribs across entire shell surface. Ribs narrow, smooth-topped, solid underneath, and project beyond rib interspaces. Rows of spines in interspaces between ribs. Spines of two different sizes (termed primary and secondary), but spines

within a single row all of one size. Spines within a single row connected by a raised thread, but raised thread never present without spines. Interspaces that bear rows of primary spines raised higher than other interspaces. Spines in microstructural continuity with shell. Concentric sculpture and cross-striae absent.

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A NEW GENUS AND FIVE NEW SPECIES OF MUSSELS (BIVALVIA, MYTILIDAE) FROM DEEP-SEA SULFIDE/HYDROCARBON SEEPS IN THE GULF OF MEXICO

Richard G. Gustafson[1]*, Ruth D. Turner[2], Richard A. Lutz[1], & Robert C. Vrijenhoek[1]

ABSTRACT

Five new species of modioliform mussels in the family Mytilidae are described from material collected at sulfide/hydrocarbon seeps in the Gulf of Mexico. New definitive taxa, placed in the subfamily Bathymodiolinae, include the genus Tamu and the species Tamu fisheri from hydrocarbon seeps on the Louisiana Continental Slope, Bathymodiolus heckerae from brine seeps at the base of the West Florida Escarpment in the eastern Gulf of Mexico, and Bathymodiolus brooksi from the West Florida Escarpment site and from hydrocarbon seeps at Alamiños Canyon in the western Gulf of Mexico. An additional two new mussel species, which exhibit combinations of morphological characters unlike any existing mytilid genus but for which molecular data are equivocal, are provisionally placed in the genera Bathymodiolus and Idas, respectively. These are: "Bathymodiolus" childressi from hydrocarbon seeps at Alamiños Canyon and the Louisiana Continental Slope, and "Idas" macdonaldi (in the subfamily Modiolinae) from hydrocarbon seeps on the Louisiana Continental Slope.

Key words: Mytilidae, deep-sea, sulfide seeps, hydrocarbon seeps, Bathymodiolinae.

INTRODUCTION

Modioliform mussels in the family Mytilidae are conspicuous members of many deep-sea hydrothermal vent and cold-water methane/sulfide seep environments. A common feature of these mussels is their dependence on sulfide-oxidizing or methanotrophic symbionts (Fisher, 1990; Cavanaugh, 1992). The first vent mussel described was Bathymodiolus thermophilus Kenk & Wilson, 1985, which occurs at hydrothermal vents on the Galápagos Rift and the East Pacific Rise (EPR). Recently described species are: B. platifrons Hashimoto & Okutani, 1994; B. japonicus Hashimoto & Okutani, 1994; B. aduloides Hashimoto & Okutani, 1994; and B. septemdierum Hashimoto & Okutani, 1994, from vent and cold seep sites around Japan; B. brevior Cosel, Métivier & Hashimoto, 1994, and B. elongatus Cosel, Métivier & Hashimoto, 1994, from vent sites in the south Pacific; and B. puteoserpentis Cosel, Métivier & Hashimoto, 1994, from the Snake Pit site on the Mid-Atlantic Ridge. In addition, the small mussel Idas washingtonia (Bernard, 1978) occurs at hydrothermal vents on the Juan de Fuca Ridge in the north-eastern Pacific (Juniper et al., 1992) and Amygdalum politum (Verrill & Smith, in Verrill, 1880), a small thin-shelled mytilid, occurs near cold water hydrocarbon seeps on the Louisiana Continental Slope (Turner, 1985).

As yet undescribed modioliform mussels were reported from hydrothermal vents or cold-seeps in the Pacific Ocean at Guaymas Basin (Turner, 1985), Middle Valley (Juniper et al., 1992), the Mariana Back-Arc Basin (Hessler & Lonsdale, 1991), and the Mid-Okinawa Trough (Hashimoto et al., 1995); and in the Atlantic Ocean at the South Barbados accretionary prism (Jollivet et al., 1990) and on the Mid-Atlantic Ridge at 37°50′N ("Menez Gwen" site), 37°17′N ("Lucky Strike" site), 29°N ("Broken Spur" site), and 14°45′N (Cosel et al., 1997).

An allozyme survey by Craddock et al. (1995) identified several additional modioliform taxa from sulfide/hydrocarbon seeps in the Gulf of Mexico. A subsequent analysis of these specimens for DNA sequences from a region of the mitochondrial Cytochrome c Ox-

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TABLE 1. New species and type localities of modioliform mussels from the Gulf of Mexico.

New species	Location	Latitude Longitude	Depth (m)
Bathymodiolus heckerae	West Florida Escarpment	26°02.2′ N 84°54.5′ W	3314
Bathymodiolus brooksi	Alamiños Canyon	26°21.3′ N 94°29.7′ W	2222
Bathymodiolus brooksi	West Florida Escarpment	26°02.2′ N 84°54.5′ W	3314
"Bathymodiolus" childressi	Bush Hill, Louisiana Continental Slope	27°46.9′ N 91°30.4′ W	546
"Bathymodiolus" childressi	Brine Pool-NR 1, Louisiana Continental Slope	27°43.4′ N 91°16.6′ W	650
"Bathymodiolus" childressi	Alamiños Canyon 26°21.3′ N, 94°29.7′ W		2222
Tamu fisheri	Bush Hill, Louisiana Continental Slope	27°46.9′ N 91°30.4′ W	546
Tamu fisheri	Near Garden Banks-386, Louisiana Continental Slope	27°50′ N 92°10′ W	650
"Idas" macdonaldi	Near Garden Banks-386, Louisiana Continental Slope	27°50′ N 92°10′ W	650

idase Subunit-I (COI) gene corroborated the discrete nature of these taxa (W. R. Hoeh, pers. comm., unpublished data).

Herein, we describe five of the mytilid species identified in Craddock et al. (1995) from the Gulf of Mexico (Table 1, Fig. 1). Following the suggestion of Soot-Ryen (1955), characters used for classification of these new mytilid species have been taken from the shell or from easily visible parts of the anatomy, such as muscles, gill, and mantle margins. Of special importance to classification in the Mytilidae is the comparative placement of the retractor muscles of the foot and byssus (Soot-Ryen, 1955; Knudsen 1970). However, where deemed important, taxonomic characters associated with the internal anatomy, such as the course taken by the digestive tract, have been included.

MATERIALS AND METHODS

Specimens

Mussel specimens were collected during dives of the DSV ALVIN (A) and DSRV JOHNSON SEA-LINK-I (JSL) (Tables 1–7) and subsequently prepared as described in Craddock et al. (1995). Additional specimens were provided by Colleen M. Cavanaugh (Harvard Univ.), James J. Childress (Univ. California – Santa Barbara), Charles R. Fisher (Pennsylvania State Univ.), Ian R. MacDonald (Texas A & M Univ.), and Craig R. Smith (Univ. Hawaii Manoa).

Holotypes and a series of paratypes are deposited in the Academy of Natural Sciences of Philadelphia (ANSP). Additional paratypes are deposited in the following institutions: United States National Museum of Natural History, Washington, D.C. (USNM); Museum of Comparative Zoology, Harvard University (MCZ); Houston Museum of Natural Science, Houston, Texas (HMNS), Museum National d'Histoire Naturelle, Paris (MNHN), and Rutgers University (RU). Catalogue numbers and other pertinent information concerning holotypes and paratypes are summarized in Appendix 1.

Shell and anatomical features of specimens of the following species were examined for this report: Bathymodiolus thermophilus and B. puteoserpentis from their respective type localities; paratypes of Benthomodiolus abyssicola (Knudsen, 1970) borrowed from ZMUC; Idas argenteus Jeffreys, 1876, from the Tongue of the Ocean (TOTO) east of Andros Island in the Bahama Islands; Idas washingtonia from South Cleft hydrothermal vent on the Juan de Fuca Ridge off southern British Columbia and from whale bone in the Santa Catalina Basin off California; Adipicola sp. from Middle Valley on the Juan de Fuca Ridge; and undescribed deep-sea mussels from Mariana Back-Arc Basin in the Pacific and Lucky Strike on the Mid-Atlantic Ridge.

Small shells examined by scanning electron microscopy were air dried, glued to stubs, coated with approximately 400 Å of gold/palladium, and viewed on an Hitachi S-450 scanning electron microscope. Drawings of shells

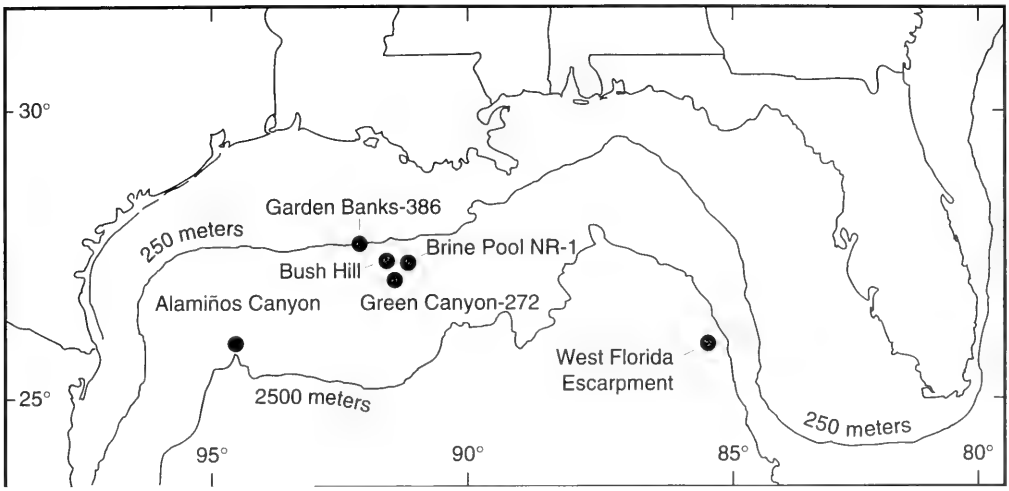

FIG. 1. Location of submersible dive sites in the Gulf of Mexico where mussels were collected.

and tissues were made either freehand or with the aid of a camera lucida.

Morphological Terminology

The "horizontal branchial septum" is a thin, membranous horizontal shelf separating incurrent and excurrent chambers, posterior to the posterior adductor (commonly extends from the ventral side of posterior adductor to the base of the excurrent siphon). The "valvular siphonal membrane" is an extension of the branchial septum formed by fusion of right and left mantle lobes ventral to the excurrent siphon and extending a variable distance into the pedal-byssal gape; a small centrally placed papilla is sometimes present at the anterior end of the valvular siphonal membrane.

Morphometrics

Shell measurements used to statistically discriminate among the five new species were: L = length of valve; H = height of valve; W = width of valves, G = length of the ligament; and A = anterior length or the distance from the anterior shell margin to an imaginary line drawn vertically from the anterior edge of the beak or umbonal bulge (Fig. 2). Measurements were made with hand-held calipers (±0.1 mm). All analyses were performed on log10 transformations of the original variables. Multivariate analyses were performed on standardized variables with Varimax rotation using the statistical computer program JMP 3.0.2 (SAS Statistics Inst., Inc, Raleigh, North Carolina).

SYSTEMATIC SECTION

Family Mytilidae

Subfamily Bathymodiolinae Kenk & Wilson, 1985

Type genus: Bathymodiolus Kenk & Wilson, 1985

Revised Diagnosis: Shell smooth, modioliform, with subterminal umbones; adult hinge edentulous, juvenile hinge with small denticulations anterior and posterior of ligament; posterior byssal retractors divided into anterior and posterior portions with separate insertion points on the adult shell producing separate muscle scars; intestine short, either straight or with a very short recurrent loop; demibranchs of hypertrophied ctenidia thick and fleshy, inner and outer demibranchs of equal length, filaments broadly thickened. Ctenidia associated with symbiotic bacteria.

Remarks: As originally described this subfamily contained the single genus Bathymodiolus (Kenk & Wilson, 1985). Eight members of this subfamily have been previously described: B. thermophilus, B. brevior, B. elongatus, B. puteoserpentis, B. platifrons, B. japonicus, B. aduloides, and B. septemdierum (Kenk & Wilson, 1985; Hashimoto & Okutani, 1994; Cosel

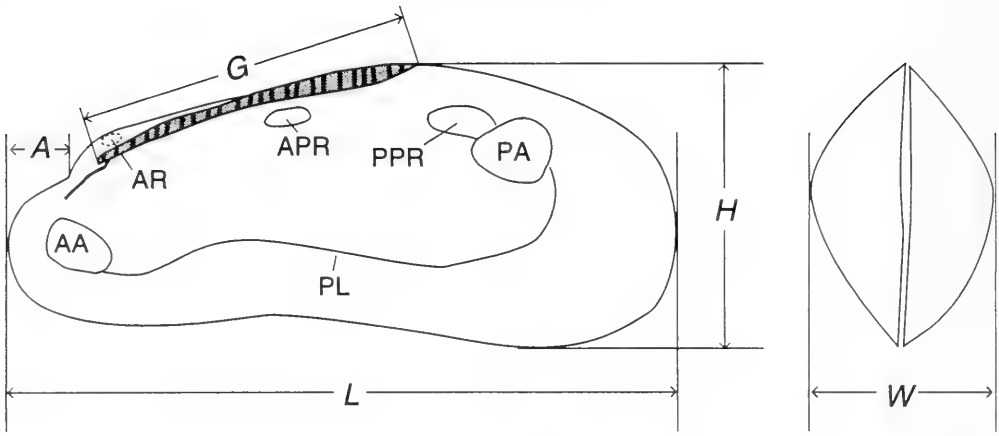

FIG. 2. Diagram depicting measurements taken and generalized shell characters. A, anterior length (distance from anterior shell margin to anterior edge of umbo); AA, anterior adductor; APR, anterior portion of posterior byssal-pedal retractor; AR, anterior byssal-pedal retractor; H, shell height; L, shell length; G, ligament length; PA, posterior adductor; PL, pallial line; PPR, posterior portion of posterior byssal-pedal retractor; W, width of shell valves.

et al., 1994). The current contribution adds the genus Tamu and the species T. fisheri, B. heckerae, and B. brooksi to the subfamily.

All members of this subfamily have hypertrophied gills associated with symbiotic bacteria that reside either within certain cells termed "bacteriocytes" or on the gill surface (Fisher, 1990; Fisher et al., 1993; Cavanaugh, 1992; Cavanaugh et al., 1987; C.M. Cavanaugh, pers. comm.). The simplified alimentary system, hypertrophied gills, and symbiosis with sulfide-oxidizing or methanotrophic bacteria, indicative of a different feeding mechanism in this group, separates members of this subfamily from all other known mytilids.

Bathymodiolus Kenk & Wilson, 1985

Bathymodiolus LePennec et al. 1983: 70; Le Pennec & Hily, 1984: 517; Laubier & Desbruyères, 1984: 1507; Smith, 1985: 1068 [nomen nudum].

Bathymodiolus Kenk & Wilson, 1985: 255 (type species, by original designation, Bathymodiolus thermophilus Kenk & Wilson, 1985).

Revised Diagnosis: Shell large (maximum size greater than 90 mm), smooth, modioliform, with sub-terminal umbones; adult hinge edentulous, juvenile hinge with small denticulations anterior and posterior of ligament (Figs. 3–5); posterior byssal retractors divided into posterior and anterior portion, retractor scars separate; labial palp suspensors and pedal retractors present; demibranchs of ctenidia thick and fleshy; filaments broadly thickened, with reduced ventral food grooves, containing intracellular bacterial symbionts; intestine straight without recurrent loop; rectum enters ventricle anterior to the auricular ostia.

Remarks: The manuscript name Bathymodiolus was introduced as a nomen nudum by LePennec et al. (1983: 70) and subsequently appeared in Le Pennec & Hily (1984), Laubier & Desbruyères (1984), and Smith (1985; publication date, May) prior to its valid introduction, under the rules of the International Code of Zoological Nomenclature (ICZN), by Kenk & Wilson (1985; publication date, 9 July).

The extremely reduced pedal gape of B. thermophilus appears to be a derived character, absent in other species referred to this genus (Hashimoto & Okutani, 1994; Cosel et al., 1994, 1997). Bathymodiolus brevior, B. elongatus, B. puteoserpentis (Cosel et al., 1994), and "Bathymodiolus" childressi have been referred to Bathymodiolus on a provisional basis. The final systematic placement of these species, and others placed in Bathymodiolus, must await complete morphological analyses and molecular studies on the entire group of deep sea mytilids.

Bathymodiolus thermophilus Kenk & Wilson, 1985 Figures 3–5

Bathymodiolus thermophilis (sic) Laubier & Desbruyères, 1984: 1510 [nomen nudum].

Bathymodiolus thermophilus Smith, 1985 (May): 1068 [nomen nudum].

Bathymodiolus thermophilus Kenk & Wilson, 1985 (9 July): 255, figs. 2–13 (type locality, "Mussel Bed" hydrothermal vent, Galápagos Rift, 0°47.89′N; 86°9.21′W in 2495 m, ALVIN Dive 879; holotype USNM 803661).

Description: Shell large, up to 180 mm long, modioliform, with sub-terminal umbones, elliptical in juveniles, arcuate in older specimens. Ventral shell margin nearly straight in young specimens, slightly concave in specimens larger than 10 cm. Adult hinge edentulous, juvenile hinge with small denticulations anterior and posterior to ligament. Posterior byssal retractors divided, retractor scars separate; separate pedal retractors prominent; slender labial palp suspensors extend anteriorly from anterior retractors to support the muscularized labial palps. Ventral pallial line with a dorsally directed concavity in byssal region about one-third of the distance from the anterior end. Inner fold of mantle lobes fused in postero-ventral and antero-ventral midline creating valvular siphonal membrane, with papilla, and an extremely reduced pedal gape. Dorsal edges of ascending lamellae attached to muscular longitudinal ridges on surfaces of mantle lobe and visceral mass. Horizontal branchial septum, extending from the base of the excurrent siphon and the ventral side of the posterior adductor, separates incurrent and excurrent chambers posteriorly. Inner and outer demibranchs essentially equal-sized, thick and fleshy, filaments broadly thickened, with reduced ventral food grooves. Ctenidia contain intracellular symbiotic bacteria. Muscularized inner palps long and slender, attached over most of their length to visceral mass, extending farther posteriorly than smaller muscularized outer palps. Intestine straight without recurrent loop; intestine/rectum enters ventricle anterior to the position of the auricular ostia.

Remarks: The manuscript species name Bathymodiolus thermophilis (sic) was introduced as a nomen nudum by Laubier & Desbruyères (1984) and as B. thermophilus by Smith (1985; publication date, May) prior to the valid description of this species, under the rules of the ICZN, by Kenk & Wilson (1985; publication date, 9 July).

Kenk & Wilson (1985) described Bathymodiolus as having a small pedal gape resulting from extensive ventral fusion of the inner folds of the mantle lobes. This feature is present in the type species B. thermophilus, but is lacking in other described members of this genus (Hashimoto & Okutani, 1994; Cosel et al., 1994), as well as in all other known mytilids. As pointed out in Kenk & Wilson (1985: 260), the dorsal ends of the ascending lamellae are attached to muscular longitudinal ridges on the surfaces of the mantle lobes and the visceral mass. These muscular longitudinal ridges are also unique to B. thermophilus and were not evident in any other mussel examined for this report.

The hinge of B. thermophilus was originally described as edentulous (Kenk & Wilson, 1985). However, in specimens of B. thermophilus smaller than about 10 mm there are up to 25 "vertical striations" or denticles immediately posterior of the ligament and about 6 denticles located immediately below the umbones (Fig. 3–5). Other deep-sea mussel species described herein (Figs. 6–28) also have hinge denticulations as juveniles (Figs. 8–10, 18–20, 23, 25–27). These denticulations are lost in adult members of the genus Bathymodiolus

Although Bathymodiolus was described as lacking ventral food grooves on the ctenidia (Kenk & Wilson, 1985), we observed reduced food grooves in all specimens of B. thermophilus we examined. Food grooves were first described in B. thermophilus by Le Pennec et al. (1983), Le Pennec & Hily (1984), and Fiala-Médioni et al. (1986).

Kenk & Wilson (1985) described the periostracum of Bathymodiolus as "hirsute"; meaning hairy, bristly or shaggy. However, these "periostracal hairs" are probably of byssal origin (Bottjer & Carter, 1980; Ockelmann, 1983) and not of taxonomic value. The original description of Bathymodiolus described the labial palps as "small," whereas the labial palps of B. thermophilus specimens we examined, from the type-locality and elsewhere, were large and muscular.

Range: This species appears confined to the area of hydrothermal vent activity on the Galápagos Rift and along the EPR at 9° to 10°N, 11°24′N and 13°N (Table 2). In addition,

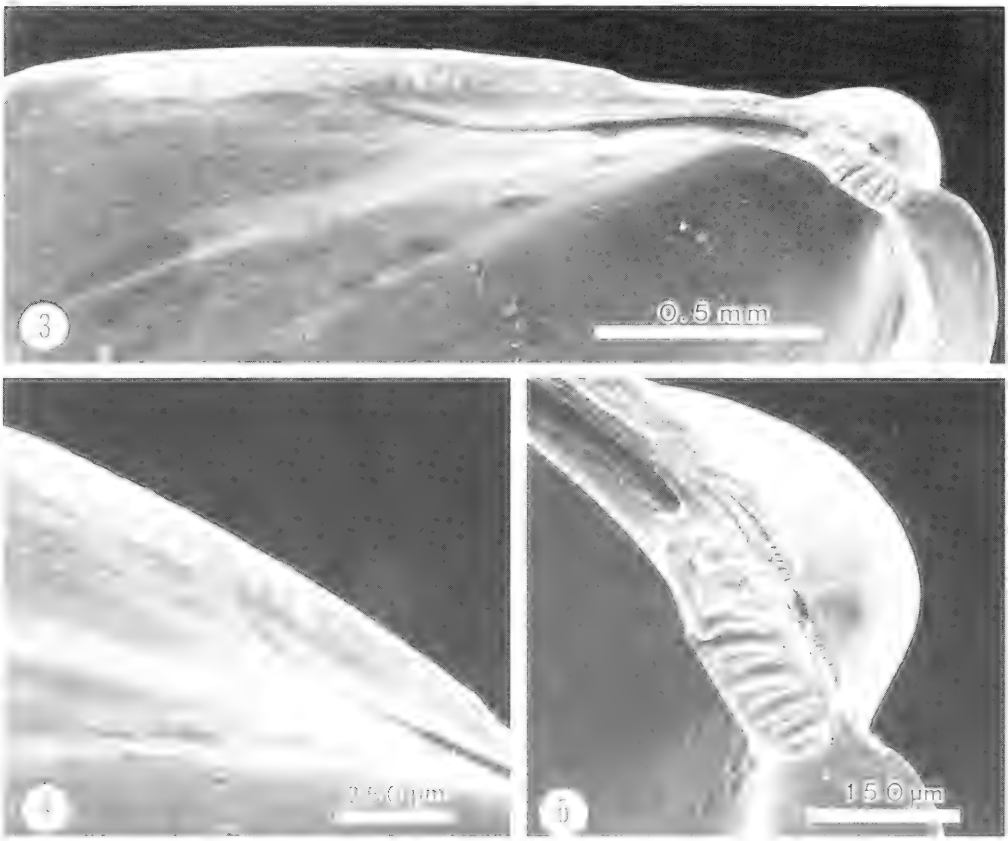

FIG. 3. Bathymodiolus thermophilus Kenk & Wilson. Juvenile hinge line of specimen 4.5 mm in length.
FIG. 4. Bathymodiolus thermophilus Kenk & Wilson. Hinge denticles, located immediately posterior to ligament in juvenile specimen 4.5 mm in length.
FIG. 5. Bathymodiolus thermophilus Kenk & Wilson. Hinge denticles, located immediately below the umbo in juvenile specimen 4.5 mm in length.

preliminary comparison of mtDNA COI sequences between B. thermophilus from the type locality and mussels collected from 17°S on the EPR revealed essentially no differences (R.C. Vrijenhoek, unpublished data).

Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek, new species
Figures 6–13

This species, known since 1984, has been referred to in literature concerning seep and vent biology but was never formally described. The following is a list of these references.

"Mussel" – Paull et al., 1984: 965, fig. 2 [mussels visible in habitat photo].

"Mussels" – Florida Escarpment Cruise Participants, 1984: 32, fig. 1 [mussels visible in habitat photo].

"Large mussel" – Turner & Lutz, 1984: 60, figs. 1 (site #9 = Florida Escarpment, diagram of mussel shell), 5, 6, [mussels visible in habitat photo], 8 (left) [micrograph of prodissoconch].

"Large, elongate mussels" – Turner, 1985: 29, figs. 4B–C, 6.

"Mytilid" – Southward, 1985: 673.

"Mytilid mussel" – Paull et al., 1985: 710.

"Large mussels," "large golden-brown mytilids" – Hecker, 1985: 465, 466, figs. 2, 4, 5, 6 [mussels visible in habitat photos].

"Large mussels" – Grassle, 1986: 338.

"Seep mussels," "Florida Escarpment mussel" – Cavanaugh et al., 1987: 346, 347,

TABLE 2. Specimens of Bathymodiolus thermophilus examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
ALVIN Dives, Galápagos Rift				
887	12 Feb. 1979	2488	00°48.5′N; 86°09.1′W	1 - shell & tissue
983	30 Nov. 1979	2457	00°48.2′N; 86°13.4′W	2 - shell, 7 - shell & tissue
2223	28 May 1990	2503	00°47.9′N; 86°09.2′W	42 - shell
2224	29 May 1990	2461	00°48.2′N; 86°13.5′W	35 - shell
ALVIN Dives, East Pacific Rise 11°N				
2225	3 June 1990	2515	11°24.9′N; 103°47.3′W	15 - shell, 2 - shell & tissue
2226	4 June 1990	2515	11°24.9′N; 103°47.3′W	63 - shell
ALVIN Dives, East Pacific Rise 13°N				
2228	6 June 1990	2630	12°48.6′N; 103°56.5′W	14 - shell
2229	7 June 1990	2630	12°48.6′N; 103°56.5′W	51 - shell, 1 - shell & tissue
ALVIN Dives, East Pacific Rise near 9°N–10°N				
2350	31 March 1991	2585	09°30.9′N; 104°14.5′W	4 - shell
2351	1 April 1991	2550	09°50.1′N; 104°17.4′W	3 - shell
2352	2 April 1991	2567	09°33.5′N; 104°14.1′W	47 - shell
2354	4 April 1991	2527	09°47.7′N; 104°17.1′W	8 - shell
2356	6 April 1991	2556	09°40.9′N; 104°15.8′W	3 - shell
2358	8 April 1991	2578	09°30.9′N; 104°14.6′W	3 - shell & tissue
2359	9 April 1991	2564	09°30.9′N; 104°17.7′W	6 - shell
2368	19 April 1991	2539	09°51.1′N; 104°17.5′W	2 - shell
2498	6 March 1992	2525	09°50.5′N; 104°17.5′W	4 - shell & tissue

TABLE 3. Specimens of Bathymodiolus heckerae examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
ALVIN Dives, Gulf of Mexico - West Florida Escarpment				
1343	9 March 1984	3270	26°03′N; 84°54′W	14 - shell & tissue
1344	10 March 1984	3270	26°03′N; 84°56′W	1 - shell
1346	12 March 1984	3286	26°03′N; 84°54′W	1 - shell & tissue
1753	14 Oct. 1986	3277	26°02.4′N; 84°54.2′W	16 - shell
1754	15 Oct. 1986	3303	26°02.4′N; 84°55.3′W	4 - shell; 6, shell & tissue
1755	16 Oct. 1986	3300	26°01.5′N; 84°55.3′W	14 - shell, 2 - shell & tissue
1756	17 Oct. 1986	3243	26°01′N; 84°55′W	27 - shell
1758	20 Oct. 1986	3266	26°01.8′N; 84°54.9′W	4 - shell
2196	26 March 1990	3314	26°02.4′N; 84°54.4′W	91 - shell, 17 - shell & tissue
2197	29 March 1990	3314	26°02.2′N; 84°54.5′W	60 - shell
2542	3 June 1992	3313	26°01.8′N; 84°54.6′W	49 - shell, 40 -shell & tissue

TABLE 4. Specimens of Bathymodiolus brooksi examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
ALVIN Dives, Gulf of Mexico - Alamiños Canyon				
2209	11 April 1990	2340	26°21.1′N; 94°30.3′W	18 - shell
2211	13 April 1990	2222	26°21.3′N; 94°29.7′W	65 - shell, 20 - shell & tissue
2535	22 May 1992	2220	26°21.1′N; 94°29.5′W	6 - shell & tissue
ALVIN Dives, Gulf of Mexico - West Florida Escarpment				
1343	9 March 1984	3270	26°03′N; 84°54′W	1 - shell & tissue
2196	26 March 1990	3314	26°02.4′N; 84°54.4′W	1 - shell
2542	3 June 1992	3313	26 °01.8′N; 84°54.6′W	4 - shell, 3 -shell & tissue

TABLE 5. Specimens of "Bathymodiolus" childressi examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Bush Hill				
1877	27 Sept. 1986	548	27°46.9′N; 91°30.4′W	5 - shell & tissue
3108	31 Aug. 1991	548	27°46.9′N; 91°30.4′W	3 - shell & tissue
3129	15 Sept. 1991	546	27°46.9′N; 91°30.4′W	119 - shell, 59 - shell & tissue
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Green Canyon-272				
3133	17 Sept. 1991	737	27°41.3′N; 91°32.5′W	4 - shell
3137	19 Sept. 1991	723	27°41.1′N; 91°32.2′W	44 - shell, 8 -shell & tissue
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Brine Pool NR-1				
3145	27 Sept. 1991	650	27°43.4′N; 91°16.6′W	29 - shell
ALVIN Dives, Gulf of Mexico - Alamiños Canyon				
2211	13 April 1990	2222	26°21.3′N; 94°29.7′W	31 - shell, 8 - shell & tissue

TABLE 6. Specimens of Tamu fisheri examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Bush Hill				
3108	31 Aug. 1991	548	27°46.9′N; 91°30.4′W	6 - shell, 3 - shell & tissue
3129	15 Sept. 1991	546	27°46.9′N; 91°30.4′W	3 - shell & tissue
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope - Near Garden Banks-386				
3131	16 Sept. 1991	701	27°50′N; 92°10′W	1 - single valve
3149	29 Sept. 1991	650	27°50′N; 92°10′W	6 - shell
MCZ No. 296151 (Texas A & M University, Louisiana Slope, Cruise #85-6-5, Trawl #5)				
L2787 (right valve)				
L2788 (left valve)				
L2789 (left valve)				
MCZ No. 296152 (Texas A & M University, Louisiana Slope, Cruise #85-6-5, Trawl #10)				
L2742 (right valve)				
L2743 (left valve)				
L2744 (left valve)				
L2745 (left valve)				

TABLE 7. Specimens of "Idas" macdonaldi examined.

Dive	Date	Depth	Latitude; Longitude	Number and condition of specimens
JOHNSON SEA LINK-I Dives, Gulf of Mexico - Louisiana Continental Slope				
3149	29 Sept. 1991	650	27°50′N; 92°10′W	4 - shell, 6 - shell & tissue

fig. 1a–b [micrographs of bacteriocyte and symbiotic bacterium].

"Mussels (c.f. Bathymodiolus)" – Hook & Golubic, 1988: 348, fig. 1 [mussels visible in habitat photos], fig. 2.

"Mytilid bivalve," "seep mussel" – Cary et al., 1989: 411.

"Deep-sea mussel, cf. Bathymodiolus" – Hook & Golubic, 1990: 240.

"Mytilid" – Petrecca & Grassle, 1990: 281.

"West Florida Escarpment mussel (common)" – Craddock et al., 1991: p. 302.

"Florida Escarpment mussel" – Dahlhoff & Somero, 1991: 475 (table 1).

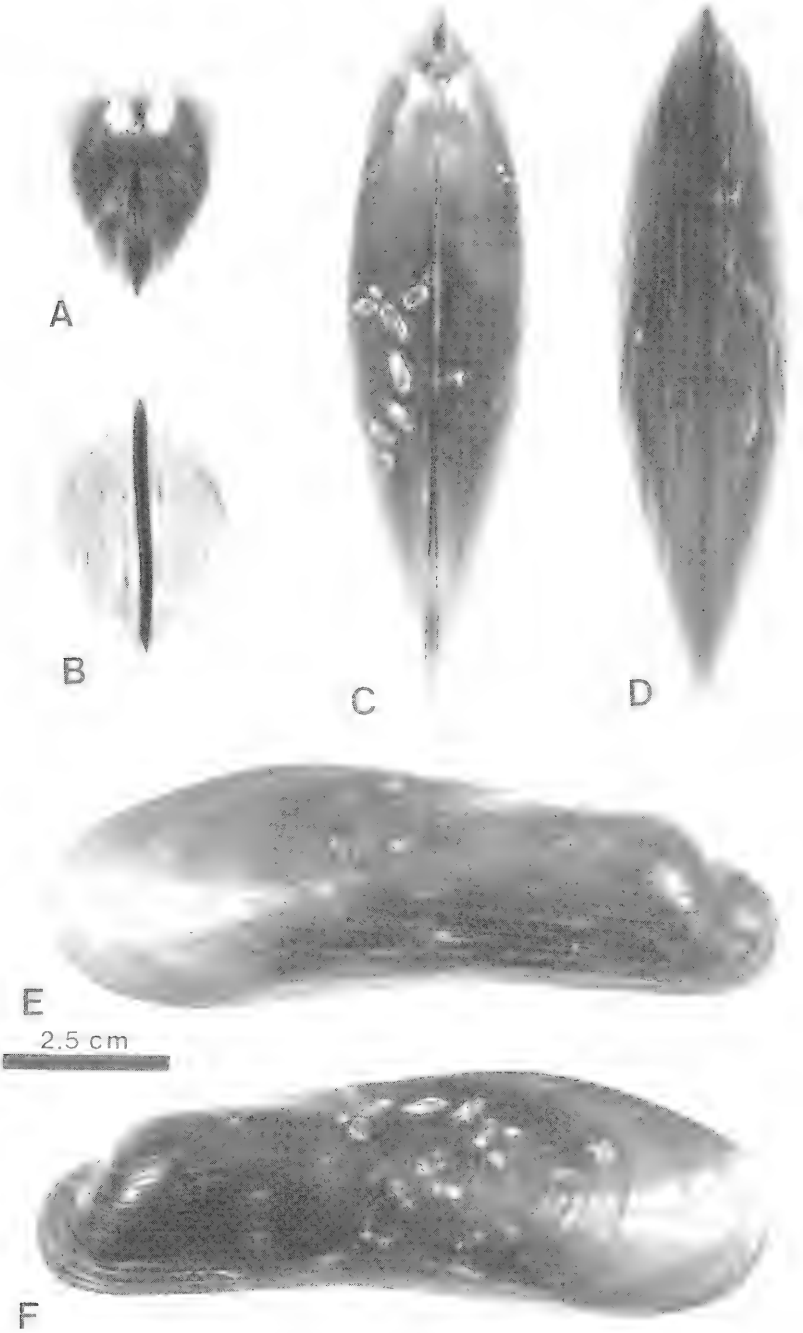

FIG. 6. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. Holotype, ANSP A18846. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view of right valve; F, lateral view of ieft valve.

FIG. 7. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. External views of a growth series of shells illustrating ontogenetic change in shape.

"FL mytilid" – Cavanaugh, 1992: 316.
"Bathymodiolus-like mussels" – Hook & Golubic, 1992: 120.
"Seep mytilid Va" – Fisher, 1993: 609.
"Deep-sea mussel (an undescribed new genus similar to Bathymodiolus)" – Hook & Golubic, 1993: 81.
"SM Va" – Fisher et al., 1993: 278, 284.
"FL/Va" – Craddock, et al., 1995: 479–483.
"Seep Mytilid Va" – Nelson & Fisher, 1995: table 3.

Types: Holotype ANSP A18846 from ALVIN Dive 1343 along the base of the West Florida Escarpment in the eastern Gulf of Mexico at 26°03′N; 84°54′W, in 3270 m. Paratypes are from ALVIN Dive 1754 at 26°02.4′N; 84°55.3′W in 3303 m (USNM); ALVIN Dive 1755 at 26°01.5′N; 84°55.3′W in 3300 m (MCZ); ALVIN Dive 2196 at 26°02.4′N; 84°54.4′W in 3314 m (ANSP 400772;, USNM, HMNS, MNHN); ALVIN Dive 2197 at 26°02.2′N; 84°54.5′W in 3314 m (HMNS); and ALVIN Dive 2542 at 26°01.8′N; 84°54.6′W in 3314 m (ANSP 400771, 400773; MNHN).

Shell Morphology: Shell large, up to 190 mm long, modioliform, thin, fragile, essentially equivalve, elongately elliptical. Anterior margin sharply rounded; posterior margin broadly rounded; ventral margin straight in young specimens, with a slight ventral concavity in medium sized specimens, concavity more pronounced in larger specimens; dorsal margin broadly convex, more or less straight over span of the ligament (Figs. 6, 7, 11, 12). Umbones often eroded; prosogyrate; subterminal, positioned between 6% and 16% of the length of the shell from anterior end. An indistinct, raised, broadly rounded ridge extends from umbonal region to posterior-ventral margin.

External sculpture lacking; surface smooth except for concentric growth lines; fine radial lines in periostracum extending from umbo to ventral margin, most prominent posteriorly; and fine radial periostracal corrugations along the ventral margin in the region of the byssal gape. Shell dull-white, periostracum straw-yellow to light-brown in young specimens, older specimens have dark-brown perios-

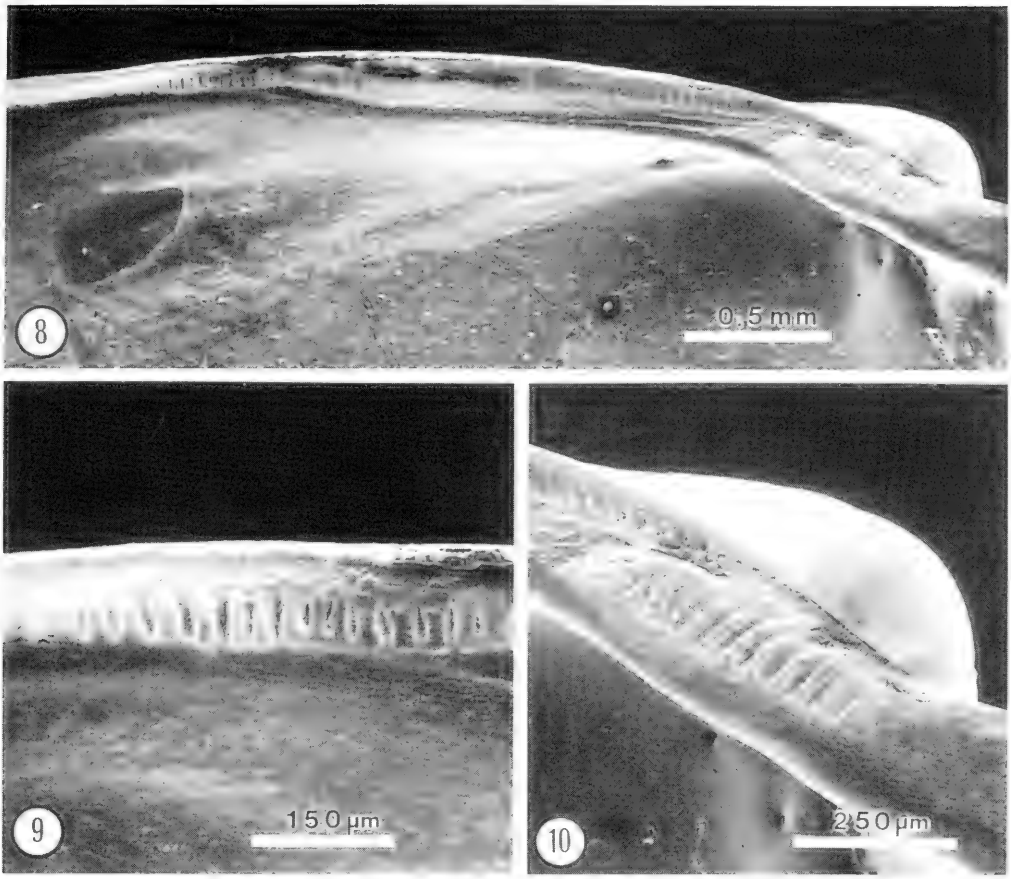

FIG. 8. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. Juvenile hinge line of specimen 7.5 mm in length.
FIG. 9. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. Hinge denticles located immediately posterior of the ligament in juvenile specimen 7.5 mm in length.
FIG. 10. Bathymodiolus heckerae Turner, Gustafson, Lutz & Vrijenhoek. Hinge denticles located immediately below the umbo in juvenile specimen 7.5 mm in length.

tracum that becomes straw-yellow peripherally. Periostracum of older specimens sometimes marked by irregularly shaped dark brown pigment patches, overlain by numerous byssal thread attachment plates. Interior off-white, predominately nacreous.

Ligament opisthodetic, parivincular, extending posteriorly from umbones to occupy from 32% to 49% of dorsal margin. Adult hinge edentulous, except for small posteriorly directed projection of anterior hinge margin beneath ligament's anterior end; hinge somewhat thickened below and anterior to umbo. Juvenile hinge with about 15 denticles immediately posterior to ligament and approximately 10 denticles located immediately below umbones (Figs. 8–10). Hinge denticles become obsolete in specimens greater than 18 mm in length.

Muscle Scars: Muscle scars and pallial line indistinct. Anterior adductor scar rounded but truncated posteriorly; located ventral and partially anterior to umbo in small specimens, entirely in front of umbo in medium and large specimens. Posterior adductor scar round to oblong, usually contiguous with small siphonal retractor scar ventrally and posterior portion of

posterior byssal-pedal retractor scar dorsally. Anterior retractor scar located within upper extremity of umbonal cavity directly beneath umbo. Posterior byssal retractors form two scars with very large intervening gap, anterior one obliquely elliptical, directly beneath or slightly anterior of posterior end of ligament in small specimens, well anterior of posterior end of ligament in medium and large specimens, second one elliptical, parallel to antero-posterior axis of shell and located antero-dorsally to and bordering posterior adductor scar (Fig. 12). Pallial line distant from shell margin, extending from postero-ventral edge of anterior adductor scar to postero-ventral edge of posterior adductor, curving slightly upwards and then downwards to form slight indentation in byssal gape region at about one-quarter to one-third of distance from anterior, end. Small siphonal retractor scar located at posterior end of ventral pallial line, usually but not always contiguous with posterior adductor (Fig. 12).

Selected Measurements (in mm):

length	height	width	anterior length	Dive	
110.6	36.0	28.1	—	A 1343	Holotype ANSP
75.2	27.8	22.3	9.7	A 1754	Paratype USNM
134.2	43.0	32.8	15.5	A 1755	Paratype MCZ
98.0	33.3	25.0	13.8	A 2196	Paratype HMNS
84.5	27.0	24.0	8.2	A 2196	Paratype MNHN
148.0	47.4	36.1	16.7	A 2196	Paratype Rutgers
22.6	11.4	7.8	1.8	A 2196	Paratype MNHN
38.7	17.5	13.8	3.2	A 2197	Paratype HMNS
102.0	34.0	25.5	11.5	A 2542	Paratype Rutgers
99.0	36.5	24.8	10.5	A 2542	Paratype ANSP
132.5	45.0	31.7	16.6	A 2542	Paratype ANSP
122.9	39.7	29.8	16.1	A 2196	Paratype ANSP
148.1	41.1	37.3	23.0	A 2196	Paratype HMNS
79.2	26.8	21.6	7.2	A 2196	Paratype USNM
164.0	47.0	41.7	18.4	A 2542	Paratype Rutgers

Internal Morphology

Musculature: Main features of musculature evident from previous description of muscle scars and illustrated in Figure 13. Posterior byssal retractors divided into two widely divergent main bundles that attach separately to shell, a posterior portion inserting along antero-dorsal edge of posterior adductor and an anterior portion inserting below and anterior to ligament's posterior end. Posterior portion of posterior byssal retractor long and slender resulting in an elongate and quite narrow region of shell attachment. Pedal retractors large and prominent, arising from dorso-lateral surface of foot mass and passing posteriorly along lateral aspect of anterior byssal retractors to become integrated with anterior and lateral region of anterior portion of posterior byssal retractors at point of shell attachment. Siphonal retractors integrated with pallial musculature, although there does appear to be a siphonal retractor scar on the shell. Anterior retractors long and slender, arising from dorso-lateral aspect of byssal-pedal mass and passing anteriorly to insert in antero-dorsal extremity of umbonal cavity. Pair of slender labial palp suspensors extend forward as branches of anterior retractors to attach to shell just behind and adjacent to anterior adductor. Posterior adductor rounded, anterior adductor rounded; one-half the size of posterior adductor.

Foot and Byssus: Foot long, thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands gray to brown, wide, flat, unornamented. Byssal gland extending down foot behind byssal groove, without extension dorsal to origin of anterior retractors.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260). Ventral edges of inner mantle lobes not unusually thickened or muscular. Excurrent tubuliform siphon short, not capable of extension beyond perimeter of shell, lacking internal diaphragm in specimens examined. Horizontal branchial septum incomplete; fusion of inner mantle immediately below excurrent siphon forming short horizontal shelf, not directly attached to ventral edge of posterior adductor. Incurrent and excurrent chambers not completely separated posterior of posterior adductor; posterior end of gill axes attached

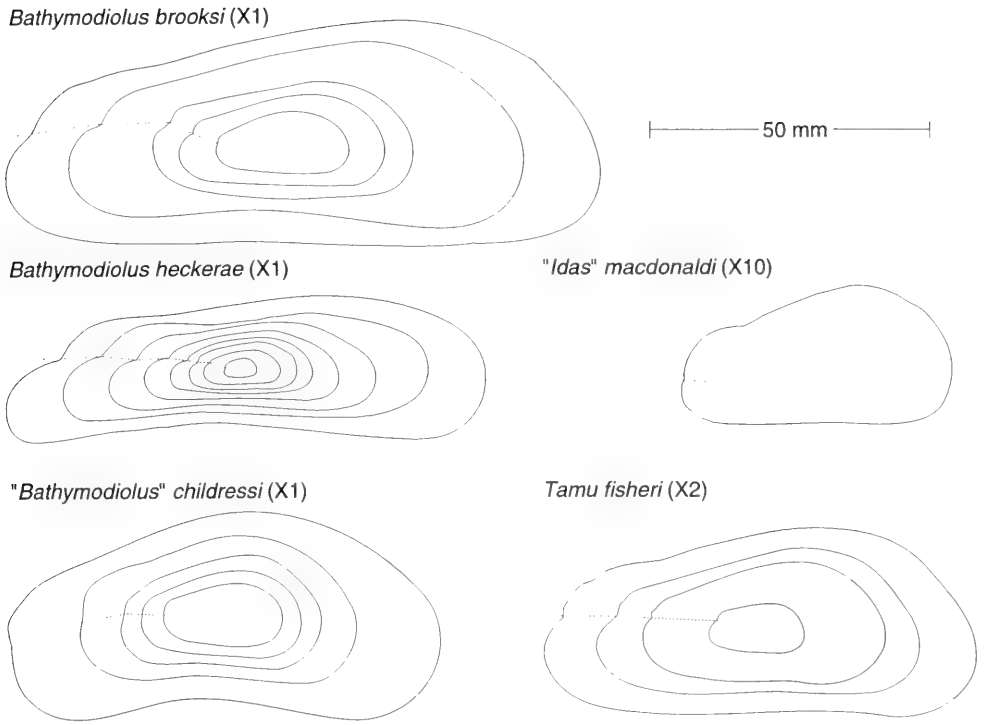

FIG. 11. Bathymodiolus heckerae, B. brooksi, "Bathymodiolus" childressi, Tamu fisheri, and "Idas" macdonaldi. Inset outlines of a graded series of shell outlines illustrating change in shape with increase in size. Only one specimen of "Idas" macdonaldi is illustrated. Dotted lines connect the relative positions of the anterior edge of the umbones in specimens of different size. Note scale bar and magnifications.

to ventral surface of horizontal branchial septum. Short extension as valvular siphonal membrane joins right and left mantle lobes, extending anteriorly only a short distance into pedal gape; small central papilla on anteriormost ventral extension of valvular siphonal membrane extends anteriorly into pedal gape. Pedo-byssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Demibranchs thick, short; approximately equal-sized, both demibranchs extend anteriorly to same degree; ascending lamellae slightly shorter than descending. Ventral edges of demibranchs with poorly developed food grooves; dorsal food grooves present in deep folds just below junction of ascending lamellae and areas of attachment to mantle lobes and visceral mass. Filaments wide, fleshy; ctenidia and filaments light-brown. Distal interlamellar junctions lacking; descending and ascending portion of each filament connected apically to one-quarter height of demibranch; every 2nd to 6th filament is "principal filament" [see Atkins, 1937: text fig. 18, type B(1b)] with septum rising to one-third height of demibranch. A single posterior "tubular connection" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes sometimes present, indiscernible in some individuals.

Labial Palps: Paired labial palps greatly modified from typical filter-feeding type, appearing to function as sorting area for material gathered by foot rather than ctenidia. Base of inner and outer palp pair widely separated; ctenidia lie lateral of labial palps in preserved specimens. Mouth situated at basal mid-point of anterior end of inner pair of labial palps, farther posterior than typical for mytilids. Inner palp pair placed posteriorly, large and muscular, elongately triangular. Outer pair of palps more anterior, triangular, muscular, but smaller than inner pair. Oral groove on inner surface of both pair of palps, bordered by pli-

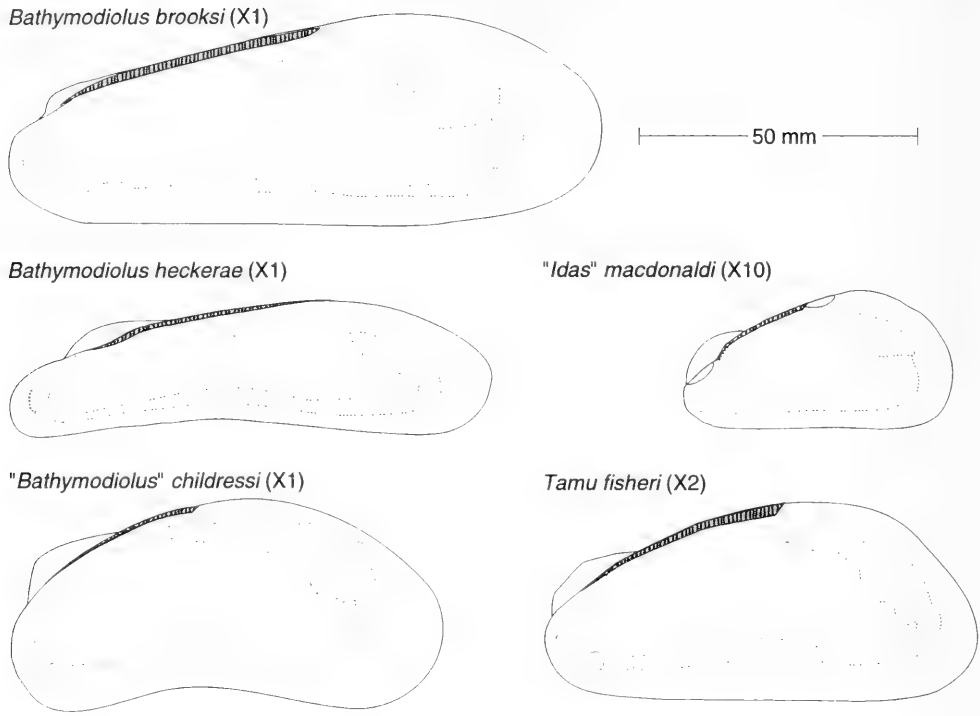

FIG. 12. Bathymodiolus heckerae, B. brooksi, "Bathymodiolus" childressi, Tamu fisheri, and "Idas" macdonaldi. Diagrams of left-lateral view of shell illustrating generalized location of muscle scars, pallial line and ligament. Lighter shading anterior and posterior to ligament in diagram of "Idas" macdonaldi indicates location of adult hinge denticles. Note scale bar and magnifications.

cations, running from near tip of proboscid-like extensions to mouth. Outer surfaces of palps smooth, non-plicate.

Digestive System: Alimentary tract straight with no recurrent loop, situated directly on body mid-line. Intestine leaves posterior end of stomach and traverses short distance posteriorly, merging with rectum; rectum enters extreme antero-ventral aspect of pericardium and ventricle, anterior to the level of the auricular openings into the ventricle.

Remarks: Bathymodiolus heckerae lacks both the extensive mid-ventral mantle fusion and the muscular longitudinal ridge in the mantle cavity, supporting the ascending lamellae, which are diagnostic characters of B. thermophilus. Bathymodiolus heckerae differs from B. brooksi in having a more arcuate shape, a greater relative shell length anterior to the umbo (A/L), larger and more prominent pedal retractors, and a smaller height to length ratio at a given length (Fig. 28). It differs from "Bathymodiolus" childressi in having umbones more distant from the anterior, a less robust shell, widely separated posterior byssal retractors and associated scars, and a central papilla on the anterior rim of the valvular siphonal membrane.

Relationship with B. brevior, B. elongatus, and B. puteoserpentis (which were placed in this genus only provisionally) is difficult to assess since we know little about the internal anatomy of these species (Cosel et al., 1994), although the recently reported presence of two recurrent loops in the intestine of B. puteoserpentis (Cosel et al., 1997) distinguishes this species from B. heckerae and other mussels examined in this report. Bathymodiolus heckerae differs from these three species in being much more arcuate and elongated (Cosel et al., 1994). The shell shape of adult B. heckerae is also much more

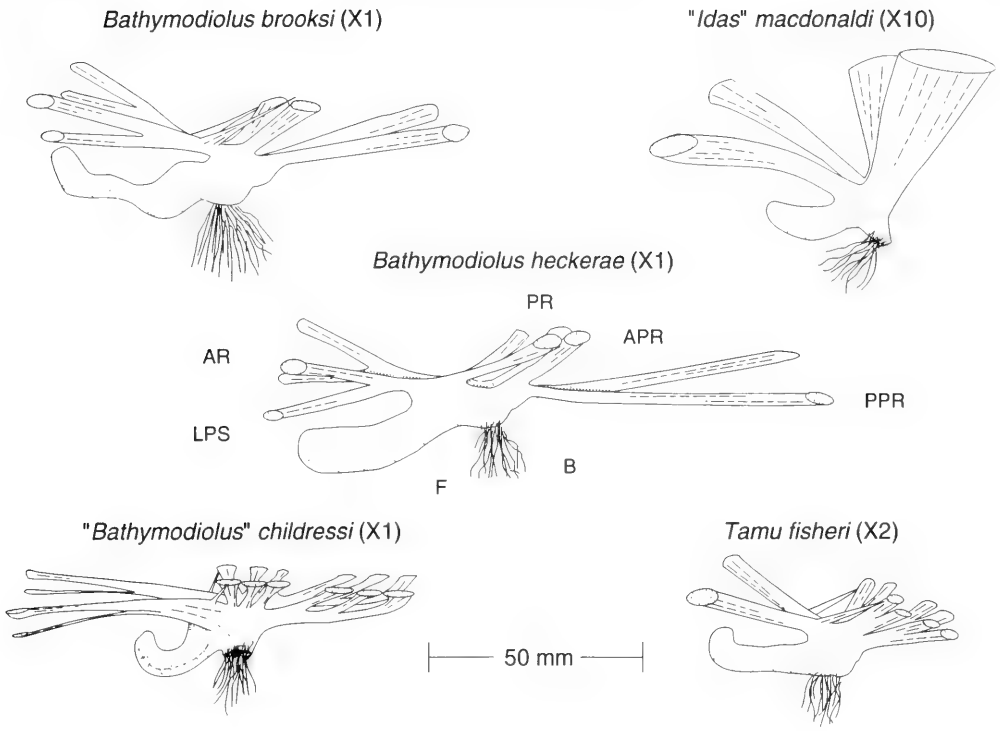

FIG. 13. Bathymodiolus heckerae, B. brooksi, "Bathymodiolus" childressi, Tamu fisheri, and "Idas" macdonaldi. Foot and retractor muscle masses as viewed from a left-lateral orientation. Anterior is to the left. Note scale bar and magnifications. AR, anterior byssal-pedal retractor; APR, anterior portion of posterior byssal retractor; B, byssus; F, foot; LPS, labial palp suspensor; PPR, posterior portion of posterior byssal retractor; PR, pedal retractor.

arcuate than any of the four Bathymodiolus species (platifrons, japonicus, aduloides, and septemdierum) from deep-sea sites off Japan. Bathymodiolus heckerae also differs from B. platifrons in having subterminal umbones (located between 6% and 16% of the anterior end of the shell) in comparison to the terminal umbones of B. platifrons (Hashimoto & Okutani, 1994).

In a protein electrophoretic study, Craddock et al. (1995) showed that B. heckerae (as FL/Va) and B. thermophilus (as MB/Bt) had no shared alleles at 17 of 26 gene loci and that these two species had a Nei's genetic distance (D) of 1.085 (Nei, 1978). Nei's genetic distance between B. heckerae, from the West Florida Escarpment site, and the two populations of B. brooksi from the West Florida Escarpment and Alamiños Canyon sites were 0.528 and 0.719, respectively. These genetic distances are within the range of values for species-level separation. Bathymodiolus heckerae was more highly divergent in pairwise comparisons with "Bathymodiolus" childressi (D = 2.188 and 2.086 for Bush Hill and Alamiños Canyon samples), T. fisheri (D = 1.983), and "Idas" macdonaldi (D = 2.556) (Table 8; Craddock et al., 1995).

Analysis of a 246 bp region of the mtDNA COI gene showed a sequence divergence of 14.7% between B. heckerae and B. brooksi, and 17.6% to 18.7% between B. heckerae and "Bathmodiolus" childressi (Table 8; W. R. Hoeh, unpublished data). Percent sequence divergence between B. heckerae and T. fisheri was 52.2%, and 44.9% between B. heckerae and "Idas" macdonaldi (Table 8). These levels of allozymic and mtDNA divergence support separate species status for B. heckerae, as well as separation at the generic level from T. fisheri and "Idas" macdonaldi.

Two genetically (Cavanaugh, 1992; Ca-

TABLE 8. Genetic distance matrix. Nei's (1978) unbiased genetic distance (above diagonal) based on 26 allozyme loci (from Craddock et al., 1995). Percent sequence divergence (below diagonal) for 246 bp of mitochondrial COI (W. R. Hoeh, unpublished data). Site and Operational Taxonomic Unit (OTU) designations as in Craddock et al. (1995). Ia, Ib = "Bathymodiolus" childressi; II, Vb = Bathymodiolus brooksi; III = Tamu fisheri; IV = "Idas" macdonaldi; Va = B. heckerae; BH = Bush Hill, Louisiana Continental Slope; AC = Alamiños Canyon; GB = Garden Banks, Louisiana Continental Slope; FL = West Florida Escarpment.

Site/OTU	BH/Ia	AC/Ib	AC/II	GB/III	GB/IV	FL/Va	FL/Vb
BH/Ia	—	0.042	1.507	2.209	2.656	2.188	2.531
AC/Ib	0.83	—	1.531	2.138	2.570	2.086	2.434
AC/II	17.16	17.16	—	1.992	5.688	0.719	*
GB/III	48.74	47.91	50.28	—	1.859	1.983	2.552
GB/IV	44.95	43.37	41.85	37.97	—	2.556	3.258
FL/Va	17.63	18.73	14.73	52.22	44.95	—	0.528
FL/Vb	17.16	17.16	0.00	50.28	41.85	14.73	—

*Some minor allozyme differences may exist but they remain to be adequately resolved.

vanaugh et al., 1992) and morphologically distinct (Cavanaugh et al., 1987) bacteria are found within gill bacteriocytes of B. heckerae. One of these is a large coccus, about 1.6 μm in diameter, with stacked internal membranes typical of Type I methanotrophs and the other is a smaller coccus or rodshaped cell, about 0.4 μm in diameter, without internal membranes. Stable carbon isotope ratios, methanol dehydrogenase activity, and the presence of a gill symbiont with stacked internal membranes indicate that B. heckerae relies on its methanotrophic symbionts to some degree as a source of carbon and energy (Cavanaugh et al., 1987; Cary et al., 1989).

Many but not all specimens of B. heckerae harbor a commensal polynoid polychaete Branchipolynoe seepensis Pettibone, 1986, within the mantle cavity. A second polychaete, the nautiliniellid Laubierus mucronatus Blake, 1993, has also been described from the mantle cavity of B. heckerae (Blake, 1993). An additional nautiliniellid Flascarpia alvinae Blake, 1993, is present at the West Florida Escarpment site but its supposed bivalve host has not been determined (Blake, 1993).

An electrophoretic analysis of B. heckerae at this site (Craddock et al., 1991, 1995) revealed the presence of a single individual of a morphologically distinct congeneric mussel. Subsequently, eight additional specimens of this congener B. brooksi (described herein) were identified. Other faunal components of this site include the vestimentiferan Escarpia laminata Jones, 1985; the bresiliid shrimp Alvinocaris muricola Williams, 1988; the neolepetopsid limpet Paralepetopsis floridensis McLean, 1990; an undescribed vesicomyid bivalve, a coiled archaeogastropod, a large white turrid gastropod, serpulid polychaetes, galatheid crabs, anemones, holothurians, ophiuroids, and zoarcid fish (Paull et al., 1984; Hecker, 1985). Newly settled B. heckerae are often found attached by byssal threads within the eroded apices of the unnamed small coiled archaeogastropods which themselves are found crawling on the adult mussel shells at this site (Turner & Lutz, 1984; Turner, 1985). The small prodissoconch I and large prodissoconch II of B. heckerae suggests a planktotrophic mode of larval development (Turner & Lutz, 1984).

Etymology: The specific name honors Dr. Barbara Hecker who was among the first scientists to describe the cold-water seep fauna of the West Florida Escarpment. The working designation "Seep Mytilid Va" was given to this species.

Range: Known only from cold-water methane/sulfide seeps at the base of the West Florida Escarpment in the eastern Gulf of Mexico near 26°02′N and 84°55′W, in depths from 3243 to 3314 m (Table 3).

Bathymodiolus brooksi Gustafson, Turner, Lutz & Vrijenhoek, new species
Figures 11–15

This species, known since 1990, has been referred to in literature concerning seep and vent biology but was never formally described. The following is a list of these references.

"Mussels" (in part) – Brooks et al., 1990: 1772.

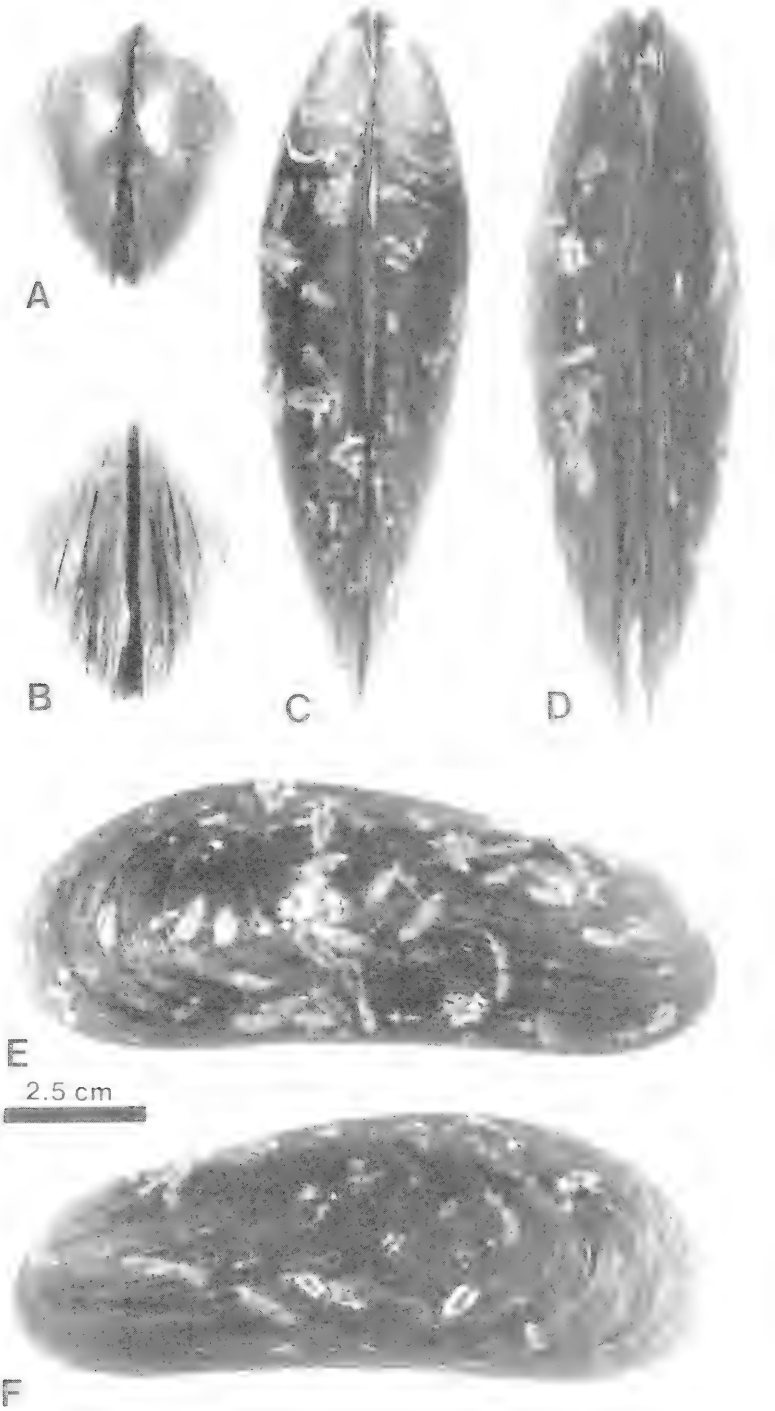

FIG. 14. Bathymodiolus brooksi Gustafson, Turner, Lutz & Vrijenhoek. Holotype, ANSP A18847. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view of right valve; F, lateral view of left valve.

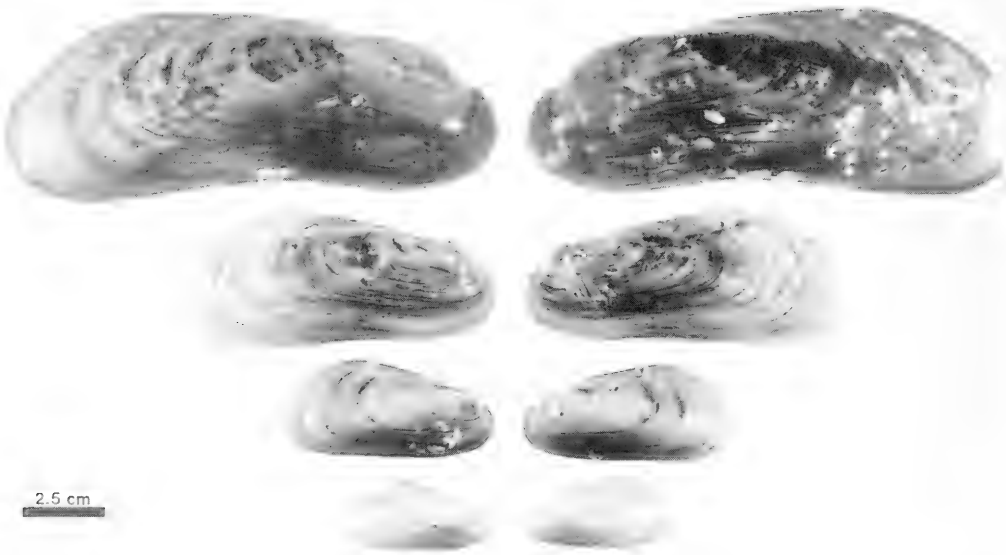

FIG. 15. Bathymodiolus brooksi Gustafson, Turner, Lutz & Vrijenhoek. External views of a growth series of shells illustrating ontogenetic change in shape.

"Alaminos Canyon more common mussel" – Craddock et al., 1991: 302.
"West Florida Escarpment mussel (one individual)" – Craddock et al., 1991: 302.
"Alaminos Canyon sp. A" - Fisher et al., 1991: 134A.
"Seep mytilid II," "Seep mytilid Vb" – Fisher, 1993: 609.
"Seep Mytilid II," "SM II" – Fisher et al., 1993: 278, 280–287, fig. 1 [mussels in habitat photo], figs. 2, 3 [micrographs of symbiotic bacteria in gills].
"AC/II, FL/Vb" – Craddock, et al., 1995: 479–483.
"Seep Mytilid II" – Nelson & Fisher, 1995: 134, table 3.

Types: Holotype ANSP A18847 from ALVIN Dive 2211 in the western Gulf of Mexico at a hydrocarbon seep in Alamiños Canyon at 26°21.3′N; 94°29.7′W in 2222 m. A number of paratypes (ANSP 400775, USNM, MCZ, HMNS, MNHN) are from the same dive and locality. Additional paratypes are from ALVIN Dive 2209 in Alamiños Canyon at 26°21.1′N; 94°30.3′W in 2340 m (ANSP 400774, USNM, MCZ, HMNS) and from the base of the West Florida Escarpment in the eastern Gulf of Mexico from ALVIN Dive 2196 at 26°02.4′N; 84°54.4′W in 3314 m (ANSP 400777), and ALVIN Dive 2542 at 26°01.8′N; 84°54.6′W in 3313 m (ANSP 400776, USNM, HMNS).

Shell Morphology: Shell large, up to 180 mm long, modioliform, elongate, elliptical, thin and fragile, essentially equivalve. Anterior margin moderately rounded; posterior margin broadly rounded; ventral margin straight in young specimens, with slight ventral concavity in medium sized specimens, concavity more pronounced in larger specimens; dorsal margin very broadly convex, more or less straight over span of the ligament (Figs. 11, 12, 14, 15). Umbones of largest specimens eroded; prosogyrate; subterminal, positioned within anterior one-tenth. An indistinct, raised, broadly rounded ridge extends from umbonal region to posterior-ventral margin.

External surface sculpture lacking, smooth except for concentric growth lines, fine radial lines in periostracum extending from umbo to ventral margin, and fine radial periostracal corrugations in the median ventral area. Shell dull-white beneath dark-brown to straw-yellow periostracum. Periostracum often marked by irregularly shaped dark brown pigment patches, overlain by numerous byssal thread attachment plates. Interior off-white, predominately nacreous.

Ligament opisthodetic, parivincular, ex-

tending posteriorly from umbones to occupy from 41% to 59% of dorsal margin. Adult hinge edentulous, except for posteriorly directed projection of anterior hinge margin beneath anterior end of ligament, hinge thickened below and anterior to umbo. Hinge denticles absent in smallest specimen (36 mm length) observed.

Muscle Scars: Anterior adductor scar rounded but truncated posteriorly, located below and partially anterior to umbo, distant from antero-ventral margin. Posterior adductor scar round, contiguous with small siphonal retractor scar ventrally and posterior portion of posterior byssal retractor scar dorsally. Anterior retractor scar located in posterior portion of umbonal cavity. Posterior byssal retractors form two scars with large intervening gap; anterior one elliptical, directly beneath or slightly anterior of posterior end of ligament; second one elliptical, parallel to antero-posterior axis of shell and located antero-dorsally to and bordering posterior adductor scar (Fig. 12). Pallial line distant from shell margin, extending from postero-ventral edge of anterior adductor scar to posterior adductor, curving slightly upwards and then more strongly downwards to form an indentation in byssal gape region at about one-quarter to one-third of distance from anterior; small siphonal retractor scar located at posterior end of ventral pallial line, usually but not always contiguous with posterior adductor.

Measurements (in mm):

length	height	width	anterior length	Dive	
121.3	46.8	35.4	—	A 2211	Holotype ANSP
152.0	60.3	45.8	12.6	A 2211	Paratype MCZ
142.2	54.4	39.7	11.3	A 2211	Paratype USNM
125.9	48.6	44.5	9.0	A 2211	Paratype MNHN
40.0	20.3	13.0	2.7	A 2211	Paratype ANSP
171.0	64.9	49.0	10.5	A 2209	Paratype MCZ
132.7	48.4	36.0	12.7	A 2209	Paratype MCZ
116.4	44.6	30.5	9.3	A 2209	Paratype MCZ
141.4	51.0	38.9	11.3	A 2209	Paratype ANSP
166.0	61.8	44.0	14.4	A 2209	Paratype Rutgers
132.3	54.4	40.3	9.4	A 2211	Paratype MNHN
146.0	49.5	42.0	12.5	A 2209	Paratype Rutgers
143.4	55.5	42.0	13.0	A 2209	Paratype HMNS
106.3	42.2	34.7	8.8	A 2211	Paratype Rutgers
85.5	35.7	24.6	5.0	A 2196	Paratype ANSP
127.7	55.4	40.1	9.0	A 2542	Paratype USNM
117.5	42.4	30.0	6.0	A 2542	Paratype HMNS
88.2	36.7	28.6	5.2	A 2542	Paratype ANSP

Internal Morphology

Musculature: Main features of musculature evident from previous description of muscle scars and Figure 13. Posterior byssal retractors divided into two widely divergent main bundles that attach separately to shell, a posterior portion inserting along postero-dorsal edge of posterior adductor and an anterior portion attaching to shell just below ligament's posterior end. Posterior pedal retractors very thin, arising from antero-dorsal part of foot, passing lateral to anterior retractors and inserting on shell anterior and lateral to posterior portion of posterior byssal retractors. Siphonal retractors integrated with pallial musculature. Anterior retractors arising from dorso-lateral section of byssal-pedal mass and passing anteriorly to insert in antero-dorsal extremity of umbonal cavity. Pair of slender labial palp suspensors extend forward as branches of anterior retractors to attach to shell just behind and adjacent to anterior adductor. Posterior adductor oblong; anterior adductor round in cross-section, about one-half size of posterior adductor.

Foot and Byssus: Foot long, thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands light to dark brown, wide, flat, unornamented. Byssal gland extending down foot behind byssal groove, without extension dorsal to origin of anterior byssal retractors.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260).

Ventral edges of inner mantle lobes thickened, muscular. Excurrent tubuliform siphon capable of slight extension beyond perimeter of shell, lacking internal diaphragm in specimens examined. Horizontal branchial septum incomplete; fusion of inner mantle immediately below excurrent siphon forms short horizontal shelf, not directly attached to ventral edge of posterior adductor. Incurrent and excurrent chambers not completely separated posterior of posterior adductor; posterior end of gill axes attach to ventral surface of horizontal branchial septum. Short extension as valvular siphonal membrane joins right and left mantle lobes, extending anteriorly a short distance into pedal gape; small central papilla on valvular siphonal membrane extending anteriorly into pedal gape. Pedo-byssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Demibranchs approximately equal-sized, thick, short; ventral edges with poorly developed food grooves; dorsal food grooves present in deep folds just below junction of ascending lamellae and areas of attachment to mantle lobes and visceral mass. Filaments wide, fleshy; ctenidia and filaments light-brown. Distal interlamellar junctions lacking; descending and ascending portion of each filament connected apically to one-quarter height of demibranch; every 2nd to 5th filament is "principal filament" (see Atkins, 1937: text fig. 18, type B [1b]) with septum rising to greater than one-third height of demibranch. Lacking "tubular connections" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes.

Labial Palps: Paired labial palps broadly triangular, thick, muscular; inner pair more posterior than outer pair, but not markedly so; plicate ventral to oral groove on inner surface of inner palp and dorsal to oral groove on inner surface of outer palp; outer palp surfaces smooth. Mouth situated in normal anterior position at basal junction of inner and outer palps. Antero-ventral portion of demibranchs situated between inner and outer palps coincident with plicate palp surfaces.

Digestive System: Alimentary tract essentially straight, without recurrent loop, situated directly on body mia-line. Intestine leaves posterior end of stomach and traverses posteriorly ventral to pericardium to a level just posterior to ventricle's mid-point; rectum enters pericardium and ventricle from below at mid-point of ventricle, but anterior to level of auricular openings.

Remarks: Although specimens of B. brooksi from the West Florida Escarpment were more variable in shell shape than those from Alamiños Canyon, overall morphological differences between these were minor. Craddock et al. (1995) identified a single unique individual (with the OTU label FL/Vb; B. brooksi) among 94 specimens of FL/Va (B. heckerae) from this site. Once aware of the existence of a genotypically unique individual in this collection, visual examination of the voucher shell collection readily identified the lone individual. Although this one specimen appeared to differ genetically from all other deep-sea mussels examined by Craddock et al. (1995), analysis of additional specimens of FL/Vb (B. brooksi) collected from this site in 1993 showed that these new FL/Vb samples did not differ from AC/II (B. brooksi from Alamiños Canyon), indicating that B. brooksi is present both at Alamiños Canyon and the West Florida Escarpment sites (Table 8). In addition, analysis of mt DNA COI sequences revealed that the new FL/Vb specimens from West Florida Escarpment were identical with B. brooksi from Alamiños Canyon (AC/II) (Table 8; W. R. Hoeh, unpublished data).

Bathymodiolus brooksi lacks both the extensive ventral mantle fusion and the muscular longitudinal ridge in the mantle cavity, supporting the ascending lamellae, that are characteristic of B. thermophilus. Bathymodiolus brooksi differs from B. heckerae in having a more anteriorly located umbo, a less arcuate ventral shell margin, and relatively thin pedal retractors. In addition, the height to length ratio of B. brooksi is normally greater than B. heckerae at a given length (Fig. 28). Bathymodiolus brooksi differs from "Bathymodiolus" childressi in having widely separated anterior and posterior portions of the posterior byssal retractors, whereas posterior byssal retractors are separated into multiple bundles with a single muscle scar in "Bathymodiolus" childressi. Bathymodiolus brooksi has a central papilla on the anterior margin of the valvular siphonal membrane, which is missing in "Bathymodiolus" childressi. In B. brooksi, the intestine is straight and the rectum enters the ventricle anterior to the auricular ostia; whereas in "Bathymodiolus" childressi, the intestine has a very short recurrent

loop and the rectum enters the ventricle posterior to the auricular ostia. In addition, B. brooksi differs from "Bathymodiolus" childressi in having a more elongate, more slender and less tumid shell shape.

Bathymodiolus brooksi differs from B. platifrons in having subterminal umbones (within 3% to 10% of the anterior) in comparison to the terminal position of the umbo in B. platifrons. The relative height of the posterior portion of the shell is much less in B. brooksi (H/L ranges from 0.34 to 0.51) than in B. platifrons (H/L range; 0.50 to 0.68) and B. japonicus (H/L range; 0.51 to 0.61). Bathymodiolus brooksi differs from B. aduloides in having a straight, unlooped intestine and a central papilla on the valvular siphonal membrane. A central papilla on the valvular siphonal membrane is also lacking in B. septemdierum (Hashimoto & Okutani, 1994).

Relationship between B. brooksi and B. brevior, B. elongatus, and B. puteoserpentis is difficult to assess since we know little about the internal anatomy of the latter three species (Cosel et al., 1994), although the recently reported presence of two recurrent loops in the intestine of B. puteoserpentis (Cosel et al., 1997) distinguishes this species from B. brooksi and other mussels examined in this report. Bathymodiolus brevior, B. elongatus, and B. puteoserpentis are much wider relative to their length than is B. brooksi; the ratio of width over length for B. brooksi ranges from 0.25 to 0.35, whereas these ratios in B. brevior, B. elongatus, and B. puteoserpentis are greater than 0.35.

The protein electrophoretic study of Craddock et al. (1995) showed that B. brooksi from Alamiños Canyon (designated as AC/II) and B. thermophilus (designated as MB/Bt) had no shared alleles at 17 of 26 gene loci and that these two species had a Nei's genetic distance (D) of 1.280. Nei's genetic distance between B. brooksi from Alamiños Canyon and B. heckerae from the West Florida Escarpment site was 0.719 (Craddock et al., 1995; see Table 8). These genetic distances are within the range of values for species-level separation. Bathymodiolus brooksi was more highly divergent in pairwise comparisons with "Bathymodiolus" childressi (D = 1.507 and 1.531 for Bush Hill and Alamiños Canyon samples), T. fisheri (D = 1.992), and "Idas" macdonaldi (D = 5.688) (Table 8; Craddock et al., 1995). Bathymodiolus brooksi shared only 8 to 9 of 26 alleles with "Bathymodiolus" childressi, only 4 of 26 alleles with T. fisheri, and only 1 of 26 with "Idas" macdonaldi (Craddock et al., 1995). Since most congeneric groupings of animals have Nei's D values less than 2.0 (Nei, 1987), these results support generic separation of T. fisheri and "Idas" macdonaldi from B. brooksi.

Analysis of a 246 bp region of the mtDNA COI gene showed a sequence divergence of 14.7% between B. brooksi and B. heckerae, and 17.1% between B. brooksi and " Bathymodiolus" childressi (Table 8; W. R. Hoeh, unpublished data). Percent sequence divergence between B. brooksi and T. fisheri was 50.3%, and 41.8% between B. brooksi and "Idas" macdonaldi (Table 8). These levels of allozymic and mtDNA divergence support separate species status for B. brooksi, as well as separation at the generic level from T. fisheri and "Idas" macdonaldi.

General features of the Alamiños Canyon hydrocarbon/brine seep sites are presented in Brooks et al. (1990). Simultaneous occurrence of sulfur-oxidizing and methanotrophic bacterial symbionts in gill tissue, as well as the presence of two morphological types of symbionts visible in transmission electron micrographs of the gill tissue, suggests that B. brooksi harbors both thiotrophic and methanotrophic bacterial symbionts within its gill bacteriocytes (Fisher et al., 1993). Specimens of this species from the West Florida Escarpment site also harbor two morphologically distinct bacterial endosymbionts (C. M. Cavanaugh, pers. comm.).

Bathymodiolus brooksi shares the Alamiños Canyon site with the methanotrophic mussel "Bathymodiolus" childressi, two species of vestimentiferan tubeworms, a white shrimp, and galatheid crabs (Brooks et al., 1990). This species shares the West Florida Escarpment site with B. heckerae. Other West Florida Escarpment site fauna are described in the remarks section for B. heckerae.

Etymology: The specific name honors Dr. James M. Brooks, Texas A & M University, who has been one of the driving forces behind exploration of deep-sea hydrocarbon/brine seeps in the Gulf of Mexico. The working designation "Seep Mytilid II" was given to this species from Alamiños Canyon and "Seep Mytilid Vb" to members of this species from the West Florida Escarpment.

Range: Known from hydrocarbon seeps at Alamiños Canyon in the western Gulf of Mexico in depths from 2222 to 2340 m and from

cold-water methane/sulfide seeps at the base of the West Florida Escarpment in the eastern Gulf of Mexico near 26°02′N; 84°55′W in depths from 3270 to 3314 m (Table 4).

"Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek, new species
Figures 11–13, 16–20

This species, known since 1985, has been referred to in literature concerning seep and vent ecology but was never formally described. The following is a list of these references.

"Mytilid (large, brown)" – Turner, 1985: 29 (Louisiana Slope).
"Undescribed mussel" – Childress et al., 1986: 1306, fig. 2 [micrographs of gill filament and symbiotic bacteria].
"Mytilid" – Grassle, 1986: 339.
"Undescribed mytilid" – Fisher et al., 1986: 6A.
"Mussels" – Brooks et al., 1987a: 498.
"Mussels," "Mytilidae undescribed" – Brooks et al., 1987b: 1138, 1139.
"Seep mussels," "symbiont-containing mytilid bivalve" – Cary et al., 1988: 78, 79.
"Undescribed hydrocarbon-seep mussels" – Fisher et al., 1987: 59, figs. 1a, 1b, 2a, 3a, 3c [micrographs of gill filaments, bacteriocytes, symbiotic bacteria].
"Mussels from Louisiana hydrocarbon seeps" – Hook & Golubic, 1988: 361–362.
"Mussel" – Kennicutt et al., 1988a: 44, figs. 1, 2 [mussels visible in habitat photos].
"Mussel" – Kennicutt et al., 1988b: 1639.
"Undescribed seep mussel" – Page et al., 1988: 192A.
"Undescribed mussel (Mytilidae)" – Brooks et al., 1989:2.
"Methane-oxidizing mussel," "Bathymodiolus-like," "seep mussels" – MacDonald et al., 1989: 235, figs. 3C and 3D [mussels visible in habitat photos].
"Mussels," "Mytilidae sp." – Wade et al., 1989: 19, 22.
"Bathymodiolus n. sp." – MacDonald et al., 1990a: 1096, figs. 3, 4 [mussels visible in habitat photos].
"Seep mussel (Bathymodiolus n. sp.: Mytilidae)" – MacDonald et al., 1990b: 248, fig. 4 [mussels visible in habitat photos].
"Methanotrophic mussels" – MacDonald et al., 1990c: 15, figs. 2a–c [mussels visible in habitat photos].
"Mussels" – Alper, 1990a: 536, fig. p. 537 [mussels visible in habitat photo].
"Mussels" – Alper, 1990b: 23, figs. pp. 22, 26, 28 [mussels visible in habitat photos].
"Undescribed seep mussel" – Page et al., 1990: 251.
"Louisiana seep mussel" – Dahlhoff & Somero, 1991: 475 (table 1).
"Bathymodiolus sp." – Warén & Ponder, 1991: 54.
"Alaminos Canyon less common mussel" – Craddock et al., 1991: 302.
"Alaminos Canyon sp. B" – Fisher et al., 1991: 134A.
"Bathymodiolus sp., undescribed" – Kochevar et al., 1992: 389, fig. 4 [micrographs of gill filament and symbiotic bacteria].
"Bathymodiolus sp., undescribed" – Lee et al., 1992: 99.
"Louisiana seep mussel" – Kennicutt et al., 1992: 298.
"Seep Mytilid Ia" – Fisher & Childress, 1992: 223, fig. 2 [micrographs of bacteriocytes, symbiotic bacteria].
"LA mytilid" – Cavanaugh, 1992: 316.
"Seep mytilid Ia," "Seep mytilid Ib" – Fisher, 1993: 609.
"SM Ia, SM Ib" – Fisher et al., 1993: 278, 280.
"Seep Mytilid Ia" – Gustafson & Lutz, 1994: 80, figs. 4.1, 4.2 [micrographs of prodissoconch I and II].
"BH/Ia, AC/Ib" – Craddock et al., 1995: 479–483.
"Seep Mytilid Ia," "Seep Mytilid Ib" – Nelson & Fisher, 1995: 133–134, table 3.
"Seep mytilid Ia" – Lee & Childress, 1995: 137.
"Seep Mytilid Ia" – Nix et al., 1995: 605, 606, 609–613.
"Seep mytilid Ia" – Lee & Childress, 1996: 373.
"Seep Mytilid Ia" – Kochevar & Childress, 1996: tables 1, 2.

Types: Holotype ANSP A18848 from JOHNSON SEA-LINK-I Dive 3129, Bush Hill hydrocarbon seep, 27°46.9′N; 91°30.4′W, about 210 km south southwest of Grand Isle, Louisiana in 546 m. The type-locality is on the Louisiana Continental Slope between Blocks 184 and 185 in the Green Canyon offshore petroleum leasing area. Several paratypes (ANSP 400778, MCZ, HMNS, MNHN) are from the same locality. Additional paratypes are from JOHNSON SEA LINK-I Dive 3137 at 27°41.1′N; 91°32.2′W in 723 m (Green Canyon-272) (MCZ, HMNS, MNHN); JOHNSON SEA LINK-I Dive 3145 at 27°43.4′N; 91°16.6′W in 650 m (Brine Pool NR-1)

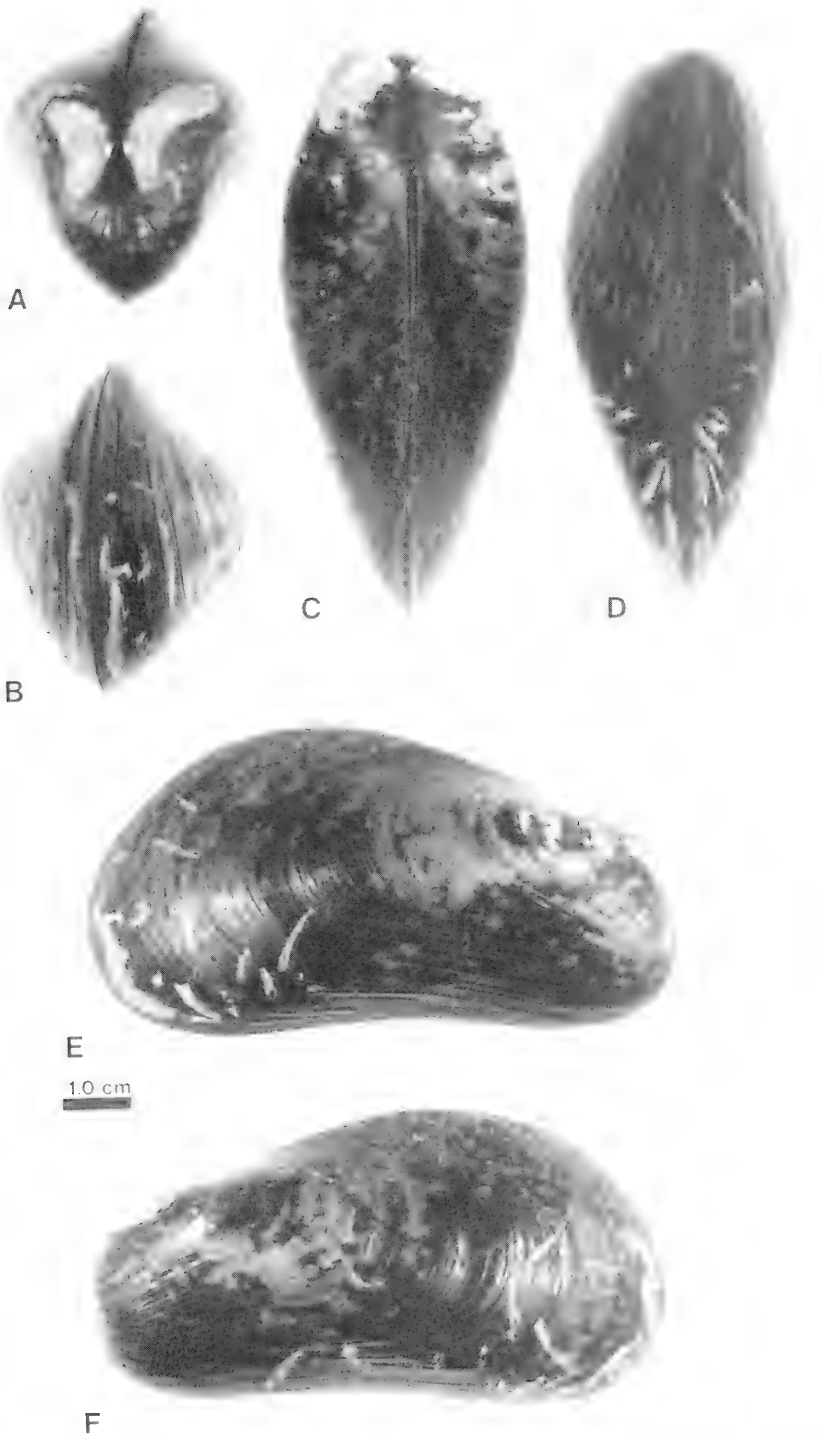

FIG. 16. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. Holotype, ANSP A18848. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view of right valve; F, lateral view of left valve.

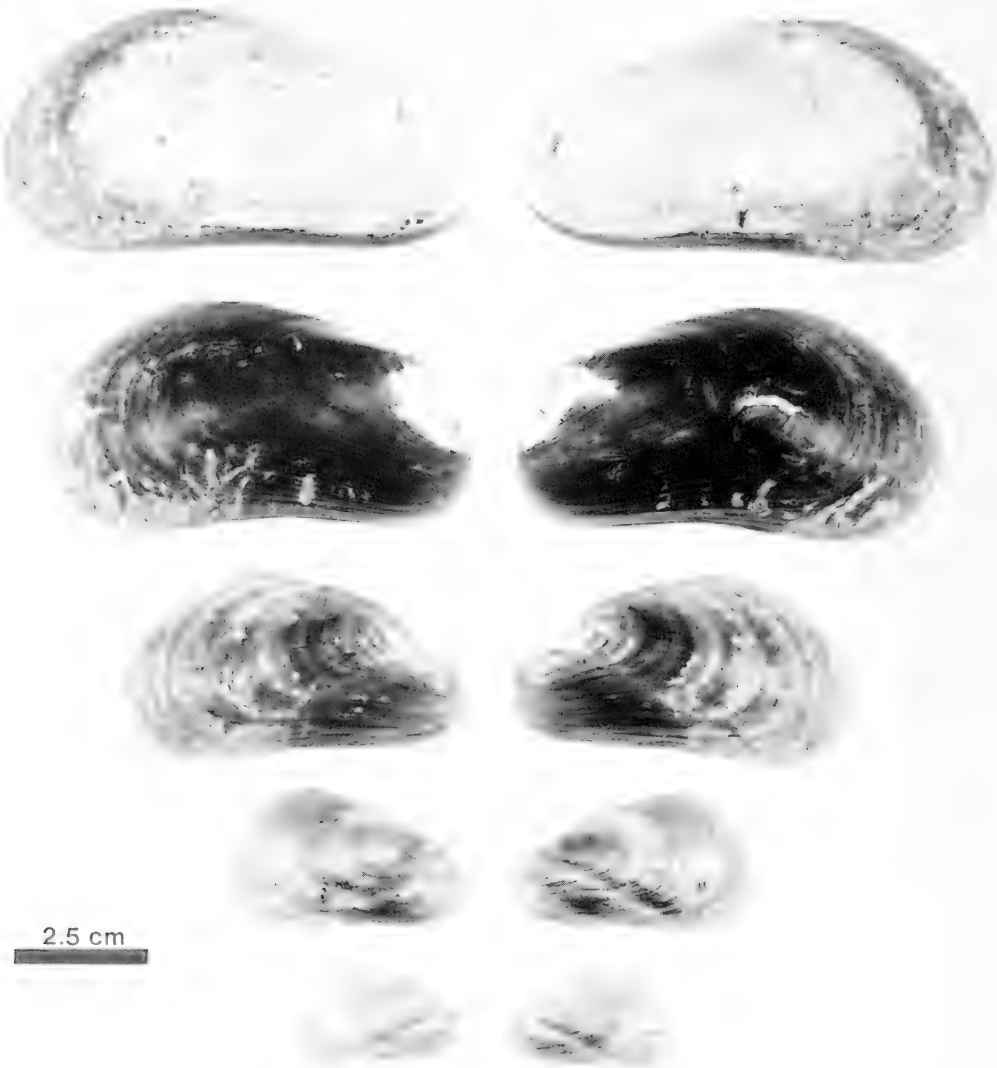

FIG. 17. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. External views of a growth series of shells illustrating ontogenetic change in shape.

(USNM, MCZ); and ALVIN Dive 2211 at 26°21.3′N; 94°29.7′W in 2222 m (Alamiños Canyon) (ANSP 400779, USNM, HMNS, MNHN).

Shell Morphology: Shell large, up to 120 mm long, modioliform, thin and fragile, essentially equivalve, elliptical in immature specimens, becoming increasingly arcuate in larger, old specimens (Figs. 11, 12, 16, 17). Anterior margin narrowly rounded; posterior margin broadly rounded; ventral margin straight to slightly concave in small specimens, becoming increasingly concave in larger specimens; dorsal margin convex (Fig. 11). Umbones often eroded; prosogyrate; nearly terminal to slightly subterminal; prodissoconch I from 100 to 110 μm in length; prodissoconch II reddish, 385 to 404 μm in length. An indistinct, raised, broadly rounded ridge or keel extends from the umbonal region to the postero-ventral margin.

External sculpture lacking, surface smooth except for concentric growth lines and fine ra-

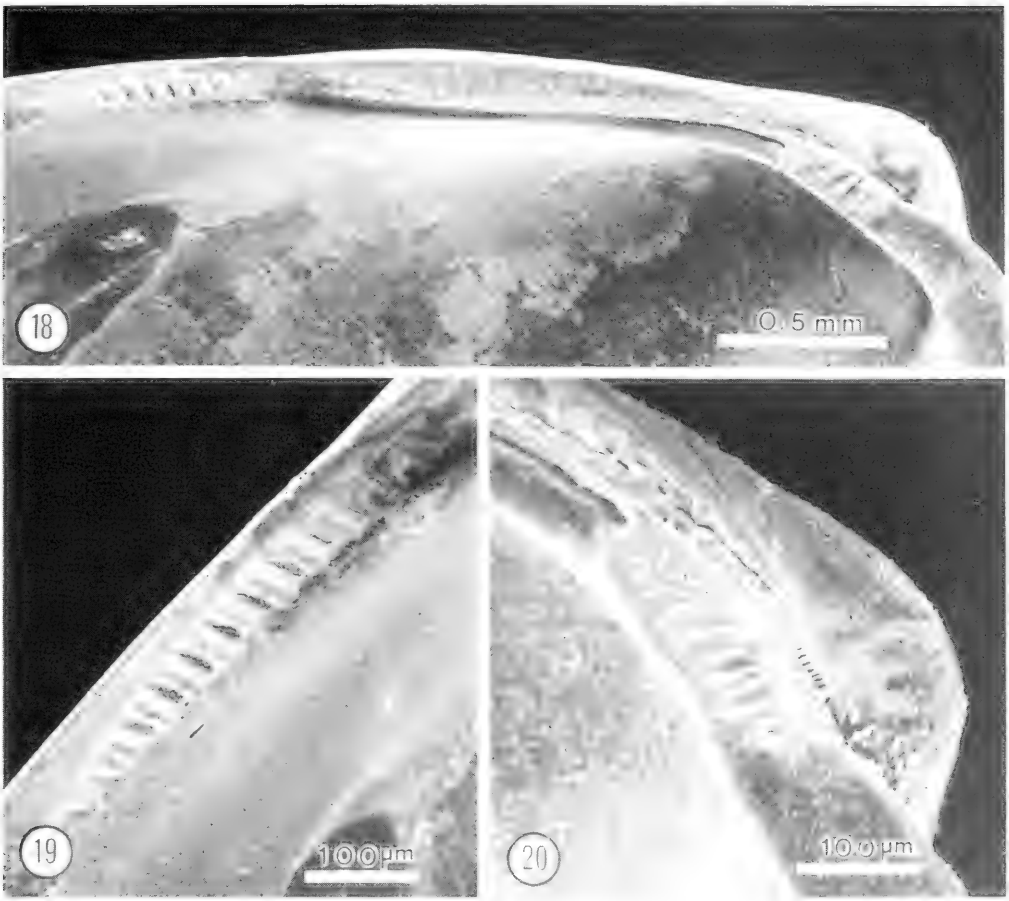

FIG. 18. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. Juvenile hinge line of specimen 4.5 mm in length. Scale bar = 0.5 mm.
FIG. 19. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. Hinge denticles located immediately posterior of the ligament in juvenile specimen 4.5 mm in length.
FIG. 20. "Bathymodiolus" childressi Gustafson, Turner, Lutz & Vrijenhoek. Hinge denticles located immediately below the umbo in juvenile specimen 4.5 mm in length.

dial periostracal corrugations in the median ventral area. Shell dull-white beneath a dark-brown to straw-yellow periostracum. Antero-dorsal portion of shell variably eroded depending on age and collection site. Interior off-white, predominately nacreous.

Ligament opisthodetic, parivincular, extending posteriorly from umbones to occupy 38% to 58% of dorsal margin. Adult hinge edentulous, thickened below and anterior to umbo. Juvenile hinge with 8 to 9 denticles immediately posterior to ligament and with 4 to 5 denticles located immediately below umbones (Figs. 18–20). Hinge denticles obsolete in specimens greater than 11 mm in length.

Muscle Scars: Muscle scars and pallial line indistinct. Anterior adductor scar oblong, below and posterior to the umbo; posterior adductor scar round, contiguous dorsally with single posterior byssal-pedal retractor scar; anterior retractor scar located in posterior portion of umbonal cavity; posterior byssal retractors forming continuous scar extending from directly beneath posterior end of ligament to antero-dorsal edge of posterior adductor scar (Fig. 12). Ventral pallial line straight, well

inset, paralleling the ventral shell margin and extending from postero-ventral edge of anterior adductor scar to posterior adductor.

Selected measurements (in mm):

length	height	width	anterior length	Dive	
88.7	46.1	37.7	—	JSL 3129	Holotype ANSP
83.3	43.3	29.6	1.1	JSL 3129	Paratype MNHN
73.4	39.5	30.0	3.8	JSL 3129	Paratype ANSP
67.6	36.5	29.3	2.6	JSL 3129	Paratype Rutgers
86.1	44.3	36.5	2.1	JSL 3137	Paratype HMNS
123.6	58.4	46.0	4.5	JSL 3145	Paratype USNM
118.5	53.3	46.0	2.4	JSL 3145	Paratype MCZ
45.9	23.4	20.5	0.2	A 2211	Paratype HMNS
56.7	30.2	25.2	1.3	A 2211	Paratype Rutgers
63.5	32.6	28.6	2.7	A 2211	Paratype ANSP
106.8	48.9	41.5	2.3	JSL 3145	Paratype USNM
94.1	45.5	39.4	4.2	JSL 3137	Paratype Rutgers
78.4	39.6	28.5	1.5	JSL 3129	Paratype HMNS
90.6	45.5	37.6	2.5	JSL 3137	Paratype MNHN
61.4	30.7	28.1	1.1	JSL 3137	Paratype MNHN

Internal Morphology

Musculature: Although the posterior byssal retractors form one continuous muscle scar in each valve (see description above, Fig. 12), posterior byssal retractors are subdivided into six main muscle bundles (Fig. 13). Posterior pedal retractors small, thin, arising from antero-dorsal portion of the foot mass and passing lateral to anterior bundle of posterior byssal retractors. Siphonal retractors not evident. Anterior retractors arising just ventral to origin of anterior portion of posterior byssal retractors on dorsal surface of byssal-pedal mass and passing anteriorly to insert in posterior portion of umbonal cavity (Fig. 13). Paired labial palp suspensors slender, extending forward as branches of anterior retractors to attach just behind and adjacent to anterior adductor. Posterior adductor oblong; anterior adductor small, round in cross-section.

Foot and Byssus: Foot thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands light-to dark-brown, wide, flat, unornamented. Byssal gland extending down foot behind byssal groove.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260). Ventral edges of inner mantle lobes thickened and muscular. In life, excurrent tubuliform siphon capable of moderate extension beyond end of shell. Lacking horizontal branchial septum between incurrent and excurrent chambers; incurrent and excurrent chambers not physically separated posterior to the posterior adductor. Posterior end of gill axes attach to inner wall of fused inner mantle lobes just ventral to excurrent siphon. Short valvular siphonal membrane joins right and left lobes, extending anteriorly a short distance into pedal gape; anterior edge of valvular siphonal membrane smooth, lacking central papilla. Pedobyssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Demibranchs approximately equal-sized, tall, fleshy; ventral margins with well-developed food grooves; dorsal food grooves in deep folds just below the junction between the ascending lamellae and both the mantle lobes and the visceral mass. Ctenidia off-white; filaments thin for the group examined in this report, but broader than typical for mytilids. Distal interlamellar junctions lacking; descending and ascending portion of each filament connected apically to one-quarter height of demibranch; every 2nd to 6th filament is a "principal filament" (see Atkins, 1937: text fig. 18, type B[1b]) exhibiting short interlamellar septum extending dorsally to a slight degree. Lacking "tubular connections" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes.

Labial Palps: Paired labial palps greatly modified from the typical filter-feeding type, appearing to function as sorting area for material gathered by the foot rather than the

ctenidia. Base of inner and outer palp pair widely separated. Inner pair placed farther posteriorly, large and muscular with long proboscid-like extension of far posterior end. Mouth situated at basal mid-point of anterior end of inner pair of labial palps, farther posterior than typical for mytilids. Outer pair of palps more anterior, triangular, muscular, but smaller than inner pair with shorter proboscid-like extension.

Digestive System: Stomach and direct intestine situated left of the mid-line; rectum on mid-line posterior to entry into ventricle. Intestine leaves posterior end of stomach and traverses a short distance posteriorly to the left of the mid-line; intestine/rectum with a very short recurrent loop, which turns in a clockwise direction when viewed dorsally, just prior to turning upwards to enter the ventral aspect of the ventricle just posterior to the auricular ostia.

Remarks: "Bathymodiolus" childressi possesses a combination of morphological characters not seen in any previously described deep-sea mytilid genus; however, genetic distance measures (Nei's D and percent sequence divergence for 246 bp of the mtDNA COI gene) do not clearly separate this species from other members of the genus Bathymodiolus. So as to avoid erecting a new mono-specific genus, this species is provisionally placed in Bathymodiolus. Specimens of "Bathymodiolus" childressi previously designated Seep Mytilid Ia (Louisiana Continental Slope) and Ib (Alamiños Canyon) appear identical in all particulars and are here regarded as conspecific.

"Bathymodiolus" childressi differs from all other species referred to Bathymodiolus in having multiple separation of the posterior byssal retractors (similar to what is seen in Modiolus), a single posterior byssal retractor scar, and a rectum that enters the ventricle posterior to the level of the auricular ostia. "Bathymodiolus" childressi differs from B. heckerae and B. brooksi in having a more anteriorly located umbo, a recurrent intestinal loop, and lacking a papilla on the valvular siphonal membrane. "Bathymodiolus" childressi differs from all other Bathymodiolus species, except B. platifrons, in having the umbo located at the extreme anterior end of the shell, in an almost terminal position. Although superficially similar to B. platifrons, "Bathymodiolus" childressi differs from B. platifrons in having a single posterior byssal retractor scar, a rectum that enters the ventricle posterior to the level of the auricular ostia, a recurrent intestine, and lacking a papilla on the valvular siphonal membrane (Hashimoto & Okutani, 1994).

The protein electrophoretic study of Craddock et al. (1995) showed that "Bathymodiolus" childressi (designated as AC/Ib and BH/Ia) and B. heckerae (designated as FL/Va) had pairwise Nei's D values of 2.086 and 2.188, whereas comparison of these two populations of "Bathymodiolus" childressi with B. brooksi (designated as AC/II) yielded D values of 1.531 and 1.507, respectively. Pairwise comparison of the two "Bathymodiolus" childressi populations and B. thermophilus (designated as MB/Bt) yielded Nei's D values of 1.831 and 1.833 (Craddock et al., 1995; Table 8). These genetic distances straddle the range of values for species-level separation and are not sufficient evidence to support erection of a new genus for "Bathymodiolus" childressi.

The two populations of "Bathymodiolus" childressi were more highly divergent in pairwise comparisons with T. fisheri (D = 2.209 and 2.138), and "Idas" macdonaldi (D = 2.656 and 2.570) (Table 8; Craddock et al., 1995). Since most congeneric groupings of animals have Nei's D values less than 2.0 (Nei, 1987), these results support generic separation of T. fisheri and "Idas" macdonaldi from "Bathymodiolus" childressi

Analysis of a 246 bp region of the mtDNA COI gene showed a sequence divergence of 17.6% to 18.7% between "Bathymodiolus" childressi and B. heckerae, and 17.2% between "Bathymodiolus" childressi and B. brooksi (Table 8; W. R. Hoeh, unpublished data). Sequence divergence between "Bathymodiolus" childressi and T. fisheri ranged from 47.9% to 48.7%. Similar values for "Bathymodiolus" childressi and "Idas" macdonaldi ranged from 43.4% to 45.0% (Table 8). These levels of mtDNA divergence support separate species status for "Bathymodiolus" childressi, and separation at the generic level from T. fisheri and "Idas" macdonaldi.

"Bathymodiolus" childressi occurs over a depth range of at least 1670 m, which is not remarkable considering that Knudsen (1970) recorded at least 15 abyssal and hadal bivalves with depth ranges greater than 2000 m and numerous other deep-sea bivalves with similar or greater vertical distributions are on record (references in Allen, 1983).

"Bathymodiolus" childressi from both the Louisiana Continental Slope and Alamiños Canyon contain methanotrophic symbionts in their gills (Fisher, 1993), which provide a source of carbon and energy to the host mussel via oxidation of environmental methane (Childress et al., 1986; Fisher et al., 1987). Intracellular bacteria are limited to bacteriocytes within the gill filaments and have internal membrane structures typical of Type I methanotrophs (Childress et al., 1986; Fisher et al., 1987). Analysis of 16S rRNA gene sequence data reveals the presence of only a single bacterial species in "Bathymodiolus" childressi (Cavanaugh, 1992).

The labial palp suspensors of "Bathymodiolus" childressi provide support for the large labial palps. Although rare in the Mytilidae in general, similar muscles occur in the deep sea mytilids Dacrydium ockelmanni Mattson & Warén, 1977 (mislabelled "pedobyssal retractors"), D. angulare Ockelmann, 1983 ("labial palp suspensors") and B. thermophilus ("labial palp muscles") (Kenk & Wilson, 1985), as well as in B. heckerae and B. brooksi described in this report.

The fine scale distribution of "Bathymodiolus" childressi at hydrocarbon/brine seeps on the Louisiana Continental Slope is significantly correlated with methane concentration (MacDonald et al., 1989). Living mussels occur in clusters near gas vents, around areas of general fluid discharge where seeping brine may be a carrier of methane (MacDonald et al., 1989, 1990a), and around brine-filled depressions on the sea-floor where the density of brine (up to 3.5 times normal seawater) traps methane in close proximity to oxygen laden seawater (MacDonald et al., 1990c). Although "Bathymodiolus" childressi form discrete beds on soft sediments and among carbonate outcrops, they also occur on and among clumps of the vestimentiferan tubeworm Lamellibrachia sp. (MacDonald et al., 1989). Two other species of mussel, T. fisheri and "Idas" macdonaldi co-occur with "Bathymodiolus" childressi at some sites on the Louisiana Continental Slope, but they are far less common and were only recently recognized (Fisher & Childress, 1992; I. R. MacDonald, pers. comm.). Other fauna associated with "Bathymodiolus" childressi at Louisiana Continental Slope sites include the trochid gastropod Cataegis meroglypta McLean & Quinn, 1987; the nerite gastropod Bathynerita naticoidea Clarke, 1989; the shrimp Alvinocaris stactophila Williams, 1988; and the crabs Rochinia crassa (A. Milne Edwards, 1879), Benthochascon schmitti Rathbun, 1931, and Munidopsis sp. (MacDonald et al., 1989, 1990a, c).

Published information on communities at Alamiños Canyon are scanty but we know that "Bathymodiolus" childressi shares this site with the mussel B. brooksi, vestimentiferan tubeworms, galatheid crabs, and swarms of white shrimp.

Numerous, round, white-rimmed, egg capsule scars (or the egg capsules themselves) are often found on the posterior and posterodorsal portion of the shell of "Bathymodiolus" childressi from Bush Hill, Green Canyon, and Brine Pool NR-1. These capsules are deposited by Bathynerita naticoidea (C. R. Fisher, pers. comm.).

Micrographs depicting the prodissoconchs I and II of "Bathymodiolus" childressi have been published in Gustafson & Lutz (1994: figs. 4.1, 4.2). The prodissoconch I length of 100 to 110 μm, the prodissoconch II length of 385 to 404 μm and the sculpture of concentric growth lines on the prodissoconch II are consistent with characteristics indicative of planktotrophic development (Gustafson & Lutz, 1994).

Etymology: The specific name honors Dr. James J. Childress, University of California - Santa Barbara, whose seminal work on the physiology of this species revealed its reliance on a methane-based symbiosis with intracellular bacteria (Childress et al., 1986). The working designation "Seep Mytilid Ia" was given to this species from the Louisiana seeps and "Seep Mytilid Ib" to members of this species from Alamiños Canyon.

Range: Known from the northern Gulf of Mexico on the Louisiana Continental Slope in 546 to 737 m and from the western Gulf of Mexico at Alamiños Canyon in 2222 m (Table 5).

Tamu Gustafson, Turner, Lutz & Vrijenhoek, new genus

Type species: Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek, new species.

Description: Shell smooth, modioliform, with sub-terminal umbones; adult hinge edentulous, juvenile hinge with small denticulations anterior and posterior to ligament; posterior retractors divided into anterior and posterior portions, posterior retractor scars separate; small pedal retractors present; mantle open ventrally; demibranchs of ctenidia hypertro-

phied and fleshy, filaments broadly thickened, with well-developed ventral food grooves; symbiotic bacteria associated with external gill surfaces; intestine with a short recurrent loop beneath the ventricle, rectum entering ventricle anterior to the auricular ostia.

Remarks: Tamu possesses a combination of morphological characteristics not seen in any existing mytilid genus (Table 9) and exhibits genetic distance measures (Nei's D and percent sequence divergence for 246 bp of the mtDNA COI gene) that clearly separate the type species from the genus Bathymodiolus (Table 8). Comparison of Tamu with existing genera is hampered by the fact that most deep-sea mytilid genera have been described without benefit of anatomical studies; in many cases, surviving type specimens consist of shell material only. Tamu differs from Bathymodiolus in having thickened gills that contain symbiotic bacteria in "pockets," open to the mantle cavity; by its relatively small size; and by the absence of palp suspensors. Tamu differs from Idas and Adipicola in having posterior byssal retractors that are divided into anterior and posterior portions and in loosing the hinge denticulations at maturity. Tamu further differs from Idas (as represented by putative I. argenteus, the type species, and I. washingtonia) in having thickened versus filamentous gills, lateral versus medial placement of the pedal retractors (relative to the posterior byssal retractors), and outer and inner demibranchs of equal length. Tamu further differs from Adipicola (as represented by Adipicola sp. from the Middle Valley hydrothermal vent site on the Juan de Fuca Ridge in the northwest Pacific) in having separate pedal retractors that are not integrated with the posterior byssal retractors. Tamu differs from other deep-sea mytilid genera (Amygdalum, Benthomodiolus, and Dacrydium) in having thickened ctenidia versus filamentous ctenidia. In addition, the outer demibranchs are only one half the length of the inner demibranchs in Benthomodiolus and Dacrydium, whereas outer and inner demibranchs are of equal size in Tamu. Palp suspensors are absent in Tamu, but present in both Benthomodiolus (type species) and Dacrydium (Ockelmann, 1983).

Nei's genetic distance based on 26 allozyme loci between T. fisheri and members of the genus Bathymodiolus, ranged from 1.983 to 3.305 (Craddock et al. 1995; Table 8). These Nei's D values are outside the range of those for most congeneric groupings of animals (Nei, 1987). Percent sequence divergence for a 246 bp region of the mtDNA COI gene ranged from 47.9% to 52.2% between T. fisheri and members of the genus Bathymodiolus. Tamu fisheri and "Idas" macdonaldi were somewhat closer related, with a pairwise Nei's D value of 1.859 and a COI sequence divergence of 38% (Table 8).

The generic name derives from the abbreviation for Texas A & M University (TAMU). Members of the Geochemical and Environmental Research Group at Texas A & M University have been instrumental in the discovery and exploration of numerous hydrocarbon/brine seeps on the Louisiana and Texas Continental Slope where many of these mussel taxa were first discovered.

Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek, new species
Figures 11–13, 21–23

This species, known since 1991, has been referred to in literature concerning seep and vent biology but was never formally described. The following is a list of these references.

"Seep mytilid III" – Fisher, 1993: 609.
"Seep mytilid III" – Gustafson & Lutz, 1994: 81, fig. 4.3 [micrograph of prodissoconch II].
"GB/III" – Craddock et al., 1995: 479–483.
"Seep mytilid III" – Nelson & Fisher, 1995: table 3.
"Seep mytilid III" – Kochevar & Childress, 1996: tables 1, 2.

Types: Holotype ANSP A18849 from JOHNSON SEA-LINK-I Dive 3108 at Bush Hill hydrocarbon seep at 27°46.91′N; 91°30.36′W, 210 km south southwest of Grand Isle, Louisiana in 548 m. The type-locality is between Blocks 184 and 185 in the Green Canyon offshore petroleum leasing area in the Gulf of Mexico on the Louisiana Continental Slope. Five paratypes (ANSP 400780, 400781; USNM, MCZ) are from the same dive and locality. Additional paratypes are from JOHNSON SEA-LINK-I Dives 3131 and 3149 at approximately 27°50′N; 91°10′W in 701 and 650 m, respectively (ANSP 400782; MCZ, HMNS).

Shell Morphology: Shell small, length no greater than 60 mm. Modioliform, thick and sturdy, essentially equivalve. Anterior margin

TABLE 9. Comparison of morphological characters among genera of deep-sea mytilid mussels.

Character/ Genus	Adipicola[1]	Amygdalum	Bathymodiolus (type species)	Benthomodiolus (type species)	Dacrydium	Idas[2]	Modiolus	Tamu (type species)
Maximum shell length	36 mm	44 mm	160 mm	18 mm	4 mm	9 mm	230 mm	54 mm
Hinge denticulations	retained in some species	?	juvenile only	absent	retained in adult	retained in adult	?	juvenile only
Ventral mantle fusion	absent	absent	extensive[3]	absent	absent	absent	absent	absent
Posterior byssal retractors	undivided	separate	separate	separate	undivided	undivided	multiple muscle bundles, single scar	separate
Pedal retractors	absent	absent	present	present	absent	present	present	present
Palp suspensors	?	?	present	present	present	absent	absent	absent
Intestine	?	?	straight	1 short recurrent loop	1 recurrent loop	1 recurrent loop	2 recurrent loops	1 recurrent loop
Entry point of rectum into ventricle	?	?	anterior to auricular ostia	anterior to auricular ostia	anterior to auricular ostia	anterior to auricular ostia	?	anterior to auricular ostia
Ctenidia	thickened	filamentous	thickened, endosymbiotic bacteria	filamentous	filamentous	filamentous	filamentous	thickened, ectosymbiotic bacteria
Outer demibranchs	equal with inner demibranchs	?	equal with inner demibranchs	1/2 length of inner demibranchs	1/2 length of inner demibranchs	1/2 length of inner demibranchs	equal with inner demibranchs	equal with inner demibranchs

[1]Based on Adipicola sp. from Middle Valley on the Juan de Fuca Ridge.
[2]Based on Idas argenteus from the Tongue of the Ocean (TOTO) site and I. washingtonia from South Cleft hydrothermal vent on the Juan de Fuca Ridge off southern British Columbia and from whale bone in the Santa Catalina Basin off southern California.
[3]Character present in type species only, absent in other members of Bathymodiolus.

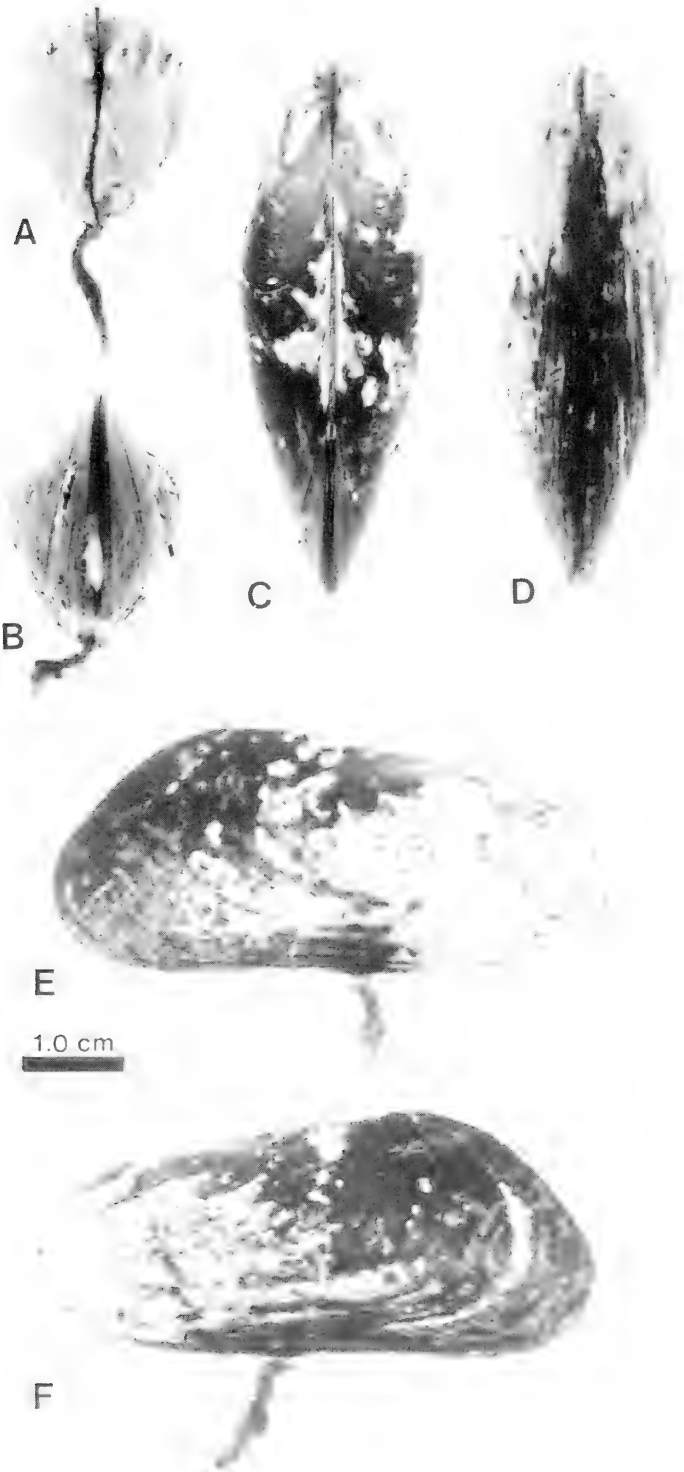

FIG. 21. Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek. Holotype, ANSP A18849. A, anterior view; B, posterior view; C, dorsal view; D, ventral view; E, lateral view of right valve; F, lateral view of left valve.

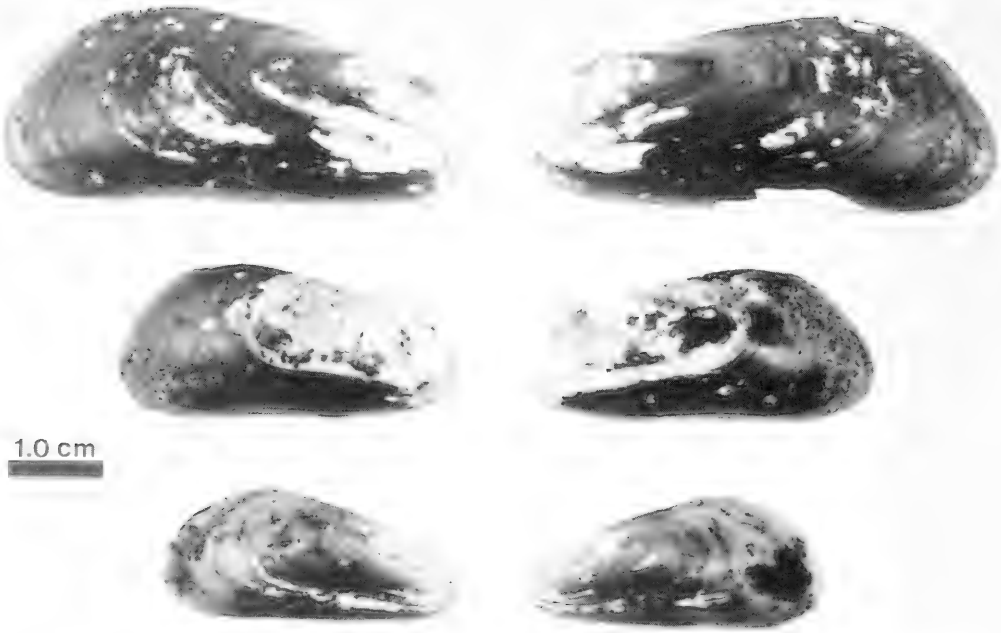

FIG. 22. Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek. External views of a growth series of shells illustrating ontogenetic change in shape.

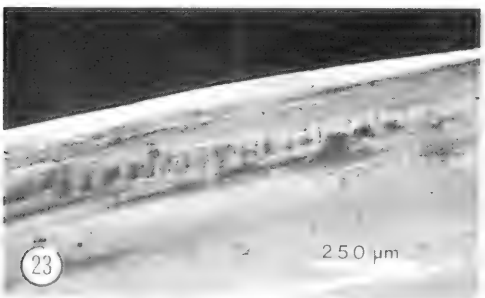

FIG. 23. Tamu fisheri Gustafson, Turner, Lutz & Vrijenhoek. Remnants of juvenile hinge denticles located immediately posterior of the ligament in juvenile specimen 16.9 mm in length.

sharply rounded; posterior margin broadly rounded, becoming angular dorsally; ventral margin straight, very slightly concave in region of byssal gape in largest specimens; dorsal margin very broadly convex (Figs. 11, 12, 21, 22). Shell length greater than twice the height. Umbones often eroded; prosogyrate; subterminal, positioned within the anterior one-twentieth. Prodissoconch II red, 460 µm in length. A raised, broadly rounded ridge extends from the umbonal ridge to the posterior-ventral margin.

External sculpture lacking, surface smooth except for concentric growth lines and very fine radial periostracal corrugations in the median ventral area. Shell dull-white beneath dark-brown to straw-yellow periostracum. Antero-dorsal portion of periostracum and shell variably eroded depending on age and collection site. Interior polished, off-white, predominately nacreous.

Ligament opisthodetic, parivincular, extending posteriorly from the umbones to occupy from 37% to 50% of the dorsal margin. Adult hinge edentulous, thickened below and anterior to the umbo. Juvenile hinge with denticles immediately posterior of the ligament and immediately below the umbones (Fig. 23). Hinge denticles obsolete in specimens greater than 17 mm in length.

Muscle Scars: Anterior adductor scar oblong, positioned at an oblique angle near the antero-ventral margin, below the umbo. Posterior adductor scar round, contiguous with small siphonal retractor scar ventrally and posterior portion of posterior byssal-pedal retractor scar dorsally. Anterior retractor scar located within upper extremity of umbonal cavity directly beneath umbo. Posterior byssal retractors form two scars with a moderate gap between them; anterior scar obliquely elliptical, directly beneath the posterior end of the ligament, poste-

rior scar elliptical, parallel to the antero-posterior axis of the shell and located antero-dorsally to and bordering the posterior adductor scar (Fig. 12). Ventral pallial line prominent, extending from the median posterior aspect of the anterior adductor scar to the posterior adductor, curving slightly upwards and then downwards to form an indentation in the byssal gape region at about the mid-point of the antero-posterior axis; small siphonal retractor scar located at posterior end of ventral pallial line contiguous with posterior adductor.

Measurements (in mm):

length	height	width	anterior length	Dive	
53.5	23.8	17.6	—	JSL 3108	Holotype ANSP
46.8	21.4	16.2	2.2	JSL 3108	Paratype Rutgers
50.0	21.9	17.0	2.8	JSL 3108	Paratype USNM
51.4	21.0	18.5	1.9	JSL 3108	Paratype ANSP
48.8	20.6	16.1	2.2	JSL 3108	Paratype ANSP
49.6	20.5	16.2	2.0	JSL 3108	Paratype USNM
31.6	14.1	10.1	2.0	JSL 3149	Paratype HMNS
33.9	15.2	12.3	2.0	JSL 3149	Paratype Rutgers
33.9	15.9	10.6	1.7	JSL 3149	Paratype MCZ
37.0	16.3	13.3	2.9	JSL 3149	Paratype ANSP

Internal Morphology

Musculature: Main features of musculature evident from previous description of muscle scars and Figure 13. Posterior byssal retractors separated into posterior and anterior portions, each consisting of two main muscle bundles, that attach separately to the shell; the posterior portion inserting along the postero-dorsal edge of the posterior adductor and the anterior portion inserting just below and posterior to the posterior end of the ligament. Pedal retractors very slender, arising from antero-dorsal portion of foot, passing lateral to the anterior retractors and inserting lateral to posterior portion of the posterior byssal retractors. Siphonal retractors indistinct, originating in inner mantle margin around the excurrent siphon and attaching along postero-ventral edge of the posterior adductor. Anterior retractors arising from dorso-lateral portion of the foot mass and passing anteriorly to insert in the antero-dorsal extremity of the umbonal cavity. Labial palp suspensors not evident. Posterior and anterior adductor rounded.

Foot and Byssus: Foot long, thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands few to profuse, gray to light-brown, thin, flat, unornamented. Byssal gland extending down foot behind byssal groove, without extension dorsal to origin of anterior retractors.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260). Ventral edges of inner mantle lobes not thickened and muscular. Excurrent siphonal opening small, tubuliform siphon capable of moderate extension beyond perimeter of shell, lacking internal diaphragm. Fusion of inner mantle immediately below excurrent siphon forms short, incomplete, horizontal branchial septum between incurrent and excurrent chambers; incurrent and excurrent chambers not completely separated posterior of posterior adductor; posterior ends of gill axes attach to underside of horizontal branchial septum. Short valvular siphonal membrane joins right and left lobes, extending anteriorly a short distance into pedal gape; anterior edge of valvular siphonal membrane smooth, lacking central papilla. Pedo-byssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Lamellae of unequal height; ascending lamellae two-thirds height of descending, resulting in inner and outer demibranchs forming short-armed W-shaped gill when viewed in cross-section. Demibranchs unequal in length; inner demibranch slightly longer anteriorly than outer. Demibranchs hypertrophied, thick, short; ventral edges have well-developed, recessed food grooves; dorsal food grooves present in deep folds just below junction of ascending lamellae and areas of attachment to mantle lobes and visceral mass. Filaments broad, moderately fleshy; ctenidia and filaments white. Distal interlamellar junctions lacking; lamellae joined apically to approximately one-half height of descending and three-quarter height of ascending lamellae; "principal filaments" (see Atkins, 1937: text fig. 18, type B[1b]) lacking.

TABLE 10. Means (mm) and standard errors (in parentheses) of mensural characters in five new species of seep mytilids from the Gulf of Mexico. N = sample size; L = shell length; H = shell height; W = width of shell valves; A = anterior length; and G = ligament length (see Fig. 2).

Species	Site	N	L	H	W	A	G
Bathymodiolus heckerae	West Florida Escarpment	236	90.6 (2.8)	31.2 (0.8)	24.2 (0.6)	10.7 (0.4)	38.0 (1.2)
Bathymodiolus brooksi	Alamiños Canyon	75	115.1 (3.5)	46.1 (1.2)	34.7 (1.0)	8.3 (0.3)	58.8 (1.8)
Bathymodiolus brooksi	West Florida Escarpment	5	100.0 (9.6)	40.4 (4.1)	29.9 (2.7)	5.8 (0.9)	40.7 (6.1)
"Bathymodiolus" childressi	Alamiños Canyon	29	54.7 (1.3)	29.5 (0.8)	24.3 (0.7)	1.5 (0.1)	27.5 (0.8)
"Bathymodiolus" childressi	Bush Hill	91	78.6 (0.9)	40.2 (0.4)	32.2 (0.4)	2.5 (0.1)	36.1 (0.5)
"Bathymodiolus" childressi	Brine Pool NR-1	27	107.7 (3.1)	50.1 (1.2)	40.7 (1.3)	3.6 (0.2)	49.7 (1.5)
Tamu fisheri	Bush Hill	13	37.9 (3.2)	16.7 (1.3)	13.0 (1.1)	2.1 (0.1)	18.0 (1.7)
"Idas" macdonaldi	Garden Banks-386	5	11.8 (0.9)	5.8 (0.5)	6.0 (0.4)	0.6 (0.1)	4.1 (0.4)

Lacking "tubular connections" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes.

Labial Palps: Paired labial palps short, broad, flat, triangular; inner surfaces plicate, outer surfaces smooth; bases of inner and outer pair coincident; both pairs in normal anterior position, without proboscid-like extensions. Outer pair of palps larger, up to twice the size of inner pair. Mouth situated normally, at the basal junction of inner and outer palps. Extreme anterior portions of gill placed between inner and outer palps coincident with plicate palp surfaces.

Digestive System: Alimentary system well developed for the group; stomach and direct intestine located on body mid-line. Intestine leaves posterior end of stomach and passes posteriorly down midline ventral to ventricle; short recurrent loop to the right begins immediately below posterior end of ventricle; recurrent intestine passes anteriorly on right side. Rectum turns to the mid-line and enters extreme antero-ventral portion of ventricle anterior to the auricular openings.

Remarks: Some characters that separate T. fisheri and other deep-sea mytilids have been previously discussed in the remarks section for the genus description. The small adult size of T. fisheri and the bifurcation of both posterior and anterior portions of the posterior byssal retractors further differentiate this species from "Bathymodiolus" childressi, B. brooksi, and B. heckerae. Conversely, T. fisheri is much larger than the largest specimens of "Idas" macdonaldi (Table 10). Tamu fisheri has a short recurrent intestinal loop similar to "Bathymodiolus" childressi, but in contrast to the straight intestine present in most species of Bathymodiolus.

Tamu fisheri is rare at both Bush Hill and the site near Garden Banks, in contrast to the much more abundant "Bathymodiolus" childressi. Fauna associated with T. fisheri at Bush Hill are discussed in the remarks section for "Bathymodiolus" childressi. The site near Garden Banks is "extremely oily," but lacking in "major community development (stunted tube worms, isolated bivalves)" (I. R. MacDonald, pers. comm.). The new mussel "Idas" macdonaldi is also found at the site near Garden Banks. Tamu fisheri has an association with sulfur-oxidizing symbiotic bacteria on the surface of the gills (C. R. Fisher, pers. comm.). These bacteria express high activities of the enzyme ribulose biphosphate carboxylase/oxygenase. Two specimens of T. fisheri, including the holotype, contained an unidentified commensal polynoid polychaete within the mantle cavity.

Round, white-rimmed, egg capsule scars identical to those commonly deposited by the snail Bathynerita naticoidea on the shell of "Bathymodiolus" childressi (C. R. Fisher, pers. comm.) were found on the postero-dorsal portion of one shell of T. fisheri from Bush Hill. Gustafson & Lutz (1994: fig. 4.3) illustrate the prodissoconch II of T. fisheri (designated "Seep Mytilid III") with a length of approximately 460 μm, and a surface sculpture of

concentric growth lines alone, which is consistent with characteristics indicative of planktotrophic development.

Etymology: The specific name honors Dr. Charles R. Fisher of The Pennsylvania State University, who has provided us with many of the specimens examined in this report and who has done a great deal of the seminal work on the physiology of these symbiotic mussel taxa. The working designation "Seep Mytilid III" was given to this species from the Louisiana Continental Slope cold-water seeps.

Range: Known only from hydrocarbon seeps at Bush Hill in Green Canyon and from a site within Garden Banks petroleum lease block 386 on the Louisiana Continental Slope in the northern Gulf of Mexico in depths from 546 to 650 m (Table 6).

Subfamily Modiolinae
Type genus: Modiolus Lamarck, 1799

Idas Jeffreys, 1876
Idas Jeffreys, 1876: 428 (type species, by monotype, Idas argenteus Jeffreys, 1876, non Idas Mulsant, 1876).
Idasola Iredale, 1915: 340 (unnecessary replacement name for Idas Jeffreys, 1876: 428, non Mulsant, 1876 [Warén, 1991: 116]).
(For further synonymy, see Dell 1987:25).

Revised Diagnosis: Shell small (8 to 22 mm maximum length), modioliform, rhomboidal to oblong, smooth, umbones subterminal; periostracum light-yellow to brownish-yellow; prodissoconch reddish-brown; ligament extending along most of postero-dorsal margin; fine hinge denticulations present anterior and posterior to ligament. Posterior retractors undivided; posterior retractor scars continuous with posterior adductor scar. Separate pedal retractors present. All of the species assigned to this genus occur in deep-water and are commonly collected in association with sunken organic matter, including wood, whale bone, and fish skeletons.

Remarks: Warén (1991: 116) presented convincing evidence, based on the requirements of the ICZN, for the maintenance of Jeffrey's name Idas in contrast to the replacement name Idasola of Iredale (1915). Warén (1991) also synonymized Idas and Adipicola, stating that he could not see why Dell (1987) distinguished between these two genera. Warén (1991: 116) presumed that Dell based his generic distinction on the presence or absence of "crenulated areas along the hinge line," which Warén (1991) considered to be a juvenile character, lost with growth in adult Adipicola but retained in adult Idas due to the latter's smaller size at maturity. In support of Warén's (1991) position, hinge denticulations were also present in all juvenile specimens of the species described in this report, being retained only in adult "Idas" macdonaldi, the smallest species examined. However, Dell (1987) also pointed out that in Idas the pedal retractor is associated with the posterior byssal retractor, whereas there is no sign of a separate pedal retractor in Adipicola.

Other anatomical differences have not been studied in the type specimens of these genera (type specimens consist of shells only); however, analyses for this report of the anatomy in putative I. argenteus (the type species of the genus), I. washingtonia, and Adipicola sp. (see Materials and Methods section for source material) revealed further differences between these two genera. Specimens of I. argenteus and I. washingtonia have outer demibranchs that are only one-half the length of the inner demibranchs, whereas specimens of Adipicola sp. have outer demibranchs equal in size to the inner demibranchs. In addition, Adipicola sp. have thick fleshy gills, whereas specimens of I. argenteus and I. washingtonia have thin, filamentous gills and "Idas" macdonaldi have moderately thickened but still essentially filamentous gills. These anatomical observations argue against placing Idas and Adipicola in synonymy.

Idas differs from Bathymodiolus, Benthomodiolus, and Tamu in having undivided posterior byssal retractors (Dell, 1987), medial versus lateral placement of the pedal retractors (relative to the position of the posterior byssal retractors), and hinge denticulations anterior and posterior of the ligament in adult specimens. Idas further differs from Bathymodiolus and Tamu in its small adult size and in having thin filamentous ctenidia, the outer demibranchs of which are only one-half the length of the inner demibranchs (as exemplified by I. argenteus and I. washingtonia). Idas further differs from Bathymodiolus in lacking palp suspensors (as exemplified by I. argenteus, I. washingtonia, and "Idas" macdonaldi).

Idas differs from Dacrydium in having sepa-

rate posterior pedal retractors (in I. argenteus, I. washingtonia, and "Idas" macdonaldi), umbones located some distance from the anterior end, and in lacking palp suspensors.

"Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek, new species
Figures 11–13, 24–27

Types: Holotype ANSP A18850 from JOHNSON SEA-LINK-I Dive 3149 at 27°50′N; 92°10′W, in 650 m in the Gulf of Mexico on the Louisiana Continental Slope near Garden Banks block 386 offshore petroleum leasing area. Two paratypes (ANSP 400783, 400784) and 6 additional specimens (Rutgers) are from the same dive and locality.

Shell Morphology: Shell small, less than 15 mm long, modioliform, sturdy and stout, translucent, essentially equivalve. Anterior margin sharply rounded; posterior margin broadly rounded; ventral margin straight but with concave indentation in region of byssal gape, indentation more pronounced in longest specimens; dorsal margin broadly convex, more or less straight over the span of the ligament (Figs. 11, 12, 24). Umbones often eroded; prosogyrate; subterminal, positioned within anterior one-twentieth. Raised, broadly rounded external ridge extends from umbonal region to posterior-ventral margin.

External sculpture lacking, surface smooth except for concentric growth lines. Shell dull-white beneath straw-yellow periostracum. Antero-dorsal portion of periostracum variably eroded, periostracum sometimes lacking on dorsal three-quarters. Interior off-white, predominately nacreous.

Ligament opisthodetic, parivincular, extending posteriorly from the umbones to occupy from 31% to 37% of dorsal margin. Adult hinge thickened below and anterior to umbones, with 12 to 28 denticles immediately posterior to ligament and 9 to 19 denticles immediately below umbones on a thickened boss (Figs. 25–27).

Muscle Scars: Muscle scars and pallial line indistinct. Anterior adductor scar round, somewhat truncated posteriorly, positioned near antero-ventral margin, below umbo. Posterior adductor scar round, contiguous with posterior byssal-pedal retractor scar dorsally. Anterior byssal retractor scar located within upper extremity of umbonal cavity directly beneath umbo. Elongated posterior byssal-pedal retractor scar not divided; parallel to antero-posterior axis of shell; posterior end of muscle scar bordering posterior adductor scar antero-dorsally, anterior end terminating below posterior hinge denticles (Fig. 12). Ventral pallial line straight without dorsal concavity, extending from postero-ventral aspect of anterior adductor scar to postero-ventral edge of posterior adductor.

Measurements (in mm):

length	height	width	anterior length	Dive	
10.6	4.9	5.1	—	JSL 3149	Holotype ANSP
9.9	4.8	4.5	—	JSL 3149	Paratype ANSP
11.2	5.3	4.8	—	JSL 3149	Paratype ANSP
9.9	5.0	5.3	0.7	JSL 3149	Specimen Rutgers
11.2	5.4	5.6	0.5	JSL 3149	Specimen MCZ
13.4	5.8	6.2	0.8	JSL 3149	Specimen Rutgers
6.6	3.7	3.3	—	JSL 3149	Specimen Rutgers
8.4	4.0	3.6	—	JSL 3149	Specimen USNM
8.2	4.3	3.8	—	JSL 3149	Specimen HMNS

Internal Morphology

Musculature: Main features of musculature evident from previous description of muscle scars and Figure 13. Posterior byssal retractors continuous, not divided into posterior and anterior portions; attaching to shell from antero-dorsal edge of posterior adductor to just posterior of and below ligament's posterior end. Separate pedal retractors located medially, between posterior byssal retractors, partially obscured when viewed from a lateral aspect; becoming integrated with posterior byssal retractors at point of shell attachment. Anterior retractors arising from dorso-lateral aspects of foot mass and extending anteriorly to attach to shell in antero-dorsal extremity of umbonal cavity. Labial palp suspensors not evident. Posterior adductor rounded, anterior adductor slightly oblong.

Foot and Byssus: Foot thick; shape in preserved specimens variable, dependent on degree of contraction. Byssal strands white to light-brown, thin, flat, unornamented. Purple tinted byssal gland extending down foot be-

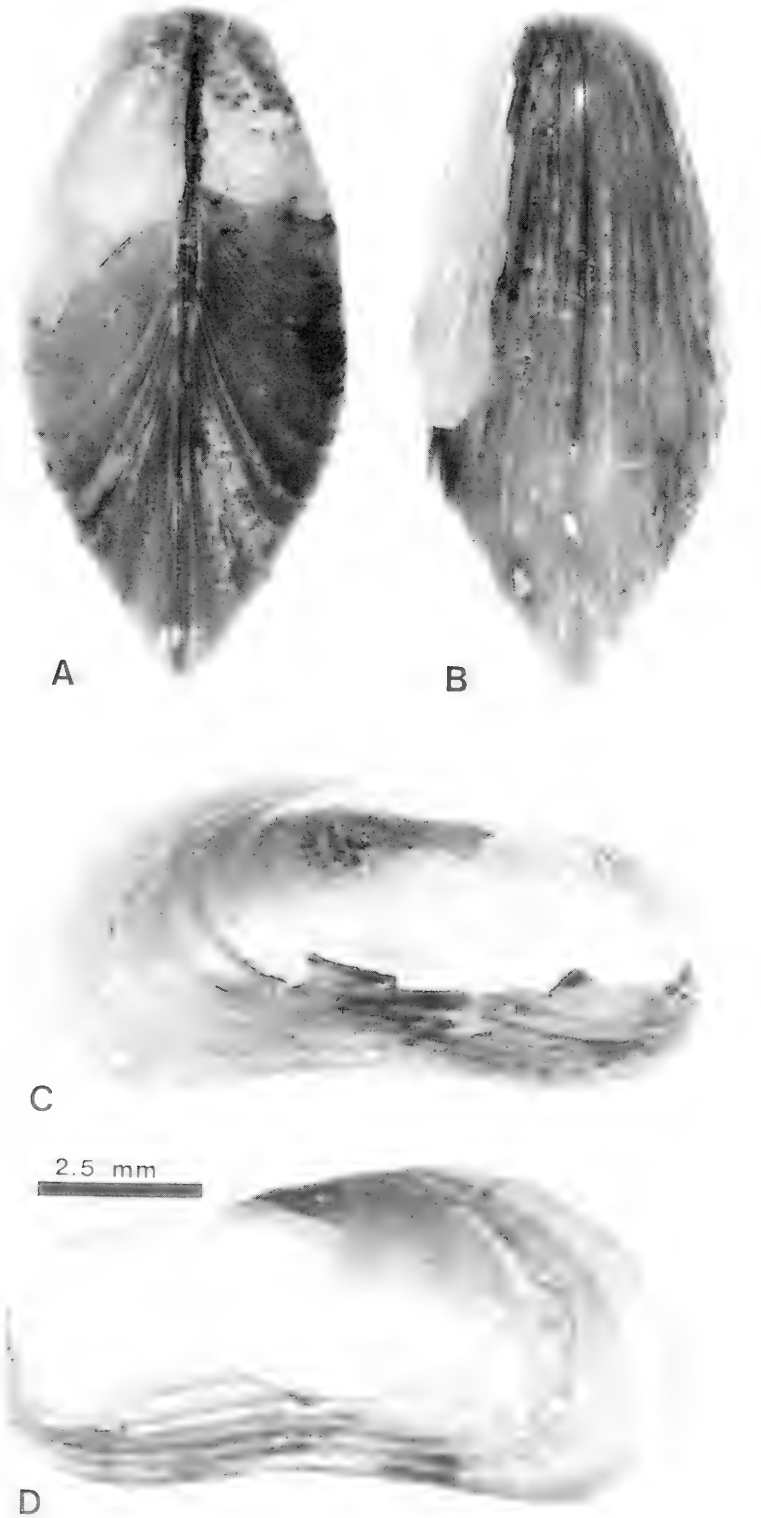

FIG. 24. "Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek. Holotype, ANSP A18849. A, dorsal view; B, ventral view; C, lateral view of right valve; D, lateral view of left valve.

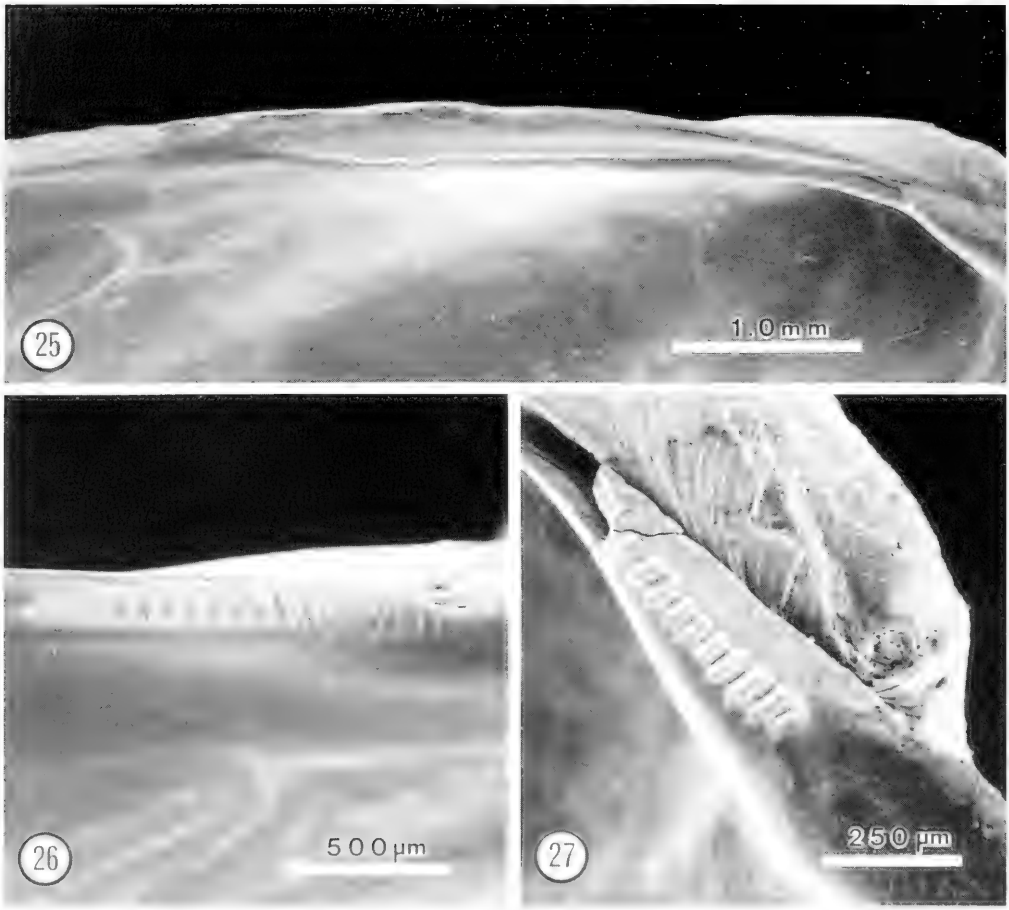

FIG. 25. "Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek. Juvenile hinge line of specimen 10.4 mm in length.
FIG. 26. "Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek. Hinge denticles located immediately posterior of the ligament in juvenile specimen 10.4 mm in length.
FIG. 27. "Idas" macdonaldi Gustafson, Turner, Lutz & Vrijenhoek. Hinge denticles located immediately below the umbo in juvenile specimen 10.4 mm in length.

hind byssal groove; extending laterally and slightly dorsal to origin of anterior retractors.

Mantle and Mantle Cavity: Connections between edge of ascending lamellae and surface of mantle lobes and visceral mass weak or lacking, resulting in incomplete separation of incurrent and excurrent chambers. Lacking muscular longitudinal ridges for attachment of ascending lamellae to mantle lobes and visceral mass (see Kenk & Wilson, 1985: 260). Ventral edges of inner mantle lobes not thickened and muscular. Excurrent siphon little more than a simple slit with short extensible collar, not capable of extension beyond perimeter of shell. Unusual internal diaphragm occludes ventral two-thirds of excurrent siphonal opening, attached dorsally to slender muscular bridge that connects side walls of internal opening approximately two-thirds of distance from the siphon floor. Lacking horizontal branchial septum; incurrent and excurrent chambers not separated posterior of posterior adductor. Posterior end of gill axes attach to inner wall of fused inner mantle lobes just ventral to exhalent siphon. Short valvular siphonal membrane joins right and left mantle lobes, extending anteriorly a short distance into pedal gape; anterior edge of valvular siphonal membrane smooth, lacking central papilla.

Pedo-byssal gape extensive; incurrent aperture extending from anterior end of valvular siphonal membrane to posterior edge of anterior adductor.

Ctenidia: Lamellae of unequal height; ascending lamellae two-thirds to three-quarters height of descending, resulting in inner and outer demibranchs forming short-armed W-shaped gill. Demibranchs unequal; outer demibranchs shorter anteriorly, approximately 90% to 95% the length of the inner demibranchs. Status of food grooves not determined due to poor preservation. Ctenidia filamentous to moderately thickened; filaments off-white in color. Distal interlamellar junctions lacking; lamellae joined apically to approximately one-third height of gill; "principal filaments" (see Atkins, 1937: text fig. 18, type B [1b]) lacking. Lacking "tubular connections" (see Kenk & Wilson, 1985) between free edges of ascending lamellae and gill axes.

Labial Palps: Paired labial palps short, thickened, broadly triangular; inner surfaces plicate, outer surfaces smooth; bases of inner and outer pair coincident; both pairs in normal anterior position, without proboscid-like extensions. Outer pair of palps larger, up to twice the size of inner pair. Mouth situated normally, at the basal junction of inner and outer palps.

Digestive System: Alimentary system well developed for group; stomach and direct intestine located slightly to left of body mid-line. Intestine leaves posterior end of stomach and passes posteriorly left of mid-line and ventral to ventricle; very short recurrent loop to the right begins before ventricle's mid-point; recurrent intestine then passes beneath ventricle to right side of mid-line and proceeds anteriorly for a short distance. Rectum then returns to mid-line and enters floor of ventricle anterior to auricular openings and about one-fifth of distance from ventricle's anterior.

Remarks: "Idas" macdonaldi possesses a combination of morphological features not seen in any described genus of mytilid mussel. So as to avoid erecting a new mono-specific genus, this species is provisionally placed in Idas. Although most morphological features place "Idas" macdonaldi in the genus Idas, the ctenidial structure is radically different from that seen in other species of this genus. In "Idas" macdonaldi, the outer demibranchs extend to 90% to 95% the length of the inner demibranchs and are moderately thickened. However, examination of adult I. argenteus (type species of Idas) collected at The Tongue of The Ocean (TOTO) in the North Atlantic, revealed filamentous outer demibranchs that are only half the length of the inner demibranchs. Long, thick outer demibranchs have not been previously reported for the genus Idas. Reduced outer demibranchs were also observed in I. washingtonia from the South Cleft hydrothermal vent site on the Juan de Fuca Ridge and in I. washingtonia from whale bone in the Santa Catalina Basin. Type specimens of I. argenteus (type material consists of shell only) and I. washingtonia were not examined for this feature.

Reduced outer demibranchs have also been observed in Dacrydium ockelmanni (Mattson & Warén, 1977) and in paratypes of Benthomodiolus abyssicola (Knudsen, 1970; see Discussion below). Other morphological characters of "Idas" macdonaldi correspond with those of the genus Idas, although specimens of "Idas" macdonaldi are larger than most other known species of this genus.

Several features of "Idas" macdonaldi serve to distinguish this species from other mussels described herein; small size, rhomboidal shape, unseparated posterior byssal retractors, and lack of palp suspensors (although the latter are also lacking in T. fisheri). No previous records of Idas or Adipicola from the Gulf of Mexico exist. Other Atlantic species of Idas and Adipicola include I. argenteus, A. simpsoni (Marshall, 1900) and A. pelagica (Woodward, 1854). Although listed as arising in the Recent geological period in Moore (1969), Idas has been recorded from the Miocene of northern Germany (Janssen, 1972; I. lignicola) and the Cretaceous of Egypt (Abbass, 1962; I. faragi and I. nakadyi).

"Idas" macdonaldi differs from I. coopingeri (Smith, 1885) (reported from deep-water sites off Australia), I. japonica (Habe, 1976) (from off Japan and New Zealand), I. argenteus, and I. washingtonia in having the umbones located in an almost terminal position; the anterior length (A) of the shell occupies the anterior 3% to 7% of the shell in "Idas" macdonaldi, the anterior 16% in I. coopingeri, the anterior 10% to 14% in I. japonica, the anterior 12% to 20% in I. argenteus, and the anterior 23% to 33% in I. washingtonia (Dell, 1987). "Idas" macdonaldi further differs from I. japonica in having a less narrow and elongate shell and in having the pedal and posterior byssal retractors almost at

TABLE 11. Correlation matrix of mensural characters (log_{10} transformed) from five new species of mytilids from the Gulf of Mexico. The PC-1 and PC-2 columns represent loadings of each character on the first two, Varimax rotated, principal component axes. PC-1 plus PC-2 explained 98.97% of the variance in these five characters. L = shell length; H = shell height; W = width of shell valves; A = anterior length; and G = ligament length.

Variable	L	H	W	A	G	PC-1	PC-2
L	1.0000	0.9425	0.9297	0.7170	0.9821	0.8507	0.5136
H		1.0000	0.9842	0.4811	0.9565	0.9670	0.2358
W			1.0000	0.4516	0.9450	0.9750	0.2043
A				1.0000	0.6497	0.2614	0.9649
G					1.0000	0.8845	0.4302

right angles to the plane of the anterior byssal retractors (the posterior and anterior retractors are essentially in the same plane in I. japonica) (Dell, 1987).

"Idas" macdonaldi differs from I. ghisottii (Warén & Carrozza, 1990), from the Mediterranean Sea, in having a more rhomboidal and less elongate shell shape and in maintaining hinge denticulations anterior of the ligament up to adult size. "Idas" macdonaldi differs from I. indica (Smith, 1904), from off the Andaman Islands, in having a smooth shell surface and more anteriorly located umbones. Myrina modiolaeformis Sturany, 1896, was placed in Idas by Dell (1987); however, Warén (1991) questioned whether this species really belongs in Idas. This species has not been found since the original description and its systematic placement is uncertain. Narrow, elongate specimens described as Idas dalli Smith, 1885, from off Culebra Island, West Indies, also apparently do not belong in Idas, according to K. W. Ockelmann, as reported in Dell (1987).

The largest paratype of "Idas" macdonaldi was found attached by byssal threads to the external shell surface of a specimen of the vesicomyid bivalve Vesicomya cordata Boss, 1968. Other specimens were "found interstitially in a mass of pea-sized carbonate rubble" (I. R. MacDonald, pers. comm.). Other fauna at this "extremely oily" site, which "lacked major community development," are T. fisheri, "Bathymodiolus" childressi, stunted tubeworms, and isolated vesicomyid bivalves (I. R. MacDonald, pers. comm.). Two specimens of "Idas" macdonaldi contained a single large unidentified polynoid polychaete within the mantle cavity. These polynoids have been forwarded to Dr. James Blake for taxonomic description.

Etymology: The specific name honors Dr. Ian R. MacDonald of the Geochemical and Environmental Research Group at Texas A & M University, who is responsible for the collection, preservation, and forwarding of this new species. The working designation "Seep Mytilid IV" was given to this species from the Louisiana Continental Slope cold-water seeps.

Range: Known only from the northern Gulf of Mexico on the Louisiana Continental Slope in the vicinity of Garden Banks block 386 offshore petroleum leasing area in 650 m (Table 7).

MORPHOMETRIC ANALYSIS

The new mytilid species fall into three discrete size classes (Table 10). The two Bathymodiolus species and "Bathymodiolus" childressi were generally large, although differences in size existed among samples within two of the species. Tamu fisheri was intermediate in size and "Idas" macdonaldi was small. Principle components analyses proceeded from a correlation matrix (Table 11) of the five characters illustrated in Figure 2. The first principal components axis (PCI) represented covariates of overall size (L, W, H, and G). Length of the shell anterior to the beak (character A) loaded highly on PC2.

The five species of mussels separated reasonably well according to the PCI and PC2 axes (Fig. 29). The two Bathymodiolus species found at the West Florida Escarpment site, although similar in size, can be discriminated because the anterior length (A) of B. heckerae is proportionally larger than in B. brooksi. Similarly, B. brooksi and "Bathymodiolus" childressi at the Alamiños Canyon site can be discriminated because the anterior length (A) of B. brooksi is greater than in "Bathymodiolus" childressi, at a given size. Adult specimens of the three species found along the Louisiana Continental Slope sites can be discriminated easily because of their non-

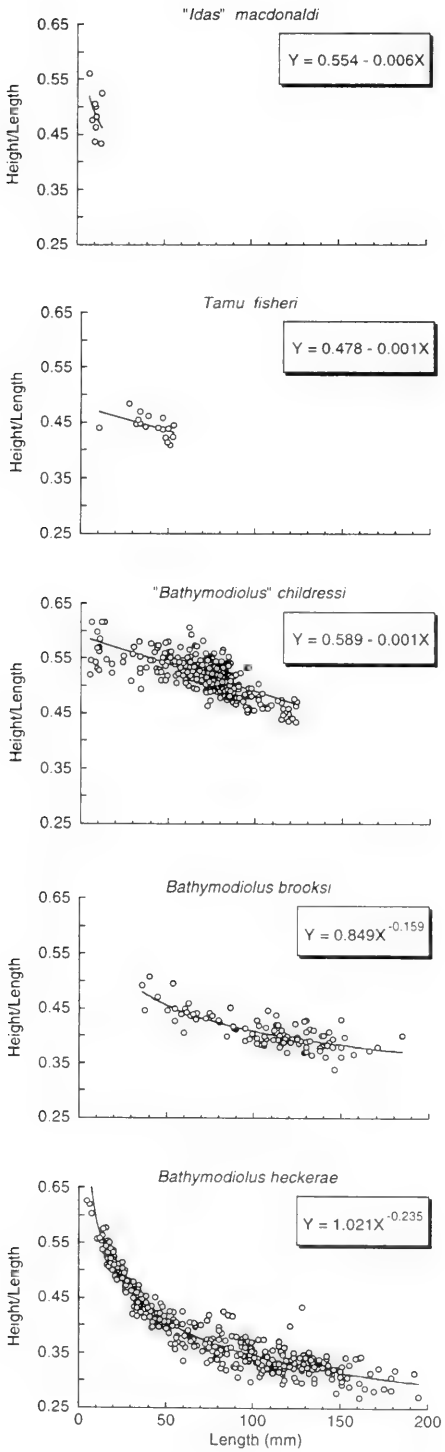

FIG. 28. Plots of the ratio of height to length against length for *"Idas" macdonaldi, Tamu fisheri, "Bathymodiolus" childressi, Bathymodiolus brooksi,* and *Bathymodiolus heckerae.*

specimens of the three species found along the Louisiana Continental Slope sites can be discriminated easily because of their non-overlapping size distributions; "*Bathymodiolus*" *childressi* being largest, *T. fisheri* being intermediate, and "*Idas*" *macdonaldi* being smallest (Table 10).

DISCUSSION

Prior to the discovery of the species described in this study, mytilid mussel genera with representatives in the deep sea (defined as those whose range extends below 600 m) included *Adipicola, Amygdalum, Bathymodiolus, Benthomodiolus, Crenella, Dacrydium, Idas, Modiolus,* and *Musculus* (Clarke, 1962; Knudsen, 1979; Dell, 1987; Kenk & Wilson, 1985). Of these genera, only *Bathymodiolus* was known to contain endosymbiotic bacteria in specialized gill cells (Felbeck et al., 1981; Cavanaugh, 1983; Fiala-Médioni, 1984), although a mussel species retrieved from whale bone on the deep-sea floor and referred to *I. washingtonia* was reported to "host" chemoautotrophic bacteria (Smith et al., 1989), and two mussels from the Middle Valley hydrothermal vent on the northern Juan de Fuca Ridge referred to *I. washingtonia* and *Adipicola* sp. respectively, were reported to have bacteria associated with the microvillar surface of the gill cells (Juniper et al., 1992). With the exception of "*Idas*" *macdonaldi,* the mussel species described in this study, possess fleshy, thickened gills, similar to *B. thermophilus.* Gills of this type are thought to indicate the presence of a bacterial association (Fisher, 1990). Both *B. brooksi* and *B. heckerae* harbor two distinct populations of endosymbiotic gill bacteria (one having the morphology of a type I methanotroph and the other resembling a sulfide oxidizing bacterium); *B. thermophilus* (sulfide-oxidizing endosymbiont) and "*Bathymodiolus*" *childressi* (methanotrophic endosymbiont) have only one symbiont (Childress et al., 1986; Cavanaugh et al., 1987; Fisher et al., 1991; Cavanaugh, 1992; Cavanaugh et al., 1992; C. M. Cavanaugh, pers. comm.). *Tamu fisheri* apparently has an association with bacteria on the surface of the gill (C. R. Fisher, pers. comm.).

Anatomical characters used to separate the new species herein described from each other and from previously described *Bathymodiolus* species are summarized in Table 12. Cosel et al. (1994) were not able to inves-

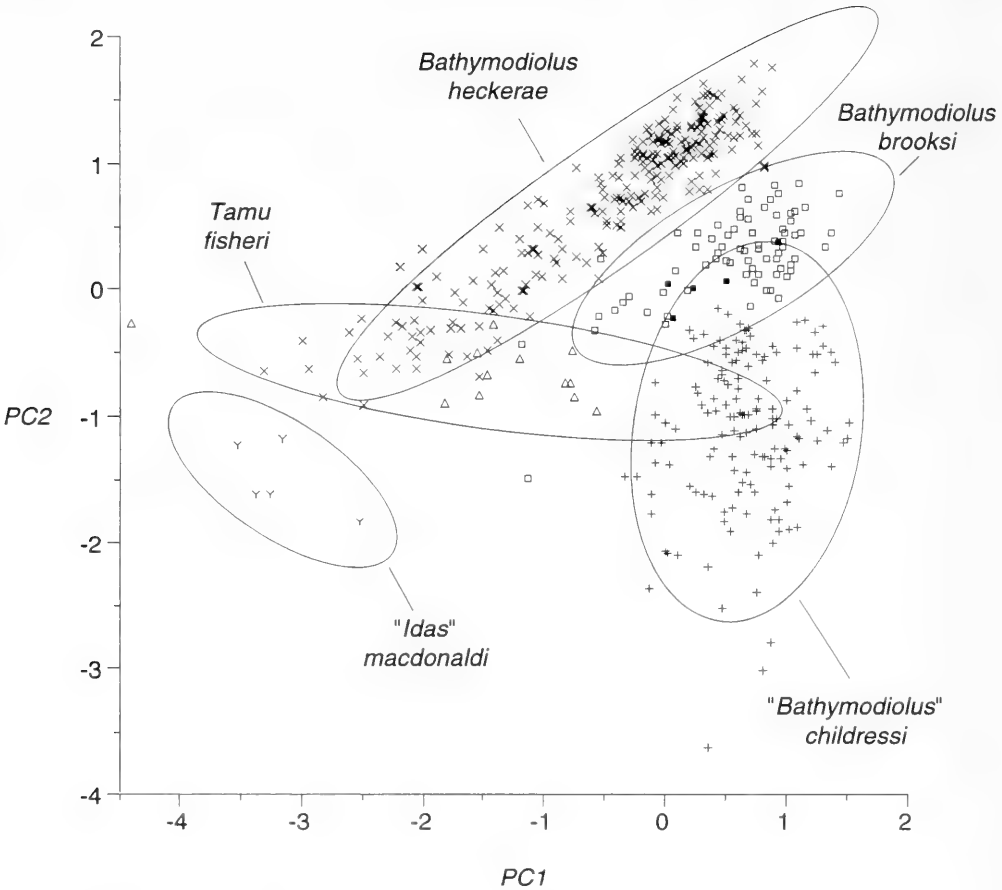

FIG. 29. Scatter plots of the first two principle components (PC1 and PC2) for shell measurements of all available specimens. Ellipses encompass 95% confidence limits for each species. Bathymodiolus heckerae = (x), Bathymodiolus brooksi (Alamiños Canyon = □; West Florida Escarpment = ■), "Bathymodiolus" childressi = (+), Tamu fisheri = (△), and "Idas"macdonaldi = (Y).

Bathymodiolus by Hashimoto & Okutani (1994) and Cosel et al., (1994), as well as the species of Bathymodiolus herein described, lack the extensive ventral mantle fusion and the prominent longitudinal muscular ridge for attachment of the ascending lamellae to the mantle, diagnostic of the type species B. thermophilus (Kenk & Wilson 1985). In most species of Bathymodiolus, the intestine is more or less straight, lacking a recurrent loop, whereas a short or very short recurrent intestinal loop is present in B. aduloides, "Bathymodiolus" childressi, T. fisheri, and "Idas" macdonaldi. The rectum enters the ventricle in "Bathymodiolus" childressi at a point posterior to the level of the auricular ostia, whereas in other Bathymodiolus species the rectum enters the ventricle at a point anterior to the level of the auricular ostia (Table 12). The posterior byssal retractors are separated into separate anterior and posterior portions in Bathymodiolus, but not in "Bathymodiolus" childressi.

The affinities of the new deep-sea mytilid taxa described herein to existing deep-sea mytilids, including B. thermophilus, are not at all certain. The genera Amygdalum, Crenella, and Musculus all have typically filamentous filibranch gills and shell characters which separate them from the other genera under discussion. Modiolus also has typically filamentous gills. Relationships with Benthomodiolus, Dacrydium, and Adipicola are more problematical. Major anatomical characters of these deep-sea genera are summarized in Table 9.

Recently, the validity of two primary diag-

TABLE 12. Comparison of morphological characters among previously described species of Bathymodiolus and new mytilid mussel species described herein. Morphological characters are numbered 1–13 and character states are explained below. Dash (–) indicates data were unavailable.

Species\Character	1	2	3	4	5	6	7	8	9	10	11	12	13
B. thermophilus	1	1	1	1	1	0	0	1	0	0.42–0.57	0.32–0.50	0.05–0.09	184
B. japonicus	0	—	1	—	—	0	0	0	—	0.51–0.63	0.34–0.49	—	106
B. platifrons	0	—	1	—	1	0	0	1	—	0.50–0.68	0.34–0.47	—	115
B. aduloides	0	—	1	—	1	0	1	0	—	0.41–0.52	0.30–0.37	—	96
B. septemdierum	0	—	1	—	1	0	0	0	—	0.43–0.66	0.29–0.46	—	124
B. brevior	0	—	1	1	—	—	—	0	—	0.45–0.61	0.36–0.45	—	143
B. elongatus	0	—	1	1	—	—	—	0	—	0.37–0.56	0.35–0.44	—	156
B. puteoserpentis	0	—	1	1	—	—	2	—	—	0.49–0.62	0.38–0.52	—	119
B. heckerae	0	0	1	1	1	0	0	1	0	0.27–0.63	0.20–0.41	0.06–0.16	192
B. brooksi	0	0	1	1	1	0	0	1	—	0.34–0.51	0.25–0.35	0.03–0.10	185
"B." childressi	0	0	2	0	1	1	1	0	0	0.43–0.62	0.33–0.51	0.00–0.06	124
Tamu fisheri	0	0	1	0	0	0	1	0	0	0.41–0.48	0.28–0.37	0.04–0.13	54
"Idas" macdonaldi	0	0	0	2	0	0	1	0	1	0.43–0.56	0.43–0.54	0.03–0.07	14

Morphological characters and character states
(1) Mid-ventral mantle fusion: 0 = absent; 1 = present.
(2) Muscular longitudinal ridge on mantle surface at attachment point of dorsal edges of ascending lamellae: 0 = absent; 1 = present.
(3) Separation of posterior byssal retractors into anterior and posterior portions: 0 = unseparated, single muscle scar; 1 = widely separated, separate muscle scars; 2 = multiple separation, single muscle scar.
(4) Pedal retractor muscles: 0 = thin, reduced; 1 = prominent; 2 = medial to pedo-byssal retractors.
(5) Palp suspensor muscles: 0 = absent; 1 = present.
(6) Entry point of rectum into ventricle: 0 = anterior to auricular ostia; 1 = posterior to auricular ostia.
(7) Recurrent loop of intestine: 0 = absent; 1 = single loop; 2 = double loop.
(8) Central papilla on anterior rim of valvular siphonal membrane: 0 = absent; 1 = present.
(9) Hinge denticulations: 0 = present in juvenile only; 1 = retained in adult.
(10) Height/length.
(11) Width/length.
(12) Anterior length/length.
(13) Maximum length (mm).

nostic characters that have been used to separate the smaller of these deep-sea mytilid taxa, the presence or absence of "periostracal hairs" and "vertical hinge striations," have come under question. The so-called periostracal hairs considered by some to be a diagnostic character of Idas, Benthomodiolus (Dell, 1987), and some other mytilids may not be of periostracal origin (Bottjer & Carter, 1980), but may merely be byssal gland secretions laid down over the exterior of the normal periostracum by the foot, as suggested by Ockelmann (1983). A scanning electron microscopic examination of "periostracal hairs" on small specimens of several species described herein suggests that the hairs on the surface of these shells are of byssal origin. Likewise, the vertical hinge denticles, thought to be a diagnostic character of Idas and of some Adipicola (Dell, 1987), are a character common to most juvenile modioliform mussels. These hinge denticulations are maintained in adult Idas and in some species of Adipicola as a consequence of their small size (Warén, 1991). In the present study, small specimens of every species examined had hinge denticles both in front of and behind the hinge ligament. With the exception of "Idas" macdonaldi, these denticles were absent in adult specimens.

We have examined paratypes, on loan from the Zoologisk Museum, University of Copenhagen, of Benthomodiolus abyssicola (Knudsen, 1970), the type species of Benthomodiolus. Although the intestine has a short recurrent loop and the posterior retractors are divided in this small mussel (17.2 mm maximum length) from 3270 to 3670 m in the Gulf of Panama, there are no hinge denticulations even in the smallest specimens, the gills are thin and filamentous as in typical filter-feeders, and the outer demibranchs are incomplete, extending forward only to the middle of the inner demibranchs. These characters lead us to reject a close relationship between Benthomodiolus and the five new species described herein. Kenk & Wilson (1985) came to the same conclusion concerning a relationship between Benthomodiolus and Bathymodiolus.

The genus Dacrydium consists of small (about 5 mm maximum size) "nest-building" neotenous deep-sea mussels that lack separate pedal retractors, but have reduced outer demibranchs, unseparated posterior retractors, a long recurrent intestinal loop, labial palp suspensors, and provincular and juvenile hinge teeth that persist throughout the animal's life (Mattson & Warén, 1977; Ockelmann, 1983). This combination of characters, although similar in some respects, distinguishes Dacrydium from the five new species described herein.

Several species of small deep-sea mussels referred to the genus Modiolus (Verco, 1908; Pelseneer, 1911; Prashad, 1932) may ultimately be placed in one or the other of the above discussed genera. Recently, Modiolus willapaensis Squires & Goedert, 1991, was described from Late Eocene deposits representing ancient subduction-related methane seeps in southwestern Washington, USA (Goedert & Squires, 1990; Squires & Goedert, 1991). This species apparently did not obtain lengths greater than 27 mm. Although superficially resembling seep mussels described in this study, no internal features of the shell (hinge denticulations or muscle scars) were observed in the articulated fossils and therefore relationship of M. willapaensis with extant seep mussels cannot be determined. Similarly, fossil M. exbrocchii exbrocchii Sacco have been described from Miocene (Tortonian) deposits in Italy, in association with other mollusks, such as Lucina, characteristic of seep environments (Moroni, 1966).

Although some anatomical features of B. heckerae and B. brooksi (extensive ventral pedo-byssal gape and lack of muscular attachment ridge for ascending lamellae), "Bathymodiolus" childressi (multiple posterior byssal retractors, short recurrent loop of intestine and position of rectum relative to the ventricle) and "Idas" macdonaldi (complete outer demibranchs and relatively large size) differ from that seen in the respective type species of these genera, we hesitate in erecting additional deep-sea mytilid genera for these species. On the other hand, the level of genetic divergence (Craddock et al., 1995) and the unique combination of anatomical features in T. fisheri (bifurcate posterior and anterior portions of the posterior byssal retractors, short recurrent loop of intestine, and lack of palp suspensors) argue for generic level differentiation of this species.

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APPENDIX 1

The ID#, location and museum catalog numbers of the mussel holotypes and paratypes. The holotypes and a series of paratypes are deposited in the Academy of Natural Sciences of Philadelphia (ANSP). Additional paratypes are deposited in the following institutions: United States National Museum of Natural History, Washington, D.C. (USNM): Museum of Comparative Zoology, Harvard University (MCZ); Houston Museum of Natural Science, Houston, Texas (HMNS), Museum National d'Histoire Naturelle, Paris (MNHN), and Rutgers Univerisity (RU). MNHN and RU do not assign catalog numbers to their collections.

Bathymodiolus heckerae

ID #	Location	Cat. #
A 1343	Holotype ANSP	A18846
A 1754-3	Paratype USNM	880270
A 1755-13	Paratype MCZ	316977
A 2196-8	Paratype HMNS	45307
A 2196	Paratype MNHN	
A 2196-1	Paratype RU	
A 2196-40	Paratype MNHN	
A 2197-33	Paratype HMNS	45306
A 2542-40	Paratype ANSP	400773
A 2542	Paratype ANSP	400771
A 2196	Paratype ANSP	40072
A 2196-17	Paratype HMNS	45299
A 2196-56	Paratype RU	
A 2542-13	Paratype MNHN	

Bathymodiolus booksi

ID #	Location	Cat. #
A 2211	Holotype ANSP	A18847
A 2211-13	Paratype MCZ	319676
A 2211-7	Paratype USNM	88-268
A 2211-22	Paratype MNHN	
A 2211	Paratype ANSP	400775
A 2209-11	Paratype MCZ	316973
A 2209-20	Paratype MCZ	316975
A 2209-14	Paratype MCZ	316974
A 2209	Paratype ANSP	400774
A 2209-2	Paratype RU	
A 2211-6	Paratype MNHN	
A 2209-9	Paratype RU	
A 2209-18	Paratype HMNS	45300
A 2211-36	Paratype RU	
A 2196	Paratype ANSP	400777
A 2542-7	Paratype USNM	880269
A 2542-60	Paratype HMNS	84302
A 2542	Paratype ANSP	40076

"Bathymodiolus" childressi

ID #	Location	Cat. #
JSL 3129	Holotype ANSP	A18848
JSL 3129	Paratype MNHN	
JSL 3129	Paratype ANSP	400778
JSL 3129-61	Paratype RU	
JSL 3137-39	Paratype HMNS	45303
JSL 3145-41	Paratype USNM	880272
JSL 3145-23	Paratype MCZ	316978
A 2211-39	Paratype HMNS	45308
A 2211-44	Paratype RU	
A 2211	Paratype ANSP	400779
JSL 3145-37	Paratype USNM	880271

JSL 3137-27	Paratype RU	
JSL 3129-112	Paratype HMNS	45305
JSL 3137	Paratype MNHN	
JSL 3137	Paratype MNHN	

Tamu fisheri

ID #	Location	Cat. #
JSL 3108	Holotype ANSP	A18849
JSL 3108-1	Paratype MCZ	
JSL 3108-3	Paratype USNM	880273
JSL 3108	Paratype ANSP	400780
JSL 3108	Paratype ANSP	400781
JSL 3108-11	Paratype USNM	880274
JSL 3149-1.3	Paratype HMNS	316979
JSL 3149-3.3	Paratype RU	
JSL 3149-4.3	Paratype MCZ	45301
JSL 3149	Paratype ANSP	400782

"Idas" macdonaldi

ID #	Location	Cat. #
JSL 3149	Holotype ANSP	A18850
JSL 3149	Paratype ANSP	400784
JSL 3149-11.6	Paratype ANSP	400783
JSL 3149-12.2	Paratype RU	
JSL 3149-12.3	Paratype MCZ	316980
JSL 3149-12.4	Paratype RU	
JSL 3149	Paratype RU	
JSL 3149-11.2	Paratype USNM	880275
JSL 3149-11.6	Paratype HMNS	45304

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PROTOBRANCHIA (MOLLUSCA: BIVALVIA) CHILENOS RECIENTES Y ALGUNOS FÓSILES

María Villarroel[1] José Stuardo[2]

RESUMEN

Se estudian 15 especies de protobranquios recientes de Chile continental, 5 especies antárticas y 7 fósiles. De un total de 35 especies recientes citadas para la costa chilena y antártica, se aceptan sólo las 27 siguientes: *Nucula austrobenthalis, N.* (*N.*) *falklandica, N.* (*N.*) *fernandensis, N.* (*N.*) *interflucta, N.* (*N.*) *pisum, Ennucula eltanini, E. grayi, E. puelcha, Nuculana* (*Saccella*) *cuneata, N.* (*Borissia*) *inaequisculpta, Propeleda longicaudata, Tindariopsis sulculata, Silicula patagonica, S. rouchi, Yoldia* (*Aequiyoldia*) *eightsi, Yoldiella chilenica, Y. ecaudata, Y. granula, Y. indolens, Malletia chilensis, M. magellanica, M. patagonica, M. inaequalis, Malletiella sorror, Tindaria virens, T. salaria, y Acharax macrodactyla.* Se agrega a esta lista la especie nueva: ***Nucula (N.) pseudoexigua,*** encontrada en el Estrecho de Magallanes. Se amplía la distribución de la especie antártica *Propeleda longicaudata* al Estrecho de Magallanes.

Se da especial énfasis a la descripción de las partes blandas, junto a los caracteres de la concha utilizados tradicionalmente en el estudio de los moluscos.

Se estudió las siguientes características y estructuras morfológicas externas e internas: tamaño, forma y ornamentación de la concha; charnela, dientes charnelares y ligamento; manto y musculatura paleal; sifones, tentáculo sifonal, glándula hipobranquial y ctenidios; pie, musculatura pedal, visceral y aductores; boca, palpos labiales, tentáculo del palpo y lamelas del palpo; esófago, estómago, tiflosoles, divertículos digestivos, intestino y recto; corazón, glándula pericárdica; riñones; ganglios supraesofágicos, cerebro-pleurales, pedales y viscerales; y gónadas. Se considera, además, la información disponible sobre la distribución y ecología de las especies chilenas. En un estudio comparativo general, se corrobora el valor de las partes blandas en la diferenciación de categorías superiores dentro de la clase, pero con el limitado conocimiento que se tiene de ellas y debido al escaso número de especies estudiadas, su valor a nivel específico es todavía impreciso. Por otra parte, la complejidad observada en algunas de las estructuras estudiadas permitió sugerir modificaciones en la interpretación filogenética de ellas, especialmente en el caso de la estructura del estómago, la posición del corazón y la estructura de los sifones.

Se consideran válidas las familias Nuculidae, Nuculanidae, Sareptidae, Tindariidae, Siliculidae, Malletiidae, y Acharacidae.

Se trata a las especies fósiles con un criterio taxonómico similar al de las especies recientes y se compila una lista de alrededor de 54, efectuando y/o sugiriendo los cambios genéricos apropiados, cuando las descripciones e ilustraciones lo permitían. Como resultado del material colectado en distintas zonas fosilíferas se describen en detalle las especies siguientes: *Ennucula araucana, E. ¿nogalis?, E. lebuensis, E. valdiviana, Propeleda medinae, Tindariopsis elegans,* y *Malletia volckmanni.* Por último se discute la distribución geográfica y batimétrica de las especies recientes estudiadas.

EXPANDED ENGLISH ABSTRACT

The classification of the subclass Protobranchia followed here considers the families Nuculidae, Nuculanidae, Siliculidae, Sareptidae, Malletiidae, and Tindariidae in the order Nuculoida, and the family Acharacidae in the order Solemyoida. We also follow the separatation of Malletiidae from Nuculanidae, further justifying it on anatomical grounds.

Fifteen protobranch species of Recent distribution in continental Chile, five Antarctic, and seven fossil species were studied. Out of a total of 35 species cited for the coast of Chile and Graham Land in Antarctica, only the following 27 are here accepted as valid: *Nucula austroben-*

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thalis Dell, 1990; *Nucula* (*Nucula*) *falklandica* Preston, 1912; *Nucula* (*Nucula*) *fernandensis* Villarroel, 1971; *Nucula* (*Nucula*) *interflucta* Marincovich, 1973; *Nucula* (*Nucula*) *pisum* Sowerby I, 1833; *Ennucula eltanini* Dell, 1990; *Ennucula grayi* (d'Orbigny, 1846); *Ennucula puelcha* (d'Orbigny, 1842); *Nuculana* (*Saccella*) *cuneata* (Sowerby I, 1833); *Nuculana* (*Borissia*) *inaequisculpta* (Lamy, 1906); *Propeleda longicaudata* Thiele, 1912; *Tindariopsis sulculata* (Gould, 1852); *Silicula patagonica* Dall, 1908; *Silicula rouchi* Lamy, 1911; *Yoldia* (*Aequiyoldia*) *eightsi* (Jay, 1839); *Yoldiella chilenica* (Dall, 1908); *Yoldiella ecaudata* (Pelseneer, 1903); *Yoldiella granula* (Dall, 1908); *Yoldiella indolens* (Dall, 1908); *Malletia chilensis* des Moulins, 1832; *Malletia magellanica* Smith, 1875; *Malletia patagonica* Mabille & Rochebrune, 1889; *Malletia inaequalis* Dall, 1908; *Malletiella sorror* Soot Ryen, 1959; *Tindaria virens* (Dall, 1890); *Tindaria salaria* Dall, 1908; and *Acharax macrodactyla* (Mabille & Rochebrune, 1889). ***Nucula*** (***N.***) ***pseudoexigua*** Villarroel & Stuardo, a new species from the Strait of Magellan is described. The Antarctic species *Propeleda longicaudata* Thiele, 1912, is reported for the first time from the Strait of Magellan.

A diagnosis for every taxonomic category and a detailed description for every species are given, including the shell features traditionally utilized, as well as the soft parts. Most features having so far been studied only on a few species of the subclass, allow a comparative analysis with the Chilean representatives, summarized as follows.

(1) Size varies within the different families. Living nuculids are in general smaller than nuculanaceans and solemyaceans. The largest size found in the Chilean Nuculidae reaches 20.6 mm length in *Ennucula grayi,* whereas among Nuculanidae and Malletiidae, a maximum measured length of 51.0 mm was found in *Malletia chilensis.* A Chilean fossil of this genus measured 60 mm.

(2) The studied species fall within the three known basic forms: nuculoid, nuculanoid, and solemyoid (Fig. 61).

(3) No comprehensive study of hinge tendencies within each family has been attempted; such study would possibly permit to examine affinities and divergencies at lower taxonomic ranks.

(4) The study of the ligament in specific taxa should be used to test the validity of prevailing models and interpretations. So far, the study of the ligament in Nuculidae and Nuculanidae has followed Owen's (1959) interpretation of an external or lamellar layer connected with the mantle margins, and another internal, fibrous layer connected to the isthmus of the mantle. A resilifer or chondrophore interrupts the two teeth series, and is directed anteriorly in *Nucula* and *Ennucula* (Fig. 3A, cdr), is more or less straight in *Yoldia* (Fig. 129), and is directed posteriorly in *Nuculana* (Fig. 3). Previously, Stempell (1898a) demonstrated that the ligament in *Malletia* can be divided in anterior, central and posterior parts, the central part corresponding to the resilium (inner layer of the ligament), and the anterior and posterior parts with an external origin. Thus, such similar differentiation in Nuculidae, Nuculanidae and Malletiidae, suggested that the resilium of internal position in *Nucula* and *Nuculana,* had migrated to become external in Malletiidae, without dissapearing. An intermediate stage in its position is observed in *Tindariopsis,* as was shown by Stempell (1898a).

Relevance is given to the novel and most stimulating interpretation on the evolution of the ligament in the bivalves advanced by Waller (1990). He questions the traditional model of an amphidetic primary ligament of three layers, and proposes a protobranch stem group from which two major types of ligament for the bivalves evolved.

(5) Variation in number and size of hinge teeth does not allow to use them as taxonomic features of generic or suprageneric value, but size and form may sometimes offer specific taxonomic value, as noted by Knudsen (1970) and Villarroel (1971).

(6) The palps are very similar in the Nuculacea and Nuculanacea, but their homology with the Solemyidae is not well known. The palps in *Solemya* are not interpreted as doubled palps appendixes of other protobranchs; the palps sheets would be reduced to simple ridges (Fig. 11) in the edge of the furrow that joins the mouth with the appendixes (Figs. 15–17)(Ridewood, 1903; Morse, 1913; Yonge, 1939; Reid, 1980).

The appendix or palp tentacle on the external sheet of every palp considered by Drew (1901) be equivalent of a pair of hypertrophiated fold (Figs. 10, 12, other figs., tp) differ in position according to family (Fig. 61). In the Nuculanacea, the palp appendix is located on the terminal portion of the external palp sheet (e.g., Fig. 5, *Silicula rouchi;* Fig. 77, *Nuculana* (*S.*) *cuneata;* Fig. 90, *Nuculana* (*B.*) *inaequisculpta*). In the Nuculidae, the palp appendix is displaced to the end, because behind it there is an additional, non-extensible structure termed the "palp caecum," which represents a pair of hypertrophiated folds (Stasek, 1965).

The proximal end of the palp appendix is linked with the surface of the palp external sheets and the palp caecum (Fig. 10, bp); its musculature is fused with the posterior foot retractor. Stasek's (1961) observation of this feature in *Acila* was corroborated, without exception, in every species studied. Nevertheless, in almost all the cases, the appendix was found in different degrees of contraction, preventing recognition of specific differences (Figs. 4 and 62, 74 and 76, tp).

(7) In a general comparative analysis, the value of the soft parts in the differentiation of the higher categories within the subclass, is corroborated; however, due to the limited available knowledge of many internal structures and the few studied species, their taxonomic role at the specific level cannot be always ascertained. On the other hand, the complexity observed in some of the internal morphological parts permitted us to set forth complementary interpretations on their possible phylogenetic value, particularly in the case of the stomach, the position of the heart, and the configuration of the various types of siphons.

Although stomach morphology has been described for species of *Nucula, Nuculana* and *Malletia,* a comparison became necessary, resulting in the identification of a new caecum and changes in the interpretation of the features observed by previous authors. In fact, its study in the available species allowed the conclusion that there is not one basic type or "Gastroproteia," as proposed by Purchon (1956, 1959), but three. These are:

Type Ia. Common to the genera *Nucula* and *Ennucula* and characterized by several (three or four) ciliary sorting areas and a wide extension of the typhlosole (Figs. 18–32, 60).

Type Ib. Common to the genera of Nuculanidae and Malletiidae and characterized by three ciliary sorting areas and a small extension of the minor typhlosole (Figs. 33–56, 60).

Type Ic. Common to the genera of Solemyidae and Nucinellidae and characterized by the absence of distinct sorting areas and lack of typhlosoles.

It is not difficult to differentiate the internal and external features recognized in the stomach of Nuculacea and Nuculanacea. The dorsal hood is smaller in Nuculanacea than in Nuculacea, and the three ducts that communicate the stomach with the digestive diverticula are also different in these two superfamilies (Figs. 18–56, 60).

Similar differences were found in the ciliary sorting areas and the number of folds. For instance, the three additional sorting areas as^1, as^2 and as^3 described by Purchon (1956), although not present in all species, can also be used in interspecific differentiation. Thus, the first one was found only in *Nucula* (*Nucula*) *pisum* (Fig. 21) and *Ennucula puelcha* (Figs. 29–31), but not in the other studied species of these genera; the second sorting area was found presenting different sizes in *Nucula* (*Nucula*) *pisum, Nucula* (*Nucula*) *fernandensis,* and *Ennucula puelcha,* being largest in the latter. The third above named sorting area was not observed in the studied Nuculacea, and none were found in the studied Nuculanacea. Such differences do not back Purchon's (1987b) generalization that one description can embody all of them (Fig. 60).

Undoubtedly, the complexity of the gastric shield with its biggest modification in *Propeleda* and *Malletia* is larger in Nuculanacea than in Nuculidae and Solemyidae, but presently it is difficult to establish generic or specific differences. On the other hand, folding of the typhlosoles entering the style-sac has shown specific constancy in the studied species of *Nucula* and *Ennucula.* Development of the typhlosoles in Nuculanacea shows a different pattern.

(8) Attention has also been given to the number of loops observed in the gastric and medium intestine with a pattern of coiling, which according to Heath (1937) is specific, with minimal intraspecific variation as observed in *Nucula* (*Nucula*) *pisum* and *Nucula* (*Nucula*) *pseudoexigua* (Figs. 63–67). It begins on the side of the stomach and continues anteriorly in some species almost reaching the mouth. It turns then dorsally to the esophagus and continues posteriorly above the stomach, or continues ventrally to form the coils prior to its final turn backwards.

Heath (1937) was the first to demonstrate that in Nuculacea the intestine does not extend forwards as much as in Nuculanacea. He associated the species of *Nucula* and *Acila* with life in shallow water in the case of simple coiling and life in deep water in the case of complex coiling. However, the many coils in the Chilean species of *Nucula* and *Ennucula* is not associated with depth, and a high degree of coiling was also described by Knudsen (1970) in various abyssal species of *Nucula, Ennucula* and *Brevinucula.* He, furthermore, found a large number of coils in species of Nuculanidae-species of *Spinula* with 1, 6 and 7 coils; species of *Ledella* with 1, 4 and 5 coils; and *Phaseolus* with two. Thus, there seem to be two tendencies within the nuculanids: one with a high number of coils in the above-named genera, and another with only one coil in *Nuculana, Propeleda, Yoldia* and *Yoldiella.*

The species of the genera *Neilonella, Tindaria, Tindariopsis* and *Malletia* always have only one coil and show no variation with depth.

Schileyko (1989) observed that the number of coils is associated to the quality of the nutrients rather than the depth. This observation explains why *Nucula* (*N.*) *fernandensis,* collected at shallow depth in a sandy sustratum had a large number of coils. Schileyko (1989) proposed six tendencies in the pattern of coils.

Although there is no clear functional relationship between number of coils and life habits, there seems to be a clear association between coiling and shell volume for species of some genera. Such a relationship is observed in short but inflated species of *Nucula, Ennucula, Spinula* and *Ledella,* all of which have an intestine with more than 3 or 4 coils. On the other hand, species of genera with a flat, elongate shape, such as *Malletia,* have almost always only one coil. Excep-

tions of inflated species with only one coil within the genus *Nuculana* may be explained by the anterior position of the intestine, typical of nuculanaceans.

(9) The phylogenetic value of the relationship between position of the heart and rectum suggested by Pelseneer (1888, 1911) for the bivalves, seems to be applicable to the evolution of the Protobranchia, as well. In fact, species of Nuculidae, recognized as the more primitive family, have a heart located dorsal to the rectum (*Nucula, Ennucula*) or surrounding it (*Nucula proxima*), whereas in more specialized families of Nuculanacea, the heart may be found surrounding the rectum (Nuculanidae) or located underneath (Malletiidae) (Figs. 58, 59). Thus, the studied species of *Nuculana, Propeleda, Silicula, Yoldiella* and *Yoldia* had without exception a heart surrounding the rectum (Figs. 76, 78, 85, 89). In the species of *Malletia, Tindaria,* and *Tindariopsis,* the heart can be positioned ventral to the rectum (*Malletia chilensis* and *Tindaria virens;* Figs. 92, 95) or surrounding it (*Malletia patagonica* and *Tindariopsis sulculata;* Figs. 81, 82).

According to Owen (1959; fig. 7) in *Solemya* the heart surrounds the rectum.

(10) The structure of the siphons in the Nuculanacea seems to indicate clearly differentiated morphological adaptations. Yonge (1939, 1957), based on species of Nuculanidae and Malletiidae, recognized three different types of fusion for the walls of the siphonal tubes correlated with length (Fig. 57a–c): (a) with both siphons fused by tissue; (b) with the exhalant siphon closed, and ciliary junctions completing the inhalant siphon; and (c) with ciliary junctions completing both siphons.

Our study of the Chilean species and the information provided by Knudsen (1970), Filatova & Schileyko (1985), and Allen (1985), allow us to propose the following five additional types (Fig. 57 d–h): (d) siphons united dorsally and ventrally only by ciliary junctions; (e) Exhalant siphon open dorsally and ventrally; with or without a variable number of tentacles or papillae along the margin of the mantle corresponding to the inhalant siphon; (f) with exhalant siphon only, closed ventrally; mantle margins corresponding to the inhalant siphon serrated; (g) Exhalant siphon only partially separated from the inhalant one; and (h) Siphons only dorsally united.

To study the precise type of union, examination of several specimens was required; however, it was often difficult to differentiate a close ciliary junction from a tissular one, and we risk possible confusion in some cases. In fact, we agree with Drew (1899), Pelseneer (1911), and Heath (1937) in that a fusion by tissue, due to its ontogenetic origin, keeps a line of fusion indicated by a medial ventral line which breaks easily when pressed by a dissecting instrument. For species not examined by us, we trusted the descriptions.

Coupling our observations with those by Knudsen (1970), Allen (1963), Allen & Sanders (1973, 1982), and Sanders & Allen (1977), we are permitted to establish the following relationships among the genera of Nuculanacea (genera in parenthesis indicate that description of the siphons is not sufficiently detailed to be certain of the type of union):

Fusion of type a. Observed in species of *Malletia, Yoldia, Yoldiella,* (*Spinula?*), (*Ledella*), *Jupiteria, Lembulus,* and *Nuculana.*

Fusion of type b. Observed in species of *Yoldia, Yoldiella,* (*Spinula?*), (*Ledella*), and *Nuculana.*

Fusion of type c. Observed in species of *Neilonella, Malletia, Nuculana,* (*Phaseolus*), *Tindariopsis,* and *Propeleda;* however, in this last genus the ventral borders are divergent.

Fusion of type d. Observed in species of *Neilonella* and *Tindaria.*

Fusion of type e. Observed in species of *Sarepta.*

Fusion of type f. Observed in species of *Tindaria.*

Fusion of siphons in Nuculanacea does not follow definite evolutionary lines, and to understand their adaptive significance will require both ecological and functional studies. Pelseneer (1911) noticed the presence of the siphonal tentacle generally on the left in species of *Yoldia* and *Nuculana.* Stempell (1899) found it indistinctly on one side or the other in *Yoldiella ecaudata,* but mainly on the right side in *Malletia chilensis,* Yonge (1939) located it in general mainly to the right, but in the species here studied it was indistinctly found on one side or the other; the same was observed by Knudsen (1970) in abyssal and hadal species.

(11) Regarding geographic distribution, the study of the Chilean protobranchs has demonstrated that the extraordinary wide distribution recorded for some species is doubtful, and this is probably also the case of species from other geographic regions with purported very wide distribution. For instance, the identification of species of *Nucula* in Chile with a wide interregional distribution may be erroneous, as we have established for *Nucula exigua* Sowerby I, 1833; *Nucula carlottensis* Dall, 1897; *Nucula declivis* Hinds, 1843; *Ennucula colombiana* (Dall, 1908); and *Nuculana callimene* (Dall, 1908). In other cases, the distribution may appear wide due to a wrong synonymy as in the case of *Malletia chilensis,* mistakingly recorded up to Magellan.

Table 2 indicates the existence of two faunistic groups of Protobranchia (also acknowledged for bivalves in general by Woodward, 1851–1856; Soot-Ryen, 1959; Stuardo, 1964, 1988), with a limited overlapping of species. In fact, only the species *Nucula* (*Nucula*) *pisum, Ennucula grayi,*

and *Ennucula puelcha* present a wider distribution within the two recognized "Provinces," whereas *Malletia chilensis* and *Tindariopsis sulculata* cover limits that may be considered transitional zones.

This table also helps to demonstrate possible interspecific relationships. For instance, morphological affinities among *Nucula* (*Nucula*) *pisum, N.* (*N.*) *fernandensis, N.* (*N.*) *interflucta,* and *N.* (*N.*) *falklandica* seem to be the result of allopatric radiation, the first being the stem from which the other two radiated. The fossil record of *N.* (*N.*) *pisum* supports this conclusion (Philippi, 1887).

Ennucula grayi and *E. puelcha* seem to be sympatric species, or may correspond to only one.

(12) Little is known of the ecology of the Chilean species, as they have been studied in some detail only in two places in central Chile: Bahía Concepción (this study) and Bahía Valparaíso (Ramorino, 1968).

Three species are present at Bahía Concepción: *Nucula* (*Nucula*) *pisum, Nuculana* (*Saccella*) *cuneata,* and *Malletia chilensis.* The first two were found living mainly in sandy-mud, whereas *Malletia* usually lives in mud, difference that agree with Ramorino's observations (1968) at the Bahía Valparaiso. *Ennucula grayi,* which lives at Valparaiso, is not found at the Bahía Concepción, probably due to the seasonal environmental variations in temperature, salinity and oxygen (Ahumada & Chuecas, 1979). Abundance of the three reported species is neither comparable to the values reported for Valparaiso, as discussed in the taxonomic part under each species.

(13) Regarding distribution in depth, all the species listed in Table 2 have an extended range of bathymetric distribution, as is well known for the group; however, following the bathymetric division of the oceans (Hedgpeth, 1957), there is only one intertidal species: *Nucula* (*N.*) *interflucta,* from Iquique, and only one abyssal species: *Tindaria salaria* collected off Islas Salas y Gomez. All the other are sublittoral or sublittoral-bathyal species. In general, the sublitoral contains the better known Chilean fauna of protobranchs; the abyssal fauna and that of the oceanic islands remain to be collected and studied.

(14) The Chilean fossil protobranchs have not been recently reviewed, and their taxonomic status is rather poorly known. However, a revision of the literature yielded about 50 species described for the Paleozoic, Mesozoic, and Cenozoic. The collections available to us allowed the detailed description of only five species belonging to the genera *Ennucula, Propeleda, Tindariopsis,* and *Malletia.* For the remaining species, we confirm or suggest the appropriate generic changes when the description and illustrations permitted it.

Key Words: Protobranchia, Chilean, Antarctic, taxonomy, anatomy, distribution, Nuculoida, Solemyoida.

INTRODUCION

En el estudio de los moluscos es de aceptación general que los protobranquios constituyen el grupo más primitivo entre los bivalvos. Tal conclusión se ha alcanzado por el estudio de las partes blandas, estructuras cuyo valor filogenético se postula como fundamental en la clasificación de este complejo grupo, y de los bivalvos en general (Yonge, 1959).

A pesar de su primitivismo, los protobranquios presentan una mezcla de estructuras especializadas, resultado de una gran radiación observable tanto en las especies recientes (en particular en formas de la fauna abisal), como en las especies fósiles. En ellos el pie es todavía una suela plana; los ctenidios, aún cuando deben considerarse grandes, no dominan todavía la cavidad del manto, yacen en lo que se considera una posición primitiva, posterior y sus filamentos permanecen triangulares; entre los órganos paleales, son los palpos labiales más que los ctenidios, los que colectan el alimento. Es por ello que la clasificación de los protobranquios debe considerar fundamentalmente el estudio detallado de sus partes blandas.

No todos los caracteres utilizados en la clasificación taxonómica tienen el mismo valor filogenético ya que, en general, los bivalvos muestran un grado de evolución en mosaico con muchos ejemplos de convergencia (Morton y Yonge, 1964), al cual los protobranquios no escapan. Esta podría ser una de las razones de la prevalencia de una clasificación simplificada de este grupo hasta la década de los años sesenta, que consideraba sólo a unas pocas familias. Sin embargo, el estudio de las formas abisales y sus adaptaciones funcionales, ha permitido ampliar la clasificación de los protobranquios para incluir a nuevas familias y reforzar así la importancia que en esta nueva clasificación tienen las partes blandas (Allen y Hannah, 1986).

De acuerdo a estos planteamientos los objetivos más importantes del presente estudio fueron dos. En primer lugar, realizar el estudio taxonómico de casi todas las especies chilenas conocidas, considerando una combinación de caracteres tanto de la concha como de las partes blandas; en segundo lugar, llevar a cabo el estudio anatómico comparativo de las distintas especies de protobranquios encontradas. Esto, permitió la evaluación de algunos caracteres anatómicos considerados en la clasificación y en la evolución del grupo, esperándose que sea este aspecto de la revisión, lo que estimule mayores investigaciones.

El estudio anatómico permitió, además, discutir la interpretación de estructura y función de los órganos más importantes.

Finalmente, se logró compilar una sinopsis de todas las especies fósiles chilenas conocidas, proyectando los resultados del análisis taxonómico-anatómico realizado con las especies actuales, a la interpretación de ellos. Sin embargo, el deficiente conocimiento taxonómico previo, el escaso número de especies fósiles chilenas disponibles y, en menor grado, la falta de literatura, permitió sólo un estudio parcial de ellas.

Antecedentes Históricos Sobre La Clasificación de los Protobranquios

Hay escasos estudios sobre los protobranquios de Chile, aunque los catálogos sobre la fauna de moluscos de este país han compilado las especies descritas incluyendo ocasionalmente comentarios taxonómicos y sinonimias. Estudios que junto a la identificación consideran datos sobre profundidad, substrato y abundancia relativa son los de Hupé (1854), Smith (1881), Mabille y Rochebrune (1889), Stempell (1898a), Dall (1908a, 1909) y Soot-Ryen (1959).

Dos trabajos taxonómicos importantes son: el de Ramorino (1968) que incluye, además, estudios de densidad en los fondos de la Bahía de Valparaíso, y el de Marincovich (1973) sobre moluscos intermareales de Iquique, que describe una nueva especie de *Nucula*.

Otros autores han examinado diversas especies de protobranquios chilenos en estudios faunísticos de gran extensión latitudinal. Entre ellos destacan: el de Hertlein y Strong (1940) sobre especies de la costa de México y América Central; el catálogo de Carcelles y Williamson (1951) sobre los moluscos de la provincia Magallánica; las monografías de Keen (1958, 1971) y Olsson (1961) sobre moluscos de la Provincia Panameña; los de Soot-Ryen (1951), Powell (1951), y Dell (1964, 1990) sobre fauna Antártica, y el de Bernard (1983) sobre bivalvos del Pacífico Oriental. Respecto de los moluscos del Pacífico central, Rehder (1980) describió a un protobranquio entre los moluscos de la Isla de Pascua.

Coan y Scott (1997) presentan el estado taxonómico actual de los protobranquios en su inventario de los bivalvos marinos del Noreste del Océano Pacífico, basados en el examen de material tipo de colecciones de varios museos y toda la literatura publicada.

Las investigaciones sobre anatomía del grupo son escasas. De todas las especies chilenas, sólo tres han sido anteriormente estudiadas en detalle: *Malletia chilensis, Tindariopsis sulculata* (Stempell, 1898a; Heath, 1937), y *Nucula* (*Nucula*) *fernandensis* Villarroel, 1971, lo cual refleja el estado del conocimiento sobre la anatomía de los moluscos chilenos en general. La descripción anatómica de *Petrasma atacama* Kuznetzov y Schileyko, 1984, designada por estos autores para la zona peruano-chilena, por la latitud que ellos señalan (7°41′N; 79°47′W) corresponde a Ecuador.

Por otra parte, la importancia de los estudios anatómicos en la clasificación de los protobranquios ha sido incorporada en las contribuciones de Pelseneer (1891, 1911), Davies (1933), Yonge (1939), Allen (1954, 1978, 1985), Purchon (1956, 1959, 1978, 1987a), Filatova (1958, 1976), Morton (1963, 1967), Stasek (1963), Savitskii (1969a, 1969b, 1974), Allen y Sanders (1973, 1982), Sanders y Allen (1973, 1977), Schileyko (1983, 1985, 1989), Filatova y Schileyko (1984, 1985), y Allen y Hannah (1986, 1989).

La fauna de bivalvos fósiles chilenos, descrita en su mayoría por Philippi (1887, 1899), no ha vuelto a ser revisada y los nombres propuestos originalmente se usan todavía en trabajos de índole puramente estratigráfica, tales como los recopilados por Steinmann (1856–1929), Wilckens (1904), Fuenzalida (1938, 1942), Tavera (1942, 1956, 1960), Tavera y Veyl (1958) y otros. Zinsmeister (1984) describió un género y tres especies nuevas para el Eoceno Superior, Formación La Meseta, Isla Seymour, Península Antártica y Stinnesbeck (1986), una subespecie y dos

especies nuevas de la Formación Quiriquina (Maastrichtiano) de Chile Central.

A partir de la propuesta inicial de Neumayr (1884), quien basándose en los caracteres de la concha incluyó este taxón junto a los Arcacea en el orden Taxodonta, la clasificación de los protobranquios ha combinado las interpretaciones filogenéticas de paleontólogos y neontólogos.

La historia geológica de los protobranquios y su filogenia, comenzó a ser discutida en detalle, combinando estas tendencias, por Cox (1959). Con posterioridad, McAlester (1964) en un estudio de los Nuculoides del Paleozoico temprano, y considerando los trabajos anatómicos de especies recientes, concluyó que dentro de los protobranquios existe una radiación evolutiva primaria en dos grupos distintos, representados por las formas nuculoides y nuculanoides, asignándole a cada una el rango de superfamilia: Nuculacea y Nuculanacea, respectivamente.

Estos antecedentes fueron considerados por Newell (1965, 1969) para proponer la separación de la subclase de los protobranquiados en dos categorías diferentes: los Palaeotaxodonta Korobkov, 1954, y los Cryptodonta Neumayr, 1884, en contraste a clasificaciones más conservadoras (Yonge, 1939; Purchon, 1959, 1978). Newell se basó en que trabajos modernos en el género *Solemya,* tendían a demostrar numerosas diferencias morfológicas en la concha entre Nuculoides y Solemyoides, las que sumadas a una larga historia geológica que no evidenciaba su origen común, sugería dos líneas evolutivas completamente diferentes.

La clasificación de Newell (1969) fue modificada por Salvini-Plawen (1980), quien al igual que Nevesskaya et al. (1971) sugiere considerar las subclases como superórdenes, proponiendo además el nombre de Ctenidiobranchia Salvini-Plawen, 1980, en lugar de Palaeotaxodonta Korobkov, y Palaeobranchia Iredale, 1939, en vez de Cryptodonta Neumayr. Incluye a estos superórdenes en la subclase Pelecypoda Goldfuss, 1820, considerando al orden Nuculida Dall, 1889, dentro de los Ctenidiobranchia y a los órdenes Solemyida Dall, 1889, y Praecardiida Newell, 1965, dentro de los Palaeobranchia.

Schileyko (1983) considera al superorden Protobranchia conformado por los órdenes Solemyioda y Nuculida

Allen y Hannah (1986) reactualizaron la subclase Protobranchia Pelseneer, 1889, dividiéndola en los órdenes Solemyoida, y Nuculoida y a esta última en dos superfamilias: Nuculoidea y Nuculanoidea.

Warén (1989) demostró que la superfamilia Nuculanoidea debería ser asignada a H. Adams y A. Adams, 1858, y no a Gray, 1824, como concluyeran Allen y Hannah (1986). También la distribución de familias propuesta por estos autores fue criticada por Maxwell (1988), quien justificadamente, sugiere en primer lugar, la división de la familia Nuculidae en dos subfamilias (Nuculinae Gray, 1824, y Nuculominae Maxwell, 1988), y luego, USÓ la familia Sareptidae Stoliczka, 1871, en reemplazo de Yoldiidae, a cuyas subfamilias Yoldiinae Habe, 1977, y Yoldiellinae Allen y Hannah, 1986, agrega la subfamilia Sareptinae Stoliczka, 1871. El género *Sarepta* A. Adams, 1860, es incluído por Allen y Hannah (1986) en la subfamilia Yoldiellinae, lo que con los antecedentes existentes consideramos justificado. Por otra parte, la separación de los Nuculidae propuesta por Maxwell nos parece un caracter filogenético importante, susceptible de complementarse con caracteres anatómicos, como se ha intentado desarrollar en este trabajo.

Convencidos de la necesidad de profundizar el estudio anatómico de las partes blandas en este grupo y por su trascendencia taxonómica mantenemos para la subclase el nombre Protobranchia Pelseneer, 1889, prefiriéndolo a la proposición reciente de Palaeotaxodonta Korobkov (Carter, 1990).

Carter (1990) resume una clasificación para el orden Solemyoida que incluye a las superfamilias Solemyoidea "H. Adams y A. Adams, 1857 [1840]" (con la familia Solemyidae y las subfamilias Solemyinae y Clinopisthinae Pojeta, 1988, fósil) y la superfamilia Nucinelloidea Vokes, 1956, con las familias Nucinellidae y Manzanellidae Chronic, 1952 (fósil).

El género *Acharax* Dall, 1908, es incluido en los Solemyinae por las características de ligamento afín a *Solenomya.*

Considerando a las especies discutidas en este trabajo, la clasificación aquí seguida, es la siguiente:

Clase Bivalvia Linné, 1758
Subclase Protobranchia Pelseneer, 1889
Orden Nuculoida Dall, 1889
Superfamilia Nuculacea Gray, 1824
Familia Nuculidae Gray, 1824
Subfamilia Nuculinae Gray, 1824

Subfamilia Nuculominae Maxwell, 1988
Superfamilia Nuculanacea H. Adams y A. Adams, 1858
Familia Nuculanidae H. Adams y A. Adams, 1858
Subfamilia Nuculaninae H. Adams y A. Adams, 1858
Subfamilia Ledellinae Allen y Sanders, 1982
Familia Siliculidae Allen y Sanders, 1973
Familia Sareptidae Stoliczka, 1871
Subfamilia Sareptinae Stoliczka, 1871
Subfamilia Yoldiellinae Allen & Hannah, 1986
Familia Malletiidae H. Adams y A. Adams, 1858
Familia Tindariidae Verrill & Bush, 1897
Orden Solemyoida Dall, 1889
Superfamilia Solemyacea Gray, 1840
Familia Acharacidae Scarlato y Starobogatov, 1979

MATERIALES Y MÉTODOS

Materiales Examinados

Especies Actuales: De un total de 27 especies aquí aceptadas para Chile, se estudiaron 20, de las cuales 15 son continentales y 5 antárticas. Las áreas de recolección se representan en los Mapas 1 y 2.

En la lista de especies incluida en la Tabla 2, se han marcado con un asterisco aquellas de las que no se obtuvieron ejemplares, y con interrogante, aquellas otras citadas cuya presencia se considera improbable. Las especies restantes fueron identificadas en muestras depositadas en las colecciones de bivalvos del Museo del Departamento de Zoología, Universidad de Concepción, Chile (MZUC), provenientes de las expediciones, donaciones y recolecciones siguientes, cuyas abreviaciones se utilizan en el texto:

(1) Expedición Mar-Chile I, entre Coquimbo (29°57′24″S) y el extremo S de la Isla de Chiloé (42°55′S), Febrero-Marzo 1960 (M. Ch. I.).

(2) Expedición Mar-Chile II, entre la frontera con el Perú (18°28′S) y Punta Patache (20°48′S), Julio 1962 (M. Ch. II).

(3) Crucero 69-5 del buque "Hero", de la National Science Foundation, realizado entre el Estrecho de Magallanes (53°30′S y el Archipiélago Madre de Dios (50°9′30″S), 18 de Octubre a 5 de Noviembre 1969 ("Hero" 69-5).

(4) Material proporcionado por el Instituto de Fomento Pesquero, Chile, proveniente de uno de sus cruceros frente a la costa centro-norte chilena (IFOP-01), Noviembre 1964.

(5) Muestras de la Bahía de Valparaíso enviadas por la Estación de Biología Marina de Montemar, Departamento de Oceanología, Universidad de Chile, Valparaíso.

(6) XIXa Expedición Antártica Chilena, Diciembre 1964-Enero 1965 (Ant. XIX).

(7) XXIIa Expedición Antártica Chilena. Diciembre 1967-Enero 1968 (Ant. XXII).

(8) Operación Centolla, Mayo 1962 (Op. Centolla).

(9) Muestreo cuali y cuantitativo en la Bahía de Concepción, Febrero 1968 y Diciembre-Enero 1969.

Especies Fósiles: Las muestras estudiadas abarcan, tanto la mayoría de las formaciones marinas que afloran en las Provincias de Concepción y Arauco, como también las de algunas de las Provincias de Santiago y Coquimbo (Mapa 1). Fueron proporcionadas por el Profesor Lajos Biró (Q.E.P.D.), del Laboratorio de Paleontología de la Universidad de Concepción.

(1) Lo Valdés, 14 al 31 de Enero de 1964.

(2) Navidad, 1 a 4 de Noviembre de 1968.

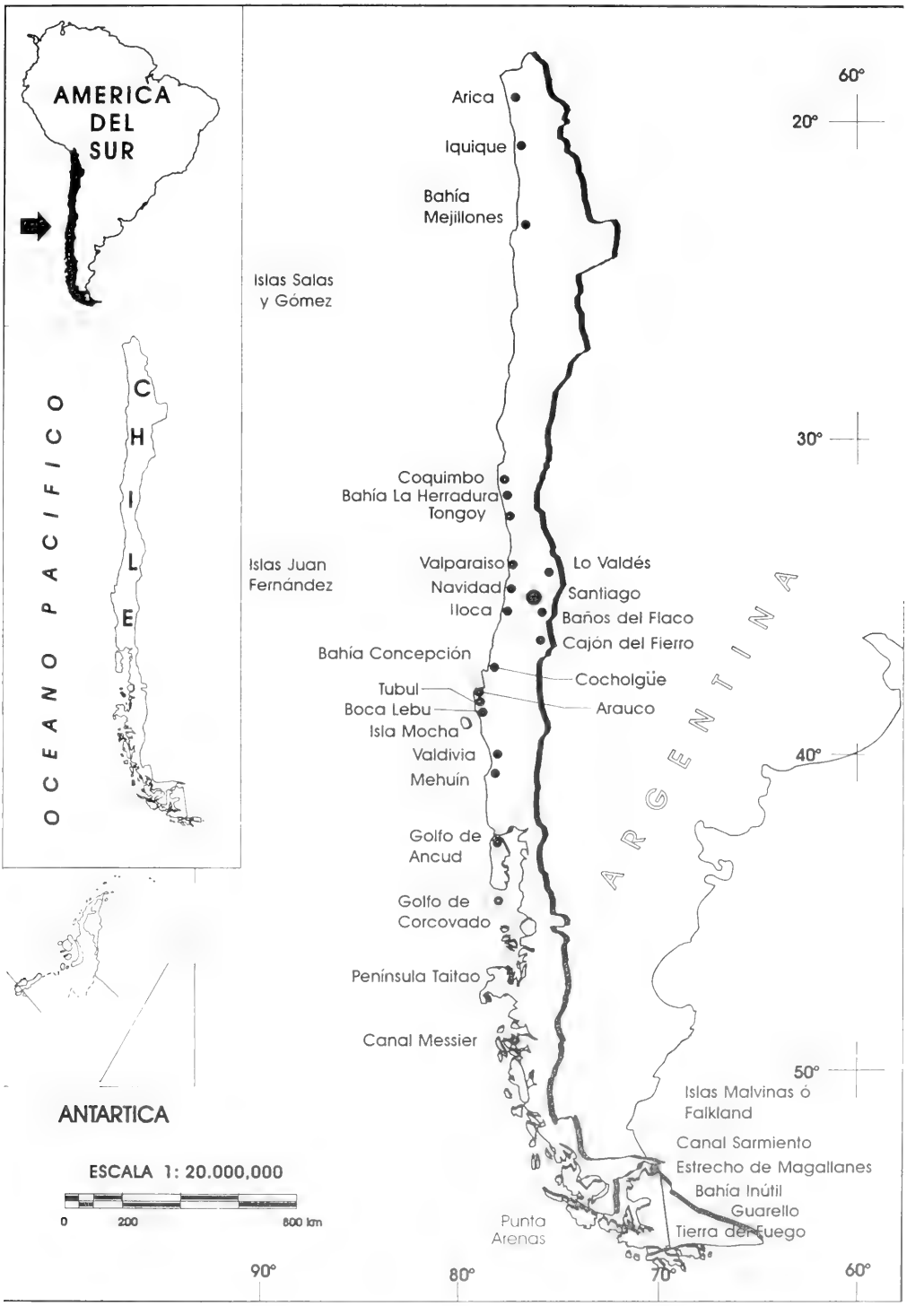
(3) Tubul, Noviembre de 1965 y visitas esporádicas posteriores.

En colectas efectuadas por el autor principal en Coquimbo, Tongoy (Prov. Coquimbo), Cajón del Fierro-Baños del Flaco (Prov. de Colchagua), Cocholgüe, Lirquén, San Vicente, Tumbes y Quiriquina (Prov. de Concepción) no se encontraron protobranquios fósiles. Algunas muestras adicionales provenientes de Navidad, se examinaron en la Escuela de Geología de la Universidad de Chile, Santiago.

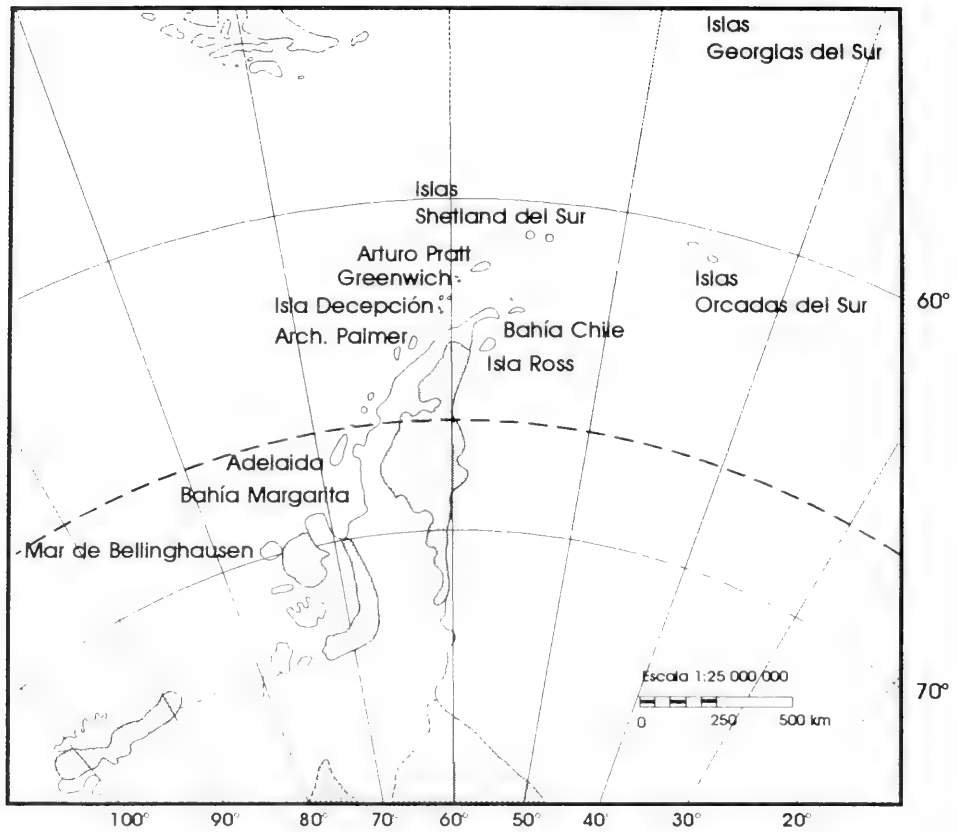
Las muestras estudiadas sólo cubren cortos tramos del tiempo transcurrido desde el Paleozoico Superior (Carbonífero-Pérmico), piso más antiguo en que se han encontrado protobranquios hasta el presente (Tabla 1).

Aunque el número de fósiles revisados en las distintas colecciones ascendió a más de 10,000 ejemplares, sólo 140 individuos, 742 valvas y 32 moldes internos son protobranquios correspondientes a las siete especies fósiles analizadas.

En la colección de fósiles de R. A. Philippi (1887, 1899) existente en el Museo Nacional de Historia Natural en Santiago, no se encontró ningún protobranquio.



MAPA 1. Localidades principales mencionadas en el texto agrupadas de acuerdo a su latitud aproximada.
Main geographic references cited in the text, grouped according to their approximate latitude.



MAPA 2. Principales localidades Antárticas mencionadas en el texto. Main Antarctic localities cited in the text.

Métodos

En las citas sinonímicas de las especies se señalan aquellas que incluyen descripciones anatómicas con la abreviación (anat.).

Las muestras de especies actuales con partes blandas fueron conservadas en alcohol al 75%. Entre los fósiles, no siempre se tuvieron ejemplares completos y conchas originales, por lo que fue necesario efectuar algunas determinaciones utilizando conchas incompletas, moldes externos, internos e/o impresiones.

Los términos técnicos usados en las descripciones de las especies son los usuales (e.g., Arnold, 1965) para definir los caracteres de la concha. La observación de estas estructuras y las disecciones de las partes blandas teñidas con rojo neutro diluído en alcohol, se efectuaron utilizando un microscopio estereoscópico Zeiss.

En el estudio de las partes blandas se hicieron cortes histológicos, para precisar la interpretación de los ciegos estomacales. En la lista de especies estudiadas, aparte de las especies marcadas con asterisco (*), cuya existencia en Chile es dudosa, no se estudió la anatomía interna de *Silicula patagonica,* ni de *Yoldiella indolens.*

Las dimensiones de la concha medidas en cada especie fueron: longitud, altura y espesor y se efectuaron en la forma representada en las Figuras 1y 2. Debido a la gran variabilidad de las medidas observadas no se calcularon índices.

El material estudiado y su procedencia se

TABLA 1. Ubicación cronológica de las localidades de donde provienen las colecciones revisadas. En todas se han mencionado protobranquios fósiles, pero en este estudio se encontraron sólo en las marcadas con asterisco (*). Las edades referidas a localidades distintas se agrupan de acuerdo a otros autores. Chronological location of the studied samples of fossil protobranchs (*). Strata and localities arranged according to various authors.

Período	Época	Localidades
Cuaternario	Pleistoceno	Coquimbo
		Tongoy
		Tubul*
	Plioceno	Coquimbo
		Tongoy
		Tubul*
Terciario	Mioceno Inferior	Navidad*
	Eoceno	Isla Seymour
	Eoceno Inferior	Boca Lebu
	Paleoceno Superior	Boca Lebu
Cretácico	Superior	Quiriquina
		San Vicente
		Lirquén
		Cocholgüe
		Tumbes
	Inferior	Lo Valdés*
		Baños del Flaco
		Rio Maitenes
		Cajón del Fierro
Jurásico	Superior	Lo Valdés*
		Baños del Flaco
		Río Maitenes
		Cajón del Fierro

indican en detalle después de la sinonimia de cada especie. En cada una de las muestras se señala el número de ejemplares completos estudiados (ej), y/o el número de valvas (v), su ubicación lateral izquierda o derecha (i o d) y el tamaño máximo y mínimo. Si la abreviación ej va acompañada de s, significa que se trata de ejemplares completos, pero secos. Si la abreviación ej va sola, indica que se trata de una muestra conservada en alcohol. En el caso de los fósiles los moldes internos se abrevian mi.

Para cada muestra se indica también en orden continuado: No. de Museo (colección del Museo del Departamento de Zoología de la Universidad de Concepción, MZUC o de la Colección de Paleontología, DGUC), nombre de la expedición y de la estación en que fue obtenida (si la hubiere), posición geográfica, tipo de substrato y profundidad (expresada en m). Las referencias a los tipos de substrato fueron tomadas directamente de las etiquetas. En el caso de los fósiles, se incluye también indicaciones de edad y naturaleza de las rocas en que se encontraron.

En las Figuras 1 a 3 se ilustran los caracteres de la concha; en las restantes, se han representado solamente las estructuras de la concha y de las partes blandas que se discuten en el texto; se hace referencia a ellas, cuando se estimó necesario.

Las conchas de las especies de pequeño tamaño se lavaron con jabón suave y se limpiaron durante un minuto en un vibrador Bransonic 220. Luego se montaron en grafito coloidal sólido en isopropanol al 20%. Se metalizaron con oro en un sistema SPUTER S 150 coater y se fotografiaron con el microscopio de barrido Siemen ETEC Autoscan U-1 en el Laboratorio de Microscopía Electrónica de la Dirección de Investigación de la Universidad de Concepción. Las especies de mayor tamaño se fotografiaron con un microscopio estereoscópico Carl Zeiss Modelo IV,

provisto de una cámara Carl Zeiss C 35 para microfotografía. Los dibujos de las partes blandas se hicieron con una cámara clara Carl Zeiss. Todos los dibujos, excepto las figuras 3, 9–12, 66, 75, 80 y 95 fueron hechos a escala y las medidas se expresan en cada caso en mm o en décimas de mm.

La numeración tanto de dibujos como de fotografías es consecutiva y se designan como figuras (Figs.). En el caso de las fotografías se indica el número de Museo de la muestra, el tamaño del ejemplar o el aumento utilizado y su procedencia.

En el caso de las especies fósiles, se numera en forma consecutiva las especies de las cuales se revisó material.

Abreviaciones Empleadas

ct	ctenidio
a	aurícula
aa	aorta anterior
ada	aductor anterior de la concha
adp	aductor posterior de la concha
an	ano
ap	ápice
apt	aorta posterior
apl	área plegada (FA de otros autores)
as (1–4)	área de selección (SA de otros autores)
b	boca
bp	ciego del palpo
cav p	cavidad pericárdica
ccp	conectivo cerebro pedal
ccv	conectivo cerebro visceral
cd	capuchón dorsal (DH de otros autores)
cdr	condróforo
con	escultura concéntrica
cp	ciego posterior
cp′	entrada ciego posterior
cq	cinturón quitinoso
cs	cinturón de separación del estómago y saco del estilo
dch	dientes charnelares
dd	conductos de los conductos digestivos
dd^2	conducto del divertículo digestivo derecho
$dd^{2'}$	entrada del ducto digestivo derecho al estómago
$dd^{1.3}$	conductos de los divertículos digestivos izquierdos
$dd^{1'.3'}$	entrada de los divertículos en el estómago
ddg	divertículos digestivos
deg	dientes del escudo gástrico
div	escultura divergente
dm	músculo dorsal medio
dp	disco pedal
dq	dientes quitinosos
dva	escultura divaricada
e	esófago
e′	entrada del esófago
eg	escudo gástrico
es	estatocisto
est	estómago
esc	escutelo
esp	espesor
fl	filamento del palpo
g	gónada
gl b	glándula del biso
gl h	glándula hipobranquial
gse	ganglio supraesofágico
gp	ganglio pedal
gv	ganglio visceral
h	altura
i	intestino
iaa	impresión aductor anterior
iap	impresión aductor posterior
im	intestino medio
iv	intestino visceral
l	longitud
le	lamela externa del palpo
lig	ligamento (int = interno; ext = externo)
li	lamela interna del palpo
lp	lámina del palpo
lpl	línea paleal
lun	lúnula
mbr	músculo branquial
mi	músculo interior del palpo
mm	músculos medios
mp	músculos paleales
ms	músculos sifonales
msp	membrana suspensora del palpo
nbr	nervio branquial
npa	nervio paleal anterior
npl	nervio del palpo
npp	nervio paleal posterior
o′	entrada al estómago
p	pie
per	pericardio
pl	palpo labial
pm	papilas del manto
pr	perióstraco
pp	músculos protractores pedales
rad	escultura radial
r	recto
ret	escultura reticulada
ri	riñón
rm	músculos retractores del manto

ra	músculo retractor pedal anterior
rpp	músculo retractor pedal posterior (rp)
rs	músculos retractores sifonales
s	sifón
se	saco del estilo
sex	sifón exhalante
si	surco intestinal
si′	continuación del surco intestinal del estómago
sin	sifón inhalante
sp	seno paleal
sol	surco oral lateral
tm	tentáculos del manto
tma	tiflosol mayor (TY de otros autores)
tme	tiflosol menor (TY′ de otros autores)
tp	tentáculo del palpo
tpd	talón pedal
ts	tentáculo sifonal
um	umbo
v	ventrículo
vm	músculo ventral medio

TAXONOMIA DE LOS PROTOBRANQUIADOS CHILENOS RECIENTES

Clase Bivalvia (Lamellibranchiata) Linné, 1758
Subclase Protobranchia Pelseneer, 1889

Diagnosis

Bivalvos con pie sagital y longitudinalmente surcado, suela con márgenes papilados; filamentos branquiales simples, generalmente aplanados, no reflejados, con manojos de cilios abfrontales; sin glándula del biso, pero con una glándula pedal (o "bisal") en la quilla del pie que no produce biso.

Clave Para Las Familias Y Géneros De Protobranquios Chilenos Recientes Y Fósiles

1. Concha de forma variable con el extremo posterior no alargado. Sin seno paleal. Animal sin sifones 2

1′. Concha oval, oblonga o alargada; extremo posterior generalmente más largo y a menudo rostrado. Con seno paleal generalmente presente. Tubos sifonales parcial o totalmente unidos 4

2. Concha alargada, soleniforme; entreabierta. Perióstraco sobrepasando los bordes de las valvas. Charnela sin dientes. Ligamento externo. Bordes del manto unidos en su parte media. Palpos labiales muy pequeños. Ctenidios muy grandes ocupando un tercio de la cavidad paleal . . . . Acharacidae . . . . . *Acharax*

2′. Concha corta, ovalada, subtriangular o redondeada; no entreabierta. Perióstraco no sobrepasando los bordes de las valvas. Charnela provista de numerosos dientes. Bordes del manto libres. Palpos labiales y ctenidios casi del mismo tamaño Nuculidae.3

3. Márgenes internos de las valvas crenulados (tamaño hasta 5 mm) . . . . . *Nucula*

3′. Márgenes internos de las valvas lisos (tamaño hasta 20.6 mm) . . . . . *Ennucula*

4. Ligamento externo o parcialmente interno. Corazón ventral al recto o atravesado por él. Tamaño a grande 5

4′. Ligamento interno. Corazón atravesado por el recto. Tamaño pequeño, mediano o grande . . . . . .Nuculanidae . . . 7

5. Ligamento externo 6

5′. Ligamento parcialmente interno; su parte externa alojada en una cavidad posterior a los umbos. Sifón exhalante completo; inhalante abierto ventralmente . . . Ledellinae (hasta 13.3 mm) . . . . . *Tindariopsis*

6. Concha más o menos veneriforme, inflada, de umbos prominentes. Sin seno paleal. Sifones formados sólo por unión de papilas o repliegues del manto..Tindariidae (hasta 6 mm) . . . . . *Tindaria*

6′. Concha ovalada, comprimida lateralmente, de umbos bajos. Con seno paleal. Sifones unidos, cerrados o abiertos ventralmente . .Malletiidae (hasta 51 mm) . *Malletia*

7. Concha más o menos rostrada. Extremo posterior generalmente realzado por una quilla 8

7′. Concha redondeada. Extremo posterior sin quilla . . . . . .Yoldiidae. 10

8. Ornamentación formada por costillas concéntricas. Charnela provista de dientes chevronados (en "v") . . . .Nuculaninae . . . 9

8′. Sin ornamentación concéntrica. Charnela provista de dientes lamelares muy oblicuos . . . . . .Siliculidae (hasta 12 mm) . . . . . *Silicula*

9. Rostro romo, muy largo, bicarinado (hasta 18.9 mm) . . . . . .*Propeleda*

9′. Rostro corto no carinado (hasta 12.5 mm) . . . . . *Nuculana*

10. Concha de regular tamaño, entreabierta posteriormente. Seno paleal profundo. Condróforo triangular .Yoldiinae (hasta 35.5 mm) . . . . . *Yoldia*

10′. Concha muy pequeña, cerrada estrechamente. Seno paleal poco profundo. Sin condróforo . . . . . .Yoldiellinae (hasta 12 mm) . . . . . *Yoldiella*

Orden Nuculoida Dall, 1889
Superfamilia Nuculacea Gray, 1824
Los mismos caracteres de la familia.
Familia Nuculidae Gray, 1824

Diagnosis

Concha equivalva, hasta 50 mm de longitud (30 mm en las especies chilenas), subtriangular u oval. Valvas inequilaterales; parte posterior corta, a menudo truncada, la anterior más larga; extremo redondeado. Umbo opistogiro. Lúnula casi siempre cordiforme. Generalmente sin escutelo; sólo algunas veces existe un escutelo o un pseudo-escutelo bien definido. Prodisoconcha lisa. Escultura, si la hay, formada por estrías concéntricas, concéntricas y radiales, radiales bifurcadas, o modificaciones y combinaciones de las anteriores. Margen ventral interno liso o crenulado. Interior nacarado. Placa de la charnela generalmente fuerte, curvada o acodada en el medio; condróforo bordeado por una serie anterior y otra posterior de dientes taxodontos. No hay ligamento externo; resilium interno. Línea paleal entera. Bordes del manto libres. Pie voluminoso. Aductores grandes, subiguales. Glándula hipobranquial sobre la pared de la cavidad suprabranquial. Corazón sobre el recto. Palpos labiales muy grandes, cada uno con un largo apéndice tentacular. Estómago (en las especies chilenas) con o sin un ciego dorsal posterior; al menos con dos áreas de selección distintas. Eje de los ctenidios de posición oblicua o vertical con filamentos simples, que dividen la cavidad paleal en una gran cámara inhalante anterior y una pequeña cámara exhalante posterior. Ganglio visceral más pequeño que el cerebral. Sin órgano sensorial en el manto anterior. Sin sifones.

Distribución

Los representantes de esta familia viven en la actualidad en todos los mares, tanto en aguas someras como profundas, en fondos que van desde grava y arena gruesa hasta sedimento fino. Algunas especies son de aguas tropicales, pero la mayoría de ellas se encuentran en aguas templadas y boreales (Hertlein y Strong, 1940).

Observaciones

Un resumen de algunas especies de Nuculidae recientes descritas y/o citadas para Chile fue publicado por Villarroel (1971).

Subfamilia Nuculinae Gray, 1824

Con una capa superficial de finos prismas radiales, de sección rectangular.

Género *Nucula* Lamarck, 1799

Nucula Lamarck, 1799:87. Especie tipo por monotipia: *Arca nucleus* Linné, 1758 (Hertlein y Strong, 1940).

Diagnosis

Concha oval o subtriangular, sólida; escultura lisa o concéntrica con estrías radiales finas, anchas y aplastadas, a menudo difíciles de ver en la parte media de la concha, pero distintas cerca del borde ventral de ella en donde forman un margen crenulado; interespacios angostos, cerca de 1/10 del ancho de las estrías. Eje del condróforo, oblicuo, dirigido anteriormente. Borde del manto liso, sin papilas.

Subgénero *Nucula* s. s. (= *Lamellinucula* Schenck, 1944)

Concha oval o subtriangular, truncada; escultura lisa o concéntrica, generalmente con estrías radiales y margen crenulado; placa de la charnela en ángulo; dientes proximales junto a un condróforo relativamente pequeño; ligamento oblicuo.

Especies encontradas en Chile:

1. *Nucula* (*N.*) *falklandica* Preston, 1912
2. *Nucula* (*N.*) *fernandensis* Villarroel, 1971
3. *Nucula* (*N.*) *interflucta* Marincovich, 1973
4. *Nucula* (*N.*) *pisum* Sowerby I, 1833
5. *Nucula* (*N.*) *pseudoexigua,* sp. nov.

De las especies encontradas en Chile continental, sólo *Nucula* (*Nucula*) *interflucta* no fue estudiada. Esta es la más pequeña de las especies chilenas y la única que habita en la zona intermareal. No ha sido registrada de otras partes.

Nucula polynesica Rehder, 1980, descrita para la Isla de Pascua, es una especie con

aparentes afinidades a la fauna del Pacífico Central.

Dell (1990) describió a *Nucula austrobenthalis* con un amplio rango de distribución en las profundidades antárticas ubicadas al Sur de los 56°S en 3519–4209 m.

Clave Para las Especies de *Nucula* Estudiadas

1. Escultura de la concha conspícua, formada por costillas concéntricas que generalmente se interrumpen en algún punto de su curso, y por estrías radiales. Estómago con un ciego posterior. Especie de la región magallánica .... *N.* (*N.*) *pseudoexigua* sp. nov.

1′. Escultura de la concha inconspícua de apariencia lisa, formada por estrías concéntricas y radiales débiles. Estómago con o sin ciego posterior 2

2. Concha casi orbicular. Estómago con un ciego posterior. Especie de las Islas Juan Fernández .....*N.* (*N.*) *fernandensis*

2′. Concha alargada antero-ventralmente 3

3. Concha con la región anterior elevada. Márgenes internos de las valvas crenulados. Estómago con un ciego posterior. Especie de la región magallánica ....*N.* (*N.*) *falklandica*

3′. Concha con la región dorsal anterior semitruncada. Estómago sin ciego posterior. Sólo los márgenes ventrales internos de las valvas son crenulados. Especie de amplia distribución en Chile .....*N.* (*N.*) *pisum*

Se han citado otras tres especies dudosas para Chile. *Nucula exigua* Sowerby I, 1833, registrada entre el Golfo de California y Perú, ha sido citada para el Estrecho de Magallanes por Dall (1908) y otros autores (Hertlein y Strong, 1940; Soot Ryen, 1959). *Nucula declivis* Hinds, 1843, otra especie con distribución muy similar a la anterior, fue también citada por Dall (1908) para el Estrecho de Magallanes. Soot-Ryen (1959) comentando la improbabilidad de que estos dos nucúlidos se encuentren en Chile, sugirió que las identificaciones en cuestión, pudieran pertenecer a una forma de otra especie, *N. carlottensis* Dall, 1897, que parecería estar ampliamente distribuída a lo largo de la costa oeste de América.

Ningún otro autor ha fundamentado esta sugerencia que consideramos también dudosa. En consecuencia, la inclusión de estas tres especies en la fauna malacológica chilena no se justifica.

Nucula (*N.*) *falklandica* Preston, 1912
Figs. 1, 27, 28, 68, 69, 102, 103

Nucula falklandica Preston, 1912: 637, lám. 21, fig. 3 (Loc. tipo: Islas Falkland); Carcelles y Williamson, 1951: 322; Powell, 1960:169; Dell, 1964: 139, fig. 1 (17). Dell, 1990: 5, figs. 8 y 9.

Nucula minuscula Melvill y Standen, 1907: 113 (*non* Pfeffer, 1886).

Material Estudiado

9 ejemplares (ej) y 20 valvas (v). MZUC. Procedencia: (1) 1 ej, 2.5 mm (No. 4548), Op. Centolla, Est. 2, E. de Magallanes, Bahía Inútil; fango con abundantes restos de conchas, 46 m. (2) 3 ej, 2.5–3 mm (No. 4553), Op. Centolla, Est. P5M6, E. de Magallanes, Bahía Inútil; fango con algas, esponjas, briozoos y conchas, 46 m. (3) ej, y 20 v, 1–2 mm (No. 4662) "Hero" 69-5, Est. 210, E. de Magallanes, Bahía Corbeta Papudo (Guarello) (50°21′17″S; 74°43′25″W), fango amarillo verdoso, 500 m.

Descripción

Concha: Concha pequeña (hasta 3 mm de longitud), semiovalada, blanca, de aspecto vítreo. Prodisoconcha más blanca y opaca que el resto de la concha. Perióstraco amarillo muy pálido. Umbos ubicados en el tercio posterior de la concha, ligeramente abultados. Margen dorsal anterior arqueado y notoriamente elevado en su región media, lo que le da a la concha un aspecto de truncamiento dorso anterior; margen ventral redondeado; margen dorsal posterior elevado. Extremo posterior, levemente truncado. Ornamentación reticulada, formada por líneas radiales finas y densas que cubren toda la superficie de la concha, pero se hacen poco visibles sobre los umbos. Líneas de crecimiento distribuídas irregularmente, aumentando su densidad hacia el margen ventral. Superficie interna de las valvas lisa, transparentando la reticulación externa. Todo el margen interior de la concha finamente crenulado. Charnela arqueada, con dientes poco numerosos, muy poco curvados hacia arriba: 3 a 7 anteriores y 2 a 4 posteriores. (Dell, 1964, cita a un ejemplar del Museo Británico de 3.6 × 3.3 mm con 9 dientes anteriores y 5 posteriores.) Primeros dos dientes anteriores próximos al condróforo, distintos en posición y forma de los que les siguen. Impresiones de los músculos

aductores iguales, alargadas verticalmente. Otras impresiones musculares no visibles.

Anatomía Interna: Disco pedal con incisiones cortas y largas, dando un aspecto dentado. Glándula hipobranquial voluminosa, de aspecto granular con pequeñas gotas de apariencia oleaginosa. Palpo alargado, con tentáculo muy ancho. Ctenidios con filamentos externos de forma triangular muy aristada; filamentos internos más largos que los externos, no aristados. Corazón con aurículas y ventrículo globosos. Estómago con área de selección (as) con menos de 12 repliegues. Ciego posterior del estómago muy notorio como en *N.* (*N.*) *pseudoexigua* y *N.* (*N.*) *fernandensis.* Intestino corto con no más de dos vueltas.

Observaciones

Aunque ninguno de los ejemplares estudiados alcanza el tamaño del ejemplar tipo (3.6 mm, *fide* Dell, 1964), es posible encontrar en ellos todos los rasgos de la concha que caracterizan a esta especie.

En la descripción original, Preston (1912) incluyó una figura que ha sido considerada poco representativa por autores posteriores, sin embargo, Dell (1964) publicó una figura del tipo en vista interna que permite reconocerla fácilmente. Una vista externa e interna de la especie y dibujos de la concha y de su anatomía se dan en las Figuras 1, 27, 28, 68 y 69.

Tanto la concha como las partes blandas permiten diferenciar fácilmente a esta especie de las otras. Es particularmente interesante, el que en esta especie aparezca un ciego en el estómago, igual al descrito en *N.* (*N.*)*fernandensis* y *N.* (*N.*) *pseudoexgua,* sugiriendo una posible relación filogenética.

Distribución Geográfica

La especie se conocía previamente sólo de las Islas Falkland (Preston, 1912; Dell, 1964); Orcadas del Sur y Península Antártica (Dell, 1990). El material estudiado permite extender su distribución al Estrecho de Magallanes y Bahía Inútil.

Hábitat

Las muestras estudiadas cubren toda el área de dispersión de la especie. Se encontraron ejemplares grandes viviendo en profundidades hasta de 46 m, en fango con restos de conchas; y ejemplares pequeños y valvas sueltas hasta 500 m de profundidad, en fango. Parece presentar gran tolerancia batimétrica, pero esta especie es aparentemente poco abundante.

Nucula (N.) fernandensis Villarroel, 1971
Figs. 23–26, 99–101

Nucula fernandensis Villarroel, 1971: 159–171; Cekalovic y Artigas, 1981: 80. *Nucula (Linucula) fernandensis* Villarroel, Bernard, 1983: 10.

Material Estudiado

Serie tipo (Villarroel, 1971); MZUC (Loc Tipo: Islas Juan Fernández). MZUC No. 10387. Paratipos: No. 4577, 4580, 10295, 10296, 10297, 10298, 10299, 10300.

Descripción

Concha: Concha pequeña (hasta 4.5 mm de longitud), redondeada, de perióstraco amarillo pálido. Umbos anchos y abultados, de superficie lisa, sin ornamentación, generalmente erosionados. Prodisoconcha blanca. Escultura formada por líneas radiales finas, que cubren completamente la concha; en algunos ejemplares son visibles en la región posterior sólo con fuerte aumento; líneas concéntricas débiles, irregularmente distribuidas, más densas hacia el margen ventral; con finísimas líneas divergentes, superpuestas a las radiales, sólo en la región anterior y posterior, como en *N. (N.) pisum.* Región posterior delimitada por líneas radiales algo más fuertes que en el resto de la concha. Condróforo angosto. Dientes pequeños, anchos, obtusos (no agudizados); los anteriores varían entre 8 (ejemplares de menor tamaño) y 12 (mayor tamaño); los posteriores varían entre 4 y 6 en los mismos casos. Impresiones de los aductores desiguales, el anterior de mayor altura que el posterior. Impresiones de los músculos dorsal medio y ventral medio, continuas, ubicadas bajo un condróforo. Impresiones puntiformes no alineadas; dos de ellas más marcadas.

Anatomía Interna: Manto, glándula del biso, corazón, ganglios y musculatura pedal aparentemente similares a los de *N. sulcata, N. rugosa y Acila castrensis* y como en *N.* (*N.*) *pisum.* Riñón semejante al de *N. nucleus.*

Músculos dorsal medio y ventral medio, jun-

tos, situados aproximadamente debajo del condróforo. Haces musculares que fijan la masa visceral a la concha, separados y desiguales, ubicados en una línea curva, concordando con las impresiones que se observan en la cara interna de las valvas. Aductores anterior y posterior aproximadamente del mismo grosor, el posterior de sección más oval que el anterior.

Boca situada junto al aductor anterior. Palpos alargados, más altos en la región posterior junto al tentáculo.

Branquias grandes, de filamentos deltoídeos (tendiendo a lo triangular), siendo la rama externa de cada filamento de tamaño aproximadamente igual a la mitad de la rama interna.

Estómago de gran tamaño, la mitad de su altura corresponde al saco del estilo, que puede aparecer ensanchado o alargado dependiendo del grado de contracción del pie. Capuchón dorsal terminando sobre el lado izquierdo en un ciego digitiforme. Región dorso-lateral izquierda a la entrada del esófago, con cuatro pliegues. Con un gran saco (ciego) de posición dorsal a la región de selección del lado derecho, cuyo extremo se dirige posteriormente a la izquierda; sin repliegues en su interior. Tiflosol menor extendiéndose desde la proximidad de la abertura del esófago, rodeando el área de selección, hasta el saco del estilo. No existen otras áreas de selección. Aberturas de los divertículos digestivos situadas una bajo el esófago, ligeramente a la derecha, las otras dos sobre el lado izquierdo del estómago. Los conductos que nacen de las dos aberturas más próximas al esófago se dirigen hacia el lado derecho; el tercero lo hace hacia la izquierda. Intestino muy largo, con un enrollamiento notable y un tiflosol dorsal. A consecuencia del enrollamiento tan acentuado, el esófago y el estómago se hallan desplazados considerablemente hacia la izquierda.

Observaciones

La presencia en esta especie de un ciego estomacal no conocido o descrito anteriormente, nos lleva a sugerir el valor que este caracter podría tener en la separación de especies del género *Nucula*. Este ciego no se encontró en *N.* (*N.*) *pisum*.

Distribución Geográfica

Conocida sólo de la localidad tipo: frente a las Islas Juan Fernández (33°35′S; 78°31′2″W); en arena fina, entre 220 y 280 m de profundidad.

Nucula (N.) pisum Sowerby I, 1833
Figs. 4, 21, 22, 62–64, 97, 98

Nucula pisum Sowerby I, 1833: *Nucula* fig. 23 (Feb.); Sowerby I, in Broderip & Sowerby, 1833: 198 (13 March) (Localidad tipo: Valparaíso); Hanley, 1843: 172, lám. 20, fig. 23; d'Orbigny, 1846: 625; Hupé, 1854: 340; Hanley, 1856: 376, lám 20 fig. 12; Hanley, 1860: 153, lám. 229, fig. 133; Sowerby II, 1870: *Nucula* lám. 4, fig. 24; Philippi, 1887: 190, lám. 41, fig. 25 (Fósil en la Hacienda de la Cueva); Dall, 1909: 250; Hertlein y Strong, 1940: 387; Carcelles, 1950: 73; Soot-Ryen, 1959: 12, lám. 1, figs. 1, 2; Powell, 1960, 5: 170.

Linucula pisum (Sowerby), Dell, 1964: 144, lám. 2, figs. 7, 8; Ramorino, 1968: 183, lám. 1, fig. 4, lám. 4, fig. 2.

Nucula (Linucula) pisum Sowerby, Bernard, 1983: 10.

Material Estudiado

450 ejemplares (ej) y 8 valvas (v); MZUC. Procedencia: (1) 14 ej, 1.2–4.1 mm (No. 4653), Bahía Mejillones, Punta Cuartel (cerca Pta. Angamos); arena, 2–3 m. (2) 61 ej, 2–5 mm (No. 4604), Coquimbo, Bahía La Herradura (29° 57′S; 71°22′W). (3) 3 ej, 6 v. 2.8–3.5 mm (No. 4594), M.Ch.I, Est. 1, frente a Coquimbo (29°57.4′S; 71°22.4′W); fango conchífero, 82–88 m. (4) 1 ej s, 2.4 mm (No. 4590), M. Ch. I, Est. 20–21, al S de Coquimbo (31°51.5′S; 71°35′W); restos de conchas, 88 m. (5) 150 ej, 1.5–4 mm (No. 4735), Bahía de Valparaíso (33°S); fango, 200 m. (6) 20 ej s, 2–3.4 mm (No. 4675), M. Ch.I, Est. 39, Chile central (34°08.4′S; 72°02.5′W); fango-arena, 90 m. (7) 185 ej, 2.3–4 mm (No. 4683–4685, 4688, 4690, 4693, 4698, 4699, 4701, 4718, 4721, 4722, 4725, 4728), draga van Veen, Bahía de Concepción (36°S); fango, 10–27 m. (8) 7 ej s, 2.5–3.8 mm (No. 4596), M. Ch. I, Est. 68, frente a Arauco (37°06′S; 73°38′W); arena gruesa-roca y "cascajo", 58 m. (9) 1 ej s, 2.7 mm (No. 4595), M. Ch. I. Est. 77, al S de Lebu (38°16′S; 73°41′W); fango, arena fina, 120–160 m. (10) 4 ej, 2–3 mm (No. 4737), M. Ch. I, Est. 79, al S de Lebu (38°16′S; 74°06′W); fango-arena fina, 110 m. (11) 1 ej, 2 mm (No. 4681), M. Ch. I, Est. (117) X 1, Golfo de Concorvado (42°55′S; 72°55′W); arena-fango-cantos, 190 m. (12) 3 ej, s, 2.2–3.3 mm (No. 4549), Op. Centolla, Est. P5M2, draga

Petersen 0.1 m^2, E. de Magallanes, Bahía Inútil (53°30′S; 69°49′W); fango calcáreo, abundantes conchas, 46 m. (13) 3 ej 2.4–3 mm (No. 4550), Op. Centolla, Est. P4M2, draga Petersen 0.1 m^2, E. de Magallanes, Bahía Inútil (53°30′S; 69°49′W); fango calcáreo con conchas, 52 m. (14) 2 ej, 2v, 2.6–2.7 mm (No. 4551), Op. Centolla, Est. P4M1, draga Petersen 0.1 m^2, E. de Magallanes, Bahía Inútil (53°30′S; 69°49′W); fango calcáreo con conchas, 52 m. (15) 3 ej, 2.9–3 mm (No. 4739), Op. Centolla, Est. P5M6, draga Petersen 0.1 m^2, E. de Magallanes, Bahía Inútil (53°30′S; 69°49′W); fango con algas, esponjas, briozoos y conchas, 46 m. (16) 6 ej, 2.5–3 mm (No. 4554), Op. Centolla, Est. P5M5, draga Petersen 0.1 m^2, E. de Magallanes, Bahía Inútil (53°30′S; 69°49′W); fango calcáreo con conchas, 46 m.

Descripción

Concha: Concha pequeña (hasta 5 mm de longitud), subtrígona, oblicua y semiinflada, de aspecto vitreo, a veces con viso nacarado. Prodisoconcha frecuentemente blanca, muy prominente. Perióstraco crema o anaranjado, generalmente cubierto en las regiones anterior y posterior con depósitos de color rojizo. Umbos posteriores poco elevados. Bordes dorsal anterior y ventral levemente curvados; dorsal posterior extremadamente corto y curvo. Extremo anterior muy largo y arqueado, posterior casi truncado. Ornamentación de líneas radiales finas, visibles por transparencia, que nacen en los umbos y cubren toda la superficie; en el área lunular y escutelar se observan sólo con fuerte aumento. Estrías de crecimiento distribuídas irregularmente, más notorias hacia el borde dorsal o anterior y posterior; interrumpen a las radiales originando una aparente ornamentación reticulada. Areas lunular y escutelar más brillantes que el resto de la concha, cubiertas densamente con finas líneas divergentes. Margen ventral interno crenulado. Charnela con 7 a 14 dientes anteriores y 3 a 7 posteriores, según la talla del individuo; los dientes son aguzados y curvados hacia afuera. Condróforo piriforme, pequeño, dirigido anteriormente formando un ángulo casi recto con la corrida de dientes posteriores. Impresión del aductor anterior subcircular; la del posterior alargada verticalmente. Impresiones de los músculos medio-dorsal y medio-ventral contiguas, ubicadas muy cerca de la charnela, por delante del condróforo. Impresiones punctiformes cercanas a la charnela. La mayor situada a mitad de camino entre el aductor anterior y la impresión de los músculos medios; el resto, próximas a las impresiones de los músculos medios

Anatomía Interna: Bordes del manto lisos sin papilas. Glándula del biso grande. Glándula hipobranquial voluminosa cubriendo más de la mitad de las branquias y parte del palpo. Lamelas del palpo más altas en su parte media. Ctenidios grandes con sus ramas dirigidas anteriormente. Filamentos branquiales delgados y numerosos, con ambas ramas prolongándose sobre el eje; la rama externa es aflechada. Corazón con aurículas grandes; ventrículo alargado. Area de selección del estómago con pocos pliegues (no más de 10). Con sólo un área plegada (¿área de selección?) sobre la entrada del esófago. Intestino, relativamente largo, con pocas vueltas (no más de tres); su distribución varía individualmente, pero conserva un plan general, en forma de 8.

Observaciones

El tipo de *N.* (*N.*) *pisum* fue examinado por Dell (1964), y transferido al género *Linucula,* subgénero propuesto por Marwick (1931) para algunas especies fósiles neozelandesas. Dell (1956) describió las primeras especies vivientes de Nueva Zelandia y discutiendo una de ellas, concluyó que la escultura divergente tan peculiar a estas especies, su restricción geográfica a Nueva Zelandia y la historia del grupo durante el terciario, permitían considerarlo como un género. Dell (1964) al discutir nuevamente la posición de *Linucula,* fundamentó el género en la combinación de los siguientes caracteres: "Margen crenulado, a menudo extendiéndose alrededor de las valvas; radiales bien marcadas; escultura divergente sobre la lúnula y el escutelo y falta de hinchamiento." Maxwell (1988), siguiendo a Dell (1964), lo considera digno de rango genérico.

El estudio de la concha de *N.* (*N.*) *pisum* y de *N.* (*N.*) *fernandensis* mostró (Villarroel, 1971), que ambas especies presentan los caracteres descritos por Dell (1956, 1964) para el género *Linucula* y que, en consecuencia, este último se diferenciaría del género *Nucula* sólo por la presencia de las líneas finísimas que cruzan a las radiales en la lúnula y escutelo, dando la impresión de di-

vergencia. Sin embargo, Villarroel (1971) considera que el valor taxonómico de estas líneas parece relativo, ya que además de constatar diferencias en estas dos especies en la charnela y en la forma y disposición de los distintos órganos, *N.* (*N.*) *fernandensis* presenta un ciego posterior en el estómago que existe también en *N.* (*N.*) *pseudoexigua* y *N.* (*N.*) *falklandica,* pero no en *N.* (*N.*) *pisum.* Este ciego podría corresponder a un carácter filogenético importante, pero ésto podrá ser valorado sólo cuando se estudie la anatomía de las especies neozelandesas de *Linucula.*

La variación en el número y forma de los dientes no permite utilizarlos como caracteres de valor genérico o supragenérico, ya que varía considerablemente con el crecimiento en una misma especie y aún en individuos del mismo tamaño; sin embargo, la forma y el tamaño de los dientes presentan a menudo valor específico, como lo han hecho notar algunos autores (Knudsen, 1970; Villarroel, 1971).

En esta especie es común encontrar epizoos tubícolas sobre las valvas, los que se ubican preferentemente en las áreas dorsal anterior y posterior, además de, o en lugar de los depósitos de color rojizo que la caracterizan.

Distribución Geográfica

Bahía de Mejillones (Antofagasta) a Estrecho de Magallanes.

La distribución de *N.* (*N.*) *pisum,* que hasta hace poco sólo se conocía para la localidad tipo de Valparaíso, fue ampliada por Ramorino (1968) hacia el S hasta Chiloé. El abundante material aquí estudiado permite, sin lugar a dudas, extender su distribución por el N, hasta Bahía Mejillones (Antofagasta) y hacia el S, hasta el Estrecho de Magallanes y Bahía Inútil. Las localidades de recolección estudiadas permiten, además, demostrar la continuidad de su distribución entre Antofagasta y el Golfo de Corcovado, pero no existen datos que permitan asegurar tal continuidad desde el Golfo de Corcovado hasta el Estrecho de Magallanes. Esa zona ha sido muy pobremente muestreada.

Hábitat

Esta especie se encuentra en un amplio rango de distribución vertical, desde 8 a 200 m, en fondo arenoso, arena fangosa y fango arenoso.

Se encontró gran diferencia de densidad de *N.* (*N.*) *pisum,* al comparar los datos obtenidos por Ramorino (1968) en la Bahía de Valparaíso, con los logrados en la Bahía de Concepción. En esta última, la profundidad máxima de rastreo fue de 50 m (no existen profundidades mayores), encontrándose *N.* (*N.*) *pisum* sólo entre 10 y 27 m con una densidad de aproximadamente 30 ejemplares/m^2. En cambio, en la Bahía de Valparaíso se rastreó hasta los 200 m, encontrándose la densidad mínima (465/m^2) en zona arenosa entre 20 y 50 m y una máxima (848 ejemplares/m^2) en fango arenoso entre 51 y 80 m.

Ambas coinciden, sin embargo, al demostrar la mayor densidad en un substrato de fango arenoso.

Nucula (N.) pseudoexigua sp. nov.
Figs. 18–20, 65–67, 104–106

Material Estudiado

9 ejemplares (ej) y 7 valvas (v); MZUC. Procedencia: (1) 1 ej, 4v, 2.5–4 mm (No. 10304, 10305, Paratipos), "Hero" 69-5, Est. 9 (201), Confluencia Canales Trinidad y Concepción (50°9′55″S; 74°43′75″W); arena y grava, 390–460 m. (2) 7 ej, 2.3–5.1 mm (No. 10306, 10308, Paratipos), "Hero" 69–5, Est. 57, (50°0′50″S; 74°14′10″W); fango, 223 m. (3) 1 ej s, 3.5 mm (No. 10293, Holotipo), 3v 3.2–3.5 mm (No. 10307, Paratipos), "Hero" 69-5, Est. 211, Canal Sarmiento (51°12′S; 74°9′W); fango, 500 m.

Localidad Tipo

Canales del sur de Chile entre 50°9′S; 74°43′W y 51°12′S; 74°9′W; 223 a 500 m de profundidad.

Descripción

Concha: Concha pequeña (hasta 5.1 mm de longitud), suborbicular, débilmente globosa, blanca, translúcida de aspecto vítreo con viso nacarado. Prodisoconcha blanca, opaca, lisa. Perióstraco amarillo verdoso claro. Umbos poco prominentes. Borde dorsal anterior arqueado y formando un ángulo con el borde ventral curvado; borde posterior suavemente arqueado, no truncado. Ornamentación de las valvas formada por costillas concéntricas, fuertes, espaciadas regularmente, cuya direc-

ción no cambia sobre las áreas dorsales; son más débiles sobre la lúnula y en algunos ejemplares se interrumpen en uno o dos puntos de su curso aparentando una bifurcación. Hay estrías radiales finísimas y densas sobre las concéntricas, que tienden a desaparecer hacia los extremos anterior y posterior. Lúnula delimitada por un surco débil. Areas dorsales con finas líneas microscópicas divergentes que cruzan a las radiales y las concéntricas. Superficie interna de las valvas lisa, transparentando la ornamentación externa; margen ventral interno crenulado. Dientes de la charnela fuertes, agudizados, curvados débilmente hacia afuera; se cuentan 7 a 12 anteriores y 4 a 7 posteriores, según la talla del individuo; en la valva derecha, el diente posterior al condróforo tiene una base equivalente a dos dientes juntos.

Anatomía Interna: Disco pedal con incisiones bien marcadas en sus bordes, los que aparecen parcialmente divididos. Glándula hipobranquial grande, cubriendo más de la mitad de la branquia. Palpos con un surco lateral externo notorio y tentáculo grande. Branquias con filamentos internos y externos casi iguales. Cavidad pericárdica ubicada detrás del condróforo. Corazón simétrico con el ventrículo alargado y globoso y las aurículas trilobuladas en su unión con los ventrículos. Estómago grande, con el área de selección mayor provista de numerosos repliegues (hasta 18); área de selección en la entrada del esófago (as[1]) muy desarrollada; ciego posterior del estómago, grande. Intestino largo, con dos surcos (tiflosoles), y no menos de cuatro vueltas.

Observaciones

Nucula (*N.*) *pseudoexigua* se caracteriza por su ornamentación de costillas concéntricas bien marcadas y difiere de *N. semiornata* d'Orbigny, 1846, del Atlántico, la especie que más se le parece, porque estas costillas no cambian de dirección abruptamente. En *N. semiornata* se observa un cambio de dirección en las estrías concéntricas, tan notorio como en *N. exigua* Sowerby I, 1833, una especie tropical circunscrita a la Provincia Panameña.

Probablemente sea esta nueva especie la que condujo a error a Dall (1908a) al citarla como *N. exigua* para el Estrecho de Magallanes; difiere de esta última principalmente por las costillas concéntricas que no sufren cambio de dirección sobre la lúnula y el escutelo, y por el menor inflamiento de las valvas.

Distribución Geográfica

Conocida sólo de la localidad tipo.

Hábitat

La mayor densidad de esta especie se encontró a una profundidad de 223 m en substrato de fango, disminuyendo entre 390 y 460 m en substrato de arena y grava; su menor abundancia se halló a 500 m, en substrato de fango.

Subfamilia Nuculominae Maxwell, 1988

Sin prismas radiales.

Género *Ennucula* Iredale, 1931

Ennucula Iredale, 1931: 202, 231. Especie tipo designación original: *Nucula obliqua* Lamarck, 1819.

Diagnosis

Concha subovalada a oval-alargada, moderadamente inflada; sin ornamentación externa conspicua, sólo provista de líneas de crecimiento. Margen ventral de las valvas liso. Condróforo notablemente oblicuo. Margen del manto provisto de papilas.

Especies encontradas en Chile:

1. *Ennucula grayi* (d'Orbigny, 1846)
2. *Ennucula puelcha* (d'Orbigny, 1842)
3. *Ennucula eltanini* Dell, 1990

Las revisiones de bivalvos chilenos recientes (Soot-Ryen, 1959; Dell, 1964, 1990), han concluído que existen cuatro especies de *Ennucula* en Chile: *E. colombiana, E. puelcha, E. grayi* y *E. eltanini.*

Ennucula colombiana (Dall, 1908a) fue descrita originalmente de Panamá, Colombia y Ecuador entre 29.5 y 401 brazas y citada también en el S de Chile, en 122 y 194 brazas (224.5 y 357 m) y en la costa W de la Patagonia, 51°12′S en 258 brazas (516 m). Su distribución en la parte S de Sudamérica fue mantenida por autores subsecuentes (Hertlein y Strong, 1940; Olsson, 1961 y Dell, 1964), pero Ramorino (1968) puso estas citas en duda al considerarlas como correspondientes a probables ejemplares juveniles de *E. grayi.*

La revisión de abundante material del área

magallánica permite concluir que existen ahí sólo tres especies de *Ennucula: E. eltanini, E. grayi,* y *E. puelcha.* Los juveniles de las dos últimas especies son fácilmente diferenciables; sin embargo, la conclusión de Ramorino (1968) de que los juveniles de *E. grayi* correspondan a la especie *E. colombiana* Dall (1908), no se justifica, ya que son los juveniles de *E. puelcha* los que se asemejan más a la descriptción de Dall y a las figuras de Olsson (1961: lám. 1, fig. 3, 3a). Parece poco probable que, de existir *E. colombiana* en la zona de Magallanes, se haya escapado al intenso muestreo de que ha sido objeto esa zona.

Dell (1990) describió la pequeña especie *E. eltanini,* de 4.1 × 3.2 mm, para la zona del Estrecho de Magallanes y Oeste de Tierra del Fuego entre 307 y 544 m. Esta especie se diferencía facilmente de *E. grayi* y *E. puelcha* por la prominencia de sus umbos y su pequeño condróforo.

La descripción y distribución de las dos especies estudiadas se discute a continuación.

Clave Para las Especies de *Ennucula* Estudiadas

1. Concha subovalada, inflada; margen dorsal anterior no elevado; lúnula plana, subcordada. Impresiones de los aductores conspicuas, sobre un área cóncava. Borde anterior del manto generalmente sin papilas; si las hay, sólo se las encuentra dorsal y anteriormente al aductor; bordes posteriores con papilas mameliformes . . . . . *E. grayi*

1'. Concha oval-alargada, poco inflada; margen dorsal anterior y área lunular de las valvas, elevadas. Impresiones de los aductores poco visibles y ubicadas en un área plana. Bordes del manto con papilas, las anteriores mameliformes y las posteriores digitiformes . . . . . *E. puelcha*

Ennucula grayi (d'Orbigny, 1846) (Figs. 8, 70, 71, 73, 107–109)

Nucula obligua Lamarck, Sowerby I, 1833: *Nucula* fig. 21, *non* Lamarck, 1819; Hanley, 1860: 156–157 lám. 229, fig. 150.

Nucula grayi d'Orbigny, 1846: 625; Hupé, 1854: 304; Sowerby II, 1870: *Nucula* lám. fig. 13. Mabille y Rochebrune, 1889: H112; Dall, 1909: 250; Hertlein y Strong, 1940: 385.

Nucula tanneri Dall, 1908a: 219, 367 (Loc. tipo: Estrecho de Magallanes en 369 brazas); Hertlein y Strong, 1940: 388; Carcelles, 1950: 73; Carcelles y Williamson, 1951: 322.

Ennucula grayi (d'Orbigny), Soot-Ryen, 1959: 13, lám. 1, fig. 3; Dell, 1964: 142, lám. 2, figs. 3–6; Linse, 1997: 45.

Nucula (*Leionucula*) *grayi* d'Orbigny, Bernard, 1983: 10.

Material Estudiado

85 ejemplares (ej) y 50 valvas (v); MZUC. Procedencia: (1) 1 v i, 14 mm (No. 4600), Exp. M. Ch. I, Est. 21–22, al S de Coquimbo (31°51′S; 71°40′30″W); fango-arena, 130–200 m. (2) 1 ej, 16 mm (No. 4736), Bahía de Valparaíso (33°S); fango. (3) 1 v i, 20.6 mm (No. 4564); IFOP 01, Est. 57, frente a Iloca (34°56′54″S; 72°19′30″W), 94 m. (4) 6 v, 16–17 mm (No. 4598 Exp. M. Ch. I, Est. 69, frente a Coronel (37°06′S; 73°38′W); roca, 96–100 m. (5) 1 ej s, 16 mm (No. 4599), Exp. M. Ch. I, Est. 79, al S de Lebu (38°16′S; 74°06′W); fango-arena fina, 110 m. (6) 13 v, 14–18 mm (No. 4676), Exp. M. Ch. I, Est. 77, Chile austral (38°16′S; 73°41′W); fango-arena fina, 120–160 m. (7) 1 ej s, 17 mm (No. 4567), Exp. M. Ch. I, Est. 90, Chile austral (39°03′S; 73°51′W); "cascajo", 174 m. (8) 1 ej, 2 v, 2–3.5 mm (No. 4738), "Hero" 69-5, Est. 210, draga Petersen 0.1 m^2, Bahía Corbeta Papudo (Guarello) (50°21′17″S; 75°17′25″W); fango amarillo verdoso, 70–78 m. (9) 23 ej, 2.5–4 mm (No. 4555), "Hero" 69-5, Est. 56, (51°0′50″S; 74°14′10″W); fango fino, 221 m. (10) 10 ej, 2–8 mm (No. 4615), "Hero" 69-5, Est. 213 (51°27′30″S; 74°03′W); fango, 722 m. (11) 40 ej, 24 v, 2–15 mm (Nos. 4617, 4619, 4621), "Hero" 69-5, Est. 280, draga Petersen 0.1 m^2, E. de Magallanes (53°17′18″S; 70°48′36″W); fango-arenoso, 180–210 m. (12) 2 ej, 14 mm (No. 4628), "Hero" 69-5, Est. 280 B, draga Petersen 0.1 m^2, E. de Magallanes (53°17′18″S; 70°48′36″W); fango con muy poca arena, 178,5 m. (13) 3 ej, 12–14 mm (No. 4629), "Hero" 69-5, Est. 280 C, draga Petersen 0.1 m^2, E. de Magallanes (53°17′18″S; 70°48′36″W); fango con muy poca arena, 179 m. (14) 3 ej, 3v, 13–14 mm (No. 4606), "Hero" 69-5, Est. 279 C, draga Petersen 0.1 m^2, E. de Magallanes (53°15′S; 70°50′18″W); fango, 156 m.

Descripción

Concha: Concha de regular tamaño (hasta 20.6 mm de longitud), gruesa subovalada, inflada, de color blanco amarillento, opaca. Perióstraco brillante, con bandas concéntricas irregulares de color oliva claro, que se alternan con bandas más oscuras y aumentan su tono hacia el borde ventral, llegando hasta

pardo negruzco. Con depósitos de un material oscuro en la región dorsal, que pueden llegar a cubrir la concha completamente. Umbos inflados, amplios, ubicados en el tercio posterior de la concha; ápices opistogiros. Borde dorsal anterior suavemente arqueado y casi el doble más largo que el posterior, que es recto; márgenes anterior, ventral y posterior redondeados. Ornamentación formada por estrías de crecimiento que, al cruzar el borde del escutelo se dirigen en forma oblicua hacia los ápices y estrías radiales tenues e irregularmente dispuestas, visibles con mayor facilidad en la parte ventral y en los individuos jóvenes. Lúnula subcordada, plana junto a los ápices, delimitada por una línea más clara en el perióstraco; escutelo no delimitado. Interior de las valvas blanco verdoso, nacarado con brillo iridiscente, rara vez de color verde. Serie de dientes de la charnela formando un ángulo casi recto. Condróforo ancho. Impresiones de los aductores muy profundas y ubicadas en la mayor curvatura producida por el inflamiento de las valvas. Impresión de los músculos medios una más arriba que la otra. Impresiones puntiformes dispersas.

Anatomía Interna: Borde anterior del manto sin papilas; si existen son pequeñas, poco notorias y sólo ubicadas dorsal y anteriormente al aductor; borde posterior con papilas mameliformes. Palpos generalmente más anchos en la región media. Corazón con aurículas globosas; origen de la aorta anterior alejado del recto, junto a la aurícula. Estómago como en *E. puelcha.*

Observaciones

Ennucula grayi se presenta generalmente cubierta con depósitos oscuros color rojizo en la región dorsal principalmente. Las muestras de la zona sur se caracterizaron por la frecuencia de un epizoo Hidroídeo que cubría las valvas, ubicándose preferentemente en la región dorsal y en la ventral anterior.

Esta especie fue la que presentó el mayor tamaño entre los nucúlidos estudiados (20.6 mm de longitud).

Las diferencias de esta especie con *E. puelcha* se discuten en las observaciones de esta última.

Distribución Geográfica

Desde 45° Lat S en la Costa Atlántica al Estrecho de Magallanes y la costa de Chile, hasta Coquimbo (31°51′S) hacia el N.

Ramorino (1968) concluyó que las citas de *Ennucula savatieri* y *Nucula cardara* Dall, 1916, de San Diego por Parker (1964), eran sinónimos de *E. grayi,* lo que le permitió extender la distribución de esta especie hasta América Central y California. No existiendo mayor información taxonómica que lo justifique, tales citas nos parecen dudosas.

Hábitat

Las muestras estudiadas cubren toda el área de dispersión conocida de esta especie en la costa chilena, desde 31°51′S; 71°40′W (al S de Coquimbo) hasta el Estrecho de Magallanes, en profundidades de 94 hasta 722 m en substrato de fango arenoso, presentando una mayor abundancia entre 180 y 221 m.

Ennucula puelcha (d'Orbigny, 1842)
(Figs. 29–32, 72, 110–112)

Nucula puelcha d'Orbigny, 1842: 162 (Loc. tipo: Bahía San Blas, Patagonia); d'Orbigny, 1846: 644, lám. 84, figs. 24–26; Hanley, 1860: 156, lám. 230, fig. 149; Sowerby II, 1870, *Nucula* lám. 1, sp. 7 Figueiras y Sicardi, 1968: 258.

Nucula uruguayensis Smith, 1880: 320 (Loc. tipo: Río de la Plata); Smith, 1885: 229, lám. 18, fig. 12–12b; Pilsbry, 1897: 9; Smith, 1915: 97; Carcelles, 1994: 26; Figueiras y Sicardi, 1968: 258.

Nucula savatieri Mabille y Rochebrune, 1889: H112, lám. 8, fig. 2a–c (Loc. tipo: Canal Beagle.); Dall, 1908a: 367, lám, 18, fig. 11; Hertlein y Strong, 1940: 387; Carcelles, 1950: 73, lám. 3, fig. 62; Carcelles y Williamson, 1951: 323.

Nucula pigafettae Dall, 1908a: 219, 368 (Loc. tipo: Estrecho de Magallanes); Hertlein y Strong, 1940: 386; Carcelles y Williamson, 1951: 322.

Nucula agujana Dall, 1908a: 370, lám. 10, figs. 6, 7 (Loc. tipo: Punta Agujas, Perú).

Nucula (?) *agujana* Dall, Hertlein y Strong, 1940: 384.

Nucula felipponei Marshall, 1929: 6, lám. 4, figs. 10–12 (Río de la Plata; en estómago de *Micropogon undulatus* Linné).

Nucula (*Ennucula*) *puelcha* d'Orbigny, Schenck, 1939: 30, lám. 8, figs. 5–8.

Ennucula savatieri Mabille y Rochebrune, Soot-Ryen, 1959: 13.

Ennucula puelcha (d'Orbigny), Dell, 1964: 141.

Nucula (*Leionucula*) *puelcha* d'Orbigny, Bernard, 1983: 10.

Material Estudiado

34 ejemplares (ej) y 15 valvas (v); MZUC. Procedencia: (1) 1 ej, 10 mm (No. 4603), M. Ch. I, Est. 51, Chile central (34°56′S; 72°14′W); fango-arena, 50 m. (2) 1 ej, 10 mm (No. 4602), M. Ch. I, Est. 77, Chile central (38°16′S; 73° 41′W); fango-arena fina, 80 m. (3) 9 v, 14.4–16.2 mm (No. 4566), M. Ch. I, Est. 96, al S de Mehuín, Valdivia (39°59′55″S; 74°01′7″W); arena gruesa-cantos, 260–295 m. (4) 1 ej, 5 mm (No. 4601), M. Ch. I, Golfo de Ancud (42°55′S; 72°55′W); arena-fango-cantos, 190 m. (5) 4 ej, 4.6–10.5 mm, 1v, 4.5 mm (Nos. 4645, 4654), "Hero" 69-5, Est. 56, Puerto Bueno, Canal Sarmiento (51°0′50″S; 74°14′10″W); fango, 221 m. (6) 1 ej, 10 mm (No. 4608), "Hero" 69-5, Est. 279 C, E. de Magallanes (53°15′S; 70°50′3″W); arena fina con piedrecillas, 156 m. (7) 10 ej, 4 v, 10.3–12 mm (Nos. 4618, 4622), "Hero" 69-5, E. de Magallanes (53°17′18″-53°18′40″S; 70°48′36″-70°42′20″W); fango arenoso, 180–210 m. (8) 4 ej, 5–8 mm (No. 4635), "Hero" 69-5, Est. 280 B. E. de Magallanes (53°17′18″S; 70°48′36″W); fango arenoso, 178, 5 m. (9) 1 ej, 2v, 5 mm (No. 4638), "Hero" 69-5, Est. 244(27), E. de Magallanes (53°03′3″S; 71°46′36″W).

Descripción

Concha: Concha de regular tamaño (hasta 16.2 mm de longitud), subovalada, alargada en sentido antero-posterior, poco inflada, blanca. Perióstraco brillante, bandeado de tono oliva claro, rara vez pardo negruzco en su margen ventral; su color aumenta de intensidad en los adultos (algunos ejemplares poseen depósitos de color ferruginoso sobre la región dorsal). Umbos poco abultados con ápices levemente opistogiros. Borde dorsal anterior más largo que el posterior, elevado; borde anterior truncado, formando un ángulo con el borde ventral; bordes restantes redondeados. Ornamentación de las valvas formada por leves estrías de crecimiento, más aparentes hacia el margen ventral; estrías radiales tenues e irregularmente dispuestas, más conspícuas en la parte ventral y en individuos jóvenes. Lúnula de color más claro que el resto de la concha, levemente elevada, delimitada por una banda clara del perióstraco. Escutelo delimitado por un surco débil. Interior de las valvas generalmente verde intenso. Condróforo angosto. Impresiones de los aductores poco marcadas y ubicadas sobre un área casi plana. Impresiones de los músculos medios una al lado de la otra. La mayoría de las impresiones puntiformes se encuentran agrupadas cercanas al aductor anterior.

Anatomía Interna: Bordes anterior y posterior del manto con papilas; las anteriores como botones y las posteriores digitiformes. Palpos generalmente más anchos en la región posterior junto al tentáculo. Corazón con aurículas cónicas; origen de la aorta anterior cercana al recto. Estómago con el área de selección mayor (as) muy grande, con innumerables repliegues. Otras áreas de selección muy desarrolladas, especialmente as^2 que cubre el lado izquierdo y dorsal de la entrada del esófago. Con una vuelta en la región gástrica del intestino.

Observaciones

Ennucula puelcha se differencia de *E. grayi* por una menor convexidad y menor razón espesor/longitud de las valvas, una lúnula elevada, por poseer papilas en el borde del manto tanto en su borde anterior como posterior, y el origen de la aorta anterior junto al recto. Además, no alcanza nunca colores tan oscuros como *E. grayi* y sobre su superficie no se encontraron epizoos.

Según Dell (1964) tanto *E. puelcha* como *E. grayi* deberían considerarse como subespecies de una especie polítipica, dada el amplia área de superposición conocida para ambas especies y el número de formas (especies) descritas que han pasado a la sinonimia de la una y de la otra. Dell señala también que estudios de especies vivientes de *Ennucula* a nivel mundial, han mostrado que en cualquier área faunística es raro encontrar más de una especie.

Tal apreciación parece respaldada con el estudio de algunas partes de la concha, pero para precisar criterios definitivos de politipia es necesario considerar también el estudio comparativo de las partes blandas y la ecología de cada especie. Por el momento las diferencias indicadas justifican su separación.

Las vueltas de la región gástrica del intestino fueron consideradas por Yonge (1939) características de la familia Nuculanidae, como consecuencia de una mayor actividad; sin embargo, las encontramos también en *Nucula (N.) fernandensis* y en *Ennucula puelcha,* entre las especies de la familia Nuculidae aquí estudiadas (Figs. 24,30). Si la

función postulada por Yonge es correcta, este caracter indicaría que las especies nombradas son también muy activas, aunque hasta este momento es más cauto sugerir solamente que, este caracter se encuentra presente en algunas especies tanto de Nuculacea como de Nuculanacea, sin precisar una función determinada.

Distribución Geográfica

Desde el Estrecho de Magallanes a Río Grande do Sul por el Atlántico y hasta Punta Aguja, Perú, por el Pacífico.

Hábitat

Las muestras estudiadas cubren sólo parte del área de dispersión de esta especie. *Ennucula puelcha* es muy poco abundante; se encontró desde los 34°56'S (Chile central) hasta el Estrecho de Magallanes, entre 50 y 295 m de profundidad, en sustrato de fango arenoso. Su mayor densidad se obtuvo entre 180 y 210 m de profundidad. En las muestras del Estrecho de Magallanes se halló junto a *E. grayi, Tindaria virens* y *Yoldiella chilenica.*

Con anterioridad *E. puelcha* ha sido registrada en fondos de fango (como *E. pigafettae* Dall y *E. agujana* Dall) en profundidades que varían entre 77 y 1036 brazas (139 m y 186.4 m, respectivamente). Originalmente fue descrita sobre bancos de arenas someras que se descubren con la marea baja.

Superfamilia Nuculanacea H. Adams y A. Adams, 1858

Descripción

Concha algo alargada posteriormente, equivalva, inequilateral; parte anterior corta, redondeada y convexa, parte posterior generalmente más larga que la anterior; extremo angosto y a menudo rostrado. Apices orto u opistogiros. Ligamento interno o externo. Interior aporcelanado, rara vez nacarado. Charnela acodada o casi recta, con o sin condróforo. Generalmente con seno paleal. Con o sin glándula hipobranquial. Bordes del manto más o menos unidos. Aductor anterior más grande que el posterior. Ctenidios de posición horizontal, más o menos angostos, sujetos en toda su extensión. Corazón atravesado por el recto o ventral a él.

Nuculanidae H. Adams y A. Adams, 1858
(= Ledidae H. Adams y A. Adams, 1858)

Descripción

Concha alargada, rara vez entreabierta anteriormente. Ligamento generalmente interno, proyectado a veces hacia el margen dorsal, llegando a ser parcialmente externo. Interior aporcelanado. Línea paleal con seno paleal. Sifones desarrollados; por lo general, el exhalante forma un tubo completo y el inhalante es abierto ventralmente. Glándula hipobranquial pequeña, a veces, ausente. Corazón atravesado por el recto.

Los representantes recientes de esta familia viven en la actualidad en todos los mares y a distintas profundidades, preferentemente en fondos blandos.

Observaciones

Algunos autores utilizaron esta familia bajo el nombre de Ledidae, pero a pesar de que como fuera demonstrado por Bowen y Heppell (1966), Ledidae H. Adams y A. Adams, 1858, tiene 10 meses de prioridad sobre Nuculanidae, el nombre aceptado generalmente para esta familia ha sido Nuculanidae, lo que valida su conservación bajo los términos de Artículo 40(a) del Código Internacional de Nomenclatura Zoológica.

Subfamilia Nuculaninae H. Adams y A. Adams, 1858

Diagnosis

Concha alargada, dorsoventralmente angosta, generalmente fuerte; escultura concéntrica bien definida; rostro formado por extensión del margen posterodorsal cóncavo; umbo anterior; margen posteroventral cuando es sinuoso no es profundo; lumen de los sifones generalmente entero; intestino generalmente con una vuelta simple a la derecha del cuerpo.

Género *Nuculana* Link, 1807

Nuculana Link, 1807: 155. Especie tipo por monotipia: *Arca rostrata* Bruguière, 1789, *ex* Chemnitz MS; = *Arca pernula* Müller, 1779.

Leda Schumacher, 1817: 55, 172, 173, lám. 19, fig. 4. 551. Especie tipo por monotipia:

Arca rostrata Bruguière, 1789, *ex* Chemnitz MS, = *Arca pernula* Müller, 1789.

Otros sinónimos propuestos por Allen y Hannah (1986) son: *Exocholeda* Iredale, 1939; *Kamaleda* Iredale, 1939; *Zygonoleda* Iredale, 1939; *Eptoleda* Iredale, 1939; *Thestyleda* Iredale, 1929; *Scaeoleda* Iredale, 1929; *Politoleda* Hertlein y Strong, 1940; *Costelloleda* Hertlein y Strong, 1940; *Robaia* Habe, 1958.

Diagnosis

Concha con la parte posterior más o menos larga, a menudo arqueada y aguzada o redondeada; parte anterior más corta, elevada y redondeada; por lo general con ornamentación concéntrica. Apices pequeños opistogiros. Ligamento interno; cartílago del ligamento corto, colocado bajo el vértice, a veces dirigido oblicuamente hacia atrás. Sifones completamente unidos o al menos en parte. Seno paleal pequeño, poco profundo.

Observaciones

Dell (1955) aclaró la confusión que ha existido en la literatura sobre el uso del nombre *Nuculana* con preferencia a *Leda.* Plantea que *Leda* Schumacher, 1817, es un nombre sustituto para *Nucula* Lamarck, 1799, y en consecuencia no es válido. Por otra parte, *Nuculana* Link, 1807, tiene 10 años de prioridad y parece un nombre legalmente válido, conclusión aceptada por muchos investigadores, por ejemplo, Grant y Gale (1931), Prashad (1932), Cox (1940), Hertlein y Strong (1940), Fletcher (1945), Soot-Ryen (1959).

Savitskii (1969a) analiza la problemática del género *Nuculana* y agrega detalles de las razones que han creado tanta confusión. Entre ellas señala que se estableció el género *Leda* Schumacher, 1817, con la especie tipo: *Arca rostrata* Bruguière, 1789, *ex* Chemnitz ms, la cual Hanley (1860) presentó como un sinónimo de *Arca pernula* Müller, 1779. Lo anterior no solo demuestra prioridad, sino que también sinonimia. Además, Hanley (1860) al mismo tiempo aclaró que *Arca rostrata* Montagu, 1803, era diferente de *Arca rostrata* "Chemnitz, 1784."

Verrill y Bush (1897) al revisar los Ledidae y Nuculidae de la costa del Atlántico de Estados Unidos aceptan como especie tipo para el género *Leda* a *Arca rostrata* "Montagu" y propusieron limitar el género *Leda* a las especies *Leda pernula* (Müller); *L. cuspidata* Gould; *Leda caudata* Donovan, y *L. tenuisculata* (Couthouy), y otras. Esto último Savitskii (1969) lo invalida por las notables diferencias entre estas especies y la citada por Verrill y Bush (1897).

Savitskii (1969) propone agrupar a las *Nuculana* en dos grupos probables de subgéneros, el Grupo I, *Nuculana* Link, 1807, con la especie tipo *Arca pernula* Müller, 1779, con los tres subgéneros: *Nuculana* s.s., *Thestyleda* Iredale, 1929, y *Poroleda* Hutton, 1893, y el Grupo II, *Leda* Schumacher emend. Verrill y Bush, 1897 con la especie tipo *Arca rostrata* "Montagu, 1803," para seguir usando el nombre de *Leda* que ha sido empleado por tanto tiempo, con tres subgéneros: *Saccella* Woodring, 1925, *Lembulus* Risso, 1826, *ex* Leach ms, y *Borissia* Slodkewitch, 1938. Su agrupación nos permite separar muy bién a las especies de *Nuculana* y *Propeleda* aquí estudiadas.

Especies Estudiadas:

1. *Nuculana (Saccella) cuneata* (Sowerby I, 1833)
2. *Nuculana (Borissia) inaequisculpta* (Lamy, 1906)

Además de *N.* (*S.*) *cuneata* descrita originalmente para Valparaíso, y de *N.* (*B.*) *inaequisculpta* aparentemente restringida a la Península de Palmer, Antártica y archipiélagos vecinos, se han citado impropiamente para Chile otras dos especies recientes. *Nuculana (Saccella) acuta* Conrad, 1832, de la costa atlántica estadounidense, citada también por Dall (1909) para California, Golfo de Panamá y región al S de Valparaíso, es una especie diferente que no se encuentra en la costa oeste de las Américas (Hertlein y Strong, 1940) y no puede ser considerada un sinónimo de *N.* (*S.*) *cuneata* (Sowerby), como Dall concluyera.

Nuculana (*Saccella*) *callimene* Dall es otra especie descrita originalmente del Golfo de Panamá y mencionada también para Tomé, Chile. Sin embargo, como se discute más adelante, el registro de Tomé corresponde a *N.* (*S.*) *cuneata.* La presencia de *N. callimene* en Chile es dudosa y su validez debe ser confirmada, en primer lugar, por un estudio de su variación y anatomía, en la localidad tipo.

Clave para las Especies de *Nuculana* Estudiadas

1. Concha con un rostro corto. Ornamentación formada por costillas concéntricas fuertes que cubren toda la concha . . . *N.* (*S.*) *cuneata*

1′. Concha no rostrada. Ornamentación formada por costillas concéntricas débiles sólo en la parte central de la concha . . . *N.* (*B.*) *inaequisculpta*

Subgénero *Saccella* Woodring, 1925

Saccella Woodring, 1925: 15. Especie tipo por designación original *Arca fragilis* Deshayes, 1858, *ex* Chemnitz ms, = *Leda commutata* Philippi, 1844. Nuevo nombre para *Ledina* Sacco, 1898, (Dec.) *non Ledina* Dall, 1898 (Abril)

Diagnosis

Concha elongada-ovada con un angosto (o agudo) rostro y una más o menos marcada quilla posteroumbonal, típicamente con escultura de prominentes costillas marginales. Seno paleal más profundo que en *Jupiteria*. (Savitskii, 1969; Maxwell, 1988)

Nuculana (*S.*) *cuneata* (Sowerby I, 1833)
Figs. 7, 42, 43, 77–79, 115–118

Nucula cuneata Sowerby I, 1833: fig. 15 (Feb); Sowerby I, in Broderip y Sowerby I, 1833: 198 (13 March) (Loc. tipo: Valparaíso); Reeve, 1841: 111, lám 85, fig. 15; Philippi, 1860: 158; Philippi, 1887: 190, lám. 41, fig. 4.

Leda cuneata (Sowerby), d'Orbigny, 1846: 546; Hupé, 1854: 307; Hanley, 1860: 128, lám. 228, figs. 92, 93; Sowerby II, 1871, *Laeda* lám. 6, fig. 35a, b.

Nuculana cuneata Sowerby, Hertlein y Strong, 1940: 403, lám. 1, fig. 20; Soot-Ryen, 1959: 14.

Leda (*Jupiteria*) *callimene* Dall, 1908a: 372, lám. 17, figs. 3, 4 (ex parte Tomé, Chile, en 14 brazas).

Leda callimene, Dall, 1909: 250 (ex parte); Zetek, 1918: 37.

Nuculana callimene (Dall), Carcelles y Williamson, 1951: 324 (ex parte).

Nuculana (*Saccella*) *callimene* Dall, Hertlein y Strong, 1940: 393, lám. 1, fig. 13 (ex parte); Keen, 1958: 18, fig. 8; Olsson, 1961: 64, lám. 1, figs. 7a, b (ex parte); Keen, 1971: 29, fig. 21; Bernard, 1983: 12.

Nuculana (*Saccella*) *cuneata* Sowerby, Ramorino, 1968: 189, lám. 1, figs. 3, 8, lám. 4, fig. 3 (ex parte); Bernard, 1983: 12.

Material Estudiado

241 ejemplares (ej) y 5833 valvas (v); MZUC. Procedencia: (1) 48 ej, 92 ej s, 5719 v, 4–11 mm (No. 4562), M. Ch. I, Est. 1, Punta Tortuga, Coquimbo (29°57′24″S; 71°4′22″W); fango, conchilla, 82 m. (2) 83 ej s, 6–11 mm (No. 4680), M. Ch. I, Est. 2, Punta Tortuga, Coquimbo (29°57′24″S; 71°24′48″W); fango, conchilla, roca, 122 m. (3) 4 v, 2–8 mm (No. 4589), M. Ch. I, Est. 19, zona Norte (31° 51′54″S; 71°42′42″W); fango, 169 m. (4) 2 v, 4–6 mm (No. 4592), M. Ch. I, Est. 20, zona Norte (31°51′30″S; 71°35′W); conchilla, 200 m. (5) 22 v, 3–9 mm (No. 4584), M. Ch. I, Est. 37, Valparaíso (33°06′S; 71°47′W); fango, 135 m. (6) 1 ej s, 7 mm (No. 4572), M. Ch. I, Est. 74, frente a Punta Talca (33°25′S; 71°43′W); fango, 52 m. (7) 7 ej, 4 v d, 4–7 mm (No. 4734), Bahía de Valparaíso (33°S). (8) 3 ej s, 4–8 mm (No. 4678), M. Ch. I, Est. 39, Chile central (34°8′24″S; 72°2′30″W); fango, arena, 90 m. (9) v i, 3–4 mm (No. 4587), M. Ch. I, Est. 40, Chile central (34°6′48″S; 72°30′W); arena, 28 m. (10) 7 ej, 5–9 mm (No. 4591), M. Ch. I, Est. 41, Chile central (34°56′S; 72°9′W); arena, fango, trozos de roca, 160 m. (11) Restos de v (No. 4574), IFOP 01, Est. 61, frente a Carranza (35°38′S; 72°39′W); conchilla, 107 m. (12) 3 v d, 4 v i, 5–8 mm (No. 4585), M. Ch. I, Est. 64, frente a Bahía Concepción (36°32′S; 73°21′W); fango, 125 m. (13) 4 v i, 5 v d, 5–8 mm (No. 4573), IFOP 01, Est. 73, frente a Dichato (Punta Iloca y Tumbes) (36°32′S; 72°57′W); 76 m. (14) 47 v, 3–8 mm (Nos. 4687, 4689, 4696, 4706, 4708, 4710, 4712, 4714, 4726, 4729), draga van Veen, Bahía de Concepción; fango, 16–23 m. (15) 7 ej, 12 v, 3–6 mm (Nos. 4557, 4559, 4560), Golfo de Arauco (37°13′S; 73°19′W); fango arenoso, 60–65 m. (16) Restos de v (No. 4679), M. Ch. I, Est. 77, zona Sur (38°16′S; 73°41′W); fango, arena fina, 120–160 m. (17) 4 v, 4–6 mm (No. 4558), M. Ch. I, Est. 108, al S de Mehuín, Valdivia (40°54′S; 73°56′W); fango, 136 m. (18) 1 v, 5 mm (No. 4571), IFOP 01, Est. 31 frente a Islas Juan Fernández (33°35′S; 78°31′12″W); arena, 220–280 m.

Descripción

Concha: Concha de regular tamaño (hasta 11.5 mm de longitud), subtriangular, gruesa,

blanca. Perióstraco blanco, ocre o amarillento. Umbos inflados con los ápices adyacentes, débilmente opistogiros. Márgenes redondeados. Parte posterior poco alargada, suavemente cóncava; extremo curvado. Ornamentación formada por numerosas costillas concéntricas, separadas por surcos subiguales, más densas en la base; cubren toda la concha, excepto en un angosto espacio cercano a la carena radial dorso-posterior, donde son casi obsoletas. Con un surco débil que se extiende desde los umbos hasta la base del margen anterior. No hay lúnula ni escutelo, pero la carena radial marcada y el área dorsal posterior plana forman un pseudoescutelo con finas costillas longitudinales. Interior de las valvas blanco arcilloso. Charnela acodada con dientes fuertes, sólidos; la serie posterior con 2 ó 3 dientes menos que la anterior y separada de ella por un condróforo triangular, profundo, ubicado directamente bajo los ápices. Línea paleal bien marcada, seno paleal poco profundo, aguzado hacia atrás. Impresiones de los aductores pequeñas, bien marcadas y distintas; la anterior de doble tamaño que la posterior. Impresiones de los músculos medios, adyacentes, bein marcadas, ubicadas bajo y ligeramente anterior al condróforo.

Anatomía Interna: Manto uniforme con un notable repliegue en todo su borde libre. Pie posteriormente muy geniculado. Glándula hipobranquial grande. Palpos labiales tan largos como los ctenidios con pliegues anchos y con su extremo posterior alargado en un filamento. Tentáculo del palpo relativamente pequeño; su inserción es muy anterior a la lamela del palpo. Ctenidios con filamentos gruesos y triangulares. Cavidad pericárdica bastante grande; origen de la aorta posterior junto a la unión del ventrículo con la aurícula. Estómago con sólo un área de selección (as). Riñón grande, poco lobulado. Sifones unidos en parte; inhalante incompleto.

Observaciones

Después de haber observado más de 1000 valvas de una de las muestras procedentes de Coquimbo, y de compararlas con las de otras localidades chilenas, se llega a la conclusión de que en Chile existe una sola especie de *Nuculana* que corresponde a *N.* (*S.*) *cuneata.* En la mayoría de las muestras se observan dos extremos de variación: uno corresponde a ejemplares con la concha proporcionalmente más alta y el umbo más inflado y el otro a conchas proporcionalmente más bajas con umbos menos inflados. La comparación de varias series de conchas de distintas localidades, demostró una gradación de forma que une a ambos extremos. Además, al hacer mediciones de una submuestra obtenida por cuarteo desde la muestra mayor que contiene alrededor de 6000 ejemplares (Punta Tortuga, Coquimbo; fango conchífero, 82 m), se constató que todos, sin excepción, presentaban: (1) la misma disposición de las costillas concéntricas, las que se hacen más densas a medida que se acercan al margen ventral; (2) una carena dorsal posterior que delimita un área que semeja a un escutelo; y (3) en la región anterior un débil surco que nace en el umbo y termina en el margen ventral. La anatomía y el interior de la concha no mostraron tampoco mayores diferencias. Probablemente fue este tipo de variación poblacional, lo que llevó a Dall (1908a) a identificar a ejemplares de Tomé con la especie *Nuculana callimene* (Dall, 1908) del Golfo de Panamá.

Los dos extremos de variación se muestran en las Figuras 117 y 118; esta última muestra un ejemplar que coincide con la figura y descripción de la especie de Dall, lo que sugiere que fueron ejemplares de este tipo los estudiados por él. Por otra parte, no hay referencias de que Dall haya visto ejemplares de *N.* (*S.*) *cuneata* al hacer la descripción de *N. callimene* o que haya considerado su existencia. A juzgar por las medidas del tipo y de otros ejemplares dados por Dall (1908a) y Olsson (1961) el tamaño de esta especie (15–16 mm) parece mucho mayor que el encontrado en los ejemplares más grandes de las muestras chilenas (11.5 mm), y en estas últimas son muy pocos los ejemplares que tienen la relación longitud-alto de *N. callimene.* Es factible que se trate de dos especies alopátricas.

Ramorino (1968) basándose en una información proporcionada por el fallecido Dr. Joseph Rosewater del United States National Museum comenta que "*N.* (*Saccella*) *cuneata* es muy parecida en su aspecto general a *N.* (*Saccella*) *callimene* (Dall, 1908), y que las posibles diferencias fundamentales estarían dadas por la cantidad de dientes charnelares y el radio G/A (la razón espesor/altura), aunque las tallas comparadas no son equivalentes." Efectivamente, el número de dientes anteriores y posteriores del ejemplar tipo (15.5 mm de longitud) es de 26 y 20, respec-

tivamente, mientras que el promedio de 11 ejemplares medidos por Ramorino con un tamaño (longitud) variable entre 5.96 y 9.60 mm fue de 10 a 17 dientes anteriores y 8 a 15 dientes posteriores. Ejemplares de Coquimbo de 11 mm de longitud presentaron un máximo de 18 dientes anteriores y 16 dientes posteriores, lo que corrobora y confirma que en ésta como en otras especies el número de dientes varía con la talla.

Es notable, sin embargo, que en la vista interior de un ejemplar del USNM de 15.5 mm (¿el Holotipo?) del Golfo de Panamá dada por Olsson (1961: lám. 1, fig. 7a) se cuentan sólo 17 dientes en la serie anterior y 19 (¿20?) en la serie posterior.

Distribución Geográfica

Desde Mejillones (23°S) hasta el S de Valdivia (40°54′S) y alrededor de las Islas Juan Fernández (33°35′S).

Hábitat

Las muestras estudiadas cubren toda el área de dispersión conocida. Se encontraron en profundidades entre 28 y 200 m, en substrato de fango arenoso y frente a las Islas Juan Fernández entre 220 y 280 m de profundidad, en arena.

Esta especie presenta su mayor abundancia entre Coquimbo y Valparaíso, disminuyendo hacia el S donde llega a ser más o menos rara. En *N.* (*S.*) *cuneata* al igual que *N.* (*N.*) *pisum,* y *M. chilensis,* se encontraron diferencias de densidad al comparar los datos obtenidos por Ramorino (1968) en la Bahía de Valparaíso, con los logrados en la Bahía de Concepción. En esta última se obtuvo una densidad de 10 ejemplares/m^2 (promedio de 10 muestras) en sustrato de fango entre 16 y 23 m, valor levemente inferior al obtenido por Ramorino (1968) entre 20 y 50 m de profundidad, en la Bahía de Valparaíso, igual a 15 ejemplares/m^2 en fondo de fango.

Por otra parte, los datos de este autor indican una mayor densidad en fango arenoso entre 121 y 200 m, en cambio en las muestras de las localidades que aquí se estudiaron, se encontró la mayor densidad entre 82 y 122 m en fango y fango conchífero.

Con anterioridad, *N.* (*S.*) *cuneata* había sido citada en fondo de arena gruesa y grava entre 14 y 45 brazas (Sowerby I, in Broderip y Sowerby I, 1833).

Subgénero *Borissia* Slodkewitsch, 1938.

Borissia Slodkewitsch, 1938: 78, 86. Especie tipo por designatión orígional: *Nuculana* (*Borissia*) *alferovi* Slodkewitsch, 1938. Mioceno de Tyushev del Este de Kamchatka; Kafanov y Savitskii, 1995: 87.

La posición taxonómica de *Borissia* fue discutida ampliamente por Savitskii (1978, *fide* Kafanov y Savitskii, 1995).

Diagnosis

Concha oblonga-ovada, marcadamente convexa; casi subequilateral. Margen posterior de la valva más amplio que el anterior. Umbos protruidos. Escultura externa en la forma de costillas amplias, bajas y contorneadas. Costillas dispuestas a través de toda la superficie, excepto el área posterior o limitadas a un triángulo umbonal. Líneas de crecimiento transversas en áreas separadas (Kafanov y Savitskii, 1995).

Nuculana (*B.*) *inaequisculpta* (Lamy, 1906)
Figs. 37, 38, 90, 121, 122

Yoldia inaequisculpta Lamy, 1906: 125, fig. 3 (Localidad tipo: Orcadas del Sur.); Lamy, 1910: 314; Lamy, 1911: 29, lám. 1, fig. 23; Carcelles, 1953: 209, lám. 5, fig. 99.

Nuculana (*sub gen.?*) *inaequisculpta* (Lamy), Soot-Ryen, 1951: 6.

Nuculana (*s. l.*) *inaequisculpta* (Lamy), Powell, 1960: 170; Dell, 1964: 144.

¿*Malletia sabrina* Hedley?, Nicol, 1966: 17, lám. 1, figs. 3, 5, *non Malletia sabrina* Hedley, 1916.

Nuculana inaequisculpta (Lamy), Egorova, 1991: 44, fig. 2.

Material Estudiado

14 ejemplares (ej) y 1 valva (v). MZUC. Procedencia: (1) 1 ej, 3 mm (No. 4556), Ant. XXII, Estrecho de Bransfield (62°58′6″S; 60°40′6″W); fango arenoso, 60 m. (2) 1 ej s, 2 mm (No. 4540), Ant. XXII, Est. 17, E. de Bransfield (62°58′6″S; 60°40′6″W); fango arenoso, 93 m. (3) 1 v erosionada (No. 4520), Ant. XIX, Bahía Foster, Isla Decepción (62°59′24″S; 60°34′W), 160 m. (4) 1 ej, 5 mm (No. 4517), Ant. XXII, Est. 50, E. de Bransfield (62°28′36″S; 59°40′30″W); fango, 123 m. (5)

4 ej, 5.9–12.5 mm (No. 4529), Ant. XXII, Est. 19, E. de Bransfield (62°29′24″S; 59°39′24″W); fango, 70 m. (6) 1 ej, 12 mm (No. 4537), Ant. XXII, Est. 35, E. de Bransfield (62°29′S; 59°42′36″W); arena y fango, 48 m. (7) 2 ej, 5–10.1 mm (No. 4510), Ant. XIX, E. de Bransfield (63°12′S; 58°35′W); 135–150 m. (8) 4 ej, 8.5–9 mm (No. 4518), Ant. XIX, Bahía Margarita, frente Islas Jenny y Adelaida (67°50′S; 68°45′S); 150 m.

Descripción

Concha: Concha de regular tamaño (hasta 12.5 mm de longitud), oval truncada, semirectangular, no rostrada; delgada y frágil, blanca. Bordes redondeados, excepto el posterior que es levemente truncado y oblicuo. Perióstraco de color variable, blanco a amarillo verdoso o pardo claro. Umbos poco prominentes, ligeramente anteriores; ápices rectos. Ornamentación de la concha formada por finas costillas concéntricas, poco elevadas, que dejan espacios subiguales entre ellas; bien marcadas en la región central de la concha; casi imperceptibles hacia los extremos anterior y posterior. Área comprendida entre la línea que une los ápices con la base del extremo posterior aplanada. Áreas dorsales anterior y posterior elevadas, surcadas finamente por la continuación de las costillas concéntricas que se dirigen hacia los ápices. Resilium cordado, casi completamente interno; sólo una parte muy pequeña se ubica externamente por delante y detrás de los ápices. Interior de las valvas blanco brillante. Línea paleal visible, con un seno paleal pequeño, no mayor que la impresión del aductor posterior. Charnela acodada, dientes fuertes de base ancha, de mayor tamaño en el centro de cada serie anterior y posterior, muy suavemente curvados hacia arriba; serie anterior con 2 ó 3 dientes más que la posterior. Impresiones de los aductores de la concha desiguales; anterior más marcada y de doble tamaño que la posterior.

Anatomía Interna: Manto con un repliegue fuerte, cercano al borde ventral, que se engruesa a medida que se acerca al extremo posterior, donde sufre uno o más repliegues sobre sí mismo. Pie casi recto, muy poco geniculado; disco pedal con crenulaciones poco notorias. Glándula hipobranquial ausente. Palpos labiales de regular tamaño, muy surcados; tentáculos más o menos del mismo tamaño que el palpo. Un par de repliegues hipertrofiados en la base del tentáculo. Ctenidios apegados al techo de la cavidad del manto, de filamentos gruesos. Cavidad pericárdica pequeña; corazón de aurículas y ventrículos tubulosos, éste último atravesado por el recto. Estómago con saco del estilo corto. Sifones bien desarrollados, pero pequeños; sólo el exhalante es cerrado, el inhalante está formado únicamente por repliegues del manto que se unen débilmente.

Observaciones

Dell (1964) ha hecho notar que en *N.* (*B.*) *inaequisculpta* la concha "tiene algo de Malletiidae, aunque la charnela esté interrumpida por un condróforo bien desarrollado y la escultura sea más bien de un Nuculanidae."

Las variaciones de la forma de la concha fueron dibujadas por Egorova (1991).

El estudio anatómico de esta especie, especialmente en lo que se refiere a la posición del corazón con respecto al recto, la forma y posición de los sifones, y la disposición general de los órganos en la cavidad del manto, permiten incluirla sin lugar a dudas en los Nuculanidae.

El par de repliegues hipertrofiados observados en la base del tentáculo del palpo de esta especie (Fig. 90) podría corresponder en función con "la pequeña extensión (flap) de la lamela interna del palpo que rodea a la base del apéndice" representada por Yonge (1939: fig. 35, po) en *Nuculana minuta, Yoldiella lucida,* y *Malletia obtusata.*

Distribución Geográfica

Orcadas del Sur, Shetland del Sur, Georgia del Sur, Archipiélagos de Palmer y Estrecho de Bransfield, Bahía Rybiy Khvost, Océano Indico (Antártica).

Hábitat

Nuculana (*B.*) *inaequisculpta* es una especie antártica muy poco abundante. En las muestras estudiadas, fue encontrada desde el Estrecho de Bransfield (62°S) hasta Bahía Margarita, frente a las Islas Jenny y Adelaida (67°S), en profundidades de 48 a 160 m con substrato de fango y fango arenoso. Presentó su mayor densidad y tamaño en substrato de fango a 70 m de profundidad. Egorova (1991) la encontró entre 20 y 150 metros.

Con anterioridad esta especie fue encontrada a profundidades mayores a las aquí expuestas. Dell (1964) la cita de las Orcadas del Sur entre 244 y 344 m y en el Archipiélago de Palmer entre 160 y 335 m de profundidad.

Género *Propeleda* Iredale, 1924

Propeleda Iredale, 1924: 181. Especie tipo por designación original: *Leda ensicula* Angas, 1877. Reciente de Australia; figurada por Hedley (1914: lám. 78, figs. 15, 16).

Diagnosis

Concha con un rostro largo y truncado; condróforo, oblicuo y angosto, dirigido hacia atrás; dientes de la charnela casi paralelos al borde.

Propeleda longicaudata Thiele, 1912
(Figs. 33–36, 74–76, 113, 114).

Propeleda longicaudata Thiele, 1912: 229, lám. 17, fig. 22 (Loc. tipo: Estación de Gauss, Mar de Davis, Antártica.); Iredale, 1924: 186; Powell, 1951: 77; Powell, 1960: 170; Dell, 1964: 146; Nicol, 1966: 13, lám. 2, figs. 2, 4.
Poroleda longicaudata (Thiele), Hedley, 1916: 18.
Nuculana (*Poroleda*) *longicaudata* (Hedley), Soot-Ryen, 1951: 5.
Propeleda longicaudata (Thiele, 1912), Linse, 1997: 46.

Material Estudiado

35 ejemplares (ej) y 41 valvas (v); MZUC. Procedencia: (1) 1 ej, 18.2 mm (No. 4506), Ant. XIX, Bahía Margarita entre Islas Jenny y Adelaida (67°50′S; 68°45′W); cantos grandes, 150 m. (2) 1 ej, 1.2 mm (No. 4507), Ant. XXII, Est. 28, Isla Greenwich, Shetland del Sur (62°28′42″S; 59°38′30″W); fango arenoso, 93 m. (3) 14 ej, 9–18 mm (Nos. 4502, 4508, 4511, 4514), Ant. XIX, E. de Bransfield (63°12′S; 58°35′W); arena y piedrecillas, 135–150 m. (4) 8 ej, 41 v, 7–13 mm (Nos. 4610, 4627, 4642), "Hero" 69-5, Est. 201 (9), Confluencia Canales Concepción y Trinidad (50°9′55″S; 74°43′25″W); fango, 390–460 m. (5) 11 ej, 10–13.5 mm (Nos. 4646, 4652), "Hero" 69-5, Est. 56, Puerto Bueno, Canal Sarmiento (51°0′50″S; 74°14′10″W); fango, 215–220 m.

Descripción

Concha: Concha de regular tamaño (hasta 18.85 mm de longitud), sólida, muy comprimida, muy inequilateral; alargada posteriormente, con un rostro curvado hacia arriba; opaca, blanca. Perióstraco delgado, amarillo verdoso a pardo claro. Umbos inconspicuos con ápices opistogiros ubicados en el tercio anterior. Márgenes convexos (redondeados), excepto el dorsal posterior que es cóncavo y se eleva gradualmente a medida que se aproxima al margen posterior. Ornamentación formada por dos fuertes carenas (quillas) que nacen en el ápice y corren hasta el borde posterior, separándose paulatinamente; hay, además, costillas concéntricas muy densas sobre los umbos que disminuyen a medida que se aproximan al margen ventral y cambian su dirección abruptamente sobre las quillas dirigiéndose hacia arriba; con 1 a 5 cóstulas complementarias sobre las quillas. Lúnula alargada, con numerosas estrías muy finas, continuación de las concéntricas, que se dirigen oblicuamente hacia el ápice. Interior de las valvas blanco con brillo aporcelanado; con una carena posterior. Charnela acodada con dientes laminares alargados muy numerosos; los posteriores duplican en número a los anteriores. Base de los dientes proximales, de lados muy desiguales, formando prolongaciones laminares muy acentuadas. Resilium parcialmente externo y dividido, con la parte anterior de mayor tamaño que la posterior. Línea paleal poco visible; seno paleal del mismo tamaño que la impresión del aductor posterior. Impresiones de los aductores muy desiguales; la anterior redondeada, algo alargada verticalmente, la posterior de forma oval ubicada en la mitad de la parte posterior.

Anatomía Interna: Parte ventral del extremo posterior del manto reflejado hacia el interior; con 6-8 pequeños lóbulos. Pie grande. Glándula hipobranquial pequeña. Palpos labiales de tamaño regular, con un fuerte tentáculo. Ctenidios muy alargados de filamentos prolongados y gruesos. Ventrículo y aurículas alargadas, el primero atravesado por el recto. Estómago grande, con repliegues adicionales al área de selección mayor, pero separados de ésta (se asemejan a los de *Tindaria virens*, en la que son la continuación de los pliegues del área mayor); ciego dorsal muy surcado. Sifones incompletos, comunicados, formados

por un repliegue interno, posterior, que se abre ventralmente; en la parte interna del reborde posterior del manto hay dos proyecciones laterales en la base de los sifones.

Observaciones

El material estudiado permite corroborar la afirmación de Hedley (1916) y Powell (1951), de que los ejemplares de mayor tamaño de P. *longicaudata* tienden a ser proporcionalmente más angostos que los de menor tamaño; asimismo, el rostro tiende a alargarse desproporcionadamente al resto de la concha.

Las características anatómicas de esta especie no son muy diferentes a las observadas en las especies del género *Nuculana*. De hecho, *P. longicaudata* presenta solamente el cuerpo más alargado.

Distribución Geográfica

Mar de Bellinghausen, Mar de Davis, Tierra Adelaida, Mar de Ross, Archipiélago de Palmer, Orcadas del Sur, Shetland del Sur, Georgia del Sur, Costa Knox, Tierra Princesa Elizabeth (Thiele, 1912; Hedley, 1916; Soot-Ryen, 1951; Powell, 1951; Dell, 1964). Estrecho de Bransfield y Estrecho de Magallanes. Especie probablemente circumantártica.

Hábitat

Las muestras estudiadas cubren sólo en parte el área de dispersión de la especie. En las muestras procedentes del Archipiélago de Palmer, se halló esta especie en profundidades de 93 a 150 m, en substrato de fango arenoso, arena y "piedrecillas." En el Estrecho de Magallanes fue encontrada viviendo en profundidades de 215 a 460 m en fango.

Con anterioridad *P. longicaudata* había sido encontrada en profundidades mayores entre 487 y 512 m (Powell, 1951), entre 100 y 1080 m (Dell, 1964), y entre 64 y 1180 m (Linse, 1997).

Subfamilia Ledellinae Allen y Sanders, 1982

Concha robusta, moderadamente inflada, veneriforme u ovalada, con o sin rostro, escultura concéntrica generalmente presente, ocasionalmente con estrias radiales; umbo aproximadamente central; margen dorsal posterior convexo, margen ventral en ejemplares viejos ampliamente aplastado, margen posteroventral puede ser sinuoso; placa de la charnela bien desarrollada; ligamento interno y/o externo; intestino posterior con diversas configuraciones; músculos aductores, aproximadamente iguales en tamaño; sifones generalmente combinados para formar un lumen común; palpos por lo general con relativamente pocos pliegues (<30) (Allen y Sanders, 1982).

Género *Tindariopsis* Verrill y Bush, 1897

Tindariopsis Verrill y Bush, 1897: 59. Especie tipo por designación original: *Malletia* (*Tindaria*) *agathida* Dall, 1889. St. Kitts, en 687 brazas (1236.6 m) y al E de Tobago, Indias occidentales, en 880 brazas (1584 m).

Diagnosis

Concha con un rostro corto, definido por un lomo y un surco radial. Surco ligamental externo, posterior a los ápices, bien marcado. Hay una pequeña ranura bajo el ápice para una parte especializada del ligamento, que interrumpe la charnela.

Observaciones

Tindariopsis fue propuesto originalmente como un subgénero de *Tindaria* Bellardi, 1875, de la familia Malletiidae, sin que se conocieran sus características anatómicas. Verrill y Bush (1897) señalaron que "si tiene sifón y seno paleal podría formar un género distinto y ser referido a Malletinae." El estudio anatómico de la especie *Tindariopsis sulculata* (Gould, 1852), referida a este género, demostró que caracteres tales como el corazón atravesado por el recto y la presencia de seno paleal y sifones no completamente unidos, permitirían incluir a *Tindariopsis* tanto en la familia Nuculanidae como Malletiidae. Sin embargo, la inserción del ligamento parcialmente externo y un rostro formado por proyección del margen posterior de la concha, llevó a Allen y Sanders (1982) y Allen y Hannah (1986) a proponer reunir los géneros *Ledella* y *Tindariopsis* en la subfamilia Ledellinae, separándolos de otros Nuculánidos.

Entre los caracteres anatómicos estudiados en las especies incluídas en este trabajo,

un rasgo interno que caracteriza a *Tindariopsis* es la presencia de un corazón atravesado por el recto.

Tindariopsis sulculata
(Gould, 1852, ex Couthouy MS)
(Figs. 39–41, 80–82, 157–159)

Nucula sulculata "Couthouy," Gould, 1852: 424; Atlas, 1860, lám. 37, fig. 539a–e (Loc. tipo: Bahía Orange, Patagonia.); Johnson, 1964: 155.

Leda lugubris A. Adams, 1856: 49 (Loc. tipo: ?); Smith, 1881: 39; Mabille y Rochebrune, 1889: H113.

Leda sulculata ("Couthouy"), Hanley, 1860: 129; Mabille y Rochebrune, 1889: H113; Stempell, 1897: 17–28; Stempell, 1898a: 343, lám. 22, figs. 1, 5–8, 10, 11, lám. 23, figs. 19, 21, lám. 24, figs. 23–26, 28–31, lám. 25, figs. 33–38, 40, 41, 43 (Anat.).

Leda orangica Mabille y Rochebrune, 1889: H113, lám. 8, fig. 3 (Loc. tipo: Bahía Orange).

Tindaria (*Tindariopsis*) *sulculata* ("Couthouy"), Dall, 1908a: 390; Hertlein y Strong, 1940: 425; Soot-Ryen, 1959: 16; Powell, 1960: 171.

Tindaria sulculata ("Couthouy"), Dall, 1909: 251.

Tindariopsis ? sulculata ("Couthouy"), Dell, 1964: 149.

Material Estudiado

23 ejemplares (ej) y 76 valvas (v); MZUC. Procedencia: (1) 1 ej s., 8 mm (No. 4588), M. Ch. I, Est. 51, Chile central (34°56′S; 72°14′W); fango y arena, 50 m. (2) 1 ej s., 10.8 mm, 1 v d., 4.8 mm (No. 4664), M. Ch. I, Est. 76, Chile austral (38°16′S; 73°39′W); fango y arena fina, 66 m. (3) 8 ej s., 4–10 mm (No. 4586), M. Ch. I, Est. 91, Chile austral (39°03′S; 73°39′W); arena fina compacta, 71 m. (4) 10 v i, 6 v d., 4–11 mm (No. 4561), M. Ch. I, Est. (117) X-1, Golfo de Corcovado (42°55′S; 72°55′W); arena, fango y "piedras", 190 m. (5) 2 v i, 3 v d., 5–8 mm (No. 4623), "Hero" 69-5, Est. 206, draga Petersen 0, 1 m^2, Caleta Henderson (50°16′42″S; 74°48′28″W); fango con grava fina, 30 m. (6) 7 ej, 8–13 mm, 3 v d, 2 v i, 11–13 mm (No. 4640), "Hero" 69-5, Est. 58, Puerto Bueno (50°59′S; 74°13′W); fango con carbón, vidrios quebrados y escorias, parece algo negruzco, 18 m. (7) 25 v d, 7.5–13 mm, 21 v i, 11–13 mm (No. 4624), "Hero" 69-5, Bahía Isthmus, Península Zach (52°10′S; 73°37′W); fango, 32–40 m. (8) 5 ej, 4.5–13 mm, 1 v d, 11 mm (Nos. 4607 y 4631), "Hero" 69-5, E. de Magallanes, frente a Punta Arenas (53°17′S–53°18′40″S; 70°48′36″W–70°42′20″W); fango, 180–210 m. (9) 1 v d, 10 mm (No. 4644), "Hero 69-5, Est. 227, E. de Magallanes (53°14′42″S–53°14′54″S; 70°53′12″W–70°53.30″W); fango, 105 m. (10) 1 ej s, 10.8 mm, 1 v, 4.8 mm (No. 4649), "Hero" 69-5, Est. 48, E. de Magallanes, Bahía Fortescue (53°41′40″S; 72°0′45″W); grava con muchas algas rojas, 18 m.

Descripción

Concha: Concha de tamaño mediano (hasta 13.3 mm de longitud), triangular, alargada posteriormente, inflada, muy gruesa, blanca. Perióstraco delgado, pardo claro amarillento a casi negro. Umbos pequeños, ligeramente anteriores, con ápices levemente prosogiros. Margen posterior y dorsal anterior oblícuos, casi rectos; márgenes anterior y ventral redondeados; dorsal posterior ligeramente cóncavo, elevado en su extremo y generalmente aguzado. Ornamentación formada por costillas concéntricas (3–4 por mm) sobrepuestas unas a otras y muy poco curvadas; no llegan a los márgenes anterior ni posterior. Líneas de crecimiento más notorias en las regiones anterior y posterior, formando surcos que interrumpen a las concéntricas. Pequeña lúnula y escutelo delimitados por un leve surco que señala el término de las costillas concéntricas; con líneas de crecimiento muy finas. Interior de las valvas blanco, aporcelanado; con un área solevantada por un espesamiento detrás de la impresión del aductor anterior. Charnela acodada; dientes numerosos, hasta 14 anteriores y 19 posteriores, ligeramente curvados hacia arriba. Línea paleal bien marcada; seno paleal casi cuadrangular, no mayor que la impresión del aductor posterior; notorio por un engrosamiento de la concha. Impresiones de los aductores desiguales; anterior redonda; posterior ovalada. Hay también una impresión lineal única, oblícua, que sale por debajo de la ranura ligamentaria y llega hasta la cercanía de la impresión del aductor anterior.

Anatomía Interna: Bordes del manto lisos. No hay glándula hipobranquial. Palpos labiales muy grandes con tentáculo pequeño. Ctenidios muy pequeños. Corazón de ventrículo y

aurículas globosos, atravesado por el recto. Estómago con un área de selección (as) simple, cuyos repliegues sufren sólo una leve flexión; sin área de selección complementaria. Sifones pequeños, completamente unidos, pero abiertos ventralmente.

Observaciones

La ornamentació de la concha de *T. sulculata* es muy similar a la de la especie fósil *T. elegans,* que se trata posteriormente. Difiere de ella por la menor longitud y por la truncación de su extremo posterior.

Distribución Geográfica

Desde 34°S (Chile Central) hasta 35°41′S (E. de Magallanes), Islas Falkland y Río de la Plata, Argentina.

Hábitat

Las muestras estudiadas de esta especie cubren toda el área de dispersión de la costa del Pacífico. Se encontró en profundidades de 18 a 210 m en substrato de fango, fango arenoso, fango con escoria, arena fina y en grava con algas rojas.

Con anterioridad, *T. sulculata* había sido encontrada entre 13 y 300 m en fondo de arena gruesa con algo de fango (Soot-Ryen, 1959).

Familia Siliculidae Allen y Sanders, 1973

Concha alargada, extremadamente comprimida, entreabierta, sin escutelo; umbo pequeño, difícilmente visible a nivel del margen dorsal; placa de la charnela débil, dientes alargados, laminares; ligamento opistodético, interno, oblícuo; con sifones, el margen ventral del sifón inhalante formado por adhesión y no por fusión; láminas branquiales externas de la mitad del tamaño de las internas; boca ubicada muy posterior al músculo aductor; única vuelta del intestino posterior al lado derecho, o a la derecha e izquierda del cuerpo (Allen y Sanders, 1973).

Género *Silicula* Jeffreys, 1879

Silicula Jeffreys, 1879: 574, lám. 45, fig. 6, 6a. Especie tipo por monotopia: *Silicula fragilis* Jeffreys, 1879.

Diagnosis

Concha frágil, lisa, comprimida; muy inequilateral, soleniforme, truncada atrás y redondeada adelante; umbo en el tercio anterior, pequeño, obtuso. Condróforo oblicuo, dirigido posteriormente. Resilium casi totalmente interno, la parte externa obsoleta. Línea de la charnela casi recta; dientes lamelares, transversales; serie posterior más alargada; con menor número de dientes que la anterior. Seno paleal de profundidad variable.

Especies estudiadas:

1. *Silicula patagonica* Dall, 1908
2. *Silicula rouchi* Lamy, 1910

Además de la especie *S. patagonica* arriba señalada, Carcelles y Williamson (1951) han incluído también a *S. fragilis* Jeffreys, 1879, del Hemisferio Norte, en una lista de la fauna malacológica de las regiones Magallánica y Patagónica. La presencia de esta especie en el Hemisferio Sur es improbable.

Con objeto de completar el conocimiento de los caracteres anatómicos del género se incluye en esta revisión el estudio de la especie antártica *S. rouchi* Lamy, 1910.

Clave Para Las Especies
De *Silicula* Estudiadas

1. Concha con el extremo posterior redondeado; presenta su mayor altura junto a los umbos. Umbos abultados. Tamaño hasta 8 mm de longitud . . . . . .*S. patagonica*

1′. Concha con el extremo posterior truncado; presenta su mayor altura cerca del extremo. Umbos pequeños. Tamaño hasta 12 mm de longitud . . . . . .*S. rouchi*

Silicula patagonica Dall, 1908
Fig. 130

Silicula (Phaseolus) patagonicus Dall, 1908a: 392 (Loc. tipo: costa W Patagonia, 51°2′S).

Silicula patagonica Dall, Carcelles y Williamson, 1951: 324; Soot-Ryen, 1959: 14; Allen y Sanders, 1973: 283, fig. 23.

Material estudiado

1 ejemplar (ej) y 2 valvas (v); MZUC. Procedencia: (1) 1 ej, 5.7 mm (No. 4651), "Hero" 69-

5, Est. 56, Puerto Bueno, Canal Sarmiento (51°0′50″ S; 74°14′10″W); fango, 221 m. (2) 2 v, 8 mm (No. 4659), "Hero" 69-5, Est. 201, Confluencia Canales Trinidad y Concepción (50°9′55″ S; 74°43′25″W); fango, 460 m.

Descripción

Concha: Concha muy semejante a S. rouchi, pero más pequeña (hasta 8.4 mm), con el extremo posterior menos truncado y menos alto y el borde dorsal posterior más recto.

Anatomía Interna: Caracteres anatómicos muy semejantes a los de *S. rouchi.*

Observaciones

La comparación anatómica de *S. patagonica* con *S. rouchi* no estableció diferencias significativas. Aunque el ejemplar estudiado de *S. patagonica* era más pequeño que los de *S. rouchi,* (probablemente un juvenil), se considera que la conclusión anterior es válida, no así en el caso de la concha donde se encontraron diferencias que correspondían a la descripción original.

Pese a esto, es indudable que ambas especies necesitan una revisión basada en una mayor cantidad de ejemplares.

Distribución Geográfica

Conocida sólo desde Canal Sarmiento (51°02′30″ S; 74°08′30″W) hasta la confluencia de los Canales Trinidad y Concepción (59°9′55″S; 74°43′25″W).

Hábitat

Silicula patagonica parece ser una especie muy rara, ya que se encontró sólo un ejemplar vivo a 221 m de profundidad y 2 valvas a 460 m, en substrato fangoso. Con anterioridad, se conocía sólo de la localidad tipo donde fue colectada entre 223–544 m de profundidad en fango (Dell, 1990).

Silicula rouchi Lamy, 1911
Figs. 5, 14, 48, 49, 126

Silicula rouchi Lamy, 1911: 394 (Loc. tipo: Tierra Alejandro I); Lamy, 1911: 30-I, lám. 1, figs. 24, 25; Hedley, 1916: 18; Soot-Ryen, 1951: 6; Carcelles, 1953: 208; Powell, 1958: 171; Powell, 1960: 171; Dell, 1964: 147; Nicol, 1966: 15, lám. 1, figs. 1, 7; Allen y Sanders, 1973: 284, figs. 25–27; Egorova, 1982: 56, figs. 242–244; Dell, 1990: 16, fig. 13.

Material Estudiado

9 ejemplares (ej); MZUC. Procedencia: (1) 7 ej, 9–11.2 mm (Nos. 4500, 4508, 4509, 4515), Ant. XIX, Est. 2, E. de Bransfield (63°12′S; 58°35′W); fango, 135-150 m. (2) 1 ej roto (No. 4546), Ant. XXII, Est.22, draga Petersen 0.1 m^2, Isla Greenwich, Shetland del Sur (62° 28′30″S; 59°39′24″W); fango, 196 m. (3) 1 ej, 12 mm (No. 4523), Ant. XXII, Est. 56, draga Petersen 0.1 m^2, Isla Greenwich, Shetland del Sur, (62°25′48″S; 59°37′W); fango, 244 m.

Descripción

Concha: Concha de regular tamaño (hasta 12 mm de longitud), blanca, oblonga, alargada, comprimida lateralmente, delgada, frágil; entreabierta anteriormente. Parte anterior corta, semicircular; parte posterior más alargada. Borde dorsal recto; posterior oblicuamente truncado, formando casi un ángulo con el borde ventral. Perióstraco verdoso a pardo claro amarillento, con bandas más oscuras. Umbos ubicados en el tercio anterior; poco prominentes, de ápices agudos y levemente prosogiros. Ornamentación muy fina, formada por líneas de crecimiento muy densas; en la región anterior hay líneas radiales muy tenues, difícilmente observables en la zona adyacente a los umbos; en la región posterior existen dos o más surcos finísimos. Interior de las valvas de color blanco, aporcelanado, brillante. Ligamento casi totalmente interno dividido externamente en una parte anterior y otra posterior a los umbos. Línea paleal muy débil; seno paleal pequeño, ubicado inmediatamente debajo de la impresión del aductor posterior y no más grande que ella. Impresiones de los aductores poco notorias.

Anatomía Interna: Manto con pliegues y lobulaciones pequeñas, poco numerosas en la región posterior. Pie grande, muy geniculado. Sin glándula hipobranquial. Palpos labiales relativamente pequeños con surcos grandes; tentáculo del palpo con una base diferenciada de la lámina del palpo que llega hasta la proximidad de la boca. Ctenidios alargados, ubi-

cados en el techo de la cavidad del manto; filamentos triangulares con un gran poro lateral. Corazón tubular, delgado, atravesado por el recto. Estómago grande con repliegues complementarios a la gran área de selección (as). Intestino corto en forma de "S". Con un solo tubo sifonal. Tentáculo del sifón, largo y fino, ubicado sobre el lado izquierdo.

Observaciones

Algunos ejemplares presentan adherencias de color pardo rojizo sobre los umbos y los bordes anteriores.

Los ctenidios de los protobranquios han sido descritos tradicionalmente como no reflejados; sin embargo, en *Silicula rouchi* se observa un esbozo de reflejo de filamento externo (Fig. 5), correspondiendo en parte, a la condición hipotética intermedia postulada por Yonge (1959), entre la condición protobranquial y la condición filibranquial (Morton y Yonge, 1964).

Distribución Geográfica

Antártica: Shetland del Sur, Archipiélago de Palmer, Isla Alejandro, Tierra del Kaiser Wilhelm II, Tierra Adelaida, Tierra del Rey Jorge V, Tierra Oates y Mar de Ross (Dell, 1964).

Hábitat

Las muestras estudiadas cubren sólo en parte el área de dispersión de la especie. En el Estrecho de Bransfield se la encontró en profundidades de 135 y 150 m, en substrato de fango; en la Isla Greenwich de las Shetland del Sur, en 196 y 244 m, en fango. Se encontró un mayor número de ejemplares en la primera localidad mencionada.

Con anterioridad, *S. rouchi* fue encontrada en fondos de fango entre 160 y 355 m, en fondo de fango y cantos entre 278 y 500 m y en fondo de diatomeas en 720 y 826 m (Dell, 1964). En el Mar de Ross se encontró entre 311 y 1153 m (Dell, 1990).

Familia Sareptidae Stoliczka, 1871

Diagnosis

Concha generalmente frágil, marcadamente comprimida, ovalada o alargada, generalmente extendida posteriormente; puede o no ser rostrada, puede o no estar entreabierta; lisa o con finas líneas concéntricas de crecimiento; margen posterodorsal recto o convexo, raramente cóncavo; series de dientes de la charnela anterior y posterior interrumpidos; ligamento interno y/o externo puede estar ubicado en un condróforo; sifonado (Allen y Hannah, 1986).

Subfamilia Sareptinae Stoliczka, 1871

Diagnosis

Concha moderadamente grande, comprimida, alargada, ligeramente entreabierta anterior y posteriormente, levemente rostrada; escultura concéntrica fina, ocasionalmente con estrías oblicuas o radiales; ligamento en su mayor parte interno; sifones fusionados ventralmente, lumen completo.

Género *Yoldia* Möller, 1842

Yoldia Möller, 1842: 91. Especies citadas: "*Y. arctica, Nucula arctica* Gray" y "*Y. angularis* nob., *Nuc. Myalis* Couth.?" Especie tipo por designación posterior (ICZN Opinion 769 en 1966): *Yoldia hyperborea* Torell, 1859 (Nombre No. 1706), = *Nucula hyperborea* Gould, 1841, *ex* Lovén ms (*fide* Coan y Scott, 1997: 22).

Diagnosis

Algo similar a *Nuculana,* pero con la concha más delgada, subovada, débilmente rostrada, generalmente entreabierta posteriormente. Sin ornamentación; sólo con líneas de crecimiento. Charnela formada por dos series subiguales de pequeños dientes en forma de "v" invertida; condróforo grande, ubicado simétricamente entre las dos hileras de dientes. Sifones largos. Seno paleal profundo y amplio; el ápice en forma de "U" ancha.

Observaciones

Una discusión acerca de la designación de la especie tipo de *Yoldia* ha sido hecha por Grant y Gale (1931) y resumida por Hertlein y Strong (1940), quienes dan también una sinonimia detallada.

Subgénero *Aequiyoldia* Soot-Ryen, 1951

Aequiyoldia Soot-Ryen, 1951: 6. Especie tipo por designación original: *Yoldia subaequilateralis* Smith, 1875.

Diagnosis

Concha casi equilateral, débilmente rostrada. Charnela con escasos dientes, casi en igual número a cada lado; condróforo triangular y amplio. Márgenes del manto casi siempre con tentáculos solamente sobre los sifones.

Observaciones

Soot-Ryen (1951) creó este subgénero para las especies antárticas "que no están estrechamente relacionadas a las especies meridionales de *Yoldia* s. str," justificando su separación "en la apariencia general, los pocos dientes y algunas diferencias en la anatomía." Además de los dientes, la única característica anatómica que parece importante es la distribución de las papilas o tentáculos en los bordes del manto, por sobre los sifones, como se indica en la diagnosis.

Yoldia (*Aequiyoldia*) *eightsi* (Jay, 1839, *ex* Couthouy MS)
Figs. 44–46, 87–89, 128–129

Nucula eightsii Jay, 1839, *ex* Couthouy MS: 113, lám. 1, figs. 12, 13 (Loc. tipo: no indicada) (E. Coan, 1995, comunicación personal); Couthouy, in Jay, 1839 (*fide* Bernard, 1983).

Yoldia sp. n. Woodward, 1854: 270, fig. 182 (Loc. tipo: no indicada).

Leda (*Yoldia*) *eightsii* (Jay, 1839, *ex* Couthouy MS), Hanley, 1860: 142, fig. 164.

Leda (*Yoldia*) *woodwardi* Hanley, 1860: 140-141, pl. 226, figs. 17, 22 (sin localidad).

Yoldia woodwardi Hanley, Sowerby II, 1871: *Yoldia* lám. 1, fig. 2a, b; Pelseneer, 1903: 10; Lamy, 1906: 19; Lamy, 1910: 393; Lamy, 1911: 29; Melvill y Standen, 1914: 127; Carcelles, 1950: 74; Carcelles y Williamson, 1951: 325; Bernard, 1983: 13.

Yoldia cf. *woodwardi* Hanley, Linse, 1997: 46

Yoldia eightsii (Jay, 1839, *ex* Couthouy MS), Sowerby II, 1871; lám. 5, sp. 26; Smith, 1902: 211; Hedley, 1911: 3; Melvill y Standen, 1914: 127; Carcelles y Williamson, 1951: 325.

Yoldia kerguelensis Thiele y Jaeckel, 1931: 207, lám. 8, fig. 65; Gaillard, 1974: 6.

Yoldia subaequilateralis Smith, 1875: 73; 1879: 187, lám. 9, fig. 18; 1885: 242; 1902: 211; Gaillard, 1974: 6.

Yoldia (*Aequiyoldia*) *subaequilateralis* Smith, Soot-Ryen, 1951: 6; Powell, 1957: 114; 1960: 170.

Yoldia (*Aequiyoldia*) *woodwardi* Hanley, Soot-Ryen, 1951: 7, lám. 1, figs. 1–6; Carcelles, 1953: 208; Soot-Ryen, 1959: 15; Powell, 1960: 171; Bernard, 1983: 13.

Yoldia (*Aequiyoldia*) *eightsii* (Jay, 1839, *ex* Couthouy MS), Soot-Ryen, 1951: 6; Carcelles, 1953: 208.

Yoldia (*Aequiyoldia*) *eightsi* (Jay, 1839, *ex* Couthouy MS), Dell, 1963: 247, fig. 1; Dell, 1964: 146; Nicol, 1966: 11, lám. 1, figs. 6, 8; Rabarts y Whybrow, 1979: 177, figs. 3–5, 8–10, 14a, b, 15c, b; Bernard, 1983: 13; Dell, 1990: 10, figs. 2, 5.

Material Estudiado

259 ejemplares (ej) y 1 valva (v); MZUC. Procedencia: (1) 31 ej, 1–31.5 mm (No. 4503), Ant. XIX, Est. 16, Isla Decepción (62°59′24″S; 60°34W); fango, 97 m. (2) 4 ej, 22–30 mm (No. 4504), Ant. XIX, Est. 10, Bahía Chile, Puerto Soberanía (62°30′S; 59°41′W); fango, 25 m. (3) 17 ej, 4.5–31.8 mm (No. 4530), Ant. XXII, Est. 37, draga Petersen 0.1 m^2, Isla Greenwich, Shetland del Sur (62°28′24″S; 59°41′24″W); fango arenoso, 33 m. (4) 13 ej, 4.5–31.4 mm, (No. 4531) Ant. XXII, Est. 36, draga Petersen 0.1 m^2, Isla Greenwich, (62°28′42″S; 59°42′24″W); fango 33 m. (5) 1 ej, 32.5 mm (No. 4532) Ant. XXII, Est. 34, draga Petersen 0.1 m^2, Isla Greenwich, (62°29′S; 59°42′6″W); fango arenoso, 38 m. (6) 16 ej, 12.5–26 mm (No. 4533), Ant. XIX, Est. 10, Bahía Chile, Caletón Iquique, Isla Greenwich (62°30′S; 59°41′W); fango y cantos, menos de 10 m. (7) 1 ej, 28 mm (No. 4534), Ant. XXII, Est. 40, draga Petersen 0.1 m^2, Isla Greenwich (62°29′6″S; 59°40′30″W); fango arenoso, 44 m. (8) 1 ej, 24 mm (No. 4535), Ant. XXII, Est. 31, draga Petersen 0.1 m^2, Isla Greenwich (62°29′6″S; 59°41′W); fango arenoso, 39 m. (9) 2 ej, 31.7–32.5 mm (No. 4536), Ant. XXII, Est. 35, draga Petersen 0.1 m^2, Isla Greenwich (62°29′S; 59°42′ 36″W); fango arenoso, 48 m. (10) 1 ej, 28.4 mm (No. 4538), Ant. XXII, Est. 29 draga Petersen 0.1 m^2, Isla Greenwich (62°29′30″S; 59°40′6″W); fango arenoso, 49 m. (11) 1 ej, 12 mm (No. 4539), Ant. XXII, Est. 39, draga Petersen 0.1 m^2, Estrecho de Bransfield (62°28′54″S; 59°41′18″W); fango arenoso, 54 m. (12) 2 ej, 17 y 19.5 mm (No. 4541), Ant. XXII, Est. 17, draga Petersen 0.1 m^2, E. de Bransfield (62°58′6″S; 60°40′6″W); arena fina, fango, 93 m. (13) 5 ej, 3–5.5 mm (No. 4542), Ant. XXII, Est. 26, draga Petersen 0.1

m^2, Isla Greenwich, (62°28′22″S; 59°38′ 12″W); fango, 90 m. (14) 1 ej 35.5 mm (No. 4543), Ant. XXII, Est. 38, draga Petersen 0.1 m^2, Isla Greenwich (62°28′36″S; 59°41′ 36″W); arena, fango, 33 m. (15) 161 ej, 5.5–30 mm (No. 4544), Ant. XIX, Bahía Chile, Puerto Soberanía, (62°30′S; 59°41′W); fango, más o menos 25 m. (16) 1 v d, 13.3 mm (No. 4661), Base Antártica A. Prat. (17) 2 ej, 13.8 y 32.7 mm (No. 4505), Ant. XIX, Bahía Margarita frente a Islas Jenny y Adelaida (67°50′S–68°45′S); cantos glaciales, 150 m.

Descripción

Concha: Concha de regular tamaño (hasta 35.5 mm de longitud), subovalada, comprimida, gruesa, entreabierta anteriormente, blanca. Parte anterior ligeramente más larga que la posterior que es algo aguzada; bordes redondeados; el dorsal posterior levemente cóncavo, a veces anormalmente exagerado. Perióstraco amarillo verdoso en los juveniles a pardo oscuro en los ejemplares de mayor tamaño, más oscuro hacia el margen ventral; ocasionalmente con bandas concéntricas más oscuras. Umbos muy poco abultados, generalmente erosionados. Apices pequeños, opistogiros. Ornamentación formada por estrías de crecimiento finas y líneas radiales tenues, más notorias en los extremos anterior y posterior. Condróforo triangular. Resilium casi totalmente interno, dividido externamente en una parte anterior y otra posterior al condróforo, siendo la anterior de mayor tamaño. Interior de las valvas blanco, brillante, engrosado dorso posteriormente. Charnela formada por dos series subiguales de dientes fuertes, poco numerosos (hasta 12); la anterior con uno o dos dientes más que la posterior. Línea paleal débil; seno paleal subredondeado anteriormente, profundo, alcanzando hasta la altura del condróforo; posteriormente agudo. Impresión de los músculos sifonales pequeña y débil, ventral y posterior a la impresión del aductor.

Anatomía Interna: Manto de bordes gruesos especialmente sobre los sifones, con pequeñas papilas en la región anterior y posterior. Pie angosto, levemente geniculado. Masa visceral muy grande. Cavidad pericádica desplazada mucho más atrás del condróforo. Láminas del palpo muy angostas; tentáculo del palpo largo. Glándula hipobranquial pequeña. Estómago muy alargado con el área de selección mayor (as) dividida en dos regiones con diferente orientación de los pliegues ciliados; hay una área plegada adicional (¿área de selección?) sobre ella. Sifones firmemente unidos.

Observaciones

Yoldia (*A.*) *eightsi* es el protobranquiado de mayor tamaño existente en aguas antárticas.

Ejemplares de las muestras de Puerto Soberanía e Isla Decepción, presentan una concavidad dorsal posterior notoria por efecto de un crecimiento defectuoso, fenómeno observado por Dell (1963) al revisar el tipo. La comparación anatómica entre ejemplares que presentaban esta concavidad y otros normales no arrojó diferencias.

La sinonimia de esta especie fue aclarada por Dell (1963).

Peck y Bullough (1993) calcularon el incremento anual de crecimiento de *Y. (A.) eightsi* basados en una población de la Isla Signy, Antártica, en alrededor de 5 mo. Las edades para los individuos más grandes de la población (35 mm de largo) fueron calculados en ± 65 años. A los especímenes de 43 mm les calcularon 120 años. Estos mismos autores encontraron que en las zonas expuestas predominan los juveniles, lo cual explican se deba al efecto abrasivo de los iceberg sobre los bancos de *Yoldia* y a la inhibición del asentamiento de larvas por las altas densidades de individuos.

Otros autores como Davenport (1989), Rabarts (1970), y Nolan y Clarke (1993) encontraron tasas de crecimiento similares usando tres técnicas diferentes.

Distribución Geográfica

Yoldia (*A.*) *eightsi* es una especie ampliamente distribuida en la Antártica (Dell, 1990). Se la ha citado para las Islas Falkland, Georgia del Sur, Orcadas del Sur, Shetland del Sur, Islas Sandwich del Sur, Archipiélago de Palmer, Mar de Bellinghausen y Mar de Ross. Aunque considerada una especie con probable distribución circunantártica (Dell, 1964; Nicol, 1966), *Yoldia* (*A.*) *eightsi* ha sido encontrada con una distribución en parches alrededor del continente, Tierra del Fuego, Sur de Chile, hasta las Islas Kerguelen (Dell, 1990).

Rabarts y Whybrow (1979) aseveran que

Yoldia (*A.*) *woodwardi* es simpátrica con *Yoldia* (*A.*) *eightsi* en las Islas Falklands y en Tierra del Fuego.

Hábitat

En las muestras estudiadas fue encontrada en Isla Decepción, Archipiélago de Palmer, y Shetland del Sur en substrato de fango y cantos a menos de 10 m de profundidad; en fango arenoso entre 25 y 97 m y entre cantos glaciales en 150 m; en el Mar de Ross entre 4 y 55 m.

Con anterioridad, esta especie fue colectada entre 50 y 87 m de profundidad en fondos de cantos pequeños, arena con cantos, y arcilla arenosa con algas y cantos (Soot-Ryen, 1951), en fondos de arena entre 144 y 161 m de profundidad, arena verde, fango y conchas entre 135 y 144 m, en fango verde entre 244 y 344 m y en fondo rocoso entre 200 y 728 m (Dell, 1964).

Su rango total va de 4-824 m, pero es mucho más común en profundidades inferiores a los 100 m (Dell, 1990).

Yoldia (Aequiyoldia) eightsi cava relativamente poco comparada con otras especies de *Yoldia* (Davenport, 1989). Se alimenta principalmente de material orgánico presente en las capas superficiales de los sedimentos (Yonge, 1939; Davenport, 1988).

Subfamilia Yoldiellinae Allen y Hannah, 1986

Diagnosis

Concha pequeña, generalmente comprimida, ovalada o elíptica, ocasionalmente con un rostro mal definido, no entreabierta; lisa, o con escultura muy fina; ligamento anfidético, en gran parte interno; sifones de estructura variada, seno sifonal pequeño; intestino con configuraciones diversas (Allen y Hannah, 1986).

La atribución de esta subfamilia como Yoldiellidae Allen, 1978, y Yoldiellinae Allen, 1985, ha sido decretada *nomina nuda*, porque no hay suficientes caracteres para separlas de otras familias/subfamilias. Entre los autores que han seguido atribuyendo incorrectamente a la subfamilia está Oliverio (1993).

Género *Yoldiella* Verrill y Bush, 1897

Yoldiella Verrill y Bush, 1897: 55, figs. 3, 4, 11, 14. Especie tipo por designación original: *Yoldia lucida* Lovén, 1846 (ICZN Opinión 1306, en 1985); ilustrada como *Portlandia lucida* Lovén, por Sars, 1878: 37, lám. 4, figs. 8a., 8b; Schileyko, 1985: 171; Warén, 1978: 214; 1989: 226.

Diagnosis

Concha pequeña, frágil, ovalada, generalmente cuneiforme; cerrada o muy ligeramente entreabierta. Perióstraco satinado, iridiscente. Ligamento parcialmente externo; la parte interna, que es relativamente grande, interrumpe el margen de la charnela más o menos completamente y ocupa una ranura simple, generalmente delimitada por un lomo en la superficie inferior de la línea de la charnela. Seno paleal relativamente pequeño, generalmente indistinto. Sifones delgados y unidos sólo hasta la mitad de su longitud.

Especies Estudiadas

1. *Yoldiella ecaudata* (Pelseneer, 1903)
2. *Yoldiella chilenica* (Dall, 1908)
3. *Yoldiella indolens* (Dall, 1908)

Dall (1908a) describió para Chile cuatro especies de *Yoldiella,* como *Yoldia: Y. granula* del Estrecho de Magallanes, *Y. indolens, Y. chilenica,* y *Y. infrequens* de la zona de los canales al N del Estrecho de Magallanes. Ninguna de estas especies fue ilustrada originalmente, por lo que se presentan aquí por primera vez fotografías de *Y. chilenica* y *Y. indolens. Yoldiella infrequens* podría considerarse definitivamente como un sinónimo de *Tindaria virens* Dall, 1889, ya que así lo demuestran su descripción y las observaciones del tipo efectuadas por Soot-Ryen (1959).

Se incluye en este estudio a la especie *Y. ecaudata* (Pelseneer, 1903) de aguas antárticas.

Warén (1978, 1989) y Schileyko (1985) han hecho intentos basados en el análisis de las partes blandas para dilucidar la problemática de las especies atribuidas a este género. Desgraciadamente la calidad del material que estudiamos no nos permitió corroborar las observaciones hechas por ellos.

Clave Para las Especies de *Yoldiella* Estudiadas

1. Concha ovalada 2
1′ Concha subtriagular; hasta de 5.25 mm de longitud . . . . . *Y. indolens*
2. Concha muy inequilateral, con el ex-

tremo posterior alargado, dorsalmente recto y con un débil escutelo. Hasta de 12 mm de longitud . . . . . *Y. chilenica*

2′ Concha ligeramente equilateral, ambos extremos levemente aguzados; sin escutelo. Hasta de 3.5 mm de longitud . . . *Y. ecaudata*

Yoldiella ecaudata (Pelseneer, 1903)
(Figs. 83–86, 125)

Leda ecaudata Pelseneer, 1903: 22, figs, 77, 78 (Loc. tipo: Gaussberg y Archipiélago de Palmer); Thiele, 1912: 229, fig. 20, 20a.

Yoldiella ecaudata (Pelseneer), Soot-Ryen, 1951: 5; Carcelles, 1953: 208; Powell, 1960: 170; Dell, 1964: 145; Egorova, 1982: 55, figs. 234–237; Dell, 1990: 12, figs. 15, 16.

Material Estudiado

29 ejemplares (ej) y 3 valvas (v); MZUC. Procedencia: (1) 1 ej, 3.2 mm (No. 4575), Ant. XXII, Est. 61, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62°28′6″S; 59°30′48″W); fango, 188 m. (2) 2 ej, 1.5–3 mm (No. 4545), Ant. XXII, Est. 22, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62°28′S; 59°39′24″W); fango, 196 m. (3) 1 ej, 3.4 mm (No. 4569), Ant. XXII, Est. 48, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62°28′12″S; 59°40′6″W); fango arenoso, 73 m. (4) 2 ej, 3.1–3.3 mm (No. 4576), Ant. XXII, Est. 50, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur, (62°28′36″S; 59°40′30″W); fango, 123 m. (5) 1 ej, 2.5 mm (No. 4568), Ant. XXII, Est. 50, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62°28′36″S; 59°40′30″W); fango, 123 m. (6) 2 ej, 3.5 mm (No. 4228), Ant. XXII, Est. 59, draga Petersen 0.1 m^2, I. Greenwich, Shetland (62°28′36″S; 59°41′36″W); fango, 70 m. (7) 1 ej s, 3.1 mm (No. 4527), Ant. XXII, Est. 37, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62°28′24″S; 59°41′24″W); fango arenoso, 33 m. (8) 1 ej, 2.5 mm (No. 4525), Ant. XXII, Est. 41, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62° 27′12″S; 59°37′36″W), fango arenoso, 220 m. (9) 1 ej, 2 mm, 3 v, 2.5–3 mm (No. 4522), Ant. XXII, Est. 51, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62°28′48″S; 59°40′36″W); fango, 79 m. (10) 1 ej quebrado, 3.5 mm (No. 4521), Ant. XXII, Est. 20, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62°29′S; 59°39′42″W); fango, 61 m. (11) 1 ej, 3.5 mm (No. 4570), Ant. XXII, Est. 29, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62°29′30″S; 59°40′6″W); fango arenoso, 49 m. (12) 1 ej, 2 mm (No. 4524), Ant. XXII, Est. 30, draga Petersen 0.1 m^2, I. Greenwich, Shetland del Sur (62°30′S; 59°40′6″W); fango, 60 m. (13) 13 ej, 2–3 mm (Nos. 4501, 4513, 4516), Ant. I, Est. 2, E. de Bransfield (63°12′S; 58°35′W); fango, arena, "piedrecillas," 135–150 m. (14) 1 ej, 2 mm (No. 4519), Ant. I, Est. 1, I. Decepción, Bahía Foster; fango, arena y cantos pequeños, 160 m.

Descripción

Concha: Concha muy pequeña (hasta 3.5 mm de longitud), oval, ligeramente equilateral, con los extremos levemente aguzados. Perióstraco amarillo blanquecino, presentando, a veces, bandas más oscuras. Umbos prominentes de ápices levemente opistogiros, adyacentes. Sin ornamentación, pero con finas líneas de crecimiento irregularmente distribuídas. Interior de las valvas blanco brillante.

Anatomía Interna: Manto sobresaliendo de las valvas en algunos ejemplares, con un repliegue largo que rodea al margen ventral, y varios pequeños junto a los sifones. Glándula hipobranquial poco notoria. Palpos labiales de regular tamaño, con tentáculo fuerte. Ctenidios anchos, con numerosos filamentos. Cavidad pericárdica relativamente grande; corazón atravesado por el recto; aurículas y ventrículo globosos; estómago con saco del estilo pequeño; área de selección mayor con numerosos pliegues. Sifones unidos aparentando un sifón único. Tentáculo sifonal largo, sobre el lado izquierdo.

Observaciones

En algunos ejemplares el pie se encontró extendido fuera de las valvas y dirigido hacia atrás.

Distribución Geográfica

Antártica: desde 62°28′S a 70°S: Gaussberg y Archipiélago de Palmer (Dell, 1964). Parece tener una amplia distribución en aguas alrededor de la península Antártica. Descrita para el mar de Bellinghausen (desde 80°O a 92°O) ha sido posteriormente colectada en la Estación Gauss (90°E) del Mar de Davis y de la Península Antártica (Dell, 1990).

Hábitat

Las muestras estudiadas cubren sólo una parte del área de dispersión de la especie. Se encontraron ejemplares en la Isla Greenwich, Shetland del Sur, en profundidades de 60 a 196 m en substrato de fango arenoso; en Bahía Foster, Isla Decepción, en 160 m en fango con arena y cantos, y en el Estrecho de Bransfield entre 135 y 150 m, en fango con arena y cantos pequeños. Parece ser una especie abundante.

Con anterioridad, *Y. ecaudata* había sido colectada entre 278 y 500 m de profundidad fuera del Mar de Ross (Dell, 1964). En el Mar de Ross, se encuentra en profundidades entre 362 y 891 m con un único muestreo conocido a 2525 m (Dell, 1990).

Yoldiella chilenica (Dall, 1908)
Figs. 123, 124

Yoldia (*Yoldiella*) *chilenica* Dall, 1908a: 380 (Loc. tipo: Canal Sarmiento (51°52′S; 73° 41′W); en fango, entre 348 y 258 brazas (626.4 y 464.4 m); Hertlein y Strong, 1940: 416.

Portlandia (*Yoldiella*) *chilenica* (Dall), Carcelles y Williamson, 1951: 325.

Yoldiella chilenica (Dall), Soot-Ryen, 1959: 15.

Yoldiella (*Yoldiella*) *chilenica* (Dall), Bernard, 1983: 14.

Yoldia cf. *chilenica* (Dall), Linse, 1997: 46.

Material Estudiado

109 ejemplares (ej) y 541 valvas (v); MZUC. Procedencia: (1) 3 ej s., 3.5–5 mm (No. 4582), M. Ch. I, Est. X-3, Golfo de Ancud (42°S;73°W); fango, arena fina, 264 m. (2) 25 v, 1.5–7 mm (No. 4658), "Hero" 69–5, Est. 210, draga Petersen 0.1 m^2, Bahía Corbeta Papudo (50°21′17″S; 75°17′25″W); fango amarillo pardo, 70–78 m. (3) 17 ej, 4–7 mm (No. 4648), "Hero" 69–5, Est. 56, Puerto Bueno, Canal Sarmiento (51°0′50″S; 74° 14′10″W); fango, 221 m. (4) 5 ej, 3 mm, 4 v, 3–8.5 mm (No. 4632), "Hero" 69–5, Est. 211, Canal Sarmiento (51°12′S; 74°9′W); fango, 480 m. (5) 10 ej, 1.5–7 mm (No. 4616), "Hero" 69–5, Est. 213, Canal Sarmiento (51°27′ 30″S; 74°03′W); fango, 722m. (6) 3 ej, 7–7.5 mm, 10 v, 3–8 mm (No. 4625), "Hero" 69-5, Est. 279 C, draga Petersen 0.1 m^2, E. de Magallanes (53°15′S; 70°50′18″W); fango, 156 m. (7) 2 ej, 6.5–7 mm, 10 ej, 1.5–2.1 mm, 10 v, 1.5–2 mm, 16 v, 5–6.5 mm (No. 4630), "Hero" 69-5, Est. 280 C, draga Petersen 0.1 m^2, E. de Magallanes (53°15′18″S; 70°48′ 18″W); fango, 179 m. (8) 4 ej, 7–7.5 mm, 10 v, 3–8 mm (No. 4634), "Hero" 69-5, Est. 280, E. de Magallanes (53°17′18″S; 70°48′36″W); fango, 175 m. (9) 2 ej, 7 mm, 4 ej, 1.5–1.7 mm, 16 v, 3.5–7.5 mm (No. 4633), "Hero" 69–5, Est. 280 B, E. de Magallanes (53° 17′18″S: 70°48′18″W); fango, 178 m. (10) 422 v, 3–8.6 mm (No. 4609), "Hero" 69-5, E. de Magallanes, frente a Punta Arenas (53°17′18″S; 70°48′36″W); fango, 180–210 m. (11) 40 ej, 3–7 mm (No. 4620), "Hero" 69-5, frente a Punta Arenas, E. de Magallanes (53°17′18″S-53°18′40″S;70°48′36″W–70°42′20″W); fango, 180–210 m. (12) 9 ej, 28 v, 4–5 mm (No. 4612), "Hero" 69-5, Est. 201 (9), Confluencia Canales Concepción y Trinidad, (50°9′55″S; 74°43′25″W); fango, 460 m.

Descripción

Concha: Concha pequeña (hasta 11.5 mm de longitud), oval, alargada posteriormente, blanca, inequilateral, la parte anterior más corta y redondeada. Borde dorsal posterior ligeramente recto. Perióstraco amarillo pálido a amarillo verdoso y con bandas de tono más oscuro, de ancho y distribución variables. Prodisoconcha diferenciada. Sin ornamentación, pero con líneas de crecimiento muy finas. Escutelo débilmente impreso con los márgenes de las valvas elevados. Ligamento oscuro, anfidético. Interior de las valvas blanco, aporcelanado, muy brillante. Seno paleal amplio y corto, redondeado hacia adelante. Serie de dientes anteriores generalmente con dos dientes más que los posteriores.

Observaciones

No presenta diferencias anatómicas muy características que la separen de *Y. ecaudata* (descrita anteriormente), excepto que en esta última, el manto sobrepasa el margen de las valvas.

Distribución Geográfica

Desde el Golfo de Ancud (42°S; 73°W) al Estrecho de Magallanes (53°17′18″S; 70°48′36″W).

Hábitat

Con anterioridad, *Y. chilenica* se conocía sólo de la localidad tipo en el Canal Sarmiento.

En las muestras estudiadas se encontró en el Golfo de Ancud a una profundidad de 264 m, en substrato de arena fina y en el Estrecho de Magallanes en profundidades entre 70 y 722 m, en substrato fangoso. Su mayor densidad se observó entre 180 y 210 m de profundidad.

Es una especie muy abundante en los fondos fangosos del Estrecho de Magallanes. Se la encuentra viviendo preferentemente junto a *Tindaria virens* y *Ennucula grayi*.

Yoldiella indolens (Dall, 1908)
Fig. 127

Yoldia (*Yoldiella*) *indolens* Dall, 1908a: 381 (Loc. tipo: Costas del S. de Chile, Canal Messier (48°41′S; 74°24′W–48°9′S; 74° 36′W); 194 brazas (349.2 m), fango); Hertlein y Strong, 1940: 417.

Yoldia indolens (Dall), Carcelles y Williamson, 1951: 325.

Material Estudiado

2 ejemplares (ej) y 18 valvas (v); MZUC. Procedencia: (1) 1 ej, 2 mm, 4 v, 1.3–1.4 mm (No. 4520), "Hero" 69-5, Est. 280-C draga Petersen 0.1 m^2, E. de Magallanes (53°15′18″S; 70°48′36″W); fango, 179 m. (2) 1 ej, 2 mm, 6 v, 1.8–2.2 mm (No. 4626), "Hero" 69-5, Est. 280-B, draga Petersen 0.1 m^2, E. de Magallanes (53°17′18″S; 70°48′36″W); fango, 178 m. 3) 18 v, 1.5–2 mm (No. 4643), Hero" 69–5, Est. 210, draga Petersen 0.1 m^2, Bahía Corbeta Papudo (Guarello), (50°21′17″S; 75°17′25″W); fango, 70–78 m.

Descripción

Concha: Concha muy pequeña (hasta 5.25 mm de longitud), oval, inflada, translúcida; inequilateral con el lado anterior más corto. Extremos redondeados, el posterior con un débil ángulo superior. Perióstraco oliváceo, opaco, con 2 ó 3 bandas angostas más oscuras de distribución variable. Umbos amplios, abultados. Sin ornamentación. Interior de las valvas aporcelanado. Seno paleal pequeño. Dientes anteriores y posteriores en número igual.

Anatonia Interna: Partes blandas aparentemente como en *Y. ecaudata*.

Observaciones

El color blanquecino opaco de algunas valvas de esta especie pequeña, sugiere un cambio de aspecto por alteración de la concha al enterrarse en el fango. Además, por efecto del desgaste, algunas se ven equilaterales, sugiriendo las características de la especie *Y. granula* descrita por Dall (1908); sin embargo, estas valvas no presentan el diente distinto a los otros, mientras que en otras se constatan focos de calcificación incipiente.

Aunque los ejemplares estudiados no alcanzan el tamaño del ejemplar tipo (5.25 mm), se observan en ellos todos los rasgos de la concha que caracterizan e esta especie.

Distribución Geográfica

Estrecho de Magallanes entre 53°15′S y 53°17′S.

Hábitat

Con anterioridad, *Y. indolens* se conocía sólo de la localidad tipo en el Canal Messier, en substrato de fango a 349 m de profundidad. En las muestras estudiadas se encontró en el Estrecho de Magallanes en profundidades entre 70 y 179 m en sustrato fangoso.

Familia Malletiidae H. Adams y A. Adams, 1858

Diagnosis

Concha redondeada, alargada o veneriforme, a veces posteriormente aguzada o truncada; equivalva; inequilateral o equilateral. Charnela casi recta, con dientes más o menos numerosos; serie anterior con un número menor de dientes que la serie posterior. Ligamento externo, alargado, prominente, opisto o anfidético, o parcialmente interno, corto y alojado en una cavidad de las valvas. Apices orto u opistogiros. Con o sin seno paleal. Glándula hipobranquial grande. Corazón ventral al recto o atravesado por él. Ctenidios con un poro ventral. Sifones separados ventralmente o unidos por manojos de cilios o por tejido.

Los representantes recientes de esta familia viven en todos los mares, preferentemente en aguas profundas y fondos blandos.

Observaciones

El rango taxonómico de la familia Malletiidae ha sido muy discutido. Este taxón fue descrito originalmente como subfamilia de Nuculanidae por H. Adams y A. Adams (1858) y elevada de rango por autores posteriores, quienes la separaron de los Nuculanidae esencialmente por la presencia de un ligamento externo. Se sugería, así, dar importancia filogenética primaria a la utilización de la posición del ligamento en la clasificación de los protobranquios recientes y fósiles, incluyendo a la familia fósil Ctenodontidae, principalmente paleozoica. Sin embargo, Yonge (1939, 1959) al realizar un estudio anatómico y funcional de los protobranquios, concluyó que las características de *Malletia* y otros géneros incluídos tradicionalmente en esta familia no justificaban su separación, ya que no pasaban de ser nuculánidos especializados para vivir de preferencia en los fondos blandos de profundidad, donde la competencia es escasa. Este modo de vida estaría demostrado por una concha de apariencia delicada y más o menos comprimida lateralmente. Además, no serían diferentes, ya que mostrarían la misma anatomía básica y las mismas adaptaciones encontradas en todos los representantes vivientes de la familia Nuculanidae. Agregó, que el ligamento externo de *Malletia* no tendría mayor peso para indicar relación filogenética que el complejo total de una morfología y caracteres adaptativos esencialmente idénticos, por lo que sugirió reunir ambas familias. La validez de estos argumentos parecía irrefutable y así fue considerado subsecuentemente por algunos autores.

McAlester (1964), junto con reconocer el valor de las conclusiones de Yonge de que las diferencias en el modelo del ligamento no indican una divergencia filogenética primaria de los géneros nuculoides, hizo notar la falta de conocimiento sobre la morfología de otros géneros externamente ligamentados, que no se parecen mucho a *Malletia*. Concluyó, que un mayor estudio podría descubrir que estas formas son fundamentalmente diferentes tanto a *Malletia* como a otros nuculánidos vivientes, lo que fue corroborado con posterioridad por Sanders y Allen (1985). Sin embargo, el estudio anatómico comparativo de especies pertenecientes a los géneros *Malletia, Tindaria,* y *Tindariopsis* y las descripciones de las partes blandas de *Neilonella* y otras especies de *Malletia* y *Tindaria* dadas por Knudsen (1970), sugerían la utilización de caracteres adicionales para la diferenciación taxonómica de estos grupos, tales como las vueltas del intestino, la estructura de los sifones, la disposición de las áreas de selección del estómago y la posición del corazón en relación al recto. Como ya ha sido discutido, sólo el último de estos caracteres parece encerrar valor taxonómico a nivel de familia, ya que mientras las especies estudiadas de los géneros *Nuculana, Propeleda* (Nuculanidae), *Silicula* (Siliculidae), *Yoldia* y *Yoldiella* (Sareptidae) tienen un corazón atravesado por el recto, especies de los géneros *Malletia* (Malletiidae), *Tindaria* (Tindariidae), y *Tindariopsis* (Nuculanidae) tienen el corazón ventral al recto o atravesado por él.

La estructura de los sifones y del estómago parece presentar tendencias evolutivas múltiples (algunas de las cuales es necesario estudiar mejor) cuyo valor taxonómico es difícil de precisar. Así por ejemplo, *Malletia* presenta sifones completamente unidos y cerrados o abiertos ventralmente, mientras que en los otros géneros de Malletiidae y Nuculanidae, pueden estar separados o unidos parcial o totalmente y ventralmente abiertos, en parte o por completo. Las vueltas del intestino, pueden tener también algún valor taxonómico como lo ha sugerido Knudsen (1970). Sin embargo, sólo el estudio de un número mayor de especies de cada género permitirá en último término sancionar el valor de estos caracteres.

Las especies chilenas con estas características están incluídas en los géneros: *Malletia, Tindaria, Tindariopsis,* y *Malletiela.* Este último representado sólo por *M. sorror* Soot-Ryen, 1959: 18, lám. 1, figs. 4, 5. "Albatross" Est. 2791, costas SW de Chile en 677 brazas = 1218.6 m, es conocido sólo en la localidad tipo. Esta especie no se halló en las muestras estudiadas.

Género *Malletia* des Moulins,1832

Malletia des Moulins, 1832: 85. Especie tipo por monotipia: *Malletia chilensis* des Moulins, 1832.

Diagnosis

Concha de tamaño mediano, oval, comprimida lateralmente, alargada; posteriormente aguzada o redondeada; por lo general bastante delgada. Lisa o concéntricamente estriada. Interior subnacarado. Charnela con la serie posterior de dientes separada de la

anterior. Ligamento externo, alargado, prominente. Seno paleal grande y profundo. Sifones, completamente unidos, cerrados o abiertos ventralmente.

Especies Estudiadas

1. *Malletia chilensis* des Moulins, 1832
2. *Malletia patagonica* Mabille y Rochebrune, 1889

Otras tres especies recientes han sido descritas para Chile:
M. inequalis Dall, 1908; *M. magellanica* (Smith, 1875); y *M. hyadesi* Mabille y Rochebrune, 1889. La validez de algunas de estas especies se discute más adelante.

Clave Para las Especies Chilenas de *Malletia*

1. Extremo posterior aguzado . *M. magellanica*
1′. Extremo posterior redondeado o algo truncado 2
2. Extremo posterior redondeado; anterior más o menos truncado . . . . . .*M. chilensis*
2′. Extremo anterior redondeado; posterior algo truncado 3
3. Parte anterior mucho más larga que la posterior. Borde dorsal anterior redondeado. Sin escutelo . . . . . .*M. inequalis*
3′. Parte anterior más corta o igual. Bordes dorsal anterior y posterior casi rectos. Con escutelo . . . . . .*M. patagonica*

Malletia chilensis des Moulins, 1832
(Figs. 17, 50–53, 56, 91, 92, 133, 146, 147)

Malletia chilensis des Moulins, 1832: 85, lám. 1, figs. 1–8; H. Adams y A. Adams, 1858: 549, lám. 126, figs. 6, 6a; Chenu, 1862: 181, fig. 913; Kolbelt, 1881: 372, lám. 109, fig. 3; Tryon, 1884: 249, lám. 126, fig. 34 (expl. en lám. 126 como *Yoldia* (*Malletia*) *chilensis*); Fischer, 1886: 987, lám. 17, fig. 22; Verrill y Bush, 1897: 56, 60, fig. 9; Stempell, 1898a: 343, lám. 22, figs. 2, 3, 4, 9, 12; lám. 23, figs. 13–17; lám. 24, fig. 32 (Anat.); Stempell, 1902: 219; Dall, 1909: 251; Carcelles y Williamson, 1951: 322; Soot-Ryen, 1959: 16, figs. 1, b; Franc, 1960: 2074, fig. 1731; Dell, 1964: 148; Ramorino, 1968: 191, lám. 1, fig. 1, lám. 4, fig. 1.

Malletia (*Malletia*) *chilensis* des Moulins, Hertlein y Strong, 1940: 421; Bernard, 1983: 10

Solenella norrisii Sowerby I, 1833: 197 (Localidad tipo: Valparaíso); Reeve, 1841: 48, lám. 30, 4 figs.; Hanley, 1843: 17, fig. 8; Hanley, 1856?: 337; d'Orbigny, 1846: 543; Woodward, 1851–1856: 270, lám. 17, fig. 22; Hupé, 1854: 306; Deshayes, 1839: 270; 1850: lám. 34, figs. 5, 6, 7; Hanley, 1860: 164, lám. 226, figs. 1, 2 (var. *brevior*); Sowerby II, 1870: Solenella lám. 1, figs. 2a, b.

Material Estudiado

126 ejemplares (ej) y 53 valvas (v); MZUC. Procedencia: (1) 23 ej, 4.5–51 mm (No. 4733), Bahía de Valparaíso (33°S); fango, 45–100 m. (2) 1 ej s, 21.5 mm, 1 v rota, 19 mm (No. 4665) M. Ch. I, Est. 49, Chile central (34°56′S; 72°14′W); fango, arena, "rocas", 150 m. (3) 20 ej, 12–26 mm, 11 ej s, 11–13 mm, 20 v, 18.6–25 mm (Nos. 4666, 4667, 4672, 4673), M. Ch. I, Est. 51, Chile central (34°36′S; 72°14′W); fango, arena, 50 m. (4) 2 ej s, 31–39 mm (No. 4671), Barra Río Carampague, Arauco (37°20′S); arena, 1 m. (5) 15 ej, 6–22 mm (Nos. 4682, 4686, 4691, 4692, 4694, 4695, 4697), draga van Veen, Bahía de Concepción (36°S); fango, 20–27 m. (6) 84 ej, 9–32 mm, 17 v, 15–16 mm (Nos. 4700, 4702, 4705, 4707, 4709, 4711, 4713, 4715–4717, 4719, 4720, 4723, 4724, 4730, 4731), Bahía de Concepción (36°S); fango, 10–35 m. (7) 8 ej s, 18–21 mm (No. 4669), M. Ch. I, Est. 76, Chile austral (38°16′S; 73°39′W); fango, arena fina, 60 m. (8) 1 ej s, roto, 21 mm (No. 4668), M. Ch. I. Est. 93, Chile austral (39°58′S; 73°45′W); fango, arena fina, 86 m. (9) 4 v d, 7 v i, 21–26 mm (No. 4670), M. Ch. I, Canal Desertores, Sur de Chile (42°24′S; 72°34′W); fango, arena fina, 240 m. (10) 11 ej s, 20–24 mm, 4 v, 22–25 mm (No. 4563), M. Ch. I, corte X-2, Est. 51, Canal Desertores, Sur de Chile (42°24′S; 72°34′W); fango, arena fina, 240 m.

Descripción

Concha: Concha de gran tamaño (hasta 51 mm de longitud), blanca, oblonga, comprimida, entreabierta, delgada, generalmente inequilateral. Márgenes redondeados; el dorsal anterior casi recto. Perióstraco de color variable: amarillo, verde oliva o pardo, generalmente en bandas. Umbos pequeños, generalmente erosionados; ápices agudos; anteriores en los ejemplares grandes, posteriores en los pequeños. Ornamentación de la concha formada por estrías radiales muy tenues y escasas en la región anterior, y por dos carenas muy débiles en la región poste-

rior. Ligamento de la misma longitud que la serie posterior de dientes.

Interior de las valvas blanco mate o plomizo, algunas veces algo nacarado. Charnela casi recta; con 3 a 7 dientes anteriores como nudosidades y 14 a 40 posteriores, aguzados; los dientes posteriores cuadriplican en número, a los anteriores. La placa que sustenta los dientes anteriores se prolonga hasta el nivel del aductor, formando una quilla. Línea paleal bien marcada. Seno paleal amplio, profundo, sobrepasando al umbo; de contorno algo irregular, con el borde anterior casi recto; oblícuo con respecto a la vertical al eje anteroposterior que pasa por el umbo; borde inferior más o menos coalescente con la línea paleal; borde superior generalmente interrumpido por la impresión del aductor, continuando más allá de ésta.

Anatomía Interna: Papilas tentaculiformes bífidas o trífidas, poco numerosas sobre los bordes dorso anteriores del manto; hay numerosos tentáculos ramificados sobre los bordes dorso posteriores y posteriores del manto. Tentáculo del palpo muy largo, dos veces la longitud de la lámina; con un filamento laminar. Ctenidios pequeños; filamentos con un poro ventral. Corazón ventral al recto; ventrículo globoso. Area de selección mayor del estómago con repliegues divergentes que encierran otra área plegada, perpendicular a los pliegues inferiores.

Sifones largos, grandes, completamente unidos. Tentáculo sifonal ubicado en el lado derecho o izquierdo.

Observaciones

La comparación anatómica de ejemplares provenientes de Valparaíso y Concepción, y otros colectados en Valdivia y Chiloé con diferente coloración del perióstraco, no demostró diferencias. Los ejemplares de las muestras australes presentan un color pardo oscuro con bandas más claras, a diferencia del tono predominantemente verdoso encontrado en las poblaciones del centro y norte de Chile.

El mayor tamaño alcanzado por los ejemplares de la Bahía de Concepción fue de 32 mm, en contraste a los de Bahía de Valparaíso que alcanzan un tamaño hasta de 51 mm, siendo el mayor tamaño entre las especies estudiadas. Estas differencias de tamaño y color sugieren extremos de variación clinal.

Ramorino (1968) realizó un estudio de la variación de la concha en ejemplares de *M. chilensis* de Bahía de Valparaíso, donde hace ver que las descripciones de Soot-Ryen de ejemplares del área de Chiloé asignadas a *M. inequalis* Dall, 1908a (una especie del Estrecho de Magallanes), no muestran diferencias con los de Valparaíso. Aún cuando Ramorino no examinó ejemplares de esta especie en otras localidades, concluye que *M. inequalis* debería, en consecuencia, ser considerada como sinónimo de *M. chilensis.*

Abundante material examinado proveniente de Chiloé, y su comparación con poblaciones de diferentes localidades de la zona central y Valparaíso, demuestran que efectivamente se trata de una sola especie que corresponde a *M. chilensis.* Sin embargo, la conclusión de Ramorino (basada sólo en la identificación de Soot-Ryen) de que esta especie es igual a *M. inequalis* no se justifica, mientras no se ilustre y se estudie en detalle el tipo de esta última y se compare con muestras del Estrecho de Magallanes, la localidad tipo. Además, las características dadas por Dall para *M. inequalis* son diferentes de M. *chilensis* como se demuestra en la clave adjunta.

Es factible, en consecuencia, que en el área magallánica existan al menos tres especies diferentes: *M. inequalis, M. patagonica,* y *M. magellanica* a menos que la primera demuestre ser sinónimo de una de las otras dos. Mientras ésto no se compruebe, sólo se justifica incluir en la sinonimia de *M. chilensis* a *M. inequalis* Soot-Ryen, 1959 (*non* Dall).

Malletia magellanica y *M. patagonica* son especies tan diferentes de *M. chilensis* que no puede pensarse en sinonimizarlas con esta última o entre sí. *Malletia hyadesi* Mabille y Rochebrune, 1889, especie también descrita del Estrecho de Magallanes, ha sido considerada como un sinónimo de *M. magellanica* Mabille y Rochebrune por Dall (1908a) (aunque es obvio que se refiere a *M. patagonica* de Mabille y Rochebrune) y como sinónimo de *M. patagonica* Mabille y Rochebrune por Hertlein y Strong (1940); desgraciadamente, sin discusión alguna. *Malletia hyadesi* se diferencia de todas las otras especies, por presentar la charnela más corta y por la posición de las inserciones musculares (muy abajo la anterior y muy anterior la posterior). A no ser que se demostrara que se trata de un ejemplar anómalo o que las impresiones musculares han sido dibujadas sólo en parte (precisar límites de las impresiones musculares es a veces difícil), no se justifica que se identi-

fique con *M. patagonica*. Hasta que ello pueda demostrarse, se propone considerarla sólo como un probable sinónimo de esta última.

Distribución Geográfica

Desde Coquimbo (30°S) hasta el Canal Desertores (42°S).

Hábitat

Las muestras estudiadas cubren la mayor parte del área de dispersión de esta especie y fueron colectadas en profundidades que varían entre 1 y 240 m, en substrato de fango con arena fina.

Malletia chilensis (al igual que *N.* (*N.*) *pisum* y *N.* (*S.*) *cuneata*) parece presentar grandes diferencias de densidad si se comparan los datos publicados por Ramorino (1968) para la Bahía de Valparaíso, con los obtenidos en la Bahía de Concepción. En esta última se obtuvo una densidad de 30 ejemplares/m^2 (promedio de 7 muestras) en substrato de fango entre 20 y 27 m. Este valor es muy inferior al calculado por Ramorino (1968) entre 20 y 50 m en la Bahía de Valparaíso que fue de 1373 ejemplares/m^2, en fondo arenoso entre 51 y 80 m de profundidad. En los fondos de fango arenoso de la Bahía de Concepción no se encontró *M. chilensis*.

Malletia patagonica Mabille y Rochebrune, 1889
Fig. 91

Malletia patagonica Mabille y Rochebrune, 1889: H 114, lám. 8, fig. 1 (Loc. tipo: Punta Arenas); Hertlein y Strong, 1940: 424; Carcelles, 1950: 74, lám. 3, fig. 65; Carcelles y Williamson, 1951: 324; Dell, 1964: 148

?*Malletia hyadesi* Mabille y Rochebrune, 1889: H 114, lám. 7, fig. 8 (Loc. tipo: Punta Arenas).

Malletia magallanica Smith (*non M. magallanica* [Smith, 1875]), Dall, 1908a: 383 (E. de Magallanes).

Malletia (*Malletia*) *patagonica* Mabille y Rochebrune, Bernard, 1983: 10.

Material Estudiado

1 ej, 33.5 mm (No. 4636), "Hero" 69-5, Est. 280 A, E. de Magallanes (53°17′18″S; 70°48′36″W), fango con muy poca arena, 177 m. MZUC.

Descripción

Concha: Concha de tamaño mediano (hasta 42 mm de longitud), eliptica, gruesa, entreabierta, algo comprimida, inequilateral; parte posterior más larga, oblicuamente truncada. Márgenes redondeados, excepto el dorsal posterior que es casi recto. Perióstraco pardo amarillento. Umbos conspícuos. Concha sin ornamentación. Estrías de crecimiento distribuídas irregularmente. Ligamento de la misma longitud que la serie de dientes posteriores. Escutelo muy largo.

Interior de las valvas rosado o blanco con manchas amarillas. Charnela corta, con 10 dientes anteriores y 29 posteriores; los posteriores triplican en número a los anteriores. Línea paleal muy poco marcada; seno paleal pequeño, estrecho, con el borde anterior redondeado, subcircular; borde superior interrumpido por la impresión del aductor, continuando más allá de éste.

Anatomía Interna: Borde dorsal posterior del manto con tentáculos simples. Tentáculo del palpo corto, casi la mitad del tamaño de la lámina, originándose en el extremo posterior de ella; con un músculo fuerte que lo une a la masa visceral; con filamento laminar. Corazón atravesado por el recto; ventrículo y aurículas muy angostas y aplastadas. Sifones pequeños, cortos. Tentáculo sifonal a la derecha del sifón.

Observaciones

Después de su hallazgo original, esta especie fue encontrada por la expedición del "Albatross" (Dall, 1908a) en distintos puntos del Estrecho de Magallanes, cercanos a la localidad tipo. Desgraciadamente, ella fue identificada erróneamente por Dall (1908a) como *M. magellanica* Mabille y Rochebrune, 1889, aunque es obvio que en la discusión de esta especie se refiere a *M. patagonica*. *Malletia magellanica* es una especie creada por Smith (1875), y sólo citada, pero no descrita por Mabille y Rochebrune (1889). También la localidad original citada por Dall para *M. magellanica* es la de *M. patagonica*.

Esta especie se diferencia fácilmente de las otras presentes en esa zona, por su forma elíptica y los bordes dorsales anterior y posterior casi rectos.

Es importante hacer resaltar que, además de *Malletia gigantea* Smith, ésta es la única

otra especie de *Malletia* conocida en la que el corazón es atravesado por el recto.

Distribución Geográfica

Estrecho de Magallanes (53°01′S–53°17′ 18″S; 68°13′W–70°48′36″W).

Hábitat

La muestra estudiada fue obtenida cerca de Punta Arenas, la localidad tipo, a una profundidad de 177 m en fango, con muy poca arena. Con anterioridad, Dall (1908a) la citó del Estrecho de Magallanes entre 56.7 m y 664.2 m en fondos de arena, fango verde y fango de diatomeas.

Familia Tindariidae Verrill y Bush, 1897

Diagnosis

Concha ovalada, robusta; escultura concéntrica, ocasionalmente con líneas radiales; placa de la charnela fuerte con dientes en forma de "v" invertida bien desarrollados, continuos bajo el umbo; umbos grandes, ortogiro o prosogiro; ligamento externo, más elongado posteriormente que anteriormente; faltan verdaderos sifones; abertura inhalante posterior rodeada por papilas alargadas; palpos relativamente pequeños con pocos surcos; intestino con una vuelta simple a la derecha del cuerpo; puede penetrar en el manto (Sanders y Allen, 1977).

Género *Tindaria* Bellardi, 1875

Tindaria Bellardi, 1875: 28. Especie tipo por monotipia: *T. arata* Bellardi, 1875. (= *Deminucula* Iredale, 1931).

Diagnosis

Concha pequeña, ovalada, redondeada o veneriforme; inflada, gruesa. Sin ornamentación o formada sólo por costillas concéntricas de desarrollo variable. Umbos abultados; ápices prosogiros. Charnela más o menos interrumpida bajo el umbo; dientes de la serie posterior muy curvados; la serie anterior con dientes fuertes, cortos y rectos. Sin seno paleal; abertura exhalante formada sólo por papilas del borde del manto; con o sin sifón inhalante. Palpos grandes.

Observaciones

Este género se encuentra representado en Chile por *T. salaria* (Dall, 1908a) conocida sólo frente a las Islas Salas y Gómez, la localidad tipo, en 1142 brazas (2055.6 m) de profundidad, y por *T. virens* (Dall, 1889), la especie aquí tratada.

Tindaria virens (Dall, 1890)
Figs. 52, 54, 55, 93–96, 119, 120

Malletia (*Tindaria*) *virens* Dall, 1890: 254, lám. 13, fig. 3 (Loc. tipo: Costa Oeste de Chile, 48°9′S–51°52′S, entre 122 y 449 brazas de profundidad).

Tindaria virens Dall, Dall, 1908a: 389; Hertlein y Strong, 1940: 428 (Cit.); Clarke, 1961: 371; Carcelles y Williamson, 1951: 323; Bernard, 1983: 11.

Yoldia (*Yoldiella*) *infrequens* Dall, 1908a: 219, 381.

Tindaria cf. *virens* Dall, Linse, 1997: 47

Material Estudiado

247 Ejemplares (ej) Y 129 valvas (v); MZUC Procedencia: (1) 7 ej s, 1.9–4.2 mm, 4 v i, 5 v d, 3–4.3 mm (N. 4597), M. Ch. I, Est. X-3, Golfo de Ancud (42°00′S; 73°00′W); fango, arena fina, 264 m. (2) 11 ej, 3.1–5 mm, 2 ej s., 4.5–6 mm, 6 v, 5.5–2 mm (Nos. 4611, 4642, 4660), "Hero" 69-5, Est. 9 (201), Confluencia Canales Concepción y Trinidad, (50°9′55″S; 74°43′25″W); arena, grava, etc., 460 m. (3) 5 ej, 3.2–4.3 mm, 30 v d, 10 v i, 2–4.4 mm (N. 4657), "Hero" 69-5, Est. 210, draga Petersen 0.1 m^2, Bahía Corbeta Papudo (50°21′17″S; 75°17′25″W); fango amarillo verdoso, 70–78 m. (4) 5 ej, 4 v, 4.2–5.2 mm (No. 4647), "Hero" 69-5, Est. 56, Puerto Bueno, Canal Sarmiento (51°0′50″S; 74°14′10″W); fango, 236 m. (5) 181 ej, 2.8–5.1 mm, 39 v s, 2.2–5.4 mm (No. 4650), "Hero" 69-5, Est. 57, Puerto Bueno, Canal Sarmiento (51°0′50″S; 74°14′ 10″W); fango, 223 m. (6) 30 ej, 3.6 mm, 20 v s, 2–5.5 mm (No. 4614), "Hero" 69-5, Est. 213, Canal Sarmiento (51°27′30″S; 74°3′W); fango, 722 m. (7) 6 ej, 2–3 mm, (No. 4637), "Hero" 69-5, Est. 243 (26), draga Petersen 0.1 m^2, E. de Magallanes (53°3′S; 71°33′12″W); fango, 151 m. (8) 11 v s, 2–5 mm (No. 4639), "Hero" 69-5, Est. 244 (27), draga Petersen 0.1 m^2, E. de Magallanes (53°3′3″S; 71°46′ 36″W); fango, 184 m.

Descripción

Concha: Concha pequeña (hasta 6 mm de longitud), de contorno triangular, gruesa, inflada; inequilateral, con el lado anterior más corto que el posterior; blanca. Perióstraco amarillo verdoso a pardo claro, rara vez con bandas. Prodisoconcha blanca. Umbos ligeramente anteriores, elevados, de ápices ortogiros. Márgenes redondeados, excepto el dorsal posterior que es oblícuo, casi recto, formando un margen posterior angular. Ornamentación de la concha formada por costillas concéntricas generalmente muy regulares, notorias aun sobre la prodisoconcha. Sin lúnula ni escutelo.

Interior de las valvas blanco, con brillo aporcelanado. Charnela acodada con numerosos dientes en forma de "v" invertida; los posteriores (hasta 18) en mayor número que los anteriores (hasta 13). Línea paleal difícilmente visible. Impresiones de los aductores ovaladas, a veces de tono oscuro; la anterior alargada en sentido vertical, de doble tamaño que la posterior que es alargada en sentido horizontal. No se observan otras impresiones musculares.

Anatomía Interna: Manto de bordes lisos, más delgado sobre los sifones. Pie grande, fuerte; disco pedal crenulado. Glándula hipobranquial grande, cubre por completo los ctenidios. Palpos labiales muy grandes; tentáculo del palpo fuerte, del mismo tamaño que los ctenidios. Ctenidios grandes de posición horizontal; filamentos subtriangulares. Corazón ventral al recto. Estómago grande con repliegues adicionales al área de selección mayor. Intestino relativamente corto (1 vuelta). Sifones parcialmente unidos en su parte interna por un tabique formado por dos mitades no fusionadas. Tentáculo del sifón pequeño, fino, ubicado más abajo y a la derecha del sifón.

Observaciones

Clarke (1961) identificó a esta especie en la fauna abisal de la Costa del Congo Belga, basándose en 12 ejemplares obtenidos por el "Vema" a 1675 brazas; sin embargo, una diferencia encontrada entre éstos y los paratipos de *T. virens* por él examinados, fue la presencia de dientes un poco más fuertes, disparidad que supone de escaso valor taxonómico. Es de esperar que el estudio anatómico comparativo de ejemplares de un área tan distante al área tipo, logre precisar si se trata de la misma especie o no.

Distribución Geográfica

Desde el Golfo de Ancud (42°S; 73°W) al Estrecho de Magallanes (53°S; 71°46′W). Con anterioridad, *T. virens* era conocida sólo de la localidad tipo, costa oeste de Chile (48°09′S–51°52′S).

Hábitat

En las muestras estudiadas esta especie se encontró en profundidades de 70 a 460 m, en substrato de fango. Su mayor densidad se observó en 236 m de profundidad.

Orden Solemyoida Dall, 1889

Paleotaxodontos con charnela sin dientes o con dientes taxodontos subumbonales separados de los dientes laterales anteriores por un espacio edentado; concha equivalva alargada anterior o anteroventralmente; huella muscular del aductor posterior reducida o ausente; periostraco grueso; branquias grandes, anchas, cubriendo todo el cuerpo; proboscis del palpo ausente o muy pequeña; palpos pequeños, triangulares, sin surcos; aparato digestivo simple reducido o ausente (Allen y Hannah, 1986; Pojeta, 1988).

Superfamilia Solemyacea Gray, 1840

Concha pequeña a grande, entreabierta; anterior a anteroventralmente alargada, sin dientes; músculo aductor posterior más pequeño que el anterior, con una huella muscular arqueada o recta desde el aductor anterior, indicando la unión del integumento a la masa visceral y continúa con las huellas de los músculos del pie. Ligamento variable con o sin ninfas o condróforos. Con una extensa fusión ventral del manto; lúmen del tubo digestivo estrecho o ausente.

Observaciones

La inclusión de las familias Solemyidae y Acharacidae entre los protobranquios se ha basado en la estructura de los ctenidios (Pelseneer, 1888, 1911; Yonge, 1939; Cox,

1959). Sin embargo, Newell (1969) considerando las grandes diferencias morfológicas observadas y la antigüedad de Solemyidae y los nuculoideos (Nuculacea y Nuculanacea), considera que, aunque ambos grupos han ocupado nichos ecológicos similares, no han alcanzado paralelismo alguno en la concha. Tampoco hay evidencia paleontológica de que hayan sido derivados el uno del otro, ni están conectados por formas intermedias, aunque Allen y Sanders (1969) y Allen (1978) han postulado un ancestro actinodontiano común. Pojeta (1988) ha indicado evidencia de la evolución de este grupo a partir de la familia "nuculoide" Ctenodontidae. De la misma manera Yonge (1939), Purchon (1956), Allen y Sanders (1969) y Allen (1978) han comentado que las similaridades anatómicas de los Solemyidae indican claramente una derivación de un tronco común con los nuculoideos (Fig. 61). Allen (1985) también ha discutido la morfología más primitiva de los Solemyoidea y analizado sus adaptaciones morfológicas a los sedimentos blandos, incluyendo el significado funcional de su aparato digestivo muy reducido y el papel de las bacterias quimoautotróficas (Felbeck et al., 1981, 1983; Cavanaugh, 1983; Reid y Brand, 1986) en los bacteriocitos, similares a los descritos para las *Calyptogena* de las fuentes hidrotermales (Fiala-Médioni y Métivier, 1986; Childress et al., 1987; Stuardo y Valdovinos, 1988).

Familia Acharacidae Scarlato y Starobogatov, 1979

Scarlato y Starobogatov (1979) crearon la familia Acharacidae y la superfamilia Acharacoidea, caracterizándolas por la ausencia total de un ligamento interno y un ligamento externo reforzado por ninfas.

Estudios detallados de la anatomía de las partes blandas de especies de *Acharax* pueden apoyar o rechazar esta separación. Desde el punto de vista de la microestructura de la concha y del ligamento, Carter (1990), considera al género *Acharax* dentro de una subfamilia Solemyinae; sin embargo, preferimos seguir a otros autores que consideran a Acharacidae una buena familia, mientrás no hayan mayores contribuciones anatómicas al grupo.

Género *Acharax* Dall, 1908

Acharax Dall, 1908b: 364. Especie tipo por designación original: *Solemya johnsoni* Dall, 1908b: 364.

Diagnosis

Concha alargada, oval o subrectangular, comprimida o circular en sección transversal; ligamento opistodético, completamente externo; visible internamente sólo donde cruza el espacio entre los márgenes de las valvas. Ninfas sin reborde de sustentación ("prop") [Traducción descripción original].

Observaciones

Dall (1908b) incluyó en su subgénero *Acharax* a dos especies del Sur de Chile: *Solemya patagonica* Smith, 1885, y *S. macrodactila* Mabille y Rochebrune, 1889, sugiriendo que la primera parecería ser un ejemplar anómalo y que la segunda podría ser, en consecuencia, sólo un sinónimo.

Acharax patagonica (Smith, 1885) fue descrita de la costa oeste de la Patagonia (52°45′30″; 73°46′W, en 245 brazas = 441 m) basado en un único ejemplar, caracterizado por un engrosamiento dorsal. Baratini (1951) citó también a esta especie para Uruguay, sobre la base de ejemplares procedentes de la desembocadura del Río de la Plata; sin embargo, en un estudio de la fauna uruguaya, Figueiras y Sicardi (1968), al referirse a *S. patagonica* comentan que encontraron en esa zona "especímenes de este género que indudablemente pertenecen a otra especie."

Acharax macrodactyla (Mabille y Rochebrune, 1889) fue descrita originalmente para la Bahía Orange y citada por Dall (1908b) hasta el norte de Chiloé.

Dell (1995) quien informa haber examinado recientemente material del sur de Sudamérica, concluye al igual que Dall (1908b) que *Acharax macrodactyla* no puede ser diferenciada de *Acharax patagonica* y que esta última es muy afin a *A. johnsoni* (Dall, 1891) registrada desde Puget Sound, Washington, a Perú.

En el material estudiado se encontraron 4 valvas pequeñas y un ejemplar minúsculo de una especie no descrita de este género.

Acharax sp.
Figs. 6, 9, 13, 131, 132

Material Estudiado

1 ej, 2.7 mm, 2 v, 8.1 mm, 2 v, 3.2 mm (No. 4613), "Hero" 69-5, Est. 213, Canal Sarmiento (51°27.5′S; 74°03′W); fango, 722 m. MZUC.

Descripción

*Concha: C*oncha de tamaño muy pequeño (hasta 8.1 mm de longitud), alargada, delgada, lisa, blanca; muy inequilateral. Bordes dorsal anterior y ventral paralelos; extremos redondeados, el posterior más bajo que el anterior. Perióstraco grueso, de color pardo oscuro, con franjas radiales más oscuras, casi negras, que nacen del umbo y se prolongan en procesos digitiformes más allá del borde de la concha, dejando espacios entre ellas, equivalentes a su mitad. Las franjas están provistas de costillas que se hacen más notorias hacia el extremo de las digitaciones. (En los ejemplares más pequeños, menores de 2.7 mm de longitud, el perióstraco café muy claro no sobresale de los bordes de la concha, sino que está doblado hacia el interior de ella; las franjas radiales apenas se insinúan y la concha es transparente.)

Umbos en el tercio posterior de la concha, poco prominentes; ápices inconspicuos. Ligamento externo, ancho, ubicado muy posteriormente en una cavidad formada por el borde de las valvas. Interior de las valvas blanco, opaco, sin ornamentación. Impresiones de los aductores desiguales; posterior pequeña, ovalada, ubicada bajo el ligamento; impresión anterior más grande, alargada, ubicada dorsalmente cerca del margen.

Anatomía Interna: Bordes del manto libres, subperiféricos (sin llegar a los bordes de la concha); el posterior con 8 lóbulos, de los cuales los 3 inferiores son de mayor tamaño que el resto. Glándula hipobranquial muy desarrollada, cubierta totalmente por los ctenidios. Palpo pequeño de forma triangular, sin ápendices; su parte ventral posterior (correspondiente al tentáculo del palpo) como una lengüeta corta y ancha. Ctenidios grandes, ocupando casi la mitad de la cavidad paleal; inequilaterales respecto al eje ctenidial, con la parte superior de mayor tamaño que la inferior.

Observaciones

El examen del palpo labial en *Acharax* sp. (Figs. 6, 9, pl), mostró diferencias considerables con respecto al de *Solemya togata* descrito e ilustrado por Yonge (1939), ya que no existe el subapéndice del tentáculo del palpo. Sin embargo, la falta de este subapéndice en *Acharax* sp. podría deberse a un caracter juvenil, dado el pequeño tamaño del ejemplar estudiado. Fue imposible determinar la posición exacta del corazón con respecto al recto. Parece ser inferior a él, aunque White (1942) describe el ventrículo rodeando al recto en *Solemya velum* Say, del hemisferio Norte.

Distribución Geográfica

Canal Sarmiento (51°27.5′S; 74°03′W).

Hábitat

Fue encontrada a 722 m de profundidad, en un substrato de fango con gran contenido de materia orgánica.

Especie aparentemente escasa.

SINOPSIS TAXONÓMICA DE LAS ESPECIES FÓSILES

Los representantes más antiguos de los protobranquios fósiles encontrados en Chile provienen del Paleozoico Superior (Carbonífero-Pérmico); sin embargo, la historia geológica de este grupo se remonta prácticamente a los orígenes de los bivalvos, a comienzos del Paleozoico.

Pojeta y Runnegar (1985) han discutido la evolución temprana de este grupo (como Paleotaxodonta), y hacen ver que ya en el Ordovícico se conocen a lo menos tres docenas de géneros y cientos de especies. Entre otros, los denominados prenucúlidos se han encontrado a comienzos del Ordovícico, y una de las interpretaciones propuestas (Runnegar y Bentley, 1983) han colocado a *Pojetaia,* uno de los primeros bivalvos conocidos, con los "paleotaxodontos" prenucúlidos. De ser esto correcto, significa que el origen de los protobranquios puede trazarse desde el Cámbrico temprano al Ordovícico. *Tironucula* tiene dientes tan simples como *Pojetaia* y similares impresiones musculares umbonales (Morris y Fortey, 1976; Pojeta y Runnegar, 1985) y se propone que formas como *Tironucula* pueden haber sido intermedias entre los nuculoides y los actinodontoides (Pojeta, 1978).

Pese a que la clasificación supragenérica de los "paleotaxodontos" Ordovícicos se encuentra en revisión, se distinguen dos amplios morfogrupos: (a) aquellos en los que las conchas son casi equidimensionales en longitud y altura; y (b) aquellos en los que la concha es significativamente más larga que alta. Según Pojeta y Runnegar (1985), estos morfogrupos muestran, aparentemente, la di-

visión de los primeros "paleotaxodontos" en formas de tipo-*Nucula* y de tipo-*Nuculana*. En opinión de estos autores, hay también considerable evidencia paleontológica sugiriendo que los Solemyidae se derivaron de los "paleotaxodontos," probabilidad documentada por especies del Ordovícico (e.g. *Paleosolemya ordovicicus* Pojeta y Runnegar, 1985). De este modo, la separación de los órdenes Nuculoida y Solemyoida, dentro de la subclase Protobranchia, punto de vista compartido en este trabajo, parece más probable que la separación de los Solemyidae como un orden de una subclase Cryptodonta.

En Chile, sólo los Nuculidae de los géneros *Nucula* y *Ennucula* están representados por especies fósiles. Una única especie asignada al género *Acila* por Tavera (1942) es un *nomen nudum*.

El número de especies fósiles chilenas referidas al género *Nucula* es muy grande, pero sólo un número reducido de ellas han sido lo suficientemente bien descritas como para permitir su identificación. Entre éstas, algunas no se han vuelto a encontrar desde su descripción y otras pertenecen ahora a géneros diferentes. Todas provienen del Mesozoico y Cenozoico.

Especies adscritas con anterioridad al género *Nucula* pertenecen al género *Ennucula* si se considera la falta de ornamentación radial, margen ventral liso y gran inclinación del condróforo. Se trata de especies mesozoicas y cenozoicas.

Los representantes más antigüos de los Nuculanidae pertenecen al Silúrico (Dechaseaux, 1952), pero los fósiles chilenos asignados a ella provienen del Mesozoico y Cenozoico.

Sólo para los géneros *Nuculana, Australoportlandia, Propeleda* y *Tindariopsis* se han descrito representantes fósiles chilenos.

Hay muy pocas especies fósiles referidas al género *Nuculana* (= *Leda*) en Chile, aunque se conocen muchas citas de especies identificadas (pero no descritas) sólo a nivel genérico. Por otra parte, se han descrito especies de *Nucula,* que por su forma podrían corresponder a este género, como se indica en la lista de *nomina dubia*.

Hasta ahora ninguna especie fósil chilena parece haber sido asignada al género *Propeleda* en la literatura revisada, pero las especies de Philippi (1887) *Nucula medinae, N. darwini,* y *N. dorbigny* pueden ser referidas a este género, por poseer un rostro largo y truncado, condróforo oblícuo y angosto, dirigido hacia atrás, y dientes de la charnela casi paralelos al borde. De ellas se estudió sólo *Nucula medinae* sobre la base de fragmentos de la concha y moldes.

Kafanov y Savitskii (1995) en su revisión de los taxa de un grupo genérico de la familia Nuculanidae registrados en depósitos Cenozoicos del Pacífico Noroccidental proponen incluir a *Propeleda* Iredale, 1924 (= *Lamellileda* Cotton, 1930), en la subfamilia Poroledinae Scarlato y Starobogatov, 1979, lo cual Maxwell (1988) había considerado de valor dudoso.

No se han mencionado especies fósiles pertenecientes al género *Tindariopsis* en la literatura consultada, pero es indudable que *Nucula elegans* Hupé, 1854, debe incluirse en él.

De los Yoldiidae se encontró descrita solo una especie, *Yoldia levitestata* Stinnesbeck, 1987.

La familia Malletiidae es, sin duda, la de origen más reciente entre los protobranquios (McAlester, 1964), y está representada por especies principalmente Cenozoicas y Recientes.

Las especies chilenas fósiles de Malletiidae pueden referirse a los géneros *Australoneilo* y *Malletia*. Las dos especies de este último género encontradas en Chile, se incluyen aquí en el subgénero *Neilo* H. Adams y A. Adams, 1852, caracterizado por poseer una concha con ornamentación concéntrica y forma arcoide. Según Hertlein y Strong (1940), este subgénero ha sido citado del Cretácico Superior al Reciente de la Patagonia, del Helvetiano, Mioceno Inferior de Francia y del Oligoceno Superior al Reciente en Nueva Zelandia. A esto hay que agregar el registro del Mesozoico de *Neilo* (*Neilo*) *quiriquinae* Stinnesbeck, 1986, de la Formación Quiriquina, Maastrichtiano y los del Cenozoico de Chile.

La familia Solemyidae, que está representada en las especies chilenas recientes por el género *Acharax,* se conoce por una sola especie fósil incluída con propiedad en el género *Solemya*.

Se conocen especies de *Solemya* desde el Paleozoico al Reciente (Carbonífero y posiblemente Silúrico a Reciente, según Hertlein y Strong, 1940). La única especie chilena conocida, fue descrita para el Piso de Navidad (Mioceno Inferior).

Por otra parte, esta compilación ha mos-

trado también el enorme número de especies que, por deficiencias de descripción y figuras, se hace necesario considerar como *nomina dubia* y, por ellos, se incluyen con los nuculánidos en igual condición, al final de esta sinopsis.

Las especies que sobre la base de sus descripciones y figuras pueden ser consideradas en el género *Nucula,* no estaban representadas en las colecciones estudiadas. En cada caso, se incluye a las referencias bibliográficas consultadas, las localidades conocidas y el rango estratigráfico.

Especie Paleozoica
Nuculana bellistriata Stevens?

Nuculana bellistriata Stevens, Brüggen, 1950: 11 (Huentelauquen); Hoffstetter et al., 1956: 149 (Huentelauquen; NW Prov. Aconcagua 31°40′S y Prov. Coquimbo 31°30′S) (Capas de la desembocadura del Choapa, Carbonífero Sup. o Pérmico Inf.).

Especies Mesozoicas

Pertenecientes al Cretácico según Philippi (1887) en su obra sobre fósiles Terciarios y Cuartarios donde incluye 161 moluscos del Cretácico.

Nucula ceciliana (d' Orbigny, 1842)

Mactra ceciliana d' Orbigny, 1842: 126, lám. 15, figs. 5, 6; 1850: 235; Philippi, 1887: 142, lám. 32, fig, 8 (Isla Quiriquina).

Nuculana ceciliana (d' Orbigny), Wilckens, 1904: 228, 272, 277, lám. 19, fig. 5 (Quiriquina: 25 ejemplares; Tomé: 100 ejemplares; San Vicente: 6 ejemplares); Tavera, 1942: 587 (Piso de Quiriquina). Cretácico Superior.

Nucula (*Leionucula*) *ceciliana* (d' Orbigny), Stinnesbeck, 1986: 162, lám. 1, fig. 1–3 (Formación Quiriquina, Maastrichtiano).

Nucula albertina d' Orbigny, 1850: 243; Philippi, 1887: 194, lám. 31, fig. 8 (Cretácico de Puerto del Hambre (Port Famine), Orange).

Nucula apicina Philippi, 1887: 193, lám. 41, fig. 19 (Cretácico de Tumbes).

Observaciones

La comparación de las descripciones e ilustraciones de *Nucula albertina* d'Orbigny y *N. apicina* Philippi demuestran, que éstas son sólo sinónimos de *N. ceciliana* d'Orbigny, corroborando la conclusión de Wilckens (1904), quien comparó un gran número de ejemplares.

Nucula compressiuscula Philippi, 1899

Nucula compressiuscula Philippi, 1899: 61, lám. 26, fig. 11 (Portezuelo del Tinguiririca; Jurásico Superior-Cretácico Inferior).

Nucula discors Philippi, 1887

Nucula discors Philippi, 1887: 189, lám. 41, fig. 23 (Provincia de Arauco).

Nucula patagonica Philippi, 1887

Nucula patagonica Philippi, 1887: 191, lám. 41, fig. 8 (Terciario de Santa Cruz, Argentina); von Ihering, 1899: 15 (Patagoniano Inferior y Medio); Ortmann, 1900: 379; Ortmann, 1902: 80-82, lám. 25, fig. 7a, b (Desembocadura Río Santa Cruz, Lago Pueyrredón, Argentina); Fuenzalida, 1942: 412, 413, 423, 424 (Patagoniano Inferior, Medio y Superior y cf. en los Estratos de Boquerón); Tavera, 1942: 607 (Piso de Navidad en Arauco); Feruglio, 1949: 100, 128, 156, 253 (cf. en Juliense. Comodoro Rivadavia y Patagoniense, Argentina y Chile, Boquerón); Hoffstetter et al., 1956: 44 (Estratos de Boquerón, Eoceno y Paleoceno).

Nucula tricesima von Ihering, 1897: 243, lám. 4, fig. 21, lám. 5, fig. 27.

Observaciones

Ortmann (1902) designó como sinónimo de esta especie a *Nucula tricesima* von Ihering, 1897, del Superpatagónico, sobre la base de una serie de 20 ejemplares y un molde interno. De ellos, uno presenta las características de *N. tricesima* y otros, más o menos las de *N. patagonica* Philippi, existiendo además, una serie de individuos intermedios.

Fuenzalida (1942), insistió posteriormente en las diferencias señaladas por von Ihering (1907): mayor altura con relación al ancho (espesor o longitud?) en *N. tricesima* y mayor número de dientes en la serie anterior ("posterior") de la charnela (11 a 13 en *N. patagonica* y 15 a 17 en *N. tricesima*). No obstante estas diferencias, *N. tricesima* podría repre-

sentar un sinónimo de *N. patagonica,* ya que las características comparadas por estos autores varían de acuerdo al tamaño de los ejemplares.

Nucula ovallei Philippi, 1887

Nucula ovallei Philippi, 1887: 186, lám. 41, fig. 12 (Tumbes); Neuman, 1892: 111 (Tumbes).

Nucula pusilla Philippi, 1899

Nucula pusilla Philippi, 1899: 61 lám. 24, fig. 12 (Portezuelo del Tinguiririca); Klohn, 1960: 52 (cf. Formación Baños del Flaco, en el faldeo occidental del Valle Barroso, Prov. Santiago. Valanginiano).

Ennucula ¿nogalis ? (Philippi, 1899)
(Figs. 140, 141)

Nucula nogalis Philippi, 1899: 62, lám. 28, fig. 9 (Loc. Tipo: Nogales, al N del Agua de los Pajaritos).
Nucula sp. Biró, 1964: 54 (Lo Valdés, Berriasiano Inferior).

Material Estudiado

1 v i, 15 mm de longitud, 11.4 mm de altura, 4 mm espesor, (V/132), Lo Valdés, Prov. de Santiago, 1964. Depto. Geociencias Universidad de Concepción.

Descripción

Concha de regular tamaño (15 mm de longitud), ovalada, inflada; lado posterior extremadamente corto y cóncavo, casi recto; anterior largo y convexo. Bordes dorsal y ventral redondeados. Umbos abultados. Ornamentación de la valva formada por estrías concéntricas finas y densas en número de 6–7 por mm. No existe lúnula ni escutelo.

Observaciones

El único ejemplar estudiado, citado por Biró (1964) como *Nucula* sp., es de tamaño menor que el descrito por Philippi (1899), y muestra alguna diferencia en el contorno de la concha, atribuible probablemente a una quebradura dorsal.

Rango Estratigráfico

Neocomiano (Berriasiano Inferior). Biró (1964).

Distribución Geográfica

Nogales (Prov. Aconcagua), Lo Valdés (Prov. Santiago).

Nuculana amuriensis rostrata
Stinnesbeck, 1986

Nuculana amuriensis rostrata Stinnesbeck, 1986: 163, lám. 1, figs. 4–6 (Formación Quiriquina, Maastrichtiano).

Nuculana cuneiformis Stinnesbeck, 1986

Nuculana cuneiformis Stinnesbeck, 1986: 164, lám. 1, figs. 7–9 (Formación Quiriquina, Maastrichtiano).

Neilo (*Neilo*) *quiriquinae* Stinnesbeck, 1986

Neilo (*Neilo*) *quiriquinae* Stinnesbeck, 1986: 167, lám. 1, figs. 15, 16 (Formación Quiriquina, Maastrichtiano).

Especies Cenozoicas (Terciario)

Nucula (Nucula) pisum Sowerby I, 1833

Nucula pisum Sowerby I, 1833: 198 (Véase sinonimia para especie reciente).

Observaciones

Nucula (*N.*) *pisum,* descrita como especie reciente, fue citada por Philippi (1887) del Terciario de Coquimbo, Caldera, La Cueva, Navidad, Lebu, Valdivia y Chiloé y del Cuaternario de Mejillones del Sur, Caldera, Coquimbo y Cahuil. Sin embargo, aunque algunas de estas localidades han sido estudiadas con posterioridad, no se han encontrado otros ejemplares de esta especie.

Nucula semiornata D'Orbigny, 1846

Nucula semiornata d'Orbigny, 1846: 624, lám. 84, figs. 27–29; von Ihering, 1907; Fuenzalida, 1942: 404 (cf. al Terciario de Magallanes); Feruglio, 1949: 156, 196, 253 (Pata-

goniense, Entrerriense y Actual; Estratos de Loreto; Sierra de Carmen Silva); Hoffstetter et al., 1956: 202 (Formación Loreto, Oligoceno (y/o) Eoceno Sup. ?), Magallanes, 53°7′S).

Nucula (*Leionucula*) *palmeri*
Zinsmeister, 1984

Nucula (*Leionucula*) *palmeri* Zinsmeister, 1984: fig. 3A, B (Isla Seymour, Antártica, Eoceno); Stilwell y Zinsmeister, 1992: 47 (Isla Seymour, Antártica).

Ennucula araucana (Philippi, 1887)
Figs. 142, 143

Nucula araucana Philippi, 1887: 191, lám. 41, figs, 7, 7b (Lebu y ¿Navidad? Terciario); Grzybowsky, 1892: 614, 631 (Terciario de Talara, Perú); Tavera 1942: 602, 607, 612, 627 (Piso de Navidad, Mioceno de Arauco); Fenner y Wenzel, 1942: 1004 (Piso de Navidad); Feruglio, 1949: 156, 240, cf. (Tierra del Fuego, Magallanes y Navidad); Hoffstetter et al. 1956: 306, 243 (Ranquil, Prov. Arauco y Navidad); Tavera y Veyl, 1958: 160.

Material Estudiado

2 ejemplares (ej), 1 valva (v) y 1 molde interno (mi). DGUC. Procedencia: (1) 1 ej 12 mm de longitud, 9 mm altura, 5.8 mm de espesor, con sólo la capa interna de la concha y con una perforación de 1.6 mm de diámetro; 1 v d, 17 mm de longitud, 13 mm altura, ca. 8.7 mm de espesor, con su molde interno; fragmentos de valvas, una de ellas alcanzaría 20 mm de longitud. (T/16), Tubul, 24. X. 1969. (2) 1 ej ca. 15 mm de longitud, ca. 13 mm altura, con una perforación de 2.3 mm (T/17), Tubul, 11. X. 1970. (3) 1 impresión de una v i, 17 mm longitud, 12 mm altura, con 21 dientes anteriores y 8 posteriores (T/18), Tubul, 11. X. 1970.

Descripción

Concha de regular tamaño (hasta 20 mm de longitud), triangular. Umbos prominentes. Bordes redondeados, excepto el posterior que es casi recto, formando un ángulo con el margen ventral. Líneas de crecimiento más notorias en la región ventral, donde originan costillas concéntricas irregularmente distribuídas. Lúnula bien delimitada, casi plana; escutelo poco notorio. Charnela con 21 dientes anteriores y 8 posteriores (contados en la impresión de una valva de 17 mm de longitud).

Observaciones

Se distingue de *E. valdiviana* (Philippi, 1887) y *E. lebuensis* (Philippi, 1887) por su contorno triangular y por el ángulo que forma el borde posterior con el borde ventral.

El ejemplar de "Navidad", descrito por Philippi (1887, lám. 41, fig. 7 b), sin medidas y que consideró una "variedad", parece corresponder a un ejemplar de esta especie. Este material no se encuentra en las colecciones existentes en el Museo Nacional de Historia Natural, Santiago.

Distribución Geográfica y
Rango Estratigráfico

Ennucula araucana Philippi ha sido encontrada en los afloramientos del Piso de Navidad, en (Mioceno Inferior) Navidad (Prov. Santiago), Arauco, Ranquil, Lebu (Prov. Arauco), e Isla Mocha, ¿Tierra del Fuego? (Eoceno-Plioceno) (Prov. Magallanes), en los afloramientos Plio-Pleistocénicos de Tubul y en Talara, Perú (no se especifica Piso).

Ennucula lebuensis (Philippi, 1887)
Figs. 138, 139

Nucula lebuensis Philippi, 1887: 191, lám. 41, fig. 5 (Loc. tipo: Lebu, Terciario); Tavera, 1942: 602, 604, 612, 626, 627 (Piso de Navidad en Arauco y Ranquil y Oligoceno del Perú); Fenner y Wenzel, 1942: 1004 (Piso de Navidad); Feruglio, 1949: 302; 2: 250 (Navidense); Hoffstetter et al., 1956: 243, 245, 306.

Material Estudiado

(1) 2 moldes internos. 19 mm longitud, 13.7 mm altura, 8.7 mm espesor; 19 mm longitud, 14 mm altura, 10 mm espesor (T/19), Tubul, 24.X.1969. DGUC.

Descripción

Concha de regular tamaño (hasta 26 mm de longitud), ovalada, ligeramente comprimida; muy inequilateral. Bordes redondeados. Al-

tura del extremo posterior, igual a la mitad de la altura máxima de la concha. Umbos poco prominentes; ápices aplastados, líneas de crecimiento irregularmente distribuídas, débilmente visibles. Lúnula plana, lanceolada.

Observaciones

Como lo hiciera notar Philippi (1887) esta especie, en comparación a *E. valdiviana,* se caracteriza por su forma elíptica y su extremo posterior poco elevado.

Al igual que en el caso de otras especies, el material tipo de Philippi parece haberse perdido y no se encuentra en las colecciones del Museo Nacional de Historia Natural, Santiago.

Distribución Geográfica y
Rango Estratigráfico

Piso de Navidad, Mioceno Inferior, en Arauco, Ranquil y Lebu; Plio-Pleistoceno de Tubul (Prov. de Arauco) y Oligoceno del Perú (sin localidad).

Ennucula valdiviana (Philippi, 1887)
Figs. 134–137

Nucula valdiviana Philippi, 1887:190, lám. 41, fig. 22 (Localidad tipo: Llancahue, Boca del Río Rapel, Terciario); Tavera, 1942: 619 (Piso de Navidad).

Material Estudiado

1 ejemplar (ej), 4 valvas (v) 1 molde interno (mi). DGUC. Procedencia: (1) 1 ej, 17 mm longitud, 10.5 mm altura, 7.2 mm espesor (sólo capa interna de la concha), 1 v de 19.5 mm longitud, 12.9 mm altura, 1 resto de valva (tiene 21 dientes anteriores) (T/13), Tubul, 24.X.1969. (2) 2 v, 15.7 mm longitud, 14.2 mm altura (T/14) Tubul, 7.X.1968. (3) 1 v d, 19.5 mm de longitud, 13 mm, dientes anteriores 19, (MV/1), Tubul, 10. I. 1971. (4) 1 mi de aproximadamente 16 mm de longitud, 12 mm altura, 7 mm espesor (T/15), Tubul, 24.X.1969.

Descripción

Concha de regular tamaño (hasta 30 mm de longitud), elíptica, débilmente globosa; muy inequilateral, en la parte posterior muy corta. Bordes redondeados; extremos anterior y posterior levemente rostrados; la altura de este último es casi 2/3 de la altura máxima de la concha. Umbos poco prominentes. Ornamentación de las valvas formada por finas estrías concéntricas y líneas radiales poco notorias. Lúnula y escutelo alargado y bien delimitados. Serie anterior con 19 dientes en un ejemplar de 19.5 mm de largo.

Observaciones

Esta especie es más o menos frecuente en el Plio-Pleistoceno de Tubul. Se la encuentra con la concha original bien conservada, en la que se distingue la capa de nacar característica de los Nuculidae. También se encuentra en moldes internos. Las líneas radiales no fueron descritas por Philippi, pero el resto de los caracteres están en perfecta concordancia con su descripción.

La característica más notable para diferenciarla de *E. lebuensis,* es la relación altura extremo posterior/altura máximo de la concha, igual a 2/3 en *E. valdiviana* y a 1/2 en *E. lebuensis.*

El material estudiado por Philippi no se encuentra en las colecciones del Museo Nacional de Historia Natural, Santiago.

E. valdiviana es fácil de reconocer por su forma alargada.

Distribución Geográfica y
Rango Estratigráfico

Ennucula valdiviana ha sido encontrada en los afloramientos del Piso de Navidad (Mioceno Inferior), Boca del Río Rapel (Prov. de Santiago), Tubul (Prov. de Arauco) y Llancahue (Prov. de Valdivia).

Nuculana errazurizi (Philippi, 1887)

Nucula errazurizi Philippi, 1887: 189 lám. 41, fig. 11 (Terciario de Lebu); Fuenzalida, 1942: 404 (cf. al Terciario de Magallanes).

Leda errazurizi (Philippi), Ortmann, 1900: 378; Ortmann, 1902: 84, 85, lám. 26, figs. 3a, b (Desembocadura Río Santa Cruz, Cañon cerca Cerro Oveja, Rio Chico, Arroyo Gio, Lago Pueyrredón; Argentina); Feruglio, 1949: 156, (Terciario Tierra del Fuego y Punta Arenas en general) Estratos de Boquerón; Hoffstetter et al., 1956: 44, 222, (Boquerón, Eoceno (y Paleoceno?) 52°30′-54°S).

Nuculana oxyrrhyncha (Philippi, 1887)

Nucula oxyrrhyncha Philippi, 1887: 190 lám. 41, fig. 21 (Terciario de Lota, Lebu y Navidad); Brüggen, 1950: 44 (Algarrobo, Lebu, Rumena Quidico, Navidad).

Leda oxyrrhyncha (Philippi), Ortmann, 1900: 378; Ortmann, 1902: 83, lám. 26, figs. 2a, b (Desembocadura Río Santa Cruz, Arroyo Gio.); Fuenzalida, 1942: 412, 413, 424 (Patagoniano); Tavera, 1942: 592, 593, 594, 599, 626, 627 (Piso Boca Lebu, Millongue) Oligoceno del Perú); Feruglio, 1949: 156, 234, 237, 240 (Navidad, Boquerón, Lebu, Millongue); Hoffstetter et al., 1956: 40, 44, 95, 227, 228, 243; Tavera y Veyl, 1958: 160, lám. 1, fig. 2a (Formación Ranquil en Isla Mocha); *non* Jaworski, in Steinmann 1922: 114, 117, lám. 4, figs. 7a–e.

Observaciones

La cita de esta especie por Tavera (1942) para el Oligoceno del Perú, basada probablemente en *Leda oxyrrhyncha* Jaworski, 1922, es errónea, ya que las figuras de la especie de Jaworski son muy diferentes a las de Philippi (1887), y parecen corresponder a otra especie.

Jupiteria (*Surojupiteria*) *dissensa* Stilwell y Zinsmeister, 1992

Jupiteria (*Surojupiteria*) *dissensa* Stilwell y Zinsmeister, 1992: 48 (Terciario Inferior, Isla Seymour, Antártica).

Australoportlandia antarctica Zinsmeister, 1984

Australoportlandia antarctica Zinsmeister, 1984: 1504, fig. 3F, G (Formación La Meseta, Eoceno, Isla Seymour, Antártica); Stilwell y Zinsmeister, 1992: 50 (Formación La Meseta, Eoceno, Isla Seymour, Antártica).

Propeleda medinae (Philippi, 1887)

Nucula medinae Philippi, 1887: 188, lám. 41, fig. 24 (Loc. tipo: Boca del Río Rapel, Terciario); Fenner y Wenzel, 1942: 1003 (Punta del Fraile y Ranquil, Piso de Navidad; Millongue, Piso Millongue, Prov. de Arauco).

Leda medinae (Philippi), Tavera, 1942: 595, 596, 599 (Piso de Millongue); Feruglio, 1949: 44 (Algarrobo, Rumena Quidico, Navidad); Hoffstetter et al., 1956: 227 (Eoceno de Millongue).

Material Estudiado

4 moldes internos (mi) y fragmentos de concha; DGUC. Procedencia: 1 mi, 11 mm longitud, 5 mm altura; pedazo de mi con fragmentos de concha; 1 mi, 15 mm longitud, sólo visible dorsalmente; 1 mi 8 mm longitud, 3 mm altura; 1 mi 12 mm longitud, 5 mm altura, (P/1.), Pique Pilpilco, Curanilahue en arenisca dura.

Descripción

Concha de regular tamaño (hasta 15 mm de longitud) delgada, alargada, comprimida, rostrada posteriormente. Bordes redondeados; dorsal posterior cóncavo. Umbos poco abultados. Ornamentación de las valvas formada por costillas concéntricas finas y densas, 10 por mm. No hay lúnula ni escutelo.

Observaciones

En el aspecto externo, la semejanza de esta especie fósil con la especie reciente antártica *P. longicaudata* es notable.

Distribución Geográfica y Rango Estratigráfico

Propeleda medinae se ha encontrado en los afloramientos del Piso de Navidad (Mioceno Inferior), en Boca del Río Rapel (Prov. Santiago), Punta del Fraile y Ranquil (Prov. de Arauco), y en el Piso de Millongue (Eoceno Superior y parte del Eoceno Medio), en Millongue (Prov. Arauco) y en Algarrobo y Rumena Quidico (Prov. Santiago).

Propeleda darwini (Philippi, 1887)

Nucula darwini Philippi, 1887: 188, lám. 41, fig. 17 (Terciario de Lebu); Fenner y Wenzel, 1942: 1004 (cf. al Piso de Navidad); Feruglio, 1949: 302; 2: 237, 240, 250 (Fauna de Millongue, Piso de Navidad).

Leda darwini (Philippi), Fenner y Wenzel, 1942: 1016 (Puente Río Pilpilco, Estero Pata Vacas); Hoffstetter et al., 1956: 227, 243 (Millongue).

Propeleda dorbigny (Philippi, 1887)

Nucula dorbigny Philippi, 1887: 188, lám. 41, fig. 10 (Lebu).

Leda D'Orbigny (Philippi), Fenner y Wenzel, 1942: 1004, 1016 (Piso Millongue en Millongue, Puente Río Pilpilco, Estero Pata Vacas, Puente Río Trongol, Río Curanilahue).

Leda D'Orbigny (Philippi), Tavera, 1942: 526, 596, 599, 626 (Piso Millongue y Oligo-

ceno del Perú); Hoffstetter et al., 1956: 227.

Leda orbigny (Philippi), Feruglio, 1949: 237 (Millongue).

Tindariopsis elegans (Hupé, 1854)
Figs. 2, 148–156

Nucula elegans Hupé, 1854: 305, lám. 5, fig. 7 (Loc. tipo: Coquimbo, Eoceno); Philippi, 1887: 189, lám. 31, fig. 6 (Terciario de Tubul); Möricke y Steinmann, 1895: 230, 240 (Tubul, Coquimbo); Fenner y Wenzel, 1942: 1004 "*var angusta,*" (Piso Navidad); Hoffstetter et al., 1956: 84, 243 (Plioceno de Coquimbo, Paleoceno-Mioceno de Navidad).

Leda elegans (Hupé), Tavera, 1942: 614 (Plioceno y Cuaternario de Arauco); Feruglio, 1949: 230, 240 (Capas Terciarias de Tubul y Piso Navidad).

Nuculana elegans (Hupé), Frassinetti y Covacevich, 1995 (Plioceno Superior de Isla Guamblín, Archipiélago de los Chonos, Sur de Chile).

Material Estudiado

137 ejemplares (ej), 736 valvas (v) y 24 moldes internos (mi); DGUC. Procedencia: (1) 13 ej, 5–13 mm, 185 v s, 6–15 mm (T/10), Canal Los Patos, Arauco, I. 1964. (2) 3 ej, 12–13.5 mm, 6 v s, 8–12 mm (T/7) Tubul, 7.X.1968. (3) 10 ej, 5–11.5 mm, 40 v s, 5–14 mm (T/8) Tubul, 7.X.1968. (4) 4 ej, 4–14 mm, 20 v s, 9–12.5 mm (T/9) Tubul, 10.X.1968. (5) 5 ej, 10–13 mm, 10 v s, 14.5–11.5 mm (T/2) Tubul, 10.X.1968. (6) 17 v s, 6–10 mm (T/4), Tubul, 10.X.1968. (7) 35 v s, 7–12 mm (T/5) 10.X.1968. (8) 9 ej, 7–15 mm, 66 v s, 4–14.5 mm (T/3) Tubul, 17.X.1968. (9) 5 ej, 6.3–13.6 mm, 88 v s, 4.7–14.8 mm (T/8) Tubul, 24.XI.1968. (10) 50 ej, 3–13 mm, 216 v s, 4.7–13.5 mm (T/1) Tubul, 24.X.1969. (11) 17 mi, 9–11.5 mm (T/11) Tubul, 24.X.1969. (12) 21 ej, 8–13.5 mm, 7 mi, 4–8.5 mm, 70 v s, 4–13.5 mm (T/12) Tubul, 11.X.1970.

Descripción

Concha de tamaño mediano (hasta 15 mm de longitud), gruesa, elíptica, inflada. Umbos anteriores con ápices prosogiros. Bordes redondeados; el dorsal y el ventral posterior tienden a ser rectos; extremo posterior truncado. Ornamentación formada por costillas concéntricas sobrepuestas, densas (3.5 por mm) y flectadas sobre la carina posterior. Lúnula y escutelo débilmente delimitados. Seno paleal amplio. Impresiones de los aductores desiguales: la anterior redondeada y la posterior ovalada.

Observaciones

En *T. elegans,* como en otros bivalvos (Waller, 1967), existe gran variación en la forma y escultura de las valvas por efecto de un mayor o menor grado de abrasión postmortem, antes o después de la fosilización. Efectivamente, algunos ejemplares (Figs. 152, 154, 155) presentan en la región anterior sólo costillas concéntricas, sin que se distingan las costillas sobrepuestas que caracterizan a esta especie. Otros, (Fig. 153) que han sufrido mayor desgaste, exhiben la parte posterior lisa, dejando ver un surco carinal y asemejándose a *Nucula amblyrrhyncha* Philippi, 1887. Sin embargo, algunos individuos (muestra 1) presentan parte del perióstraco, que se observa plegado, contándose más o menos 10 finísimos pliegues por costilla de la concha.

El seno paleal de esta especie es poco profundo, pero nunca tan angular como el figurado por Philippi (1887; lám. 31, fig. 6).

Tindariopsis elegans es uno de los bivalvos más abundantes en los estratos de Tubul, Arauco, y fue recientemente redescrita del Plioceno Superior de Isla Guamblin (44° 47′45″ S; 75° 05′15″ W) (Francinetti y Covacevich, 1995). Parece muy afin a la especie reciente *T. sulculata* en lo que se refiere a la ornamentación y forma general, diferenciándose por su rostro más largo y truncado, menor convexidad de las valvas, mayor densidad de costillas concéntricas y mayor amplitud del seno paleal.

De 137 ejemplares completos y 753 valvas examinados, 20 resultaron con perforaciones, generalmente en el centro de la valva, producidas por un depredador. En general, su asociación faunística, por la presencia de pectínidos, se puede comparar con la asociación magallánica actual.

Distribución Geográfica y
Rango Estratigráfico

Ha sido encontrada en los afloramientos del Eoceno y Plioceno de Coquimbo (Prov. Coquimbo), Paleoceno y Mioceno de Navidad (Prov. Santiago), Plioceno y Pleistoceno de Arauco y Tubul (Prov. Arauco), Plioceno superior de Isla Guanblín, Archipiélago de los Chonos, Sur de Chile.

Yoldia levitestata Stinnesbeck, 1986.

Yoldia levitestata Stinnesbeck, 1986: 165, lám. 1, figs. 10, 11 (Formación Quiriquina, Maastrichtiano).

Observaciones

Aparentemente hay sólo dos especies indeterminadas referidas a este género, una del Plioceno de la Isla Mocha (Tavera y Veyl, 1958), y la otra, aún de determinación genérica dudosa, del Plioceno de Valparaíso (Tavera, 1960).

El género *Yoldia,* tiene un rango estratigráfico probable desde el Eoceno al Reciente, aunque ha sido citado también del Carbonífero (Hertlein y Strong, 1940) y del Maastrichtiano.

Yoldiella leurovata Stilwell y Zinsmeister, 1992

Yoldiella leurovata Stilwell y Zinsmeister, 1992: 51 (Eoceno tardío de la Formación La Meseta, Isla Seymour, Antártica).

Australoneilo rossi Zinsmeister, 1984

Australoneilo rossi Zinsmeister, 1984: 1503, figs. 3H–K (Isla Seymour, Antártica, Eoceno). Stilwell y Zinsmeister, 1992: 51

Solenomya antarctica Philippi, 1887

Solenomya antarctica Philippi, 1887: 179, lám. 42, fig. 5 (Loc. tipo: Boca del Río Rapel); Tavera, 1942: 602, 626 (Piso Navidad); Feruglio, 1949: 241 (Piso Navidad).

Solemya peteri Zinsmeister, 1984

Solemya peteri Zinsmeister, 1984: 1505, fig. 3L (Formación La Meseta, Eoceno. Isla Seymour, Antártica). Stilwell y Zinsmeister, 1992: 52 (Terciario Inferior Isla Seymour, Antártica).

Especies Mesozoicas y Cenozoicas

Nucula (*Leionucula*) *nova* Wilckens, 1991

Nucula nova Wilckens, 1911: 5, lám. 1, figs. 4a, 4b, 5 (Mesozoico); Fuenzalida, 1942: 414, 424 (Terciario Islas Seymour, Patagoniano Inferior); Feruglio, 1949: 156 (Boquerón); Hoffstetter et al., 1956: 44 (Eoceno y Paleoceno de Boquerón, región Magallánica).

Nucula (*Leionucula*) *nova* Wilckens, Zinsmeister, 1984: 1501, figs. 3C–E (Isla Seymour, Antártica, Eoceno); Stilwell y Zinsmeister, 1992: 47 (Terciario Inferior Isla Seymour, Antártica).

Malletia (*Neilo*) *pencana* (Philippi, 1887)

Nucula pencana Philippi, 1887: 185, lám. 41, fig. 5 (Cretácico de Hualpén); Steinmann, 1892: 111 (Hualpén).

Malletia pencana (Philippi), Wilckens, 1904: 230, 269, 272, 278 (Quiriquina); Wetzel, 1930: 75; Tavera, 1942: 587, 619 (Piso Quiriquina; Pilpilco, Antihuala, Piso de Navidad); Feruglio, 1949: 266, 303 (Estratos Cerro Dorotea); Hoffstetter et al., 1956: 64, 303 (Estratos Cerro Dorotea, Crét. Sup. Maastrichtiano Ultima Esperanza, 51°2′18″S; Capas de Quiriquina Crét. Sup. Maastrichtiano).

Neilo (*Neilo*) *pencana* (Philippi), Stinnesbeck, 1986: 166 lám. 1, figs. 12–14.

Neilo beui Stilwell y Zinsmeister, 1992

Neilo beui Stilwell y Zinsmeister, 1992: 52 (Terciario Inferior Isla Seymour, Antártica).

Neilo maxwelli Stilwell y Zinsmeister, 1992

Neilo maxwelli Stilwell y Zinsmeister, 1992: 52 (Terciario Inferior Isla Seymour, Antártica).

Malletia (*Neilo*) *volckmanni* (Philippi, 1887)
Figs. 144, 145

Nucula volckmanni, Philippi, 1887: 188, lám. 41, fig. 9 (Loc. tipo: Tubul y Lebu, Terciario); Tavera, 1942: 606, 612 (Piso de Navidad, Patagónico y Magallánico); Fuenzalida, 1942: 404 (Terciario de Magallanes); Feruglio, 1949: 156 (Piso Navidad).

Malletia volckmanni (Philippi), Tavera, 1942: 602, 604, 612, 619 (Piso Navidad en Ránquil); Wilckens, 1904: 278 (Terciario); Brüggen, 1950: 45 (Punta del Fraile, Arauco).

Malletia volckmanni (Philippi), Hoffstetter et al., 1956: 243, 245, 306 (Piso de Ránquil, Mioceno de Arauco 37°30′S); Feruglio, 1949: 240 (Terciario de Magallanes).

Material Estudiado

1 v d, 46 mm longitud, 24 mm altura (N/1). Terciario de Navidad. 15.1.1968. DGUC. De esta valva falta la parte ventral posterior y no se puede observar su interior, por estar unida

a una arenisca arcillosa, gris de grano fino, bien cementada.

Descripción

Concha de gran tamaño (46 mm de longitud), oval-oblonga, inflada, posteriormente algo rostrada. Umbos poco prominentes. Bordes, anterior y dorsal-anterior, redondeados; dorsal-posterior y posterior casi rectos, con una ligera concavidad. Ornamentación formada por costillas concéntricas regulares (1 por mm), que cambian de dirección sobre dos carenas débiles que nacen desde el ápice y separándose un poco terminan en la unión del borde ventral con el posterior; en el área comprendida entre estas carenas y el borde dorsal posterior, las costas se flectan hacia el ápice. Existe un escutelo muy alargado y angosto que encierra al ligamento.

Observaciones

A juzgar por la naturaleza de la roca en la que se encontró, *M. volckmanni* vivía en fondo fangoso; las especies actuales de este género viven en substrato similar.

Distribución Geográfica y
Rango Estratigráfico

Malletia volckmanni ha sido encontrada en los afloramientos del Piso de Navidad (Prov. de Santiago) (Mioceno Inferior), Tubul, Rada Ranquil, Punta del Fraile (Provincia de Arauco), y en los Pisos Patagónico (Argentina) y Magallánico, Eoceno-Plioceno (Prov. Magallanes).

OTRAS REFERENCIAS A *NUCULA* y *NUCULANA*

(1) Especies fósiles indeterminadas, referidas al género *Nucula,* han sido mencionadas para diferentes niveles estratigráficos por los siguientes autores:

Nucula sp. Steinmann, 1892: 10 (Piso de Navidad;¿Quiriquina?).

Nucula sp. Biese-Nickel, 1942: 443, 460, 442, (Cretácico al S de Copiapó, Caliza de Pabellón alfa 30–35 m, Caliza de Nantoco ß 250–300 m. Kinmeridgiano y Neocomiano).

Nucula sp. Fuenzalida, 1942: 404 (Terciario de Magallanes).

Nucula sp. Fenner y Wenzel, 1942: 1003, 1004, 1018 (Piso de Navidad, Ranquil, Punta del Fraile; Quebrada el Molino, Arauco).

Nucula sp. Tavera, 1956: 208 (Cretácico Inferior de Copiapó; Totoralillo; Barremiano-Aptiano).

Nucula sp. Segerström, 1959: 8 (Hauteriviano Superior, Formación Totoralillo).

Nucula sp. Galli y Dingman, 1962: 31 (Piso Lotharingiano y Sinemuriano del Liásico, Formación Longacho. Tal vez una especie distinta).

(2) Especies fósiles chilenas indeterminadas referidas al género *Nuculana* han sido mencionadas para diferentes niveles estratigráficos por los siguientes autores:

Nuculana sp. Biese-Nickel, 1942: 442 (Cretácico Inferior al S de Copiapó, Caliza Pabellón alfa 30–35 m).

Nuculana sp. Tavera, 1942: 599, 602 (Piso Millongue y Piso Navidad).

Nuculana sp. Fenner y Wenzel, 1942: 1004, 1016 (Lorcura, Terciario carbonífero de Arauco, Piso de Navidad).

Nuculana sp. Tavera, 1956: 208 (Cretácico Inferior de Copiapó).

Nuculana sp. Corvalán, 1959: 47 (Hauteriviano Superior de Vallenar y Barremiano de las Ventanas, (28°30′S, 70°52′W; Chañar Quemado, 28°21′S, 70°52′W).

Nuculana sp. Segerström, 1959a: 9, "una nueva especie" (Jurásico Inferior, Formación Lautaro, ribera oeste del Río Copiapó).

Nuculana sp. Segerström, 1959b: 8 (Hauteriviano Superior, Formación Totoralillo, Totoralillo).

Nuculana sp. Levi, 1960: 246, "aff. *Leda striatissima* Geotsche (La Calera)."

Nuculana sp. Zinsmeister, 1984: 1504 (Formación La Meseta, Eoceno, Isla Seymour, Antártica).

Nuculana spp. Biró, 1964: 57, 58 (Formación Lo Valdés, Titoniano Superior).

Nomina Dubia

Las especies que se incluyen en la lista adjunta, no están lo suficientemente bien descritas ni ilustradas como para permitir precisar su posición génerica, y en algunos casos, aún su posición a nivel de familia.

Nuculidae?

Nucula andina Philippi, 1899: 60, lám. 26, fig. 8 (Portezuelo del Tinguiririca). De género dudoso.

Nucula arcaeformis Philippi, 1887: 187, lám. 41, fig. 18 (Cretácico en Hualpén); Steinmann et al., 1892: 111; Wilckens, 1904: 271 (Piso Quiriquina). Probablemente una *Barbatia.*

Nucula? cornuta Philippi, 1887: 186, lám. 41, fig. 20 (Cretácico de Tumbes); Wilckens, 1904: 271, 272 (Piso Quiriquina). De posición taxonómica incierta.

Nucula hualpensis Philippi, 1887: 187, lám. 41, fig. 3 (Cretácico de Hualpén). Podría ser Malletiidae.

Nucula largillierti d'Orbigny, 1842: 128, lám. 15, figs. 9, 10; Hupé, 1854: 304; Philippi, 1887: 187, lám. 31, fig. 7 (Cretácico Isla Quiriquina). D'Orbigny, 1846: lám. 5, figs. 5, 6, describe aparentemente a esta especie como *Tellina largillierti.*

Nucula? quisquilia Philippi, 1899: 60, lám. 24, fig. 9 (Portezuelo de Tinguiririca). No parece ser un protobranquio.

Nucula? quiriquinae Philippi, 1887: 185, lám. 41, fig. 6 (Cretácico Isla Quiriquina); Steinmann et al., 1892: 111; Wilckens, 1904: 271, 272 (Piso Quiriquina). En apariencia un nuculanáceo, pero de posición genérica incierta.

Nucula subcarinata Philippi, 1899: 59, lám. 26, fig. 6 (Portezuelo del Tinguiririca). De género dudoso.

Nucula subradiata Philippi, 1899: 59, lám. 26, fig. 5. Probablemente un nuculanáceo. Sin localidad.

Nucula? tinguiriricana Philippi, 1899: 60, lám. 26, fig. 7. Probablemente un nuculanáceo. Sin localidad.

Nucula triangula Philippi, 1899: 60, lám. 26, fig. 10 (Portezuelo del Tinguiririca). De género dudoso.

Nucula barrosi Philippi, 1887: 191, lám. 41, fig. 14 (Boca Río Rapel); Steinmann et al., 1892: 23 (Piso Quiriquina); Wilckens, 1904: 271. ¿Un venérido?

Nucula lauta Philippi, 1887: 189, lám. 31, fig. 2 (Lebu); Brüggen, 1950: 44. No parece un protobranquio. Probablemente pertenezca a otro orden.

Nuculanidae?

Nucula andina Philippi, 1887: 60, lám. 26, fig. 8 (Portezuelo del Tinguiririca). Podría ser una *Nuculana.*

Nucula angusta Philippi, 1887: 186, lám. 41, fig. 13 (Cretácico de Algarrobo); Steinmann et al., 1892: 111 (Algarrobo).

Leda angusta (Philippi), Fuenzalida, 1942: 412, 413, 423 (Boquerón, Patagoniano, Piso Concepción); Fenner y Wenzel, 1942: 1004, (Arauco); Feruglio, 1949: 156 (Costa austral, Seno Skyring, parte superior estratos Boquerón); Hoffstetter et al., 1956: 44 (Estratos Boquerón, 52°30′–54°S, Eoceno [y Paleoceno ?]). De género dudoso; su rango estratigráfico muy amplio necesita ser revisado.

Leda minuta Wilkens? *non Nuculana minuta* (Müller, 1776), Tavera, 1942: 587, cf. (en Pilpilco y Antihuala); Feruglio, 1949: 301, 302 (Senoniano Patagonia austral, Salamanquense del subsuelo de Comodoro Rivadavia). Posiblemente una *Nuculana. Nuculana minuta* (Müller) es una especie reciente de amplia distribución en el hemisferio norte, siendo conocida desde el Artico hasta el Canal Inglés y la Bahía de Fundy, en el Atlántico, y en el Pacífico hasta California y Japón (Tebble, 1966).

Nucula lunularis Philippi, 1899: 62, sin fig. (Loc. tipo: Portezuelo del Tinguiririca). Philippi (1899), menciona que el único ejemplar usado para describir esta especie, se extravió, razón por la cual no la ilustró. Por la descripción original se podría considerar como un posible nuculanáceo.

Nucula amblyrryncha Philippi, 1887: 190, lám. 41, fig. 3 (Terciario de Rapel). Probablemente una *Nuculana.*

Nucula sanctaemariae Philippi, 1887: 188, lám. 41, fig. 2 (Terciario Isla Santa María); Fuenzalida, 1942: 425 (Estero Vitracic, Península Brunswick).

Leda sanctamariae (Philippi), Feruglio, 1949: 302; 2: 156, 250 (Loreto, Cabo Domingo Sunday); Hoffstetter et al., 1956: 202 (Oligoceno (y/o Eoceno Sup.?), Formación Loreto, región Magallánica (51°30′–54°S). Probablemente una *Nuculana.*

Nomina Nuda

Acila brueggeni Tavera, 1942: 599 (Piso Boca Lebu y Piso Millongue); Feruglio, 1949: 237–239 (Millongue, Prov. Arauco, 37°30′S, Eoceno); Hoffstetter et al., 1956: 227.

Acila bruggeni Fenner y Wenzel, 1942: 1016, 1003 (Pino Huacho). No existe de esta especie descripción ni figura.

DISCUSIÓN Y CONCLUSIONES

La clasificación de la subclase Protobranchia aquí aceptada comprende a las fa-

milias Nuculidae, Nuculanidae, Siliculidae, Sareptidae, Tindariidae y Malletiidae dentro del orden Nuculoida y la familia Acharacidae dentro del orden Solemyoida.

Los estudios de McAlester (1964), Knudsen (1970), Allen y Hannah (1986), Maxwell (1988), y Coan y Scott (1997), sugieren la conveniencia de mantener a la familia Malletiidae separada de Nuculanidae, en la que ha sido incluída por otros autores. El presente estudio ha intentado corroborar tal separación, basado especialmente sobre caracteres anatómicos de las partes blandas (e.g., corazón atravesado por el recto o generalmente bajo él; intestino con una sola vuelta).

De un total de 35 especies recientes descritas y/o citadas para la costa de Chile se aceptan 28, de las cuales *Propeleda longicaudata* era conocida con anterioridad sólo de aguas antárticas y *Nucula pseudoexigua* corresponde a una especie nueva.

Las cuatro especies de Malletiidae aceptadas en este trabajo, podrían corresponder quizá sólo a dos, si las diferencias reconocidas para las distintas especies, sobre todo de aquellas que no han vuelto a encontrarse después de su descripción original, resultan ser sólo el resultado de variación o anormalidades.

Pese a que se ha elevado de rango al taxón *Tindariopsis* Verrill y Bush escrito originalmente como subgénero, su posición es incierta y podría corresponder solo a un sinónimo de *Neilonella* Dall.

La mayoría de los caracteres anatómicos de la concha o de las partes blandas conocidos para los protobranquios es el resultado del estudio de sólo algunas especies y no existen trabajos en que se analice de manera general la relación de los diversos caracteres. Su análisis, en el caso de las especies chilenas, nos permite puntualizar las siguientes relaciones con las generalizaciones del grupo.

(1) El tamaño de las distintas familias de los protobranquios es variable. Los nucúlidos vivientes, en general, son más pequeños que los nuculanáceos y solemiáceos; el menor tamaño adulto conocido, igual a 600 µ fue registrado por Moore (1977) para *Condylonucula cynthiae* y se conoce un máximo de 49 a 50 mm de largo en *Acila divaricata* (Hinds) del Japón. Las especies chilenas no hacen excepción a los límites conocidos; por ejemplo, el mayor tamaño encontrado fue igual a 20.6 mm de longitud en *Ennucula grayi* (d'Orbigny, 1846). En Nuculanidae y Malletiidae el mayor tamaño medido fue de 51 mm de longitud en *Malletia chilensis,* aunque se ha descrito un fósil chileno de este mismo género que alcanza a 60 mm, y se conoce una especie reciente de Kerguelen *Malletia gigantea* (Smith 1875) que mide 62 mm.

(2) Se pueden distinguir tres formas básicas: nuculoide (elevada y corta), nuculanoide (elevada y larga) y solemyoide (larga), representadas en las Figuras 1, 3, 131 y 132. Las especies asignadas a las distintas familias, caen dentro de estas tres formas fundamentales, con distintos grados de variación adaptativa (Fig. 61). En Solemyacea (*Acharax*, Figs. 131–132; *Solemya*) la parte anterior del umbo es generalmente más larga, al contrario de lo que ocurre en Nuculanacea, en donde la parte posterior es generalmente igual a (e.g., especies de *Neilonella*) o mayor que la anterior (e.g., *Nuculana, Silicula, Yoldia, Yoldiella, Ledella, Malletia,* excepto en *M. inequalis,* Figs. 113–130, 133, 144–158).

(3) No se ha hecho un estudio comparativo de la forma y variación de la charnela, dentro de cada familia y su evolución ha seguido líneas evolutivas diferentes, donde, sin embargo, el conocimiento alcanzado no permite precisar afinidades y divergencias.

(4) Merece alguna discusión el ligamento por la importancia que ha revestido en la clasificación de los bivalvos en general, pero su estructura en los protobranquios es todavía problemática (Stempell, 1898a; Dall, 1908a; Trueman, 1952, 1969; Owen, 1959; Waller, 1990).

Tradicionalmente la posición del ligamento se ha descrito: interna en Nuculidae, Siliculidae y algunos Nuculanidae; parcialmente interna en algunos Nuculanidae y Malletiidae; predominantemente externa en algunos Malletiidae; externa y/o interna en Tindariidae. Pero, esta generalización se complica al considerar el origen de las dos capas del ligamento descrito por Trueman (1952, 1969) y Owen (1959).

Según Owen (1959), el ligamento de *Nucula* y *Nuculana* está formado por una capa externa, denominada también lamelar (dividida en una capa externa anterior y otra posterior), conectada con los márgenes del manto, y otra interna o fibrosa, conectada por el istmo del manto, que corresponde a capas similares del ligamento primario de los bivalvos (Yonge, 1957; Trueman, 1969). Esta característica puede aplicarse, en general, a todos los Nuculidae y Nuculanidae y va

acompañada por el desarrollo variable de un resilífero o condróforo, que interrumpe a las dos series de dientes y está dirigido hacia adelante en *Nucula* y *Ennucula* (Fig. 3A, cdr); es más o menos recto en *Yoldia* (Fig. 129) y dirigido hacia atrás en *Nuculana* (Fig. 3).

En los otros géneros la diferenciación de la parte externa e interna del ligamento, es difícil de precisar macroscópicamente y plantea interrogantes difíciles de responder sin estudios histoquímicos y de microscopía electrónica (pero véase a Waller, 1990).

Owen (1959) describió una estructura similar a la de *Nucula* y *Nuculana* (con un ligamento considerado de tipo amfidético, alivincular) en el ligamento de *Solemya parkinsoni* Smith (considerado de tipo opistodético y transversal), en la cual, la parte anterior de la capa externa se extiende a lo largo de la línea charnelar, y la capa interna queda desplazada bajo la posterior de la externa (Fig. 3C). *Malletia,* presenta según Trueman (1969) un ligamento externo opistodético y parivincular; pero, si el ligamento externo observado en *Malletia* fuera similar a la estructura del ligamento en *Solemya,* podría corresponder al de la capa externa del ligamento, lo que significaría que la capa externa (el resilium) habría desaparecido como lo sugiere Dall (1890). Sin embargo, McAlester (1964), basado en Stempell (1898a), concluye que, en los Malletiidae como en los Ctenodontidae fósiles, las áreas de inserción del ligamento no muestran esta separación de las capas, y por el contrario, conservan el tipo más corriente en los bivalvos, en los cuales la capa externa e interna están unidas para formar un ligamento externo prominente. Desgraciadamente, McAlester no comenta mayormente el trabajo de Stempell, ya que éste no solamente refuta a Dall, sino que demuestra que el ligamento de *Malletia* puede dividirse en tres partes: anterior, central y posterior, con la central correspondiendo al resilium (capa interna del ligamento) y la anterior y posterior con un mismo origen. De este modo, la equivalencia de la diferenciación de las capas del ligamento hecha por Owen y Stempell, parece corresponder exactamente en Nuculidae, Nuculanidae y Malletiidae, sugiriendo que el resilium de posición interna en *Nucula* y *Nuculana,* ha emigrado para hacerse externo en Malletiidae, sin desaparecer. Un estado intermedio en la posición del resilium se observa en *Tindariopsis* como lo muestra también Stempell.

A diferencia de estos autores Schileyko (1983), basado en la observación de series morfológicas, considera que ha habido una penetración gradual del ligamento externo en el espacio entre las dos valvas, lo que ha sido acompañado con la formación del resilifer. Las razones de este cambio serían: (1) Las posibilidades de aumento de volumen de la sustancia elástica del resilium más que del ligamento externo. (2) El ligamento interno proporciona un refuerzo concentrado, en cambio el externo distribuye el esfuerzo a todo el largo. (3) El ligamento externo impide el desarrollo de los umbos y (4) El ligamento interno está aislado de la influencia de los factores externos negativos y no se lo puede dañar sin destruir la concha.

En el caso de los Solemyoida se han descrito tres posiciones del ligamento: anfidético principalmente interno en *Solemya,* opistodético interno en *Petrasma* y opistodético completamente externo en *Acharax.* La evolución del ligamento en Solemyoida parece, en consecuencia, seguir líneas paralelas al de los Nuculoida.

En una interpretación novedosa y fundamentada sobre la evolución del ligamento en los bivalvos, Waller (1990) cuestiona el modelo anfidético de tres capas del ligamento primario, aduciendo que éste quizá no era así; que las tres capas no necesariamente corresponden a las tres capas de la concha y que el primer tipo de ligamento fue opistodético. Concluye que en los protobranquios el ligamento lamelar no se diferencia en dos subcapas como en otras subclases; no presenta ninguna relación especial a ninguna capa externa de la concha (que carece de una capa prismática columnar) y, en el hecho, es secretado sobre las partes adyacentes de ella, pudiendo haberse originado como material de reparación de la concha. En los Nuculidae, el resilium consiste de una parte media no calcificada y una parte lateral calcificada. La parte media no calcificada es contínua en sus lados anterior y posterior con el ligamento lamelar sin evidencia física de un límite que lo separe de las regiones vecinas. Esto llevó a Waller (1990) a postular que el resilium es ya sea ligamento primario o que ha invadido secundariamente la región central.

De estos sistemas más simples de ligamento presentes en todos los Protobranchia, salvo por los Solemyidae, se habrían originado dos tipos principales de ligamento presentes en los bivalvos actuales.

(5) La variación en el número y forma de los dientes en Nuculoidea no permite utilizarlos como caracteres de valor genérico o supragenérico, ya que varía considerablemente con el crecimiento en una misma especie y aún en individuos del mismo tamaño; aunque conservando constante la relación: número de dientes anteriores/número de dientes posteriores (Savitskii, 1969a). Sin embargo, la forma y el tamaño de los dientes presentan a menudo valor específico, como lo han hecho notar algunos autores (Knudsen, 1970; Villarroel, 1971).

(6) Los palpos son muy semejantes en los Nuculacea y Nuculanacea, pero su homología con los Solemyidae aun no se conoce bien. En *Solemya* se interpretan como apéndices del palpo no pareados de los otros protobranquios, y las láminas estarían reducidas a simples lomos (Fig. 11) en los bordes del surco que une a la boca con estos apéndices (Figs. 15–17) (Ridewood, 1903; Morse, 1913; Yonge, 1939; Reid, 1980).

El apéndice o tentáculo del palpo sobre la lámina externa de cada uno de los palpos, considerado por Drew (1901) equivalente de un par de repliegues hipertrofiados (Figs. 10, 12, y siguientes, tp) cambia su posición según la familia (Fig. 61). En los Nuculanacea, el apéndice del palpo está ubicado sobre la porción terminal de la lamela externa del palpo (e.g., Fig. 5, *Silicula rouchi;* Fig, 77, *Nuculana* (*S.*) *cuneata;* Fig. 90, *Nuculana* (*B.*) *inaequisculpta*). En cambio en los Nuculidae está desplazado al extremo, ya que detrás de él hay una estructura adicional, no extensible, denominada "ciego del palpo," que según Stasek (1965) también representa un par de repliegues hipertrofiados.

El apéndice del palpo se une en su extremo proximal con la superficie externa de la lámina del palpo y con el ciego del palpo (Fig. 10, bp); su musculatura pasa a fusionarse con el retractor posterior del pie. Estas observaciones efectuadas inicialmente en *Acila* por Stasek (1961) fueron corroboradas, sin excepción, en cada una de las especies aquí estudiadas. Sin embargo, en la mayoría de los casos, los apéndices se encontraron en distintos grados de contracción, impidiendo establecer diferencias específicas (Figs. 4 y 62, 74 y 76, tp).

(7) De las estructuras internas estudiadas, sólo estómago e intestino, la posición del corazón y los sifones permiten extrapolar conclusiones generalizables al grupo.

Aunque la morfología del estómago ha sido descrita en detalle para especies de *Nucula, Nuculana* y *Malletia* (Stempell, 1898a; Health, 1937; Yonge, 1939; Graham, 1949; Owen, 1956; Purchon, 1956), se hace necesaria una descripción comparativa de los Nuculacea y Nuculanacea sobre la base de las especies estudiadas. Esta comparación incluye la identificación de una estructura nueva (ciego posterior), y cambios en la interpretación de las estructuras observadas por autores precedentes, a los que hemos tratado de designar, siguiendo la nomenclatura más usada.

El tamaño y apariencia externa del estómago es similar en Nuculacea y Nuculanacea, pero en Solemyacea es extraordinariamente pequeño, apenas una dilatación (Yonge, 1939; Owen, 1961; Purchon, 1987b) (Figs. 13, 18–56) o puede faltar (Reid, 1980, en *Solemya* sp.). Su posición, que se aprecia mejor en las Figuras 13, 14, 71 y 79, varía como lo hiciera ver Yonge, por efecto de una mayor o menor extensión del pie en el momento de fijar al animal. La separación de este órgano del resto del cuerpo es relativamente fácil en este grupo (excepto en los Solemyidae), porque a diferencia de los filibranquios y eulamelibranquios, está fijo débilmente a los órganos y tejidos adyacentes, lo que Yonge (1939) interpreta como resultado de la acción de trituración muscular que debe realizar el estómago.

La estructura del estómago en Nuculacea y Nuculanacea ha sido dividida en una región superior, glandular, llamada estómago propiamente tal y una región alargada que se extiende ventralmente en el pie, denominado saco del estilo (Figs. 18–56, se). Según Yonge (1939), Graham (1949), y Purchon (1956), esta parte es homóloga con el saco del estilo de los otros bivalvos.

La estructura del estómago en los Solemyacea, posee los caracteres normales internos básicos, incluyendo un capuchón dorsal y un escudo gástrico (Owen, 1961). Yonge (1939: fig. 38) ha diferenciado interiormente tres regiones, las que no nos fue posible observar en *Acharax* (Fig. 13, est.), debido al pequeño tamaño del ejemplar estudiado.

Purchon (1956, 1959) caracterizó el estómago de todos los protobranquios como pertenecientes a un único tipo denominado por él "tipo de estómago 1 o Gastroproteia." El examen de este órgano en las especies chilenas y antárticas estudiadas permite concluir que no existe sólo un tipo básico de estómago, sino que éste puede subdividirse de acuerdo a las ilustraciones de la Figura 60. Aceptando

las relaciones que guardan entre si los tipos de estómagos encontrados o descritos en la literatura pertinente, y que la familia Nucinellidae forma parte de los protobranquios como lo demuestran Allen y Sanders (1969) es posible distinguir al menos tres tipos básicos:

Tipo Ia. Común a los géneros de *Nucula* y *Ennucula* (Nuculidae) y caracterizado por varias áreas de selección (tres a cuatro) y una gran extensión del tiflosol menor.

Tipo Ib. Común a los géneros de Nuculanidae y Malletiidae y caracterizado por tres áreas de selección y una pequeña extensión del tiflosol menor.

Tipo Ic. Común a los géneros de Solemyidae y Nucinellidae y caracterizado por la ausencia de áreas de selección distintas y ausencia de tiflosoles.

La diferenciación de las partes reconocidas interna y externamente en Nuculacea y Nuculanacea, no es difícil y como ha sido indicado por diversos autores para otras especies, en las aquí estudiadas el estómago propiamente tal presenta regiones pardo oscuras externamente lisas (quitinosas, verde oscuro en preparaciones) y otras claras, amarillas, entre las anteriores, ambas fácilmente distinguibles. La entrada del esófago está ubicada anteriormente y un poco hacia la izquierda en Nuculacea, y dorsoanteriormente en Nuculanacea.

En Nuculidae el estómago presenta dorsalmente un capuchón, que muestra en su interior dos pliegues (lomos) longitudinales, y se curva hacia la izquierda terminando en un ciego digitiforme (Figs. 20–32, cd). En Nuculanacea, este capuchón es pequeño y está ubicado dorsalmente a la izquierda (Figs. 33–56, cd). Al igual que en Nuculidae es recorrido por dos pliegues (lomos) que están situados transversalmente.

Los tres conductos (Fig. 18–56; dd, o dd^1, dd^2, dd^3) que comunican al estómago con los divertículos digestivos que lo rodean, entran uno por la izquierda (dd^2) y dos por la derecha (dd^1, dd^3). Dos de ellos (dd^2 y dd^1) están en comunicación con la masa izquierda de los divertículos, y el tercero (dd^3), con la masa de divertículos del lado derecho, como puede observarse en los esquemas adjuntos. La posición de estos conductos es diferente en Nuculacea y Nuculanacea. En los primeros, los orificios de los conductos dd^2 y dd^1 se ubican más o menos simétricamente a los lados o bajo la entrada del esófago, sobre áreas planas (Figs. 18–32). En Nuculanacea, en cambio, el conducto dd^2 se encuentra ubicado generalmente sobre un surco, bajo la entrada del esófago (Figs. 33–56), y los otros dos (dd^1 y dd^3), se abren sobre surcos que corren entre pliegues, dirigidos hacia el esófago en un bolsillo denominado as^4 (Figs. 36, 41, 44).

Las denominadas áreas de selección del estómago, son igualmente importantes en la diferenciación taxonómica de los Nuculacea y Nuculanacea. El área de selección mayor as, presente en Nuculacea y Nuculanacea, descrita por Graham (1949) en *Nucula hanleyi,* mostró en el material estudiado variaciones interespecíficas en cuanto al número de repliegues y a la orientación de éstos.

La variación observada en el número y tamaño de los repliegues, en *Nucula* y *Ennucula* (Nuculacea), se representa en las Figuras 18–31. En las figuras siguientes (Figs. 32–56), se muestra la variación en los Nuculanacea, cuyos pliegues aparecen de tamaño mucho mayor y con orientaciones distintas. Sin embargo, no parece haber modelos que representen a todas las especies de un género (compare Figs. 37, 38 y Figs. 42, 43 ilustrando a dos especies distintas de *Nuculana*).

Después de Graham (1949), Purchon (1956) describió en *Nucula nucleus* (Linné, 1758), tres áreas adicionales denominadas as^1, as^2 y as^3, que pueden o no estar presentes en las distintas especies. En consecuencia, la presencia y distribución de dichas áreas también parece servir como un buen caracter específico. Así por ejemplo, as^1 se encontró sólo en *Nucula* (*Nucula*) *pisum* (Fig. 21) y en *Ennucula puelcha* (Figs. 29–31) y no en las otras especies estudiadas de este género; as^2 se encontró presentando diferente tamaño en *Nucula* (*Nucula*) *pisum. Nucula* (*Nucula*) *fernandensis* y *Ennucula puelcha,* siendo mayor en esta última. En cambio, as^3, no se observó en ninguna de las especies de Nuculanacea estudiadas.

En una posición que corresponde a esta última área de selección (as^3), existe un gran saco (ciego), de posición dorsal a la región de selección mayor "as", sin repliegues en su interior, cuyo extremo se dirige posteriormente a la izquierda. Villarroel (1971) describió este ciego en *Nucula (Nucula) fernandensis* (Figs. 23–26, cp). Se encuentra también en *Nucula* (*Nucula*) *pseudoexigua,* sp. nov., y *Nucula (Nucula) falklandica* (Figs. 18–20 y 27–28, cp).

Purchon (1956) describió también un área plegada en *Nucula nucleus* Linné, que Owen (1956: fig. 2) denominó tracto de expulsión

("rejection tract") en *Nucula sulcata* Bronn. Esta área fue descrita, además, en *Nucula layardi* por Dinamani (1967: fig. 1) pero no fue encontrada por Graham (1949) en *Nucula hanleyi* Winckworth. En el caso de las especies chilenas se observó en *Nucula (Nucula) fernandensis* y *Ennucula puelcha* (Figs. 26, 32, apl), pero no se encontró en *Nucula* (*Nucula*) *pisum,* o *Nucula* (*Nucula*) *pseudoexigua,* sp. nov.

En los nuculanáceos estudiados, no existen las áreas as[1], as[2], as[3], pero en cambio se encuentra también en el tracto de expulsión un área selectiva adicional denominada "as[4]" por Purchon (1956: fig. 3 de *Nuculana minuta* [Müller]), considerada con anterioridad por Yonge (1939) como un ciego (Figs. 36, 41, 42, 49, 50, apl, as4). Según Purchon (1956), estas áreas pueden haberse derivado de un área de selección, pero no tendrían en la actualidad función selectiva.

Aparte de las áreas ya descritas, se encontró una aparente área de selección pequeña en *Malletia chilensis* y *Propeleda longicaudata* (Figs. 36, 50, 56, as?).

Las diferencias indicadas existentes entre los estómagos de Nuculacea y Nuculanacea no apoyan la generalización de Purchon (1987b) de que son básicamente comparables y que una sola descripción puede englobarlos (Fig. 60).

Además de las áreas de selección, y de aquellas ya descritas en que se abren los conductos de los divertículos digestivos, en el interior del estómago existe una tercera parte, revestida por una pared quitinosa que deja libre sólo las áreas de selección, y un surco que une el estómago con el saco del estilo.

La pared quitinosa forma un amplio cinturón alrededor del estómago, y presenta su mayor complejidad en *Propeleda* y *Malletia,* donde se observan modificaciones pectinadas cerca del área de selección mayor (as), y dientes en el escudo (Figs. 36, 56, dq y deg).

Es indudable que la complejidad del escudo gástrico es mayor en Nuculanacea que en Nuculidae y Solemyidae, pero en la actualidad, es difícil juzgar su valor como caracter de diferenciación genérica o específica. Según Yonge (1939), el escudo de los protobranquios sería homólogo con el de los otros moluscos.

La parte inferior del estómago o saco del estilo en Nuculacea y Nuculanacea, longitud y diámetro que alcanza en algunos géneros. Es indudablemente más largo en *Yoldia* (Fig. 44) que, por ejemplo, en *Silicula* (Fig. 48), *Nuculana* (Figs. 37, 42), *Malletia* (Fig. 50) y *Tindaria* (Figs. 52, 55); y entre los nucúlidos, más largo en *Ennucula* (Fig. 29) que en *Nucula* (Figs. 18–28). Hay dos repliegues ciliados o tiflosoles a lo largo de la pared anterior del saco del estilo, que dejan entre ellos el llamado "surco intestinal." Los dos tiflosoles fueron denominados originalmente tiflosol mayor y tiflosol menor por Graham (1949), nombres que continuaron siendo utilizados por Owen (1956) y Purchon (1956), aunque parte del tiflosol menor ha sido denominado también "pliegue derecho" (right fold, Owen, 1956) y "lomo o reborde longitudinal" (longitudinal ridge, Purchon, 1956).

Ventralmente, en la unión del saco del estilo con el intestino, ambos tiflosoles dan origen a numerosos repliegues longitudinales que corren a lo largo de este último (Fig. 73, im). Su número varía especificamente, como se pudo constatar en las especies estudiadas de *Nucula* y *Ennucula.*

Al llegar al estómago ambos tiflosoles se separan. En Nuculacea, el tiflosol menor se dirige hacia atrás y rodea gran parte del área de selección mayor, pudiendo terminar en el lado derecho cerca de la abertura esofágica, como ocurre en *Ennucula puelcha* (Fig. 32, tme), *Nucula nucleus* (Linné, 1758) (Purchon, 1956: fig. 2) y en *Nucula hanleyi* Winckworth (Graham, 1949: fig. 8); o seguir por sobre la abertura esofágica y entrar en el capuchón dorsal, en *Nucula* (*Nucula*) *fernandensis* (Fig. 26), *Nucula sulcata* Bronn (Purchon, 1956) y *Nucula layardi* (Dinamani, 1967: fig. 1).

Dinamani (1967) ha sugerido que la extensión de este tiflosol hasta el capuchón dorsal representaría una modificación única en los Nuculacea, ya que podría también considerarse que dicho tiflosol está interrumpido por el repliegue que divide las dos partes del estómago, haciendo terminar el tiflosol dentro del saco del estilo mismo y no en el capuchón dorsal. De acuerdo con ésto, el lomo que se extiende en el estómago sería sólo una parte del pliegue que nace del capuchón dorsal. Desgraciadamente, este autor no hizo comentarios con respecto al recorrido del tiflosol menor en Nuculanacea. En este grupo, a diferencia de Nuculacea, no circunda el área de selección posteriormente, sino que sólo parcialmente en la parte anterior, acompañando al surco intestinal como se ha observado en *Propeleda longicaudata* y *Malletia chilensis* (Figs. 36, 56, tme), y como lo ilustrara Purchon (1956: fig. 3) en *Nuculana minuta* (Müller).

(8) De interés ha resultado la observación del número de vueltas en los denominados intestino gástrico y medio de diversas especies y sus interpretaciones.

Según Yonge (1939), la porción correspondiente al intestino gástrico se extiende en la base del pie, por lo que cuando éste es proyectado hacia afuera se estiraría formando una sola vuelta.

Las vueltas en esta región del intestino fueron consideradas por Yonge (1939) características de la familia Nuculanidae, como consecuencia de una mayor actividad; sin embargo, ellas se encuentran también en Nuculidae, como ocurre en *Nucula* (*Nucula*) *fernandensis* y *Ennucula puelcha* entre las especies aquí estudiadas (Figs. 24, 30). Si la función postulada por Yonge es correcta, este caracter indicaría que las especies nombradas son también muy activas, aunque como se argumenta a continuación, hasta este momento es más cauto sugerir solamente que este caracter se encuentra presente en algunas especies de las dos familias, sin precisar una función determinada.

Desde la base del pie, el intestino corre dorsalmente a la pared dorsal del estómago y luego se vuelve anteriormente. El intestino medio es de diámetro variable y presenta un patrón de ordenación de sus vueltas específico (Heath, 1937: figs. 2, 3, 6, 8, y siguientes), con una variación intraespecífica aparentemente mínima en las especies estudiadas (e.g. *Nucula* (*Nucula*) *pisum*). Comienza sobre o junto al estómago, y se continúa anteriormente en algunas especies, hasta alcanzar cerca de la boca. Luego, pasa dorsalmente a corta distancia del esófago, y continúa por sobre el estómago a la parte dorsal posterior del cuerpo, o bién, se vuelve ventralmente para formar las vueltas ya mencionadas.

Heath (1937) fue el primero en demostrar que en los Nuculacea el intestino no se extiende tan adelante como en Nuculanacea, lo que el considera una condición primitiva. Describió el número de vueltas en varias especies de *Nucula* y *Acila,* asociando un tipo simple de pocas vueltas con aguas someras, y el enrollamiento más complejo como típico de animales que viven a grandes profundidades.

Un número elevado de vueltas se observó también en las especies chilenas estudiadas de *Nucula* y *Ennucula,* aunque no existe ninguna relación con la profundidad; ha sido mencionado por Knudsen (1970) en numerosas especies abisales de los géneros *Nucula, Ennucula* y *Brevinucula.* Además, este autor describe especies de algunos géneros de la familia Nuculanidae que presentan, también, un número elevado de vueltas. Así, ocurre en especies de *Spinula* con 1, 6 y 7 vueltas, de *Ledella* con 1, 4 y 5 vueltas y de *Phaseolus* con dos vueltas.

En consecuencia, parecería que en Nuculanidae hay dos tendencias, una que corresponde a un enrollamiento acentuado en especies de los géneros ya mencionados (¿tendencia paralela a Nuculidae?); y la otra, representada especialmente por los géneros *Nuculana, Propeleda, Yoldia* y *Yoldiella,* con especies en la que existe una sola vuelta; ¿cual es especializada y cual primitiva?

Los géneros *Neilonella, Tindaria, Tindariopsis* y *Malletia* presentan siempre una sola vuelta. En estos grupos tampoco existe una relación de un mayor número de vueltas con la profundidad.

Schileyko (1989) después de revisar muchas especies de aguas someras y abisales llega a la conclusión que el alargamiento del intestino, que se da indistintamente en varias familias de protobranquios, se debe más bien a la calidad de las partículas útiles a la alimentación que a la profundidad. Encontró que las especies presentes en la fosa Kurilo-Kamchatka, donde existe abundancia de sustancias nutritivas, no presentan el intestino alargado. Esto explicaría el por qué *Nucula* (*Nucula*) *fernandensis,* que vive en fondos arenosos, con pocas sustancias nutritivas, tenga un intestino más largo que las otras *Nucula* estudiadas, cuyos hábitats son más nutritivos (limo-arcilla).

Schileyko (1989) agrupa a los protobranquios en seis grupos de variantes de la topografía del intestino:

(a) Se conserva una vuelta en el lado derecho del cuerpo (Schileyko, 1989: fig. 8, *Nucula tenuis*)

(b) Se conserva una vuelta en el lado derecho del cuerpo, pero la vuelta se alarga muchísimo. Algunas veces penetra en la hoja derecha del manto (algunos Tindariidae) (Schileyko, 1989: fig. 8, *Tindaria callistiformis*).

(c) Se conserva la disposición del intestino en el lado derecho, pero el número de vueltas aumenta hasta 5–11 (Ledellidae, en parte) (Schileyko, 1989: fig. 8, *Bathyspinula oceanica*). *Nucula proxima,* de 10 m de profundidad, tiene tres vueltas; la especie cercana *N. cancellata* de 3834 m de profundidad tiene ocho vueltas (Allen, 1978: fig. 10). En esta

misma publicación Allen menciona las mismas relaciones dentro del género *Yoldiella,* pero representa (Allen, 1978: fig. 11) diferentes géneros; el género *Yoldiella* pertenece, probablemente, al *Yoldiella* sp. L, pero *Y.* sp. K se debe trasladar a otro género (Observación hecha por Schileyko, 1986, en Schileyko, 1989).

(d) Las vueltas (una o unas) se encuentran tanto a la derecha como a la izquierda y se pasan de un lado a otro por detrás del estómago (*Pristigloma nitens, Pseudotindaria, Ledellina*) (Schileyko, 1989: fig. 8, *Ledellina olivacea*).

(e) Todas las vueltas se enrrollan casi horizontalmente encima del estómago (*Pristigloma alba, Microgloma*) o alrededor de él (*Setigloma*) (Schileyko, 1989: fig. 8, *Setigloma japonica*).

(f) Las vueltas se emplazan en diferentes superficies sin ninguna predominancia a la derecha o a la izquierda (Lametilidae) (Schileyko, 1989: fig. 8, *Lametila abyssorum* [como "*Lametyla*"], no la de Allen y Sanders, 1973: fig. 33).

De estas seis variaciones propuestas por Schileyko (1989) en las especies chilenas se presentaron solo las tres primeras: (1) Con una vuelta en el lado derecho en: *Silicula rouchi* (Fig. 14); *Nuculana* (*S.*) *cuneata* (Figs. 78, 79); *Tindariopsis sulculata* (Figs. 81, 82); *Yoldiella ecaudata* (Fig. 84); *Yoldiella chilenica* (Fig. 86); *Yoldia* (*Aequiyoldia*) *eightsi* (Fig. 89); *Tindaria virens* (Figs. 95, 96). (2) Se conserva una vuelta en el lado derecho del cuerpo, pero la vuelta se alarga muchísimo o forma dos vueltas en: *Nucula* (*N.*) *pisum* (Fig. 64); *Ennucula grayi* (Fig. 71); y *Propeleda longicaudata* (Fig. 76). (3) Se conserva la disposición del intestino en el lado derecho, pero el número de vueltas aumenta en: *Nucula* (*N.*) *fernandensis; Nucula* (*N.*) *pseudoexigua* (Fig. 66); y *Ennucula puelcha* (Fig. 73).

Parece existir una relación entre especies muy anchas, pero cortas de *Nucula* y *Ennucula, Spinula* y *Ledella* y un número superior a 3 ó 4 vueltas. Por el contrario, géneros caracterizados por especies aplastadas y largas presentan casi siempre una sola vuelta, aunque de longitud y forma variable (e.g., *Malletia*).

Sin embargo, las excepciones demostradas por el género *Nuculana* que contiene especies bastante anchas, pero con una sola vuelta, sugiere tendencias que aún en el caso de *Propeleda, Yoldia, Yoldiella, Malletiidae,* y otros géneros, podrían explicarse mejor por la posición adelantada del intestino, como lo propone Heath (1937). Warén (1978: figs. 1–7) muestra como la configuración de las vueltas del intestino pueden variar según el grado de compresión de la masa visceral.

(9) El valor filogenético de la posición del corazón en relación al recto, sugerido por Pelseneer (1888, 1911) para todos los bivalvos, parece poder aplicarse también a la evolución de este órgano dentro de los protobranquios. Familias reconocidas como más primitivas (Nuculidae), presentan un corazón dorsal al recto o envolviendo al recto (atravesado por él), mientras que en familias más especializadas (Nuculanidae, Malletiidae), el corazón puede estar envolviendo al recto (Nuculanidae) o bajo él (Malletiidae) (Figs. 58, 59).

Efectivamente, se observó que en las especies de *Nucula* y *Ennucula* aquí estudiadas (Nuculidae), el corazón es dorsal al recto, al igual que en la especie europea *Nucula nucleus* (Linné) (Figs. 63, 65, 67, 71, 73), pero diferente a *N. proxima,* en la que White (1942) describió al ventrículo atravesado por el recto. A este respecto, es igualmente importante mencionar que según Drew (1901), en *N. delphinodonta* el corazón rodea al recto durante su desarrollo y solamente llega a ser dorsal a él, cuando el animal alcanza su madurez sexual. En consecuencia, en Nuculidae se conocen dos tipos de posición del corazón en relación al recto: dorsal a él y envolviéndolo.

En las especies estudiadas de los géneros *Nuculana, Propeleda, Silicula, Yoldiella,* y *Yoldia,* el corazón se observó envolviendo al recto y no existen en la literatura citas de otras especies de estos géneros en que se presente en una posición distinta (Figs. 76, 78, 85, 89). En las de los géneros *Malletia, Tindaria,* y *Tindariopsis* el corazón puede ser, ventral al recto (*Malletia chilensis* y *Tindaria virens;* Figs. 92, 95) o estar envolviéndolo (*Malletia patagonica* y *Tindariopsis sulculata;* Figs. 81, 82). El corazón también parece estar envolviendo al recto en *M. gigantea* (Smith, 1875) (White, 1942).

Segun Owen (1959: fig. 7), en *Solemya* (Solemyidae) el corazón está envolviendo al recto. Desgraciadamente, no se ha descrito su posición en el género *Acharax* y, en la especie de este género estudiada por nosotros, no pudo establecerse debido al tamaño reducido del ejemplar estudiado.

(10) La plasticidad de la estructura sifonal

en el proceso adaptativo frente a condiciones ambientales diferentes, parece ser otra de las tendencias que esta marcando la diferenciación de especies entre los nuculanáceos, pero sin una secuencia filogenética clara. Estructuralmente, los sifones representan la hipertrófia de las regiones posteriores de los márgenes del manto que rodean las aberturas exhalante e inhalante y de los músculos paleales asociados.

Yonge (1939, 1957) basado en especies de Nuculanidae y Malletiidae señaló tres formas diferentes de fusión de las paredes de los tubos sifonales, que supuso correlacionadas con el largo de los sifones:

1, con ambos sifones fusionados por tejidos (tercera forma de Schileyko, 1983);

2, sifón exhalante cerrado, con unión ciliar completando sólo el sifón inhalante (segunda forma de Schileyko, 1983);

3, con unión ciliar completando ambos sifones (Fig. 57a–c) (primera forma de Schileyko, 1983).

El estudio de las especies chilenas aquí tratadas y el de las especies abisales y hadales de protobranquios realizado por Knudsen (1970), Schileyko (1983), y Allen (1985), permite ampliar las tres formas fundamentales de Yonge a ocho (Fig. 57a–h), agregando a las anteriores aquellas que presentan:

4, sifones unidos dorsal y ventralmente solo por uniones ciliares (Fig. 57d);

5, sifón exhalante abierto dorsal y ventralmente, ya sea con un número variable de tentáculos o papilas en el margen del manto (correspondiente al sifón inhalante), o sin ellos (margen liso, Fig. 57f);

6, sifón exhalante solamente, cerrado ventralmente (cuarta forma de Schileyko, 1983), con el margen del manto correspondiente al sifón inhalante aserrado (Fig. 57e);

7, sifón exhalante solo parcialmente separado del inhalante (Fig. 57g) y

8, sifones unidos sólo dorsalmente (Fig. 57h).

La proposición de Yonge (1957) de que la formación de los sifones comenzó con el ensamble de cilios de los bordes opuestos del manto, seguido por la fusión secuencial de los tejidos, es convincente en opinión de Schileyko (1983) y Allen (1985). Schileyko (1983) agrega que cuando existe la unión ciliar como una especie de cremallera, la capacidad de conducción es mayor que cuando existe un tubo que la limita.

La diferenciación entre unión ciliar y tisular es difícil, al extremo de que, en las especies aquí estudiadas en las que se examinaron detalladamente los sifones, solo se pudo concluir si existía o no unión completa, sin precisar su origen ciliar o histológico. Se arriesga así una posible confusión de ambas, puesto que según Drew (1899) la fusión mediante tejido, por su origen ontogénico, conserva una línea de unión indicada por un surco en la línea media ventral (Pelseneer, 1911; Heath, 1937), que se rompe con cierta facilidad al ser presionada con un instrumento de disección. Precisar la unión, requirió casi siempre el examen de muchos ejemplares. La constatación definitiva debería hacerse mediante cortes histológicos e idealmente con microscopía de barrido.

En suma, se encontró que el sifón exhalante es un tubo completo, y el inhalante está formado aparentemente por unión ciliar en los Nuculanidae-*Nuculana* (*Saccella*) *cuneata* (Fig. 77); *Nuculana* (*Borissia*) *inaequisculpta* (Fig. 90); *Propeleda longicaudata* (Figs. 75, 76); *Tindariopsis sulculata* (Fig. 80); y el Tindariidae-*Tindaria virens* (Figs. 94–96). En cambio, ambos sifones forman un tubo verdadero en: *Yoldia* (*Aequiyoldia*) *eightsi* (Sareptidae, Figs. 87-89); *Silicula rouchi* (Siliculidae, Fig. 5); *Yoldiella ecaudata* (Nuculanidae); y *Malletia chilensis* (Malletiidae, Fig. 12).

Estas observaciones, sumadas a las descripciones de Knudsen (1970), Allen (1963), Allen y Sanders (1973, 1982), y Sanders y Allen (1977), permiten establecer las siguientes relaciones entre géneros de Nuculanacea y estado de fusión de los sifones:

Fusión de tipo a. Observada en especies de los géneros *Malletia, Yoldia, Yoldiella,* (*¿Spinula?*), (*Ledella*), y *Nuculana.*

Fusión de tipo b. Observada en especies de los géneros *Yoldia, Yoldiella,* (*¿Spinula?*), (*Ledella*), y *Nuculana.*

Fusión de tipo c. Observada en especies de los géneros *Neilonella, Malletia, Nuculana,* (*Phaseolus*), *Tindariopsis,* y *Propeleda.* En este último género, sin embargo, los bordes ventrales son divergentes.

Fusión de tipo d. Observada en especies de los géneros *Neilonella* y *Tindaria.*

Fusión de tipo e. Observada en especies del género *Sarepta* (Knudsen, 1970).

Fusión de tipo f. Observada en especies del género *Tindaria.*

La descripción de los sifones en los

géneros incluidas en paréntesis, no es lo suficientemente detallada como para precisar el tipo de unión.

En *Ledella kermadecensis,* Knudsen (1970), describió un solo sifón con dos aberturas, mientras que en las especies *Yoldiella ecaudata* y *Silicula rouchi* aquí estudiadas y en *Spinula oceanica* Filatova, *S. tasmanica* Knudsen, *S. vityasi* Filatova, estudiadas por este mismo autor, existe un solo tubo sifonal, no pudiendo establecerse si corresponde solamente a un sifón exhalante o a una fusión de los dos sifones.

Filatova y Schileyko (1984) agregan una importante observación en cuanto a la estructura del sifón. Ellos encontraron que las paredes del único sifón de los Nuculanidae (Ledellinae y Spinulinae) pueden contener parénquima o hemolinfa. Con el primer caracter ellos separan la subfamilia Ledellinae con los géneros *Bathyspinula* Filatova, 1958; *Ledellina* Filatova y Schileyko (1984); y *Ledella* Verrill y Bush, 1897. Con un sifón de paredes huecas con hemolinfa caracterizan a Parayoldiellinae Filatova, 1971, con los géneros *Parayoldiella* Filatova, 1971, e *Intercalaria* Filatova y Schileyko, 1984.

Además estos autores concluyen que la diferencia en la estructura del sifón hace que su alargamiento y movimiento sea también diferente. El sifón provisto de parénquima se puede alargar poco, pero se puede encorvar, en cambio el otro tipo es hidraúlico y si bien se puede alargar mucho y funcionar como una válvula peristáltica, no se puede doblar o encorvar tan facilmente. Desgraciadamente no hicimos cortes de los sifones que observamos, pero sería interesante hacerlo para todas las especies que aquí se presentan.

Filatova y Schileyko (1984) encuentran una correlación entre la longitud de los sifones y la presencia de un rostro en la concha que les proporciona protección, pero que limita la movilidad del sifón.

La fusión de los sifones dentro de los Nuculanacea no parece seguir líneas evolutivas definidas. Efectivamente, aún cuando la presencia de sifones ha sido acompañada de una reducción del tamaño de las branquias y que, como lo sugiriera Yonge (1939), el grado de unión de los sifones podría estar correlacionado con su largo, no parecen haber otras relaciones funcionales claras. Será difícil precisarlas, mientras no se conozcan en detalle los hábitos de las distintas especies.

Pelseneer (1911) observó la presencia de un tentáculo sifonal generalmente a la izquierda en especies de *Yoldia* y *Nuculana,* mientras que fue encontrado indistintamente a un lado u otro por Stempell (1899) en *Yoldiella ecaudata* y por Filatova y Schileyko (1984) en *Ledellina* y *Bathyspinula.* Stempell (1899) lo encontró de preferencia a la derecha en *Malletia chilensis.* Yonge (1939) lo ubica de preferencia a la derecha, pero en las especies aqui estudiadas — *Nuculana* (*S.*) *cuneata, Yoldia* (*Aequiyoldia*) *eightsi, Tindaria virens, Yoldiella ecaudata,* y *Malletia chilensis* se encontró indistintamente a un lado u otro (Figs. 77, 85, 89, 96, ts).

En las especies abisales y hadales descritas por Knudsen (1970), el tentáculo sifonal se encontró en un número igual de especies, tanto a la derecha como a la izquierda.

No todas las especies de *Nuculana* presentan tentáculo sifonal y a este respecto nos parece interesante la ausencia de tentáculo en la única especie descrita hasta ahora para las ventilas hidrotermales, *Nuculana grasslei* Allen, 1993. El autor de la especie lo relaciona a un desarrollo pobre del sistema nervioso y quizás a una preadaptación para vivir en sedimento con bastante material bacteriano en la superficie.

(11) Respecto de la distribución geográfica, el estudio de los protobranquios chilenos, ha demonstrado, que la distribución extraordinariamente amplia de algunas especies de protobranquios es dudosa y éste, probablemente, es el caso de muchas otras en otras regiones biogeográficas. Así ocurre con especies de *Nucula* de supuesta amplia distribución geográfica en Chile, pero erróneamente identificadas, como ya se estableció para *Nucula exigua* Sowerby I, 1833; *Nucula carlottensis* Dall, 1897; *Nucula declivis* Hinds, 1843; *Ennucula colombiana* (Dall, 1908a); y *Nuculana callimene* (Dall, 1908a).

En otros casos, la distribución geográfica aparece amplia, por la sinonimización equívoca de especies distintas, como ocurrió con *Malletia chilensis,* cuya distribución se había establecido erróneamente hasta Magallanes.

En la Tabla 2 se ha representado el rango de la distribución de las especies estudiadas, en 10 columnas, que incluyen a las siguientes áreas geográficas:

1. Islas Juan Fernández — Islas Salas y Gómez
2. Perú
3. Arica — Mejillones
4. Coquimbo — Valparaíso — Constitución

5. Talcahuano — Canal de Chacao
6. Isla de Chiloé — Península de Taitao
7. Golfo de Penas — Estrecho de Magallanes
8. Tierra del Fuego — Islas Falkland
9. Argentina
10. Antártica

La Tabla 2 demuestra la existencia de los dos grupos faunísticos reconocidos para los bivalvos (Woodward 1851–1856; Soot-Ryen, 1959; Stuardo, 1964, 1988), con una limitada sobreposición de especies. En el hecho, solo las especies *Nucula* (*N.*) *pisum, Ennucula grayi,* y *E. puelcha* presentan una distribución amplia dentro de las dos provincias, mientras que *Malletia chilensis* y *Tindariopsis sulculata* se extienden dentro de límites que podrían considerarse zonas de transición. Todas las especies restantes están circunscritas a los límites conocidos tradicionalmente para las dos unidades faunísticas, de origen subtropical y subantártico, respectivamente.

Las especies antárticas, salvo *Propeleda longicaudata,* no llegan al extremo sur de Sudamérica (Tabla 2). Por otra parte, son pocas las especies de protobranquios que se extienden al Atlántico, reforzando la impresión de Stuardo (1964, 1988) de que debe tratarse de precisar la diferencia ambiental entre la fauna de elementos magallánicos del Atlántico y del Pacífico.

La Tabla 2 muestra también posibles relaciones interespecíficas. Por ejemplo, las relaciones morfológicas entre *Nucula* (*Nucula*) *pisum, N.* (*N.*) *fernandensis,* y *N.* (*N.*) *falklandica* parecen ser el resultado de una radiación alopátrica de especies en las que *N.* (*N.*) *pisum* correspondería a la especie ancestral de la cual las otras dos se derivaron, separándose hacia los extremos de dispersión de la primera. El registro fósil de esta especie (Philippi, 1887) parece corroborar lo anterior.

Ennucula grayi y *E. puelcha* son dos especies simpátricas muy parecidas, pero cuyas relaciones entre sí y con respecto a las especies de *Ennucula* de áreas vecinas del Pacífico o del Atlántico son todavía oscuras. Podrían corresponder a una sola especie.

(12) De la ecología de estas especies, se sabe poco excepto por las indicaciones de sustrato que se dan en las descripciones.

Solo en dos lugares de la costa de Chile se han estudiado en detalle: Bahía de Concepción (este estudio) y Bahía de Valparaíso (Ramorino, 1968). Los datos son resumidos aquí brevemente.

Se han encontrado sólo tres especies en la Bahía de Concepción: *Nucula* (*Nucula*) *pisum, Nuculana* (*Saccella*) *cuneata,* y *Malletia chilensis,* de las cuales *Nucula* y *Nuculana* se encontraron viviendo preferentemente en fango arenoso, mientras que *Malletia* fue encontrada preferentemente en fango, diferencias que coincíden con las observaciones de Ramorino (1968) en la Bahía de Valparaíso. La especie *Ennucula grayi* que vive también en los fondos de la Bahía de Valparaíso no se encuentra en la Bahía de Concepción, probablemente debido a las variaciones ambientales estacionales tan extremas conocidas en esta última (Ahumada y Chuecas, 1979). La abundancia de las otras tres especies tampoco es comparable a la que Ramorino (1968) encontró en Valparaíso como se ha discutido bajo cada una de estas especies.

Las relaciones de las distintas especies a distintos tipos de fondos se ha resumido en la distribución de cada especie. En general, son pocas las que se encuentran vivas en fondos con sedimentos gruesos; la mayoría habita siempre en fondos de arena y fango, o en mezclas de ambos. Esto no difiere de lo descrito para otros protobranquios, pareciendo haber una relación estrecha entre las características del sedimento y la forma y actividad del animal. Como lo ha demostrado Allen (1954) para las especies británicas de *Nucula* y *Nuculana,* variaciones de forma dentro de la misma especie pueden también ser consecuencia de la variación del sustrato. (Ver discusión sobre longitud del intestino.)

(13) El número de especies de protobranquios que habitan grandes profundidades (2358–7000 m) es considerable, a juzgar por la lista dada por Knudsen (1970: tabla 1), Schileyko (1989). Sin embargo, siguiendo la división batimétrica de los océanos, entre los protobranquios chilenos, habría una sola especie intermareal (i): *Nucula* (*N.*) *interflucta,* descrita para Punta Morro, Iquique, encontrada en limo arenoso negro entre guijarros y cantos rodados de una playa protegida y una sola especie abisal (a, Tabla 2); *Tindaria salaria,* colectada frente a las Islas Salas y Gómez. Todas las demás son sublitorales (s, Tabla 2) o sublitorales y batiales al mismo tiempo (s-b, Tabla 2).

La distribución gradual batimétrica de las especies chilenas representa en parte (litoral-abisal) a las observaciones de Schileyko

TABLA 2. Distribución geográfica y batimétrica de los protobranquios chilenos y de algunos antárticos; a = abisal; b = batial; i = intermareal; s = sublitoral.
Geographic and batimetric distribution of Chilean and some Antarctic protobranchs; a = abyssal; b = bathyal; i = intertidal; s = sublitoral.

Especies	Áreas geográficas										Prof (m)	Distr. vert.
	1	2	3	4	5	6	7	8	9	10		
Nucula pisum			X	X	X	X	X				8–200	s
N. fernandensis	X										120–280	s
N. falklandica							X	X			46–500	s-b
N. interflucta			X									i
N. pseudoexigua							X				223–500	s-b
Ennucula grayi				X	X	X	X	X	X		92–744	s-b
E. puelcha		X	X	X	X	X	X	X	X		139–210	s
Nuculana cuneata	X		X	X	X						28–280	s
N. inaequisculpta										X	48–304	s
Propeleda longicaudata							X			X	93–1080	s-b
Sllicula patagonica							X				219–460	s-b
S. rouchi										X	135–720	s-b
Yoldia eightsi										X	25–728	s-b
Yoldiella ecaudata										X	33–891	s-b
Y. granula							X				110	s
Y. chilenica						X	X				70–722	s-b
Y. indolens							X				70–349	s
Malletia chilensis				X	X	X					1–240	s
M. magellanica							X				36–58	s
M. patagonica							X				57–664	s-b
M. inaequalis							X				56–110	s
Malletiella sorror					X						1219	s-b
Tindaria virens						X	X				70–808	s-b
T. salaria	X										2055	a
Tindariopsis sulculata				X	X	X	X	X	X		13–300	s
Acharax patagonica							X				441	s-b
A. macrodactyla						X		X			36–664	s-b

(1989) (litoral hasta ultraabisal) y que la mayor parte de los taxa de profundidad tienen representantes de poca profundidad.

Respecto a la distribución en profundidad de *Malletia chilensis,* parece extraño que Ramorino (1968) la encontrara como máximo hasta solo 102 m, probablemente por limitaciones de muestreo. Como se desprende de los datos resumidos en la Tabla 2, esta especie y todas las otras tienen un rango de distribución batimétrica mucho mayor.

De esta síntesis también se desprende que tanto el conocimiento de las especies sublitorales de protobranquios chilenos como el de las especies batiales parece adecuado, pero el de las especies abisales que viven frente a estas costas es prácticamente nulo. Se deben hacer esfuerzos para conocer mejor tanto la fauna de moluscos abisales como la de invertebrados en general. Parece igualmente pobre el conocimiento de la fauna de protobranquios en las islas oceánicas chilenas, sobre todo de las islas Juan Fernández y Pascua (Rapa Nui).

(14) Como se demuestra en este trabajo, las especies de protobranquios fósiles no han sido estudiadas recientemente, y su conocimiento taxonómico deja mucho que desear. Sin embargo, la revisión de la literatura ha permitido compilar y reubicar taxonomicamente un total de alrededor de 50 especies del Paleozoico, Mesozoico y Cenozoico. Del mismo modo, la obtención de muestras permitió redescribir en detalle cinco especies de los géneros *Ennucula, Propeleda, Tindariopsis* y *Malletia.*

SINOPSIS DE LOS PROTOBRANQUIOS RECIENTES DESCRITOS O CITADOS PARA CHILE CON INCLUSIÓN DE LAS ESPECIES ANTÁRTICAS ESTUDIADAS

(A = especies antárticas; * = especies no vistas;
? = especies cuya presencia es improbable)

FAMILIA NUCULIDAE
A **Nucula austrobenthalis* Dell, 1990
? *Nucula declivis* Hinds, 1843
? *Nucula exigua* (forma de *carlottensis?, fide* Soot-Ryen, 1958)
? *Nucula carlottensis* Dall, 1897
Nucula (*N.*) *falklandica* Preston, 1912
Nucula (*N.*) *fernandensis* Villarroel, 1971
Nucula (*N.*) *interflucta* Marincovich, 1973
Nucula (*N.*) *pisum* G.B. Sowerby I, 1833
Nucula (*N.*) *pseudoexigua,* sp. nov.
? *Ennucula colombiana* (Dall, 1908)
**Ennucula eltanini* Dell, 1990
Ennucula grayi (d'Orbigny, 1846)
Ennucula puelcha (d'Orbigny, 1842)

FAMILIA NUCULANIDAE
Nuculana (*Saccella*) *cuneata* (G. B. Sowerby I, 1833)
? *Nuculana* (*S.*) *callimene* (Dall, 1908)
A *Nuculana* (*Borissia*) *inaequisculpta* (Lamy, 1906)
A *Propeleda longicaudata* Thiele, 1912
Tindariopsis sulculata (Gould, 1852, *ex* Couthouy ms)

FAMILIA SILICULIDAE
Silicula patagonica Dall, 1908
? *Silicula fragilis* Jeffreys, 1879
A *Silicula rouchi* Lamy, 1911

FAMILIA SAREPTIDAE
A *Yoldia (Aequiyoldia) eightsi* (Jay, 1839, *ex* Couthouyms)
Yoldiella chilenica (Dall, 1908)
A *Yoldiella ecaudata* (Pelseneer, 1903)
**Yoldiella granula* (Dall, 1908)
Yoldiella indolens (Dall, 1908)

FAMILIA MALLETIIDAE
Malletia chilensis des Moulins, 1832
**Malletia magellanica* Smith, 1875
Malletia patagonica Mabille y Rochebrune, 1889
**Malletia inaequalis* Dall, 1908
**Malletiella sorror* Soot-Ryen, 1959

FAMILIA TINDARIIDAE
Tindaria virens Dall, 1890
**Tindaria salaria* Dall, 1908

FAMILIA ACHARACIDAE
?*Acharax patagonica* (Smith, 1885)
**Acharax macrodactyla* (Mabille y Rochebrune, 1889)

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Agradecemos al Dr. George M. Davis por haber revisado el manuscrito original y animarnos a actualizarlo. Al Dr. Eugene V. Coan por su crítica y cuidadosa revisión, comentarios, sugerencias y por la literatura enviada. A la Biól. Sandra Rubio por la captura del MS. A la dibujante Lourdes Espinoza por el entintado de algunas figuras. Al Laboratorio de Microscopía Electrónica de la Dirección de Investigación de la Universidad de Concepción. Al Dr. E. López por la revisión de estilo. Al Dr. Alan R. Kabat y Raye Germon por permitirnos revisar los tipos de Dall en el Museo Smithsoniano. A la Geól. Irina Musina por las traducciones del ruso al español. A la Coordinación Científica de la Universidad Michoacana cuyos proyectos CICH 5.5 y 7.11 hicieron posible terminar la revisión bibliográfica. A todos aquellos que nos tuvieron la paciencia de soportar muchas revisiones al MS, nuestros más sinceros agradecimientos

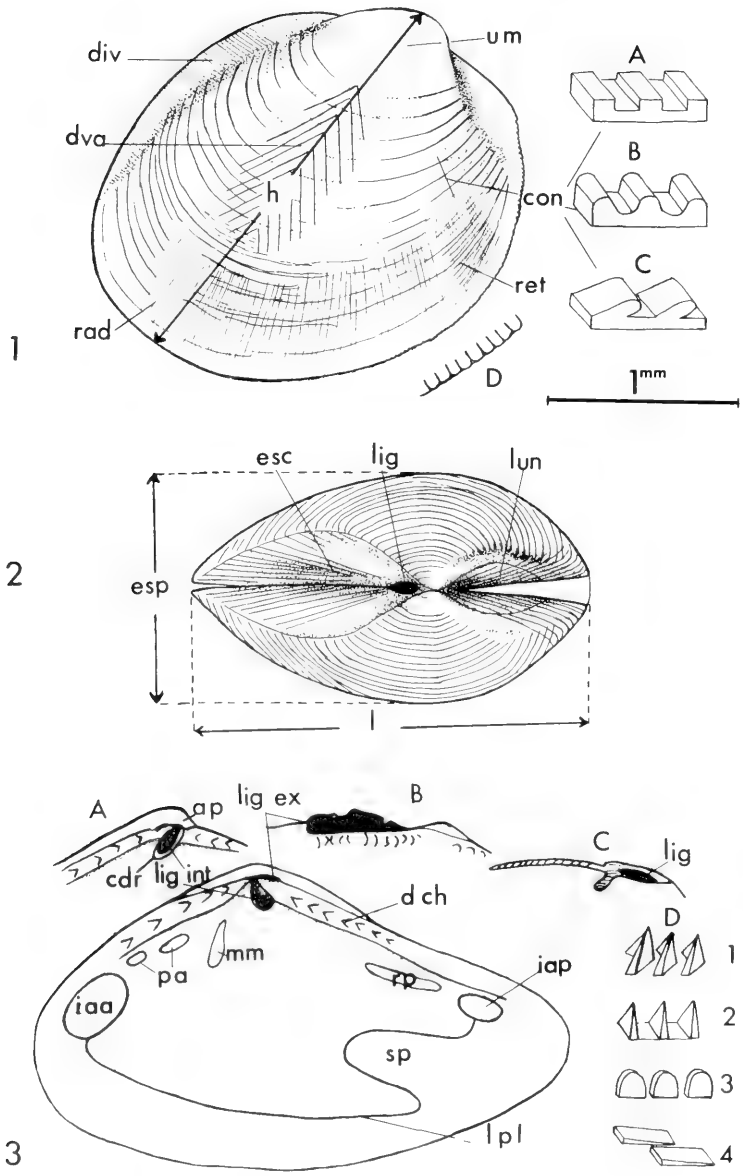


FIG. 1. *Nucula* (*N.*) *falklandica.* Valva izquierda esquematizando los tipos de ornamentación de la concha. Left valve showing the types of shell ornamentation.
A, B, C, tipos de costillas concéntricas que fueron observadas en *Tindaria virens, Nuculana* (*S.*) *cuneata* y *Tindariopsis sulculata,* respectivamente. A, B, C, types of concentric ribs observed on *T. virens, N.* (*S.*) *cuneata,* and *T. sulculata,* respectively.
D, crenulación del borde interno (género: *Nucula*). D, crenulation of the inner margin (genus: *Nucula*).

FIG. 2. *Tindariopsis elegans.* Vista dorsal mostrando escutelo, ligamento, lúnula y medidas de espesor y longitud. Dorsal view showing escutcheon, ligament, lunule and measurements for width and length.

FIG. 3. Esquema de la valva derecha de un nuculanáceo, destacando las impresiones musculares, dientes de la charnela y ligamento. Right valve outline in nuculanaceans, showing muscle scars, hinge teeth and ligament. (A) Charnela de un Nuculidae. Nuculid hinge. (B) Charnela de *Malletia* y *Tindaria.* Hinge in *Malletia* y *Tindaria.* (C) Charnela de un Solemyidae. Hinge in solemyids. (D) Tipos de dientes más característicos en las especies estudiadas. Characteristic hinge teeth in the studied species.

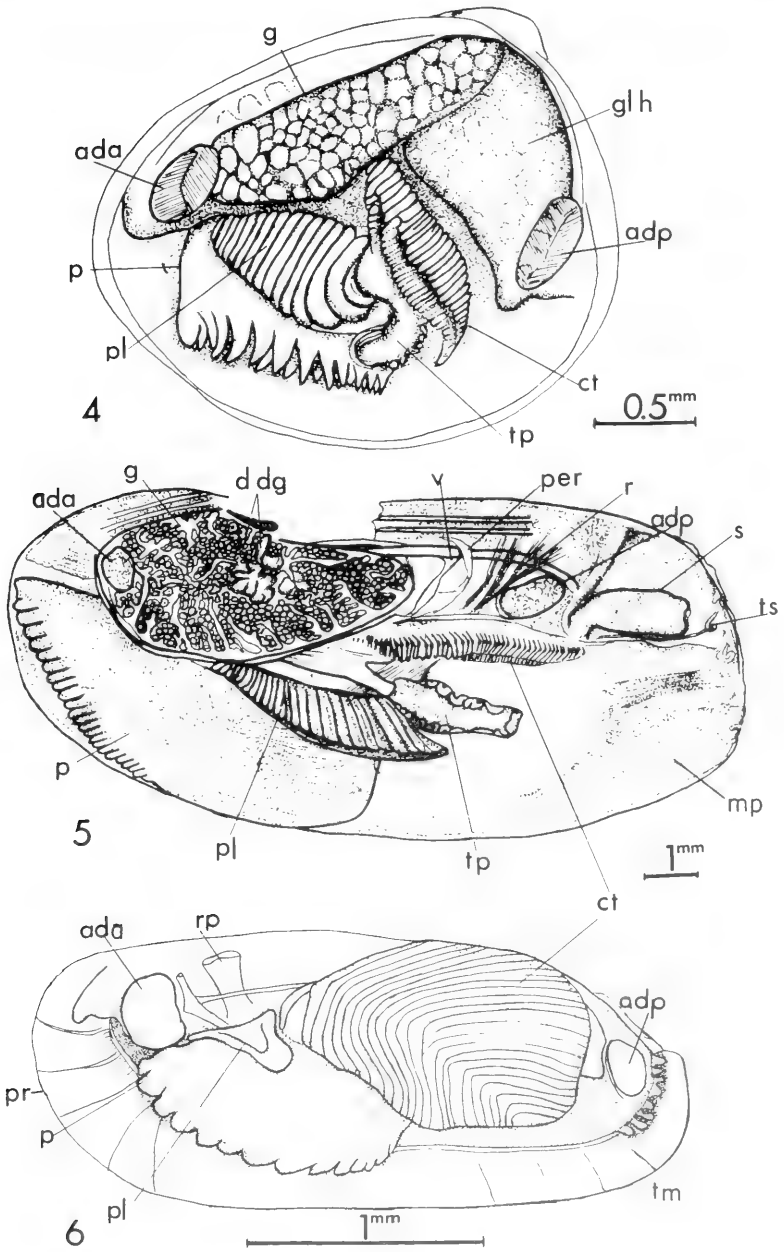


FIG. 4. *Nucula* (*N.*) *pisum.* Vista lateral izquierda de la cavidad del manto mostrando la disposición de los órganos en un Nuculidae. Parte de la glándula hipobranquial se ha omitido para señalar el ctenidio. Left lateral view of mantle cavity showing internal organs in Nuculidae. Part of hypobranchial gland omitted to show ctenidia.

FIG. 5. *Silicula rouchi.* Vista lateral izquierda mostrando la disposición de los órganos en la cavidad del manto y cavidad pericárdica de un nuculanáceo. Left lateral view showing internal organs of mantle cavity and pericardial cavity in Nuculanacea.

FIG. 6. *Acharax* sp. Vista izquierda de la cavidad del manto, indicando la disposición de los órganos de un Solemyidae. Left view of mantle cavity showing internal organs in Solemyidae.

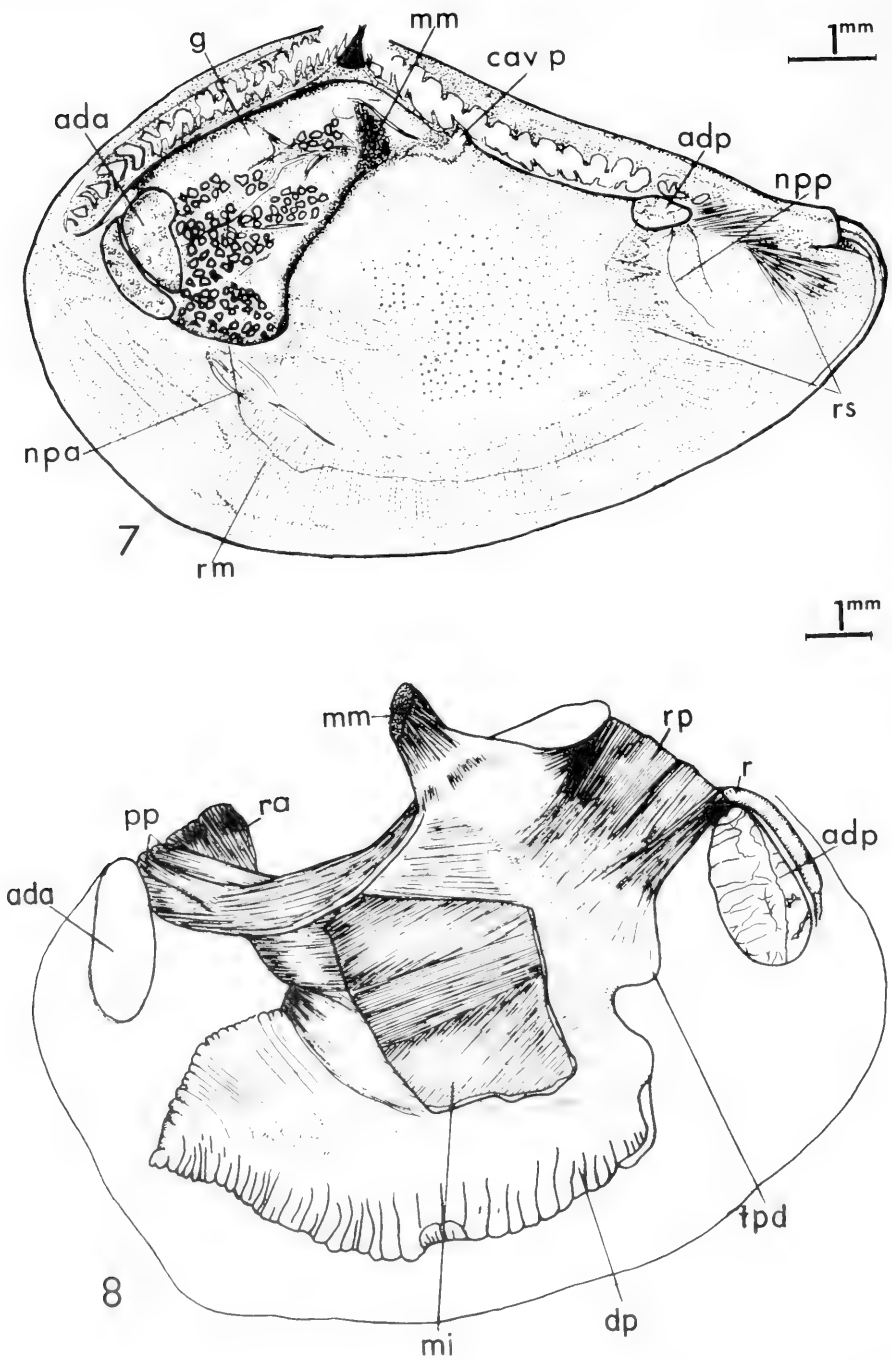


FIG. 7. *Nuculana* (*S.*) *cuneata*. Vista izquierda del manto, mostrando la disposición de los músculos del manto y de los sifones. Left view of mantle showing arrangement of mantle muscles and siphons.

FIG. 8. *Ennucula grayi*. Musculatura del pie y músculos aductores. Foot musculature and adductors.

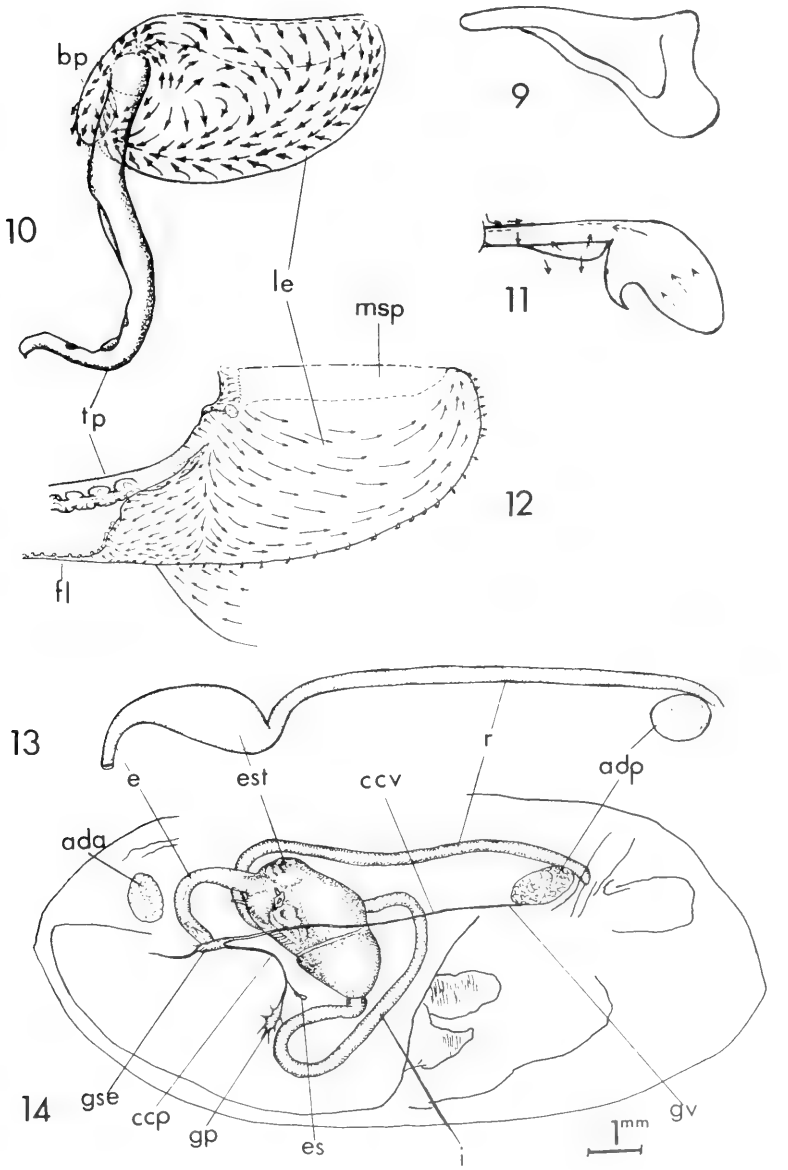


FIG. 9. *Acharax* sp. Vista externa del palpo labial izquierdo. External view of left labial palp.

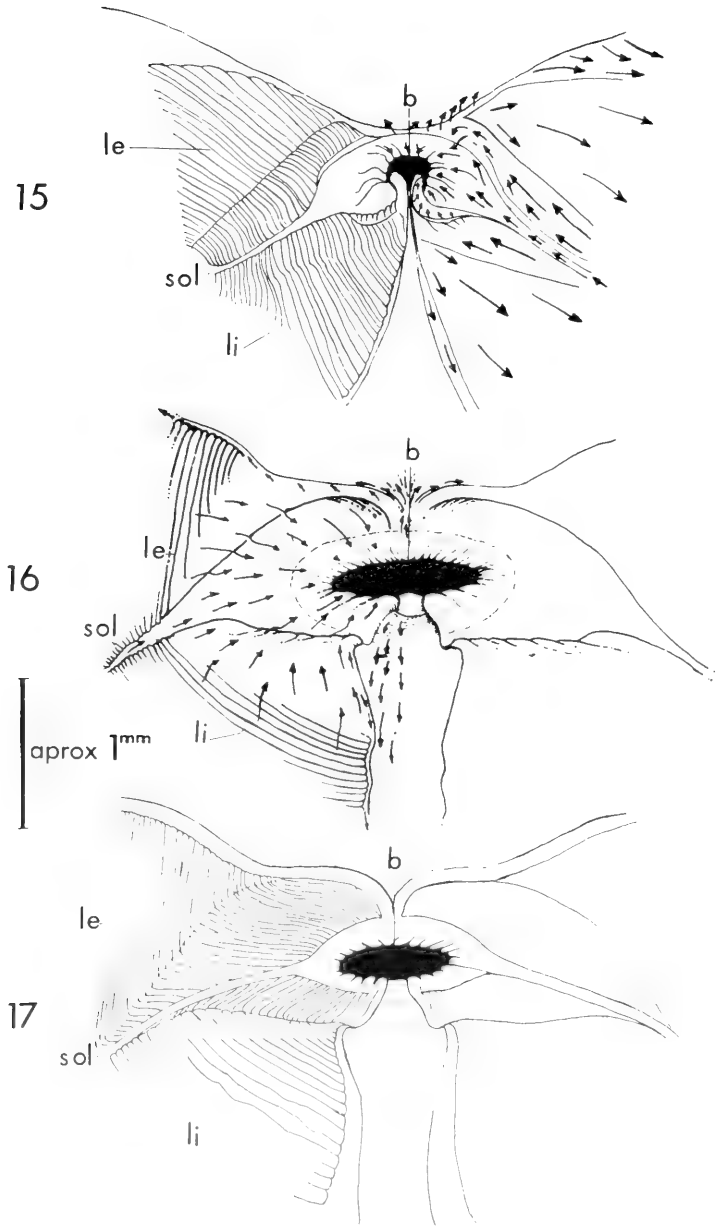
FIG. 10. *Acila castrensis*. Superficie lisa del palpo en la que se indican las corrientes ciliares (modificada de Stasek, 1961; fig. 5). Palp surface showing ciliary currents (modified from Stasek, 1961; fig. 5).

FIG. 11. *Solemya togata*. Vista externa del palpo labial izquierdo (según Yonge, 1939; fig. 34; modificada). External view of left labial palp (modified from Yonge, 1939: fig. 34).

FIG. 12. *Yoldia ensifera*. Superficie lisa del palpo en la que se indican las corrientes ciliares (según Stasek, 1965: fig. 3). Palp surface showing ciliary currents (after Stasek, 1965: fig. 3).

FIG. 13. *Acharax* sp. Aparato digestivo. Digestive system.

FIG. 14. *Silicula rouchi*. Aparato digestivo y su relación con el sistema nervioso. Digestive system in relation to nervous system.

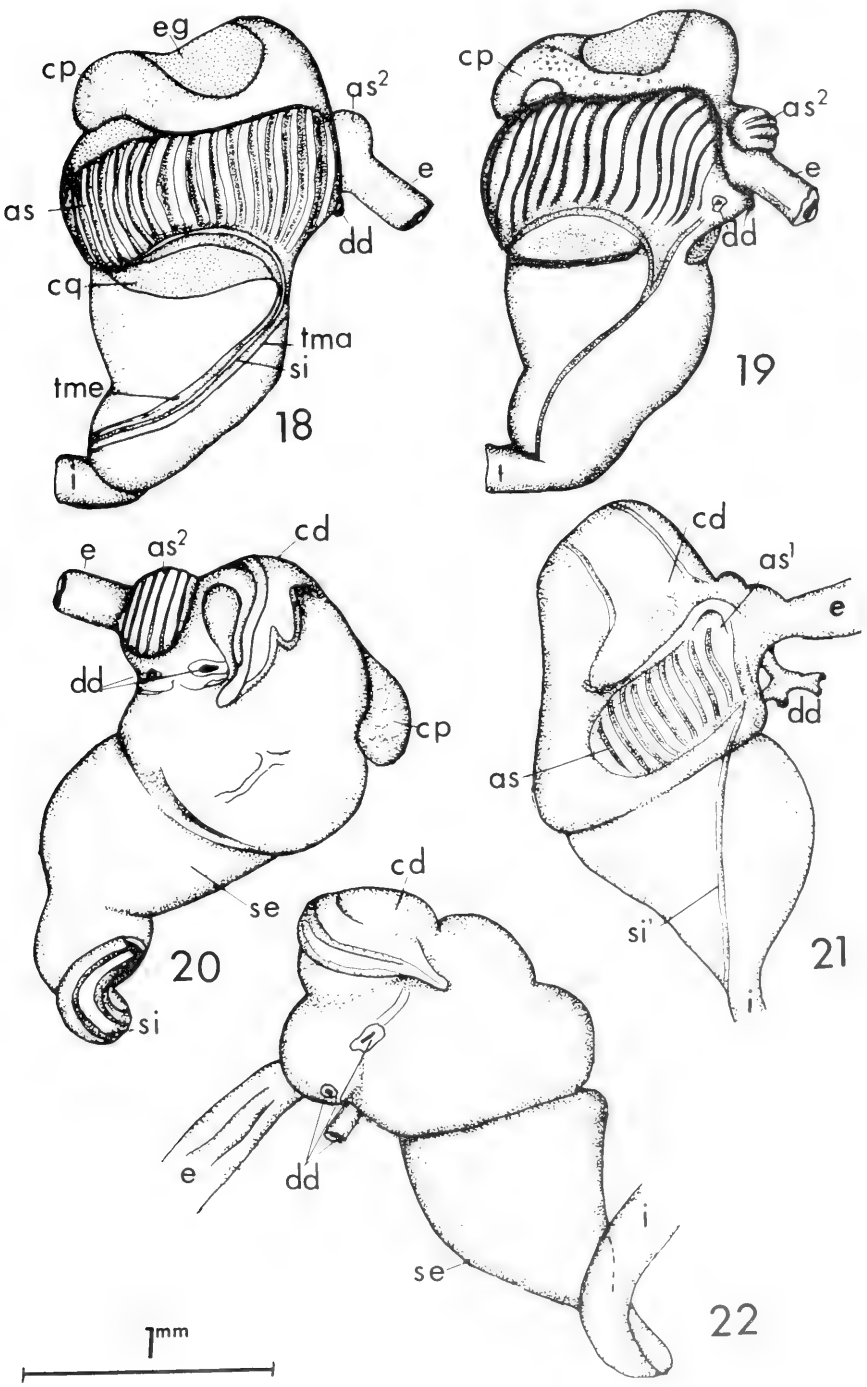


FIGS. 15–17. Relación de la lamela del palpo derecho con la boca, en Acila, Yoldia y Malletia. Right palp lamela showing relationship to mouth in Acila, Yoldia y Malletia.

FIG. 15. Acila castrensis. Las caras yuxtapuestas de las lamelas han sido separadas. La dirección del movimiento ciliar se indica sobre las lamelas izquierdas: los pliegues se han indicado en las derechas (según Stasek, 1961: fig. 4). Separated juxtaposed parts of palp lamellae. Ciliary movement shown in right lamella (after Stasek, 1961: fig. 4).

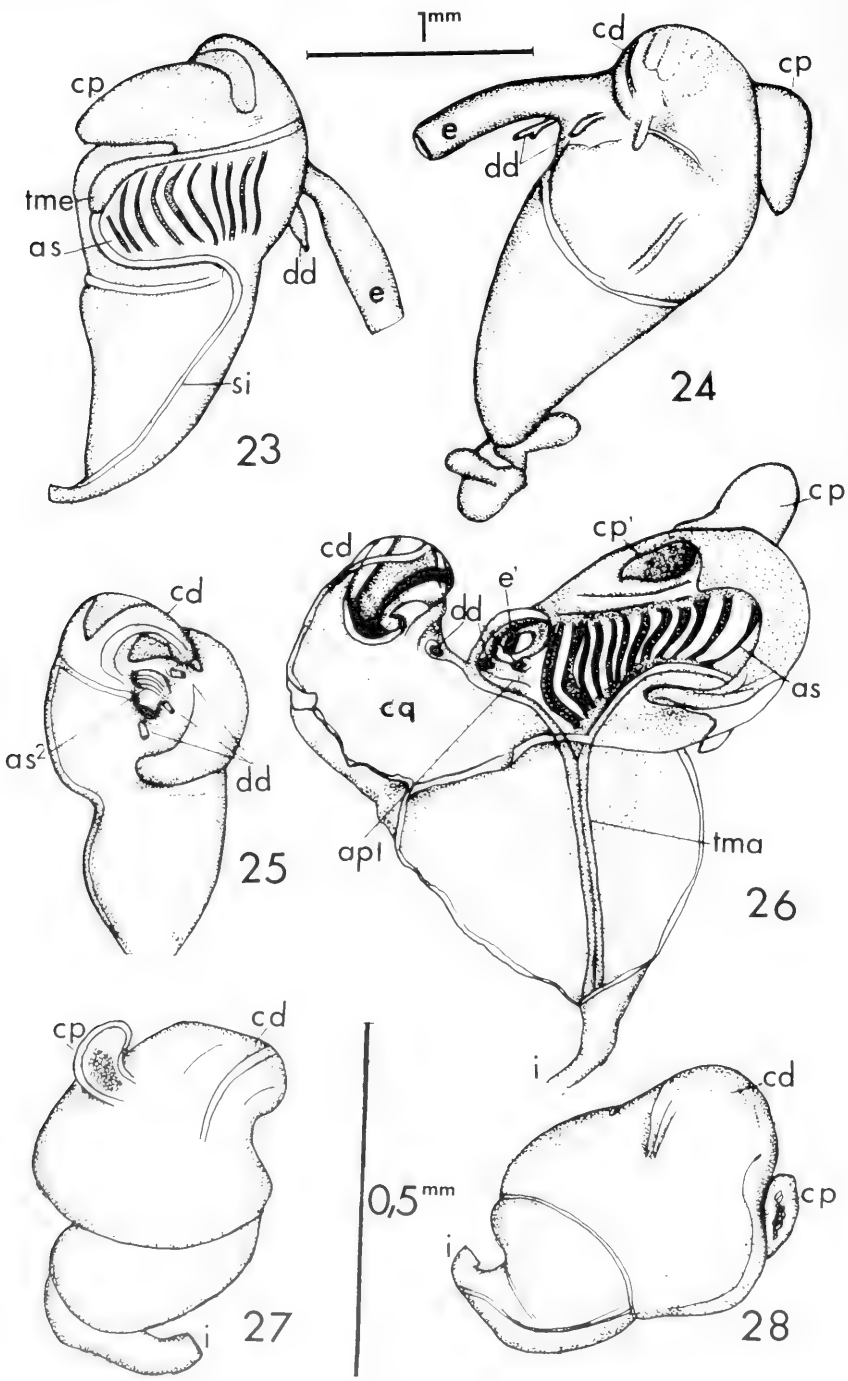
FIG. 16. Yoldia ensifera. Las corrientes ciliares se indican al lado derecho (según Stasek, 1965: fig. 2). Ciliary currents shown on right side (after Stasek, 1965: fig. 2).

FIG. 17. Malletia chilensis. Nótese la presencia de surcos ciliados en el ensanchamiento del canal oral lateral. View of ciliated grooves on embayment of lateral oral canal.



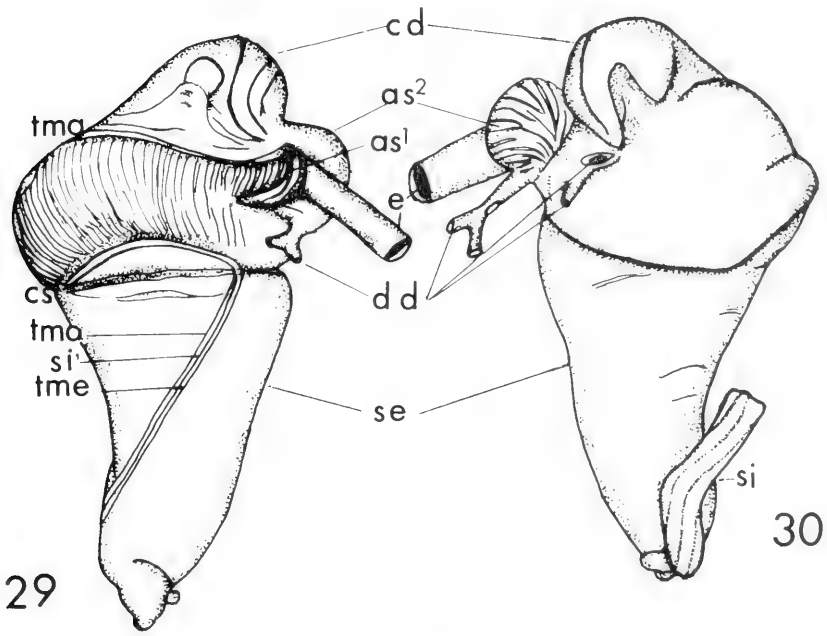
FIGS. 18–20. *Nucula* (*N.*) *pseudoexigua*. Estómago. Vistas derecha, anterior e izquierda. Stomach in right, anterior and left views.

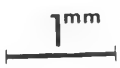
FIGS. 21–22. *Nucula* (*N.*) *pisum*. Estómago. Vistas derecha e izquierda. Stomach. Right and left views.

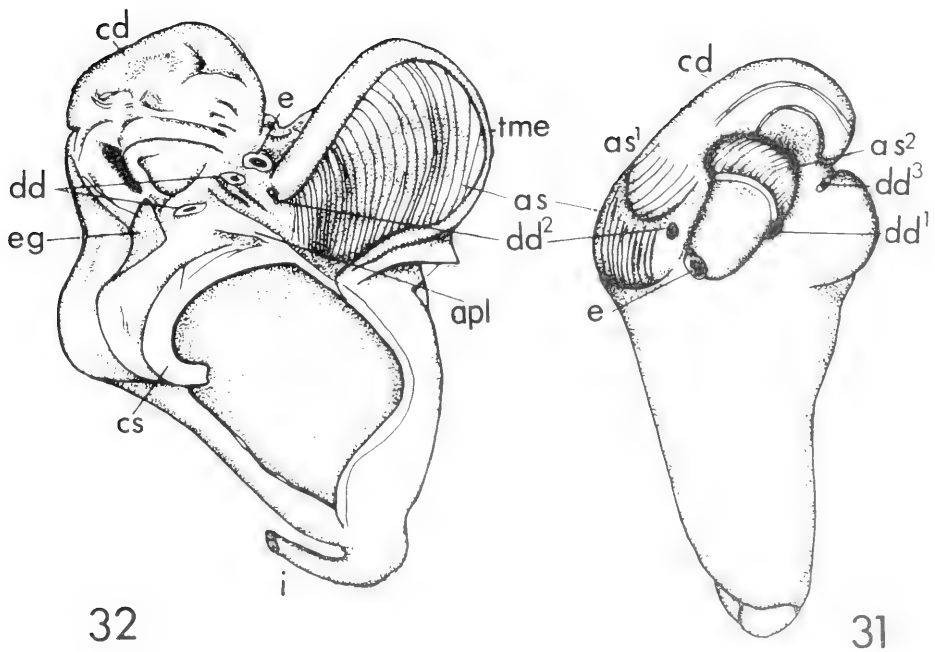


FIGS. 23–26. *Nucula* (*N.*) *fernandensis*. Estómago. Vistas derecha, izquierda, anterior e interior. Stomach. Right, left, anterior and internal views.

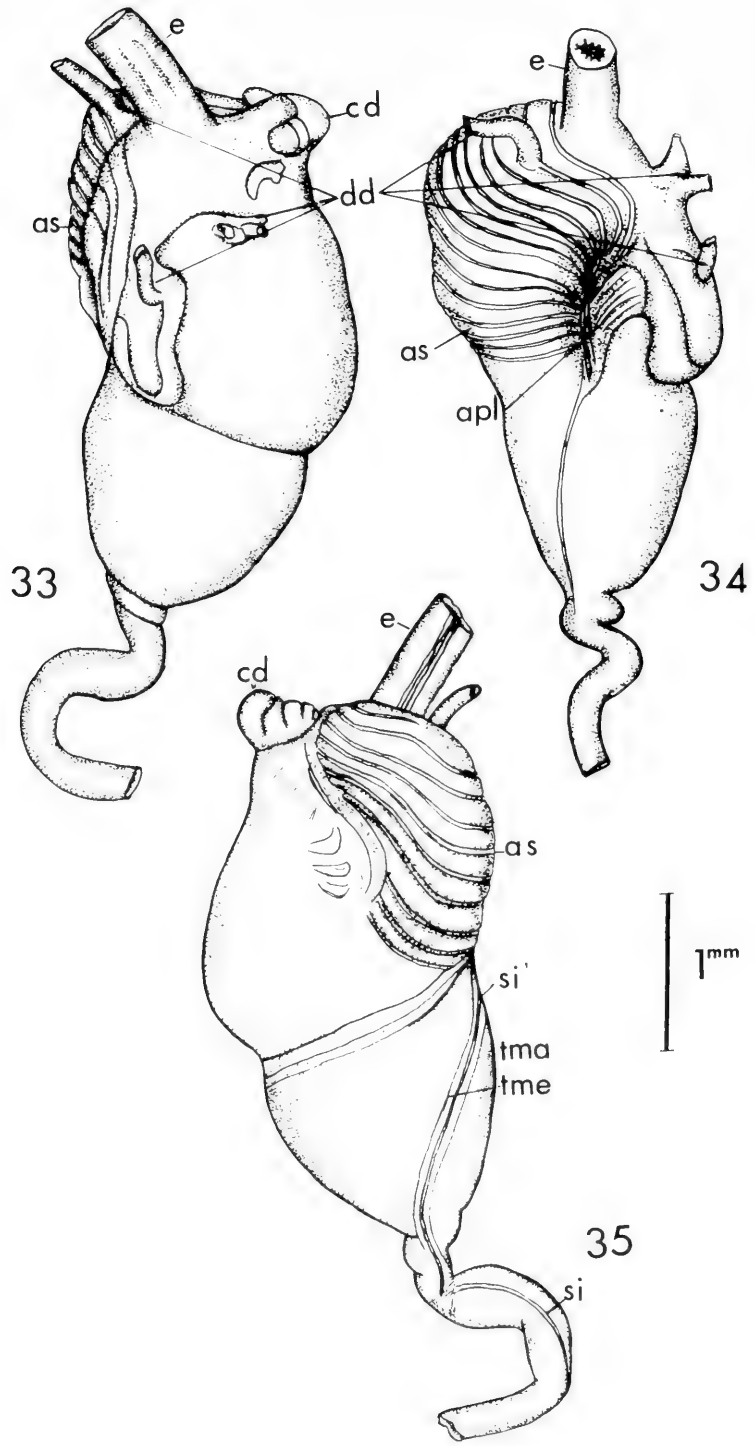
FIGS. 27–28. *Nucula* (*N.*) *falklandica*. Estómago. Vistas derecha y posterior. Stomach. Right and posterior views



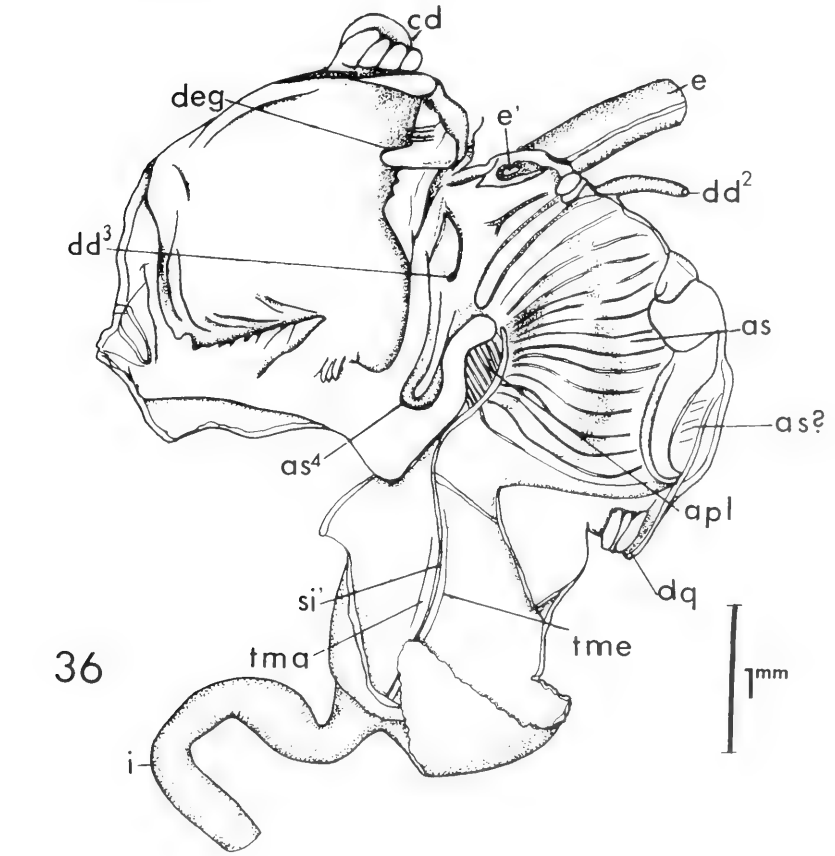




FIGS. 29–32. Ennucula puelcha. Estómago. Vistas derecha, izquierda, interior y anterior. Stomach. Right, left, interior and anterior views.



FIGS. 33–35. *Propeleda longicaudata.* Estómago. Vistas izquierda, anterior y derecha. Stomach. Left, anterior and right views.



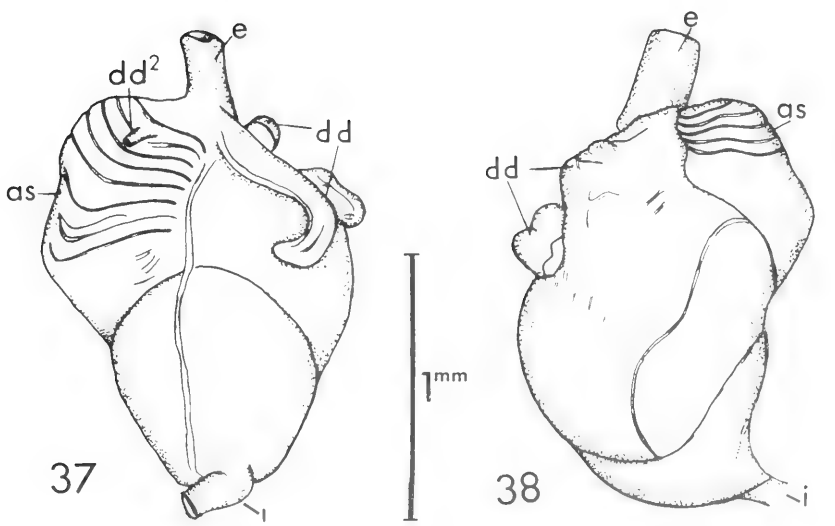
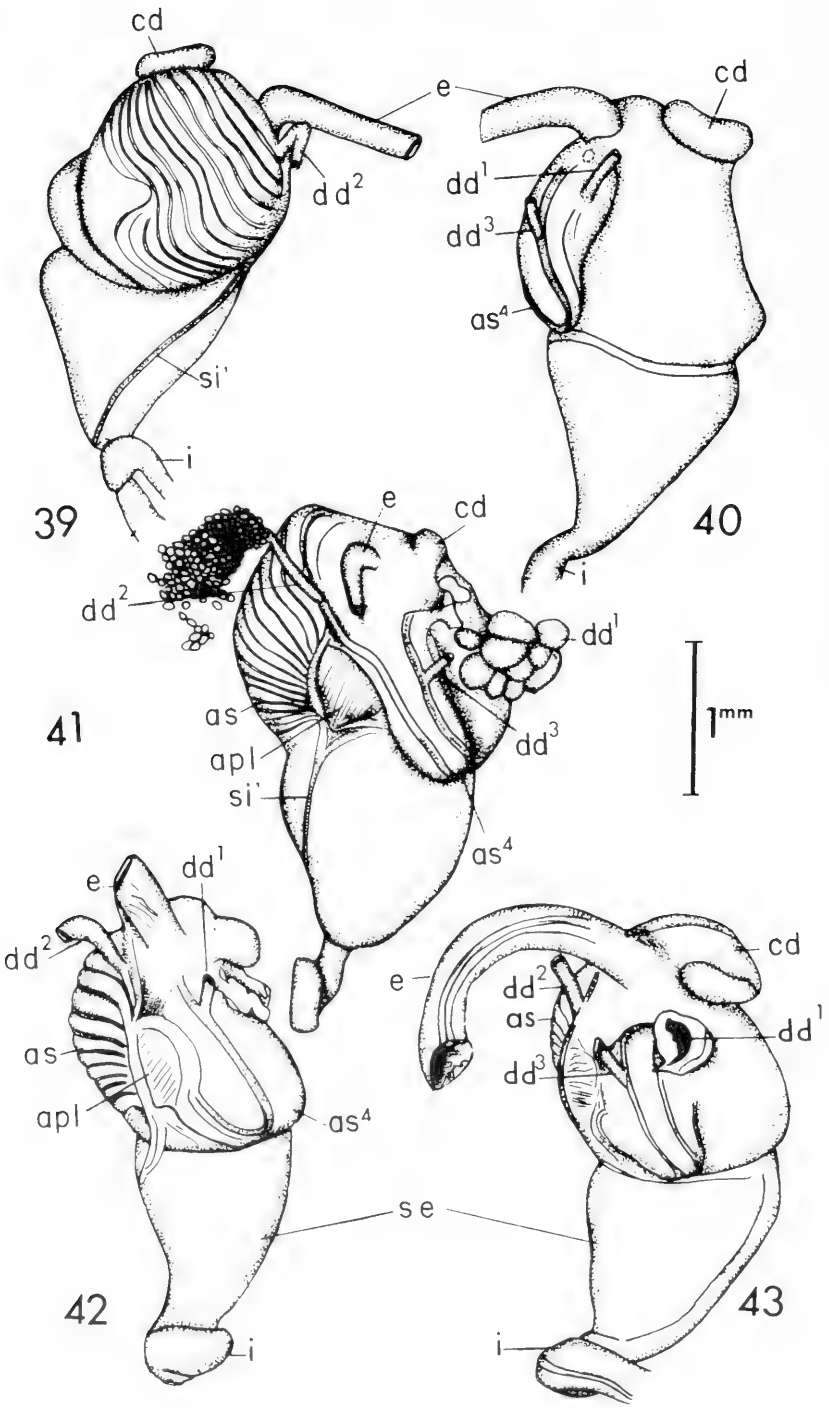


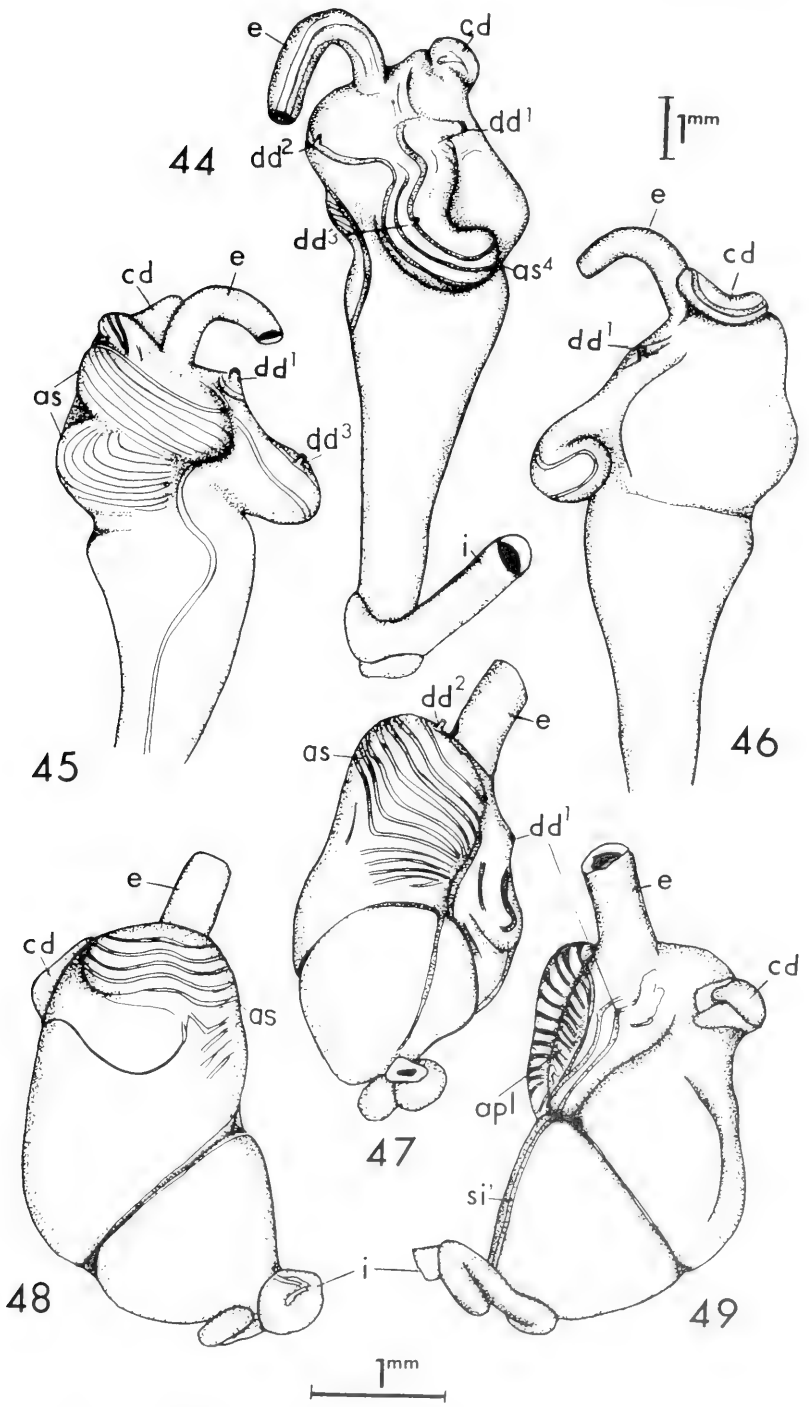
FIG. 36. *Propeleda longicaudata*. Vista interior del estómago. Stomach. Internal view.

FIGS. 37–38. *Nuculana* (*B.*) *inaequisculpta*. Estómago. Vistas anterior e izquierda. Stomach. Anterior and left views.



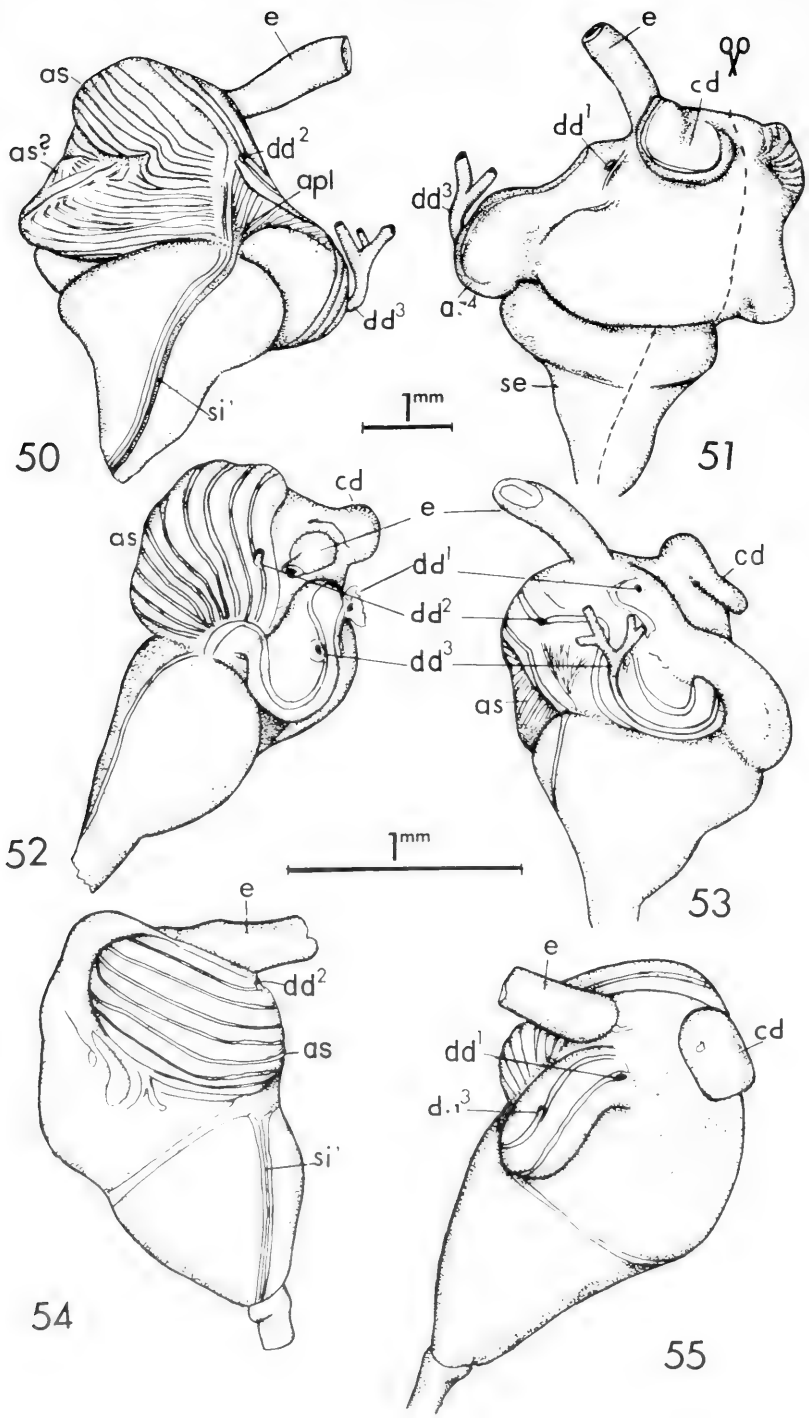
FIGS. 39–41. *Tindariopsis sulculata.* Estómago. Vistas derecha, izquierda y anterior. Stomach. Right, left and anterior views.

FIGS. 42–43. *Nuculana* (*S.*) *cuneata.* Estómago. Vistas anterior e izquierda. Stomach. Anterior and left views.



FIGS. 44–46. *Yoldia* (*Aequiyoldia*) *eightsi*. Estómago. Vistas anteriores, izquierda y posterior. Stomach. Anterior, left and posterior views.

FIGS. 47–49. *Silicula rouchi*. Estómago. Vistas anterior, derecha e izquierda. Stomach. Anterior, right and left views.



FIGS. 50, 51, 53. *Malletia chilensis*. Estómago. Vistas derecha y posterior (se indica línea de corte), anterior e izquierda. Stomach. Right, posterior (showing incision line), anterior and left views.

FIGS. 52, 54, 55. *Tindaria virens*.

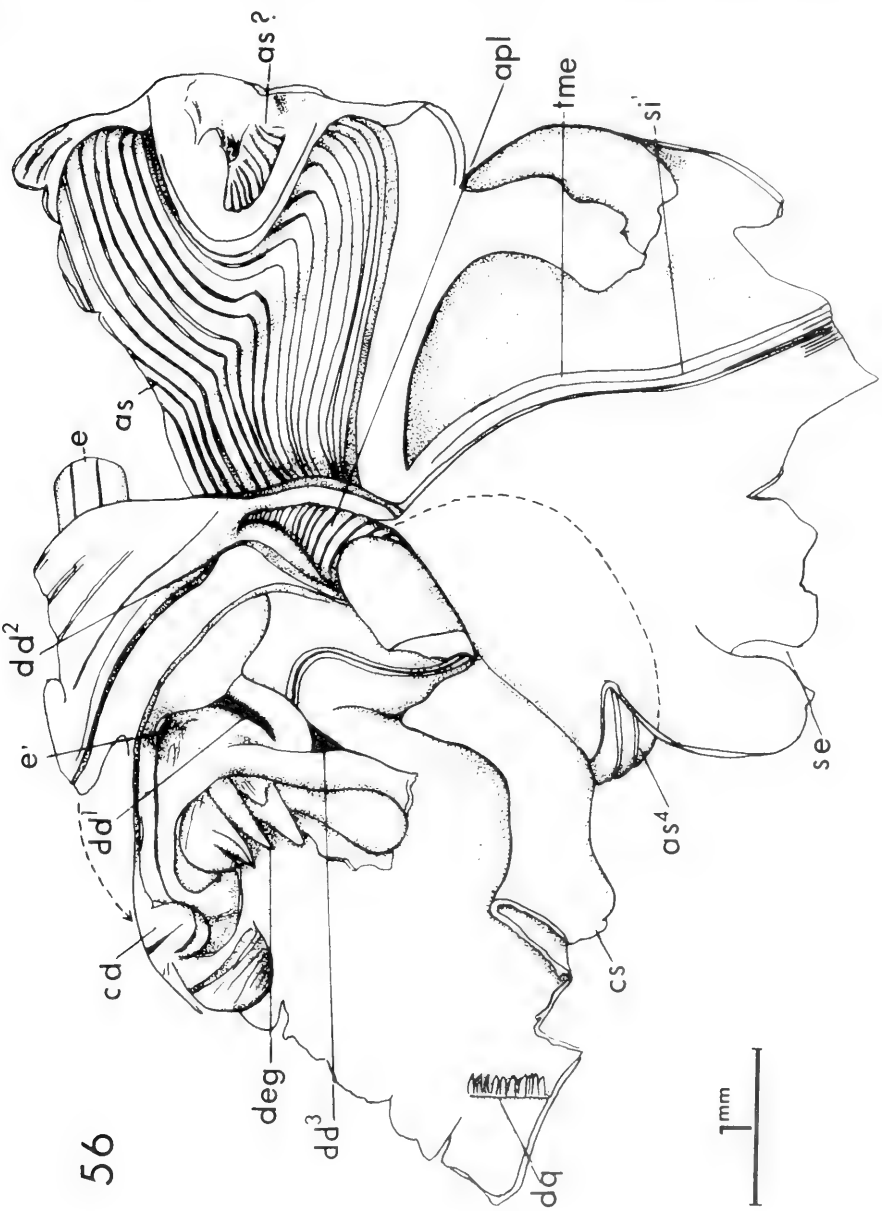
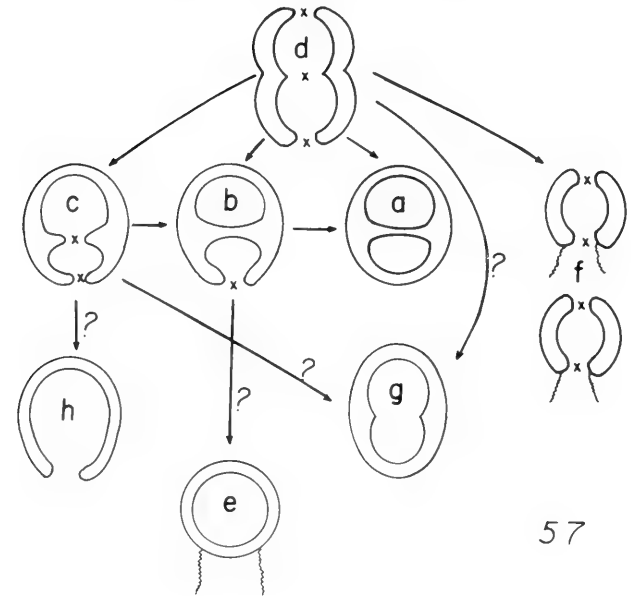


FIG. 56. *Malleia chilensis*. Vista interior del estómago (ver también Fig. 51). Stomach. Internal view (see also Fig. 51)



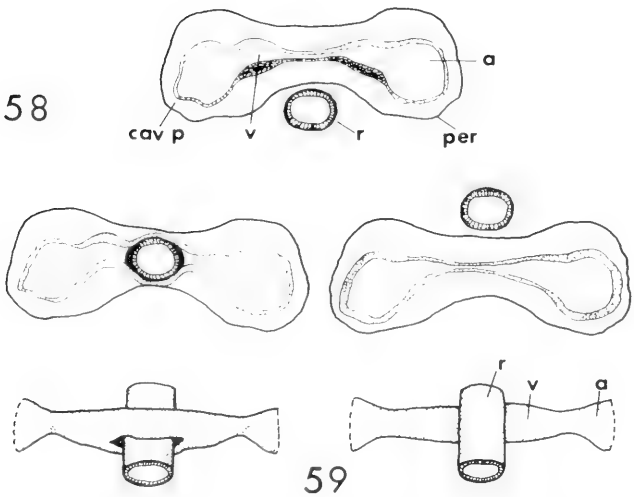


FIG. 57. Tipos de unión entre sifones, observados en los géneros de Nuculanacea. (a) Ambos sifones fusionados por tejido; (b) Sifón exhalante cerrado, inhalante abierto ventralmente; (c) Ambos sifones abiertos ventralmente; (d) Sifones abiertos dorsal y ventralmente; (e) Sifón exhalante cerrado; región correspondiente al inhalante con bordes aserrados; (f) Sifón exhalante abierto ventralmente o dorsal y ventralmente; región del sifón inhalante con bordes tentaculados o lisos. Fusion types in the genera of Nuculanacea. (a) Both siphons fused by tissue; (b) exhalant siphon closed, inhalant open ventrally; (c) both siphons open ventrally; (d) siphons open dorsally and ventrally; (e) exhalant siphon closed; part corresponding to inhalant siphon with serrated margins; (f) exhalant siphon, ventrally or dorsally and ventrally opened; inhalant siphon area with tentacles or smooth margins.

FIGS. 58, 59. Esquema diagramático de una sección transversal de la cavidad pericárdica y el recto y vista dorsal de la relación corazón-recto en la cavidad pericárdica, que muestra las modalidades fundamentales observadas en los géneros estudiados. Schematic transversal section of pericardial cavity and rectum dorsally showing the relationship heart-rectum and arrangements observed in the studied genera.

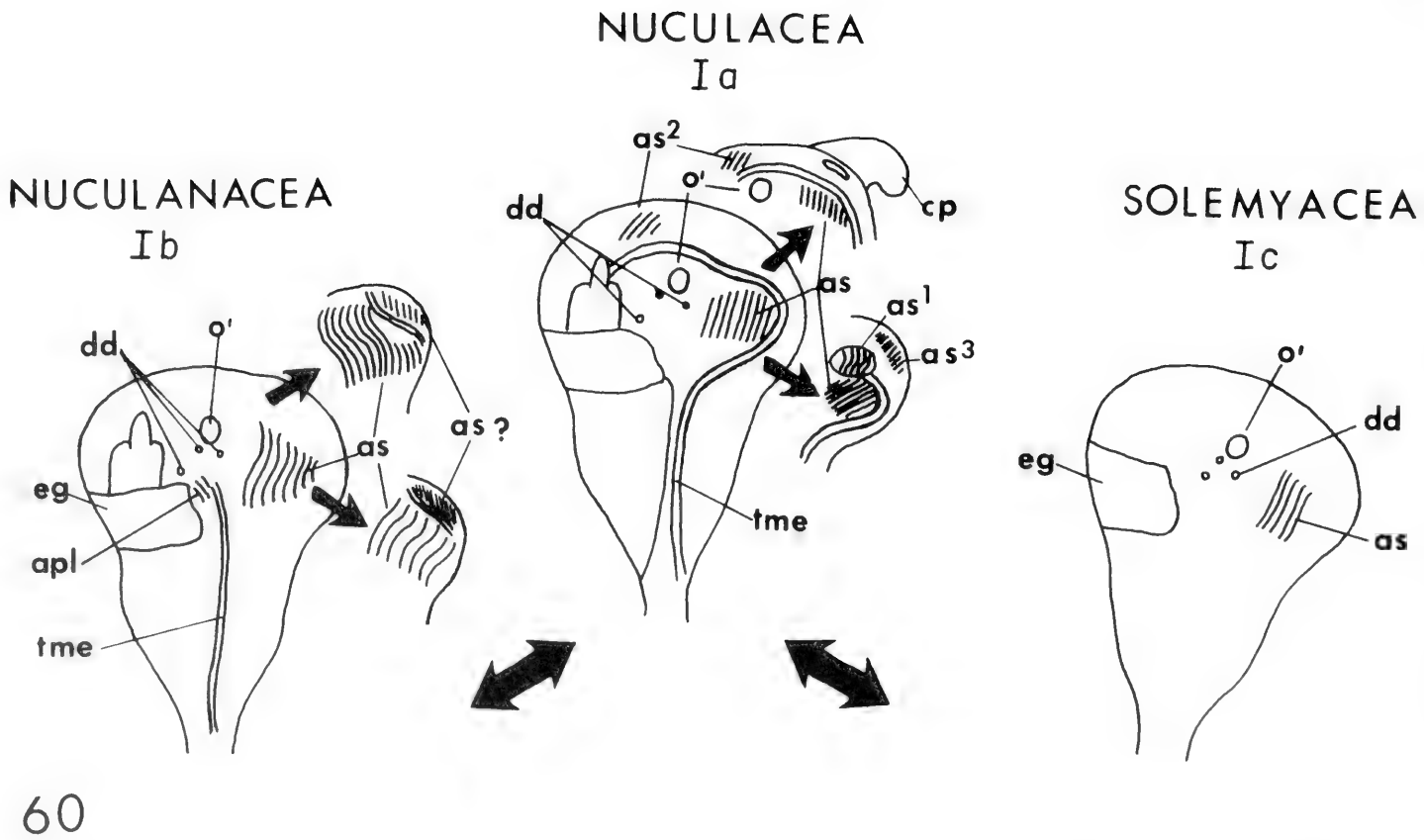


FIG. 60. Esquema filogenético de la subclase sobre la base de las áreas de selección de los estómagos de las especies estudiadas. Possible phylogenetic relationships within the subclass, based on the sorting areas of the studied stomachs.

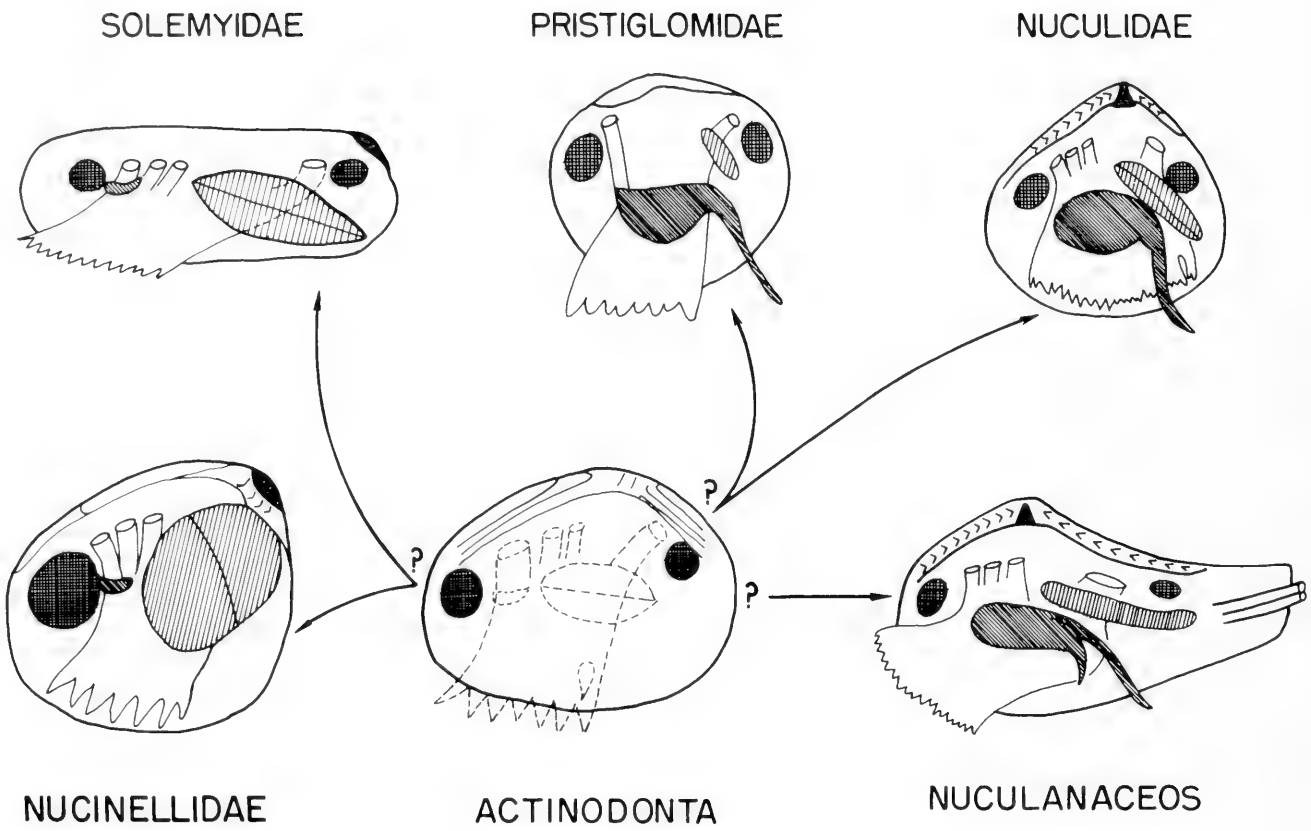
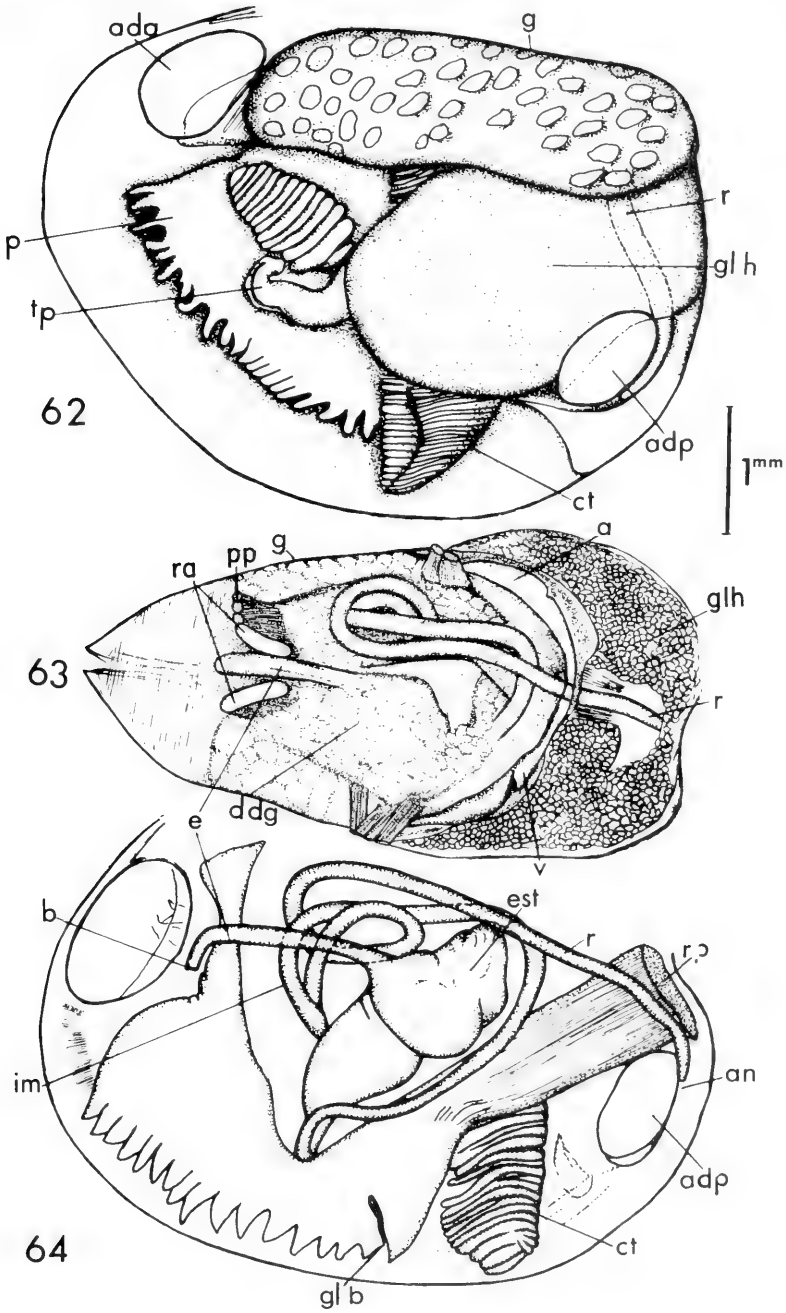


FIG. 61. Esquema filogenético de las familias estudiadas en que se señalan las diferencias en los rasgos morfológicos de ctenidios, palpos, músculos aductores y ligamento en: *Nucula* (Nuculidae), *Nuculana* (Nuculanidae), *Malletia* (Malletiidae), *Solemya* (Solemyidae) y Nucinellidae. Se indican las posibles tendencias evolutivas a partir de un actinodonto hipotético (tomado en parte de Allen y Sanders, 1969: fig. 5). Phylogenetic relationships of the studied families pointing out observed differences in ctenidia, palps, adductors muscles and ligament in *Nucula* (Nuculidae), *Nuculana* (Nuculanidae), *Malletia* (Malletiidae), *Solenomya* (Solemyidae), and Nucinellidae. Presumed evolutionary tendencies starting from a hypothetical actinodont are suggested (modified from Allen & Sanders, 1969: fig.5).

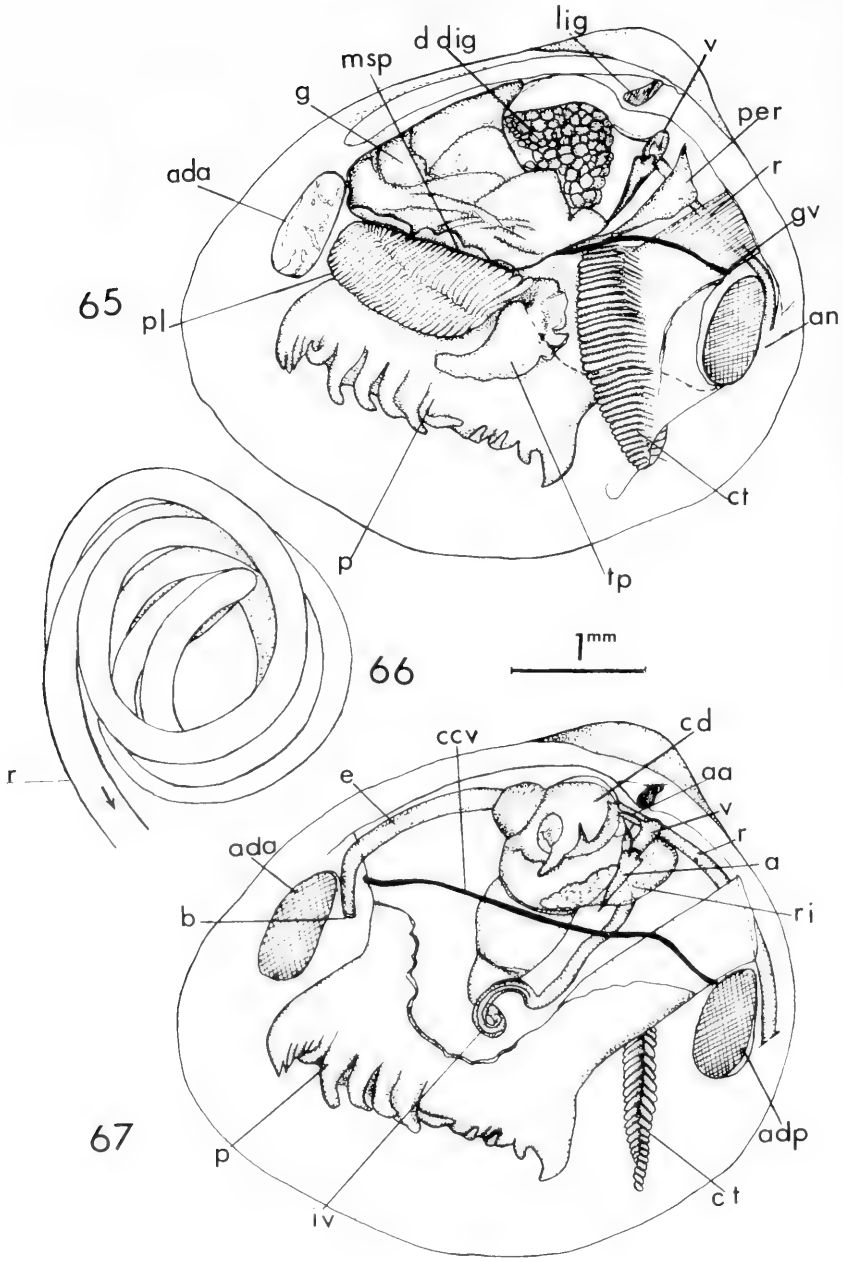


FIGS. 62–64. *Nucula* (*N.*) *pisum.*

FIG. 62. Vista lateral izquierda. Left lateral view.

FIG. 63. Vista dorsal mostrando tracto digestivo, divertículos digestivos, corazón y glándula hipobranquial derecha. Dorsal view showing: digestive tract, digestive diverticula, heart and right hypobranchial gland.

FIG. 64. Vista lateral izquierda mostrando aparato digestivo, sistema nervioso y glándula del biso. Left lateral view showing digestive tract, nervous system and byssal gland.

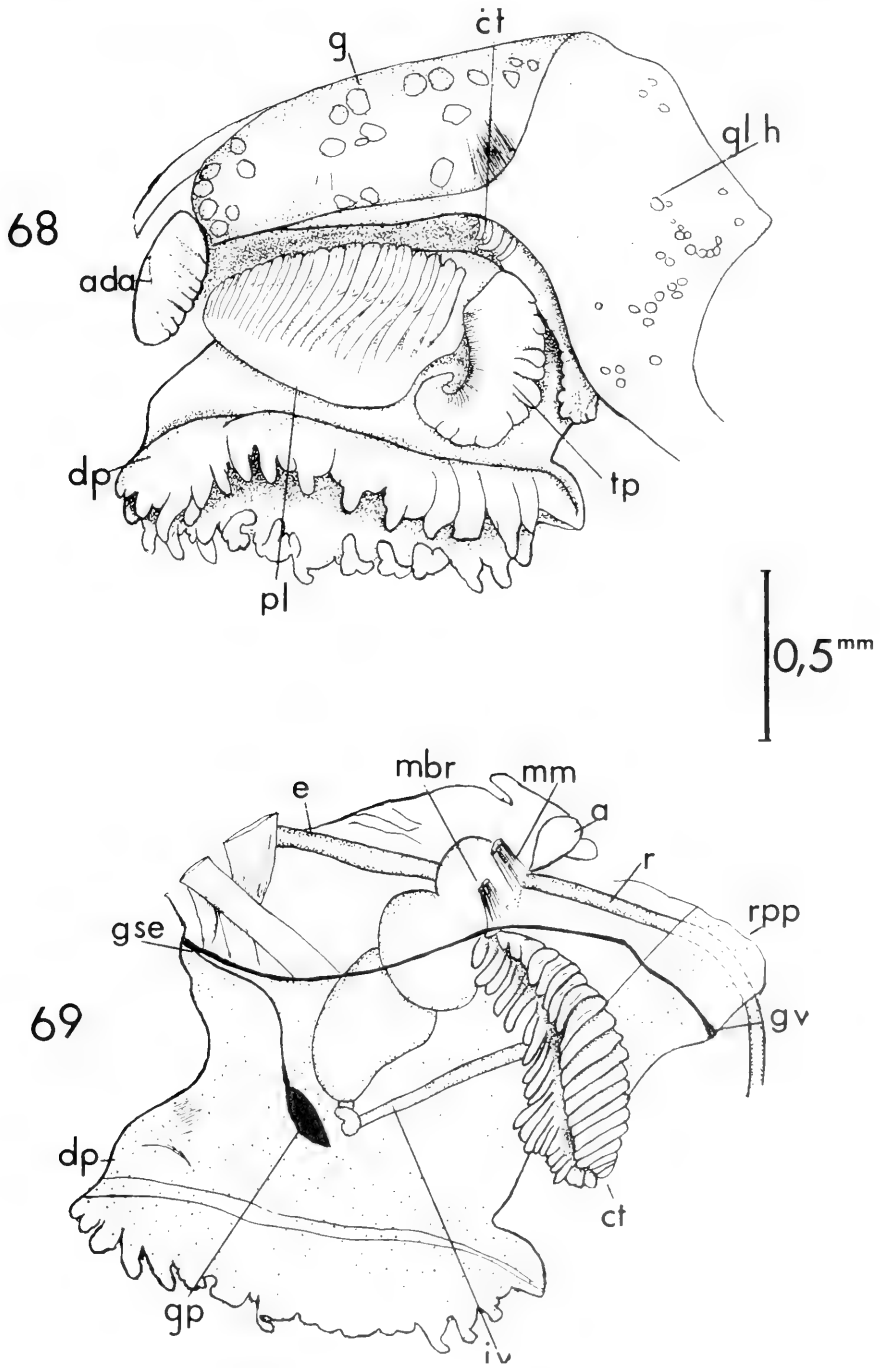


FIGS. 65–67. *Nucula* (*N.*) *pseudoexigua.*

FIG. 65. Vista lateral izquierda de la cavidad del manto y cavidad pericárdica. Left lateral view of mantle and pericardial cavity.

FIG. 66. Vista lateral derecha del intestino. Muy aumentada. Enlarged right lateral view of intestine.

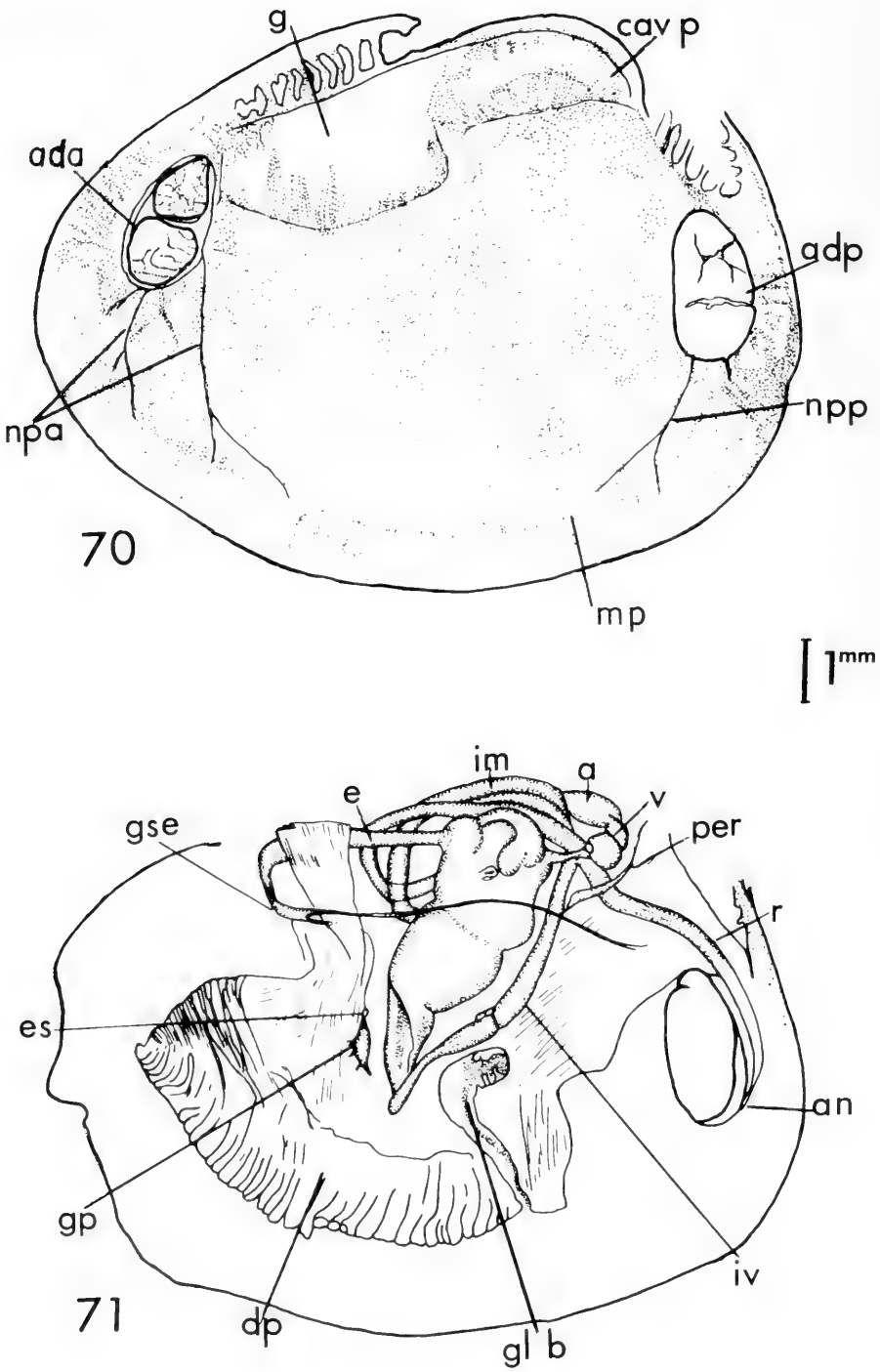
FIG. 67. Vista lateral izquierda, mostrando aparato digestivo, sistema nervioso y cavidad pericárdica con corazón y riñón. Left lateral view showing digestive tract, nervous system, pericardial cavity, heart and kidney.



FIGS. 68–69. *Nucula* (*N.*) *falklandica.*

FIG. 68. Vista lateral izquierda. Left lateral view

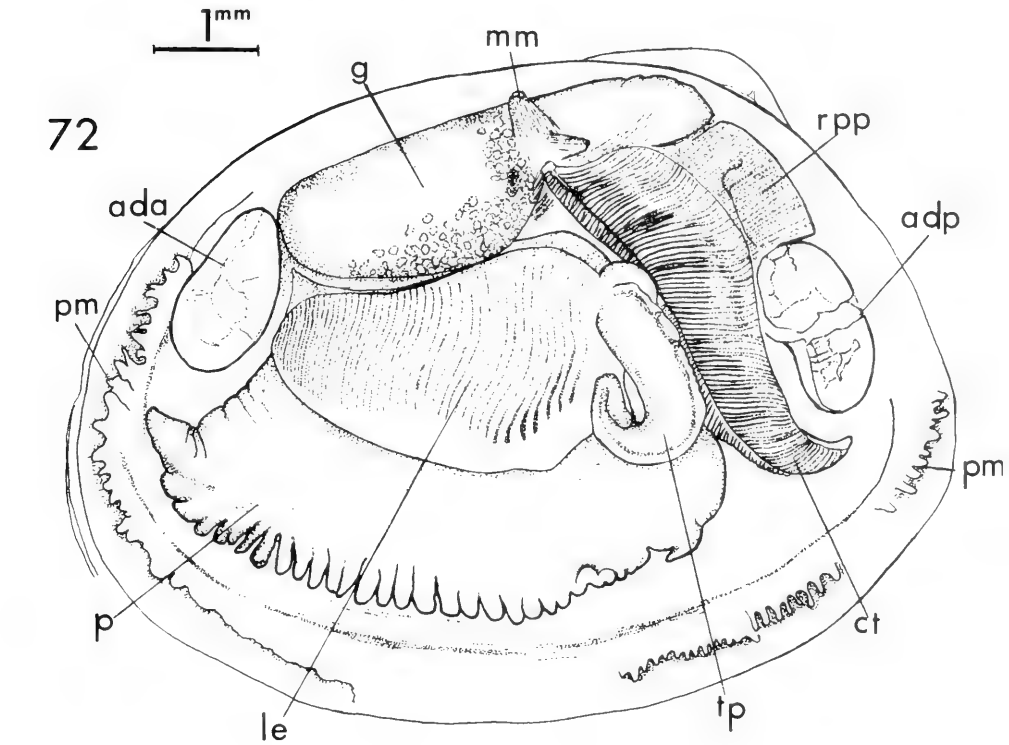
FIG. 69. Vista lateral izquierda del tracto digestivo, ctenidia y sistema nervioso. Left lateral view of the digestive tract, ctenidia and nervous system.



FIGS. 70–71. *Ennucula grayi.*

FIG. 70. Vista lateral izquierda del manto. Left lateral view of mantle.

FIG. 71. Vista lateral izquierda mostrando aparato digestivo, sistema nervioso y glándula del biso. Left lateral view showing digestive tract, nervous system and byssal gland.



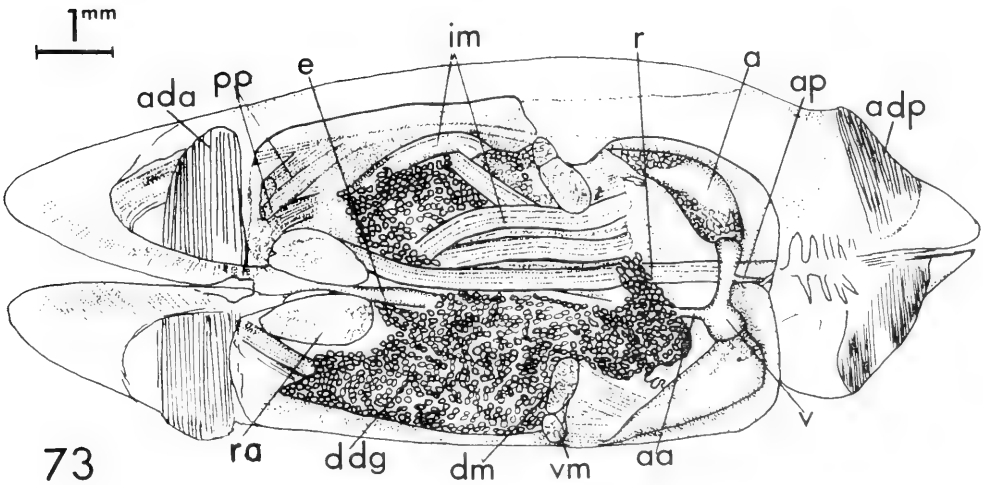
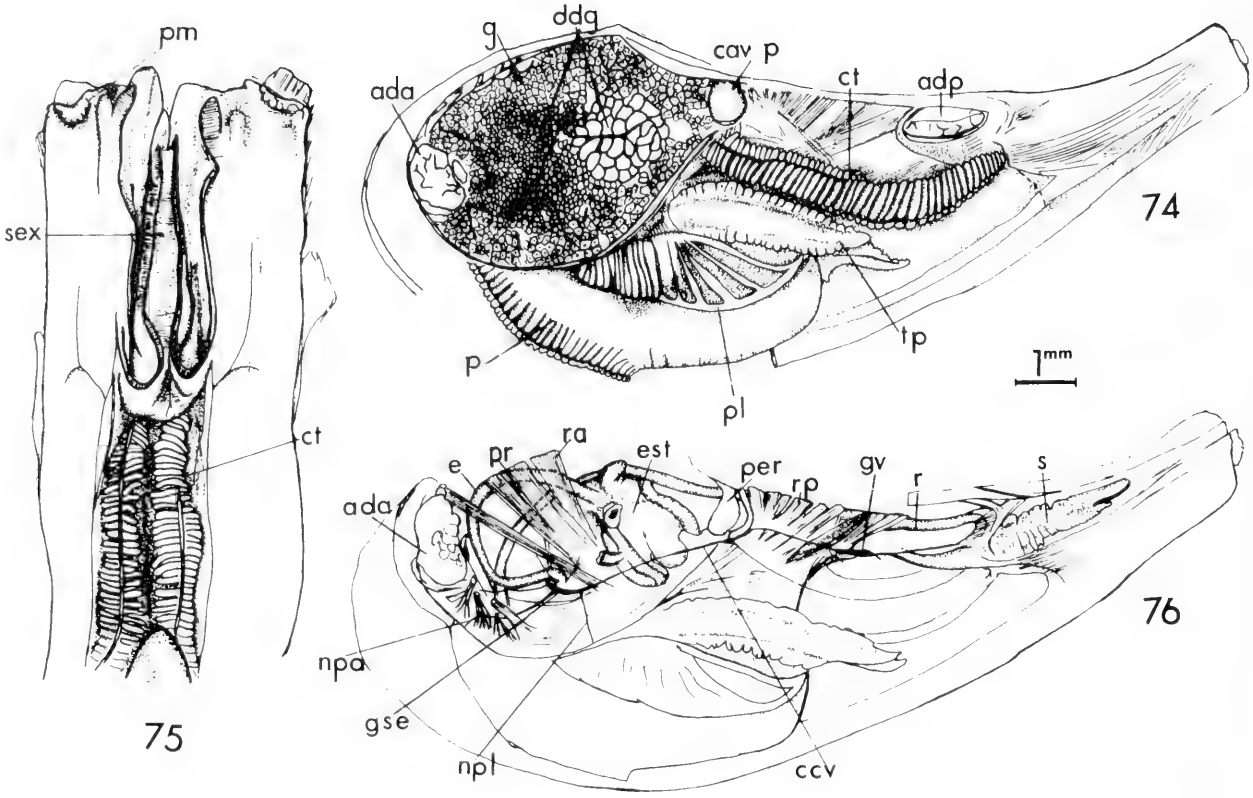


FIG. 72. *Ennucula puelcha*. Vista lateral izquierda de la cavidad paleal. Left lateral view of pallial cavity.

FIG. 73. *Ennucula grayi*. Vista dorsal mostrando tracto digestivo, corazón, glándula hipobranquial y musculatura pedal. Dorsal view showing digestive tract, heart, hypobranchial gland and pedal musculature.

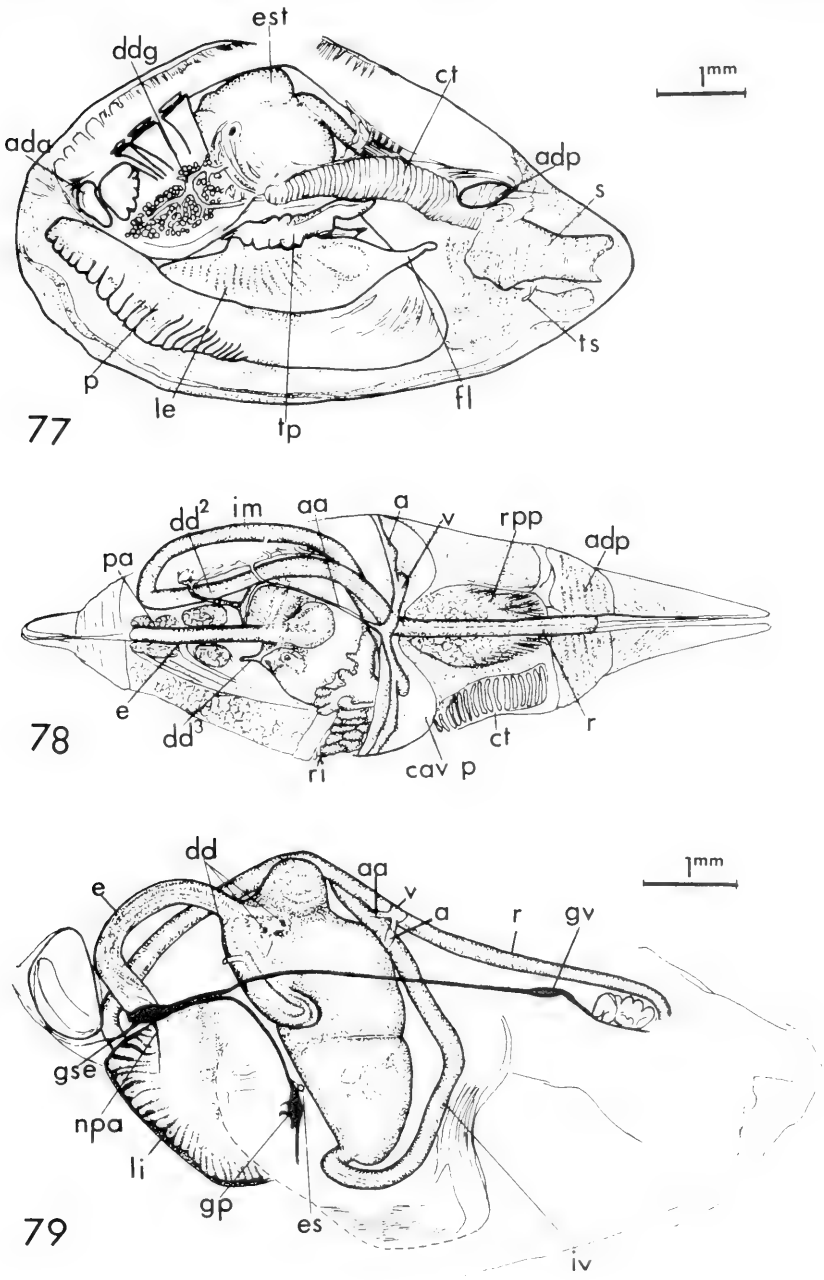


FIGS. 74–76. *Propeleda longicaudata*.

FIG. 74. Vista lateral izquierda mostrando la cavidad del manto. Left lateral view showing mantle cavity.

FIG. 75. Vista ventral del sifón inhalante y ctenidios. Ventral view of inhalant siphon and ctenidia.

FIG. 76. Vista lateral izquierda mostrando musculatura pedal, tracto digestivo y órganos de la cavidad del manto. Left lateral view showing pedal musculature, digestive tract and organs of mantle cavity.

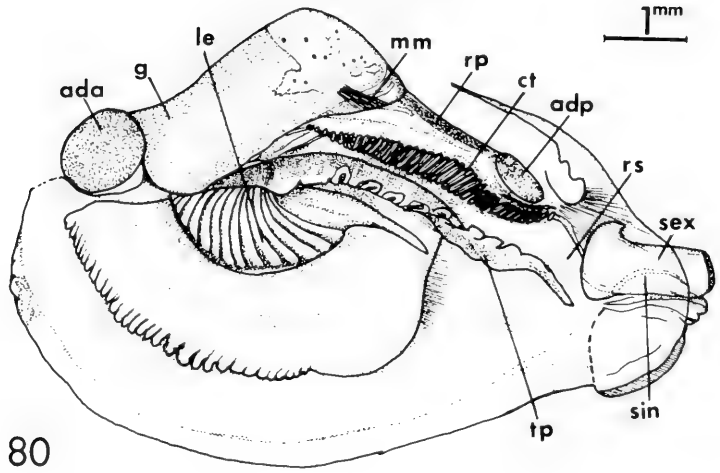


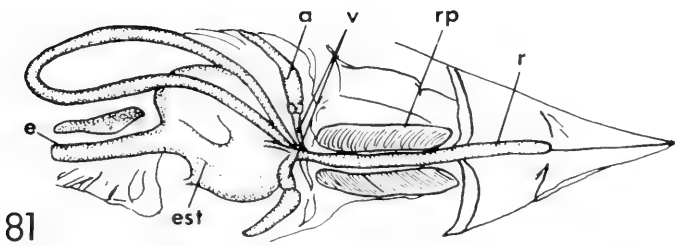
FIGS. 77–79. *Nuculana* (*S.*) *cuneata*.

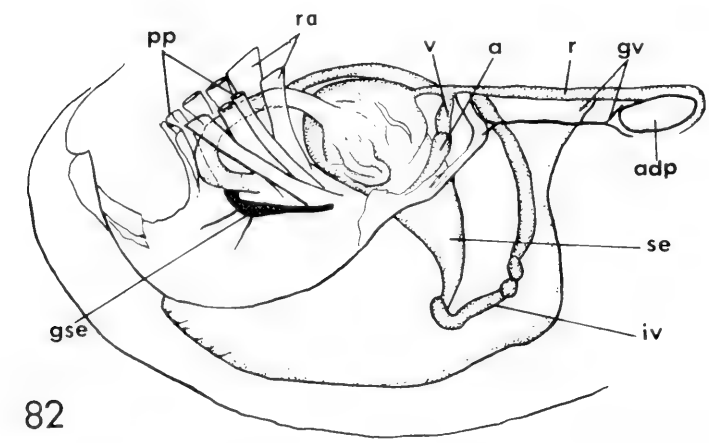
FIG. 77. Vista lateral izquierda mostrando los órganos de la cavidad paleal, divertículos digestivos izquierdos, estómago, cavidad pericárdica y corazón. Left lateral view showing organs of the pallial cavity, left digestive diverticula, stomach, pericardial cavity and hearth.

FIG. 78. Vista dorsal mostrando tracto digestivo, corazón, riñón y ctenidio derecho. Dorsal view showing digestive tract, heart, kidney and right ctenidia.

FIG. 79. Vista lateral izquierda mostrando aparato digestivo, sistema nervioso y lamela del palpo derecho. Left lateral view showing digestive tract, nervous system and right palp lamela.





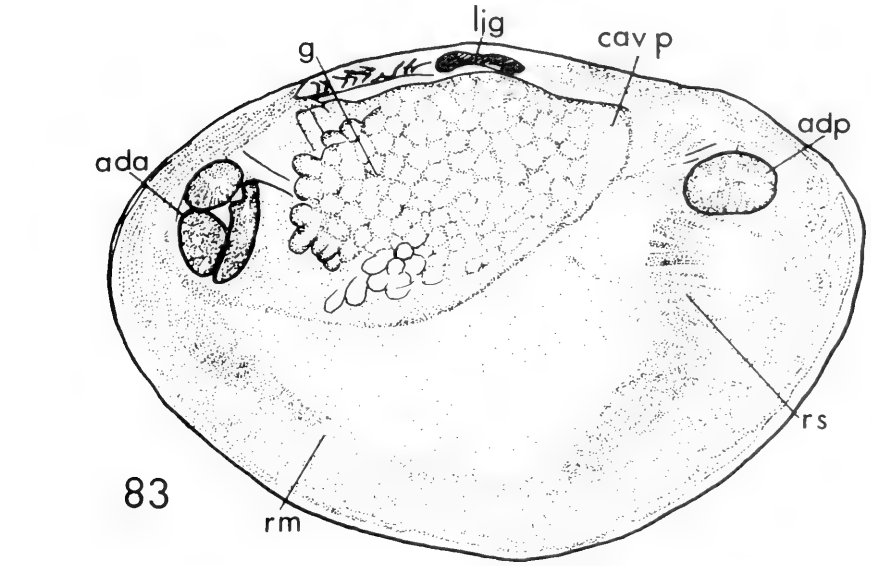


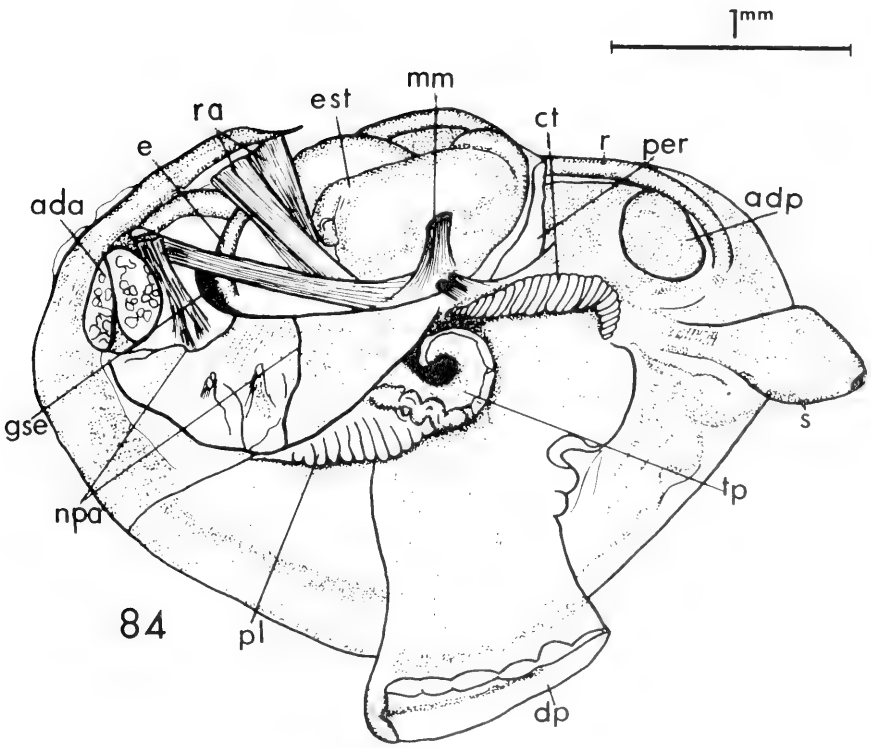
FIGS. 80–82. *Tindariopsis sulculata.*

FIG. 80. Vista lateral izquierda de la cavidad paleal con parte del manto. Left lateral view of pallial cavity with part of mantle.

FIG. 81. Vista dorsal del aparato digestivo y corazón. Dorsal view of heart and digestive tract.

FIG. 82. Vista lateral izquierda mostrando aparato digestivo, sistema nervioso y musculatura pedal anterior y visceral. Left lateral view showing digestive tract, nervous system, anterior and visceral pedal musculature.

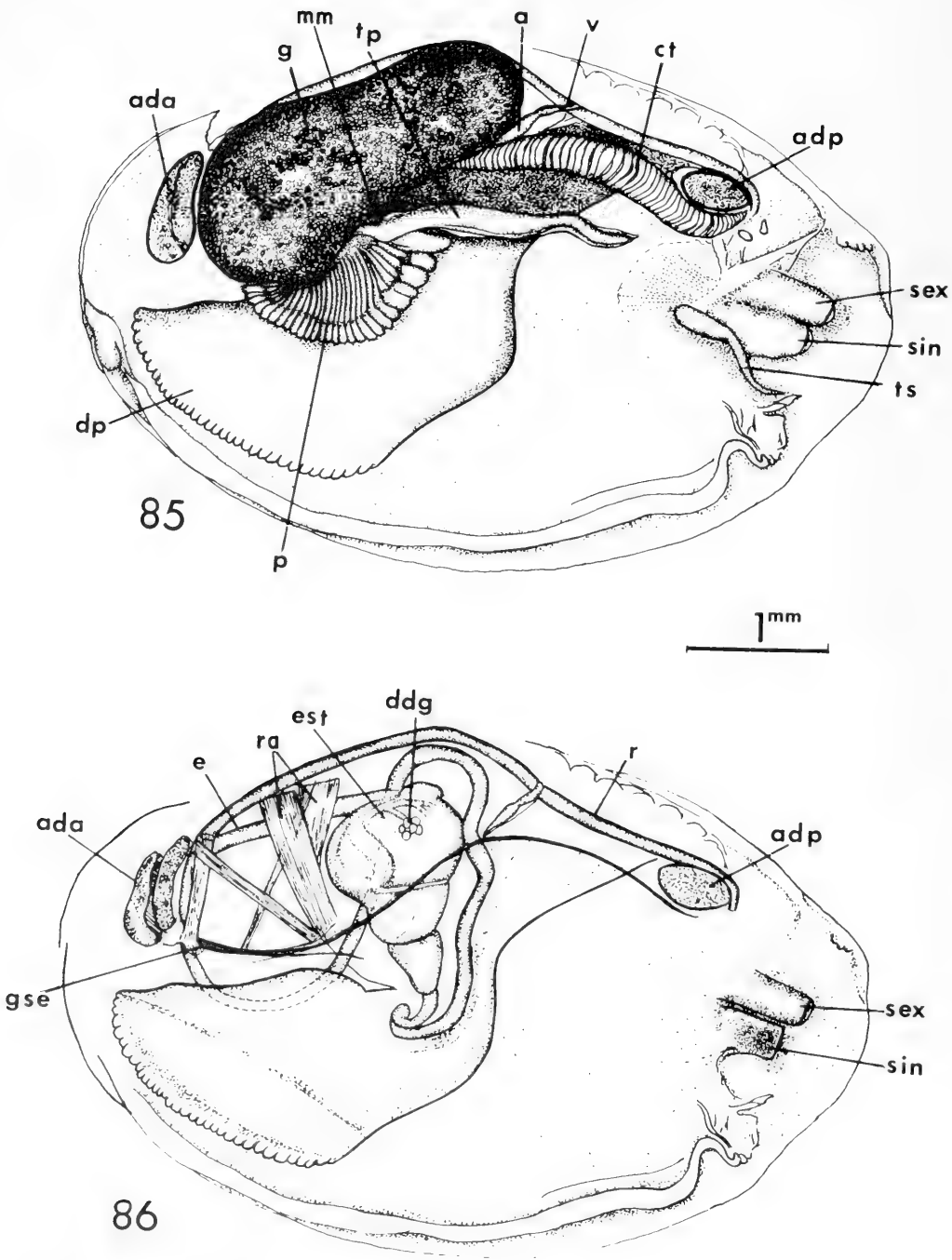




FIGS. 83–84. *Yoldiella ecaudata*.

FIG. 83. Vista lateral izquierda. Left lateral view.

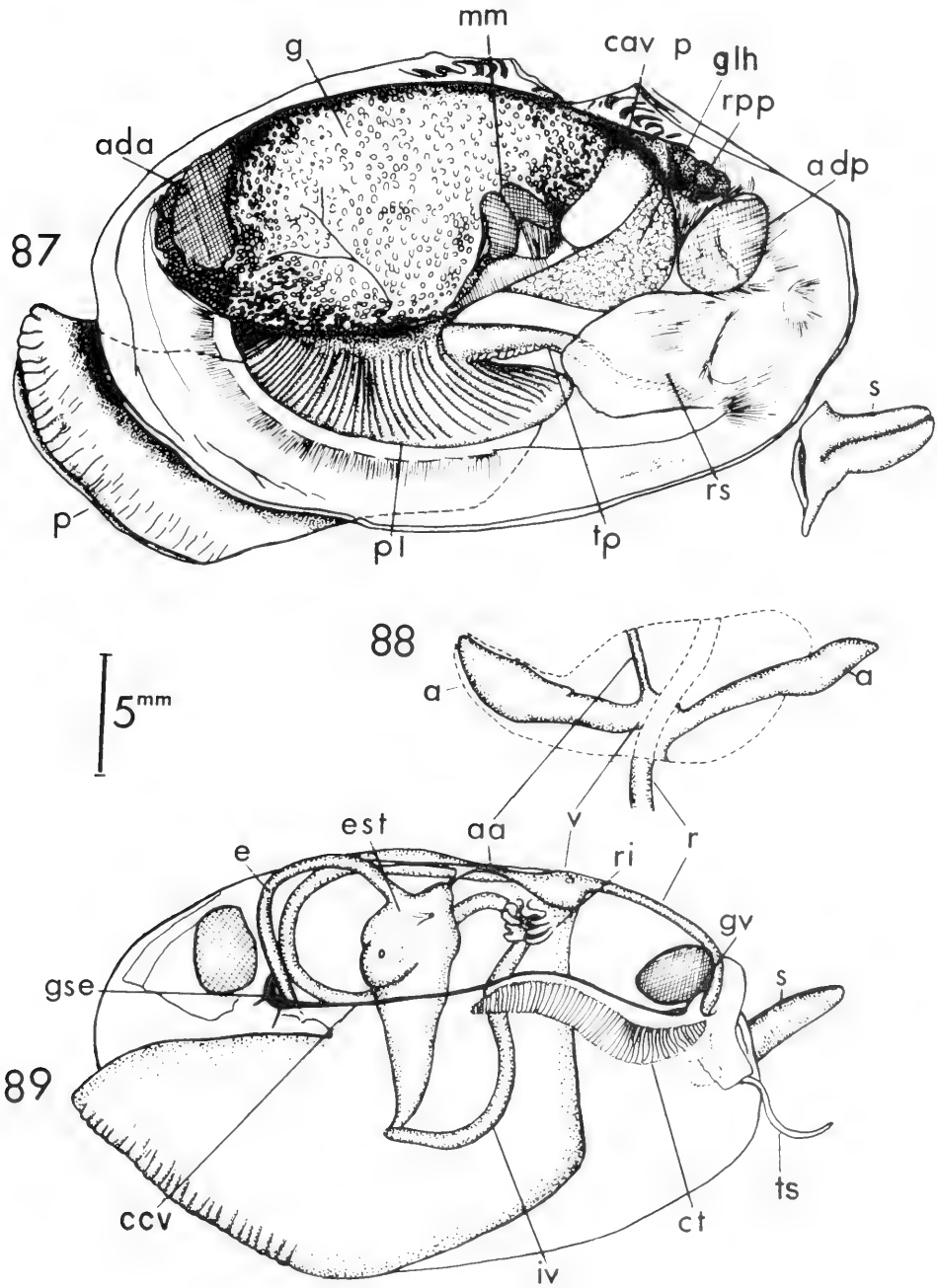
FIG. 84. Vista lateral izquierda de los órganos de la cavidad del manto. Pie y sifón extendidos. Left lateral view of the mantle cavity. Foot and extended siphons.



FIGS. 85–86. *Yoldiella chilenica.*

FIG. 85. Vista lateral izquierda de la cavidad del manto. Left lateral view of mantle cavity.

FIG. 86. Vista lateral izquierda mostrando el aparato digestivo, parte del sistema nervioso y detalle de los sifones. Left lateral view showing digestive tract, part of the nervous system and detail of siphons.



FIGS. 87–89. *Yoldia* (*Aequiyoldia*) *eightsi*.

FIG. 87. Vista lateral izquierda. Parte del manto se ha omitido para mostrar el palpo. Left lateral view. Part of mantle omitted to show palp.

FIG. 88. Vista dorsal del corazón y recto. Dorsal view of the heart and rectum.

FIG. 89. Vista lateral izquierda mostrando aparato digestivo, sistema nervioso, aparato circulatorio (la aurícula izquierda ha sido omitida para mostrar el riñón), ctenidios y sifones. Left lateral view showing digestive tract, nervous system, heart (left auricle omitted to show the kidney), ctenidia and siphons.

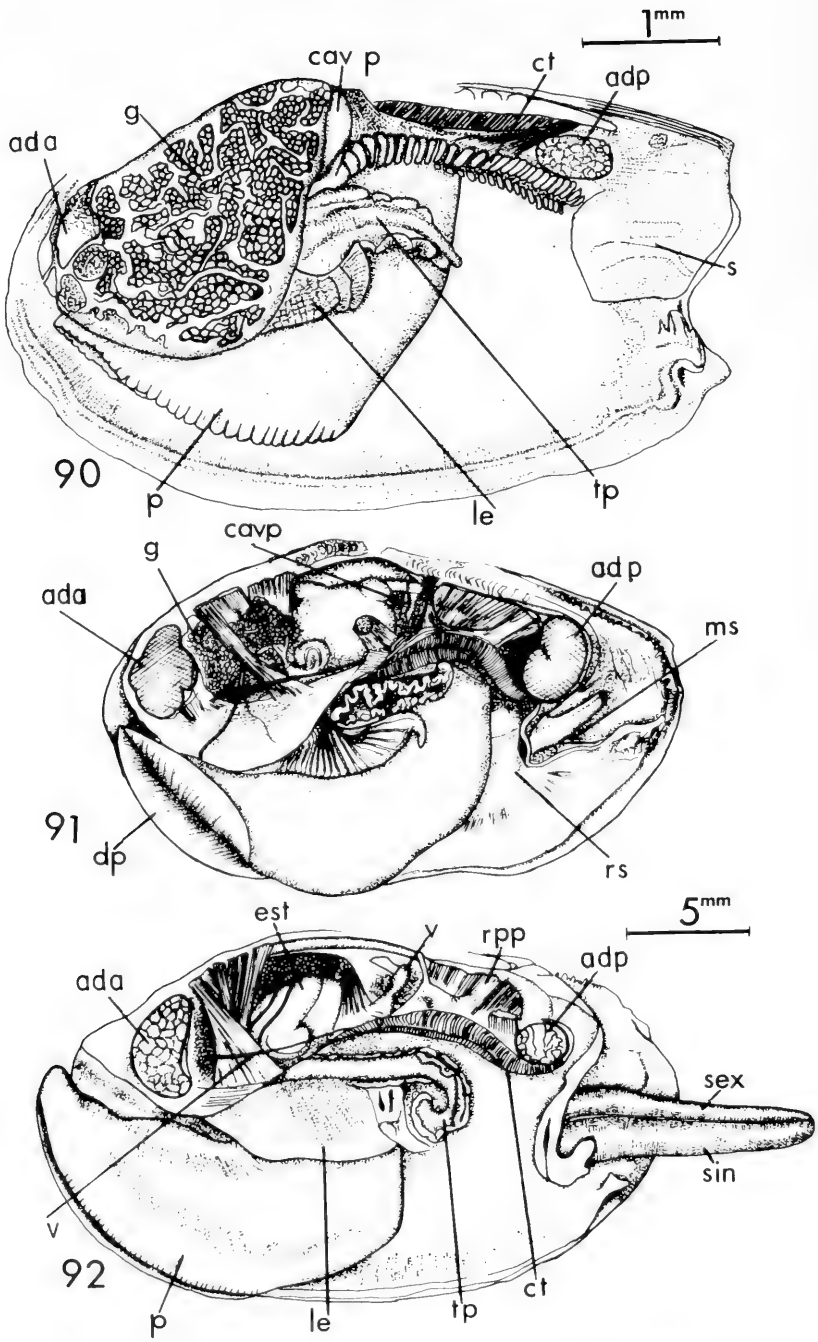
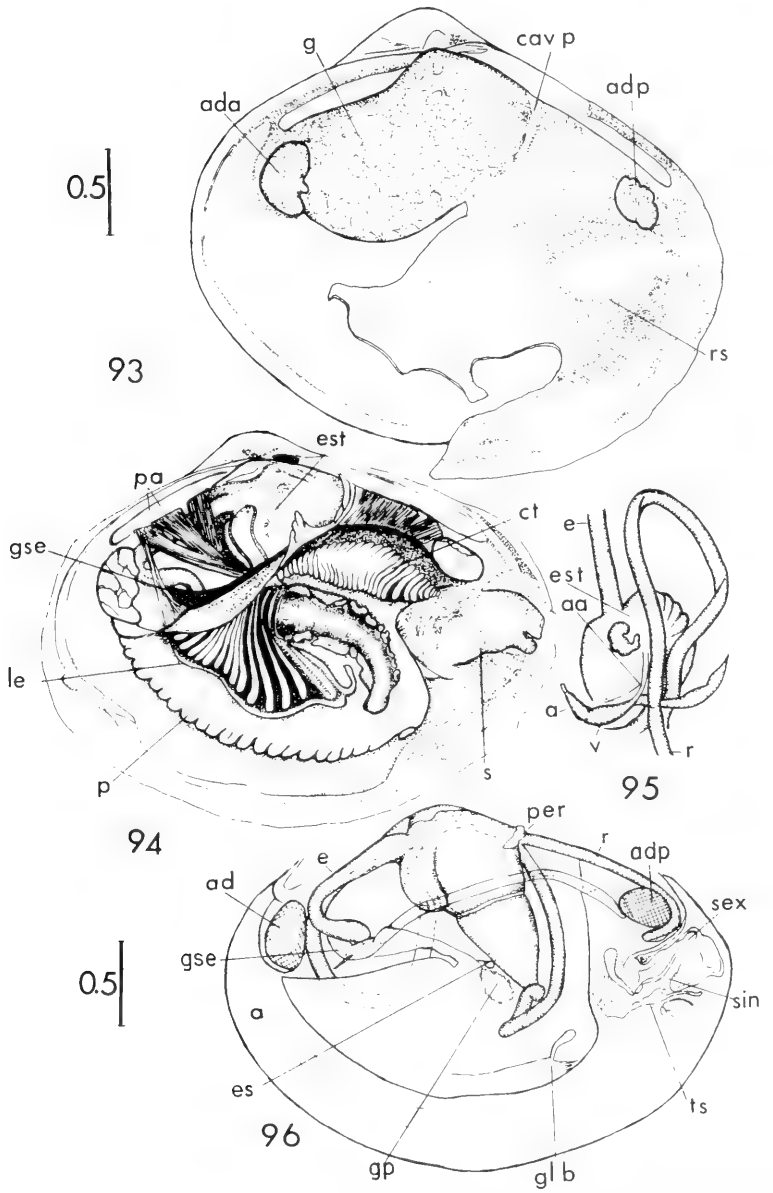


FIG. 90. *Nuculana* (*B.*) *inaequisculpta.* Vista lateral izquierda mostrando la cavidad del manto. Left lateral view showing mantle cavity.

FIG. 91. *Malletia patagonica.* Vista lateral izquierda. Left lateral view.

FIG. 92. *Maletia chilensis.* Vista lateral izquierda mostrando la cavidad del manto. Left lateral view showing mantle cavity.



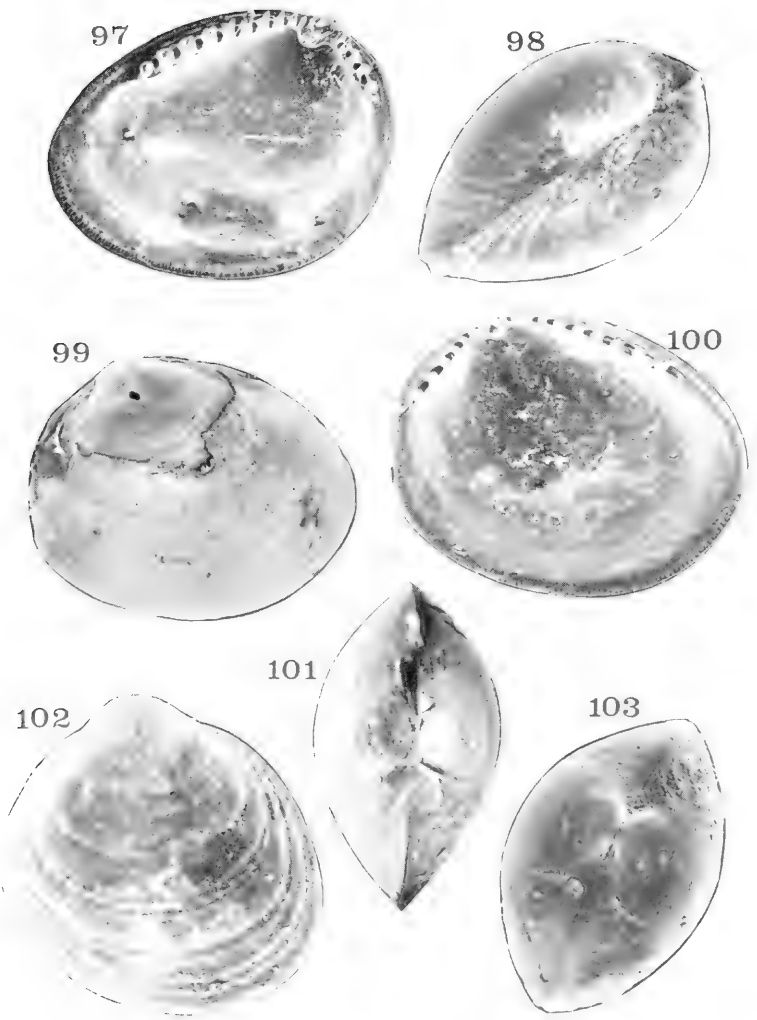
FIGS. 93–96. *Tindaria virens*.

FIG. 93. Vista lateral izquierda mostrando las gónadas y parte del manto. Left lateral view showing gonads and part of mantle.

FIG. 94. Vista lateral izquierda mostrando cavidad del manto, sifones, musculatura pedal y ganglios cerebral y visceral. Left lateral view showing mantle cavity, siphons, pedal musculature, cerebral and visceral ganglia.

FIG. 95. Vista dorsal del tracto digestivo y corazón. Dorsal view of digestive tract and heart.

FIG. 96. Vista lateral izquierda mostrando: aparato digestivo, sistema nervioso y glándula del biso. Vista frontal del sifón. Left lateral view showing digestive tract, nervous system and byssal gland. Frontal view of siphon.



FIGS. 97, 98. *Nucula* (*N.*) *pisum*.

FIG. 97. Valva derecha (MZUC 4550), 20X. Bahía Inútil, Estrecho de Magallanes. Right valve (MZUC 4550), 20X, Inutil Bay, Magellan Strait.

FIG. 98. Vista dorsal del mismo ejemplar, 28X. Dorsal view of the same specimen, 28X

FIGS. 99–101. *Nucula* (*N.*) *fernandensis*.

FIG. 99. Valva derecha (MZUC 10388), 18X, Islas Juan Fernández. Right valve (MZUC 10388), 18X, Juan Fernandez Islands.

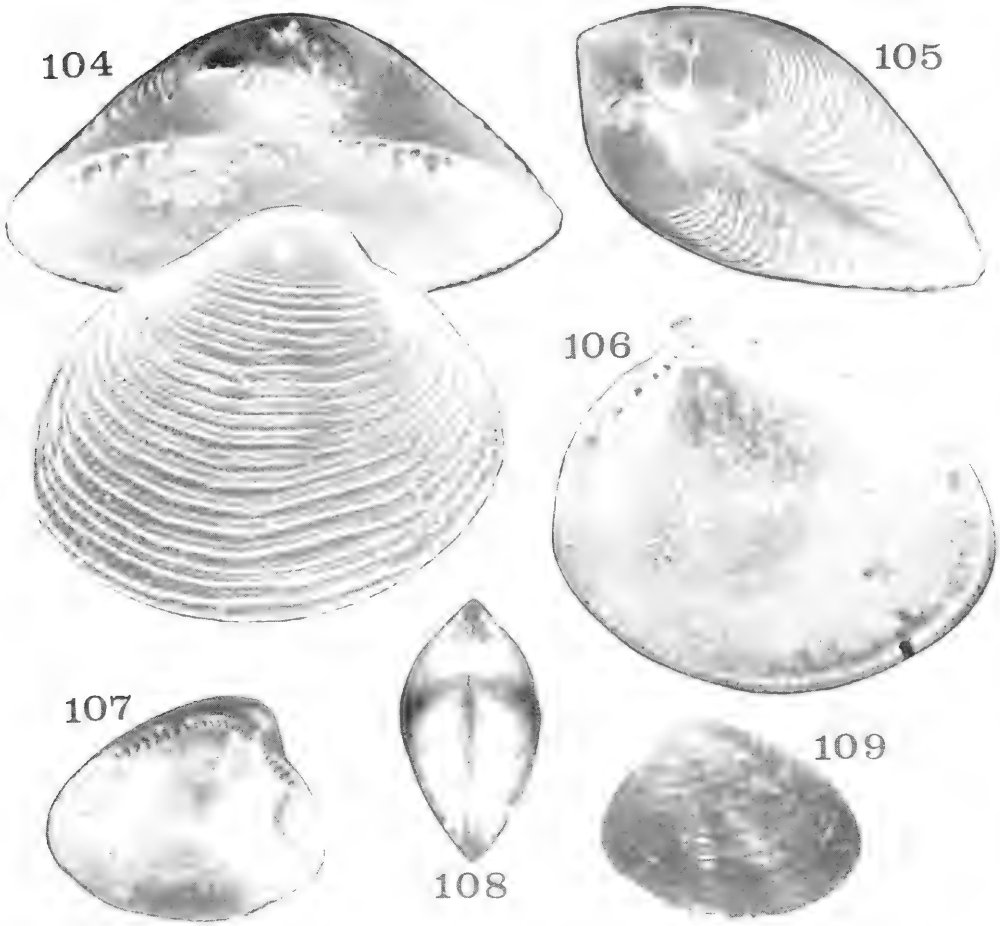
FIG. 100. Valva izquierda (MZUC 10387, paratipo), 16.5X, Islas Juan Fernández. Left valve (MZUC 10387, paratype), 16.5X, Juan Fernandez Islands.

FIG. 101. Vista dorsal (MZUC 10387, paratipo), 22X, Islas Juan Fernández. Dorsal view (MZUC 10387 paratype), 22X, Juan Fernández Islands.

FIGS. 102, 103. *Nucula* (*N.*) *falklandica*.

FIG. 102. Valva derecha (MZUC 4662), 41X, Estrecho de Magallanes. Right valve (MZUC 4662), 41X, Magellan Strait.

FIG. 103. Vista dorsal del mismo ejemplar, 41X. Dorsal view of same specimen, 41X.



FIGS. 104–106. *Nucula pseudoexigua.*

FIG. 104. Vista dorsal (MZUC 10304, paratipo), 28X, Confluencia Canales Trinidad y Concepción. Dorsal view (MZUC 10304, paratype), 28X, Confluence of Concepcion and Trinidad channels. Valva izquierda del mismo ejemplar (MZUC 10304, paratipo), 25X. Left valve of same specimen (MZUC 10304), 25X.

FIG. 105. Vista dorsal (MZUC 10293, Holotype), 20X, Canal Sarmiento. Dorsal view (MZUC 10293, Holotype), 20X, Sarmiento Channel. Paratype.

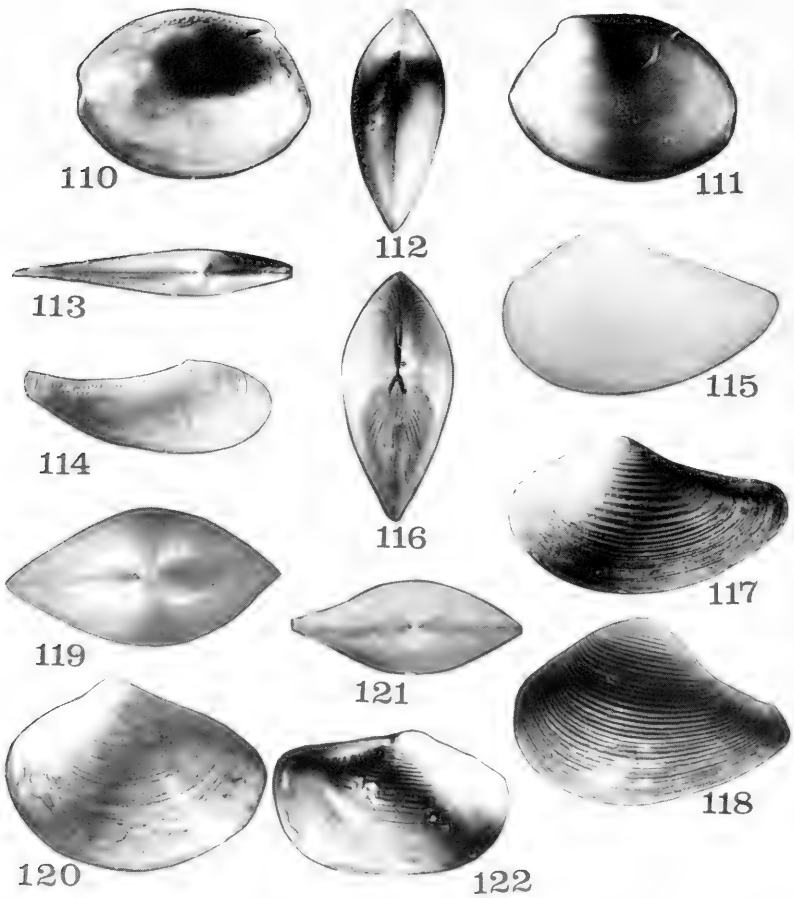
FIG. 106. Vista interior de valva izquierda (MZUC 10304), 18X, Confluencia Canales Concepción y Trinidad. Internal view left valve. (MZUC 10304), 18X, Confluence of Concepcion and Trinidad Channels.

FIGS. 107–109. *Ennucula grayi.*

FIG. 107. Vista dorsal (MZUC 4617), 14 mm, Estrecho de Magallanes. Dorsal view (MZUC 4617), 14 mm, Magellan Strait.

FIG. 108. Vista interna (MZUC 4617), 15 mm, Estrecho de Magallanes. Internal view (MZUC 4617), 15 mm, Magellan Strait.

FIG. 109. Valva derecha del ejemplar anterior. Right valve of same specimen.



FIGS. 110–112. *Ennucula puelcha*

FIG. 110. Valva derecha, vista interna (MZUC 4565), 17.7 mm, Mar Chile II Est. 24. Right valve, internal view (MZUC 4565), 17.7 mm, Mar Chile II Est. 24.

FIG. 111. Vista externa del mismo ejemplar, Estrecho de Magallanes. External view of same specimen, Magellan Strait.

FIG. 112. Vista dorsal del mismo ejemplar. Dorsal view of same specimen.

FIGS. 113, 114. *Propeleda longicaudata.*

FIG. 113. Vista dorsal (MZUC 4610), 9 mm, Confluencia Canales Concepción y Trinidad. Dorsal view (MZUC 4610), 9 mm, Confluence of Concepción and Trinidad Channels.

FIG. 114. Vista lateral del mismo ejemplar. Lateral view of same specimen.

FIGS. 115–118. *Nuculana* (*S.*) *cuneata.*

FIG. 115. Vista lateral (MZUC 4706), 8 mm, Bahía Concepción. Lateral view (MZUC 4706), 8 mm, Concepción Bay.

FIG. 116. Vista dorsal del mismo ejemplar. Dorsal view of same specimen.

FIG. 117. Valva izquierda (MZUC 4562), 112 mm, Punta Tortuga, Coquimbo. Left valve (MZUC 4562), 112 mm, Tortuga Point, Coquimbo.

FIG. 118. Valva izquierda (MZUC 4562), 11 mm, Punta Tortuga, Coquimbo. Left valve (MZUC 4562), 11 mm, Tortuga Point, Coquimbo.

FIGS. 119, 120. *Tindaria virens*

FIG. 119. Vista dorsal (MZUC 4650), 4.4 mm, Estrecho de Magallanes. Dorsal view (MZUC 4650), 4.4 mm, Magellan Strait.

FIG. 120. Vista lateral del mismo ejemplar. Lateral view of same specimen.

FIGS. 121, 122. *Nuculana* (*B.*) *inaequisculpta*

FIG. 121. Vista dorsal (MZUC 4537), 12 mm, Estrecho de Bransfield. Dorsal view (MZUC 4537), 12 mm, Bransfield Strait.

FIG. 122. Vista lateral del mismo ejemplar. Lateral view of same specimen.

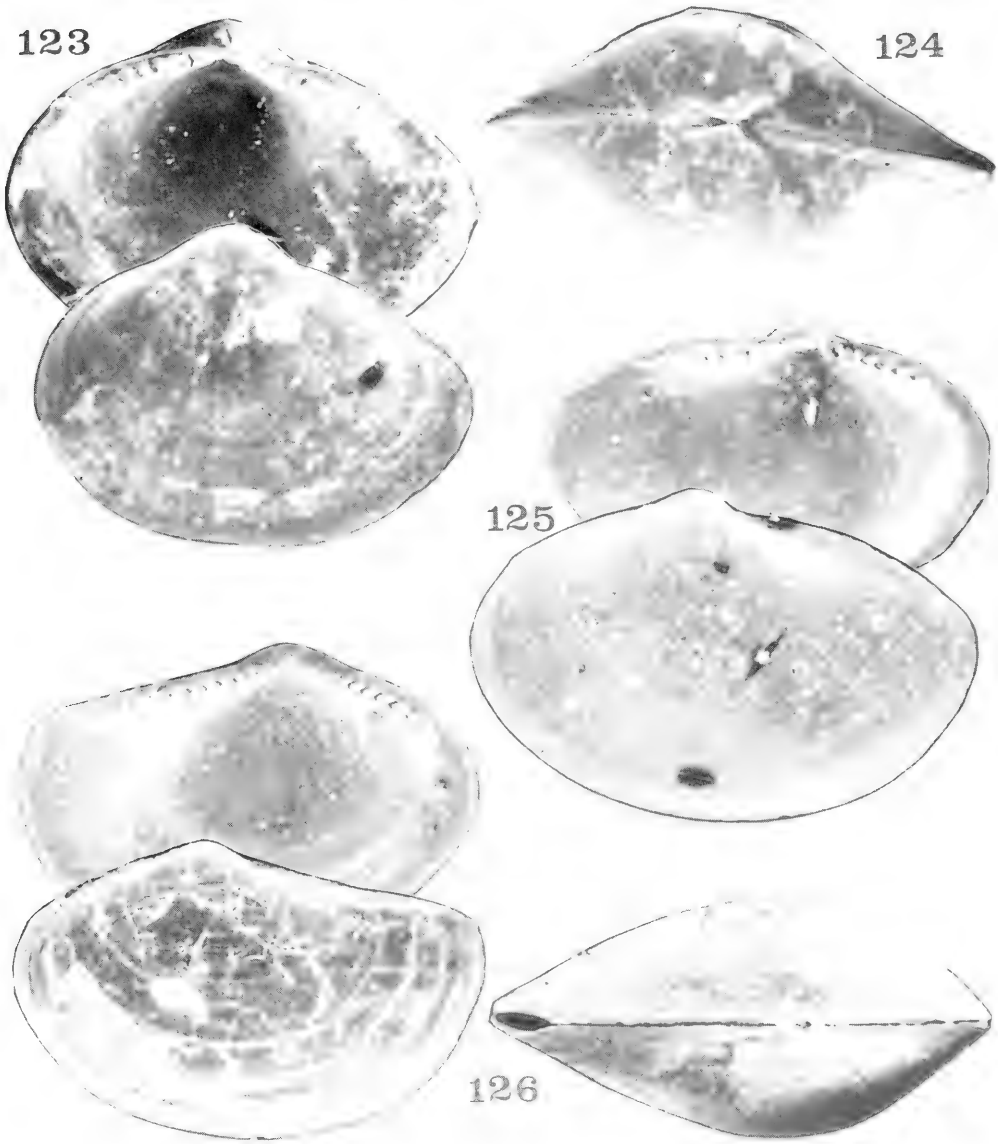


FIG. 123. *Yoldiella chilenica* Valva derecha e izquierda (MZUC 4633), 14X, Estrecho de Magallanes. Right and left valve (MZUC 4633), 14X, Magellan Strait.

FIG. 124. *Yoldiella chilenica* Vista dorsal (MZUC 4633), 12X, Bahía Corbeta Papudo. Dorsal view (MZUC 4633), 12X, Corbeta Papudo Bay.

FIG. 125. *Yoldiella ecaudata* Interior y exterior de valva izquierda (MZUC 4228), 17X y 26X, Isla Greenwich, Shetland del Sur. Interior and exterior of left valve (MZUC 4228), 17X and 26X, Greenwich Island, South Shetland.

FIG. 126. *Silicula rouchi* Interior y exterior de valva derecha (MZUC 4509), 17X y 15X, Estrecho de Bransfield. Interior and exterior of right valve (MZUC 4509) 17X y 15X, Estrecho de Bransfield. Vista dorsal (MZUC 4509), 15X, Estrecho de Bransfiel. Dorsal view (MZUC 4509), 15X, Bransfiel Strait.

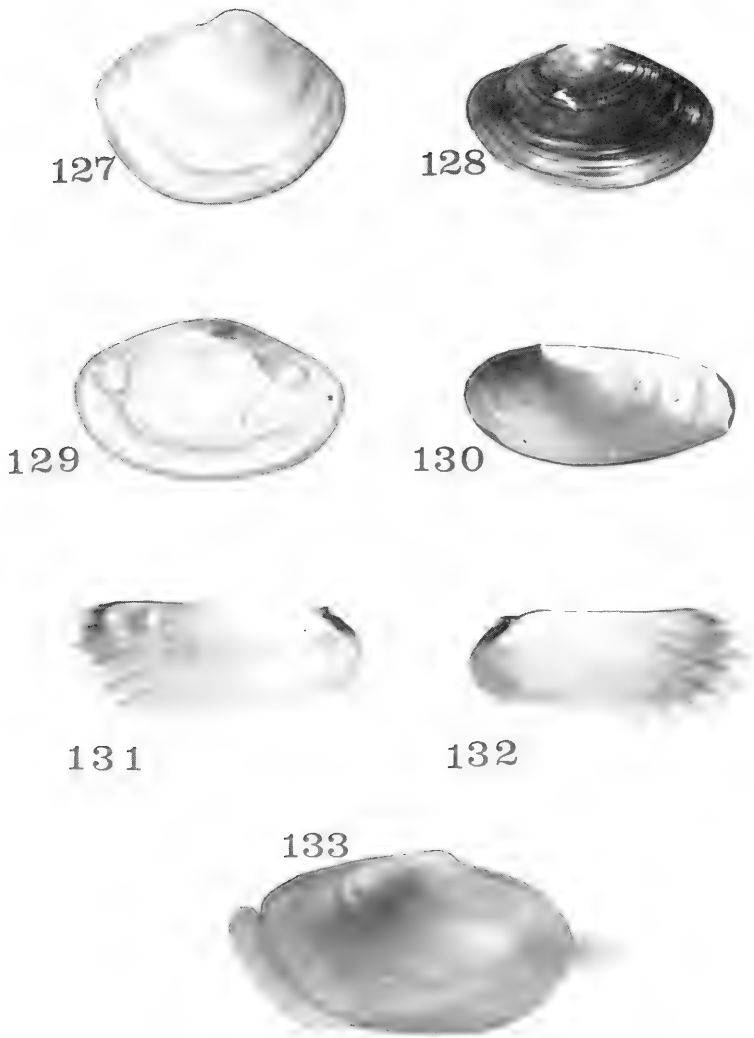


FIG. 127. *Yoldiella indolens* Valva derecha (MZUC 4520), 2 mm, Estrecho de Magallanes. Right valve (MZUC 4520), 2 mm, Magellan Strait.

FIGS. 128, 129. *Yoldia* (*Aequiyoldia*) *eightsi*

FIG. 128. Valva izquierda (MZUC 4503), 20.5 mm, Isla Decepción. Left valve (MZUC 4503), 20.5 mm, Decepción Island.

FIG. 129. Vista interna del mismo ejemplar. Internal view of same specimen.

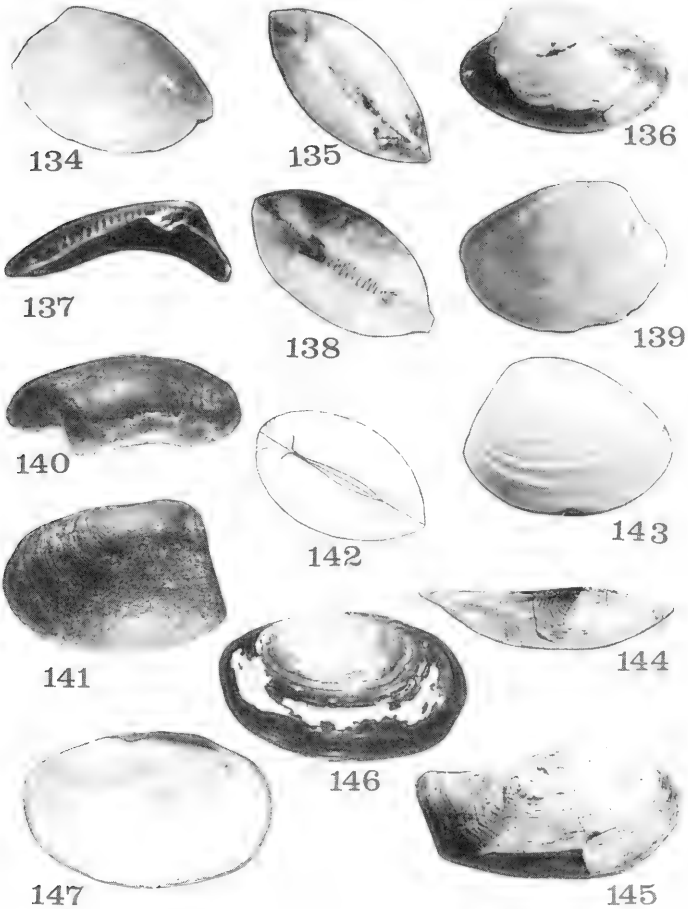
FIG. 130. *Silicula patagonica* Valva izquierda (MZUC 4659), 8 mm, Confluencia Canales Trinidad y Concepción. Left valve (MZUC 4659), 8 mm, Confluence of Trinidad and Concepción Channel.

FIGS. 131, 132. *Acharax* sp.

FIG. 131. Valva derecha (MZUC 4613), 8.1 mm, Canal Sarmiento. Right valve (MZUC 4613), 8.1 mm, Sarmiento Channel.

FIG. 132. Vista interna del mismo ejemplar. Internal view of same specimen.

FIG. 133. *Malletia chilensis.* Vista de un ejemplar con las partes blandas (MZUC 4707), 30 mm, Bahía de Concepción. Specimen with soft parts (MZUC 4707), 30 mm, Concepción Bay.



FIGS. 134–137. *Ennucula valdiviana.*

FIG. 134. Valva derecha (MV/1), 19.5 mm, Tubul. Right valve (MV/1), 19.5 mm, Tubul.

FIG. 135. Vista dorsal (T/13), 17 mm, Tubul. Dorsal view (T/13), 17 mm, Tubul.

FIG. 136. Vista lateral del ejemplar anterior. Lateral view of same specimen.

FIG. 137. Vista de la charnela del ejemplar de Fig. 134. Hinge of specimen in Fig. 134.

FIGS. 138, 139. *Ennucula lebuensis.*

FIG. 138. Vista lateral de un molde interno (T/19), 19 mm, Tubul. Lateral view of internal mold (T/19), 19 mm, Tubul.

FIG. 139. Vista dorsal del mismo. Dorsal view of same mold.

FIGS. 140, 141. *Ennucula ¿nogalis?*

FIG. 140. Vista dorsal de una valva izquierda (V/132), 15 mm, Lo Valdés. Dorsal view of left valve (V/132), 15 mm, Lo Valdés.

FIG. 141. Vista lateral de la valva anterior. Lateral view of same valve.

FIGS. 142, 143. *Ennucula araucana.*

FIG. 142. Esquema de una vista dorsal. Drawing in dorsal view.

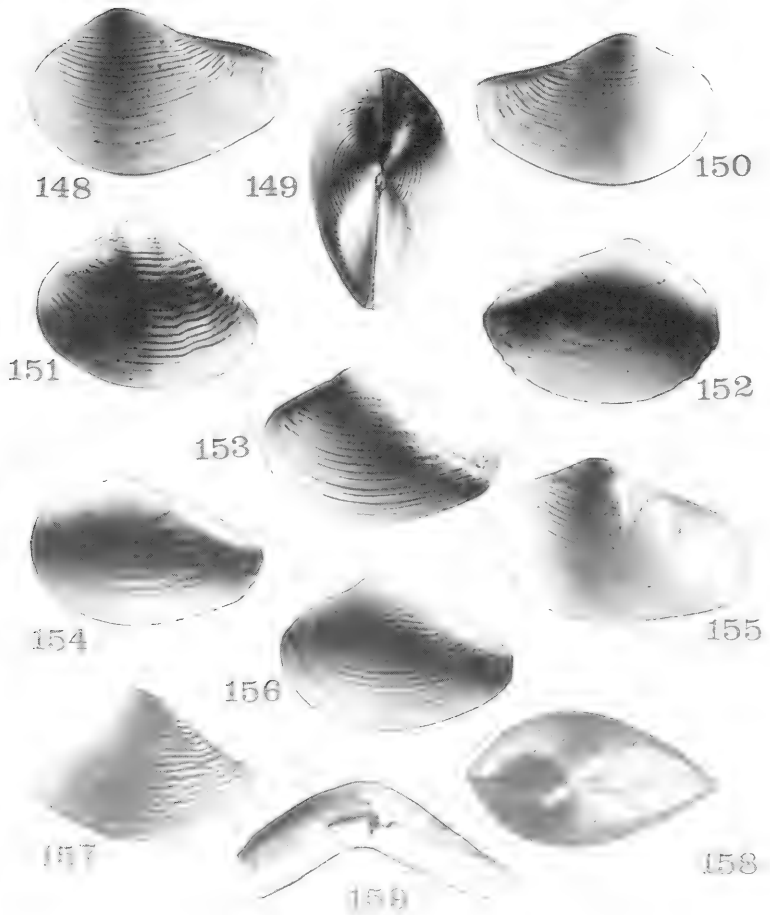
FIG. 143. Valva derecha (T/16), 17 mm, Tubul. Right valve (T/16), 17 mm, Tubul

FIGS. 144, 145. *Malletia* (*Neilo*) *volckmanni.*

FIG. 144. Vistas dorsal (N/I), 46 mm, Navidad. Dorsal view (N/I), 46 mm, Navidad.

FIG. 145. Vista lateral del mismo ejemplar. Lateral view of same specimen.

FIGS. 146, 147. *Malletia chilensis.* Vista lateral e interna de la valva izquierda (MZUC 4733), 26 mm, Bahía Valparaíso. Lateral and interior view, left valve (MZUC 4733), 26 mm, Valparaíso Bay.



FIGS. 148–156. *Tindariopsis elegans*.

FIG. 148. Valva izquierda (T/2), Tubul. Left valve (T/2), Tubul.

FIG. 149. Vista dorsal (T/1), 11 mm, Tubul. Dorsal view (T/1), 11 mm. Tubul.

FIG. 150. Valva derecha (T/3), 11 mm, Tubul. Right valve (T/3), 11 mm, Tubul.

FIG. 151. Valva izquierda (T/1), 10.5 mm, Tubul. Left valve (T/1), 10.5 mm, Tubul.

FIG. 152. Valva derecha (T/12), 8 mm, Tubul. Right valve (T/12), 8 mm, Tubul.

FIG. 153. Valva izquierda (T/1), 9 mm, Tubul. Left valve (T/1), 9 mm, Tubul.

FIG. 154. Valva izquierda (T/3) 10 mm. Tubul. Left valve (T/3), 10 mm, Tubul.

FIG. 155. Valva izquierda (T/8). 13.5 mm, Tubul. Left valve (T/8), 13.5 mm, Tubul.

FIG. 156. Valva izquierda (T/1). 8.5 mm, Tubul. Left valve (T/1), 8.5 mm, Tubul.

FIGS. 157–159. *Tindariopsis sulculata*.

FIG. 157. Vista lateral (MZUC 4631), 8 mm, Estrecho de Magallanes. Lateral view (MZUC 4631), 8 mm, Magellan Strait.

FIG. 158. Vista dorsal del mismo ejemplar. Dorsal view of same specimen.

FIG. 159. Vista de la charnela (MZUC 4631), 10 mm, Estrecho de Magallanes. Hinge (MZUC 4631), 10 mm, Magellan Strait.

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THE LAND SNAIL FAUNA OF A SQUARE KILOMETER PATCH OF RAINFOREST IN SOUTHWESTERN CAMEROON: HIGH SPECIES RICHNESS, LOW ABUNDANCE AND SEASONAL FLUCTUATIONS

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ABSTRACT

Systematic sampling of a single square km patch of rather acidic, undisturbed, fairly uniform Cameroonian rainforest during two different rainy seasons yielded 97 species of land snails, belonging to at least 12 families. Up to 45 species were collected within a single sampling site of 20 m × 20 m during a single visit, and up to 51 during two visits in different seasons. This might be the world's highest sympatric land snail diversity reported to date. Variation in species composition among the sampling sites appeared to be largely random, and not due to geographic or ecological replacement. Three (super)families make up 86% of the species, the carnivorous Streptaxidae (34%) being the most diverse. Overall snail abundance was rather low, and many species were rare. Of 64% of the species, the abundance was less than 1% of all specimens (2,654) collected. A substantial difference was observed in overall snail abundance between the two sampling periods. About 27% of the species were uniquely found in one of the two sampling periods, and many species differed more than 50% in relative abundance between these seasons. At least 27% of the species were largely or completely arboreal, and 19% were found to live both on the ground and in the vegetation; 46% of the species appear to be confined to the ground, and of 7% insufficient information was available. Major adult shell dimensions (height or diameter) range between approximately 1 and 165 mm, but the vast majority (74%) of species has adult shells smaller than 10 mm. The shell height:diameter ratio distribution is bimodal, but differs from those previously reported for other faunas by relatively many "globose" (H/D 0.8–1.2) and very tall (H/D 2.8–4.4) shells. The distribution of neither shell size nor shell shape differed between ground-dwelling and (partly) arboreal species.

Key words: Gastropoda, Africa, species diversity, biodiversity, species abundance, shell size, shell shape, vertical distribution, seasonal variation.

INTRODUCTION

Tropical rainforests in Africa and elsewhere are severely threatened by commercial timber logging and both slash-and-burn and cash crop agriculture. Huge areas of forest have already been degraded or have disappeared before information could be obtained about their biodiversity and ecology. Originally, closed forests covered large parts of Cameroon. During the period 1980–1990 approximately 140,000 ha (0.6%) were destroyed or degraded annually, and some 40% of the original forest cover now remains (Dixon et al., 1996). In view of the poor economic conditions of the country, there seems to be little hope that this trend will change in the near future. Detailed data on the biodiversity and ecology of undisturbed forest faunas are therefore urgently needed. This information would enable comparisons with various types of degraded forest, enabling, for example, conservation planning and evaluation of the usefulness of future reforestation from the viewpoint of biodiversity restoration. The lack of knowledge of the effects of disturbance on biodiversity is most apparent for invertebrates, including gastropods.

Land snails are a poorly studied group in tropical forests, including those of western Africa. Mainly on the basis of tentative ecological reasoning, Solem (1984) asserted that in rainforests land snails are "generally neither diverse nor abundant." Recent studies have challenged the universality of this statement with respect to species diversity (De Winter, 1992, 1995; Emberton, 1995; Tattersfield, 1996).

The present study describes the land snail diversity in a single square km patch of undisturbed rainforest in southwestern Cameroon in some detail, in order to obtain baseline data

for future research in this and other tropical forest regions. Data from disturbed forests in this region will be given in additional papers.

This study is carried out within the framework of the Tropenbos Cameroon Programme (TCP), which was established in 1992 by the Cameroonian Ministry of Environment and Forests (MINEF) and the Dutch Tropenbos Foundation. The general objective of this multidisciplinary programme is to develop methods and strategies for the management of natural forests enabling sustainable, that is, ecologically sound, socially acceptable, and economically viable, production of timber and other products and services (Foahom & Jonkers, 1992). The TCP study area (Fig. 1) covers 1916 km^2, and coincides with two adjacent concessions of a Dutch timber company.

THE STUDY AREA

The 1 km × 1 km patch of undisturbed rainforest studied ("block i2", as indicated on the prospection map of the timber company) is located about 15 km S of Lolodorf (about 3°06′N, 10°44′E; Figs. 1, 2). Block i2 comprises the relatively low and flat southwestern part of the so-called Biboo-Minwo catchment, a study region of c. 7.7 km^2 with an altitude between about 420 and 720 m located in the transition zone between the western lowlands and the eastern, more mountainous, part of the TCP area (Waterloo et al., 1997). Within block i2, elevations range from approximately 420 m in the western and central parts to approximately 480 m in the eastern fringes.

The geology reflects the erosion of the Precambrian shield, the region being dissected by streams and small rivers into undulating plains and remaining hills with bedrock consisting of acid gneisses. The soils are moderately to well drained, with clay and sand contents of about 35% and 45% in the topsoil (upper 0–10 cm), respectively. The topsoil is poor in nutrients (total nitrogen 0.25–0.5%, organic carbon 4–8%, available phosphorous 12–26 ppm), and very strongly to extremely acidic, with pH(H_2O) between 5 and 3.5 (Van Gemerden & Hazeu, in press). Small to very large (up to 5 m high), flat-topped rock outcrops mainly occur in the eastern and southwestern parts of block i2.

Southwest Cameroon forms part of the Guineo-Congolian domain of dense and humid evergreen rainforests. The study site lies within the Biafran Atlantic district, the flora of which is rich in Caesalpiniaceae (Letouzey, 1985). In these forests, four vegetational layers can be distinguished, with gradual transitions. The crowns of the emergent trees, sometimes surpassing 60 m in height, constitute the highest level and cover 20–30% of the ground surface. Canopies of mature trees of 25–40 m high form the second layer, covering 60–80% of the floor surface. The third layer of shrubs and small trees may reach 3–6 m, and the remaining layer of herbs is less than 1 m high. The foliage of the latter two layers covers 40–60% of the floor surface. Lianas are abundant in the canopy and in natural gaps.

The vegetation of the region, including that of block i2, may be classified as very old secondary forest, with perhaps true virgin forest on the steeper hill slopes (Van Gemerden & Hazeu, in press). The sheer size of the trees indicates that it has been left in peace for some centuries. According to Letouzey (1968) the region was subjected to extensive forest clearing by man in the 18th century. Letouzey's (1968) conclusion was based on historical research, as well as on the common occurrence of the tree *Lophira alata* ("Azobé"), the seeds of which germinate best under light conditions. His view seems to be in agreement with the presence in block i2 of a few truly giant *Ceiba pentandra* (with buttresses about 7 m wide), a tree more typical of young secondary forests and arable land. Preliminary data of M. P. M. Parren (pers. comm.) show a substantial tree diversity (diameter at breast height >10 cm) of about 125 species ha^{-1}. The area is relatively rich in valuable timber species, of which especially *Lophira alata* and others such as *Pterocarpus soyauxii* ("Padouk") and *Entandrophragma utile* ("Sipo") are exploited.

The climate is equatorial. The area receives about 2,100 mm precipitation annually, with distinctly wet periods in September-November and in April-May. There is a relatively dry period between December and March, when the monthly rainfall is well below 100 mm. Mean maximum daily precipitation is as high as 115 mm. Relative humidities are high throughout the year, with mean minimum and maximum monthly values of about 70% and 96%, respectively. The air temperature is little variable over the year (mean 24.6°C), with minimum monthly values of approximately 23°C in August and maximum values of approximately 26°C in March. The wind direction is predominantly W-SW, and wind speeds are generally low (less than 4 m s^{-1}); high wind

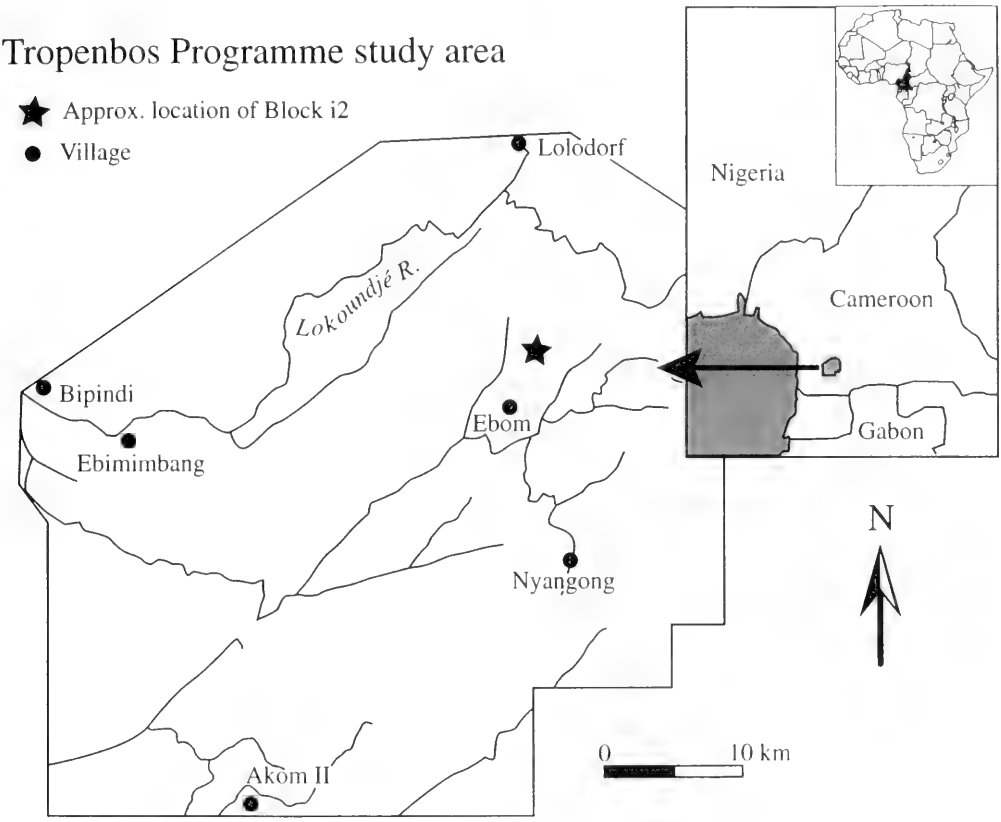

FIG. 1. The location of the square km forest site studied ("block i2") within the area covered by the Tropenbos Cameroon Programme.

speeds can occur during thunderstorms (climatic data, partly extrapolated, from Waterloo et al., 1997).

Although there is variation among the sites sampled in such characteristics as slope inclination and exposition, presence or absence of rock outcrops, and tree species, the overall nature of block i2 appeared to be fairly homogeneous: rivers are less than 5 m wide, and altitude differences are 60 m at most. During the first visit in 1995, the area was still virtually undisturbed, and the canopy closed, except for some natural gaps. However, in February/March 1996 most of the region, including block i2, was selectively logged with an intensity of about 1 tree ha^{-1}. Since the logging activities took place shortly before or during this visit, we assumed that logging could not yet have affected our results, especially since disturbed sites were avoided.

MATERIAL AND METHODS

Sampling

Sampling took place in two periods, August 29–October 6, 1995, and March 21–April 12, 1996, further referred to as "1995" and "1996." Each sampling period was early in one of the two rainy seasons.

Collections were made within patches of 20 m × 20 m that were marked with poles (called "sampling sites", "stations", or "plots" in this paper). Stations on rock boulders were considerably smaller than 20 m × 20 m. In all sites, the actual ground surface thoroughly sampled covered only a small part of the entire site.

In each sampling site, the forest floor was searched for 60 min. In this period samples of leaf-litter and a few mm of topsoil were also taken from several microhabitats that seemed

to be favourable for snails, such as beside logs and between roots of trees where dead organic material accumulates. Approximately four litres of litter from each station were sieved in a large cotton bag in which half way down a sieve of 15 mm mesh was secured. The coarse material was searched for larger species on the spot (in small portions on a plate), and the material that passed the sieve was bagged and dried. The volume of the bagged litter varied substantially, depending on the amount of decomposed matter relative to intact surface leaves and twigs on the forest floor. Litter on top of the rock boulders was often more decomposed and contained more humus than that on the forest floor proper.

At many sampling plots, the understorey vegetation (about 3/4 m to 3 m high) was systematically beaten over an open, inverted umbrella. The snails spotted in the umbrella were picked out, and the remaining leaves, twigs and fine material were bagged for later examination. In addition, the trunks of trees were carefully searched for about 30 min. The floor was searched by the senior author, whilst the understorey vegetation and tree trunks were generally sampled by E.-J. Semengue, a well-trained and dedicated local worker.

Because there is only low, herbaceous vegetation on the horizontal top surface of the rock boulders, both persons engaged in hand picking and litter sampling on the rock surface for 60 min. Also some non-boulder sites were incompletely (only the floor or the vegetation) sampled due to various logistic reasons (Table 1). In principle, sites visited in 1995 were sampled again in 1996. However, due to logging activities in 1996 a number of sites sampled in 1995 were disturbed, and new plots were chosen. The exact boundaries of a previously visited plot were not always easy to determine, because the demarcation poles had been removed after the first visit. In order to emphasize that the position of a plot visited for the second time is likely to deviate somewhat from that during the first visit, each sample was given a unique station number. In 1995, 16 sites were studied (including those on rock boulders), whilst 20 sites (including the ones sampled also in 1995) were visited in 1996. The approximate location of the sampling plots is indicated in Figure 2. Table 1 provides details of each station.

In addition, snail shells were extracted from eight litter samples taken for hydrological studies in May 1996 and kindly provided by M. Ruppert. Each of these samples consisted of all the leaf-litter present on a floor surface quadrate of 50 cm × 50 cm. The quadrates were placed randomly with respect to litter quantities within a flat patch of 50 m × 50 m forest floor, but spots with larger pieces of dead wood were avoided. The litter was dried in a stove, passed through a 15 mm mesh sieve, and the snails from the coarse fraction were removed. The fine fraction was retained and further dealt with as described below.

Analysis of Samples

Some months after collecting, the volume of the retained fraction of the floor and boulder litter samples was measured. Then the litter was passed through three sieves (5 mm, 2 mm, and 0.5 mm). The finest fraction was discarded after the first three bags were examined, because it proved to contain no molluscs. From the coarse fraction snails were picked out by eye, whilst the remaining fractions were systematically searched in small portions under a stereo-microscope.

The bagged material from the vegetation was treated in the same manner, but the volume was not measured.

Because of the considerable time interval between collecting and searching of the floor litter samples, the distinction between empty shells and shells that contain a dried-in animal proved to be difficult, especially because occasionally live specimens were observed with strongly eroded shells. In this hot, humid and acidic environment the decomposition of most empty shells (the heavy ones of some Achatinidae perhaps excluded) probably takes less than two months (De Winter, unpublished observations). We therefore decided not to distinguish between live specimens and empty shells in most of the analyses of species diversity and abundance. The relatively few snails spotted in the field were included in the data obtained from the litter, since direct searching took place at the same spots where the litter samples were taken. All snails encountered alive were preserved in ethanol in order to obtain material for future anatomical studies; this collection also served to infer information on the species' preferred habitat.

The snails collected from the tree-trunks proved to belong to the same species as those collected from the understorey vegetation, and were therefore added to these.

In the field no empty shells were found in the vegetation, probably because deceased animals will usually drop to the floor. Virtually

TABLE 1. Annotated list of sampling sites, with station number, date, type(s) of habitat sampled (B, boulder; F, floor; V, vegetation), altitude (in m above sea level), topography, direction of exposition, presence of bare rock (0, none; 1, few minor rocks; 2, large boulders), litter volume (in cc, remaining of 4 litres of litter that passed a 1.5 cm-mesh sieve), as well as numbers of specimens (Nspm) and species (Nspp) in the various habitat types and in total.

Station	Date	Habitat	Alt.	Topogr.	Exp.	Rock	Litter vol.	Nspm (Total)	Nspm (F)	Nspm (V)	Nspp (Total)	Nspp (F)	Nspp (V)	Remarks
007	29/8/95	F	420	flat	—	0	900	21	21	—	9	9	—	
008	29/8/95	F,V	430	faint slope	W	0	1100	102	97	5	31	28	6	large rotting log, old gap
009	30/8/95	F	410	valley	—	0	1000	51	51	—	13	13	—	riverine forest
010	30/8/96	F,V	410	valley	—	0	1500	113	91	22	31	23	12	riverine forest
011	30/8/97	F,V	430	upper slope	N	0	700	39	27	12	21	13	8	steep slope towards stream
012	31/8/95	F,V	420	lower slope	NNE	1	1100	72	47	25	31	16	17	dynamic forest on steep slope
013	31/8/95	B	420	valley	—	2	2100	130	—	—	31	—	—	3–4 m high boulder along stream, top surface sampled 4 × 3.5 m
014	31/8/95	B	470	upper slope	—	2	1900	65	—	—	26	—	—	3–4 m high boulder, top surface sampled 5 × 3 m
015	31/8/95	F,V	470	ridge	—	0	600	30	29	1	14	14	1	
017	19/9/95	B	480	ridge	—	2	1500	71	—	—	29	—	—	3–4 m high boulder, top surface sampled 5 × 3 m, partly sun-exposed
018	19/9/95	F, V	470	upper slope	N	1	2000	135	126	9	22	18	6	
019	20/9/95	F, V	480	upper slope	NNW	1	1400	78	69	9	35	29	8	rel. sparse understorey vegetation
020	20/9/95	B	480	ridge	—	2	1500	103	—	—	26	—	—	3–4 m high boulder, top surface sampled 4 × 4 m, partly sun-exposed
022	21/9/95	F, V	420	flat	—	1	1550	257	61	196	45	28	28	approx. 20 m from gap; dense understory vegetation
024	22/9/95	V	460	gentle slope	N	0	—	31	—	31	14	—	14	due to heavy rain only vegetation sampled
039	6/10/95	F, V	420	flat	—	0	900	64	20	44	20	7	16	

(*continued*)

TABLE 1. (*Continued*)

Station	Date	Habitat	Alt.	Topogr.	Exp.	Rock	Litter vol.	Nspm (Total)	Nspm (F)	Nspm (V)	Nspp (Total)	Nspp (F)	Nspp (V)	Remarks
055	21/3/96	F, V	470	ridge	—	1	1800	38	27	11	13	10	4	
056	21/3/96	B	470	ridge	—	2	2200	34	—	—	15	—	—	same as sta014
058	22/3/96	F	420	valley	—	0	2100	39	39	—	13	13	—	
059	26/3/96	F, V	480	upper slope	NNW	1	3100	100	68	32	40	37	13	same as sta017
060	26/3/96	B	480	ridge	—	2	1450	41	—	—	16	—	—	same as sta020
061	26/3/96	F, V	460	upper slope	N	1	2550	131	108	23	34	29	10	
062	27/3/96	F, V	410	valley	—	0	1975	76	39	37	30	20	15	same as sta010
063	27/3/96	F, V	420	lower slope	NNE	1	1525	66	44	22	37	28	12	same as sta012
064	27/3/96	B	420	valley	—	2	1700	104	—	—	22	—	—	same as sta013
065	28/3/96	F, V	420	slope	E	1	1550	67	62	5	31	27	4	rocky slope 10 m from natural gap
067	28/3/96	F, V	420	flat	—	0	700	22	11	11	14	9	5	same as sta039
068	4/01/96	F, V	420	flat	—	0	1800	78	38	40	29	20	10	
072	4/03/96	F, V	420	gentle slope	—	0	2100	73	32	41	20	12	9	
073	4/03/96	F, V	430	lower slope	N	0	3200	100	59	41	27	21	9	low understory vegetation; thin litter layer
074	4/04/96	F, V	420	undulating/ flat	—	0	1425	52	30	22	19	12	8	
075	4/4/96	F, V	420	flat	—	0	2250	99	63	36	32	22	12	
076	9/4/96	F, V	430	faint slope	—	0	1100	41	22	19	21	13	10	same as sta008
079	10/4/96	F, V	430	faint slope	—	0	1200	24	11	13	9	6	4	
082	12/4/96	F, V	420	flat	—	0	1250	67	32	35	26	15	11	
083	12/4/96	F, V	420	flat	—	0	1000	40	35	5	21	18	4	dense understorey vegetation; giant *Ceiba* tree

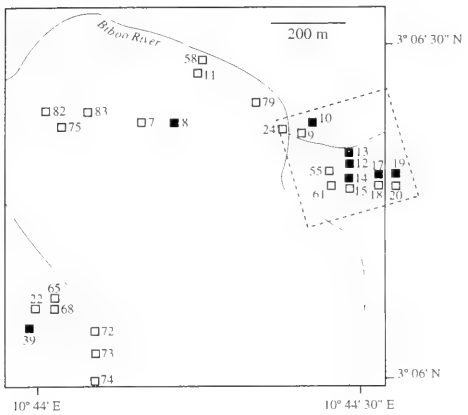

FIG. 2. The approximate location of the sampling sites within the square km forest area studied. Open squares: sites sampled once, either in 1995 or 1996; closed squares: sites sampled in both years. See Table 1 for further details. The dashed line indicates the boundaries of a 9 ha plot used for forestry studies.

all shells extracted from the vegetation litter samples were in a fresh condition and presumably caught alive.

Although in some groups (e.g., most Streptaxidae), it is possible to distinguish between adult and juvenile shells by the morphology of the aperture, most species encountered have an undetermined shell growth, and many can reproduce before reaching their maximum shell size (e.g., Subulinidae). Therefore, we did not distinguish between adult and juvenile specimens in the analyses.

Analysis of Diversity Patterns

The study is of a qualitative rather than a quantitative nature. Although searching time was standardized, and sampling took place within sites not exceeding 0.04 ha, results from different sites are not directly comparable for various reasons. Firstly, due to the heterogeneous structure of the environment, floor litter sampling was not at random, but concentrated on spots that, subjectively, seemed to be favourable for land snails. Secondly, in view of the small overall number of specimens found, and the high proportion of rare species, the presence or absence of many species often seemed to be of a stochastical rather than a systematic nature. Thirdly, numbers of live specimens obtained, especially of arboreal species, often varied greatly between days, and even within days. This seemed to be due to variation in climatic conditions, especially humidity and temperature, rather than to ecological differences between sites. Differences in circadian activity patterns of the species may also have had an effect; nocturnal species are more likely to be found early in the morning. In view of these limitations, elaborate statistical analyses of our data with respect to both species composition and abundance appeared to be of little value. However, data were sufficient to detect some general trends.

The measures of diversity used in this study are overall species richness (S), and Whittaker's index I, which is the total number of species recorded (S) divided by the mean number of species per site (α), providing a measure of diversity difference among sites (Magurran, 1988; Cameron, 1992). If I equals 1, sites have identical faunas, and higher values indicate increasing differentiation. High values of I can result from geographical or ecological replacement of taxa, or from chance effects due to sampling error. These patterns can be distinguished by comparing the variance of sites per species to the maximum variance possible for the same values of S and α, as explained in Cameron (1992). If the achieved variance is low, replacement effects will be more important than chance effects, and vice versa.

Identification and Taxonomy

The vast majority of the species were classified according to shell characters only, except for the urocyclid slug-like taxa (*Zonitarion, Verrucarion*), of which one adult specimen per sample, if available, was dissected. This means that the estimates of the numbers of species might be conservative; additional cryptic species may be present, especially among the shelled Urocyclidae. In view of the small size and overall homogeneous nature of the area studied, it seems improbable that the number of species was overestimated as the result of intraspecific variation in shell characters.

The taxonomy and distribution of most land snails in Cameroon and elsewhere in western Africa are poorly known. Most names used in this study are provisional. The use of "cf." in a name merely serves to point out a resemblance to a described species. Virtually all juvenile shells could be assigned to a species

by careful comparison of spire dimensions and sculpture, especially of the embryonic whorls. A few juvenile shells that could not be matched with adult specimens of species already recognised were treated as separate species. Most species were assigned to known genera, but it should be kept in mind that many of these probably comprise a heterogeneous assemblage of species that are more or less similar in shell characters. The anatomy of species described from western Africa, including type species of genera, is generally not or insufficiently known.

RESULTS

Faunal Composition

Table 2 lists the 97 species recognised in this study, 34 of which are probably previously described, 22 seem to be new to science, and 41 are of unclear status. A substantial portion of the latter group might be undescribed as well. The distributions of all 34 described species, as well as of a fair number of the remaining ones, extend well beyond the Biboo-Minwo region.

The species found in this study belong to at least 12 families, two of which are Prosobranchia Mesogastropoda, the remaining Pulmonata (Soleolifera and Stylommatophora) (Table 3). The family assignment of some species is at best tentative in the absence of anatomical data.

The fauna is dominated by three (super)-families, the Streptaxidae (33 species), the Achatinoidea (27 species, the majority being subulinids), and the Helicarionoidea (23 species). Together they constitute 86% of the species observed. The Streptaxidae are carnivores, the other two are vegetarians *sensu lato*, as far as is known.

Streptaxids were both surprisingly speciose and abundant, comprising 33 (34%) of the species observed and 29% of all individuals collected. *Gulella (Paucidentina)* sp. 1 was the most common species in this study, contributing about 10% of all specimens found and present in virtually all sites. Streptaxidae were comparatively less diverse and less abundant in the collections from the vegetation (25% of the species, 18% of the individuals) than in those from the forest floor (35% of the species and 33% of the individuals).

Species Diversity and Abundance

Of the 97 species recorded from the entire 100 ha area, 80 were found in 1995, nine of which were not encountered again in 1996. Of the 88 species observed in 1996, 17 were not found in 1995. High species richness was also found in smaller areas. An intensively studied subarea of 300 m × 300 m (13 sites sampled, 6 of which sampled in both seasons; Fig. 2), one of several 9 ha plots marked in the field for forestry studies and used by us for orientation, yielded 83 species, 67 of which were obtained in 1995, and 74 in 1996.

Species diversity and abundance data of the sampling sites are summarized in Table 1. The complete data table of the species and numbers of specimens per station will be deposited in the archives of the National Museum of Natural History, Leiden. The highest diversity found during a single visit (in 1995) of a 20 m × 20 m sampling site (Sta022) was 45 species, which represents 56% of all species found in 1995 and 46% of the total fauna observed in both seasons. Unfortunately, this site was disturbed in 1996 and could not be resampled. Instead, a seemingly similar site approximately 25 m to the east (Sta068) was sampled; together these two sites yielded 57 species, or 59% of the total number of species observed in block i2. The "revisited" stations comprised five plots, of which both the floor and the vegetation were sampled, and three rock boulder sites (Table 1, Fig. 2). The total number of species found during both sampling periods varied between 27 and 51 (mean 42.2) species among the floor-plus-vegetation plots, and between 29 and 39 (mean 33.3) species among the boulder sites.

The diversity patterns were quantitatively analysed for stations of which both the floor and the vegetation were sampled, as well as for collections from the major habitat types (floor, vegetation, rock boulders) separately (Table 4).

The floor-plus-vegetation sites (eight in 1995, 16 in 1996, including five "revisited" plots) yielded 95 of the 97 species observed (76 in 1995, 86 in 1996). For both years, the Whittaker's index *I* indicates substantial variation in species diversity between the stations. The proportion of the maximum possible variance achieved for stations per species was not indicative of significant replacement of species (cf. values given in Cameron, 1992; Tattersfield, 1996). Whittaker's index values

TABLE 2. List of 97 land snail species recorded in one square km of rainforest in SW. Cameroon, with numbers of specimens collected in 1995 and 1996. Species are ordered according to total number of specimens collected. Tentative type of habitat (vertical distribution) is indicated as A (arboreal), F (floor-dwelling), I ("indifferent") or ? (unknown). In the absense of anatomical data for most species, the Charopidae/Punctidae are united in the superfamily Punctoidea, the Subulinidae/Ferussaciidae are grouped with the Achatinidae in the Achatinoidea, and the Euconulidae, Urocyclidae and related (sub) families in the Helicarionoidea. If possible, the tentative family assignment is also indicated.

SPECIES	FAMILY	Number 1995	Number 1996	Total	Habitat
Gulella (*Paucidentina*) sp. 1	Streptaxidae	142	128	270	F
Pseudopeas sp. 2	Achatinoidea/Subulinidae	93	61	154	F
Trochozonites cf. *pilosus* d'Ailly	Helicarionoidea/Urocyclidae	91	40	131	I
Zonitarion semimembranaceus (Martens)	Helicarionoidea/Urocyclidae	71	47	118	A
Afropunctum sp.	Helicarionoidea/Euconulidae	43	72	115	A
Dictyoglessula sp.	Achatinoidea/Subulinidae	54	52	106	F
Philalanka cf. *delicatula* Thiele	Punctoidea	20	62	82	A
Pseudopeas sp. 3	Achatinoidea/Subulinidae	31	48	79	A
Trochozonites sp. 2	Helicarionoidea/Urocyclidae	15	63	78	A
Thapsia cf. *troglodytes* (Morelet)	Helicarionoidea/ Urocyclidae	42	30	72	I
Gulella bolocoensis Ortiz & Ortiz	Streptaxidae	38	26	64	F
Cyathopoma n.sp.	Cyclophoridae	48	14	62	F
?Endodontoid n.gen. n.sp. 2	Punctoidea	32	30	62	F
Kaliella sp.	Helicarionoidea/Euconulidae	39	23	62	I
Trochozonites cf. *bifilaris* (Dohrn)	Helicarionoidea/Urocyclidae	36	14	50	I
Gulella feai Germain	Streptaxidae	35	14	49	F
Nesopupa bisulcata (Jickeli)	Vertiginidae	26	20	46	F
Curvella sp. 1	Achatinoidea/Subulinidae	27	13	40	F
Ptychotrema (*Ennea*) *silvatica* Pilsbry	Streptaxidae	28	12	40	F
Ischnoglessula sp. 1	Achatinoidea/Subulinidae	20	17	37	I
Pseudopeas sp. 1	Achatinoidea/Subulinidae	16	21	37	I
Pileata sp. 1	Achatinoidea/Subulinidae	9	25	34	F
Gulella (*Avakubia*) *acuminata* Thiele	Streptaxidae	12	22	34	A
Pseudoglessula sp.	Achatinoidea/Subulinidae	13	20	33	F
Curvella sp. 2	Achatinoidea/Subulinidae	12	21	33	F
Trochozonites sp. 4	Helicarionoidea/Urocyclidae	25	8	33	F
Achatina iostoma (Pfeiffer)	Achatinoidea/Achatinidae	28	2	30	I
Micractaeon koptawelilense (Germain)	Achatinoidea/? Ferussaciidae	9	21	30	F
Gudeella' sp. 1	Helicarionoidea/Urocyclidae	5	25	30	I
Maizaniella (*Spirulozania*) n.sp.	Maizaniidae	14	15	29	F
Gulella (*Pupigulella*) *pupa* Thiele	Streptaxidae	15	14	29	I
Subulona sp.	Achatinoidea/Subulinidae	9	19	28	F
Streptostele sp. 3	Streptaxidae	10	14	24	F
Ptychotrema (*Ennea*) cf. *aillyi* Adam	Streptaxidae	7	16	23	A
Afroguppya sp. 1	Helicarionoidea/Euconulidae	14	9	23	F
Ischnoglessula sp. 2	Achatinoidea/Subulinidae	15	7	22	A
Gulella (*Avakubia*) cf. *avakubiensis* Pilsbry	Streptaxidae	11	11	22	A
Ptychotrema cf. *columellaris* (Martens)	Streptaxidae	11	10	21	F
Aillya sp. 1	Aillyidae	20	1	21	F
Maizaniella (*Macromaizaniella*) *preussi* (Martens)	Maizaniidae	12	8	20	F
Gulella cf. *suturalis* Degner	Streptaxidae	9	10	19	A
Ptychotrema (*Excisa*) *duseni* (d'Ailly)	Streptaxidae	4	15	19	F
Aillya sp. 2	Aillyidae	19	0	19	F
Ptychotrema (*Ennea*) cf. *perforatum* (d'Ailly)	Streptaxidae	10 8	8 10	18 18	I A
Edentulina liberiana (Lea)	Streptaxidae	4	12	16	F
Gulella (*Costigulella*) n.sp.	Streptaxidae	12	4	16	I
Prositala cf. *butumbiana* (Martens)	Punctoidea				

(*continued*)

TABLE 2. (*Continued*)

SPECIES	FAMILY	Number 1995	Number 1996	Total	Habitat
?Endodontoid n.gen. n.sp. 1	Punctoidea	7	8	15	F
Afroguppya sp. 2	Helicarionoidea/Euconulidae	5	10	15	F
Trochozonites sp. 7	Helicarionoidea/Urocyclidae	8	6	14	A
Trochozonites sp. 8	Helicarionoidea/Urocyclidae	6	7	13	A
Gulella (*Avakubia*) n.sp.	Streptaxidae	4	8	12	A
Trochozonites sp. 1	Helicarionoidea/Urocyclidae	11	1	12	A
Callistoplepa shuttleworthi (Pfeiffer)	Achatinoidea/Achatinidae	5	6	11	I
Gulella (*Conogulella*) sp.	Streptaxidae	3	8	11	I
Streptostele sp. 2	Streptaxidae	4	7	11	F
Pupisoma sp.	Vertiginidae	3	7	10	I
Gulella cf. *germaini* Connolly	Streptaxidae	0	9	9	F
Streptostele sp. 1	Streptaxidae	4	5	9	F
Gulella (*Paucidentina*) sp. 2	Streptaxidae	2	6	8	F
Pileata sp. 2	Achatinoidea/Subulinidae	5	1	6	F
Sinistrexcisa cameruniae De Winter, Gomez & Prieto	Streptaxidae	0	6	6	F
Trochozonites sp. 6	Helicarionoidea/Urocyclidae	2	4	6	A
Gonaxis camerunensis (d'Ailly)	Streptaxidae	2	3	5	F
Pseudoveronicella sp.	Veronicellidae	0	5	5	I
Archachatina marginata (Swainsson)	Achatinoidea/Achatinidae	2	2	4	I
Pseudachatina cf. *downesii* (Gray)	Achatinoidea/Achatinidae	0	4	4	A
Subulina sp.	Achatinoidea/Subulinidae	2	2	4	A
Pseudopeas sp. 4	Achatinoidea/Subulinidae	0	4	4	?
Gulella (*Paucidentina*) cf. *conica* (Martens)	Streptaxidae	2	2	4	I
Ptychotrema (*Ennea*) cf. *complicatum* (Martens)	Streptaxidae	1	3	4	F
Gudeella sp. 2	Helicarionoidea/Urocyclidae	0	4	4	F
Verrucarion sp.	Helicarionoidea/Urocyclidae	3	1	4	A
Trochozonites sp. 9	Helicarionoidea/Urocyclidae	0	4	4	A
Trochozonites sp. 10	Helicarionoidea/Urocyclidae	0	4	4	A
Gulella/*Ennea* spec.	Streptaxidae	1	2	3	?
Edentulina martensi (Smith)	Streptaxidae	2	1	3	F
Streptostele sp. 5	Streptaxidae	0	3	3	F
Trochozonites cf. *adansoniae* (Morelet)	Helicarionoidea/Urocyclidae	0	3	3	A
Trochozonites sp. 5	Helicarionoidea/Urocyclidae	2	1	3	F
Ischnoglessula sp. 3	Achatinoidea/Subulinidae	0	2	2	A
Pseudopeas cf. *feai* Germain	Achatinoidea/Subulinidae	0	2	2	F
Gulella cf. *fernandensis* Ortiz & Ortiz	Streptaxidae	2	0	2	F
Streptostele sp. 4	Streptaxidae	1	1	2	F
Trachycystis cf. *iredalei* (Preston)	Punctoidea	2	0	2	A
Trochozonites sp. 3	Helicarionoidea/Urocyclidae	1	1	2	A
Archachatina camerunensis d'Ailly	Achatinoidea/Achatinidae	1	0	1	A
Lignus solimanus (Morelet)	Achatinoidea/Achatinidae	1	0	1	A
Leptocala mollicella (Morelet)	Achatinoidea/Achatinidae	1	0	1	I
Kempioconcha sp.	Achatinoidea/Subulinidae	1	0	1	F
Opeas sp.	Achatinoidea/Subulinidae	0	1	1	?
?Ferussaciidae/Subulinidae sp.	Achatinoidea	0	1	1	?
Gulella n.sp.	Streptaxidae	0	1	1	?
Ptychotrema (*Parennea*) n.sp.	Streptaxidae	1	0	1	F
?*Gonaxis* spec.	Streptaxidae	1	0	1	?
?Endodontoid n. gen. n. sp. 3	Punctoidea	0	1	1	?
Zonitarion sp. 1	Helicarionoidea/Urocyclidae	0	1	1	F
Totals		1,362	1,292	2,654	

TABLE 3. Systematic list of (super)families and species numbers of land snails found in one square km of rainforest in southwestern Cameroon and their tentative vertical distribution.

Taxon	No. Species	VERTICAL DISTRIBUTION			
		Floor	Arboreal	"Indifferent"	Unknown
PROSOBRANCHIA					
MESOGASTROPODA					
Cyclophoridae	1	1	—	—	—
Maizaniidae	2	2	—	—	—
PULMONATA					
STYLOMMATOPHORA					
Vertiginidae	2	1	—	1	—
Achatinoidea	27	11	7	6	3
Achatinidae	7	—	3	4	—
Subulinidae	18	10	4	2	2
?Ferussaciidae	2	1	—	—	1
Streptaxidae	33	20	6	4	3
Punctoidea	6	2	2	1	1
Ailyidae	2	2	—	—	—
Helicarionoidea	23	6	12	5	—
Euconulidae	4	2	1	1	—
Urocyclidae	19	4	11	4	—
GYMNOMORPHA					
SOLEOLIFERA					
Veronicellidae	1	—	—	1	—
TOTALS	97	45	27	18	7

for samples from the floor and vegetation separately are somewhat greater than for floor-plus-vegetation plots, whilst those for the boulder sites are smallest.

Most species occurred in low numbers (Table 2). Both in 1995 and 1996, 64% of the species were represented by less than 1% of all specimens obtained, about one third took up 1-5%, and only a few species were more common.

Snail abundance was generally low. Collections from all stations in 1995 and 1996 together yielded 2,654 specimens. There was considerable variation among plots and habitats (forest floor, vegetation, boulder) in the number of specimens collected (Table 4). Boulder sites tended to yield more individuals than sites on the forest floor proper, but these differences disappear if abundance is expressed as snails per litter volume. The greater number of specimens collected from rock boulders might be at least partly due to the greater volume of boulder litter sampled, because boulder litter was generally more decomposed, and thus finer, than that on the forest floor. Numbers of snails collected from the arboreal habitats also varied greatly, which seemed to be strongly dependent on weather conditions.

The eight litter samples from 0.25 m^2 (50 cm $\times$ 50 cm) floor quadrates collected in 1996 give an impression of the magnitude and variation of snail density, species richness, and amount of leaf-litter per surface unit of forest floor (Table 5). The data illustrate some characteristic features of this forest: (1) the variability in the amount of (partly decomposed) litter on the forest floor; (2) the low abundance of snails (12–52 snails/m^2 of forest floor, 8–20 shells/l sieved litter); (3) the low specimens:species ratio; and (4) the high species diversity. Comparison of the abundance data of these randomly taken samples (Table 5) with those provided in Table 1 and Table 6 suggests that the *average* snail density per surface unit of forest floor is generally lower than appears from the data of the 0.04 ha sites, which are based on choice litter taken from seemingly favourable microhabitats.

Differences Between Sampling Periods

The total number of specimens found in both seasons was about the same (1,362 in 1995, 1,292 in 1996), but, due to the greater number of sites sampled in 1996, mean number of specimens per site was considerably smaller than in 1995 (Table 4). The total number of species found in 1995 (80) was smaller than in 1996 (88). Mean number of sites per species was relatively greater in 1995 than in 1996.

TABLE 4. Abundance and species diversity statistics of sites located within a square km patch of rainforest in southwestern Cameroon sampled in 1995 and 1996. Data are given for all sites of which both the floor and vegetation (F + V) were sampled, for all floor (F) and vegetation (V) samples separately, as well as for sites on rock boulders (B).

	F + V 1995	F + V 1996	F + V 95 + 96	F 1995	F 1996	F 95 + 96	V 1995	V 1996	V 95 + 96	B 1995	B 1996	B 95 + 96	All
No. sites	8	16	24	11	17	28	9	16	25	4	3	7	36
Total species (S)	76	86	95	64	78	87	41	36	51	47	33	54	97
Total specimens	830	1064	1894	640	720	1360	353	393	746	369	179	548	2654
Specimens/site													
Mean	103.7	66.5	78.9	58.2	42.3	48.6	39.2	24.6	29.8	92.2	59.7	78.3	
S.D.	66.6	29.9	47.9	32.1	23.9	29.1	60.1	13.0	36.9	30.2	38.5	35.4	
Range	39–257	22–131	22–257	20–126	11–108	11–126	5–196	5–41	5–196	65–130	34–104	34–130	
Species/site													
Mean (α)	29.5	25.1	26.6	18	17.8	17.9	12.7	8.7	10.2	28	17.7	23.6	
S.D.	8.6	9.0	8.9	7.9	7.2	7.3	7.2	3.6	5.4	2.4	3.8	6.2	
Range	20–45	12–40	12–45	7–29	6–29	6–31	5–28	4–15	4–28	26–31	15–22	15–31	
/ Whittaker (S/α)	2.6	3.4	3.6	3.5	4.4	4.9	3.2	4.1	5.0	1.7	1.9	2.3	
Sites/species													
Mean	3.1	4.7											
Variance	4.25	12.87											
Maximum var.	10.23	41.45											
% achieved	41	31											

TABLE 5. Snails from a 0.5 m × 0.5 m floor surface quadrat, with the number of species and specimens, the volume of sieved litter, and the number of specimens per litre and per m^2.

	Number of species	Number of shells	Litter vol. (litres)	Shells/ litre of litter	Shells/ m^2
Sample					
1	10	13	0.9	14.4	52
2	5	6	0.3	20.0	24
3	2	3	0.25	12.0	12
4	4	5	0.25	20.0	20
5	4	4	0.5	8.0	16
6	4	4	0.35	11.4	16
7	4	4	0.25	16.0	16
8	6	7	0.4	17.5	28
Totals	22	46	3.2	—	—
Mean	4.9	5.7	0.4	13	23

For many species, the number of specimens per species varied considerably between the two sampling periods (Table 2). Histograms of species frequencies ordered according to decreasing relative abundance (% of total specimens) describe a hollow curve both for 1995 and 1996, but the ranking order of the species in 1995 differed considerably from that in 1996 (Fig. 3). More than one-fourth (26) of the species was found uniquely either in 1995 or in 1996. Of 25 of the species found in both seasons, the relative abundance differed 50% or more between years. *Achatina iostoma*, for instance, was represented in 1995 by three adult shells and 25 juveniles of about 20–30 mm, whilst in 1996 only two adult specimens were encountered. Of *Trochozonites* cf. *pilosus* and *T.* cf. *bifilaris* only clearly juvenile shells were observed in the 1996 samples, whereas both adults and juveniles occurred in much larger numbers in 1995. Only one out of 40 specimens of the two *Aillya* species found was collected in 1996. Such data are suggestive of a life cycle of one year or less. The relative abundance of 46 species differed less conspicuously between years.

For both floor and boulder sites, the absolute number of individuals found per site was generally higher in 1995 than in 1996. However, the mean number of species in the floor sites did not differ between the two sampling periods, whilst in the boulder sites mean species richness was much greater in 1995 (Table 4). This general trend was also observed by comparisons of the eight sites that were sampled in both seasons. The number of individuals per species in the floor samples was significantly lower in 1996 than in 1995, whereas these ratios were the same in the boulder sites (Table 1).

Standardized per litter volume, the median number of specimens in 1995, calculated over all floor and boulder litter samples, was significantly higher than in 1996 (Table 6; one-tailed Mann-Whitney test, $Z = 3.92$, $P = 4.5 \times 10^{-5}$), as was the median number of species (Table 6; one-tailed Mann-Whitney test, $Z = 3.12$, $P = 0.91 \times 10^{-3}$). The larger total number of species found in 1996 might be due to the larger number of sites sampled, and the almost double total volume of (sieved) floor litter taken in that year, increasing the chance of finding new, rare species.

Values of Whittaker's index *I* for 1995 and 1996 (Table 4) indicate that differences in species diversity among sites were greater in 1996 than in 1995. This might well be related

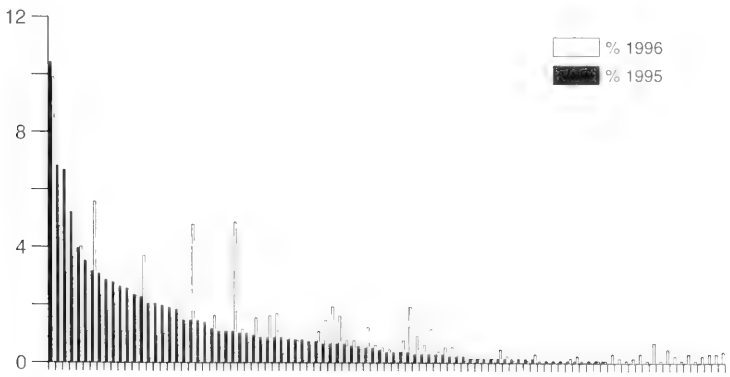

FIG. 3. Relative abundance (% of the total number of specimens collected in each season) of 97 land snail species in 1995 and 1996, ordered according to decreasing abundance in 1995.

TABLE 6. Gastropod diversity and abundance in litter samples taken from the forest floor and from rock boulder in 1995 and 1996, expressed as number of specimens or species per litre of sieved litter.

	Median	Range	Nsamples	Total litter volume	Total specimens
Specimens/litre					
1995	49.3	22.2–88.2	15	19.75	1009
1996	21.1	9.2–61.2	20	36.2	899
Species/litre					
1995	15.3	7.7–25.4	15		
1996	10.6	5.0–18.4	20		

to the lower number of specimens per station in 1996 (Table 4), and thus partly result from sampling error.

Vertical Distribution

The fauna appeared to be stratified with species confined to the ground, species confined to arboreal habitats, and species inhabiting both levels. A majority of 45 species (46%) were classified as floor dweller (F), on evidence that live specimens were almost exclusively found on the forest floor and on boulders, or because specimens of (minute) species commonly found in the floor litter were never obtained from the vegetation. This class includes seven species that were normally encountered on the floor, but of which the odd specimen was found in samples from the vegetation. Species of which live specimens were only found in the vegetation at 3/4 m or more above the ground (27 species, 28%) were considered to have arboreal habits (A), assuming that the relatively few shells found on the forest floor were from deceased animals that had dropped to the ground. The remaining snails that were regularly found alive (18 species, 19%), were classified as "indifferent" (I). Information on the vertical distribution of some uncommon species could be derived from nearby undisturbed forest sites not covered in this report. Of seven species (7%) insufficient information was available. The tentative vertical distribution of the individual species is listed in Table 2.

All major families have representatives in the three classes (F, A, I) recognised (Table 3), only the Achatinidae have no true floor-dwelling species. The majority of the Subulinidae and Streptaxidae species are ground dwellers, whilst of the Urocyclidae significantly more species have arboreal habits.

The upper, horizontal surface of the large rock boulders constitutes a special habitat. Five to 15 m^2 of horizontal rock surface yielded up to 31 species during a single visit (Table 4). Despite intensive searches, snails were never observed on the steep flanks of the 3–5 m high outcrops. Although these rocks are virtually devoid of higher vegetation, a relatively significant proportion of the shells found in the litter belongs to arboreal species. There are usually one or more spots where the woody understorey vegetation grows against the flanks of the boulder, often attached to it by climbers. Possibly some arboreal species migrate between the vegetation and the rock habitat, the microclimates of which might resemble each other.

The occurrence of a limited number of species, such as *Cyathopoma* n. sp.,. *Ptychotrema* (*Ennea*) *silvatica, Gulella bolocoensis, Gulella* (*Costigulella*) n. sp., and *Gulella* (*Pupigulella*) *pupa,* might be associated with the presence of bare rock, but none were confined to the giant boulders.

Shell Size and Shape

Shell height (H) and diameter (D) were measured from an "average" adult specimen of each of 86 species, (semi-)slugs and species known by only juvenile shells being excluded. H ranges between 0.8 and 165 mm, D between 0.9 and 94 mm. Figure 4 gives the distributions of H and D. Major shell dimension (H or D) of 32 species (37%) is less than 5 mm, and of another 32 species (37%) between 5 and 10 mm. Shells of eight species (9%) measure between 10 and 20 mm, and those of 14 species (16%) are larger than 20 mm, four of which have adult shell heights exceeding 90 mm.

Ground-dwelling species did not differ in major shell dimension (H or D) from the arboreal (two-tailed Mann-Whitney test, $Z = 1.12$, $P = 0.26$), "indifferent" ($Z = 1.64$, $P = 0.10$), or arboreal plus "indifferent" species ($Z = 1.65$, $P = 0.10$).

We examined the shell shape distribution of the floor-dwelling, arboreal and "indifferent" species separately, as well as that of these

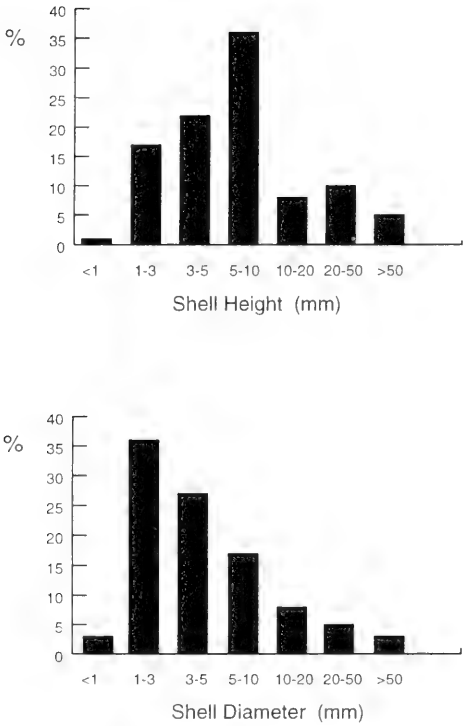

FIG. 4. Shell height (upper graph) and shell diameter (lower graph) distributions of 86 land snail species found within one square km of Cameroonian rainforest.

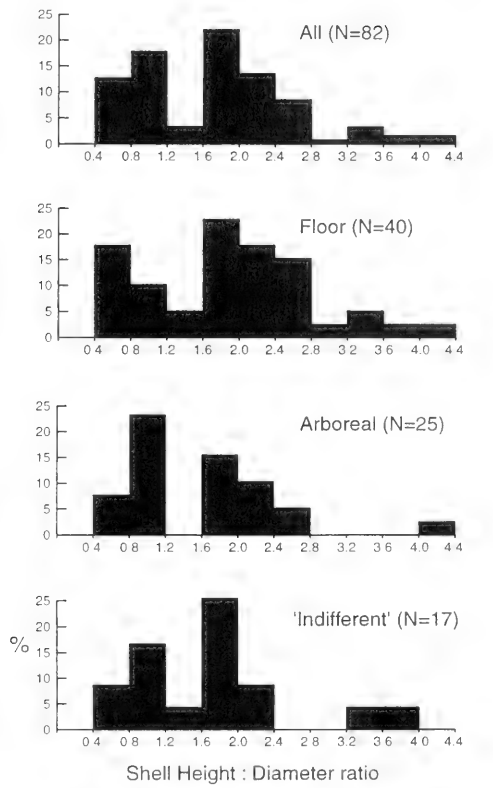

FIG. 5. Shell height:diameter ratio distributions of 82 land snail species found within one square km of Cameroonian rainforest (upper graph), as well as of the floor-dwelling, arboreal and "indifferent" species separately.

three groups together (Fig. 5). All distributions in Figure 5 are bimodal, due to relatively many species with "globose" (H/D 0.8–1.2) and moderately tall to very tall shells (H/D > 1.6). Of 82 species, H:D ratios were calculated, excluding six slug-like species (two *Zonitarion,* one *Verrucarion,* one *Pseudoveronicella,* and two *Aillya*), and nine species with unknown vertical distributions or with only juvenile shells available. The H:D ratio distribution of the floor-dwelling species did differ from neither that of the arboreal species (two-tailed Mann-Whitney test, Z = 1.26, P = 0.21), nor that of the "indifferent" species (Z = 1.01, P = 0.31) or the arboreal and "indifferent" species together (Z = 1.42, P = 0.15).

DISCUSSION

Species Richness

The malacofauna of this small patch of acid rainforest was found to be extremely rich in species. Although comparisons with other studies are hampered by a lack of standardisation with respect to area size and sampling methods, this Cameroonian area might well be the globally most species-diverse locality known with respect to land molluscs. The richest site reported so far is Waipipi Reserve, Manakau Peninsula, New Zealand. Solem et al. (1981) reported 60 species from this 4 ha site, and a total number of 72 native species from a surrounding area of approximately 50 × 15 km (but see Emberton (1985) for somewhat lower numbers). Other species-rich sites (all approx. 4 ± 2 ha) include Pine Mountain, Kentucky, U.S.A., where L. Hubricht collected 44 species, and a patch of lowland rainforest near Manombo Village, Fianarantsoa Province, Madagascar, where 52 species were found (both sites described in Emberton, 1995). Tattersfield (1997) reported 50 species from 27

plots of 40 m × 40 m each in Kakamega Forest, an area of approximates 265 km^2 in western Kenya, the richest of which yielded 33 species. In this paper, we report 97 species in 100 ha of rainforest, 83 species within a 9 ha subarea, up to 45 in a sampling site of 20 m × 20 m during a single visit, and up to 51 species in sites sampled twice. In all cases, the actual floor surface sampled is much smaller than 0.04 ha. Up to 10 species were found in litter from a 0.5 m × 0.5 m plot.

In view of the large proportion of rare species, it is likely that the actual number of species will even be greater than 97. Several parametric and non-parametric methods have been developed to estimate the actual species richness in similar situations, based on the frequency of rare species in a sampling program. According to Colwell & Coddington (1995) the Chao-2 and second-order Jackknive estimators provide the least biased estimates of true species richness for small numbers of samples. Both estimators are based on presence-absence data, and take into account the number of species that occur in only one or in two samples. These two methods were applied to all stations in 1995 (8) and 1996 (16) of which both the forest floor and vegetation were sampled. The total number of species observed in these plots was 95. The Chao-2 and second-order Jackknive estimates are 107 and 110 species, respectively. Subtracting the two species found in the remaining samples, there may be at least 105–108 species present in this 100 ha area, especially since these non-parametric estimators usually underestimate the true species richness (Colwell & Coddington, 1995).

Possible Explanations for the High Species Diversity

Of the factors favouring high land snail diversity that were discussed by Solem (1984), three might be involved in the situation described here: leaf-litter characteristics, lack of disturbance for prolonged periods of time, and stable moisture supply.

Leaf-litter associated parameters are likely to be important for the high species diversity observed. The majority of species found are floor dwellers, but since leaf-litter occurs also patchily on the understorey vegetation above the forest floor, these factors might also affect certain arboreal taxa. With more than 125 species of trees per ha, the composition and architecture of litter deposits are obviously highly variable. Leaf-litter is unequally distributed on the forest floor, and thicker litter accumulations seemed to contain more individuals and species than spots with thin litter deposits, as was also found by Solem et al. (1981) in New Zealand. Even in tropical evergreen forests trees periodically shed their leaves, but not synchronised like in temperate regions (e.g., Medway, 1972; Hladik, 1978). Thus, thickness, distribution and composition of litter layers are dynamic in both space and time. The great variety in size, shape and firmness of the leaves, combined with differential decomposition rates by spot differences in microclimate, moisture and soil conditions, potentially provides a wide array of microhabitats supporting a high land snail diversity of vegetable matter and fungi consumers, and associated predator species. These factors might partly be involved in the apparent seasonality of the snail fauna observed that might otherwise not be expected in an evergreen forest.

There are only few published reports supporting the view that litter parameters are related to land snail species diversity, for example, those by Solem et al. (1981) on New Zealand, and by Getz & Uetz (1994) on North American forests. Solem's (1984) assertion that rainforests have negligible litter deposits and, therefore, support a little diverse land snail fauna certainly does not hold for the forests of western Africa.

The fauna of this small area is also diverse in taxa above the species level, and seems to include few species that are closely related (as judged largely from conchological characters). The species belong to a considerable number of (sub)genera. Several of the larger generic entities used here are actually composed of various, as yet largely unnamed, distantly related genera. For example, anatomical studies have revealed that *Trochozonites,* the most speciose genus found, is an artificial taxon embracing at least four groups of species, despite their similarity in shell characters (Ortiz de Zárate, 1951). Local speciation therefore seems to have contributed little to the high species richness observed. It is much more probable that this land snail fauna gradually accumulated in the area, possibly over long periods of time.

In the dry and relatively cold glacial periods, the size of the African forest belt was much reduced to a small number of discrete areas.

The study area is situated within such a putative Pleistocene forest refugium (Maley, 1996). Whether this is in any way related to the high actual species richness can only be investigated by comparison with other areas, both within and outside the hypothesized refugia.

Absence of stress periods by prolonged droughts probably favours high species diversity, because the moisture regime determines the possible activity periods of land snails (Solem et al., 1981). Even in the driest periods of the year the study area receives up to 80 mm precipitation per month (Waterloo et al, 1997). According to Solem (1984) rainforests suffer from too much rain, which causes leaching of nutrients, and are therefore little diverse in land snails.

If the proportion of arboreal species in this fauna is truly greater than in other faunas, this might also be a factor contributing to the high species diversity. Waipipi Reserve in New Zealand had only 14 out of 60 species with arboreal habits, including several which live both on the floor and in the vegetation (Solem et al., 1981; Solem & Climo, 1985). There appear to be hardly any published data on the number of arboreal species in other faunas, however. Most studies appear to have adopted sampling techniques that underestimate the numbers of arboreal taxa present.

Diversity Pattern and Sampling Error

The analysis of the data suggests that the diversity of this fauna is essentially sympatric, because no indication of geographic or ecological replacement of species was found. There are no obvious barriers to dispersal; the forest cover is homogeneous, and the streams in the study area are 5 m wide at most. However, the concept of sympatric diversity is difficult to apply (De Winter, 1995; Emberton, 1995). This holds especially for rainforests, where it is almost impossible to find "restricted habitats with a homogeneous set of dominant plant species" (Solem, 1980). Although the low overall density of snails in this area is undoubtedly an effect of the low pH and the low mineral content of the soil, the actual numbers of live collected snails seemed to be very much dependent on weather conditions. The greatest numbers of live specimens were obtained during damp, warm conditions, as occur after heavy rains in the night and early morning followed by hot, sunny weather. After several days without precipitation rather few live snails were found, but during rain sampling was also less successful.

Dry conditions especially had a negative effect on the numbers of (semi)arboreal snails collected, due to problems in finding the sites where the snails hide. Solem et al. (1981) reported that some shelled arboreal taxa seal themselves firmly to the vegetation during dry periods, and in hindsight it seems possible that we not always applied enough force to shake these from their resting sites. Other species, notably slug-like taxa, probably seek shelter in holes and fissures of tree trunks.

The effect of climatic conditions is best illustrated by considering the data of the most diverse plot, Sta022, where 45 species were collected during a single visit. The richness of this plot was due to an exceptionally large number of specimens and species collected from the vegetation during optimal weather conditions as described above. The snail numbers found in the vegetation were much greater than on the floor, and the number of species found in both habitats was the same (Table 1). The number of species collected from the floor was not excessive, and several relatively common species were not represented. Under favourable conditions and by taking greater leaf-litter samples, it should be possible to find perhaps as much as 75% of the entire malacofauna within a single 0.04 ha plot.

Thus, in view of high proportion of the total fauna that can be found in a few square meter of forest, sampling error—resulting from the large proportion of rare species, the low overall snail abundance, and the varying weather conditions during sampling—has very likely had a significant effect. The differences in species composition found among the sites sampled in the same season, as indicated by the values of Whittaker's *I*, are therefore likely to be inflated. Geographic replacement of taxa also would seem unlikely in view of the small size and overall homogeneous nature of the study area. Sampling needs to be done at a much finer scale in order to detect differences in microhabitat preferences among species. Sampling error constitutes a serious problem for quantitative studies in these forests. Timed searching, as recently advocated by Emberton et al. (1996), does not seem to solve the problem, because it will inevitably result in

overlooking even more species, especially the tiniest ones.

Streptaxid Diversity

The very large proportion of carnivorous species (all Streptaxidae) in a land snail fauna is a remarkable phenomenon, which is unique to the Afrotropical region as far as known. In the Manakau Peninsula, New Zealand, only four out of 72 species are carnivores, all belonging to the Rhytididae (Solem et al., 1981). The rainforest fauna of Manombo Reserve, Madagascar, has eight (15%) streptaxid species. Substantial proportions of Streptaxidae have been reported for much larger areas elsewhere in Africa, such as the former Belgian Congo (Pilsbry, 1919) and East Africa (Kenya, Tanzania and Uganda; Verdcourt, 1983). On a smaller geographic scale the proportion of streptaxid species seems to vary greatly. Tattersfield (1996) found nine (18%) streptaxids out of 50 land snail species in Kakamega Forest in Kenya, whilst in eastern Tanzania the proportion of Streptaxidae increased with altitude from about one fourth of the species below 500 m to 46% at a single station at 1000 m, taking up to one third of the collected individuals (Emberton et al., 1997).

The conspicuous radiation of the Streptaxidae contributes substantially to the species diversity here and elsewhere in tropical Africa. Maybe these carnivorous snails occupy a segment of the ecological space filled by non-molluscan invertebrates outside the Ethiopian region. However, any data supporting this speculation are completely lacking. At present, no satisfactory explanation for this high proportion of carnivorous snails can be offered.

Emberton et al. (1997) surmised that "surely many of these streptaxid species must take nonmolluscan prey". However, in the course of six months of fieldwork in Cameroon, various streptaxid species have been only found feeding on other land snails or (in one occasion) their eggs. These incidental observations show that at least some species are not selective with respect to the species and size of their prey. *Edentulina liberiana,* for example, was found to attack some ten species of snails and semi-slugs (including observations from sites in Cameroon not described in this report), some up to twice its size. However, the considerable size-range of the streptaxids in this fauna (adult shell height 1.5–37.4 mm) is suggestive of quite some variation in feeding habits. Theoretically, Streptaxidae could live as scavengers on carrion, because at least two reports (Berry, 1963; Aiken, 1981) claim that some species feed in captivity on (mammalian) liver.

Shell Size and Shape

The malacofauna of block i2 occupies an enormous shell size range, but the vast majority of the species are rather small. Emberton (1995) provided shell size distributions of three diverse sympatric faunas, using shell diameter as an index of shell size. The shell diameter distribution reported here strongly resembles that found in the Manombo rainforest, Madagascar. The proportion of "minute species" (*sensu* Emberton, 1995; D between 0.5–5 mm) is virtually identical (66%), and in both faunas giant species (D > 40 mm) are represented. The other two faunas (Pine Mountain, U.S.A, and Waipipi Reserve, New Zealand) have very different size distributions. In New Zealand, 85% of the species are minute, and the remaining species are all smaller than 10 mm. In the U.S.A., giant species are lacking, and minute taxa constitute only 40% of the total fauna, the remaining species being approximately evenly distributed among the size classes.

Peake (1968) found in Solomon Island rainforests that ground-dwelling snails have a much more restricted shell-size range with generally smaller shells than arboreal or partly arboreal species. Here we observed that shells of species regularly exceeding 50 mm in height occur only in the arboreal and "indifferent" taxa. However, giant species (all Achatinidae) constitute a minor proportion of the total fauna, and shell dimensions of floor-dwelling and (partially) arboreal taxa were not different statistically.

The shape distribution of land snail shells was analysed by Cain (1977, 1978a, b, 1980) for a number of faunas. He observed that in most faunas species have shells that are either clearly higher than wide or wider than high, comparatively few having shells with approximately equal height and width. Cain (1978b: 219) suggested that species with high-spired shells tend to forage on vertical surfaces, and hence occur especially on rock faces and in trees; taxa with low-spired shells were hypothesized to feed more commonly on horizontal surfaces, and species with shells of about equal height and width to show little preference.

The distribution of H:D ratios of the shells found in this study deviates from those in the three sympatric faunas discussed by Emberton (1995). There are relatively many high-spired species, even more than in Madagascar, including some species in the 4.0–4.4 class, which is absent in Emberton's material. This is mainly due to the large proportion of subulinid species in the area studied. Another remarkable characteristic of this fauna is the very large proportion of shells in the 0.8–1.2 ("globose") class, and the apparent deficit of species in the 1.2–1.6 class. In the other three sympatric faunas, as well as in most large-scale faunas studied by Cain, the shell shape distribution is characteristically bimodal due to a deficit of globose-shelled snails. Most globose-shelled species are helicarionoids, especially of the heterogeneous genus *Trochozonites*, the 13 members of which have pyramidal shells, and tend to have arboreal habits, comprising only one true floor-dwelling species.

Cain (1978a) reported a relatively high proportion of globose species in the Helicostylinae of the Philippines and the Papuininae of the New Guinean area, most of which are arboreal species in rainforests. Emberton (1995) found arboreal species in a Madagascan rainforest to be globose rather than high-spired. Thus, perhaps there is some tendency in rainforest areas for globose-shelled species to have arboreal habits.

The suggestion that there might be a correlation between shell shape and preferred habitat has received experimental support for some British species (Cain & Cowie, 1978; Cameron, 1978, 1981; Cook & Jaffar, 1984), but does not seem to hold for high-spired Malagasy snails (Emberton, 1995), nor for the species studied here. Differences in shell shapes between geographically separate faunas generally appear to have a stronger taxonomic bias, like the great diversity of the high-spired Subulinidae in tropical Africa.

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CYTOCHROME OXIDASE I-BASED PHYLOGENETIC RELATIONSHIPS AMONG THE POMATIOPSIDAE, HYDROBIIDAE, RISSOIDAE AND TRUNCATELLIDAE (GASTROPODA: CAENOGASTROPODA: RISSOACEA)

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ABSTRACT

The Gondwanian-derived Asian pomatiopsid radiation is taxonomically complex, diversity-rich, and widely deployed geographically. This Asian branch of the family has coevolved with such human trematode parasites as *Schistosoma* and *Paragonimus;* it is ideally suitable for studying patterns and processes of evolution over 100 million years. Cytochrome *c* oxidase subunit I gene sequences are used here to elucidate taxonomic relationships from the subspecies to familial level. In Chinese literature, pomatiopsid taxa have been classified in the Hydrobiidae; what are the genetic relationships between *Hydrobia* and allied taxa classified as pomatiopsid?

Sixteen sequences, ranging in length from 578 to 645 nucleotides, are aligned from 11 species of nine genera assigned to seven families, four of which are rissoacean. Five different phylogenetic analyses are concordant: (1) the pomatiopsid taxa are in one distinct clade, the other rissoaceans form a second clade; (2) truncatellids are more closely allied to the hydrobiids than to the pomatiopsids; (3) the rissoid *Setia* is part of the truncatellid-hydrobiid clade; (4) two subspecies of *Oncomelania* are clearly divergent; (5) triculine taxa appear divergent from pomatiopsine taxa. However, the *Tricula* sp. node is weakly supported.

Individuals of a population differ by an average of 0.005 ± 0.004 nucleotide differences/site; the subspecies of *Oncomelania* differ by 0.148 ± 0.004; the two species of *Hydrobia* differ by 0.162 (range of 0.161 – 0.163); the triculine genera *Tricula* and *Gammatricula* differ by 0.132 (range of 0.130 – 0.133); the pomatiopsid subfamilies Pomatiopsinae and Triculinae differ by 0.179 ± 0.020; the families Hydrobiidae and Pomatiopsidae differ by 0.267 ± 0.016. Non-rissoacean and rissoacean taxa differ by 0.274 ± 0.023.

Key words: systematics, cytochrome *c* oxidase subunit I, COI, gene sequences, phylogeny, Rissoacea, Pomatiopsidae, Hydrobiidae, Truncatellidae, Rissoidae, China, Jamaica, Bulgaria, Denmark.

INTRODUCTION

This study is one of a series (reviewed in Davis, 1992) aimed at understanding the origin and evolution of the freshwater snail family Pomatiopsidae in Asia. There are compelling reasons to pursue such studies: (1) The family is ideally suited for in-depth studies of biogeography and evolution. The family is of Gondwanian origin with genera found in South Africa, South America, northern India, and Australia. Davis (1979) hypothesized an introduction of early pomatiopsids from the northeastern Indian Plate into northern Burma and western China with subsequent distribution throughout southern China, Japan, and the Philippines reaching North America via Bering Strait. (2) Pomatiopsids are ideal for studying patterns and processes of evolution over the past 100 million years. The family is taxon rich and widely deployed geographically. A series of anatomical studies on pomatiopsid taxa have yielded a rich database of characters and character-states enabling the establishment of testable phylogenetic hypotheses of the evolution of the family. Each phylogeny is tested with the addition of data from a newer study. The latest phylogeny (Davis, 1992) has not falsified the previous phylogenies. These phylogenies are mapped on area cladograms testing and reinforcing the biogeographic hypothesis. (3) A diverse array of Asian pomatiopsids are important intermediate hosts of human trematode para-

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sites. These studies are essential to study coevolution of the blood parasite *Schistosoma* with prosobranch snails. Three genera of the Pomatiopsidae — *Oncomelania, Neotricula* and *Robertsiella* — are involved in the transmission of the human blood fluke *Schistosoma* in China, the lower Mekong River, and Malaysia. The schistosome occurring in China is also distributed in Japan, Taiwan, the Philippines and Sulawesi. The genus *Schistosoma* is, as are the Pomatiopsidae, of Gondwanian origin; one branch of the *Schistosoma* clade has coevolved with Asian Pomatiopsidae, with genera distributed in two subfamilies, the Pomatiopsinae and Triculinae (reviewed in Davis, 1980, 1992). (4) Molecular data are essential to test the phylogenetic results based on anatomy. Allozyme data have, to the limited degree they have been applied, reinforced the phylogenetic hypotheses on the relationships of key genera in the aforementioned subfamilies (Davis et al., 1994); that is, the phylogenies based on allozymes and anatomical data are congruent. They have been useful to clarify subspecific status of populations of *Oncomelania hupensis* in China (Davis et al., 1995). But with the need to include numerous taxa for phylogenetic analysis, the ability to use allozyme data effectively decreases. We have found that mitochondrial gene sequences are ideally suited for testing phylogenetic relationships based on anatomical data. We have established that cytochrome *b* sequences are useful to determine patterns of divergence at the population and subspecies level within the genus *Oncomelania* (Spolsky et al., 1996).

There are a number of questions that this study was designed to answer: (1) Are the Hydrobiidae and Pomatiopsidae truly divergent separate families? From Davis (1979) onward we have argued that, on the basis of anatomy and patterns of development, the Hydrobiidae and Pomatiopsidae are highly divergent. This is an important question because up to the present, Chinese workers and others around the world have insisted on including the Pomatiopsidae within the Hydrobiidae and thus believe that some hydrobiids transmit schistosomes (Malek & Little, 1971; Brandt, 1974; Liu et al., 1974; Liu, 1979; Brown, 1980 (revised to use Pomatiopsidae in 1994); Kang, 1984, 1986; Malek, 1985). Davis (1979, 1980, 1992) has shown that the Hydrobiidae are not found in India, China or southeast Asia; further, no hydrobiid transmits *Schistosoma*.

Understanding the patterns of divergence of these two families is important to understanding the origin and coevolution of rissoacean snails with *Schistosoma*. One purpose of this paper is to present additional evidence that the two families are distinct and divergent.

(2) On the basis of anatomical data, there are two distinct subfamilies of the Pomatiopsidae; the Pomatiopsinae and Triculinae. Allozyme data reinforced the confamilial status of the two generic groupings but did not unequivocally serve to demonstrate two distinct subfamilies as anatomical data did (Davis et al., 1994). Would the cytochrome *c* oxidase subunit I (COI) gene sequences serve to clearly demonstrate family and subfamily-level generic groupings?

(3) Would the Truncatellidae (represented here by only one species) be more closely related to the Hydrobiidae or to the Pomatiopsidae? Davis (1979) and Ponder (1988) considered the Truncatellidae to be closely related to the Pomatiopsidae on the basis of anatomical data. Analyses of 28S rRNA sequences involving one species of Hydrobiidae, nine species of two genera of Truncatellidae, and one species of Pomatiopsidae (Rosenberg et al., 1997) placed the Hydrobiidae as an outgroup to a cluster consisting of two branches: one solitary branch included some of the truncatellid taxa; the second branch subdivided into two groups, one including the remaining truncatellid taxa, the other the pomatiopsid species. What would the COI sequence data tell us?

(4) Would COI data support the conclusion based on allozyme data (Davis et al., 1995) that *Oncomelania hupensis hupensis* and *O. hupensis robertsoni* are distinct subspecies?

METHODS

Taxa Studied

Pomatiopsidae: Triculinae: *Gammatricula chinensis* Davis, Liu & Chen, 1990; *Tricula* sp.

Pomatiopsidae: Pomatiopsinae: *Oncomelania hupensis hupensis* (Gredler, 1881); *Oncomelania hupensis robertsoni* Bartsch, 1946.

Hydrobiidae: Hydrobiinae: *Hydrobia* cf. *pontieuxini* Radoman, 1973; *Hydrobia neglecta* Muus, 1963.

Rissoidae: *Setia turriculata* Monterosato, 1884.

Truncatellidae: *Truncatella pulchella* (Pfeiffer, 1839).

TABLE 1. Localities and collecting information for the specimens studied.

Taxa; Preparation #	Localities	Catalog#
Pomatiopsidae:Triculinae		
Gammatricula chinensis 414/415/416	China, Zhejiang Province, Kaiwa Co, Tong Cun Town, Bai Keng Village; 118°15′47″E, 29°00′05″N	ANSP 400351 ZAMIP MO136
Tricula sp. 453/454	China, Sichuan Province, Dayi County; Tian Gong Mia Township; Huang Ba Village; 117°23′16″E, 30°35′26″N	ANSP 400352
Pomatiopsidae: Pomatiopsinae		
Oncomelania hupensis hupensis 93/96	China, Hubei Province, Han Yang County; 114°01′01″E, 30°34′08″N	ANSP 375731
Oncomelania hupensis robertsoni 45/48	China, Yunnan Province; Dali City, Da Jin Ping, Zi Ran Village; 100°12′04″E, 25°27′06″N	CIPD 0349
Hydrobiidae		
Hydrobia cf. *pontieuxini* 346/347/351	Bulgaria, 1 km W of Nessebar; 27°71′73″E, 42°65′99″N	ANSP 400353
Hydrobia neglecta 435/436/439	Denmark, Funen Island, Odense Fjord; 10°32′E, 55°30′N	ANSP 400354
Rissoidae		
Setia turriculata 474/476/477	Bulgaria, 1 km W of Nessebar; 27°71′73″E, 42°65′99″N	ANSP 400355
Truncatellidae		
Truncatella pulchella 479–480	Jamaica, W of Falmouth; 77°39′46″W, 18°29′46″N	ANSP 400356

Four molluscan taxa were used as outgroups: (1) the polyplacophoran *Katharina tunicata* (Wood, 1815), the sequence for which was obtained from GenBank (accession number U09810); (2) the cerithiacean *Cerithium atratum* (Born, 1778) (Harasewych et al., 1997); (3) the muricacean *Stramonita haemastoma* (Linnaeus, 1767) (GenBank accession number U86330, under the name *Thais*); and (4) the rissoacean *Setia turriculata* studied in this paper.

Locality data are given in Table 1. *Oncomelania hupensis hupensis, O. hupensis robertsoni* and *T. pulchella* were brought to the USA alive, *G. chinensis* and *Tricula* sp. were preserved in 100% methanol, *H.* cf. *pontieuxini* and *H. neglecta* were preserved in 70% ethanol, and *S. turriculata* was frozen. Immediately prior to isolation of DNA, the living specimens of *Oncomelania* and *Truncatella* were quick-frozen at –80°C.

DNA Preparation

The methods used for preparing DNA from individual snails were described by Spolsky et al. (1996), with the following modifications. Alcohol-preserved specimens of *Gammatricula, Tricula* and *Hydrobia* were soaked 5 min each in two changes of 300 µl of ice-cold exchange buffer before being placed in lysis buffer. Ethanol precipitation and washing were repeated and the final DNA pellet redissolved in 25 µl of water.

The quality of DNA was determined by electrophoresis through a 1% agarose gel in TBE. DNA concentration was determined using a Hoefer TKO100 fluorometer.

DNA Amplification

PCR was used to amplify a fragment of the mitochondrial COI gene using the primer pair COF14 (forward: 5′ GGTCAACAAATCATAAAGATATTGG 3′) and COR722 (reverse: 5′ TAAACTTCAGGGTGACCAAAAAAYCA 3′). COF14 is identical to primer LCO1490 as described by Folmer et al. (1994), while COR722 is a modification of Folmer et al. (1994) primer HCO2198.

Each PCR reaction mixture, in a total volume of 50 µl, contained 20-100 ng of genomic DNA, 2.5 units of cloned Pfu DNA polymerase (Stratagene), 200 µM of each dNTP, 20-40 pmol of each primer, 20 µg of BSA, and 5 µl of 10X Pfu reaction buffer. PCR amplifications

were performed using an M-J Research PTC-100 thermal controller with the following cycling conditions: initial 1 min 30 sec at 95°C, followed by 40 cycles of 1 min at 95°, 1 min 20 sec at 47°C, and 1 min 10 sec incremented by 1 sec per cycle at 73°C. After a final 5 min at 74°C, reactions were held at 4°C.

Amplified DNA products were separated by electrophoresis through a 1% low melting point agarose gel in TAE buffer. The band corresponding to a fragment of the correct size was cut out, and the DNA purified using either Microcon-100 microconcentrators (Amicon) after digesting the agarose with agarase or directly with Wizard PCR preps (Promega). DNA concentration was determined on a Hoefer TKO100 fluorometer.

Sequencing

Sequences of the COI fragment were determined by manual cycle sequencing, using the Thermo Sequenase radiolabeled terminator cycle sequencing kit (Amersham) according to their protocol.

Each reaction mixture contained 40-60 ng of purified PCR product, 4 units of Thermo Sequenase DNA polymerase, 2 µl of reaction buffer, 4 pmol of either COF14 or COR722 primer in a total reaction volume of 20 µl. One fourth of the reaction mixture was aliquoted to each of four dideoxynucleotide-specific termination mixes containing the four dNTPs at 7.5 µM each plus, for each termination, 0.15 pmol of one of the four ^{33}P-labelled ddNTPs at a specific activity of 1500 C_i/mmole. Cycling conditions consisted of 30 cycles of 60 sec at 95°C, 60 sec at 51°C and 75 sec at 72°C for the forward primer and 30 cycles of 60 sec at 95°C, 60 sec at 56°C and 75 sec at 72°C for the reverse primer. Four µl of stop solution were added after cycling and samples were stored frozen until ready to use.

Before loading, the samples were heated 5 minutes at 75°C and 3 µl of each loaded immediately on the gel. Reaction products for each primer were run on three separate gels: 2.5 h on an 8% Long Ranger gel (FMC), 4 h on a 6% gel, and 7.5 h on a 5% gel at a constant power of 37.5 Watts, providing complete sequences for both strands.

Data Analyses

COI sequences for each individual were assembled and edited using ESEE 3.0s (Cabot & Beckenbach, 1989). ESEE was also used to align our sequences with sequences obtained from GenBank and the literature.

A distance matrix was computed using DNADIST of PHYLIP version 3.57 (Felsenstein, 1989, 1993). Maximum likelihood trees were generated using DNAML (PHYLIP 3.57). Twenty repetitions, with randomized input order and optimization by global branch rearrangement, were run for each analysis. Bootstrap estimates (1,000 replicates) were made using program SEQBOOT, in conjunction with DNAML and CONSENSE. Parsimony analyses were done using Hennig86 (Farris, 1988) and PAUP 3.0s with branch and bound searching (Swofford, 1993). In analyses using PAUP, terminal nucleotides not present in all sequences were trimmed from the analyses; using DNAML, all 645 nucleotide positions were included.

We performed five different phylogenetic analyses to satisfy different conditions and compare among methods: (1) DNAML with the polyplacophoran *Katharina* and the rissoid *Setia* as outgroups; (2) As the polyplacophoran was not much more distant from the ingroup taxa than was *Setia,* we used *Setia* as the outgroup in a maximum likelihood analysis; (3) Also with *Setia* as the outgroup, we ran Hennig86 (256 variable sites; 220 informative sites); (4) We subsequently added the two Caenogastropoda; these two taxa are better outgroups (i.e., within Gastropoda but outside Rissooidea) than either *Katharina* or *Setia.* To our knowledge, there are no data available for other rissoacean taxa that might serve as outgroups. For this set of taxa, we computed a maximum likelihood tree as follows: first, we empirically determined the optimal transition/transversion ratio (ratio which minimizes the likelihood measure; we then used the optimal ratio, 1.3 in this case, in an exhaustive DNAML analysis (20 iterations, global branch swapping); (5) we also computed parsimony trees for the same set of taxa, using a 1:1 transition: transversion ratio.

RESULTS

Sequence alignments for 16 sequences, ranging in length from 578 to 645 nucleotides, are shown in Table 2. Individuals with identical sequences (414, 415; 474, 476, 477; 346, 347; 435, 436, 439; and 453, 454) were combined for alignment and subsequent analyses. A single nucleotide at position 57 is missing from the *Cerithium* sequence; we pu-

TABLE 2. Alignment of sequences of a 645 nucleotide fragment of the cytochrome *c* oxidase I gene.

Katharina tunicata	ATC	TTG	TTT	GGT	ATT	TGA	GCT	GGG	TTA	GTA	GGG	ACT	GCT	TTA	AGA	TTA	CTA	ATT	CGT	GCA	60					
Stramonita haemastoma	---	---	---	---	---	---	---	---	C.G	...	..A	..G	...	...	..T	C.T	..C	...	..G	..T						
Cerithium atratum	---	---	---	---	---	---	---	--T	.GG	A.T	..A	...	...	C.C	..T	C..	T..	...	..N	..C						
G. chinensis 414/415	..T	..A	...	...	..A	...	...	..C	...	..T	..A	...	...	C.T	...	...	T..	...	..A	..T						
G. chinensis 416	..T	..A	...	...	..A	...	...	..C	...	..T	..A	...	...	C.T	...	...	T..	...	..A	..T						
Tricula sp. 453/454	..T	..A	...	..G	..A	...	..A	..C	...	..T	..T	...	...	C.T	...	...	T..	...	..A	..T						
O. hupensis hupensis 93	..T	..A	..C	...	..A	..G	..A	..A	C.T	..T	..C	...	..C	C.T	...	...	T..	...	...	...						
O. hupensis hupensis 96	..T	..A	..C	...	..A	..G	..A	..A	C.T	..T	..C	...	..C	C.T	...	...	T..	...	...	...						
O. hupensis robertsoni 45	..T	..A	...	...	..G	..G	..A	...	...	..T	..T	...	...	C.T	...	...	T.G	...	...	...						
O.hupensis robertsoni 48	..T	..A	...	...	..G	..G	..A	...	...	..T	..T	...	...	C.T	...	...	T.G	...	...	...						
H. cf. *pontieuxini* 346/347	..T	..A	...	...	..G	...	T..	..C	C.G	..C	..T	..A	..A	C..	..T	...	...	...	...	..T						
H. cf. *pontieuxini* 351	..T	..A	...	...	..A	...	T..	..C	..G	..C	..T	..A	..A	C..	..T	...	...	...	...	..T						
H. neglecta 435/436/439	..T	..A	...	...	..G	..G	T..	..A	...	...	..T	..A	..A	C..	..T	..G	T..	...	...	..T						
S. turriculata 474/476/477	..T	..A	...	...	..A	...	T..	...	C..	..T	..A	..A	...	...	...	..T	...	...	...	..T						
T. pulchella 479	..T	...	...	..A	..G	..G	T..	..T	C.T	..T	..A	...	..A	...	..T	...	T..	...	..A	..T						
T. pulchella 480	..T	...	...	..A	..G	..G	T..	..T	C.T	..T	..A	...	..A	...	..T	...	T..	...	..A	..T						

GAG	CTA	GGT	CAA	CCA	GGG	GCT	TTA	TTG	GGG	GAT	GAC	CAA	CTG	TAT	AAT	GTT	ATT	GTC	ACA	GCT	CAT	GCT	TTT	GTT	135	
...	..C	..G	...	..C	...	...	...	C.T	..A	...	..T	...	T.A	...	...	..A	...	..G	..G	..A	...	...	...	..A		
..A	T..	..A	..G	..T	...	...	..C	C.T	C.T	..T	...	..T	..G	..A	...	...	..A	...	..A	..G	..A	...	..C	..C	..A	
...	..T	...	...	..T	..A	..A	...	..A	..T	...	..T	...	..T	...	...	...	...	...	..T	...	..A	...	..A	...	..A	
...	..T	...	...	..T	...	..A	...	..A	..T	...	..T	...	..T	...	...	...	...	...	..T	...	..A	...	..A	...	..A	
...	T..	..G	...	...	..A	..G	C..	..A	..T	...	..T	...	..T	...	...	..A	...	..T	...	..G	...	..A	...	..A	
...	T..	..A	..G	..T	...	...	..G	C.T	...	...	..T	..G	..C	...	..C	..A	...	..T	...	..A	...	..A	...	..G		
...	T..	..A	..G	..T	...	...	..G	C.T	...	...	..T	..G	..C	...	..C	..A	...	..T	...	..A	...	..A	...	..G		
...	T.G	..G	..G	...	...	...	...	C.T	..A	...	..T	...	..T	...	...	..A	...	..T	...	..A	...	..A	...	..A		
...	T.G	..G	..G	...	...	...	...	C.T	..A	...	..T	...	..T	...	...	..A	...	..T	...	..A	...	..A	...	..A		
..A	T..	..G	..G	...	..T	..A	C.T	..A	...	...	..T	..G	..C	...	..C	..G	...	..A	..T	...	...	...	...	...		
..A	T..	..G	..G	...	..T	..A	C.T	..A	...	...	..T	..G	..C	...	..C	..G	...	..A	..T	...	...	...	...	...		
..A	...	...	..G	..T	..T	..G	C.T	...	..T	...	..T	..G	..T	...	..C	..A	...	..T	..T	...	...	..C	...	...		
..A	...	...	...	..T	..A	...	...	..A	..T	...	...	..G	..T	...	..C	..A	...	..A	..T	...	...	...	...	A..		
..A	T..	..C	...	..G	..T	...	C.C	..A	..T	..C	..T	...	..T	...	...	..A	...	...	..G	...	..C	...	...	..A		
..A	T..	..C	...	..G	..T	...	C.C	..A	..T	..C	..T	...	..T	...	...	..A	...	...	..G	...	..C	...	...	..A		

ATA	ATT	TTT	TTT	TTG	GTT	ATG	CCT	ATA	ATA	ATT	GGG	GGG	TTT	GGT	AAC	TGG	CTA	GTG	CCT	TTA	ATG	TTA	GGG	GTG	210	
...	..C	..C	...	..A	...	..A	..C	..G	..G	...	..A	...	...	..C	..T	..A	..G	..T	..C	C.G	..A	...	..T	.CA		
...	...	..C	...	..A	..A	...	..A	...	...	...	..T	..A	...	..C	..T	..A	T.G	..T	..C	C.T	...	..G	..A	.CT		
...	...	...	...	..A	...	...	...	...	..G	...	..T	..T	...	..A	...	..A	..G	A.T	..A	...	...	...	...	.CT		
...	...	...	...	..A	...	...	...	...	..G	...	..T	..T	...	..A	...	..A	..G	A.T	..A	...	...	...	...	.CT		
...	...	..C	...	...	...	..A	...	...	...	...	..T	..T	...	..A	..T	..A	T..	A.T	...	C..	..A	...	..A	.CT		
...	..C	...	..C	...	..A	..A	..A	...	...	...	..T	..T	..C	...	..T	...	..G	..T	...	C.T	..A	C..	...	.CT		
...	..C	...	..C	...	..A	..A	..A	...	...	...	..T	..T	..C	...	..T	...	..G	..T	...	C.T	..A	C..	...	.CT		
...	...	...	...	..A	..A	..A	..A	...	...	...	..T	..C	...	...	..T	...	T..	..T	..A	...	..A	C.C	...	.CT		
...	...	...	...	..A	..A	..A	..A	...	...	...	..T	..C	...	...	..T	...	T..	..T	..A	...	..A	C.C	...	.CT		
...	...	...	..C	C.T	..A	..A	..C	...	...	...	..T	..C	...	..G	...	..A	...	...	...	...	..A	C.C	..T	.CA		
...	...	...	..C	C.T	..A	..A	..C	...	...	...	..T	..C	...	..G	...	...	...	...	...	...	..A	C.C	..T	.CA		
..G	...	...	..C	C.T	..A	...	...	...	...	...	..T	..C	...	..A	..T	..A	T..	...	...	...	..A	C.T	..T	.CT		
...	...	...	...	..A	..A	..A	..C	...	...	...	..A	..A	...	..A	..T	..A	T..	..T	...	...	..A	...	..C	.CT		
...	...	...	..C	..A	...	..A	..A	...	...	...	..T	..T	...	..A	...	..A	T..	..T	..G	...	..A	...	...	.CT		
...	...	...	..C	..A	...	..A	..A	...	...	...	..T	..T	...	..A	...	..A	T..	..T	..G	...	..A	...	...	.CT		

(*continued*)

TABLE 2. (*Continued*)

```
CCG GAC ATG GCT TTC CCC CGG TTA AAT AAT ATA AGT TTT TGA CTT TTG CCT CCG GCA TTA TGT CTT TTG TTA GCT  285
..A ..T ..A ... ..T ..T ..T ... ... ..C ..G ..A ... ... ..G C.T ... ..T ..G C.T CT. ..A ..A C.T T.C
..T ... ..A ... ... ..T ..A ... ... ... ... ... ..C ... ... ..A ... ..A ..T C.T CTC ..C C.T ... T..
..A ..T ..A ..A ..T ..A ..T ... ... ... ... ..A ... ... T.A C.T ..C ..A ..T C.. .TA T.A C.C C.. T..
..A ..T ..A ..A ..T ..A ..T ... ... ... ... ..A ... ... T.A C.T ..C ..A ..T C.. .TA T.A C.C C.. T..
..A ... ..A ..A ..T ..T ..T ..G ... ... ... ..A ... ... T.A C.T ... ..T ... ... .TG T.G ... ... T..
..T ... ..A ..A ... ... ... C.. ... ... ... ..A ..C ... ... C.T ... ... ... ... .TA T.A C.T C.G T..
..T ... ..A ..A ... ... ... C.. ... ... ... ..A ..C ... ... C.T ... ... ... ... .TA T.A C.T A.G T..
..T ..T ..A ..A ..T ..T ... C.. ... ... ..G ..A ... ... ..C C.T ... ..A ... C.. ..A T.G C.C C.. T.C
..T ..T ..A ..A ..T ..T ... C.. ... ... ..G ..A ... ... ..C C.T ... ..A ... C.. .TA T.G C.C C.. T.C
..A ..T ... ... ..T ..G ..A C.T ... ..C ... ... ..C ... T.A ... ... ..C ..T ... .TA ..G ..A C.. T..
..A ..T ... ... ..T ..G ..A C.T ... ..C ... ... ..C ... T.A ... ... ..C ..T ... .TA ..G ..A C.. T..
..A ..T ..A ... ..T ..T ... C.T ... ..C ... ... ..C ... ... ..A ..C ..T ..T ..G CTA ..A ..A C.T T..
..T ..T ..A ... ..T ..T ..A ... ... ... ... ..A ... ... T.A C.T ... ..T ..T ... .TA T.A ..A ... T..
..A ..T ... ..A ..T ..T ..A ... ... ..C ... ..A ... ... T.A C.T ... ..C ..T ... .TA T.G C.T C.T T..
..A ..T ... ..A ..T ..T ..A ... ... ..C ... ..A ... ... T.A C.T ... ..C ..T ... .TA T.G C.T C.T T..

TCA GGG GCG GTT GAG AGG GGG GCT GGG ACT GGG TGA ACT GTG TAT CCT CCT TTG GCG GGG AAT GTG GGG CAT GCT  360
... .CT ..C ..A ..A ..T ..A .T. ... ..A ..A ... ... ..T ..C ... ..A ... ..T ... ... C.T .C. ... ...
... .CA ..A ..A ... ... ..T .T. ..A ... ..C ... ... ..T ... ... ... ..A ..A ... ... C.A .CT ..C ..A
..G .CA ..A ... ..A ... ..A ..A ..T ..C ..A ... ..A ..C ..C ... ..A C.T ..T ..A ... T.A .CT ... ...
..G .CA ..A ... ..A ... ..A ..A ..T ..C ..A ... ..A ..C ..C ... ..A C.T ..T ..A ... T.A .CT ... ...
... .CT ..T ... ..A ..A ..A ..C ..A ... ..A ... ... ... ..A ... ..A ..A C.T ..T ..A ... T.A .CT ... ...
..G .CC ..T ... ..A ..T ..T ..A ..T ... ... ..G ..A ..A ..C ..A ..A C.T ..C ..A ... C.A .CC ... ...
..G .CC ..T ... ... ..T ..T ..A ..T ... ... ..G ..A ..A ..C ..A ..A C.T ..T ..A ... C.A .CC ..C ...
... .CT ..C ... ..A ... ..A ..C ..T ..C ..C ... ..A ... ... ..A ..A C.T ..T ..A ... T.A .CT ..C ...
... .CT ..C ... ..A ... ..A ..C ..T ..C ..C ... ..A ... ... ..A ..A C.T ..T ..A ... T.A .CT ..C ...
..T .CA ..A ... ..A ..C ..T ... ..A ..A ... ... ... ... ... ... ... C.T T.T A.C ..C T.. .CA ... ..C
..T .CA ..A ... ..A ..C ..T ... ..A ..A ... ... ... ... ... ... ... C.T T.T A.C ..C T.. .CA ... ..C
..G .CA ..T ..A ... ..A ..A ..A ... ..A ..A ... ..C ... ... ... ..C ..A ..A T.T A.T ..C A.T .CT ..C ..G
..T .CC ..A ..A ..A ... ..T .TA ..A ..A ..A ..G ... ..A ... ... ... ..A T.T ... ..C T.. .CT ... ...
..T .C. ..C ..A ..A ..A ..A ... ..T ..A ..A ... ... ..A ... ..A ..A ... ..C .CT ... T.. .CC ... ..C
..T .C. .GC ..A ..A ..A ..A ... ..T ..A ..A ... ... ..A ... ..A ..A ... ..C .CT ... T.. .CC ... ..C

GGT GGA TCT GTT GAC TTA GCT ATT TTT TCT TTA CAT TTA GCT GGA GTA TCG TCT ATT TTA GGG GCT GTT AAT TTT  435
..A ..T ..A ..A A.T C.T ..A ... ... ... C.G ... ... ..A ..T ... ..C ... ..C ..G ..T ..A ..A ..C ...
..G ... ..A ..C ... ... ... ... ..C ... C.T ..C C.. ... ..G ..T ..T ... ... ... ... ... ..A ..C ..C
..C ..T ... ... ..T ... ... ... ... ... ... ... ... ... ..T ... ..T ... ... ... ... ... ..A ... ...
..C ..T ... ... ..T ... ... ... ... ... ... ... ... ... ..T ... ..T ... ... ... ... ... ..A ... ...
... ..G ... ... ..T ... ... ... ... ... ... ... ..C ... ... ..T ... ..T ..A ... ... ..A ... ..A ... ...
... ..C ... ... ..T ... ... ... ... ... ... ... ... C.G ... ..T ..T ..A ... ... ... ..T ... ..A ..C ...
... ..C ... ... ..T ... ... ... ... ... ... ... ... C.G ... ..T ..T ..A ... ... ... ..T ... ..A ... ...
... ..T ... ..A ..T ... ... ... ... ... ... C.. ..C ... ... ..T ..T ..A ... ... ... ..T ... ..A ... ...
... ..T ... ..A ..T ... ... ... ... ... ... ... ..C ... ... ..T ..T ..A ... ... ... ..T ... ..A ... ...
... ..G ... ..A ..T ... ... ... ... ... ... C.T ..C ... ... ..T ..T ..T ..A ... C.T ... ... ..A ... ...
... ..G ... ..A ..T ... ... ... ... ... ... C.T ..C ... ... ..T ..T ..T ..A ... C.T ... ... ..A ... ...
..G ..G ... ..A ..T ... ... ... ... ... ... C.C ..C ... ..G ..T ..T ..T ... ... C.T ... ... ..A ... ...
..A ..T ... ..A ..T C.T ... ... ... ... ... ... C.. ... ..G ..T ..T ..A ... ... ..A ... ..A ... ...
..A ... ..A ..A ..T ... ..C ... ... ... C.C ... ... ..G ..T ..T ..T ..G ... ... ..T ... ..A ... ...
..A ... ..A ..A ..T ... ..C ... ... ... C.C ... ... ..G ..T ..T ..T ..G ... ... ..T ... ..A ... ...
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ATT ACT ACA ATT GTA AAT ATA CGA AGA GAA GGG ATA CAA TTA GAG CGA TTA CCT TTG TTT GTT TGG TCT GTA AAA  510
... ... ..A ... A.T ..C ... ..T G.G CGT ..T ... ..T ... ..G C.T ... ..A ... ..A ... ..G ... ...
... ... ..C ... A.T ..C ..G ... T.. CG. ..A ... ..G ..C ... ..G C.T ... C.T ... ..G ... ..A ... ...
... ... ..A ... ..T ... A.T ..C ... ... T.. CGT ..T ... ... ..T ..A ... C.T ..A ..A ... ..A ... ..A ... ...
... ... ..A ..T ... A.T ... ... ... T.. CGT ..T ... ... ..T ..A ... C.T ..A ..A ... ..A ... ..A ... ...
... ... ... ..T ... A.T ... ... ... T.. CG. ..A ... ... ..T ..A ... C.T ... ..A ... ... ... ... ... ...
... ... ... ..T ... A.T ... ... ... T.G CGT ... ..G ... ..T ..A ... C.T ... ..A ... ... ... ..A ..A ..G .T.
... ... ..C ..T ... A.T ... ... ... T.. CGG ..A ... ... ..T ..A ... C.T ... ..A ... ... ... ..A ..G ..G .T.
... ... ..C ..T ... A.T ... ... ... T.. CGG ..A ... ... ..T ..A ... C.T ... ..A ... ... ... ..G ..G ..G .T.
... ... ..A ..C ... A.C ... ... ... T.. CG. ..A ... ... ..G ..T ..A ..G C.T ... ... ... ..C ..A ... ... ..G
... ... ..A ..C ... A.C ... ... ... T.. CG. ..A ... ... ..G ..T ..A ..G C.T ... ... ... A.C ..A ... ... ..G
... ... ..A ..T ..C A.T ... ... ... ..G T.. CG. ..A ..G ..G ..T ... ..G C.T ..G ... ..C ..A ..A ... ... ...
... ... ..C ..T ... A.T ... ... ... T.. C.. ..A ..G ... ... ..T ... ..A ..T A.G ... ..A ... A.. ..A ..G ..T ...
... ... ... ..T ..C A.T ... ... ... T.. CG. ..T ..G ..G ..T ... ... ..G C.T ... ..A ... ... ..A ..A ... ...
... ... ... ..T ..C A.T ... ... ... T.. CG. ..T ..G ..G ..T ... ... ..G C.T ... ..A ... ... ..A ..A ... ...

ATT ACT GCT ATT TTG TTA TTG CTT TCC TTG CCT GTT TTA GCT GGA GGA ATT ACA ATA TTG TTA ACT GAT CGT AAT  585
..A ... ... ..A ... A.C C.C C.T T.A ..T C.T ... ... ... ... ... ... ... ... ... ... ..G C.A ... ..G ... ..A ..C
..C ... ... ..C G.. C.T ... C.T ... ... ... C.. ... ..A C.T ... ..A ..T ..CT ... ... ..T ..G C.T C.T ... ... ..C ... ..G ..C
... ... ... ..A G.. ..A C.T C.T T.A ... ... ..A ..G ... ... ... ... ..G .CT ... ... ..T ..G C.T C.T ... ... ..C ... ..A ..C
... ... ... ..A G.. ..A C.T C.T T.A ... ... ..A ..G ... ... ... ... ..G .CT ... ... ... ..A ... ... ... ... ... ..A ..C
... ... ... ..C G.. G.A ... ..A T.A ..T C.T ... ... ... ... ... ... ..T .CT ... ... ... C.A ..G ... ... ... ..A ...
..C ... ... ... G.. ..A C.C ... ... ..A ..T C.T ... ... ... ... ... ... ..G .CT ... ... ... C.T ... ... ... ..A ...
..C ... ... ... G.A ..A C.C ... ... ..A ..T C.T ... ... ... ... ... ... ..G .CT ... ... ... C.T ... ... ... ..A ...
... ... ... ... G.A C.A ... ... ..A ..T C.T ... ... ... ... ... ... ..T .CC ... ... ... C.C C.. ... ..C ... ..A ...
... ... ... ... G.A C.A ... ... ..A ..A ..T C.T ... ... ... ... ... ... ..T .CC ... ... ... C.C C.. ..C ..C ..A ...
... ... ... ... ... ..A ... ..G C.A T.A ... ..T C.A ... ... ..C ... ... ..G ... ... ..C ... ... ..T ..G C.T C.. ... ..G ... ..A ...
... ... ... ... ... ..A ..G C.A T.A ... ..T C.A ... ... ..C ... ... ..G ... ... ..C ... ... ..T ..G C.T C.. ... ..G ... ..A ...
... ... ... ... C.A ... ... ... ..A ..T ..A ... ... ..C ... ... ... ..C ... ... ..T ..CT ... ... ..T ..G C.T ... ... ..G ... ..A ...
... ... ... ... ..A ... ... ... C.C T.A ..T C.T ... ... ..C C.T ... ... ..T .C. ... ... ..T ... C.T ... ... ..A ... ..A ...
... ... ..A ... ... ..A ... ... ... ..A ..A ..T ... ... ..A ..G ... ... ..T .C. ... ... ..T ..G C.C ... ... ... ..A ... ..A ...
... ... ..A ... ... ..A ... ... ... ..A ..A ..G ... ... ..A ..G ... ... ..T .C. ... ... ..T ..G C.C ... ... ... ..A ... ..A ...

TTT AAT ACT TCT TTT TTT GAT CCT GCN GGA GGG GGG GAT CCT ATT TTA TAC CAA CAT TTG 645
... ... ..A G.A ..C ... ... ..A ..A ..G ... ... ... ... ... ... ... ... ... ... ...
... ... ..A G.. ..C ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ...
... ... ..A G.. ... ... ... ... ... ..T ..T ..T ..T ..C ..A ... C.T ..T ..T ... ... C.T
... ... ... G.. ... ... ... ... ... ..T ..T ..T ..T ..C ..A ... C.T ..T ..T ... ... C.T
... ... ... G.. ... ... ... ... ... ..T ..T ..T ..T ..A ... ..A ... C.T ..T ... ... C.T
... ... ..G G.C ... ... ... ..C ..A ..C ..G ..T ..T ..T ... ... ... ... ... ..C C.T
... ... ... G.C ... ... ... ..C ..A ..C ..G ..T ..T ..T ... ... ... ... ... ..C C.T
... ... ... G G.. ... ... ... ..G ..T ... ..T ..T ..A ... ... A N.. C.T ..T ..G AC. C.T
... ... ..G G.. ... ... ... ..G ..T ... ..T ..T ..A ... ..A ..N. C.T ..T ..N AC. C.T
... ... ..C ... ..C ... ... ... ... ..A ... ... ... ... ... ... ... ..G ..T ..G ... C.A
... ... ..C ... ..C ... ... ... ... ... ... ... ... ... ... ... ..G ..T ..G ... C.A
... ... ... ..A G.. ... ..C ..C ..A ..A ..G ..T ..A ..C ... ... ... ... ..G ..C C.T
... ... ..A ... ..G G.. ... ... ... ..T ... ..G ..A ..T ..A ... ..A ... ... ..G ... C.C
... ... ... ..G G.. ... ... ... ..C ... ... ..T ... ..A ... ... ... C.T ..T ..G ... ..A
... ... ... ..G G.. ... ... ... ..C ... ... ..T ... ..A ... ... ... C.T ..T ..G ... ..A
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tatively assign this deletion to a compression-based misreading of sequence in a GC-rich region.

Felsenstein's distance matrix of sequence divergence, based on data in Table 2, is given in Table 3. Individuals of a population differed by nucleotide divergence values of 0.005 ± 0.004 (N = 5). The subspecies of *Oncomelania hupensis* differed by 0.148 ± 0.004 (N = 4). The two species of *Hydrobia* differed by 0.162 (range 0.161 – 0.163). The genera *Tricula* vs. *Gammatricula* differed by 0.132 (range of 0.130 – 0.133). The subfamily Pomatiopsinae vs. the Triculinae differed by 0.179 ± 0.020 (N = 12). The families Hydrobiidae vs. Pomatiopsidae differed by 0.267 ± 0.016 (N = 21). The non-rissoacean outgroup snail taxa differed from the rissoaceans by 0.274 ± 0.023.

The unrooted maximum likelihood tree with the polyplacophoran as outgroup is given in Figure 1. Replacement of *Katharina* by *Setia* as the outgroup does not change the topology of the remaining tree. From these trees the following are clear: (1) The pomatiopsid taxa are one distinct clade; the other rissoaceans form a second distinct clade; (2) The truncatellids are more closely allied to the hydrobiids than to the pomatiopsids; (3) The rissoid *Setia* is part of the Truncatellidae-Hydrobiidae clade (except in Fig. 2, where it is the outgroup); (4) The two subspecies of *Oncomelania* are clearly divergent; (5) The triculine taxa appear divergent from the pomatiopsine taxa. However, the triculine node is only weakly supported (54% bootstrapping value).

The Hennig86 analysis using *Setia* as outgroup yielded two equally parsimonious trees with a length of 517, a consistency index of 0.66 and a retention index of 0.74. The Nelson consensus tree is shown in Figure 2. The pomatiopsids are in one clade, the hydrobiids and truncatellids in another. The results are the same as in the maximum likelihood analysis except that the position of *Tricula* is unresolved: there is a trifurcation in the pomatiopsid clade with *Tricula* not unequivocally within a triculine clade (it is in one of the alternative Hennig trees).

The trees obtained using *Stramonita* and *Cerithium* as outgroups are given in Figures 3 and 4. The maximum likelihood analysis (Fig. 3) yields a tree for the ingroup taxa similar to that in Figure 1 except that *Tricula* is a sister taxon to *Oncomelania* rather than to *Gammatricula*. The PAUP-based parsimony analyses (Fig. 4) again clearly define two major clades, a Pomatiopsidae clade and a Truncatellidae-Hydrobiidae clade. The analysis produced two shortest trees of 974 steps; the set of four next shortest trees required one additional step; the latter were not included in computing the Adams consensus tree. The two shortest trees differed in their placement of *Setia* within the hydrobiid clade, thus resulting in a consensus tree with a trifurcation in this clade.

DISCUSSION

Taxonomic decisions should not be made on the basis of molecular distance coefficients alone (Davis, 1994), but on anatomical, cytological and developmental data within an ecological context. Thus, the COI data presented here must be examined in light of the available anatomical data and the patterns of evolution evidenced in the clades shown here. The data provide a beginning of showing relationships; there are insufficient hydrobiid, truncatellid and rissoid genera and species involved in this study to strongly support discrete rissoid, truncatellid, and hydrobiid clades. The data are, however, sufficient to answer our questions and provide the basis for predictions concerning family relationships indicated here.

The hydrobiids and pomatiopsids are distinct clades. The genetic data coupled with anatomical data reviewed in Davis (1979, 1980, 1992) show that these clades are greatly divergent. The COI sequence data strongly support the existence of a pomatiopsid clade separate from the hydrobiids.

The distinctiveness of the pomatiopsid clade is further evidenced by the grouping of the Rissoidae and Truncatellidae with the Hydrobiidae within one clade. Thus, a second question is answered: the Truncatellidae, by these data, are more allied genetically with the Hydrobiidae than with the Pomatiopsidae. However, the truncatellid branch is weakly supported, so additional data are required. Davis (1979) and Ponder (1988) hypothesized that the Truncatellidae were closely related to the Pomatiopsidae (Rosenberg, 1996a). The Pomatiopsidae share with the Truncatellidae and Assimineidae the evolution to terrestriality from aquatic and amphibious habitats in some clades (Rosenberg, 1996b). However, the anatomical data available are insufficient to resolve whether the Truncatellidae are closer phylogenetically to the Hydrobiidae or to the Pomatiopsidae.

TABLE 3. Distance matrix of sequence divergence over 578 nucleotide positions in the cytochrome *c* oxidase I gene under maximum likelihood method.

	Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	*K. tunicata*	—															
2	*S. haemastoma*	0.3229	—														
3	*C. atratum*	0.3153	0.2895	—													
4	*G. chinensis* 414/415	0.2597	0.2360	0.2809	—												
5	*G. chinensis*	0.2571	0.2336	0.2784	0.0017	—											
6	*Tricula* sp. 453/454	0.2457	0.2608	0.2800	0.1304	0.1325	—										
7	*O. hupensis hupensis* 93	0.2752	0.2846	0.2838	0.1972	0.1949	0.1902	—									
8	*O. hupensis hupensis* 96	0.2784	0.2957	0.2820	0.2023	0.2000	0.1858	0.0122	—								
9	*O. hupensis robertsoni* 45	0.2698	0.2662	0.2647	0.1745	0.1723	0.1468	0.1526	0.1465	—							
10	*O. hupensis robertsoni* 48	0.2704	0.2661	0.2647	0.1701	0.1679	0.1425	0.1484	0.1424	0.0035	—						
11	*H.* cf. *pontieuxini* 346/347	0.2874	0.3026	0.2936	0.2761	0.2761	0.2353	0.2808	0.2844	0.2567	0.2566	—					
12	*H.* cf. *pontieuxini* 351	0.2850	0.3106	0.2964	0.2788	0.2788	0.2379	0.2835	0.2871	0.2544	0.2343	0.0052	—				
13	*H. neglecta* 435/436/439	0.3098	0.3017	0.2749	0.2665	0.2665	0.2417	0.2834	0.2769	0.2605	0.2605	0.1612	0.1634	—			
14	*S. turriculata* 474/476/477	0.2683	0.2645	0.2771	0.2269	0.2293	0.2051	0.2582	0.2589	0.2431	0.2381	0.2193	0.2218	0.2426	—		
15	*T. pulchella* 479	0.2830	0.2582	0.2872	0.2113	0.2113	0.2014	0.2413	0.2519	0.2237	0.2237	0.2164	0.2235	0.2080	0.2190	—	
16	*T. pulchella* 480	0.2862	0.2613	0.2904	0.2141	0.2141	0.2041	0.2442	0.2549	0.2266	0.2265	0.2192	0.2264	0.2108	0.2218	0.0017	—

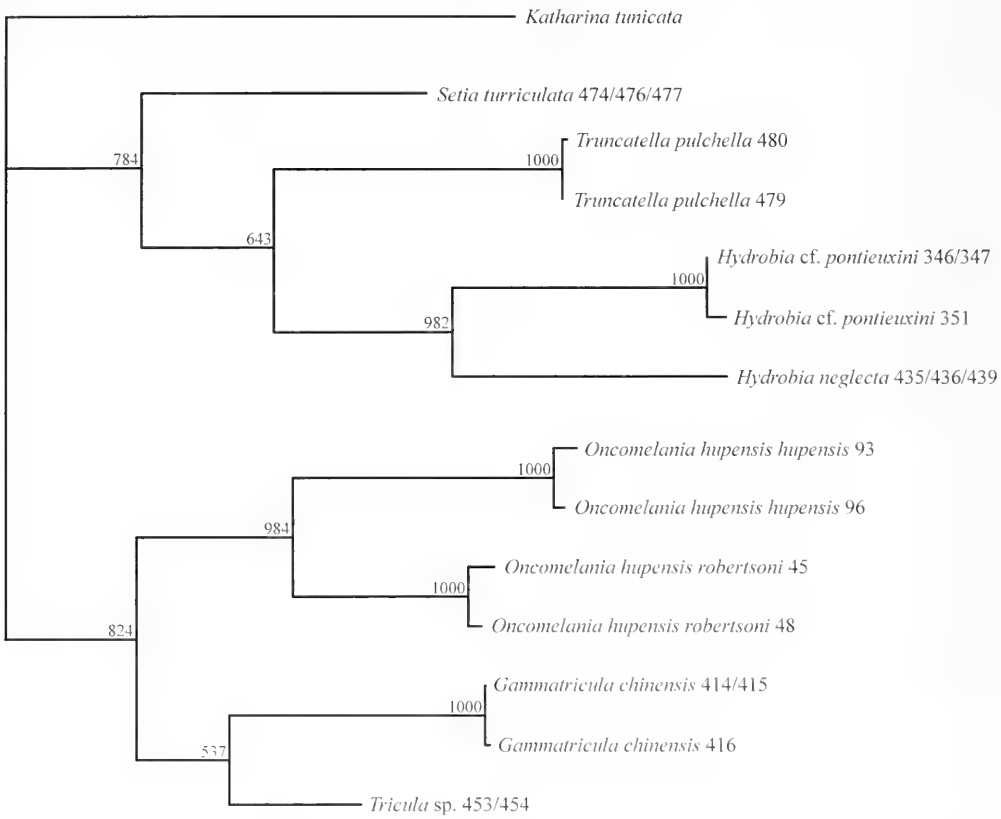

FIG. 1. Unrooted tree based on maximum likelihood with *Katharina tunicata* as the outgroup. Bootstrap values (1,000 replicates) are indicated for each node.

Anatomical data do indicate that the Rissoidae are sister taxa to the Hydrobiidae and the Truncatellidae.

A 28S ribosomal RNA phylogeny placed the Hydrobiidae as a sister group to the Truncatellidae and the Pomatiopsidae, with a terminal *Truncatella*-Pomatiopsidae clade divergent from another *Truncatella* group (Rosenberg et al., 1997). However, as Davis (1994) pointed out, one must be circumspect in assessing phylogenies based on 28S rRNA. In the results presented by both Davis (1994) and Rosenberg et al. (1994, 1997) involving rRNA, there were some considerable surprises not supported by comparative anatomy and allozyme-based phylogenies, due in part to the insufficient quantity of informative characters (85) to resolve a large assemblage (40) of divergent taxa.

In the rRNA data presented by Davis (1994: fig. 10) there were many more differences among margaritiferine taxa than among all other unionid taxa. *Cumberlandia* was basal in the unionid clade, whereas *Margaritifera margaritifera* and *M. falcata* were highly divergent from each other in a margaritiferine clade. The results were as if rRNA evolution went unexplainably berserk (greatly accelerated) in the Margaritiferidae; results not supported by any other data (see also Ledyard et al., 1996). In contrast to the rRNA sequence data, the results with mitochondrial genes have been congruent with results based on other data, and the total weight of evidence leads us to consider the truncatellids within the same clade as, and closely related to the Hydrobiidae, but divergent from the Pomatiopsidae. This is our hypothesis to be challenged with results based on yet other genes.

The COI sequence data are congruent with cytochrome *b* gene sequence data involving populations of *Oncomelania hupensis* from mainland China; the results showed evidence for two distinct subspecies: *O. h. hupensis* and *O. h. robertsoni* (Spolsky et al., 1996). Both data sets are congruent with an al-

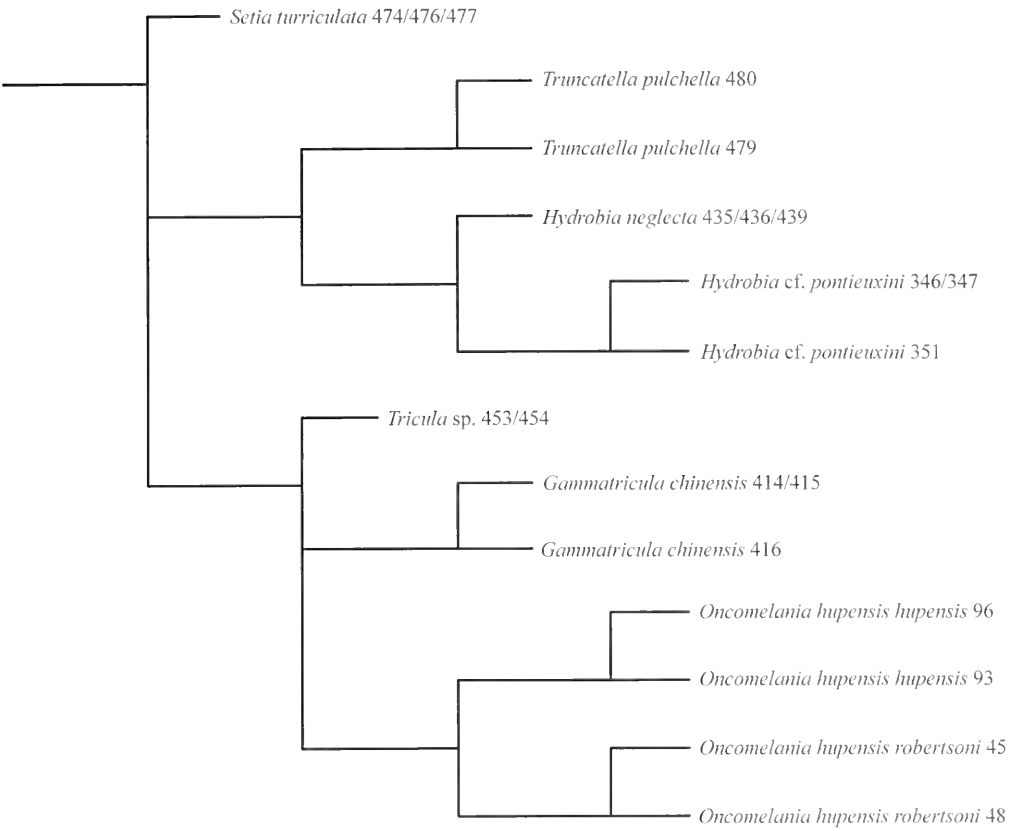

FIG. 2. Unrooted Nelson consensus tree based on Hennig86 analysis, with *Setia turriculata* as outgroup.

lozyme-based phylogeny indicating the occurrence of three subspecies of *Oncomelania hupensis* (the third, *tangi,* from Fujian Province, was not available for the DNA studies). *Oncomelania h. robertsoni* has a smooth shell, no varix, and is relatively shorter in shell length than *O. h. hupensis,* which has strong ribs and strong varix when living in the Yangtze River flood plains, but lacks ribs (although retaining a strong varix) when living above the effects of the annual flooding. *Oncomelania h. robertsoni* lives above the Three Gorges of the Yangtze, whereas *O. h. hupensis* is found below the gorges along the Yangtze River drainages. The distance coefficient between the subspecies using cytochrome *b* data averaged 0.110 (range of 0.1021 – 0.1186), based on *robertsoni* from Yunnan and Sichuan and *hupensis* from Jiang Xi Province. The equivalent average distance in this study is 0.148 ± 0.004 (N = 4) with a range of 0.142 – 0.153. In this study, *robertsoni* came from Yunnan, and *hupensis* from Hubei Province, a province upstream from Jiang Xi. This suggests that the COI gene has diverged more than the cytochrome *b* gene and thus may be more useful to detect population and subspecies divergences and patterns of evolution. That the COI gene appears to have diverged more than the cytochrome *b* is of interest given the conventional understanding that COI tends to be more conservative in most taxa.

The two species of *Hydrobia* differed from each other by a distance coefficient only about 6% greater than the distance between the subspecies of *Oncomelania hupensis,* a surprise given the considerable anatomical differences between the hydrobiid species and the great geographic distance separating them (thousands of ocean miles between Bulgaria and Denmark). In contrast to the large differences between *Oncomelania hupensis* subspecies, two populations of *O. h. robertsoni* separated by over 600 km had a cytochrome *b* difference of only 0.038, a relatively small amount of dif-

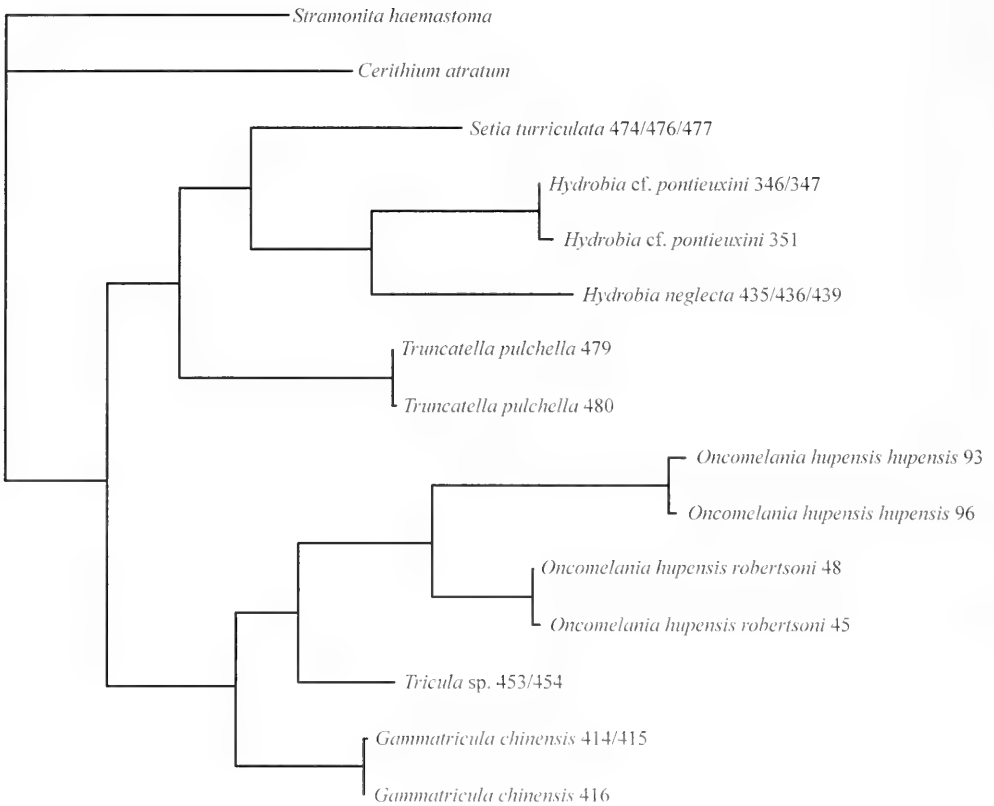

FIG. 3. Unrooted maximum likelihood tree using *Stramonita* and *Cerithium* as outgroups. Character changes were optimally weighted at 1.3:1 for transitions:transversions.

ference. It appears that the subspecies have diverged considerably since *Oncomelania* dispersed into China about 10 million years ago (Davis, 1979, 1980). The considerable genetic divergence is also seen in allozyme data (Woodruff et al., 1988; Davis et al., 1995). The Nei minimum D for *robertsoni* vs. *hupensis* was 0.257 ± 0.077 (N = 21) (Davis et al., 1995). Population variation within *hupensis* was 0.160 ± 0.085 (N = 21). Davis et al. (1995) discuss why we do not consider these taxa as full species. Our question here is what has driven such large genetic divergence when the snails are identical morphologically and anatomically (except for size and presence of ribs on some populations) and can replace each other ecologically? One hypothesis is that, as virtually all populations of *Oncomelania hupensis* throughout its range have been heavily infected with *Schistosoma japonicum*, coevolutionary pressures have been the cause. Added to this are the natural geographical isolation of Yunnan and Sichuan from the central Yangtze River basin and the mountain ranges that separate Fujian Province from the other two regions. We now need considerable population studies of COI sequences to assess the extent of population divergence across China.

Considering the Triculinae issue, it could be argued that, on the basis of anatomy, the Triculinae and Pomatiopsinae are not historically closely related. The pomatiopsine female reproductive system appears considerably different from that of the Triculinae, and what Davis has called the spermathecal duct in each taxon may not be homologous. The data presented here are congruent with allozyme data of Davis et al. (1994) that show general agreement of phylogenies based on both anatomical and allozyme data: *Oncomelania hupensis* is in a clade apart from the three triculine taxa in the allozyme study, *Gammatricula chinensis, Gammatricula songi,* and *Neotricula lilii.* However, the two clades are very close genetically. The Nei D between *On-*

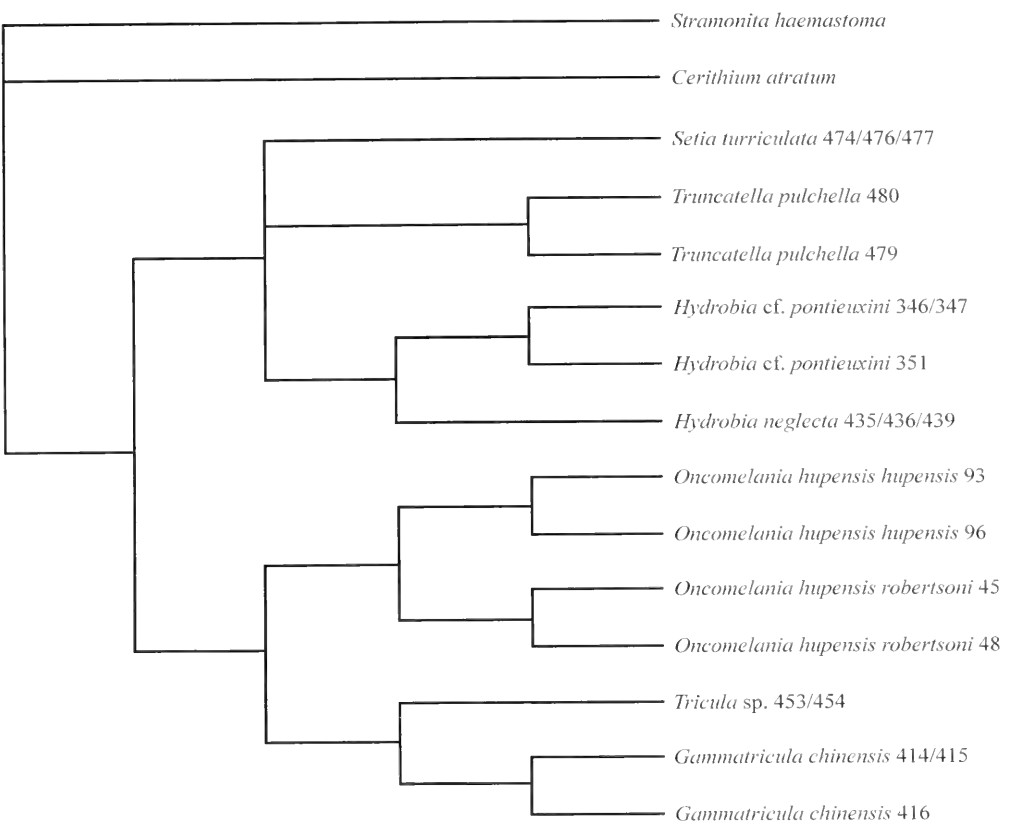

FIG. 4. Unrooted PAUP tree: Adams consensus of two shortest trees produced by a branch and bound search, with transitions and transversions weighted equally.

comelania and the three triculines was 1.293 ± 0.412 (1.000 – 1.764); D among triculines was 0.890 ± 0.301 (0.689 – 1.236). Further, *Oncomelania* was less distant from *Gammatricula chinensis* (1.116) than was *Neotricula lilii* (1.236). Accordingly, the phenogram based on Nei's D does not provide a great separation from the triculine taxa because of the closer relationship of *Oncomelania* to *N. lilii.*

The *Tricula* of this study is a new species that will be described elsewhere; anatomical data confirm its placement in *Tricula.* Hennig86 produced two trees because *O. h. robertsoni* was closer to *Tricula* sp. (0.144) than it was to *O. h. hupensis* (0.150). The two triculine taxa differed by only 0.132. This very close relationship between *Oncomelania* and some triculine taxa shows the overall close relationship between the two pomatiopsid subfamilies and possibly points the way to unraveling the pathway of evolution of the triculines from early pomatiopsids. For example, the Sichuan *Tricula* is, on the basis of anatomy, closely related to Yunnan species of *Tricula* and to the type species, *Tricula montana* from northern India. The average COI distance of *Tricula* sp. from *O. h. hupensis* is 0.188, whereas that of *Gammatricula chinensis* is 0.195; the same set of relationships to *O. h. robertsoni* is 0.144 and 0.171. The premise that emerges from these data is that *O. h. robertsoni* in Yunnan, with its generalized morphological features, is closer genetically to the basal *Oncomelania* stock that gave rise to *Tricula* than is the derived *Gammatricula* and derived *O. h. hupensis* below the Three Gorges. This premise and initial data are consistent with the hypotheses of Davis (1979, 1980, 1992) that pomatiopsids were introduced into Asia from the northeastern Indian Plate with the Himalayan orogeny, with subsequent evolution and dispersal down river systems. The closer genetic relationships of some triculine taxa to *Oncomelania* points the way to assessing the coevolution of *Schisto-*

soma spp. with both *Oncomelania* and Triculinae.

All the phylogenetic analyses combined affirm the monophyly of the Pomatiopsidae, although the placement of *Tricula* within this clade remains unresolved: using *Katharina* or *Setia* as outgroups in a maximum likelihood analysis, *Tricula* clusters with *Gammatricula;* using the closer *Stramonita* and *Cerithium* as outgroups, *Tricula* clusters with *Oncomelania* in a maximum likelihood analysis, but with *Gammatricula* in a parsimony analysis; a Nelson consensus tree of Hennig86 analyses leaves relationships within the Pomatiopsidae as an unresolved trifurcation. In the end, the bootstrap value for the *Tricula* clade tells the story; placement of *Tricula* depends on the method and choice of outgroups. It is not well resolved within the pomatiopsid clade, but all evidence places it in this clade. This question may best be answered by increasing the number of populations and species of *Tricula* and *Gammatricula* in the analyses, increasing the number of nucleotides analyzed, and sequencing an independent nuclear gene.

All five analyses place *Truncatella* in a clade with *Hydrobia.* The placement of *Setia,* however, is problematic: in analyses where it is not used as an outgroup, it clusters with the hydrobiid-truncatellid clade, but its relationships within this clade are uncertain. The unresolved trifurcations are consistent with weak bootstrapping support for those nodes in the maximum likelihood analyses.

Because the distances of *Katharina* to other taxa are not much different than distances among some ingroup members, we examined the number and kind of substitutions occurring in the COI gene. Substitution rates varied tremendously among codon positions, with strong constraints on amino acid changes: 203 of the 215 third codon positions were variable, while 51 of 215 first codon positions and only ten second codon positions were variable. Translation of the nucleotide sequences clearly pointed out the strong constraints on amino acid changes in this gene: the majority of changes were synonymous substitutions. Among this group of 16 taxa, 40 amino acid positions were variable, of which too few (28) were phylogenetically informative. PAUP analysis of the amino acid sequences produces 28 equally parsimonious shortest trees, resulting in a consensus tree with no resolution.

In an attempt to avoid saturation effects on phylogenetic tree construction, we carried out maximum likelihood analyses using only first and second codon positions: again, these analyses resulted in non-robust and implausible trees with poorly supported nodes, although in this case, the pomatiopsid clade does hold together. We plotted pairwise transition/transversion (Ts/Tv) ratios vs. pairwise distances to look for evidence of substitutional saturation. Although saturation must be occurring only at third codon positions, pairwise ratios were based on the whole sequence, as that is what the phylogenetic analyses were based on. Saturation appears to be occurring in pairwise comparisons with the three outgroup taxa *Katharina, Cerithium,* and *Stramonita,* with a mean Ts/Tv ratio of approximately 1.1, and pairwise differences greater than about 130 nucleotides. For ingroup comparisons, pairwise differences were usually less, varying from about 140 to 1. Ts/Tv ratios were roughly correlated with nucleotide differences, such that ratios approached saturation at distances greater than approximately 120 nucleotide differences. Thus, there appears to be a quantitative difference between ingroup and outgroup taxa in the substitution level. The existence of a discrete ingroup provides further support for the robustness of the phylogeny of this group. Further, although the effect of saturation is to shorten branch length, in this case it is not likely to have affected the topology, that is, branching pattern, of the trees because most of the deep branches are sufficiently long to retain the correct branching pattern.

This study should conclusively clarify two points: (1) The Hydrobiidae are not closely related historically, biogeographically, or genetically to the Pomatiopsidae; they are distinctly different families. (2) Schistosomes have evolved with the pomatiopsid lineage in Asia; hydrobiids do not transmit schistosomes. As implied by the term coevolved, there is a historical genetic linkage between the pomatiopsids and schistosomes extending back to Gondwanaland. With the progression of time, this linkage has deepened; once lost, it cannot be restored (Davis, 1992). Thus, we predict that no hydrobiid suddenly *de novo,* can become a host for any schistosome.

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TESTING ALTERNATIVE HYPOTHESES OF *NEOTRIGONIA* (BIVALVIA: TRIGONIOIDA) PHYLOGENETIC RELATIONSHIPS USING CYTOCHROME C OXIDASE SUBUNIT I DNA SEQUENCES

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ABSTRACT

Uncertainties regarding the phylogenetic history within the Bivalvia have impeded attempts to understand evolution within the group. Estimating the evolutionary relationships surrounding the Trigonioida has been especially problematic and has led to disparate hypotheses regarding (1) the origin and subsequent diversification of unionoid bivalves and (2) autobranch gill character state transitions. In order to test alternative hypotheses of trigonioid phylogeny, 613 base pairs of DNA sequence of the cytochrome *c* oxidase subunit I gene were analyzed from 14 species of bivalves (ingroup) and three species of non-bivalve mollusks (outgroup). All phylogenetic analyses, using either nucleotide or inferred amino acid sequences, produced trees that robustly placed *Neotrigonia* (Trigonioida) as the sister taxon to a monophyletic Unionoida. Furthermore, the Autobranchia, Veneroida, and Mytiloida were supported as monophyletic groups in these analyses, whereas the Bivalvia was not. These phylogenetic relationships suggest that (1) there was a single invasion of freshwater by a unionoid bivalve ancestor, (2) trigonioid rather than veneroid bivalves gave rise to the Unionoida, (3) either the eulamellibranchous or filibranchous gill condition has evolved multiple times within the Autobranchia, and (4) the molluscan bivalved body plan may have evolved more frequently than traditional phylogenetic hypotheses suggest.

Key words: Bivalvia, Trigonioida, Unionoida, cytochrome *c* oxidase I, mtDNA, phylogenetics, convergence.

INTRODUCTION

The higher-level phylogenetic relationships within the Bivalvia are poorly understood at present (e.g., Allen, 1985). This statement is corroborated by the many disparate hypotheses of evolutionary relationships that have been proposed for the higher taxa within the Bivalvia (e.g., Purchon, 1990; Waller, 1990; Starobogatov, 1992; Cope, 1996; B. Morton, 1996; Salvini-Plawen & Steiner, 1996). This plethora of phylogenetic hypotheses likely stems, in part, from arbitrary choices to exclude certain types of characters and a general lack of explicit and rigorous phylogenetic analyses. Although major anatomical character suites distinguish two of the nominal subclasses within the Bivalvia, that is, Protobranchia and Autobranchia, the ordinal-level relationships within each subclass are not strongly supported by multiple shared-derived morphological features (e.g., Waller, 1990).

Two contrasting phylogenies of the higher-level relationships within the Bivalvia have recently been proposed by Salvini-Plawen & Steiner (1996; Fig. 1A) and Waller (1990; Fig. 1B). The former study is an exemplar in that explicit data matrices and phylogenetic methodologies were presented. A major point of disagreement between the two phylogenies presented in Figure 1 is the placement of the Trigonioida, a relatively ancient bivalve taxon that, although currently depauperate, was taxonomically diverse during the Mesozoic (Cox et al., 1969; Allen, 1985). The Salvini-Plawen & Steiner hypothesis (Fig. 1A) indicates that the trigonioids are most closely related to pteriomorph bivalves (represented herein by mytiloids), with the Veneroida closely related to the Unionoida. Their proposed sister taxon relationship for the trigonioid and pteriomorph bivalves was supported by the shared presence of (1) byssate larvae and adults and (2) abdominal sense organs in these taxa (Salvini-Plawen & Steiner, 1996). Alternatively, the hypothesis of Waller (Fig. 1B) indicates that the Trigonioida is the sister taxon to the Unionoida. However, no evidential sup-

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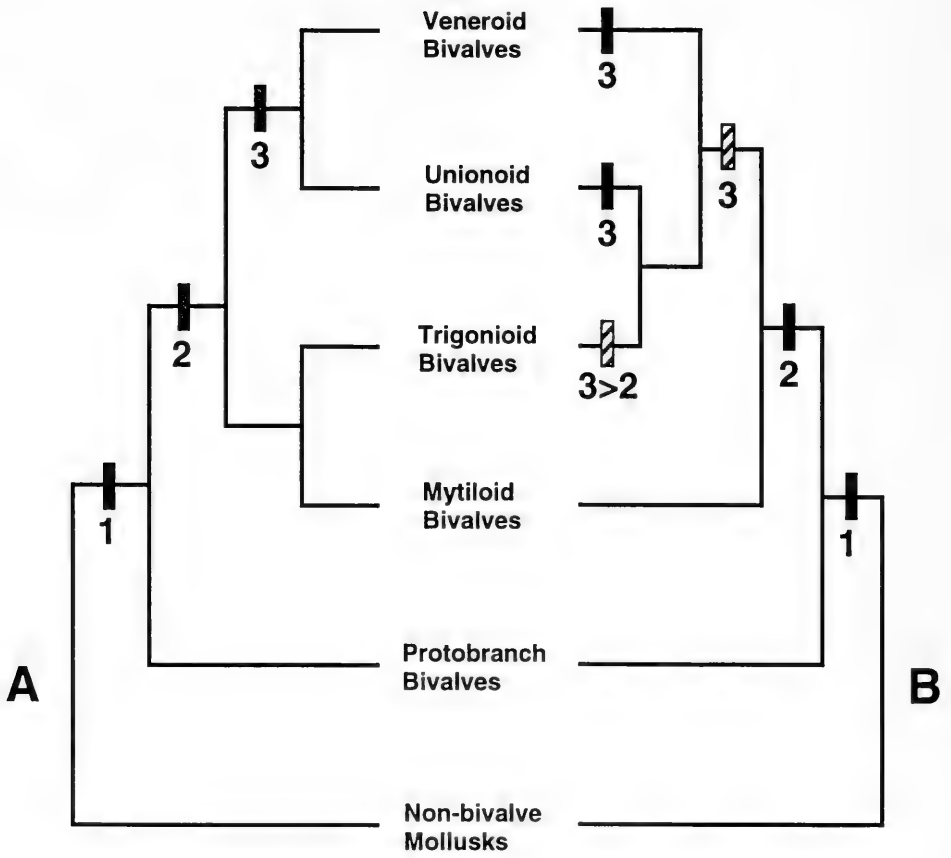

FIG. 1. Bivalve relationships, based on morphological characteristics, according to Salvini-Plawen & Steiner (1996; A) and Waller (1990; B). Both hypotheses indicate a single origin for the Bivalvia (1) and filibranchous lamellibranch gills (2) but differ in their implications for eulamellibranch gill evolution. Hypothesis A indicates a single origin for eulamellibranch gills (3) while B indicates either two origins (solid bars) or a single origin followed by a reversal to the filibranch condition in trigonioids (hatched bars).

port for this relationship was provided by Waller (1990).

The evolutionary affinities of the Trigonioida have been a contentious subject for over a hundred years (e.g., Steinmann, 1888; Neumayr, 1889; Cox, 1960; B. Morton, 1987; Healy, 1989, 1996) and are central to an understanding of bivalve mollusk character evolution, since representatives of the single extant genus (*Neotrigonia*) have a mixture of seemingly primitive (e.g., filibranchous gills [possessing ciliary-linked gill filaments], lack of posterior mantle fusion, nacreous shells; Cox, 1960; Allen, 1985; B. Morton, 1987) and derived features (e.g., multi-vesicular sperm acrosome; Healy, 1989). This mosaic of seemingly primitive and derived character states has contributed to the erection of multiple, disparate hypotheses of trigonioid evolutionary affinities. According to the hypothesis of Salvini-Plawen & Steiner (1996; Fig. 1A), the placement of the trigonioids is consistent with a single origin of eulamellibranch gills (tissue-linked gill filaments) from filibranch gills. In contrast, the phylogenetic placement of trigonioids in the hypothesis of Waller (1990; Fig. 1B) suggests that there were either (1) two origins of eulamellibranch gills or (2) a single origin of eulamellibranch gills followed by a reversal to filibranch gills in the trigonioids.

The phylogenetic uncertainty within the Bivalvia impedes the rigorous testing of evolutionary hypotheses. Therefore, the establishment of a robust phylogenetic hypothesis for higher taxa within the Bivalvia will enable criti-

cal evaluations of (1) trigonioid evolutionary relationships and (2) hypotheses of autobranch bivalve gill character state transitions. Molecular systematic analyses have been useful in situations where morphological analyses were inconclusive (e.g., Avise, 1994). Therefore, mitochondrial DNA (mtDNA) sequences, obtained from the cytochrome *c* oxidase subunit I (COI) gene, were used to construct a phylogenetic hypothesis for the major bivalve lineages represented in Figure 1. COI was chosen for this analysis because of its slow rate of evolution relative to other mitochondrial protein coding genes, relative ease of unambiguous sequence alignment (e.g., Brown, 1985; Simon et al., 1994; Russo et al., 1996), and demonstrated appropriateness for this particular analysis.

MATERIALS AND METHODS

Organisms

The molluscan taxa used in this study, with GenBank accession numbers and primary literature citation (where applicable), are as follows: (1) ingroup, Class Bivalvia, Subclass Protobranchia, Order Solemyoida, *Solemya velum* (U56852), Order Nuculoida, *Nucula tenuis* (U56851), Subclass Autobranchia, Order Unionoida, *Mutela rostrata* (U56849), *Amblema plicata* (U56841), *Anodonta cygnea* (U56842), *Margaritifera margaritifera* (U56847), Order Trigonioida, *Neotrigonia margaritacea* (U56850), Order Mytiloida, *Modiolus modiolus* (U56848), *Geukensia demissa* (U56844), Order Veneroida (the five veneroid COI sequences are from Baldwin et al. [1996]), *Corbicula fluminea* (U47647), *Rangia cuneata* (U47652), *Mercenaria mercenaria* (U47648), *Mytilopsis leucophaeata* (U47649), *Dreissena polymorpha* (U47653), (2) outgroup, Class Scaphopoda *Dentalium* sp. (U56843), Class Gastropoda *Lepetodrilus elevatus* (U56846), Class Polyplacophora *Katharina* sp. (U56845).

Methods

Total DNA was isolated from somatic (mantle) tissues of nine species of bivalves. Male gonadal tissues were specifically avoided during dissections to prevent comparisons of non-orthologous sequences (due to the actual or potential presence of doubly uniparental inheritance of mtDNA in some bivalve taxa; for example, Skibinski et al., 1994; Zouros et al., 1994; Hoeh et al., 1996). DNA was also isolated from representatives of three additional molluscan classes (i.e., Gastropoda, Polyplacophora, and Scaphopoda) for use in generating outgroup sequences. Subsequently, a 710bp fragment of COI was PCR amplified and cycle sequenced for each of the 12 taxa as described elsewhere (Folmer et al., 1994). Both strands of the COI fragment were sequenced from each of two individuals from each terminal taxon to guard against PCR-based contamination artifacts. The resulting 12 COI sequences, plus the five veneroid bivalve COI sequences from Baldwin et al. (1996), were readily aligned by eye using MacClade 3.05 (Maddison & Maddison, 1992). Sixteen of the 17 OTUs produced sequences 613 bp in length, while that of *Geukensia* was 616 bp. The increased length of the *Geukensia* sequence was due to an autapomorphic, three nucleotide (single codon) insertion event. These three contiguous nucleotides, which are phylogenetically uninformative for the taxa considered herein, were deleted prior to all phylogenetic analyses. No additional hypothesized insertion or deletion events were necessary to obtain the alignment utilized in the subsequent analyses.

The suitability of the COI data set for phylogenetic analyses at the required hierarchical level was evaluated by plotting the substitution pattern of transitions and transversions for each codon position (e.g., Orti & Meyer, 1996). Furthermore, the degree of phylogenetic signal within the COI data set was evaluated using the g_1 statistic of a random tree distribution (from 100,000 random trees; e.g., Hillis, 1991; Hillis & Huelsenbeck, 1992) as implemented in PAUP (Swofford, 1993). Phylogenetic analyses were carried out on the COI nucleotide sequences using the maximum likelihood ([ML], DNAML in PHYLIP 3.5c; Felsenstein, 1993), neighbor-joining ([NJ], MEGA 1.02; Kumar et al., 1993), and maximum parsimony ([MP], PAUP 3.1.1; Swofford, 1993) algorithms. *Katharina,* the only non-conchiferan mollusk taxon, was used to root the resulting topologies. A transition/transversion ratio of 2.0 was utilized in the ML analyses and the gamma distance (alpha = 0.5, using the Tamura-Nei model of nucleotide sequence evolution) was used to generate the pair-wise genetic distances for the NJ analyses. This particular distance takes into consideration among-site substitution rate variation (e.g., Yang, 1996). Further-

more, MP and NJ (again using gamma distances, alpha = 0.5) analyses were conducted on the inferred COI amino acid sequences (using the *Drosophila* mtDNA genetic code). Multiple random terminal taxon addition order runs, combined with global branch rearrangement options, were employed to generate topologies from ML and MP analyses. These options increased the probability of finding the actual best topology under each of the two optimality criteria (e.g., Hendy et al., 1988; Maddison, 1991). The robustness of the resulting topologies was evaluated by bootstrap analyses (1,000 replicates for MP and NJ, 100 replicates for ML).

The best COI-based topology derived from the DNAML analysis was compared with the phylogenetic hypotheses presented in Figure 1 using the Kishino-Hasegawa test (paired z test; Kishino & Hasegawa, 1989) as implemented in DNAML. To this end, the topological constraints option in PAUP was used to generate 82 user trees (all trees ≤ five steps longer than the shortest trees found by PAUP) representing the two tree topologies (for the particular taxa evaluated herein) in Figure 1. Each of these user trees was then compared to the best DNAML tree by the Kishino-Hasegawa algorithm. This test evaluated the significance of any potential incongruence between the morphology- (Figure 1) and COI-based topologies (Swofford et al., 1996). In addition, character optimization, using MacClade (Maddison & Maddison, 1992), was carried out on the COI-based topologies to investigate their implications for morphological character evolution within the Bivalvia.

RESULTS

Scatter plots of the relationship between the number of transitional and transversional substitutions at each of the three codon positions and the proportion of nucleotide differences (all positions) for the COI sequences revealed that only transitional substitutions at the third codon position had reached saturation (Fig. 2). Because saturated categories of substitution can contribute to erroneous estimates of evolutionary history (e.g., Swofford et al., 1996), all first and second position substitutions together with only transversions at the third codon position were included in the COI nucleotide data matrix used for phylogenetic analyses. Of the 613 nucleotide positions in the transformed COI data matrix, 229 were invariant, while 315 (102 from 1st codon positions; 59 from 2nd; 154 from 3rd) were phylogenetically informative using the parsimony criterion. Analysis of the tree length distribution of 100,000 randomly generated trees, using all 17 taxa, suggests that there is a significant amount of hierarchical structure within the transformed COI data set (g_1 = −0.794; with 384 variable sites, $p << 0.01$; Hillis & Huelsenbeck, 1992). This analysis was repeated using only the *Corbicula, Dentalium, Katharina, Lepetodrilus, Modiolus, Neotrigonia,* and *Solemya* COI sequences (seven taxa) in order to minimize the number of closely related taxa present in the hierarchical structure analysis. Significant structure was still present in this truncated COI data matrix ($g_1 = -0.527$; with 295 variable sites, $p < 0.01$), which suggests that the hierarchical structure present in the original data matrix was not solely due to the presence of closely related taxa. The findings from the plots of substitution pattern and g_1 statistics are consistent with the hypothesis that significant phylogenetic signal exists in the transformed COI nucleotide data matrix and validate the latter's use in this particular phylogenetic context (e.g., Swofford et al., 1996). Since amino acid substitution rates are lower than the underlying nucleotide substitution rates (e.g., Li & Graur, 1991), it follows that the inferred COI amino acid sequences are not saturated and, therefore, also appropriate for this level of phylogenetic analysis.

The best tree produced by ML analysis of the transformed COI nucleotide matrix is presented in Figure 3 along with bootstrap percentages for the NJ (above branches, 1,000 replicates), MP (below branches, 1,000 replicates), and ML (in parentheses, 100 replicates) analyses. Only bootstrap percentages greater than 50% are shown. This topology is largely congruent with the best trees produced by MP (three equally parsimonious trees) and NJ analyses (trees not shown). However, the topological relationships of the non-autobranch taxa on the best MP trees were identical to those portrayed in the trees derived from analyses of the inferred COI amino acid sequences (see below).

The Kishino-Hasegawa test results (Table 1) indicate that the morphology-based topology represented in Figure 1A was significantly worse ($p < 0.05$) than the best topology from ML analyses of the transformed COI data matrix (Figure 3). However, the morphology-based topology represented in Figure 1B was

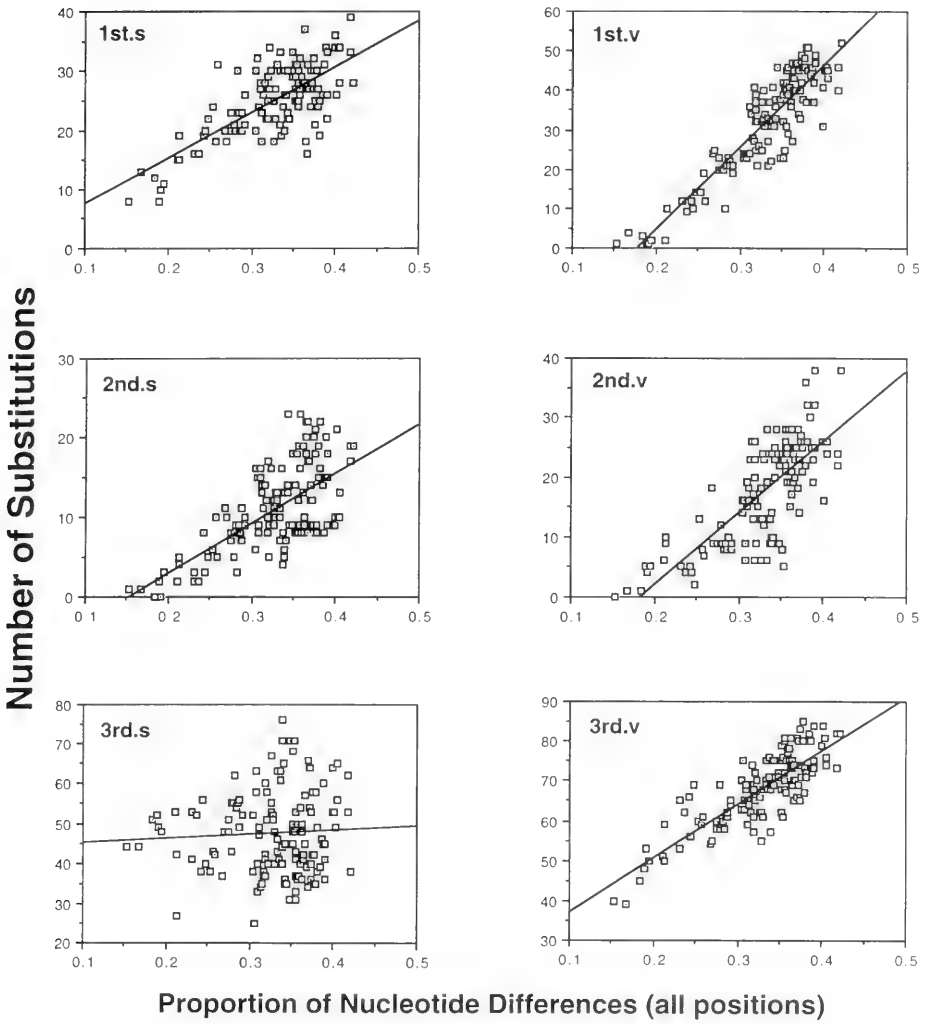

FIG. 2. Substitution pattern for transitions (s) and transversions (v) at each codon position for the COI fragment analyzed herein. The number of transitions and transversions is plotted against the proportion of nucleotide differences over all positions.

not significantly worse ($p > 0.05$) than that derived from ML analysis. These test results confirm significant discordance between the morphology-based topology represented in Figure 1A and the COI-based topology (e.g., Swofford et al., 1996).

Figure 4 represents the best topology generated from NJ analysis of the inferred COI amino acid sequences with bootstrap percentages for NJ (above branches) and MP (below branches) analyses. Only bootstrap percentages greater than 50% are shown. The strict consensus tree (not shown) of the 39 equally parsimonious trees produced by MP analysis of the inferred COI amino acid matrix is less resolved but entirely congruent with the NJ tree.

All analyses of the transformed COI nucleotide and inferred amino acid matrices were consistent with the monophyly of the Autobranchia, Veneroida, Mytiloida, and Unionoida (e.g., Figs. 3, 4). The trees in Figures 3 and 4 are especially noteworthy due to the strong inference that the filibranchous *Neotrigonia* (Trigonioida) is more closely related to eulamellibranchous freshwater mus-

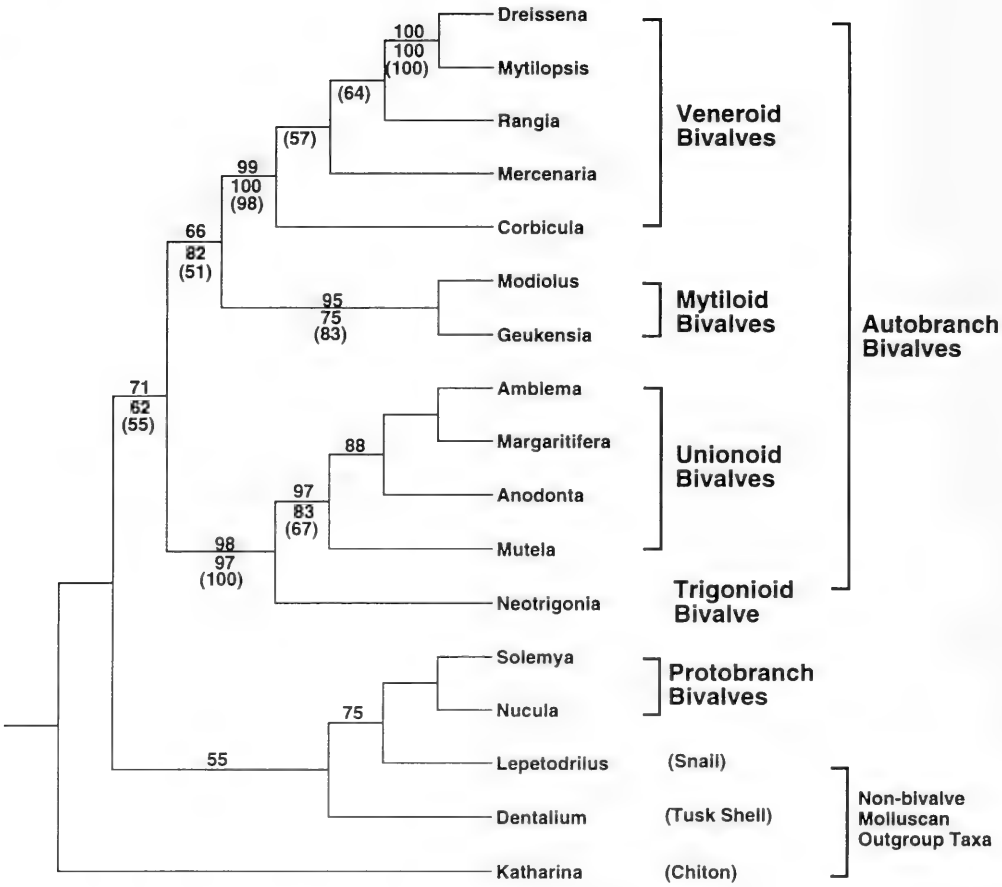

FIG. 3. Best tree topology produced by maximum likelihood analysis of the transformed COI nucleotide matrix. Numerals are bootstrap percentages for NJ (above branches, 1,000 replicates), MP (below branches, 1,000 replicates), and ML (parentheses, 100 replicates) analyses. Only bootstrap values greater than 50% are shown.

TABLE 1. Kishino-Hasegawa Test evaluation of the two phylogenetic hypotheses presented in Figure 1 against the best DNAML tree from the COI nucleotide sequence analysis (Fig. 3). User trees with Z-values (= the difference between log likelihood values of best tree and user tree divided by the standard deviation of the difference) of absolute magnitude 2.0 or greater are considered significantly worse ($p < 0.05$) than the best DNAML tree.

Tree Topology	Log likelihood value (Range of Log likelihood values)	Range of differences in Ln L	Range of Ln L S.D.	Range of Z-values
best DNAML tree	−6579.54852	—	—	—
Figure 1A (34 user trees)	(−6661.59438 to −6634.71091)	−82.04587 to −55.16240	26.3566 to 22.8030	−3.1129 to −2.4191*
Figure 1B (48 user trees)	(−6625.17868 to −6601.80601)	−45.63016 to −22.25749	27.4627 to 18.5040	−1.6615 to −1.2028

*Significantly worse than the best tree topology at the $p < 0.05$ level.

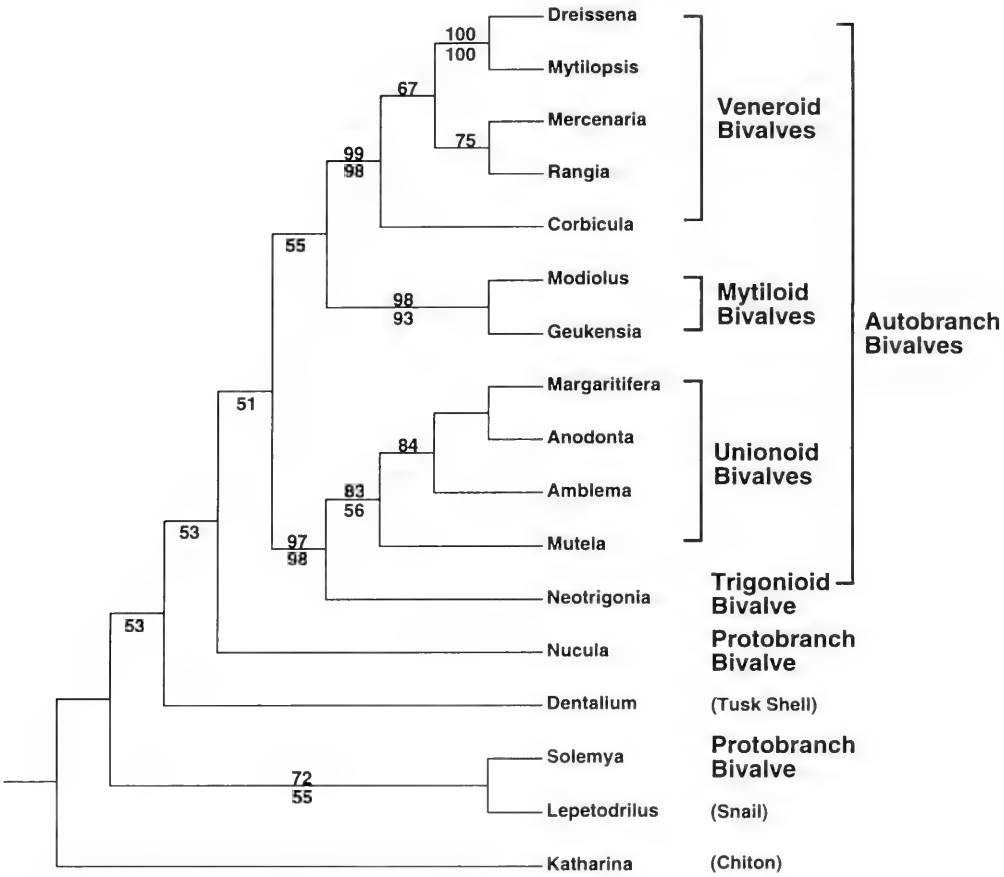

FIG. 4. Best tree topology produced by neighbor-joining analysis of the inferred COI amino acid sequences. Numerals are bootstrap percentages for NJ (above branches, 1,000 replicates) and MP (below branches, 1,000 replicates) analyses. Only bootstrap values greater than 50% are shown.

sels (Unionoida) than to the filibranchous mytiloids (mean level of bootstrap support = 98%). This level of bootstrap support suggests a robust resolution of the evolutionary relationships of *Neotrigonia* among the taxa utilized herein (Hillis & Bull, 1993).

This particular phylogenetic placement of *Neotrigonia* was also manifest in the best trees (not shown) constructed from analyses of the COI nucleotide sequences when (1) the native (untransformed) COI sequences were utilized (ML, MP, and NJ analyses), (2) all codon positions were coded for transversions only (ML, MP, and NJ analyses), and (3) only first and second codon positions were used (ML, MP, and NJ analyses). These results taken together are consonant with the hypothesis that there is a strong phylogenetic signal in the COI sequences supporting the placement of *Neotrigonia* as sister taxon to the Unionoida.

Another noteworthy aspect of all of the above phylogenetic analyses was the absence of support for bivalve mollusk monophyly. In the phylogenetic hypothesis represented in Figure 3, the protobranch bivalves, *Nucula* and *Solemya,* are portrayed as a clade, with the gastropod, *Lepetodrilus,* as the sister taxon to that clade. The phylogenetic hypothesis represented by Figure 4 portrays *Nucula* as the sister taxon of the Autobranchia while *Solemya* is the sister taxon to *Lepetodrilus.* While our analyses were somewhat limited due to the relatively small number of nucleotides and taxa analyzed, the fact that none of the best trees or bootstrap trees generated from these analyses gave support for a monophyletic Bivalvia suggests that the impli-

cations of these results be seriously considered.

DISCUSSION

Morton (1987) argued, based partially on the anatomical discontinuities between trigonioids and unionoids, that *Neotrigonia* was a transitional taxon, phylogenetically intermediate between the presumed ancestral protobranch bivalves and the more derived pteriomorph bivalves. This hypothesis is consistent with that of Salvini-Plawen & Steiner (1996; Fig. 1A). However, the results of the COI sequence analyses (Figs. 3, 4) strongly suggest that the extant representative of the Trigonioida, that is, the genus *Neotrigonia,* is the sister taxon to unionoid bivalves, as suggested in the hypothesis of Waller (1990; Fig. 1B). This phylogenetic propinquity is supported by similarities in shell structure (Taylor et al., 1969, 1973; Tevesz & Carter, 1980), gill speculation (Taylor et al., 1969, 1973), sperm morphology (Popham, 1979; Healy, 1989), and gill cilia patterns (Atkins, 1937; Tevesz, 1975). Furthermore, the indicated monophyly of the Unionoida is consistent with the hypothesis of a single invasion of freshwater by the ancestral unionoid. This finding corroborates the hypothesis of a dramatic evolutionary transition in larval morphology, that is, between glochidium and haustorium/lasidium morphology, during unionoid phylogenesis. Evaluating the directionality of this character state transition will require further, broad-scale phylogenetic analyses.

Another interesting result is the placement of *Solemya* (in Figs. 3, 4) and *Nucula* (in Fig. 3), both protobranch bivalves, among the non-bivalve outgroup taxa. This observation is not an artifact of the particular rooting scheme employed in Figures 3 and 4. It is not possible to root either of these topologies such that all of the bivalve taxa represented therein form a monophyletic group. In all of the phylogenetic analyses of the COI sequences, *Solemya* was either (1) the sister taxon to *Lepetodrilus* or (2) in a clade with *Nucula* and *Lepetodrilus.* Therefore, these analyses provide some support for the hypothesis that the currently-recognized molluscan taxon Bivalvia is a polyphyletic assemblage. The non-monophyletic status of the Bivalvia was supported by a recent phylogenetic analysis of 18S rDNA sequences (Adamkewicz et al., 1997: fig. 2). Furthermore, the topology in our Figure 3 suggests that the protobranch bivalve genera *Nucula* and *Solemya* are more closely related to the snail, *Lepetodrilus,* than to the other bivalve taxa in the analysis. Thus, the shared presence of bipectinate gills and hypobranchial glands (J. E. Morton, 1988), esophageal and stomach similarities (Salvini-Plawen, 1988), ultrafiltration site similarities (Andrews, 1988), oxygen transport molecule similarities (Mangum et al., 1987), and flattened pedal areas in both protobranch bivalves and primitive gastropods may be due to shared common ancestry rather than to the retention of ancestral character states.

The phylogenetic relationships of *Neotrigonia, Nucula,* and *Solemya,* as deduced from the COI analyses presented herein (e.g., Figs. 3, 4), suggest that a significant amount of convergent anatomical and conchological evolution has taken place within the Mollusca. There is a great deal of precedent for this statement (e.g., Allen, 1985; Purchon, 1990; Davis, 1994; Salvini-Plawen & Steiner, 1996). An important evolutionary implication that stems from the phylogenetic placement of *Neotrigonia* as sister taxon to a freshwater mussel clade is that it corroborates previous hypotheses of convergence (e.g., Waller, 1990) in the evolution of autobranch bivalve gill structure, i.e., either the filibranchous or the eulamellibranchous gill condition evolved at least twice in the evolutionary history of these bivalve taxa (Fig. 5A). The latter possibility is favored by Waller (1990). The evolution of eulamellibranchous gill organization (which facilitated larval brooding) may have been a necessary antecedent to the successful colonization and subsequent marked evolutionary diversification in freshwater habitats by unionoid bivalves.

The implications of the hypothesized phylogenetic relationships of *Nucula* and *Solemya,* as inferred from analyses of COI sequences, are more profound. It is suggested that the bivalved phenotype has evolved at least three times during the evolution of the Mollusca: (1) in the ancestor of the Juliidae, a relatively derived family within the opisthobranch gastropods (not represented in the analyses herein), (2) in the ancestor of the Autobranchia, and (3) in the ancestor of the Protobranchia (assuming a monophyletic Protobranchia, Fig. 5B). If the genera *Tuarangia* and *Pseudomyona* are found to be bivalved monoplacophorans (Runnegar, 1983) rather than autobranch bivalves (Mackinnon, 1982; Berg-Madsen, 1987), and if the Solemyoida and Nu-

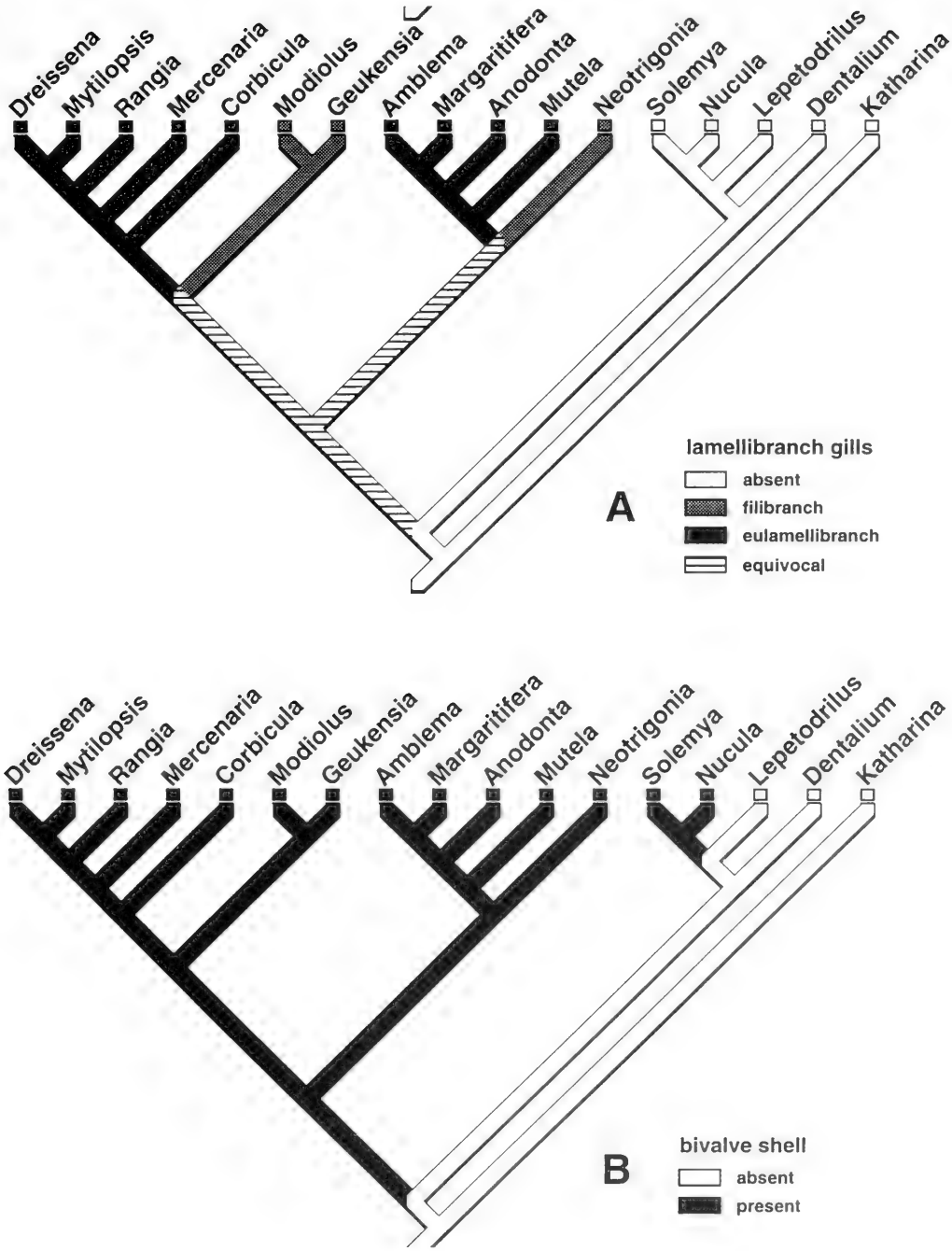

FIG. 5. Morphological character optimization using MacClade on the best topology produced from maximum likelihood analysis of the transformed COI nucleotide matrix using *Katharina* as the outgroup. A. The most parsimonious estimate of autobranch bivalve gill character state transitions for the taxa included in these analyses is that either the filibranchous or eulamellibranchous character state evolved at least twice. B. The most parsimonious estimate of character state transitions for the taxa included in these analyses suggests that the bivalved phenotype has evolved at least twice. Justification for the use of *Katharina* as the outgroup for the molluscan taxa included in this analysis is provided by numerous studies (e.g., Salvini-Plawen, 1980, 1985, 1988, 1990; Wingstrand, 1985; Eernisse, et al., 1992; Salvini-Plawen & Steiner, 1996).

culoida had independent origins (Purchon, 1978; Salvini-Plawen & Steiner, 1996), the bivalved condition would have had to evolved at least five times within the Mollusca. This striking assessment is nonetheless not totally unexpected when evaluated in the context of (1) the great evolutionary mutability of body plan exemplified by the phylum Mollusca (e.g., J. E. Morton & Yonge, 1964; Allen, 1985; Willmer, 1990) and (2) the multiple origins of bivalved external shells in four phyla (Thomas, 1988).

Under the hypothesis of a polyphyletic Bivalvia, the degree of morphological convergence on the bivalved body plan varies considerably within the extant mollusks. In the case of the opisthobranch gastropod genus *Julia,* the shell has converged on the monomyarian (= single adductor muscle) bivalve condition while the soft anatomical characteristics are clearly those of a gastropod (Kay, 1968). However, the degree of convergence in body plans between autobranch and protobranch bivalves is much greater and involves both shell and anatomical character states. The phylogenetic hypothesis displayed in Figure 3 suggests that in the distinct evolutionary histories of the autobranch and protobranch mollusks, in addition to the convergent bivalved shell, there were convergent (1) losses of head and radula, (2)origins of labial palps, (3) origins of the dimyarian adductor muscle condition, and (4) origins of fibrous ligament. Thus, the evolutionary mutability of body plans within the Mollusca may be greater than that suggested by the traditional classification schemes. Phylogenetic evaluations of additional molecular and morphological data sets are needed to test the hypothesized polyphyly of the Bivalvia and further decipher patterns of molluscan body plan evolution.

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GEOGRAPHIC AND HABITAT-SPECIFIC MORPHOLOGICAL VARIATION OF *LITTORARIA* (*LITTORINOPSIS*) *ANGULIFERA* (LAMARCK, 1822)

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ABSTRACT

Recent, detailed examination of the morphology of the Littorinidae inhabiting Indo-West Pacific mangrove forests led Reid (1986) to identify 20 species of *Littoraria,* all of which had previously been assigned to only three species within the pantropical "*Littorina scabra.*" No similar study has been done on the neotropical *Littoraria angulifera* (Lamarck), which occurs in mangrove forests on both sides of the Atlantic Ocean. We quantified variability in shell and genital morphology of *L. angulifera* throughout its range in the tropical Atlantic using material from both museum collections and new, field collections. We tested two hypotheses regarding variation in shell shape and sculpture, and frequency of color morphs in populations of *L. angulifera:* (1) observed variation is associated with the five major current regimes that could restrict its dispersal throughout the tropical Atlantic; or (2) observed variation is associated with habitat characteristics that can influence shell thermal properties. Strong geographical variation in shell shape and sculptural characteristics suggested initial support for the dispersal hypothesis. Absence of geographical variation in genital morphology, however, led to the rejection of the dispersal hypothesis. Parallel associations of habitat with geography suggests that *L. angulifera* is a single species throughout the tropical Atlantic, and observed variability results primarily from responses to local environmental conditions. However, this conclusion can be tested only with additional genetic analysis of disparate populations of *L. angulifera.*

Key words: Atlantic, currents, *Littoraria angulifera*, Littorinidae, mangroves, morphology, shell sculpture, shell shape.

INTRODUCTION

A recent, detailed examination of the morphology of the Littorinidae inhabiting Indo-West Pacific mangrove forests by Reid (1986, 1989, 1999) resulted in the identification of 21 species, all of which had previously been assigned to only three species within the pantropical "*Littorina scabra*" complex by Rosewater (1970, 1980). Reid (1986) also re-assigned these mangrove-inhabiting littorinids to the genus *Littoraria* Griffith & Pidgeon. No similar study has been done on the neotropical species *Littoraria angulifera* (Lamarck), which occurs in mangrove forests on both sides of the Atlantic Ocean, although Reid (1986, 1989) considered Eastern and Western Atlantic populations of *L. angulifera* to be a single species based on shell morphology and genital characteristics. Rosewater (1980) considered the neotropical "*Littorina angulifera*" to be a subspecies of "*Littorina scabra,*" although earlier authorities (e.g., Bequaert, 1943; Marcus & Marcus, 1964; Bandel, 1974) conferred distinct species status on *L. angulifera,* principally because of its geographical isolation from the Indo-West Pacific. Like its Indo-West Pacific congeners, *L. angulifera* is variable in shell morphology and color, and we studied this variability with respect to geography, potential dispersal routes, and habitat characteristics in the tropical Atlantic. In particular, we used museum collections and new field-collected material to test between two hypothesis that could account for observed variation in shell shape and sculpture, and frequency of color morphs in populations of *L. angulifera.* First, such variation could be associated with the five major current regimes that could restrict its dispersal throughout the tropical Atlantic. Alternatively, observed variation could be a consequence of habitat characteristics that can influence shell morphology and attendant thermal properties. We also use these

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data to discuss the need for further field studies and systematic re-evaluation of *L. angulifera* throughout its range.

Intraspecific variation in shell morphology of littorinids has been attributed both to environmental influences and genetic variability (Berry, 1961; Newkirk & Doyle, 1975; Janson, 1982a, b; Cook et al., 1985; Cook, 1992; Cook & Garbett, 1992; Lewis & Williams, 1995; Mill & Grahame, 1995). For example, supratidal and high intertidal snails subject to dessication stress tend to be highly ornamented or grooved (Vermeij, 1973). Smaller, more globose shells tend to occur in high-intertidal populations subject to frequent, high-intensity waves, while high-spired shells tend to be found in more protected areas (North, 1954; Newkirk & Doyle, 1975; Roberts & Hughes, 1980; Janson, 1982b; Johannesson, 1986; Brown & Quinn, 1988; Boulding & Van Alstyne, 1993; Lewis & Williams, 1995; Johannesson et al., 1997). Snails in low-density populations where food is abundant grow faster and tend to have rounder (low-spired) shells (Berry, 1961; Kemp & Bertness, 1984). By contrast, *Littorina subrotundata* Carpenter produces taller shells when it grows rapidly (Boulding & Hay, 1993). High levels of predation are associated with increased sculpturing (e.g., nodules and spines) and shell thickening (Reimchen, 1979, 1982; Cook, 1983; Reid, 1992; Cook & Kenyon 1993). These patterns have been documented primarily in the temperate zone, however. In contrast, studies of tropical littorines have been focused primarily on systematics (Bequaert, 1943; Rosewater, 1970, 1972; Reid, 1986, 1989), zonation (Sasekumar, 1974; Reid, 1985), predation (Reid, 1992), and intraspecific shell-color polymorphisms (Reimchen, 1979; Cook, 1983; Cook & Freeman 1986; Reid, 1987; Cook & Kenyon, 1993) of Indo-Pacific species. Little attention has been paid to intraspecific morphological variability of littorinids of the tropical Atlantic since the studies of Vermeij (1974), Borkowski (1975), and Rosewater (1981), which predate Reid's re-evaluation of the genus *Littoraria*.

Here, we document extensive morphological variability in *L. angulifera* from both sides of the Atlantic Ocean. *Littoraria angulifera* is one of only two littorinids known to occur on both sides of the Atlantic (Rosewater & Vermeij, 1972) (Fig. 1), and as such is an exemplar with which to address questions of geographically based intraspecific morphological variability. Because five distinct oceanic current occur within the range of *L. angulifera,* we expected to see regional divergence in morphology that could indicate geographically defined subpopulations based on restricted larval dispersal. In addition, the significant variation in mangrove forest structure and nutrient availability that occurs throughout the tropical Atlantic also could contribute to variability in morphology. Morphological variation caused by local environmental characteristics could either amplify or mask morphological variation of some traits due to geographic isolation. Thus, we explore how several morphological characteristics covary with geography and features of local habitats.

MATERIALS AND METHODS

Natural History and Morphology

Littoraria (*Littorinopsis*) *angulifera* (Fig. 2) is the only tropical littorinid that is found exclusively in mangrove swamps of the Atlantic and Caribbean (see distribution map in Rosewater & Vermeij, 1972). *Littoraria angulifera* is ovoviviparous, with a planktotrophic larval stage estimated to be 8–10 weeks long (Gallagher & Reid, 1979). Adult snails occur in the supralittoral zone on trunks, roots, stems, and leaves of mangroves, primarily *Rhizophora mangle* L., *Avicennia* spp., and *Laguncularia racemosa* (L.) Gaertn.f., where they feeds on epiphytic algae and marine fungi (Kohlmeyer & Bebout, 1986). Because of its supralittoral habit, local variation in wave strength and exposure is unlikely to affect *L. angulifera.* Predation on *L. angulifera* has not been studied, although omnivorous grapsid crabs and predatory wading birds (egrets, herons) are often seen feeding in and around mangrove roots at low tide (A. M. Ellison, personal observation).

The normally light-orange protoconch is characterized by 3–5 prominent spiral ridges running parallel to the 2–4 whorls. Primary grooves appear on the 1^{st}–4^{th} whorl of the teleoconch, along with the axial striae (growth lines), which do not appear to conform to any spatial pattern on the shell surface (Fig. 3). Beginning between the 3^{rd} and last whorls of the teleoconch, secondary grooves bisect the ribs between already existing primary grooves (Fig. 3). When present, tertiary grooves, like secondary grooves, appear on the ribs between already existing grooves (Fig. 3). If they

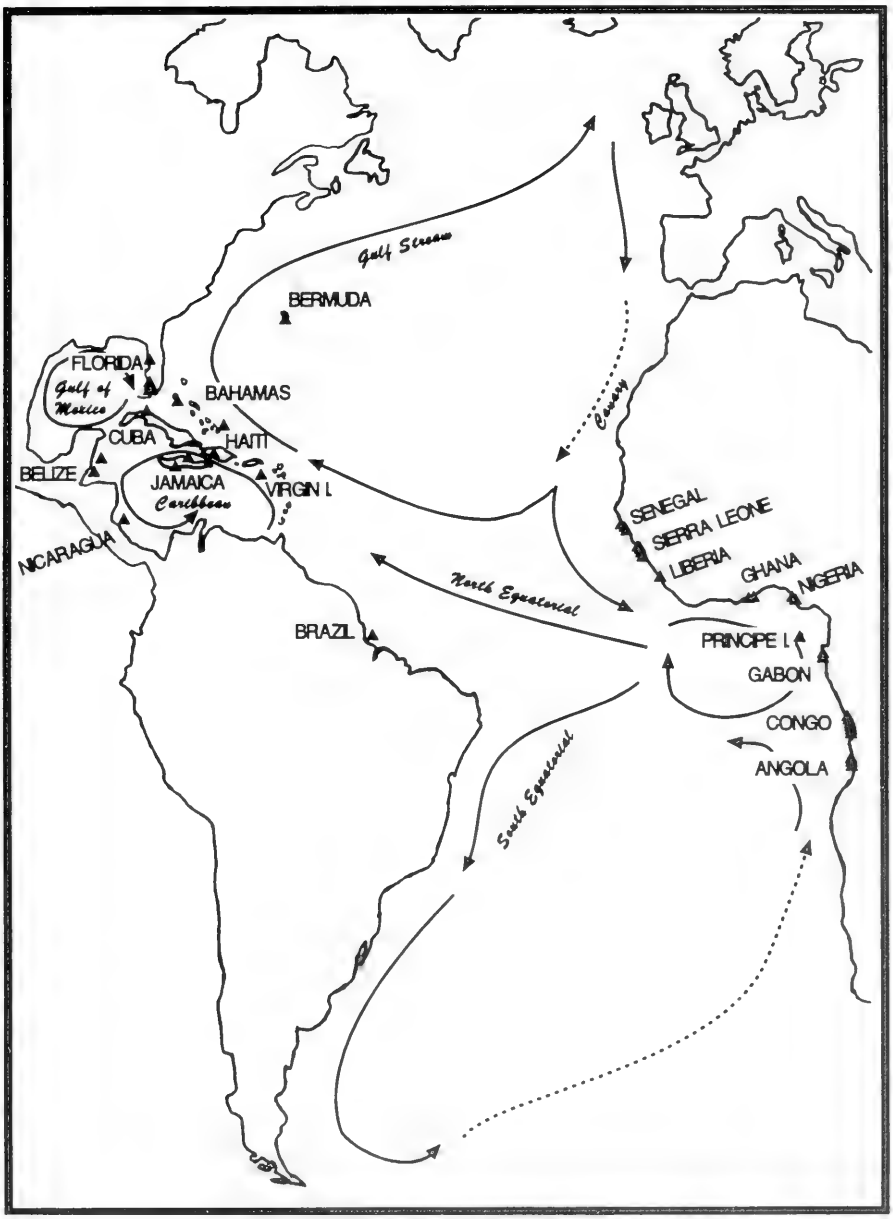
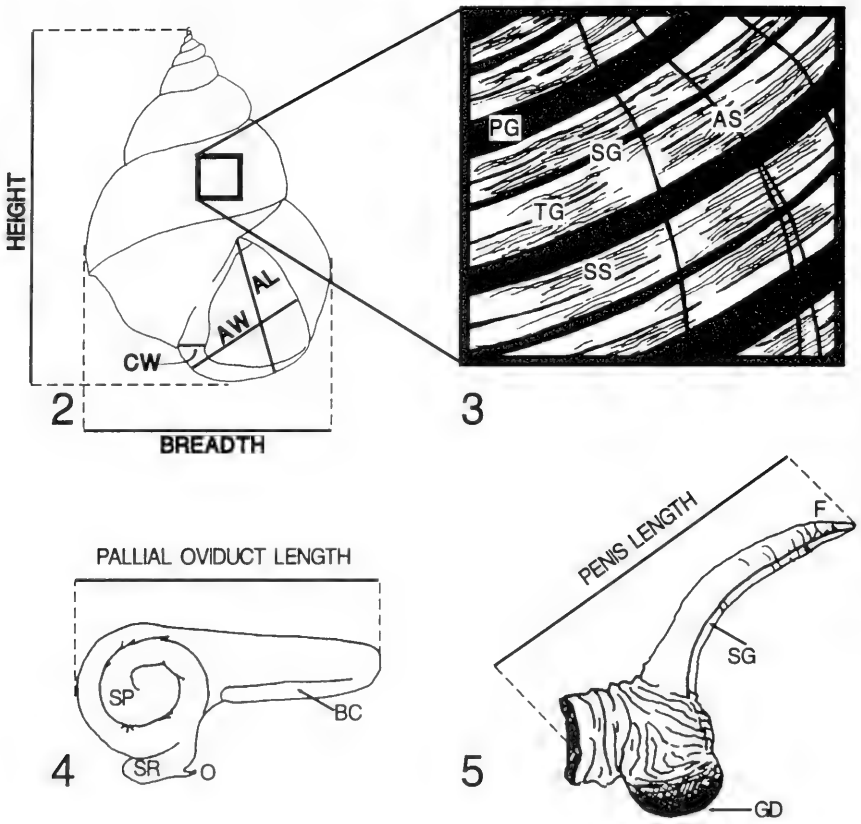


FIG. 1. Map illustrating collection localities of *Littoraria angulifera* and the prevailing currents in the Atlantic Ocean. Solid arrows are warm currents and dotted arrows are cold currents.

occur, spiral striae typically begin between the 4th and last whorls of the teleoconch (Fig. 3).

Samples and Measurements

We followed methods of Reid (1986) in collecting morphological data. A total of 1,042 specimens were examined from 41 sites throughout the distribution of *L. angulifera* (Table 1). The sample size from any single location ranged from two specimens to >100. The collections of the Academy of Natural Sciences in Philadelphia, Pennsylvania (ANSP) and The Natural History Museum, London



FIGS. 2–5. Shell shape and sculpture, and genitalia. 2. Illustration of measurements taken on an individual shell. CW: Columellar width; AW: Aperture width; AL: Aperture length. 3. Inset showing shell sculpture. PG:Primary groove; SG: Secondary groove; TG: Tertiary groove; AS: Axial stria; SS: Sprial striae. 4. Pallial oviduct. SP: Spiral loop; BC: Bursa copulatrix; SR: Seminal receptacle; O: Oviduct. 5. Penis. F: Filament; SG: Sperm groove; GD: Glandular disc.

(BMNH), were examined along with snails that we or our colleagues collected in 1996 in Florida, Belize, and Jamaica (vouchered at BMNH; Registration numbers 1996411 through 1996416). In most cases, only shells were available for study, but when preserved material was available (Florida, Belize, Jamaica, Sierra Leone, Ghana), samples were dissected and examined for comparison of anatomical characteristics as well. Dissected specimens were preserved in formalin and exhibited a certain degree of shrinkage, contortion, and discoloration. This made it impossible to identify finer characteristics, such as gamete structure and head-foot coloration. *Littoraria angulifera* secondarily has lost its egg capsule glands (Reid, 1986), so we could not use characters associated with them.

Categories of shell characteristics studied included shape, appearance, sculpture, and color (when possible) (Figs. 2, 3). The shape of *L. angulifera* shells is typical of ovoviviparous, mangrove-dwelling littorines, with a high spire and an almost circular aperture (Reid, 1986). Five measurements—height, breadth, apertural width and length, and columellar width—were taken on each shell (Fig. 2) using calipers (± 0.1 mm). Four of these measurements were collapsed into three standard composite variables: proportionality (= height/breadth), circularity (= apertural width/apertural length), and spire height (= height/apertural length).

Sculpture characteristics (Fig. 3, Table 2) were identified using a dissecting microscope. The central columella of *L. angulifera* tends to be creamy yellow in color, convex and pinched at its base, with excavation of the

TABLE 1. Collection locations (in bold) and sites (in normal font), sample source, geographic coordinates (approximate latitude, longitude), current grouping to which we assigned each location, and shell shape characteristics for all sites studies. Values given are means, with 1 SD in parentheses. Grand means for each of the 19 locations are printed in boldface type, while means for sites within locations (where there are multiple sites within a location) are printed in normal type.

Location (Site)	Source[1]	Coordinates	Current grouping	Proportionality	Circularity	Spire Height
Angola		14° E, 8° S	South Equatorial	**1.36 (0.047)**	**0.76 (0.036)**	**1.69 (0.059)**
St. Paul de Loanda	ANSP			1.37 (0.052)	0.77 (0.030)	1.67 (0.043)
Loanda	BMNH			1.39 (0.018)	0.71 (0.015)	1.81 (0.071)
Cazangai	BMNH			1.33 (0.030)	0.74 (0.032)	1.69 (0.053)
Bahamas		78° W, 27° N	Gulf Stream	**1.51 (0.091)**	**0.76 (0.026)**	**1.86 (0.078)**
Great Abaco Island	ANSP			1.55 (0.089)	0.76 (0.023)	1.86 (0.079)
Little San Salvador Island	ANSP			1.46 (0.065)	0.75 (0.034)	1.87 (0.081)
Belize		88° W, 17° N	Caribbean	**1.42 (0.060)**	**0.76 (0.029)**	**1.85 (0.080)**
Garbutt Cay	ANSP			1.47 (0.061)	0.79 (0.030)	1.84 (0.060)
Wee Wee Cay	Ellison			1.41 (0.056)	0.76 (0.026)	1.85 (0.083)
Bermuda	ANSP	65° W, 33° N	Gulf Stream	**1.53 (0.063)**	**0.77 (0.013)**	**1.87 (0.112)**
Brazil	ANSP	50° W, 0° N	North Equatorial	**1.43 (0.071)**	**0.74 (0.031)**	**1.71 (0.050)**
Congo		15° E, 6° S	South Equatorial	**1.39 (0.072)**	**0.79 (0.047)**	**1.71 (0.112)**
Banana (I)	ANSP			1.41 (0.075)	0.81 (0.063)	1.76 (0.135)
Banana (II)	ANSP			1.42 (0.049)	0.78 (0.032)	1.71 (0.093)
Banana Creek	ANSP			1.38 (0.066)	0.79 (0.026)	1.64 (0.078)
Port Gentil	ANSP			1.28 (0.042)	0.85 (0.007)	1.69 (0.142)
Kongo Town	BMNH			1.35 (0.083)	0.78 (0.021)	1.76 (0.123)
Banana (III)	ANSP			1.33 (0.052)	0.75 (0.033)	1.68 (0.090)
Cuba	ANSP	85° W, 23° N	Caribbean	**1.48 (0.062)**	**0.78 (0.034)**	**1.89 (0.108)**
Florida		82° W, 27° N	Gulf of Mexico	**1.45 (0.125)**	**0.74 (0.032)**	**1.86 (0.082)**
Little Shark River (middle)	Ellison			1.57 (0.203)	0.74 (0.032)	1.87 (0.079)
Little Shark River (upper)	Ellison			1.42 (0.053)	0.73 (0.026)	1.85 (0.070)
Little Shark River (mouth)	Ellison			1.41 (0.058)	0.74 (0.042)	1.83 (0.076)
Cockroach Bay	Ellison			1.38 (0.050)	0.74 (0.029)	1.81 (0.078)
Hurricane Island	Ellison			1.47 (0.056)	0.75 (0.022)	1.95 (0.066)

(*continued*)

TABLE 1. (*Continued*)

Location (Site)	Source[1]	Coordinates	Current grouping	Proportionality	Circularity	Spire Height
Gabon		10° E, 2° S	South Equatorial	**1.39 (0.053)**	**0.76 (0.040)**	**1.74 (0.114)**
Gabon Coast	BMNH			1.37 (0.069)	0.80 (0.024)	1.64 (0.086)
"West Africa"	BMNH			1.40 (0.040)	0.74 (0.030)	1.80 (0.079)
Ghana		2° W, 5° N	North Equatorial	**1.37 (0.046)**	**0.71 (0.041)**	**1.74 (0.089)**
Gold Coast	BMNH			1.29 (0.025)	0.73 (0.010)	1.57 (0.043)
"Ghana"	BMNH			1.38 (0.043)	0.71 (0.042)	1.74 (0.083)
Haiti	ANSP	74° W, 18° N	Gulf Stream	**1.49 (0.094)**	**0.76 (0.017)**	**1.89 (0.112)**
Jamaica		78° W, 17° N	Caribbean	**1.45 (0.083)**	**0.76 (0.035)**	**1.84 (0.085)**
Great Goat Island	ANSP			1.53 (0.090)	0.79 (0.033)	1.79 (0.088)
St. Anne's Bay	Nemeth			1.42 (0.053)	0.75 (0.025)	1.86 (0.074)
Liberia	BMNH	10° W, 7° N	North Equatorial	**1.36 (0.007)**	**0.74 (0.007)**	**1.69 (0.023)**
Nicaragua	ANSP	85° W, 13° N	Caribbean	**1.48 (0.044)**	**0.74 (0.020)**	**1.69 (0.023)**
Nigeria		5° E, 5° N	North Equatorial	**1.33 (0.030)**	**0.74 (0.053)**	**1.66 (0.079)**
Lagos Lagoon	BMNH			1.32 (0.018)	0.77 (0.039)	1.69 (0.060)
Lagos	BMNH			1.33 (0.035)	0.73 (0.057)	1.65 (0.087)
Principe Island	BMNH	8° E, 3° N	North Equatorial	**1.30 (0.055)**	**0.78 (0.082)**	**1.64 (0.087)**
Senegal		16° W, 13° N	North Equatorial	**1.54 (0.373)**	**0.75 (0.034)**	**1.79 (0.080)**
"Senegal" (I)	BMNH			1.46 (0.070)	0.74 (0.035)	1.85 (0.093)
"Senegal" (II)	BMNH			1.62 (0.504)	0.76 (0.039)	1.75 (0.050)
Solomon (Senegambia)	BMNH			1.34 (NA)	0.76 (NA)	1.76 (NA)
Sierra Leone		14° W, 8° N	North Equatorial	**1.35 (0.059)**	**0.73 (0.067)**	**1.72 (0.067)**
"Sierra Leone" (I)	BMNH			1.41 (NA)	0.77 (NA)	1.72 (NA)
"Sierra Leone" (II)	BMNH			1.35 (NA)	0.73 (NA)	1.67 (NA)
Freetown (I)	BMNH			1.36 (0.052)	0.73 (0.096)	1.72 (0.070)
"Sierra Leone" (III)	BMNH			1.32 (0.056)	0.73 (0.029)	1.67 (0.070)
Freetown (II)	BMNH			1.35 (0.065)	0.73 (0.045)	1.73 (0.063)
Virgin Islands	ANSP	65° W, 17° N	Caribbean	**1.53 (0.105)**	**0.76 (0.065)**	**1.94 (0.238)**

TABLE 2. Shell sculpture characteristics identified or measured.

Character	Measurement type
# whorls in the protoconch	numeric
# whorls in the telochonch	numeric
whorl # in which primary grooves first occur	numeric
# primary grooves at first appearance	numeric
whorl in which axial striae occur	numeric
whorl in which secondary grooves first occur	numeric
regularity of secondary grooves	categorical (0: irregular; 1: regular)
presence/absence of tertiary grooves	categorical (0: absent; 1: present)
whorl in which tertiary grooves first occur	numeric
presence/absence of spiral striae	categorical (0: absent; 1: present)
whorl in which spiral striae first occur	numeric
columella shape	categorical (0: concave; 1: vertical; 2: convex)
columella pinching	categorical (0: pinched; 1: unpinched)
columella color	categorical (0: creamy yellow; 1: otherwise)

base and lip (Fig. 2, Table 2). Shell color is variable, and two distinct color morphs, normal and orange, have been identified. The ground color of the "normal" color morph is creamy yellow to reddish-brown, and is overlaid with flecks of dark orange and brown. The ground color of the "orange" morph is light orange or yellow, and it is overlaid with faint orange flecks. Normal morphs were assigned a value of zero, and orange morphs, one.

Genital characteristics were measured for dissected specimens only (Figs. 4, 5). Length of the penis and pallial oviduct, diameter of the spiral portion of the oviduct, and length of the bursa copulatrix were measured with an ocular micrometer.

Statistical Analysis

We used discriminant analysis, cluster analysis, and principle components analysis (PCA), in SYSTAT version 7.0 (SPSS, 1997) and S-Plus for Windows version 4.0 (MathSoft, 1997), to compare morphological variation within and among populations. Because many of the samples were from sites close to each other (e.g., from within the same country), we grouped the sites into 19 discrete geographic "locations" for most of the analyses. Location groupings are indicated in Table 1. Data were transformed when necessary to meet assumptions (approximate normality, homoscedasticity) of all statistical tests (see Kroonenberg et al., 1997, for transformations appropriate for categorical data prior to application of these multivariate analyses). Details of each technique are given along with their associated results in the following section.

RESULTS

Geographic Patterns in Shell Shape

Shell shape showed pronounced changes from east to west among samples. Shells from the Western Atlantic and Caribbean have comparatively high spires and more circular apertures (Table 1, Fig. 6). The thickness of the columella also increases from east to west. Shells from the Eastern Atlantic have more whorls per mm of shell height. Primary grooves appeared earlier and in larger numbers, whereas secondary grooves occurred later on shells from the Eastern Atlantic. Discriminant analysis using these eight morphological variables (proportionality, circularity, and spire height, columellar thickness, whorls/mm, number of primary grooves, whorl on which primary and secondary grooves first appear, all expressed in standard deviation units) correctly identified 85% of the shells as coming from either the Eastern or Western Atlantic ($F = 106.6$, $P < 0.0001$; Table 3). However, shells from four localities generally were misclassified at this coarse level of geographic resolution. Shells from Liberia and Senegal were routinely assigned to the Western Atlantic, shells from Brazil were assigned more commonly to the Eastern Atlantic (Table 3), and shells from Gabon were assigned equally to each side of the Atlantic. Spire height, whorls/mm, columellar thickness, and number of primary grooves were the principle variables that discriminated between shells of the Eastern and Western Atlantic.

To investigate the hypothesis that morphological variation was associated with potential dispersal routes, we classified sites according

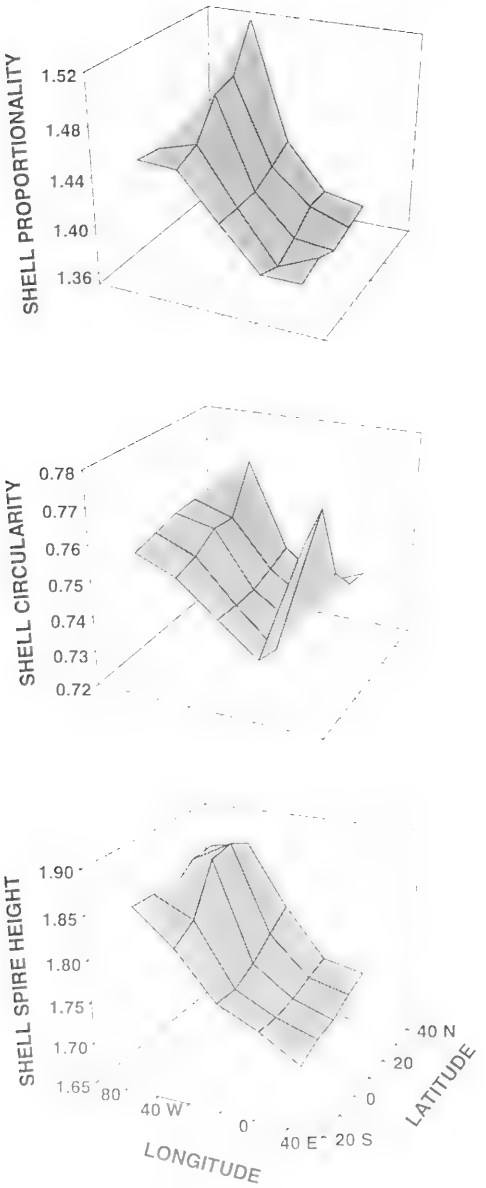


FIG. 6. Clinal patterns in shell proportionality, circularity, and spire height. Illustrations are distance-weighted, least-squares smoothing through data from all 41 sites.

to the predominant current affecting them (Caribbean, Gulf of Mexico, Gulf Stream, North Equatorial, South Equatorial; see Fig. 1; *a priori* current classifications in Table 1). We then used discriminant analysis to see if shells could be classified correctly with respect to these prevailing currents. Using the same eight standardized morphological variables, we could classify correctly 61% of the shells overall with respect to current of origin ($F = 51.7$, $P < 0.0001$). The most important morphological variables contributing to discrimination according to prevailing current were whorls/mm, spire height, columellar width, and shell circularity. In total, we could correctly classify 75% of shells from sites associated with the North Equatorial current, 71% from the South Equatorial current, 66% from the Gulf Stream, 64% from the Gulf of Mexico, and 40% from the Caribbean.

TABLE 3. Percent of shells correctly identified by discriminant analysis as coming from either the Eastern or Western Atlantic. Bold type indicates overall discrimination. Normal type indicates discrimination among locations within either the Eastern or Western Atlantic.

Location	%
Eastern Atlantic	**84**
Angola	84
Congo	70
Gabon	50
Ghana	95
Liberia	33
Nigeria	91
Principe Islands	100
Senegal	10
Sierra Leone	96
Western Atlantic	**85**
Bahamas	76
Belize	83
Bermuda	91
Brazil	40
Cuba	68
Florida	90
Haiti	88
Jamaica	84
Nicaragua	75
Virgin Islands	95

Within each current grouping, most shells from most locations were correctly classified into their respective current regimes (Fig. 7). Exceptions included Nicaragua (generally assigned to the South Equatorial current instead of the Caribbean); Brazil and Liberia (all assigned to the South Equatorial current instead of the North Equatorial current); Senegal (assigned to either the Caribbean or South Equatorial current instead of the North Equatorial current); and Gabon (30% of which were assigned to the Caribbean current). Shells from the Caribbean islands of Cuba and Jamaica frequently were assigned to the Gulf of Mexico or the Gulf Stream, whereas shells from

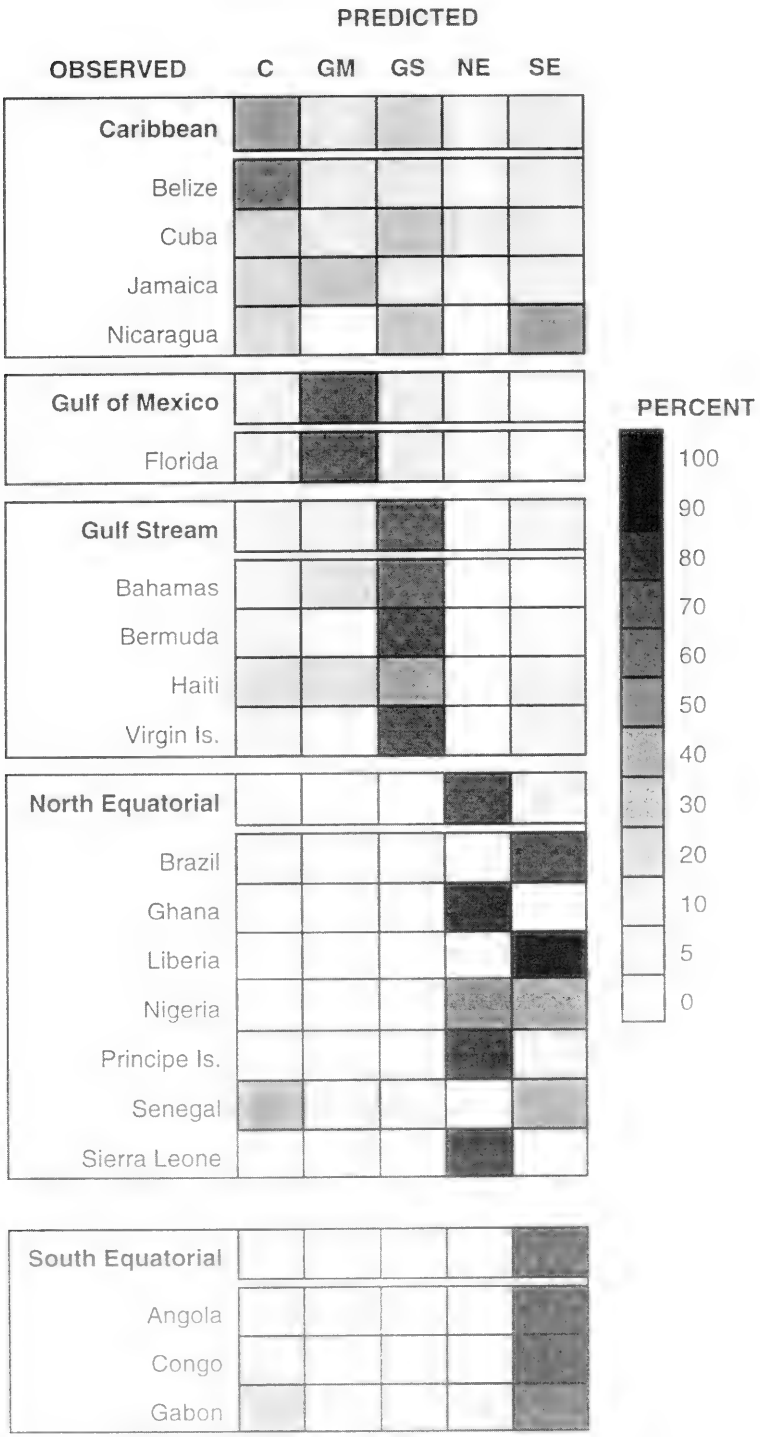


FIG. 7. Classification matrix resulting from discriminant analysis of shells from the five prevailing currents. Shading indicates percent classification into each of the five currents, with shading increasing with percentage. For each current, the overall classification is given in the first row (label in bold type), followed by the classification for each locality within that current grouping. Predicted current groupings: C—Caribbean; GM—Gulf of Mexico; GS—Gulf Stream; NE—North Equatorial; SE—South Equatorial.

TABLE 4. Loadings of shell morphological variables on the first four principal component axes. Only loadings ≥|0.1| are shown. The first four axes account for 90% of the among-location variance in shell morphology. Characters are ordered in descending order of their loadings on the first principal axis.

Variable	Axis 1	Axis 2	Axis 3	Axis 4
Thickness of columella	0.476	−0.170	−0.186	−0.318
Shell proportionality	0.471		0.401	
Whorls/mm of shell height	−0.464	0.180		0.348
Shell spire height	0.385		0.582	0.249
Whorl on which secondary groove first appears	0.276	0.503	−0.345	0.256
Number of primary grooves	0.234	−0.433	−0.457	
Whorl on which primary groove first appears	0.197	0.603	−0.326	
Shell circularity	0.137	−0.353	−0.159	0.803
Cumulative proportion of variance explained	0.42	0.66	0.78	0.90

Haiti (collected on the northern [Gulf Stream] side of the island) were mis-assigned to either the Caribbean or Gulf of Mexico.

Our eight shell morphology characteristics explained 90% of the among-location variance identified by principal components analysis (Table 4). Columellar width, proportionality, whorls/mm, and spire height loaded most heavily on the first axis, whereas whorl on which primary and secondary grooves first appeared, number of primary grooves, and shell circularity loaded most heavily on the second axis (Table 4, Fig. 8). Shells from Principe, Ghana, Sierra Leone, Nigeria, and Angola were distinguished from the others because of their low spire height and shell proportionality and their relatively large numbers of whorls/mm of shell height (Fig. 8). In other words, these five locations had the most globose shells. Shells from Angola, Congo, and Gabon had the most circular apertures (Fig. 8). Shells from the Virgin Islands, Nicaragua, Senegal, and Cuba were relatively high spired, and shells from the Virgin Islands and Bermuda had the thickest columellae.

Cluster analysis similarly illustrated the groupings of sampling localities according to these eight morphological variables (dendrogram not illustrated). We identified five clear groupings of locations from the complete-linkage dendrogram resulting from our cluster analysis: (1) Principe, Ghana, and Sierra Leone; (2) Congo, Gabon, Angola, Nigeria, and Brazil; (3) Liberia, Senegal, and Nicaragua; (4) Belize, Haiti, Jamaica, the Bahamas, Cuba, and Florida; (5) Bermuda and the Virgin Islands.

Habitat-Specific Patterns in Shell Shape

Climatic properties, stature of the mangrove forests of each location (Table 5), and primary nutrient source (oligotrophic vs. estuarine) were used to test for relationships between habitat characteristics and shell morphology. As with the morphology data, we first ordinated the sites according to the five variables using PCA. The loadings of the variables for the first two principal axes are shown in Table 6. The first axis is a function primarily of average canopy height and nutrient source (estuarine vs. oligotrophic), whereas the second axis is a function primarily of annual temperature and amount and pattern of rainfall. Together, these two composite axes encompassed 70% of the among-habitat variance. Standardized morphological and habitat scores for each location were computed by multiplying each variable by the factor coefficient derived from the PCAs morphological and habitat data, respectively. These products were then summed to yield a single standardized morphological or habitat score (computations done in Systat version 7.0). For clarity, we only illustrate the standardized scores based on the factor coefficients of the first principal component axis from each analysis. The result of this computation is a single composite morphological score and a single composite habitat score for each of the 19 locations. We found a significant association between these two scores ($r = 0.54$, $P = 0.018$; Fig. 9), which indicated a significant correlation of overall shell morphology with their local environment. This figure also illustrates clearly the similarity in overall shell morphology and habitat of Brazil, Nicaragua, and all the African samples.

Shell Color

Most shells had "normal" coloration; of the total sample, 68 shells (6.5%) were the "orange" morph. No differences in relative fre-

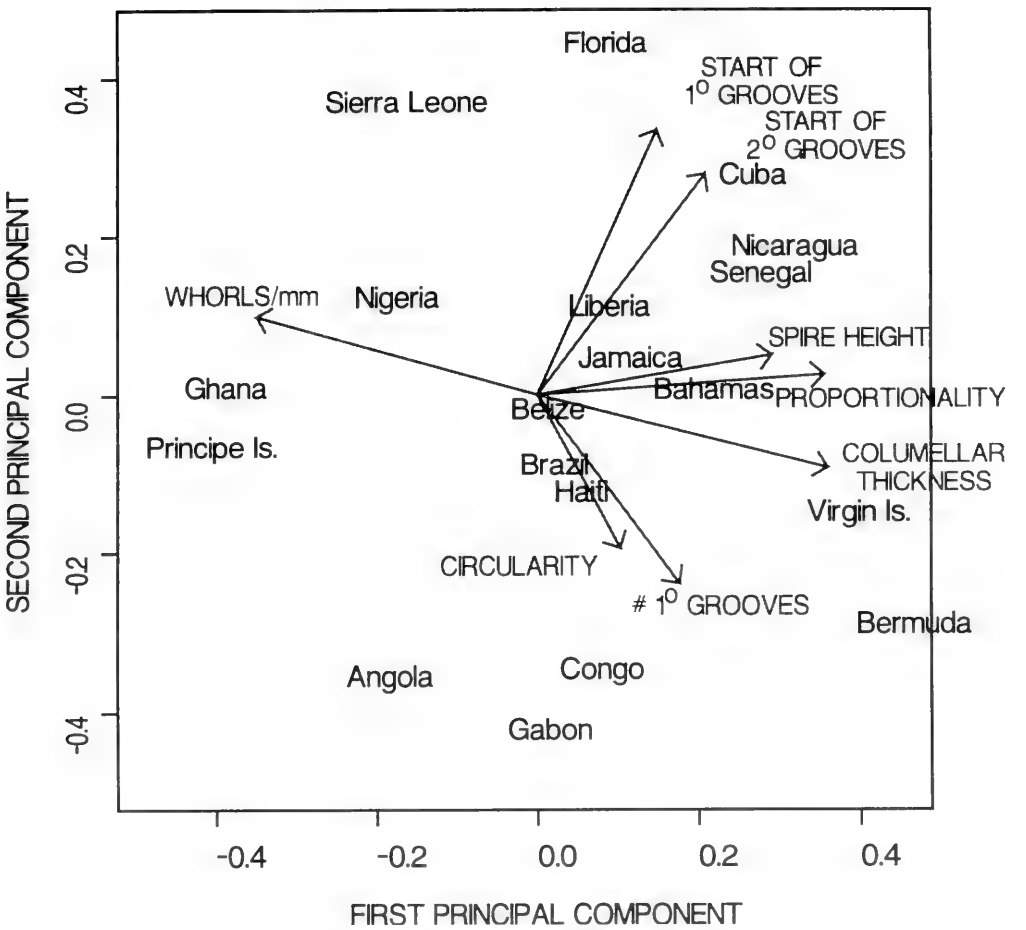


FIG. 8. Principal components biplot illustrating placement in ordination space of the 19 sampling locations with respect to eight morphological variables. All variables were standardized prior to analysis. Loadings for these two component axes, as well as axes three and four, are given in Table 4.

quencies were found between shells from the eastern and western Atlantic ($\chi^2 = 0.823$, P = 0.360, Fisher's Exact Test). Among current regimes, both the Gulf Stream and South Equatorial samples had more orange morphs than expected by chance alone (13.9% and 24%, respectively, $\chi^2 = 36.096$, $P < 0.001$, G-test). This result was due to unusually high frequencies of the orange morph in samples from Angola (24%), Bermuda (36.4%), and Virgin Islands (20%). Shell color was not clearly associated with any habitat-specific variable.

Genitalia

The pallial oviduct of the ovoviviparous *L. angulifera* has a single spiral loop that passes through the albumen and membrane glands (Fig. 4), unlike the pallial oviduct of oviparous congeners, which have four to six loops that contain additional capsule glands through which the eggs must pass before being released. The penial glandular disc is round, flattened, and darker in color than the rest of the penis, and the open sperm groove runs along the filament (Fig. 5). All specimens from which the penis was removed and drawn showed a remarkable uniformity in shape and size (Table 7). Additional multivariate analysis of sites for which we measured genital characteristics showed that those populations were distinguishable based only on characteristics of the pallial oviduct, which was much longer at one Florida site and at Wee Wee Cay than at the other sites. However, absolute

TABLE 5. Habitat characteristics of the 19 locations. Data from Walter et al. (1975); Wilcox et al. (1975); Ward & Bunyard (1992); Suman (1994); Saenger & Bellan (1995); Spalding et al. (1997).

Location	Annual rainfall (mm)	Number of dry months	Mean monthly temp. (°C)	Mean canopy height (m)	Nutrient source
Eastern Atlantic					
Angola	363	9	26.4	30	estuarine
Congo	1306	4	25.3	30	estuarine
Gabon	1904	4	26.3	30	estuarine
Ghana	858	6	26.5	15	estuarine
Liberia	3874	3	27.0	30	estuarine
Nigeria	1830	4	26.3	12	estuarine
Principe Islands	721	4	26.2	5	oligotrophic
Senegal	516	8	24.0	4	estuarine
Sierra Leone	4349	4	26.6	35	estuarine
Western Atlantic					
Bahamas	1181	2	25.1	3	oligotrophic
Belize	1500	2	29.5	8	oligotrophic
Bermuda	1483	0	21.4	3	oligotrophic
Brazil	2150	4	26.4	30	estuarine
Cuba	1481	3	25.2	10	oligotrophic
Florida	1004	1	25.3	10	oligotrophic
Haiti	1242	6	27.5	10	oligotrophic
Jamaica	800	3	26.4	12	oligotrophic
Nicaragua	3293	0	26.0	15	estuarine
Virgin Islands	1638	0	26.4	5	oligotrophic

TABLE 6. Loadings of habitat variables on the first two principal component axes. Only loadings ≥|0.1| are shown. These two axes account for 70% of the among-location variance in habitat. Characters are ordered in descending order of their loadings on the first principal axis.

Variable	Axis 1	Axis 2
Canopy height	0.898	0.122
Nutrient source	0.832	−0.207
Annual rainfall	0.525	0.788
Number of dry months	0.504	−0.807
Average annual temperature	0.412	0.133
Cumulative proportion of variance explained	0.44	0.70

shell height and pallial oviduct length were significantly correlated ($r^2 = 0.54$; $P = 0.024$), so this result simply shows that large snails had large pallial oviducts. On the other hand, shell height and penis length were not correlated ($r^2 = 0.17$; $P = 0.27$) among these sites.

DISCUSSION

Our data illustrate substantial variation in shell morphology in *Littoraria angulifera*, and this variation is associated both with potential dispersal paths and local habitat conditions. Despite an 8–10 wk planktonic larval stage, long enough to cross the Atlantic on any of the trans-Atlantic currents, populations associated with different current regimes exhibit clear and strong differences in shell morphology (Figs. 6, 7, Table 3). This observation on first glance supports the hypothesis that regional diversification associated with dispersal is occurring in this species. The strong association of habitat types with geography (Table 5), however, lends some credence to the hypothesis that morphological variation is determined primarily by local environmental conditions. Furthermore, the principal exceptions to the disperal-morphology association (Fig. 8), namely shells from Senegal, Liberia, Brazil and especially Nicaragua (which is well-isolated from easy trans-Atlantic dispersal via either equatorial current), and the uniformity in genital form and size from snails from both sides of the Atlantic (Table 7) suggest that we should reject the hypothesis of regional diversification associated with dispersal as a cause for morphological variation in *L. angulifera*.

Littoraria angulifera inhabits mangrove swamps, and we hypothesize that observed variation in its shell morphology is most likely caused by habitat-specific differences in nutrient status associated with local climate, forest structure, and prevailing geomorphology. Mangrove swamps in Florida, the Bahamas, and the Caribbean Islands are primarily found on carbonate platforms and are markedly oligotrophic (nutrient-poor) relative to the more

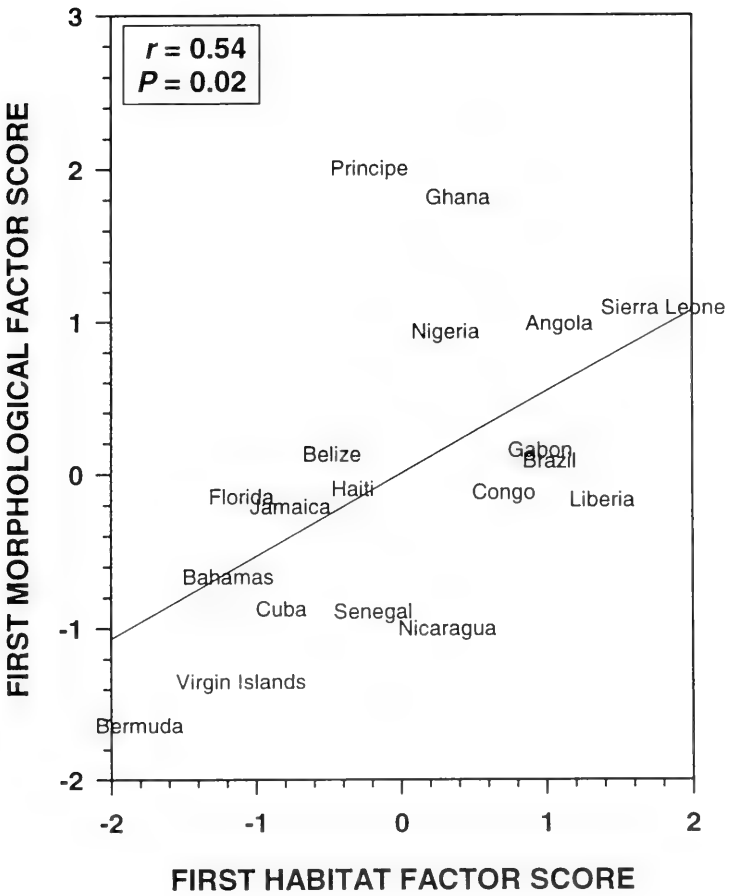


FIG. 9. Association between standardized habitat and shell morphology scores for the 19 locations.

TABLE 7. Measurements of genital characteristics (means in mm with standard deviations in parentheses). All values are lengths, except for diameter of the spiral portion of the pallial oviduct. Sample size for neotropical samples = 20; for African samples = 6.

Sample site	Penis	Pallial oviduct	Spiral Portion	Bursa copulatrix
Florida: Cockroach Bay	2.5 (2.5)	1.9 (2.2)	0.7 (0.9)	1.2 (1.5)
Florida: Little Shark River (mouth)	2.7 (3.0)	2.6 (2.8)	0.9 (1.0)	1.8 (2.1)
Florida: Little Shark River (middle)	3.1 (3.9)	4.1 (4.2)	1.7 (1.9)	2.8 (3.0)
Florida: Little Shark River (upper)	2.0 (2.9)	2.6 (2.5)	0.9 (0.9)	1.9 (1.9)
Florida: Hurricane Island	2.3 (2.8)	2.1 (2.0)	0.9 (0.9)	1.3 (1.2)
Belize: Wee Wee Cay	2.4 (3.6)	3.5 (2.6)	1.7 (1.2)	2.1 (1.6)
Jamaica: St. Anne's Bay	2.7 (2.7)	1.7 (2.1)	0.7 (0.8)	1.1 (1.4)
Ghana	1.9 (2.4)	1.0 (1.1)	0.3 (0.4)	0.8 (0.9)
Sierra Leone: Freetown (II)	2.5 (3.4)	1.7 (2.6)	0.5 (0.4)	1.9 (2.1)

eutrophic (nutrient-rich) estuarine mangroves of Africa, Nicaragua and South America (e.g., Twilley, 1995). Oligotrophic swamps have higher salinity and water clarity (Twilley, 1995), and may be associated with lower fungal biomass on the leaves where *L. angulifera* feeds (Kohlmeyer & Bebout, 1986) than estuarine ones. Lower food availability and higher salinity may result in slower growth rates of *L. angulifera*. Kemp & Bertness (1984) demon-

strated experimentally that well-fed, fast-growing *Littorina littorea* produce more rounded, globose shells (like *L. angulifera* from most of Africa, Nicaragua, and Brazil), while poorly fed, slower-growing *Littorina littorea* produced more pointed, high-spired shells (like *L. angulifera* from Florida and the Caribbean). Boulding & Hay (1993) found, in contrast, that well-fed *Littorina subrotundata* produces high-spired shells. Additional experimental work is needed to assess the role of food availability on shell shape in *L. angulifera,* and in littorines in general.

The high-spired shells from Senegal occur in short-statured mangrove forests that are more like those of the Caribbean than the rest of the sampled African locations (Table 5, Fig. 10). Caribbean and Senegalese mangroves are short (generally < 10 m) with relatively open canopies, and in such forests, insolation is likely to be higher and evaporation greater. It is likely that snails in these forests experience higher mid-day temperatures than snails in mangroves with tall, closed canopies. This observation, along with the strong association of canopy height with the first principal axis of the habitat PCA and rainfall and average temperature on the second principal axis of the habitat PCA strongly suggests that shell shape in *L. angulifera* is associated with dessication resistance (Fig. 9 links the morphology and habitat PCAs.)

Shell sculpturing may also be associated with food availability (Berry, 1961; Janson, 1982a) and dessication resistance (Vermeij, 1973). Vermeij (1973) suggested that even very small variations in shell sculpture may reduce dessication as grooves may serve to reflect heat and cause cooling through convection. Shell sculpture characteristics (number and location of primary and secondary grooves) loaded heavily on the first two principal components axes (Table 4) in the analysis of shell morphology. Figure 9 suggests additional linkages between shell sculpture and habitat characteristics. For example, shells from Bermuda, the Virgin Islands, Congo, Gabon, and Senegal are distinguished from the others by relatively many primary grooves, and mangrove forests in these areas are sparse and short in stature, or occur in regions with pronounced dry seasons (Chapman, 1976). Note that despite exceptionally low rainfall and a 9-month dry season, the canopy height in Angolan mangrove forests is very high as a consequence of high nutrient input in Angolan estuaries. We infer that the lower surface temperatures, reduced rate of evaporation, and increased nutrient levels leads to snails with globose shells (Table 1). Shell color polymorphism in *Littoraria* may also be associated with dessication avoidance (Cook, 1983; Cook & Freeman, 1986; but see Reid, 1987), but we lack detailed microclimatic data for any of these sites. In a preliminary study, however, we found no association between substrate temperature, insolation, and frequency of orange morphs of *L. angulifera* at Wee Wee Cay, Belize (A. M. Ellison, unpublished data). We note also that the frequency of rare, orange morphs of *L. angulifera* is likely to be artificially high in museum samples because of collecting bias.

Observed variation in columellar thickness may be associated with predation, but we know little about predators of *L. angulifera* and other supralittoral littorinids. Reid (1985, 1986, 1988, 1992) suggests that grapsid crabs prey on *Littoraria* in Pacific mangrove forests, and omnivorous grapsids do occur in Atlantic mangroves (Sterrer, 1986). However, there have been no studies of their diets. Shell color polymorphism may also be associated with predation (Reimchen, 1979; Cook, 1983; Reid, 1988; Cook & Kenyon 1993). Further study of both microclimate and predators of *L. angulifera* is needed, especially in Bermuda, the Virgin Islands, and Angola, where we recorded exceptionally high frequencies of orange shell morphs.

We observed site-specific differences in pallial oviduct length that were correlated with shell size, but penis length was invariant with respect to shell size. This result is not unexpected because a larger pallial oviduct would be associated with increased clutch size in larger snails. Comparable variability in penis length, however, could limit male reproductive success.

Genetic variability underlies morphological variation in some littorinids (Janson, 1982b; Cook, 1992; Cook & Garbett, 1992; Mill & Grahame, 1995). Although the lengthy larval stage (Gallagher & Reid, 1979) and likelihood of regular gene-flow among populations (at least those within current regimes) suggests that genetic differentiation among local populations of *L. angulifera* is unlikely, Janson (1985) found unexpectedly high genetic variation among Florida populations of *L. angulifera.* Janson (1985) attributed this variation either to differential selection due to abiotic factors and predation, or to restricted gene flow due to limited larval dispersal affected by

current distribution. Larger genetic divergence was found between Gulf Coast and Atlantic Coast populations of *L. angulifera* than was found among populations on either side of the peninsula. In another study of genetic variability in *L. angulifera* within the Gulf of Mexico however, Gaines et al. (1974) found no differences between observed and expected numbers of heterozygous individuals in 19 of 20 island populations.

Linking larval dispersal, distribution, and variability of genetic and phenotypic origin in oviparous and ovoviviparous gastropods is complicated by the lack of knowledge concerning the pelagic portion of the larval stage; laboratory breeding experiments and rearing of larvae generally have been unsuccessful (McQuaid, 1996). Nonetheless, more systematic study of local and regional morphology, and further genetic study of these populations, combined with the results of this study based on opportunistic museum collections would provide a more complete explanation of observed geographic and habitat-specific morphological variation of *Littoraria angulifera.*

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IS CYCLININAE A MONOPHYLETIC SUBFAMILY OF VENERIDAE (BIVALVIA)?

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ABSTRACT

Cyclininae Frizzell, 1936, consists of two extant genera, *Cyclina* Deshayes, 1850, and *Cyclinella* Dall, 1902, characterized by subcircular profiles and lack of anterior lateral hinge teeth (Keen, 1969). A cladistic analysis utilizing 14 conchological characters was performed on seven venerid taxa to determine if the venerid subfamily Cyclininae represents a monophyletic clade. Included in the analysis were the following subfamily type species: *Cyclina sinensis* (Gmelin, 1791) (Cyclininae), *Clementia vitrea* (Dillwyn, 1817) (Clementiinae), *Dosinia concentrica* (Born, 1778) (Dosiniinae), *Tapes literata* Linnaeus, 1758 (Tapetinae), as well as the type species of *Austrovenus* Finlay, 1927 (Chioninae), *A. stutchburii* (Wood, 1828), the type species of *Cyclinella, C. tenuis* (Récluz 1852), and an outgroup species, *Lucinisca nuttalli* (Conrad 1837) (Lucinidae). Methods demonstrate how continuous data can be used to quantitatively define limits of character states for cladistic analysis. Results indicate that: (1) Cyclininae is a construct of convergent traits (subcircular profiles and lack of lateral teeth), (2) *Cyclina* is a chionine genus, and (3) *Cyclinella* is a clementiinine or tapetine genus. It is proposed that: (1) Cyclininae be discarded as a venerid subfamily and possibly Clementiinae as well, (2) *Cyclina* be reclassified within the Chioninae, and (3) *Cyclinella* be reclassified within the Clementiininae or Tapetinae.

INTRODUCTION

Frizzell (1936) broke up Veneridae (Bivalvia), a large global family of marine clams, into 12 families; within this scheme, Cyclininae Frizzell, 1936, is a subfamily assigned to the family Clementiidae Frizzell, 1936. This classification was later modified by various workers (Fischer-Piette, 1975; Fischer-Piette & Métivier, 1971; Fischer-Piette & Vukadinovich, 1972, 1975, 1977; Keen, 1969, 1971; Habe, 1977), who continued to view Veneridae as a large, heterogeneous family with many subfamilies, and incorporated Frizzell's families as subfamilies. As classified by Keen (1969), Cyclininae Frizzell, 1936, is one of 12 subfamilies within Veneridae, and composed of two small extant genera, *Cyclina* Deshayes, 1850, and Cyclinella Dall, 1902, and three extinct genera, *Cyprimeria* Conrad, 1864, *Frigichione* Fletcher, 1938, and *Luciploma* Olsson, 1942. Keen (1969) defined Cyclininae as "Like Dosiniinae in form but without anterior lateral teeth or incised lunule; sculpture concentric with few faint radial traces." Dosiniinae is a large subfamily of clams that have subcircular, often discoid, valves, defined lunules, predominantly fine concentric sculpture, and anterior lateral hinge teeth. Olsson (1964) classified *Cyclinella* in Dosiniinae. Radial sculpture is present in *Cyclina* and absent in *Cyclinella* and the fossil genera.

Keen (1969) defined valves of Clementiinae as "thin, inequilateral; without escutcheon; sculpture subdued or wanting; inner ventral margin smooth; hinge without lateral teeth." In fact, *Clementia* possesses an indented escutcheon, although the structure is not as sharply defined as in, for example, the subfamily Chioninae.

Although both extant cyclinine genera are present in the fossil record, *Cyclina* contains a single extant species, the west Pacific type species *Cyclina sinensis* (Gmelin 1791); *Cyclinella* contains one moderately common extant species, the type species *Cyclinella tenuis* (Récluz, 1852), ranging from off Virginia to Brazil (Abbott, 1974), and six rarely collected species off tropical west Central America (Keen, 1971).

Despite their subcircular profiles, I observed several less obvious differences between *Cyclina* and *Cyclinella* that made me suspect they were not as closely related evolutionarily as their classification might indicate. Homoplasic profiles are common in Bivalvia, often stemming from functional convergence (Stanley, 1970); within Veneridae, numerous examples of apparent homoplasy in profile and other conchological characters exist (Jukes-

Browne, 1913; Jones, 1979; Lindberg, 1990; Harte, 1992; Roopnarine, 1996). I performed the following cladistic analysis, comparing conchological characters of *Cyclina* and *Cyclinella* and taxa of other subfamilies to test the null hypothesis that these genera were not more closely related to other subfamilies than to themselves, thus not warranting the breakup of this subfamily.

MATERIALS AND METHODS

A cladistic analysis was performed on eight taxa (Table 1), utilizing 14 conchological characters and PAUP 3.1.1 (Swofford, 1993). The characters were unweighted, character states were unordered, and every possible tree was examined. Data for the analysis were collected from the following subfamily type species: *Cyclina sinensis* (Gmelin, 1791) (Cyclininae), *Clementia vitrea* (Dillwyn, 1817)[1] (Clementiinae), *Dosinia concentrica* (Born, 1778) (Dosiniinae), *Tapes literata* Linnaeus, 1758 (Tapetinae), as well as the type species of *Austrovenus* Finlay, 1927 (Chioninae), *A. stutchburii* (Wood, 1828), the type species of *Cyclinella, C. tenuis* (Récluz 1852), *Ruditapes philippinarum* (Adams & Reeve, 1850), and an outgroup east Pacific species, *Lucinisca nuttalli* (Conrad, 1837) (Lucinidae). All specimens examined came from the U.S. National Museum Mollusca collection, the Academy of Natural Sciences at Philadelphia Mollusca collection, and the Recent Mollusca collection at the University of California Museum of Paleontology at Berkeley.

Taxa were chosen to represent those subfamilies with conchological and biogeographical affinities to Cyclininae that indicate the highest probability of evolutionary affinity. This eliminated from the analysis those subfamilies lacking both of the defining conchological characteristics of Cyclininae, subcircular profiles and the absence of lateral teeth. Like Cyclininae, all ingroup taxa except *Dosinia concentrica* lack anterior lateral teeth, three ingroup taxa have subcircular profiles, and three have radial sculpture. Like *Cyclina,* four taxa are west Pacific species. *Dosinia concentrica* is a tropical American species, like *Cyclinella* and *Clementia solida* Dall, 1902, one of the few extant species of that genus. Rather than choose the type species of the subfamily Chioninae to represent that subfamily, I chose *Austrovenus* because its biogegraphic affinities (west Pacific) to *Cyclina* (west Pacific, both fossil and Recent) increase the probability that the two taxa are more closely related, evolutionarily, than the subfamily type species, a tropical Atlantic species. *Austrovenus* is a good conchological representative of Chioninae, possessing all the subfamily characteristics; indeed, Keen (1969) classified it as subgenus of the type genus, *Chione,* although anatomical differences indicate that it is quite different from *Chione* (Jones, 1979).

TABLE 1. P-values for regressions of each of three morphometric variables on height for each taxa.

Genus	Ligament	Pallial Sinus	Profile
Clementia	0.226	0.533	0.279
Cyclinella	0.871	0.944	0.874
Cyclina	0.246	0.327	0.342
Austrovenus	0.702	0.510	0.177
Dosinia	0.855	0.473	0.679
Tapes	0.197	0.644	0.350
Ruditapes	0.547	0.530	0.116
Lucina	0.255	N/A	0.880

Conchological characters included: presence of posterior purple pigment (1), presence of radial sculpture (2), profile (3), bifidity of the 1, 2a, and 2b cardinal hinge teeth (4–6), presence of the escutcheon (7), crenulation of the ventral margin (8), presence of anterior lateral hinge teeth (9), ligament length (10), elevation of the ligament (11), pallial sinus development (12), definition of the lunule (13), and presence of radial sculpture on the lunule (14) (Fig. 1). Parenthetical numbers refer to the characters as they appear on the matrix (Table 4). Complete definitions of these characters and their character states are given in Appendix I.

Three of the above conchological characters, 3, 10, and 12, were derived from continuous data. Data were collected from 10 specimens of each species, utilizing metric calipers. For all three characters, measured variables were factored for size by dividing each by height. Height was chosen as a mea-

[1] *Mactrea vitrea* "Chemn." of Dillwyn (1817) is a senior synonym of *Venus papyracea* Gray, 1825, given by Keen (1969) as the type species of *Clementia.* Lamy (1913) asserts *Mactrea vitrea* Chemnitz, 1795 (pl. 20: figs. 1959–1960), is a species of *Clementia;* Smith (1885) notes that it is identical to *V. papyracea.* Both Kevin Lamprell (personal communication) and I agree.

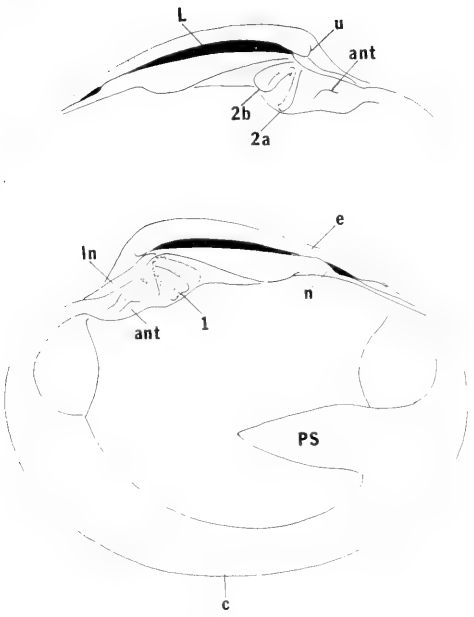

FIG. 1. A composite illustration of a right venerid valve and left hinge. ant, anterior lateral teeth; c, marginal crenulations; e, escutcheon; L, ligament; ln, lunule; n, notch at the end of an elevated nymph; PS pallial sinus; 1, a bifid right median cardinal tooth; 2a, a bifid left anterior cardinal tooth; 2b, a bifid left median cardinal tooth.

sure of size rather than valve length or width of conjoined valves, because valve height does not vary as much among venerid subfamilies (e.g., no elongation as is present in mussels), as does length (venerids vary from circular to elongate) or width (venerids vary from compressed to obese).

I utilized the software package Statistix 4.0 to analyse the resulting proportions. To determine if the proportions were affected by allometry (i.e., the proportions changed with growth, thus exhibiting significant regression), each ratio was regressed against the independent size variable, height. Means of the proportions were calculated for each variable of each species. The quantitative limits of different character states were based on a median value between the limits of nonparametrically significant clusters of means. Taxa assigned different character states but with overlapping ranges of data were tested for significant nonparametric differences in frequency distributions with the Signed Wilcoxon Rank Test.

RESULTS

Table 1 demonstrates that the three ratios representing characters derived from continuous data are proportions that are not affected by growth: no significant regressions resulted. Table 2 presents the means and ranges of characters 3, 10, and 12; in all cases variation within species is much less than among species. Table 3 demonstrates significant nonparametric differences for those taxa of different character states exhibiting overlap in raw data.

Table 4 presents the character state matrix for the cladistic analysis. The PAUP analysis results in a consensus tree (Fig. 2) derived from five most parsimonious trees (total length of 31 for each) out of 10,395 examined trees; all five trees had a consistency index (excluding uninformative characters) of 0.630. In these trees, the most homoplasic character, judging from averages derived from the homoplasy index for every variable over all five trees, is elevation of the ligament, followed by radial valve sculpture, and definition of the escutcheon and lunule. *Cyclina* clades with *Austrovenus,* and *Cyclinella* with *Clementia* and the tapetines in the consensus tree. Among the five trees, there is only one instance of *Cyclinella* forming a clade with a single other taxon, *Clementia. Clementia* clades with the tapetines in 80% of the trees. Figure 3 summarizes character states common to the clades throughout the tree.

DISCUSSION

The above results indicate that Cyclininae is not a monophyletic subfamily, but a grouping of species with a convergent conchological trait, subcircular profile. Stanley (1970) noted that shell form is an important adaptive feature of a special, ecologically significant parameter, rate of burrowing, although shell form is only one factor controlling it. His data indicate that although both *Dosinia* and *Cyclinella* are compressed subcircular species, *Dosinia* is a relatively fast burrower inhabiting cleaner, less stable sediments than the slow burrower *Cyclinella,* which lives in muddy sediments. Stanley (1970) also linked shell form with mode of burrowing. Specifically, he observed that subcircular clams (including lucinids, *Dosinia* and *Cyclinella*), whether slender (as in *Dosinia* and *Cyclinella*) or inflated (as in *Cyclina*), typically burrowed verti-

TABLE 2. Means and ranges of three morphometric variables for all taxa.

	Ligament		Pallial sinus		Profile	
Genus	Mean	Range	Mean	Range	Mean	Range
Clementia	0.38	0.32–.44	0.48	0.39–.59	1.35	1.27–1.43
Cyclinella	0.54	0.48–.64	0.49	0.41–.59	1.28	1.18–1.38
Cyclina	0.55	0.49–.61	0.39	0.35–.44	1.12	1.05–1.18
Autrovenus	0.54	0.45–.63	0.20	0.16–.26	1.36	1.23–1.47
Dosinia	0.66	0.62–.71	0.44	0.41–.48	1.27	1.22–1.31
Tapes	0.78	0.66–.86	0.54	0.43–.60	1.78	1.64–1.95
Ruditapes	0.72	0.62–.80	0.50	0.48–.55	1.57	1.48–1.62
Lucina	0.53	0.49–.57	N/A		1.07	1.01–1.10

TABLE 3. Results of Wilcoxon Signed Rank test for taxa of different character states with overlapping data ranges.

Test clusters of taxa	Variable	Σ + Ranks	Σ – Ranks	Probability (2-tailed)
Austrovenus & *Clementia* vs. *Cyclinella* & *Dosinia*	Profile	198	–12	0.0006
Clementia & *Cyclinella* vs. *Cyclina* & *Dosinia*	Pallial Sinus	207	–3	0.0002

TABLE 4. Data matrix used in the cladistic analysis of this study. *Lucinisca* is the outgroup. Characters 1–14 are fully defined in Appendix 1.

	Characters													
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Dosinia	0	0	0	0	0	1	0	0	1	1	1	1	1	0
Ruditapes	0	1	1	1	0	1	1	0	0	1	0	2	1	0
Tapes	0	0	1	1	1	1	1	0	0	1	1	2	1	0
Austrovenus	1	1	1	1	1	1	1	1	0	1	0	0	1	1
Cyclina	1	1	0	0	1	0	0	1	0	1	1	1	0	1
Clementia	0	0	1	0	0	0	1	0	0	0	0	2	0	0
Cyclinella	0	0	0	0	0	0	1	0	0	1	1	2	1	0
Lucinisca	0	1	0	2	2	2	1	1	2	1	1	3	1	1

cally downward without any forward component and "with a pronounced rocking motion to saw or slice their way into the sediment." Stanley (1970) correlated the angle of rocking most strongly with elongation of the shell—the more elongate species exhibited smaller angles of rocking.

The current analysis indicates that elevation of the ligament is also a convergent trait. Data indicate that subcircular profile (character 3, state 0) is strongly correlated with the form of the ligament, which is relatively long and sunken (characters 10 and 11, states 1 and 1) in all four subcircular taxa. No other characters within the analysis correlate so completely with subcircular profile. One might speculate that the sunken ligament increases streamlining, whereas the relative length confers adaptive strength to compensate for the greater shearing stress generated by greater rocking.

These results have several taxonomic implications. That Clementiinae does not clade separately from the tapetines in the consensus indicates the subfamily, as based solely on *Clementia,* is not monophyletic. Further cladistic analysis that includes the other extant clementiinine genus, *Compsomax* Stewart, 1930, and a larger array of characters is needed to test the monophyly of that subfamily. That *Cyclinella* clades with *Clementia* and the tapetines in the consensus tree indicates that a more accurate venerid taxonomy would be to reject the subfamilies Cyclininae and Clementiinae, and classify both *Cyclinella* and *Clementia* within Tapetinae, a position previously proposed by Deshayes (1853). Only once in the five most parsimonious trees does *Cyclinella* clade with a single other taxon, *Clementia,* a weak implication that these two taxa are slightly more related to each other

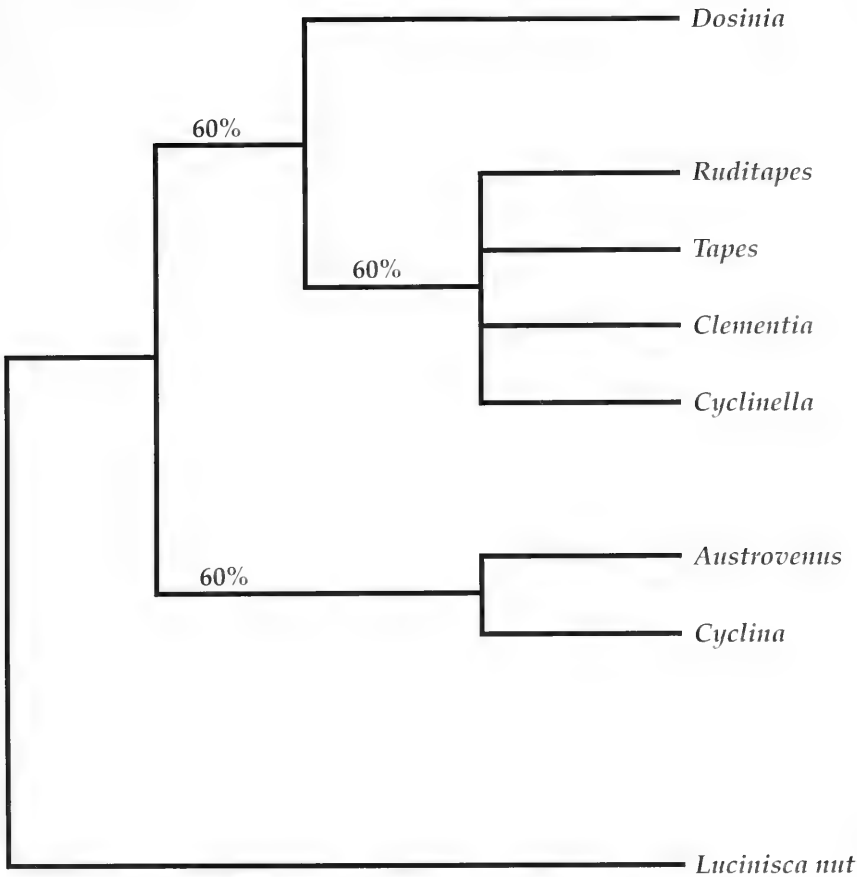

FIG. 2. A 50% majority rule consensus tree derived from five most parsimonious trees resulting from a PAUP 3.1.1 analysis of 14 conchological characters for seven venerid genera, utilizing a lucinid species, *Lucinisca,* as an outgroup. 60% = branches supported by three of the five trees.

than to other tapetines. The consensus tree is a clear rejection of the venerid taxonomy of Dall (1902), who classified *Clementia* and *Cyclinella* within the subfamily Dosiniinae. That the nominate cyclinine genus, *Cyclina,* appears to be more accurately described as a modified chionine expands the conchological range of that large subfamily.

There is no formal analytical attempt here to reconcile the placement of the extinct genera, *Cyprimeria* Conrad, 1864, *Frigichione* Fletcher, 1938, and *Luciploma* Olsson, 1942, although the conchological characteristics of each genus indicate some strong possibilities. The most problematic taxon is *Cyprimeria* Conrad, 1864 (Cretaceous), which is in some ways similar to the subfamily Sunettinae. Like Sunettinae, the shells are moderately thin, compressed, ovate, with fine concentric sculpture that forms a smooth glossy surface, and have sharply escavated escutcheons and small umbos (personal observation). Unlike Sunettinae, the hinge lacks anterior lateral teeth, the inner margins are smooth, and the geographic distribution (Americas and Europe) does not overlap with the Asian-African distribution of Sunettinae. *Cyprimeria* might be more closely linked with *Clementia* through its smooth inner margins, lack of lunule (Palmer, 1927), lack of lateral teeth, fine concentric sculpture, and moderately thin shells and it geographically overlaps with Clementiinae. Under the changes proposed above, this would argue for its placement within Tapetinae.

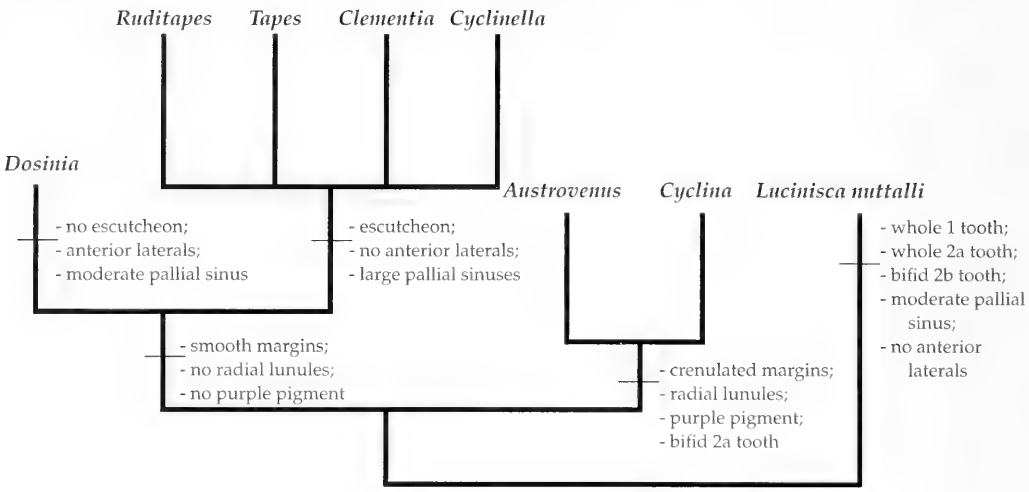

FIG. 3. Character states common to the clades of the consensus tree.

Frigichione resembles chionines in that it lacks anterior lateral teeth, and has strong concentric sculpture. The type species of *Frigichione,* an Antarctic taxon, was originally classified as a *Chione* (Fletcher, 1938), and is conchologically similar to extant *Tawera* Marwick, 1927, a chionine genus which occurs in the Antarctic (Dell, 1964). Both genera are characterized by somewhat trigonally ovate shells with heavy concentric sculpture, and with small to no pallial sinus. When specifically compared to Antarctic *Tawera,* both *Frigichione* and the Antarctic *Tawera philomela* (Smith, 1885) appear to have no pallial sinus. *Frigichione* has fine internal radial elements, but it is difficult to discern from the plates in Fletcher (1938) (the character is not mentioned in text) any marginal crenulations, a condition that is so fine in *T. philomela* that it is "only just visible to the naked eye" (Smith, 1885). Examples of chionines with smooth margins, for example, *Cryptonomella* Kuroda & Habe, 1951, exist. *Luciploma,* a Central American taxon, was probably classified within the Cyclininae, because Olsson (1942) observed that its "hinge structure agrees best with *Cyclina* and *Cyclinella*" on the basis of the right valve lacking anterior lateral teeth and having a strong medial cardinal tooth. The same, however, can be observed in many American chionine species. More important is the lack of a lunule, an apparently short ligament, the smooth ventral margins, and the moderate to weak concentric sculpture. All these conchological characters indicate that *Luciploma* most closely resembles *Clementia.* Unlike *Clementia, Luciploma* appears to have a thicker shell, with stronger hinge teeth (Olsson, 1942: pl. 3, fig. 2).

CONCLUSIONS

Cyclininae is a construct of convergently subcircular venerids and should be discarded as a subfamily of Veneridae. *Cyclinella* should be reclassified within Clementiinae or Tapetinae, and *Cyclina* within Chioninae. Conchological characters indicate that *Frigichione* can be tentatively classified as a subgenus of *Tawera* (Chioninae), and that *Cyprimeria* and *Luciploma* can be tentatively classified as genera of Clementiinae or Tapetinae pending further cladistic analysis.

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APPENDIX I

Definition of Characters and Their States

All characters are defined by either presence/absence or quantitative limits. Morphometric variables (3, 10, 12) were measured from the right valve and divided by valve height (H) to compensate for specimen size. Character state limits are based on significantly different clusters of means of the taxa for each variable derived from a minimum sample size of 10. H was measured as described below in 3 (Profile).

1. *Presence/absence of a dark purple pigment* on the inside posterior area of the valves. States: presence = 1, absence = 0.
2. *Presence/absence of radial sculpture* on the valves (excluding escutcheon

and lunule). States: presence = 1, absence = 0.

3. *Profile* is defined as a measure of the length/height (L/H) of the right valve. The right valve was placed flat on a 0.5 centimeter grid, oriented so that the dorsal tips of the adductor scars were aligned horizontally, accomplished by marking these positions on the external margins. The profile of the valve was traced onto the grid. L is the maximum horizontal, length; H is the vertical length from the tip of the umbo to the ventral margin. States: $L/H \leq = 1.31$ subcircular = 0, $L/H > 1.31$ = other = 1.
4. *Bifidity of the medial cardinal hinge tooth* in the right valve ("1"): not present (as in the outgroup) = 2, bifid = 1, not bifid = 0.
5. *Bifidity of the anterior cardinal hinge tooth* in the left valve ("2a"): not present (as in the outgroup) = 2, bifid = 1, not bifid = 0.
6. *Bifidity of the medial cardinal hinge tooth* in the left valve ("2b"): not present (as in the outgroup) = 2, bifid = 1, not bifid = 0.
7. *Presence/absence of the escutcheon:* the escutcheon was defined as present if there was any easily discernible indentated area surrounding the ligament. Present = 1, absent = 0.
8. *Crenulated ventral margin* of the valves: crenulated = 1, smooth = 0.
9. *Anterior lateral hinge teeth:* present = 1, absent = 0, not applicable (the outgroup) = 2.
10. *Ligament length* = L_{lig}/H, where L_{lig} = the length of the ligament, and H is the vertical length from the tip of the umbo to the ventral margin, as further defined in 4, above. States: $[L_{lig}/H \leq 0.45] = 0$, $[L_{lig}/H > 0.45] = 1$.
11. *Elevation of the ligament:* if the ligament was not sunken, a notch was present at the posterior end of the nymph, indicating a partial elevation of the nymph and hence, the ligament. Presence of nymphal notch = 0, absence of the notch = 1.
12. *Pallial sinus development:* = L_{pal}/H, where L_{pal} is the straight line distance from the ventral base of the pallial sinus at the pallial line to the most distal point along the ventral edge of the pallial sinus, and H is the vertical length from the tip of the umbo to the ventral margin, as further defined in 4, above. $[L_{pal}/H < 0.3] = 0$, $[L_{pal}/H \geq 0.3$ and $\leq 0.46] = 1$, $[L_{pal}/H \geq 0.46] = 2$, $[L_{pal}/H = 0] = 3$.
13. *Presence/absence of lunule:* a lunule was defined as present if a clearly incised line, an impressed area or a distinct change in sculpture within the area, or protruding rib defined its outline. Present = 1, absent = 0.
14. *Presence/absence of radial sculpture on lunule:* Present = 1, absent = 0.

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MARINE VALVATOIDEA - COMMENTS ON ANATOMY AND SYSTEMATICS WITH DESCRIPTION OF A NEW SPECIES FROM FLORIDA (HETEROBRANCHIA: CORNIROSTRIDAE)

Rüdiger Bieler[1], Alexander D. Ball[1,2], and Paula M. Mikkelsen[3]

ABSTRACT

The "lower heterobranch" gastropod family Cornirostridae Ponder, 1990 (Valvatoidea), has been previously known from only six confirmed extant species in three genera (*Cornirostra, Noerrevangia, Tomura*). Knowledge of the soft-body morphology is necessary for placement in this family. The unique "multi-tentacled, two-tailed" habitus forms a synapomorphy of this group (an appearance produced by a combination of characters of the paired anterior oral lobes, cephalic tentacles, curved foot processes, and the deeply split hindfoot). As a result of research on "lower heterobranchs" of the Florida Keys, a new species of *Cornirostra, C. floridana* Bieler & Mikkelsen, n. sp., is described from the Florida Keys, as the seventh known species in the family, the second known species in the genus, and the first member of *Cornirostra* from the Atlantic Ocean. Detailed anatomical descriptions and interpretations of the foregut and nervous system are provided from computer-assisted reconstructions of semi-thin histological sections. Shell and anatomical characters of the seven confirmed living cornirostrid species are summarized, generic and familial diagnoses are discussed, and a redescription of the family Cornirostridae is provided, based on shell and anatomical data. Distinguishing characters of other recognized families of Valvatoidea (Valvatidae, Orbitestellidae) are surveyed. The problematic assignment of fossils to this anatomically defined gastropod family is also addressed.[4]

Key words: Florida Keys, Gastropoda, lower Heterobranchia, *Cornirostra*, Atlantic Ocean, systematics, nervous system, histology.

INTRODUCTION

A focus in recent gastropod research has been on the "lower heterobranchs" (also termed Allogastropoda, Heterostropha, etc.), a grade or clade of several families that shows heterobranch anatomical organization in many organ systems, distinguishing them from the caenogastropods with which many were traditionally grouped. In addition to such relatively well-known groups as Pyramidelloidea, Architectonicoidea, and Valvatidae, this group includes families of lesser-known, small-shelled snails, such as Omalogyridae, Rissoellidae, Glacidorbidae, and the enigmatic and very recently described Tjaernoidae Warén, 1991, Hyalogyrinidae Warén & Bouchet, 1992, Xylodisculidae Warén, 1992, and Cimidae Warén, 1993. The erection of new family-group taxa is partly the result of newly discovered species, and partly because of critical reassessment of anatomical features, warranting the transfer of taxa from traditionally recognized "prosobranch" groups into the lower heterobranchs (e.g., Haszprunar, 1988; Rath, 1988; Ponder, 1991; Bieler, 1992; Warén et al., 1993).

One such example is *Tomura bicaudata* (Pilsbry & McGinty, 1946), described as a vitrinellid caenogastropod from Missouri Key in the Lower Florida Keys. Moore (1964) questioned its placement in Vitrinellidae, based on the uncharacteristic tentacle morphology illustrated in the original figures. In a reassessment of available anatomical data on Vitrinellidae, Bieler & Mikkelsen (1988) removed *T. bicaudata* from the Vitrinellidae on the basis of several head-foot characters, but also could not suggest a new taxonomic placement. While the small, thin, transparent shell

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[4]This paper is dedicated to the memory of our friend and colleague Dr. Donald R. Moore (1921–1997), who contributed extensively to the knowledge of Florida's micromollusk fauna.

of *T. bicaudata* is very similar in overall appearance to many vitrinellid species (particularly that of *Vitrinella helicoidea* C. B. Adams, 1850), its body morphology is uniquely peculiar. The oral lobes, cephalic tentacles, and curved anterior foot processes, along with a deeply split hindfoot, make the animal appear multi-tentacled and two-tailed.

Other similar "horned-snout, cleft-tail" snails have been recently discovered. Ponder (1990b) introduced the generic name *Cornirostra* for *Microdiscula pellucida* Laseron, 1954, from Australia, and placed it and *Tomura* in his new family Cornirostridae among the lower heterobranchs. Based on extensive anatomical comparisons, he recognized the position of this family in the Valvatoidea, a group previously thought restricted to freshwater. Ponder (1990b) suspected *"Cyclostrema" prestoni* Melvill, 1906, from Ceylon, and the Mediterranean *Skenea pellucida* Monterosato, 1874, also to belong to Cornirostridae. The latter species, after more detailed anatomical study, has since been transferred to Hyalogyrinidae (Warén et al., 1993); the former remains of uncertain status. Warén et al. (1993) also transferred a Mediterranean species, *Oxystele depressa* Granata, 1877, to *Tomura*, and introduced a third cornirostrid genus, *Noerrevangia,* for *N. fragilis* Warén & Schander (in Warén et al.), 1993, from the Faroe Islands. Most recently, Fukuda & Yamashita (1997) described the first cornirostrid species from the Western Pacific, *Tomura yashima* and *T. himeshima.* Thus to date the family is known from six confirmed extant species placed in three genera.

Ongoing research on "lower heterobranchs" of the Florida Keys has brought to light an additional extant species of *Cornirostra,* which is here described. Histological reconstruction and functional interpretations emphasized foregut and nervous system anatomy, particularly those structures that differed from, or were not addressed, by Ponder's studies (1990b) of cornirostrid species. Shell-morphological and anatomical characters are discussed for all known extant species, and comments are made on the reported Cretacous-Jurassic-Triassic fossil record (Schröder, 1995; Bandel, 1996).

MATERIALS AND METHODS

Specimens were collected in the Florida Keys by "rock washing" (i.e., scrubbing the surfaces of shallow-subtidal rocks that can be lifted out of the water, including the underside normally resting on the sediment, with brush and saltwater) and by shoveling, hand-dredging, and sieving of muddy and sandy shallow-water substrata. Specimens were sorted from the resulting freshly collected material in the field laboratory under a dissecting microscope.

Cornirostra floridana n. sp. was observed alive only once, sketched, and photographed with a single-lens reflex camera equipped with extension tubes. For this reason, observations of gross morphology remained incomplete. Anatomical descriptions are based upon histological sections of the single live-collected specimen; initially intended for DNA studies, the specimen had not been chemically fixed before alcohol preservation, so tis-

Figure and Table Abbreviations

agp	accessory glandular pocket
bm	buccal mass
bpl	black pigmented layer
bw	body wall
c	cuticle
cg	cerebral ganglion
co	cornea
ct	connective tissue
cs	cuticular sheath
e	eye
g	gill
h	heart
jt	jaw tooth
le	lens
lu	lumen
m	muscle
mm	mantle margin
mpp	metapodial processes
orl	oral lobe
ot	oral tube
PC	protoconch
pg	pedal ganglion
pig	pigment
plg	pleural ganglion
PMO	pigmented mantle organ
pp	propodial processes
pt	pallial tentacle
sbg	subesophageal ganglion
sg	salivary gland
sh	shell
sn	snout nerves
snt	snout
spg	supraesophageal ganglion
st	statocyst
TC	teleoconch
te	cephalic tentacle
tn	tentacle nerves
v	void

sue preparation was not ideal. Following rehydration from 70% ethanol, the shell was dissolved using saturated aqueous ethylene diamene tetraacetic acid (EDTA). After dehydration through an ascending graded ethanol series, the specimen was infiltrated with LR White resin (Polysciences, Inc.) and flat-embedded in fresh resin using an inverted BEEM capsule. Polymerization took 8 h at 70°C. The specimen was mounted in transverse orientation and serial-sectioned at 1μm thickness. Sections were stained in aqueous toluidine blue, and mounted in Polymount (Polysciences, Inc.) under coverslips. The sections were drawn at 4 μm intervals using a camera lucida and the internal anatomy was reconstructed using Jandel Scientific's PC-3D software. Where greater resolution was required, specimens were reconstructed at 1μm intervals. Individual sections were photographed using a photomicroscope with automatic camera attachment. Scanning electron micrographs (SEM) were produced from air-dried shells, coated with gold, observed and photographed using an AMRAY 1810 scanning electron microscope at FMNH. Spire angle was measured using a protractor against photographs or line drawings of shells in lateral view. Numbers of protoconch and teleoconch whorls were ascertained using the method of Taylor as summarized by Jablonski & Lutz (1980: 330, fig. 4). This method counts the initial embryonic part of the shell as part of a whorl; this explains discrepancies between our counts and those of other authors who expressly or apparently employed different methods of whorl counting.

Comparative material of *Tomura* (Figs. 14–17) was collected in the Upper Florida Keys (Sta. FK-021, Lake Surprise, northeastern end of U. S. Route 1 causeway, Mile Marker 107.5, Monroe County, Florida, sediment/algae at approximately 1.5 m depth, by hand dredge, salinity = 22 ppt, 9 July 1995, Bieler/Mikkelsen coll.). Voucher specimens are deposited in FMNH 278404 (including SEM material) and AMNH 289603. Specimens collected for this study were compared to the type specimen of *Tomura bicaudata* (ANSP 182042; Missouri Key, Lower Florida Keys, Monroe County, Florida, T. L. McGinty!, March 1945; 1.18 mm maximum shell diameter), to *Cornirosta pellucida* and other material studied by Ponder (AMS), and to other "vitrinelliform" gastropods collected by Pilsbry & McGinty in the Florida Keys (ANSP). Several major collections, including AMNH, ANSP, DMNH, and FMNH, were searched (unsuccessfully) for additional specimens of the new species.

Museum acronyms used in text are:

AMNH American Museum of Natural History, New York, U.S.A.
AMS The Australian Museum, Sydney, New South Wales, Australia
ANSP Academy of Natural Sciences of Philadelphia, Pennsylvania, U. S. A.
DMNH Delaware Museum of Natural History, Wilmington, U. S. A.
FMNH Field Museum of Natural History, Chicago, Illinois, U. S. A.
HMNS Houston Museum of Natural Science, Texas, U. S. A.
USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C., U. S. A.

RESULTS

Valvatoidea Gray, 1840[1]
Cornirostridae Ponder, 1990b

Cornirostra Ponder, 1990b; type species by original designation: *Microdiscula pellucida* Laseron, 1954.

Cornirostra floridana Bieler & Mikkelsen, new species
Figs. 1–13

Type Locality

Indian Key Fill (formerly known as "Central Supply"), Mile Marker 79, Middle Florida Keys, bay side (Gulf of Mexico), Monroe County, Florida; 24°53′25″N, 80°40′28″W.

Type Material

Holotype (FMNH 278401; shell with dried tissue remains); paratype 1 (AMNH 289256, with dried tissue remains), paratype 2 (USNM 880276, SEM specimen), and paratype 3 (FMNH 278402, SEM specimen) collected with holotype in shallow subtidal habitat by hand-dredge, 26 July 1992 (sta. RB-1582). Paratype 4 (FMNH 278405), paratype 5 (AMNH 289806), and paratype 6 (FMNH 278403, live-observed specimen, serial-sec-

[1]Availability and authorship established with ICZN Direction 27 (1955); in contrast to recent references (e.g., Riedel, 1993).

tioned on microslides) from shoveled silty mud, among turtle grass (*Thalassia testudinum* Banks ex König) and green algae [*Penicillus* cf. *dumetosus* (Lamouroux) Blainville, and *Halimeda* spp.], in shallow water (<1 m) at low tide, 1 October 1994 (sta. FK-001). All material from type locality, Bieler/Mikkelsen coll.

Dimensions:

	Diameter (mm)	Height (mm)	Teleoconch whorls
Holotype	1.70	1.60	2 7/8–
Paratype 1	1.28	0.92	2 1/10
Paratype 2	1.66	1.58	2 5/8–
Paratype 3 (damaged after SEM)	2.10	1.80	3–
Paratype 4	1.42	1.04	2 3/10
Paratype 5 (damaged, was larger)	1.20	0.90	2+

Etymology

floridanus, -a, -um; named for the State of Florida.

Description

Teleoconch (Figs. 1–3): Diameter to about 2 mm at nearly 3 convex whorls; transparent, smooth with fine growth lines, high-spired (spire angle 105–110°). Base simple, smooth, umbilicate, without umbilical keel. Aperture round; peristome simple, sharp. Fresh specimens with thin transparent periostracum, imparting very fine spiral sculpture (visible under oblique microscope light).

Protoconch (Fig. 4): 180–185 µm (paratypes 3, 2, respectively), about 1.2 whorls, coiling near-planispiral but with initial hyperstrophy (tip of apex slightly sunken). Protoconch I (embryonic shell) measuring 133–141 µm (paratypes 3, 2), with reticulated sculptural pattern as shown for other cornirostrid species (Ponder, 1990b: fig. 5F; Warén et al., 1993: fig. 3); protoconch II (larval shell, comprising about 1/5 of a whorl) smooth, divided into two sectors by a growth mark.

Head-foot (Figs. 5–6): Living animal actively and rapidly gliding. Head-foot translucent white, with pallial organs and coloration clearly visible through shell. Black pigment on snout, tentacles, and mantle as depicted in Fig. 5; digestive gland in visceral coil orange-brown, gonad milk-white; buccal mass yellow. Snout long, split anteriorly into two curved oral lobes. Cephalic tentacles long, slightly tapering with blunt tips. Large black eyes situated dorsolaterally at base of tentacles. Mantle margin reflected, overlapping shell edge, without obvious black pigment. Pallial tentacle about half the length of extended cephalic tentacle, slightly more slender, heavily ciliated, blunt-tipped, unpigmented, extended laterally and curved posteriorly in crawling animal. Large knob-shaped process ("anterior glandular pocket" of Ponder, 1990b) adjacent to base of pallial tentacle. Cephalic penis posterior to tentacle base. Foot unpigmented, with curved anterior lateral extensions (propodial processes); deeply split posteriorly into two sharply tapering metapodial processes (of unequal length), grooved at outer lateral edge, separated by U-shaped indentation (Fig. 6).

Anterior pedal mucus gland in anterior part of foot, extending posteriorly to pedal ganglia where it appears to fold around pedal commissure. Folded dorsal component passing anteriorly and then becoming untraceable in the material studied. Posterior pedal gland absent.

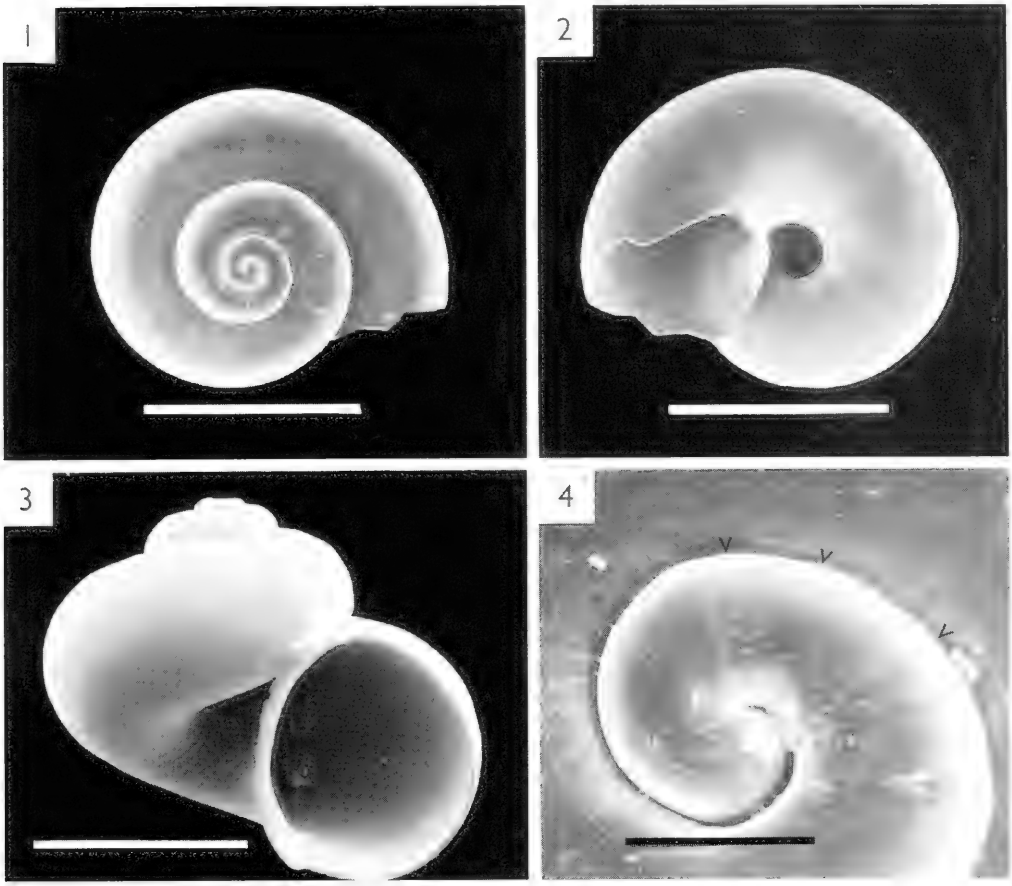
Operculum present, but not studied in detail.

Pallial cavity shallow, occupying less than half a body whorl. Gill slender-triangular, hanging freely in pallial cavity, crossing dorsal midline from left posterior to right anterior, bordered with black pigment, tip only barely emerging from beneath shell edge near right tentacle base and cephalic penis. Pulsating heart clearly visible in living animal at rear of pallial cavity.

Alimentary System: Mouth ventrally directed, slit-shaped, at tip of snout. Paired jaws (Figs. 7–8) attached to lateral walls of oral tube at approximate mid-point of its length; composed of overlapping, finely denticulate elements (8–10 elements at widest extent; each element about 10 µm in length), covered by cuticle near posteroventral limit. Each element lying above a single epithelial cell from which it was presumably secreted. Epithelium of oral tube peripheral to jaws surrounded by muscle layer [probably responsible for jaw articulation and movement].

Oral tube lined with low, cuticularized, columnar epithelium; cavity I-shaped in cross-section anterior to jaws, expanding to inverted T-shape posterior to jaws (at level of eyes), widening further to form buccal cavity.

Buccal mass lacking true odontophoral cartilages; radula supported by paired connective tissue pads, linked by approximator muscles

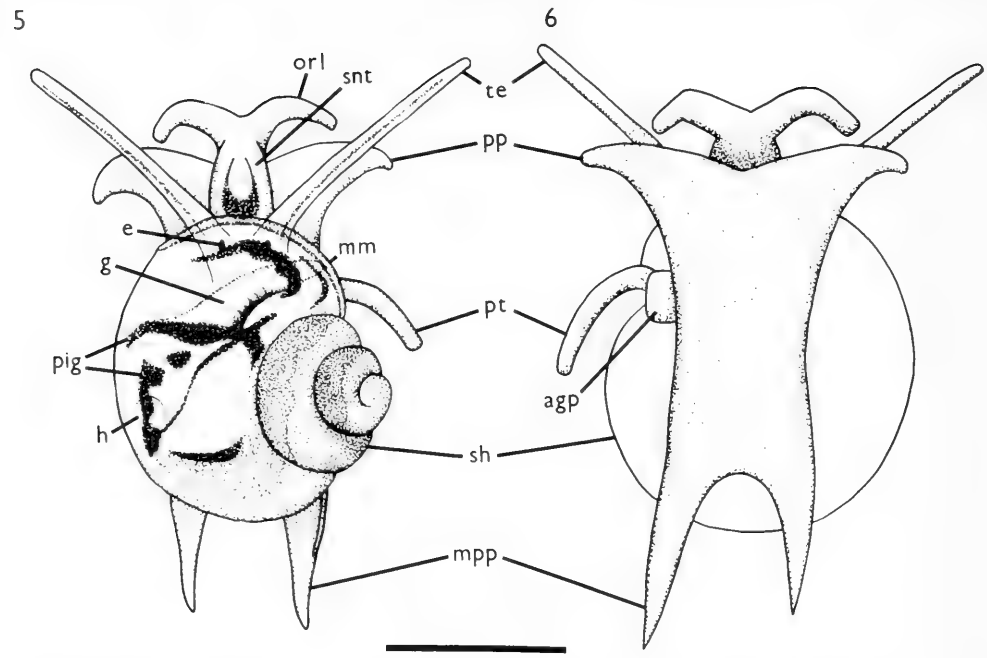


FIGS. 1–4. *Cornirostra floridana* n. sp., shell (scanning electron micrographs): (1) apical view, paratype 2; (2) basal view, paratype 2; (3) apertural view, paratype 3; (4) protoconch, paratype 3; arrows demarcating the two sectors of PC-II. Scale bars: Figs. 1–3 = 1 mm, Fig. 4 = 100 μm.

along mid-line. Longitudinal protractor muscles (dorsolateral to pads) originating in anterior body wall and passing into lateral walls of buccal mass to insert into anterior part of odontophore [probably responsible for protraction of odontophore and of buccal mass]. Paired lateral muscle bands binding buccal mass to lateral walls of haemocoel, also penetrating buccal wall, and inserting into mid-lateral part of odontophore. Wall of buccal cavity not cuticularized where muscles pass through it. (The relationship of these muscles to the buccal mass and to the odontophore suggests that these serve as lateral odontophoral protractor muscles.) Subradular membrane protractors and retractors running below radular membrane on surface of odontophore (acting antagonistically to erect and retract radular teeth during feeding). Posterior part of buccal mass lying freely in cephalic haemocoel, associated with little musculature. Radular sac not protruding from buccal mass.

Radula (interpreted from histological sections only) short, wrapped over odontophore, passing posteriorly and slightly deflected to right, terminating just beyond buccal ganglia. Radular formula and details of radular teeth not available from sections.

Salivary glands opening ventrolaterally into buccal cavity. Ducts minute, each consisting of only a circlet of 4–6 apparently ciliated, pale blue-staining cells. Glands flattened, sac-like, acinous, passing posteriorly alongside esophagus to posterior limit of cephalic haemocoel (Fig. 9). (Fixation did not permit determination of more than one cell type, however, the glands stained red in toluidine blue indicating the presence of acid mucopolysaccharides.)



FIGS. 5–6. *Cornirostra floridana* n. sp., crawling animal: (5) dorsal view; (6) ventral view. Scale bar = 1 mm.

Remainder of alimentary canal not observed in detail, but presence of style sac and localized cuticularization of stomach lining (as described by Ponder, 1990b, for *C. pellucida*) confirmed.

Nervous System (Figs. 9–12): Cerebral commissure lying immediately posterior to tentacle bases. Paired tentacle nerves originating on anterodorsal bulges on each cerebral ganglion. Paired snout nerves extending from each cerebral ganglion, down length of snout along esophagus; ventral nerve branches innervating parts of snout and esophagus.

Pleural ganglia lying lateral to esophagus and closely abutting cerebral ganglia.

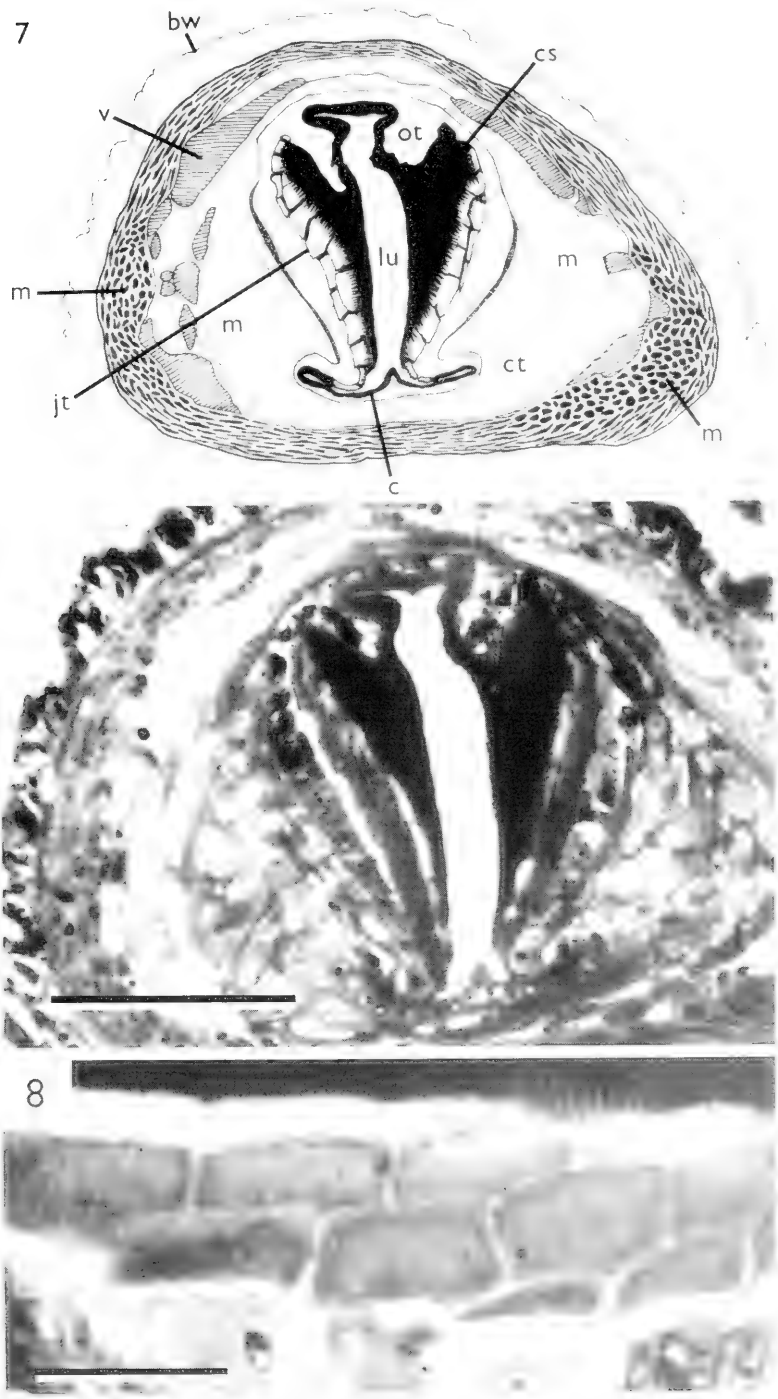
Pedal ganglia elongated, positioned ventral to cerebral ganglia. Each cerebropedal connective attached near middle of pedal ganglion; pleuropedal connective attached near posterior limit. Statocysts small, lying dorsally just posterior to cerebropleural juncture, and each containing a single statolith.

Large single pedal nerve passing anteriorly from each pedal ganglion; another nerve passing ventrally from near anterior end of ganglion anterior to cerebropedal connective. (Only anterior pedal nerves were found.) Supraesophageal ganglion (Fig. 9) closely abutting left pleural ganglion, dorsolateral to esophagus, connected to right pleural ganglion by short connective passing over esophagus. A further nerve passing toward pallial cavity to join osphradial ganglion which lies on floor of pallial cavity on left side. Subesophageal ganglion (Fig. 11) abutting right pleural ganglion, lateral to esophagus, at level of supraesophageal ganglion. Buccal ganglia situated posterior to nerve ring, behind buccal mass, forming dumbell-shaped mass due to short commissure. (Subesophageal connective, buccal connectives, and visceral ganglion not located.)

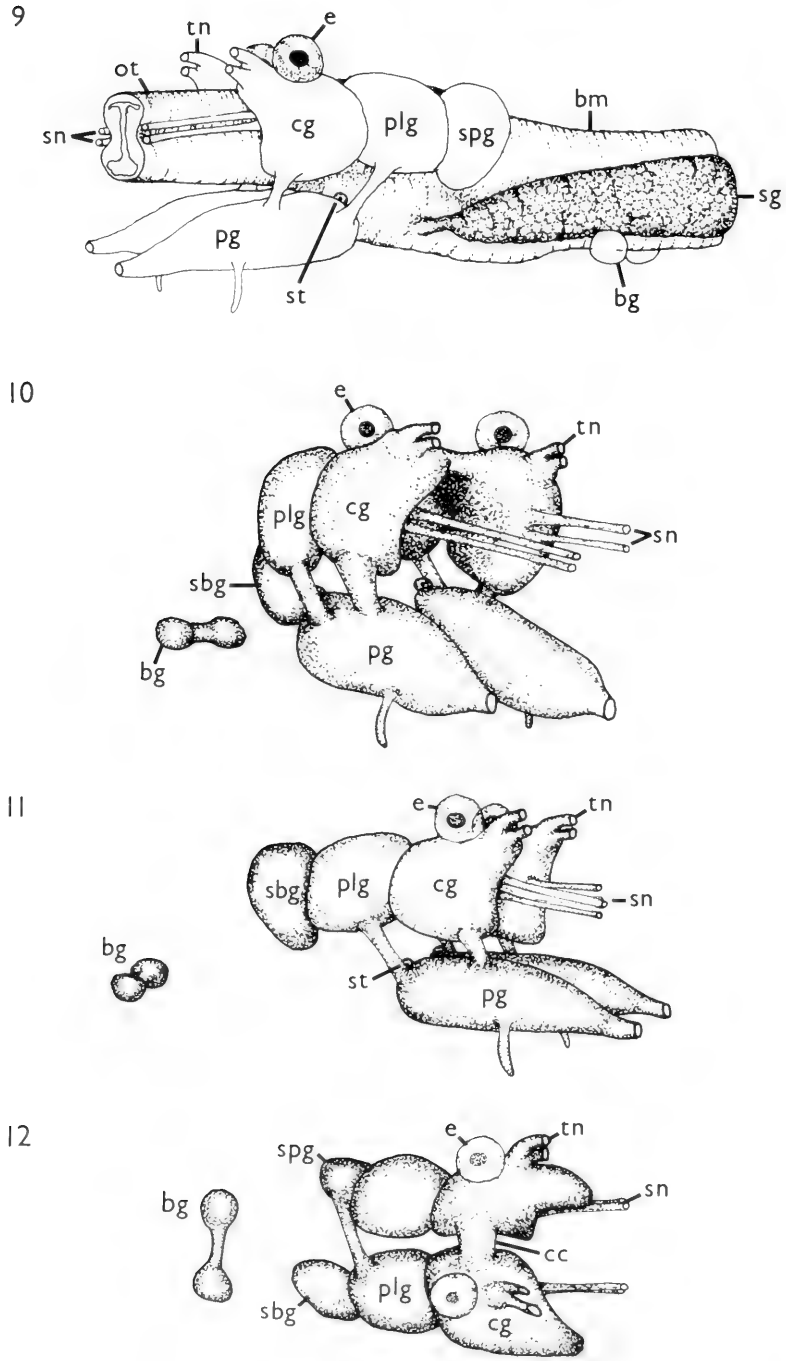
Eyes at tentacle bases, in close contact with dorsal surfaces of cerebral ganglia, innervated by short nerve at rear of each eye. Each a closed sphere (Fig. 13), with black granular pigment posteriorly; lens spherical-ovoid, solid, interior staining evenly light blue in toluidine blue.

Comparative Remarks

This new species, compared to the six other confirmed cornirostrid species (Table 1) is most similar to the Australian *Cornirostra pellucida* (as re-described by Ponder, 1990b), especially with regard to high spire angle and black mantle pigmentation. The basic organization of the nervous system and the anterior



FIGS. 7–8. *Cornirostra floridana* n. sp., jaws (1-μm sections of paratype 6 and explanatory drawing): (7) transverse section through oral tube with paired jaw; (8) jaw elements, detail. Scale bars: Fig. 7 = 50 μm, Fig. 8 = 10 μm.



FIGS. 9–12. *Cornirostra floridana* n. sp., reconstructions of the nervous system, paratype 6: (9) nerve ring and esophagus viewed from the left showing relative positions of the circumesophageal nerve ring and buccal ganglia; (10) oblique view from the right showing the origins of the snout nerves from the cerebral ganglia; (11) view from the right showing relative positions of the ganglia; (12) dorsal view showing the position of the cerebral commissure relative to the eyes and the connective linking the supraesophageal and right pleural ganglia.

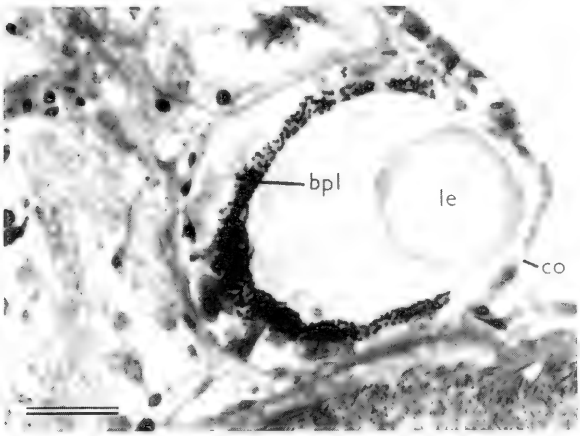


FIG. 13. *Cornirostra floridana* n. sp., eye (1-μm section of paratype 6). Scale bar = 20 μm.

pedal mucus gland are identical. Other than by geographical distribution, it differs from the latter in: smaller size, position of jaws (midpoint of oral tube versus immediately behind mouth), color of buccal mass in living animals (yellow versus white), relative position of cerebral ganglia (with commissure versus abutting), position of statocyst (near cerebropleural junctions versus on dorsal surface of pedal ganglia), number of pedal nerves (one versus two), and construction of the eye lens (solid versus hollow; also solid in *Valvata* spp. [Bernard, 1890; Ponder, 1990b]). Because so few cornirostrid specimens have been studied anatomically, some of these differences could be results of preservation artifact, varying degree of retraction, and histological technique, and warrant verification as additional material becomes available.

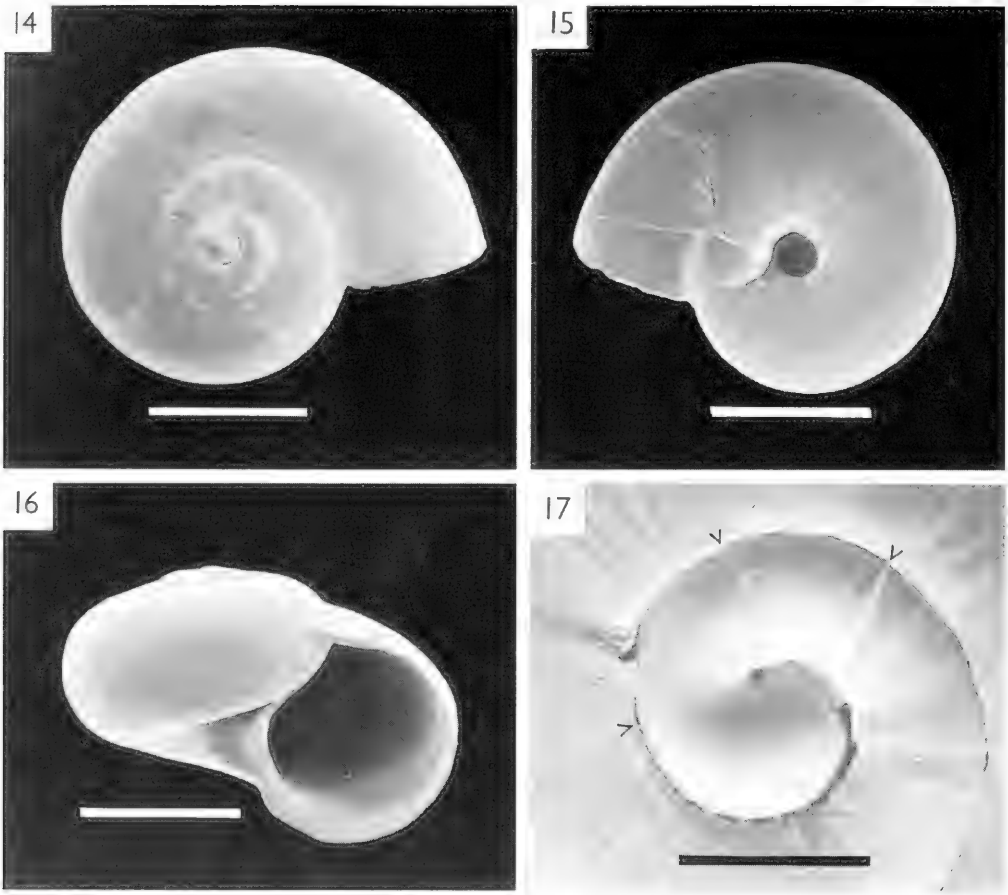
The new species differs from the single other known cornirostrid from Florida, *Tomura bicaudata* (Figs. 14–17) in: spire angle (105–110° in *C. floridana* versus 130–140° in *T. bicaudata;* compare Figures 3 and 16), umbilical keel (absent versus present; Figs. 2 and 15), black mantle pigment (present versus absent), and depth of metapodial cleft (deep versus shallow).

DISCUSSION

Cornirostra Versus *Tomura* and *Noerrevangia*

The seven confirmed cornirostrid species differ in a number of shell and anatomical characters (Table 1). These species currently reside in three nominal genera (*Cornirostra,* two species; *Tomura,* four species; *Noerrevangia,* one species). Generic characters are difficult to summarize considering the mosaic character state distribution of the few described species, but the three taxa might in fact describe natural groups. Separating characters appear to include the shape of the marginal radular teeth: triangular in *Cornirostra* (although still unknown in *C. floridana*), rectangular in *Tomura,* and slender oar-like in *Noerrevangia. Cornirostra* is further distinguished by black mantle pigment, a relatively high spire, and a deep metapodial cleft; *Noerrevangia* by a lecithotrophic-type protoconch (no PC-II) and a grooved cephalic penis. Ponder (1990b) listed the characters in which *Tomura* differed from *Cornirostra:* much smaller overall size, spiral ridge in umbilicus, non-pigmented mantle and head-foot, and radular characters. Since the transfer of *Oxystele depressa* to *Tomura* (based on gross morphology and radula; Warén et al., 1993), and the description of additional *Tomura* species from Japan (Fukuda & Yamashita, 1997), shell size and umbilical characters are now weakened as distinctions. *T. depressa* is unique in the family in having a callus-filled umbilicus, spiral sculptural ridges on the early teleoconch whorls, a small yellow pigmented mantle organ, a minute (not long) pallial tentacle, and seven (instead of nine) radular teeth per row; its size is intermediate between those of *T. bicaudata* and *C. pellucida.*

Because of the still-incomplete dataset, no cladistic analysis of the group is attempted at



FIGS. 14–17. *Tomura bicaudata* (Pilsbry & McGinty, 1946), four different shells; SEM; FMNH 278404, Lake Surprise, Florida Keys: (14) apical view; (15) basal view; note umbilical keel; (16) apertural view; (17) protoconch; arrows demarcating the two sectors of PC-II. Scale bars: Figs. 14–16 = 500 μm, Fig. 17 = 100 μm.

this time. Additional studies on reproductive system characters of cornirostrids are in progress (Ueshima, pers. comm.).

Definition of Cornirostridae

Ponder (1990b: 554) introduced the family Cornirostridae to include two monotypic genera: *Cornirostra* (based on *C. pellucida*) and *Tomura* (based on *T. bicaudata*). No formal diagnosis was given, but extensive reference was made to the numerous morphological similarities and differences with *Valvata*. Warén et al. (1993: 2) summarized the "synapomorphies" for the Cornirostridae based on Ponder's (1990b) data and new findings, and corrected earlier statements about the radulae of *C. pellucida* and *T. bicaudata* (Table 1). (Warén et al. [1993: 2] referred to the cornirostrid gill as a "ctenidium." However, Cornirostridae appear to have the same type of secondary gill as the Valvatidae [Rath, 1988; Ponder, 1990b]; like all other Heterobranchia they lack a ctenidium.) Bandel's (1996: 353) diagnosis — "A small (diameter about 2 mm) valvatiform teleoconch with simple aperture is connected to a sinistrally coiled protoconch. . . .The sinistral protoconch is smooth, consists of an embryonic and a larval shell and is coiled along the same axis as the dextral teleoconch" — is based on shell characters alone and allows the inclusion of virtually any skeneiform shell with signs of larval hyperstrophy as a member of this family, but in fact would exclude the anatomically confirmed member, *Noerrevangia*.

TABLE 1. Comparative characters of extant cornirostrid species. Data from: [1]Ponder, 1990b; [2]Warén et al., 1993; [3]R. Robertson, pers. comm.; [4]Fukuda & Yamashita, 1997; [5]this study. [*, determined from Ponder (1990b: figs. 1D-F, 5, 6); **, determined from Warén et al. (1993: figs. 1–6); ***, determined from Warén et al. (1993: figs. 14–17), ****determined from Fukuda & Yamashita (1997: figs. 18–23)].

	Cornirostra pellucida[1]	*Cornirostra floridana*[5]	*Tomura bicaudata*[1,5]	*Tomura yashima*[4]	*Tomura himeshima*[4]	*Tomura depressa*[2]	*Noerrevangia fragilis*[2]
Shell spire	115–140°**	105–110°	130–140°	>140°****	>140°****	130°**	140°***
Umbilicus	open, unkeeled	open, unkeeled	open, keeled	open, unkeeled (one juvenile described with distinct keel)	open, unkeeled	callus-filled	open, unkeeled
Maximum size	2.3 mm	2.1 mm	1.25 mm	1.5 mm	1.9 mm	1.6 mm	1.7 mm
PC size	217 µm*	108–185 µm	165–195 µm	180–200 µm	200 µm	150–175 µm	270 µm
PC coiling	initial hyperstrophy	initial hyperstrophy	initial hyperstrophy	initial hyperstrophy****	initial hyperstrophy****	hyperstrophy	orthostrophy (see text)
PC whorls	~1.25	~1.20	~1.25	~1.50	~ 1.50	~1.7**	~1.1*** [Note A]
TC whorls	2.75* [Note B]	2.05–2.95	2.0–2.25	2.0–2.5	~2.25	~2.0	2.0
PC-II sculpture	smooth	smooth	smooth, initial part with 0–2 spiral ridges	unknown (corroded)	smooth	smooth	no PC-II
TC sculpture	smooth	smooth	smooth	fine growth lines, very weak spiral threads; with thin, transparent periostracum	rough growth lines, weak spiral threads; with thick, yellowish periostracum	occassionally initially with spiral ridges	smooth
Mantle pigment	black	black	none	none	none	none	unknown
Glandular pocket	present	present	present [Note C]	not mentioned or figured	not mentioned or figured	not mentioned or figured	unknown
Cephalic penis	folded back	folded back	folded back	folded back	folded back	folded back	folded forward (artifact?)
Metrapodial cleft	deep*	deep	shallow	deep	deep	shallow**	present, but depth unknown
Pigmented pallial gland	black mantle strip	black mantle strip	not found	not found	not found	small, bright yellow (PMO)	unknown

(*continued*)

TABLE 1. (*Continued*)

	Cornirostra pellucida[1]	*Cornirostra floridana*[5]	*Tomura bicaudata*[1,5]	*Tomura yashima*[4]	*Tomura himeshima*[4]	*Tomura depressa*[2]	*Noerrevangia fragilis*[2]
Pallial tentacle	long*	long	long	long	long	minute	long
Radular formula	1-3-1-3-1[2]	unknown	2-2-1-2-2[2]	1-2-1-2-1	1-2-1-2-1	1-2-1-2-1	2-2-1-2-2
Marginal teeth	elongated triangular	unknown	rectangular	elongated rectangular	elongated rectangular	rectangular	slender oar-like
Known range	Australia	Florida	Florida, Bahamas[3]	Japan	Japan	Mediterranean	Faroe Islands

A. Given by Warén et al. (1993: 7, fig. 17) as "slightly more than half a whorl," but our method of counting indicates 1.1 whorls.
B. Given by Ponder (1990b: 539) as "about 3 whorls," but counted as 2.75 whorl by us from the SEM illustration (Ponder, 1990b: fig. 5C).
C. Ponder (1990b: 541) stated that the glandular pocket "does not appear to be present" in *Tomura bicaudata*, however our observations of living specimens suggest that it is present just posterior to the base of the pallial tentacle, as in the two *Cornirostra* species.

A re-description, summarizing existing shell and anatomical data (Table 1) is here attempted: small (<2.3 mm) valvatoideans with (almost) smooth skeneiform teleoconchs of 2–3 more-or-less convex whorls and simple peristome, and (weakly) sinistral protoconchs coiling around the same axis (this larval hyperstrophy might not be expressed if only protoconch I [embryonic shell] is present, e.g., *Noerrevangia*); snout long, with two tentacle-like oral lobes; radula with 7–9 teeth per row including 2–3 partly overlapping lateral teeth, and rachidian with highly developed lateral support; foot with propodial and metapodial extensions, appearing cleft anteriorly and posteriorly; single right pallial tentacle; bipectinate, basally attached gill; hermaphroditic reproductive system with cephalic penis.

The Cornirostrid Protoconch

A cursory survey of the literature on marine valvatoideans would imply considerable differences in the coiling of the protoconch. *Cornirostra pellucida,* for instance, was described as having the "apex slightly inrolled" (Ponder, 1990b: 539), members of Orbitestellidae were by a protoconch that "is not heterostrophic but the initial half whorl dips downward" (Ponder, 1990a: 513), while *Tomura depressa* was described (Warén et al., 1993: 3) with a "hyperstrophic" larval shell. However, all extant cornirostrids (with the exception of *Noerrevangia fragilis,* which lacks a larval shell [PC-II]), have a slightly hyperstrophically coiled larval shell. The hyperstrophy is most pronounced in *T. depressa* (Table 1), in which the protoconch has more whorls than in the other species.

Similarly weakly expressed larval hyperstrophy also occurs in other lower heterobranchs, such as *Xenoskenea* Warén & Gofas (in Warén et al.), 1993, of the Hyalogyrinidae, and in *Ammonicera* Vayssière, 1893, of the Omalogyridae (Bieler & Mikkelsen, 1998). The protoconch of freshwater members of Valvatidae has been described as without such hyperstrophy (Ponder, 1991: 22). Certain valvatid species, however, do display a weak initial hyperstrophy not unlike that seen in cornirostrids. This is demonstrated, for instance, by the SEM illustrations of the protoconch of *Valvata relicta* Polinski, 1929, by Hadžišče et al. (1976: fig. 7), and of *Valvata piscinalis* (O. F. Müller, 1774) by Riedel (1993: pl. 1). Riedel (1993: 351) explicitly referred to the "het-

erostrophic character of the apex" in the latter species [in contrast to Bandel (1996: 361), who described the protoconch of modern *Valvata* species as "planispirally coiled" with reference to the same work by Riedel, 1993]. As pointed out by Warén & Bouchet (1992: 49), larval hyperstrophy is often difficult or impossible to recognize in species with lecithotrophic development (where it might be obfuscated by distortion caused by the storage of nutrients), while it can be obvious in closely related forms with multispiral protoconchs reflecting planktotrophic development.

In spite of initial larval hyperstrophy, the cornirostrid shell does not display true heterostrophy (a divergence of the coiling direction/axes between proto- and teleoconchs) as is common for many other heterobranchs, such as Pyramidellidae, Architectonicidae, and Acteocinidae (for further explanation and definition of terms, see Bieler, 1993: 16, 18).

Another apparent difference among cornirostrid species, the sculpture of the embryonic shell (PC-I), also seems based upon differences of terminology employed by the describing authors. This has been variously described as "close-set shallow pits" (Ponder, 1990b; *Cornirostra pellucida*), or "branching small ridges" (Warén et al., 1993; *Tomura depressa*), but the illustrations accompanying these descriptions show sculpture similar or identical to the reticulated pattern observed in *C. floridana*.

A feature not previously noted in cornirostrid protoconchs is a distinct separation into three regions as observed here in both *Cornirostra floridana* and *Tomura bicaudata* (Figs. 4, 17). In both species, the PC-II is interrupted by a distinct growth mark. In the case of *T. bicaudata,* two of three specimens studied by SEM showed weak spiral ridges in the first sector of the PC-II (Fig. 17), markedly differing from the smooth second sector. A fourth specimen (here illustrated in Fig. 14) displayed strong corrosion of the PC-II, clearly indicating the border between embryonic and larval shells and suggesting mineralogical differences between the two. Such a tripartite division, although less pronounced, also occurs in *C. floridana* (two specimens investigated by SEM; one with the first sector, the other with the second sector slightly wider; Fig. 4). The biological significance of these protoconch growth marks remains unclear. Specimens of both species also show stages of arrested growth in the first teleoconch whorl.

Cornirostridae vs. Other Valvatoidea

Ponder (1990b) compared the cornirostrid species *Cornirostra pellucida* and *Tomura bicaudata* with *Valvata,* particularly *V. cristata* (Müller, 1774). Ponder inferred close relationship between marine Cornirostridae and freshwater Valvatidae based on many morphological and anatomical similarities (e.g., the long pallial tentacle, the type of secondary gill, the pallial renal organ and pericardium, organization of alimentary canal, nervous system, and much of the reproductive system), and placed Cornirostridae in the Valvatoidea. Valvatids differ in having, among other things, a protoconch with spiral sculpture as well as egg strings that are connected by chalazae; they lack the unique "cleft" foot and "horned" snout.

Ponder (1991: 22) considered another family of marine skeneiform gastropods, the Orbitestellidae, as "rather distantly related to the valvatids and cornirostrids." Healy (1990, 1993), in a parallel study of spermatozoa and spermatogenesis of members of the three families (plus the Hyalogyrinidae), also supported their combination as Valvatoidea. Members of the Orbitestellidae — *Orbitestella wareni* Ponder, 1990, and *Microdiscula charoni* (Tate, 1899) — were examined in detail by Ponder (1990a). Their anatomy is significantly different from both species of *Cornirostra.* In orbitestellids, the jaws are composed of multiple rows of cuspidate elements with a variable number of elements in each row, whereas in the Cornirostridae (Ponder, 1990b; this paper) and the Valvatidae (Cleland, 1954), the jaws are composed of a large number of teeth which interlock to form plates. The large jaws in the Orbitestellidae are associated with a muscular oral bulb, which is absent in members of Cornirostridae and Valvatidae. In addition, the oral tube is longer and the jaws lie further from the buccal cavity in cornirostrids. There are no posterior pedal glands in the two examined *Cornirostra* species or in *Valvata.* In the Orbitestellidae, there is a posterior pedal mucus gland, which passes dorsally into the cephalic haemocoel and surrounds the esophagus (Ponder, 1990a). The nervous system in Orbitestellidae species is epiathroid, and both pairs of cerebral and pleural ganglia are fused (Ponder, 1990a). The subesophageal ganglion lies ventrolateral to the buccal mass, while the supraesophageal ganglion lies dorsally and abuts the right pleural ganglion. This situation represents a clockwise rotation of the

esophageal ganglia (relative to the cerebral and pleural ganglia) compared to the two species of *Cornirostra*. Its significance however is unclear.

The described positions of the buccal mass relative to the nerve ring in the aforementioned descriptions should not be regarded as reliable, because the buccal mass is presumably brought forward during feeding and its position in the preserved specimen is therefore dependent on the degree of relaxation achieved before fixation.

In addition to these extant families currently grouped in the still ill-defined Valvatoidea, Bandel (1991) introduced the brackish-water Provalvatidae (Cretaceous to Upper Jurassic), which he later (1996: 353) hypothesized as possibly representing "the transition from fully marine Cornirostridae to fresh water Valvatidae." Bandel's statement (1996: 353) that the number of radular teeth per row is "regularly 7" in the Valvatoidea is erroneous. The inclusion of Cornirostridae and Orbitestellidae changed this number to range from five to nine. Recent placement of Cornirostridae and several other "lower heterobranch" groups in a superfamily Architectonicoidea (e.g., Bandel, 1996), is contradicted by available anatomical data (e.g., Healy, 1993; Huber, 1993).

Fossil Cornirostridae

Extant cornirostrids, with their non-descript, skeneiform/valvatiform/vitrinelliform shells can only be confirmed as members of this family through knowledge of their anatomical features. In their description of *Noerrevangia fragilis*, for instance, Warén et al. (1993: 10) stated that the shell "is featureless and it would presently be impossible to classify it from conchological characters alone." Certain protoconch characters are available, but Schröder (in a study including Jurassic and Lower Cretaceous fossils interpreted as Cornirostridae [1995: 81, our translation]) admitted that "The early ontogenetic shells of the studied Heterostropha are relatively poor in characters and are not, or only in a limited sense, useful for delimiting higher systematic units (genera, families)." Attempts to establish a deep fossil record for the family (Schröder, 1995; Bandel, 1996) by "connecting-the-dots" between Recent, Cretaceous, Jurassic, and Triassic taxa with similarly non-descript shells should thus be viewed with caution. Examples are the St. Cassian (Triassic) genus *Carboninia* Bandel, 1996,[1] the high-spired "littoriniform" shell of which has no known living counterpart in the Cornirostridae, and the Lower Cretaceous *Bandellina*[2] *laevissima* Schröder, 1995, described with turbinid-like teleoconch and architectonicid-like protoconch, but placed in Cornirostridae because of its absence of sculpture (Schröder, 1995: 79).

Pacaud & Le Renard (1996: 170) also listed the British Tertiary *Anomalorbis* Paul, 1991, as a member of the Cornirostridae. As was already noted by Paul (1991: 40), the *Anomalorbis* protoconch bears some resemblance to that of modern cornirostrids, but the teleoconch differs substantially in its sinistral coiling and compressed whorls. Another taxon tentatively assigned to Cornirostridae by Pacaud & Le Renard (1996) was *Bonnetella* Cossmann, 1918, a new name for preoccupied *Bonnetia* Cossmann, 1907, *non* Robineau-Desvoidy, 1830 (Diptera). This taxon is based on the Paris Basin Eocene species *"Bonnetia" planispira* Cossmann, 1907, which has a vitrinelliform shell with a strong callus in the umbilicus. Its affinity to extant Cornirostridae is unclear. Also tentatively placed in Cornirostridae by Pacaud & Le Renard (1996) was *Cyclostremiscus* Pilsbry & Olsson, 1945. The anatomy of extant *Cyclostremiscus* species is well known (Bieler & Mikkelsen, 1988, for *C. beauii* [Fischer, 1857]); there is no doubt that this genus belongs to the Vitrinellidae (Caenogastropoda: Rissooidea).

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[1] "*Carboninia* Bandel, 1994" of Bandel (1994a: 149; 1994b: 89) and "*Carboninia* Bandel (in Prep.)" of Schröder (1995: 79, 81) are *nomina nuda*.
[2] *Bandellina* Schröder, 1995. — "*Bandellina* Schröder, 1993" of Bandel (1994b: 89) is a *nomen nudum*.

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Note Added in Proof

A form very similar to *Cornirostra floridana* was recently described from Yucatán, México. That species, introduced as *Tomura xenoskenoides* Rubio & Rolán, 1998, appears to have near-identical teleoconch morphology and dimensions, but differs in body pigmentation pattern (with only one, grayish brown, crescent-shaped mantle-band, and more-fully pigmented snout and oral tentacles) and in protoconch size (160 µm).

Rubio, F & E. Rolán. 1998. Una nueva especie de *Tomura* (Gastropoda, Heterobranchia, Cornirostridae) del Caribe — A new species of *Tomura* (Gastropoda, Heterobranchia, Cornirostridae) from the Caribbean. Iberus, 16(1): 119–123 [June].

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PHYLOGENY OF THE CARDIIDAE (BIVALVIA): PHYLOGENETIC RELATIONSHIPS AND MORPHOLOGICAL EVOLUTION WITHIN THE SUBFAMILIES CLINOCARDIINAE, LYMNOCARDIINAE, FRAGINAE AND TRIDACNINAE

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ABSTRACT

The cardiid bivalve taxa *Plagiocardium, Maoricardium,* Clinocardiinae, Fraginae, *Goethemia,* Lymnocardiinae, and Tridacninae form a monophyletic group. The most parsimonious cladograms of this group have a topology of (*Plagiocardium* (*Maoricardium* (Clinocardiinae (Fraginae (*Goethemia* (Lymnocardiinae, Tridacninae)))))).

The giant clams form a subfamily (Tridacninae) of Cardiidae. In the ontogeny and phylogeny of giant clams, the morphology and position of the muscle scars and hinge changes from that resembling the dimyarian *Cerastoderma* to the monomyarian morphology displayed by *Hippopus* and *Tridacna,* which have lost the anterior half of the shell. This peramorphic trend is the result of differential growth: tremendous growth rate of the posterior portion of the shell and a zero or even negative growth rate of the anterior half of the shell.

All tridacnines and several species of fragines are known to harbor photosymbiotic zooxanthellae. These algae transfer excess carbon to its cardiid host. It is known that the chemosymbiotic lucinid and solemyid bivalves reduce or lose many features of their digestive systems. The sulfur-reducing bacteria in lucinids and solemyids provide most of the nutrients that the host clam needs, thus making a full digestive system unnecessary. Most fragine cardiids reduce numerous structures of their digestive systems. Only a few fragines have been examined for the presence of photosymbionts. Based upon their anatomy, it is predicted that most or all of the derived fragines harbor photosymbionts. Tridacnines harbor photosymbionts but do not appreciably reduce their digestive systems. The possession of both photosymbionts and a fully functional digestive system allows tridacnines to be the fastest growing and largest of the extant bivalves.

Key words: cardiids, giant clams, Fraginae, phylogenetics, heterochrony, paedomorphosis, peramorphosis, photosymbiosis.

INTRODUCTION

Bivalves of the family Cardiidae (cockles and giant clams) originated in the Late Triassic and have a present-day diversity of approximately two hundred species. Cardiids have been the subject of considerable taxonomic work by both paleontologists and malacologists, and numerous subfamilies, genera, and subgenera have been erected. However, few studies of the phylogenetic relationships amongst these taxa within the Cardiidae have been undertaken.

The only proposed phylogenies for the family Cardiidae are those of Kafanov & Popov (1977) and Schneider (1992). Kafanov & Popov based their phylogeny on two key character complexes: shell microstructure and morphology of the interior of the stomach. Schneider (1992) proposed a preliminary phylogenetic hypothesis for the Cardiidae based on a cladistic analysis of 54 characters of 36 taxa. In that analysis, at least one member from each of the subfamilies recognized by Kafanov & Popov (1977) and Keen (1951, 1969a, 1980) was included, as well as additional taxa of uncertain affinities. The representatives of the subfamilies Clinocardiinae, Fraginae, Tridacninae, and Lymnocardiinae were found to be a monophyletic group. The synapomorphies of this group were: (1) few tentacles, (2) oval shell shape during ontogeny, (3) shape of right anterior cardinal socket, (4) shape of right posterior cardinal tooth, (5) shape of right anterior cardinal tooth (characters and states listed in Schneider, 1993a).

MATERIALS AND METHODS

A cladistic analysis of 34 taxa and 51 characters with 140 character states was made

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using PAUP 3.1.1 (Swofford, 1993). There are 24 shell characters, 26 anatomical characters, and one periostracal character. Characters were coded from examination of specimens, unless otherwise indicated. The heuristic branch-swapping routine with random addition and tree-bisection reconnection options was used. The accelerated transformation option (ACCTRAN) was used, and steps were not added to terminal taxa with polymorphisms (Schneider [1995] explains these options.) The data matrix is presented in Table 1, and synapomorphies (shared derived characters) for one of the most parsimonious trees are presented in Table 2. With the exceptions of *Keenocardium, Maoricardium, Chametrachea, Trigoniocardia,* and *Hypanis (Monodacna),* data for each of the ingroup taxa are represented by the type species (Appendix 1). This has been termed the exemplar approach (Wheeler et al., 1993). Therefore, this analysis should be taken as a phylogeny for these species only, because character states presented may not be constant throughout all species of a given genus or subgenus. All Recent taxa were investigated anatomically, except for *Yagudinella.* Anatomical data for *Yagudinella* were taken from Kafanov (1980). Shells were examined for all taxa except *Fuscocardium,* for which data were taken from descriptions and illustrations in Oyama (1973). Missing data are coded by a question mark (?) in Table 1.

Fourty-nine of the 51 characters are unordered. Two characters, shell shape (32) and pseudocarina (41) are ordered on the basis of outgroup analysis and ontogeny. I follow Alberch's (1985) criterion for justification of the ordering of characters. Alberch argued that the only characters that can be ordered in a phylogenetic analysis are those in a casual sequence. That is, the state of a character at time 1 is dependent upon the state of that character at time 0; the state at time 2 depends upon the state at time 1, etc. Bivalves, given accretionary growth, fall under this strict criterion. The justifications for the ordering schemes of these characters are given in the character descriptions below.

Selection of Ingroup Taxa:

All genera and subgenera of the subfamilies Clinocardiinae, Fraginae, and Tridacninae are represented, along with three of the Recent genera of Lymnocardiinae.

For the subfamily Clinocardiinae, those taxa accepted by Kafanov & Popov (1977) and Kafanov (1980) are represented in the present analysis.

For the Fraginae, all taxa accepted by Keen (1969a, 1980) are represented, with the exception of *Afrocardium* (see below). Kafanov & Popov (1977) include a number of other taxa in Fraginae, such as *Parvicardium, Papillicardium, Plagiocardium,* and *Maoricardium.* These four taxa are represented in the analysis. Schneider (1992) found *Plagiocardium* and *Parvicardium* to be members of Fraginae. *Papillicardium* is usually taken to be either (1) a subgenus of *Parvicardium* (Keen, 1969a, 1980; Kafanov & Popov, 1977; Voskuil & Onverwagt, 1989), (2) a junior synonym of *Parvicardium* (Glibert & van de Poel, 1970; Popov, 1977; Lambiotte, 1979), or (3) a junior synonym of *Plagiocardium* (Spada & Della Bella, 1987). Marwick (1944) erected *Maoricardium* as a genus and considered its closest relatives to be *Clinocardium* and *Cerastoderma.* Marwick also thought that *Maoricardium* was extinct. Keen (1951, 1969a, 1980), Habe (1951), and Wilson & Stevenson (1977) classified *Maoricardium* as a subgenus of *Plagiocardium* and extended the former's range into the Recent. Popov (1977), Kafanov & Popov (1977), Beu & Maxwell (1990), and Voskuil & Onverwagt (1991) gave *Maoricardium* generic rank. Popov (1977) and Kafanov & Popov (1977) considered the Recent species placed in *Maoricardium* by Keen, Habe, and Wilson and Stevenson as belonging to *Plagiocardium.* For the present analysis, the Recent species in question are considered to belong to *Maoricardium* on the basis of shell shape and details of the cross-striae in the rib interspaces. *Maoricardium* is represented in the present analysis by the Recent species *Maoricardium pseudolatum* Voskuil & Onverwagt, 1991, for which anatomical specimens were available. Popov (1977) and Kafanov & Popov (1977) placed *Acanthocardia* and *Orthocardium* in Fraginae, but otherwise these taxa have been considered members of Cardiinae (Keen, 1951, 1969a, 1980; Nordsieck, 1969; Glibert & van de Poel, 1970, 1973; Meechan, 1987; Voskuil & Onverwagt, 1989). *Acanthocardia* and *Orthocardium* were found to be cardiines in my preliminary analysis (Schneider, 1992). Popov (1977) and Kafanov & Popov (1977) also considered *Schedocardia* and *Loxocardium* to be fragines. Keen (1951, 1969a, 1980) considered *Schedocardia* to be a subgenus of *Acanthocardia;* Popov (1977) and Kafanov & Popov (1977) considered

TABLE 1. Data matrix. "X" indicates polymorphism for states 0 and 1. "Y" indicates polymorphism for states 1 and 2. "Z" indicates polymorphism for states 1, 2 and 3.

Outgroup	1000011000	0432010000	0000100100	1011300000	00000001000
Plagiocardium	??????????	??????????	????????1?1	0111Z00000	00000001111
Maoricardium	1000011000	3032000000	00?0101001	1111300000	00000001111
Ciliatocardium	1000011100	22320X1000	0010101111	1110200000	00010001101
Profulvia	??????????	??????????	???????101	1110200?0	00010001101
Clinocardium	1010011100	32310X0010	0020100111	0000100010	10010001201
Fuscocardium	??????????	??????????	???????111	0000100?0	10010011201
Keenocardium	1010011100	22310X0010	00?0100101	0000000010	10000000201
Yagudinella	?????101??	??????????	???????211	0000100010	10010000201
Serripes	1011010100	2232001010	0010100201	0000000010	10000000201
Papillicardium	0000001001	3032000000	00?1100101	0010100000	00000000311
Parvicardium siculum	0000000001	4022000000	0??1100104	0000100000	00100000312
P. exiguum	0000011001	4012000000	0101100104	0010100000	00000000312
Cerastobyssum	0000000001	1032000000	01?1100104	0000100000	00000001311
Apiocardia	1000011101	2133000100	00?1100104	0010200000	00101112313
Trigoniocardia	0000011101	2113000100	00?1100104	0010100000	00001112313
Goniacardia	??????????	??????????	???????104	0010100000	00101112313
Lunulicardia	1000011001	4114110000	00?1100104	0010000000	01000012404
Corculum	0100000011	4114000100	0021100104	0010100000	01010000405
Fragum	0100011011	4112000100	00?1100004	0000300000	00000012303
Microfragum	01200XX011	2112100100	00?1100105	0010100000	00000001303
Ctenocardia	0100011011	2112000100	00?1100205	0010200000	00000001303
Americardia	0100011011	3112000100	00?1100105	0010000000	01000001303
Goethemia	1000000?0	3002000000	0200100102	0002100000	00000000311
Cerastoderma	1000000000	0322001001	0000100102	0000000000	00000001311
Hypanis	1000000000	5322001001	00?0100113	0000100000	0000????311
Didacna	1000000000	5322001001	00?0100113	0000100000	0000????311
Goniocardium	??????????	??????????	???????104	0012Y00001	00000000312
Avicularium	??????????	??????????	???????104	0002?10101	000????0?12
Byssocardium	??????????	??????????	???????104	0002?10102	000????0?12
Hippopus	?000100000	5320000001	10110101?4	0002?11202	000????0?12
Chametrachea	?000100000	5320000001	10112101?4	0002?11302	000????0?12
Tridacna	?001100000	5320000001	10112101?4	0002?11402	000????0?12
Persikima	?000100000	5320000001	10112101?4	0002?11502	000????0?12

Schedocardia as a genus ancestral to *Acanthocardia*. Keen (1969a, 1980) and Glibert & van de Poel (1970, 1973) also classified *Loxocardium* in the Cardiinae. Schneider (1993a, 1998) found that *Loxocardium* and *Orthocardium* were members of a monophyletic group with other Cenozoic cardiines.

Anatomical material of the type species of *Trigoniocardia, Cardium graniferum* Broderip & Sowerby, 1829, was unavailable, so *Trigoniocardia* is represented by *Cardium antillarum* Orbigny, in Ramon de la Sagra, 1842.

Sawkinsia, considered a tridacnid by Vokes (1953), Keen (1969a), and Jung (1976), was found to be a close relative of *Acanthocardia* and *Schedocardia* (Schneider, 1992, 1998). *Sawkinsia* aside, Stasek (1962), Rosewater (1965), and Keen (1969b) all agreed on the remaining genera and subgenera belonging to Tridacnidae. The type species of *Chametrachea* is *Tridacna crocea* Lamarck, 1819. *Tridachnes maxima* Röding, 1798, was selected to represent *Chametrachea* because of the availability of anatomical material.

Kafanov & Popov (1977) classified the Norian (Late Triassic) *Septocardia* as a tridacnid, and were followed by Scarlato & Starobogatov (1979). However, as Schneider (1992) pointed out, *Septocardia* does not have any of the apomorphies of tridacnines and may not even be a cardiid (Morris, 1978; Schneider, 1995).

There are over 90 named genera and subgenera of Lymnocardiinae, all but four of them extinct (Keen, 1969a; Bagdasarian, 1978; Vokes, 1980; Taktakishvili, 1987; Basch, 1990). Because specimens of the vast majority of these taxa, especially of the type species, are found only in eastern European museums, I did not attempt to undertake a detailed study of the phylogenetic relationships within the Lymnocardiinae. Lymnocardiines are represented by the Recent taxa *Cerasto-*

TABLE 2. Synapomorphies of interior nodes of tree number 15 (Fig. 34).

Node	Synapomorphies (character: state)
1	11:3, 12:0, 30:1, 31:0, 32:1, 34:4
2	49:1, 50:1, 51:1
3	16:0, 32:0, 34:0, 35:1
4	8:1, 11:2, 12:2, 23:1, 44:1, 50:0
5	17:1, 27:1, 31:1, 32:1, 35:2
6	3:1, 14:1, 19:1, 33:0, 39:1, 41:1, 49:2
7	11:3, 23:2, 29:1
8	35:0, 44:0, 48:0
9	4:1, 7:0, 14:2, 17:1, 28:2
10	6:0, 34:2, 48:0, 49:1
11	1:0, 10:1, 24:1, 34:3, 51:2
12	11:4, 22:1, 30:4
13	7:0
14	6:1, 13:1
15	11:2, 12:1, 18:1, 22:0, 23:2, 47:1, 48:2, 51:3
16	8:1, 14:3, 45:1, 46:1
17	1:1, 13:3, 43:1
18	2:1, 9:1, 50:0
19	11:4
20	14:4, 18:0, 42:1, 49:4, 51:4
21	30:5, 47:0, 48:1
22	35:2
23	7:0, 13:0, 30:2, 33:0
24	11:5, 12:3, 13:2, 20:1
25	17:1, 34:0, 48:1
26	29:1, 30:3
27	5:1, 14:0, 21:1, 23:1, 24:1, 25:0, 26:1, 30:4, 41:1, 51:2
28	36:1, 38:1
29	40:2
30	37:1, 38:2
31	25:2, 38:3
32	38:4

derma, *Hypanis* (*Monodacna*), and *Didacna*. Anatomical material of the type species of *Hypanis* (*Monodacna*), *Corbula caspia* Eichwald, 1829, was unavailable, so *H.* (*Monodacna*) is represented by *Glycimeris colorata* Eichwald, 1829.

Nordsieck (1969) erected the subfamily Cerastodermatiinae for *Cerastoderma* and *Parvicardium*. Two monotypic taxa subsequently named (*Cerastobyssum* Petersen & Russell, 1973, and *Goethemia* Lambiotte, 1979) were included in Cerastodermatiinae by Voskuil & Onverwagt (1989), who also included *Papillicardium* in Cerastodermatiinae (as a subgenus of *Parvicardium*). Nordsieck had included *Papillicardium* in Fraginae. Although each are monotypic, the relationships of *Goethemia* and *Cerastobyssum* are uncertain, and these taxa are included in the analysis. The type species of *Parvicardium* is also uncertain. Two species of *Parvicardium* are therefore included: (1) *Cardium siculum* Sowerby, 1841, which Voskuil & Onverwagt (1989) consider to be its type species; and (2) *Cardium exiguum* (Gmelin, 1791), the type species according to most other authors.

Afrocardium was erected by Tomlin (1931) as a subgenus of *Fragum*. Keen (1951, 1969a, 1980) classified *Afrocardium* as a subgenus of the fragine *Ctenocardia;* Popov (1977) synonymized *Afrocardium* with *Plagiocardium*. All eight species that Tomlin placed in *Afrocardium* are rare, have been only superficially described, are unknown anatomically, and have received virtually no attention since Tomlin (1931). Specimens were not available during the preparation of my preliminary analysis (Schneider, 1992). Subsequently, I have been able to examine the shells of several species of *Afrocardium,* including type and non-type specimens of the type species, *A. shepstonense* (Tomlin, 1931), and to dissect a specimen of *A. exochum* (Melvill, in Melvill & Standen, 1906). These species bear none of the apomorphies of Fraginae and several apomorphies of Cardiinae. Some authors (Habe, 1951; Kira, 1955, 1962; Cotton, 1961; Kuroda et al., 1971; Oyama, 1973; Fischer-Piette, 1977; Wilson & Stevenson, 1977) have included the species *Cardium ebaranum* Yokoyama, 1927 (Pleistocene to Recent), and *Cardium erugatum* Tate, 1889 (Recent), in *Afrocardium*. After examination of the shells of these species, and of the anatomy of *C. erugatum,* it was determined that they belonged in *Microfragum* (with the Pleistocene specimens of *C. erugatum* being the only known fossils attributable to *Microfragum*). *Afrocardium,* a member of the Cardiinae and not the Fraginae, is not included in the present analysis.

Selection of Outgroup

Selection of outgroup was based on the results of two previous studies. In the preliminary study (Schneider, 1992), the subfamily Cardiinae was shown to be the sister taxon to Clinocardiinae + Fraginae + Tridacninae + Lymnocardiinae. Among the least derived cardiines was *Acanthocardia*. In a phylogeny of Cretaceous to Eocene cardiids (Schneider, 1993a, 1998), the Eocene fragines and tridacnines formed a monophyletic group, with *Schedocardia* + *Sawkinsia* as its sister taxon. *Sawkinsia* is known only from molds and recrystallized specimens (Cox, 1941; Jung, 1976; Kojumdgieva & de la Torre, 1982; pers.

obs.). The morphology of many characters is still unknown, including ornamental microstructure and many hinge characters (Schneider, 1992, 1993a, 1998). *Sawkinsia* is therefore not considered in the outgroup. As stated previously, *Schedocardia* is considered closely related to *Acanthocardia* (Keen, 1951, 1969a, 1980; Kafanov & Popov, 1977; Popov, 1977). Therefore, the outgroup for the present analysis is an ancestor with conchological states taken from *Schedocardia* and anatomical states taken from *Acanthocardia.* The analysis also was run with both *Acanthocardia* and *Schedocardia* as outgroups, with the same phylogenetic results as those presented here.

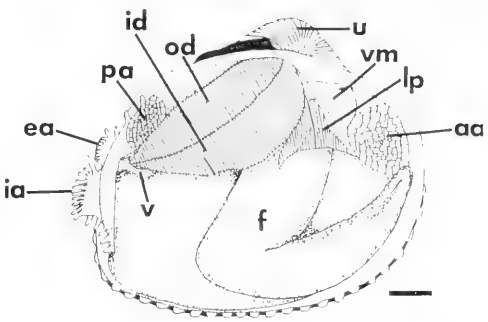


FIG. 1. Anatomy of *Clinocardium nuttallii* (live specimen, Monterey Bay; Schneider, 1994). Right valve and mantle removed. Scale bar = 5 mm.

DESCRIPTION OF CHARACTERS

I. Anatomical characters

External views (shell removed) of three taxa of cardiids is presented in Figures 1 and 2.

A. Labial palps

1. Size of labial palps (Figs. 3, 4). States: (0) small—less than one-fifth length of animal, (1) large—greater than one-fifth length of animal.

(Tridacnines are scored missing for this character. See Discussion)

2. Labial palp tips (Figs. 3, 4): (0) pointed, (1) blunt.

3. Insertion of labial palps and inner demibranch into oral groove (og; Figs. 3, 4): (0) inner demibranch inserted between labial palps, (1) inner labial palp (ip) connected to bottom of inner demibranch (id), (2) inner demibranch inserted behind inner labial palp

B. Ctenidia

4. Food groove on outer demibranch (od; Fig. 5). An outer food groove on *Serripes groenlandicus* (Mohr, 1786) is reported here for the first time. Stasek (1962) reported that *S. groenlandicus* lacked a food groove on its outer demibranch, but this structure was present on every specimen of *S. groenlandicus* that I examined. Yonge (1936) reported that *Tridacna* (*Persikima*) *derasa* (Röding, 1798) was the only giant clam with a food groove on its outer demibranch. Stasek (1962) reported that *Hippopus hippopus* (Linné, 1758) and *T. derasa* had food grooves on their outer demibranchs. Rosewater (1965) stated that a food groove on the outer demibranch was present in *Tridacna* (*Tridacna*) *gigas* (Linné, 1758) and *H. hippopus* but absent in *T. derasa* and all other giant clams. Lucas et al. (1991) report that *T. gigas* is the only giant clam with a food groove on its outer demibranch, and my anatomical studies confirm the observations of Lucas et al. States: (0) absent, (1) present.

5. Ctenidial filaments. Tridacnines have more than 60 filaments per ctenidial plica. Other cardiids have less than 30 filaments per plica (Ridewood, 1903). States: (0) few (< 30), (1) numerous (> 60).

C. Foot

6. Lateral ridges on foot (lr; Fig. 6): (0) absent, (1) present.

7. Ventral ridge on foot (vr; Fig. 6): (0) absent, (1) present.

8. Ventral papillae (vp; Figs. 6, 7). Gould (1841) named *Serripes* for "the serrated margin of the foot" of *Cardium groenlandicum* Mohr, 1786. Kafanov (1980) described ventral papillae on either side of the byssal groove on all Recent clinocardiines, and I discerned ventral papillae on either side of the byssal groove of the fragines *Trigoniocardia* and *Apiocardia.* States: (0) absent, (1) present.

D. Siphons and tentacles

9. Valvule (v; Figs. 1, 2). A semicircular flap of tissue on the interior of the siphonal apparatus, just dorsal to the incurrent aperture, was called the languette or curtain valve by Dall (1889). Pelseneer (1911) and Schneider (1992, 1994) termed this structure the valvule. Pelseneer (1911) first noted that some fragines have larger valvules. States: (0) small or absent, (1) large.

10. Perisiphonal suture (pss; mispelled as periphonal suture in Schneider [1992]; Fig. 8). The perisiphonal suture is the tissue separating the incurrent aperture from the pedal gape

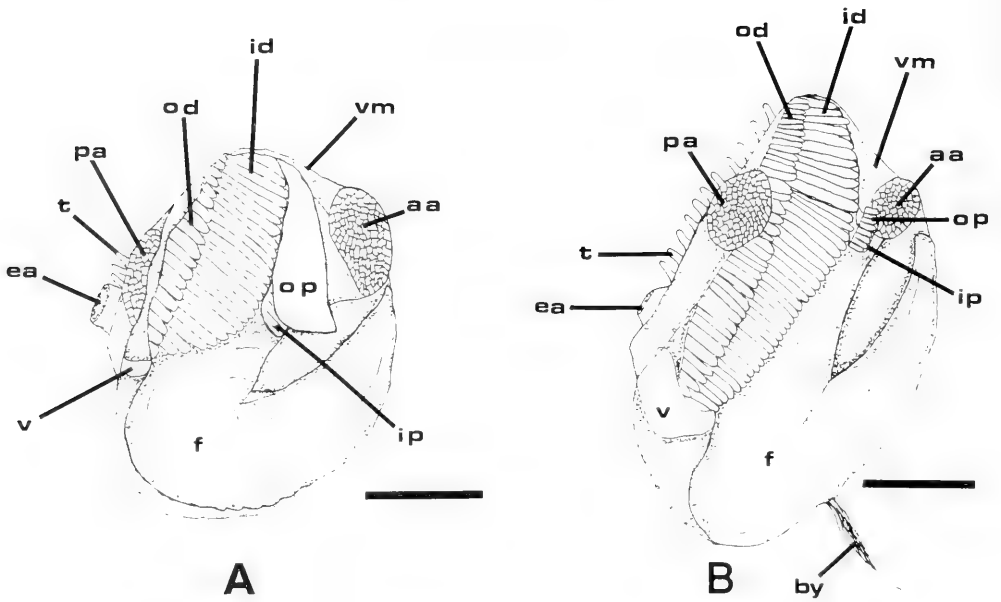


FIG. 2. Anatomy of (A) *Trigoniocardia* (*Apiocardia*) *obovale* (ANSP 316937) and (B) *Fragum fragum* (ANSP 289145). Shell and right mantle removed in both specimens. A, scale bar = 4 mm; B, scale bar = 5 mm.

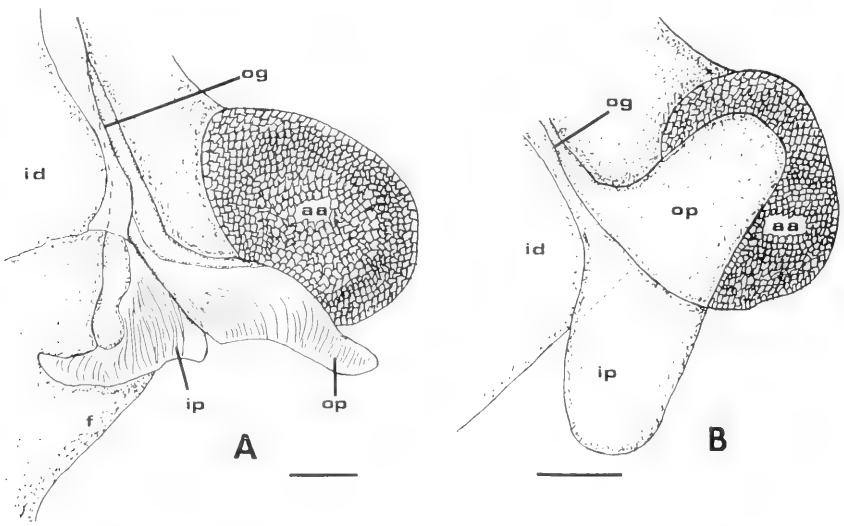


FIG. 3. Labial palps (right). A, *Ciliatocardium ciliatum* (USNM 604850). Dotted line indicates location of dorsal extension of inner palp behind inner demibranch. Scale bar = 5 mm. B, *Microfragum festivum* (AM C.164061). Dotted line indicates location of inner demibranch behind labial palps. Scale bar = 1 mm.

(pg). All fragines and only fragines lack a perisiphonal suture. Dall (1895) and Pelseneer (1911) have previously noted this anatomical structure. States: (0) present, (1) absent.

11. Location of dorsalmost tentacles around siphonal area (Fig. 8): (0) at bottom of posterior adductor muscles, (1) one-quarter up adductors, (2) half-way up adductors, (3) top of adductors, (4) beyond top of adductors, (5) around siphonal apertures only.

12. Tentacle pattern (Fig. 8): (0) numerous

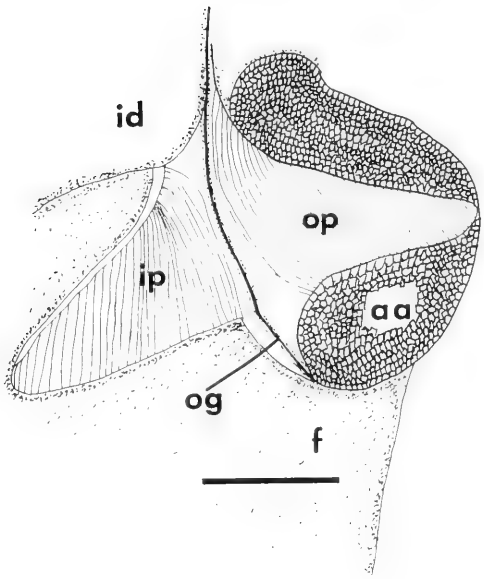


FIG. 4. Labial palps (right) of *Clinocardium nuttallii* (Schneider, 1994). Scale bar = 5 mm.

tentacles on both periphery and central portion of intersiphonal area, (1) numerous tentacles on periphery of intersiphonal area, few or no tentacles on central portion of intersiphonal area, except around siphonal apertures, (2) tentacles few, but located both on periphery and central portion of intersiphonal area, (3) on siphons only, (4) numerous tentacles around siphons, few tentacles elsewhere.

E. Intestine

13. Path of intestine (Figs. 9, 10). *Cerastoderma, Hypanis, Didacna, Parvicardium siculum,* and tridacnines have intestines that may be of either three or four loops. (Johnstone [1899] discusses the intestine of *Cerastoderma edule.*) Complex intestines are those that typically have eleven loops. Two taxa with somewhat less complicated intestines, *Apiocardia* (Fig. 10A) and *Serripes* (Fig. 10D), are also coded for this character state, for the general *pathway* of the intestine in *Apiocardia* and *Serripes* is similar to the eleven-looped form. When the data set is run with the states for *Apiocardia* and *Serripes* coded as autapomorphies, the results are the same as the results presented here, except that the most parsimonious trees are each two steps longer. The intestine of *Goethemia* has no loops. Most fragines have guts with a single loop. States: (0) no loops, (1) one loop, (2) 3 to 4 loops, (3) > 4 loops.

F. Stomach (Fig. 11).

Yonge (1936) and Purchon (1955) described and illustrated the stomach of several species of giant clams. Purchon (1960a) based his description of the cardiid stomach on Graham's (1949) description and figure of *Cerastoderma edule.* Nakazima (1964a, b) described and illustrated the stomachs of *Hippopus hippopus, Tridacna* (*Chametrachea*) *maxima* (Röding, 1798) (= *Tridacna elongata*), and *Nemocardium bechei* (Reeve, 1847). Starobogatov (in Kafanov & Popov, 1977) described, but did not illustrate, the stomachs of species belonging to twelve genera of cardiids. The species that Starobogatov examined were not stated. It is therefore important to emphasize that discrepencies between my data and those of Starobogatov's may be due to species-level differences. (Schneider, 1992, discusses use of *Cerastoderma edule* to represent *Cerastoderma* versus Starobogatov's use of *Cerastoderma glaucum* [Bruguière, 1789].) Kafanov & Popov's use of sorting areas of the stomach as key characters in bivalve phylogeny was discussed by Schneider (1992; see Purchon, 1960a: 481). Purchon (1987a) reviewed the literature on cardiid stomach anatomy. Schneider (1994) described and illustrated the stomachs of *Nemocardium* (*Keenaea*) *centifilosum* (Carpenter, 1864) and *Clinocardium nuttallii.* The terminology of stomach sorting areas is after Purchon (1960a).

14. Major typhlosole (T1) path. Purchon (1960a) put the Cardiidae and Tridacnidae into his type V stomach group. The diagnostic feature of type V bivalve stomachs is the extension of the major typhlosole and intestinal groove into two caeca (left and right). In bivalves with type V stomachs, the major typhlosole exists the combined midgut/style sac (ss), anteriorly traverses the stomach floor, and enters the right caecum (rc). The major typhlosole then emerges from the right caecum, traverses laterally across the anterior of the stomach floor, and enters the left caecum (lc). Within the left caecum, the major typhlosole may terminate in a spiral (as in tridacnines; sf). All published accounts of cardiid stomachs are consistent with this description. This is the pathway of the major typhlosole in most of the cardiids in the present analysis. However, Schneider (1994) found the major typhlosole

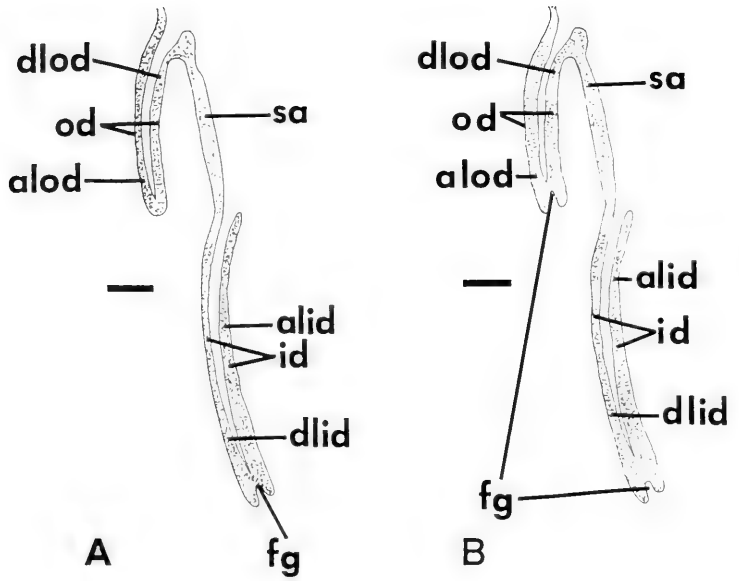


FIG. 5. Cross-section through ctenidia, showing food grooves. A, *Clinocardium nuttallii* (from Schneider, 1994). B, *Serripes groenlandicus* (USNM 600836). Scale bars = 5 mm.

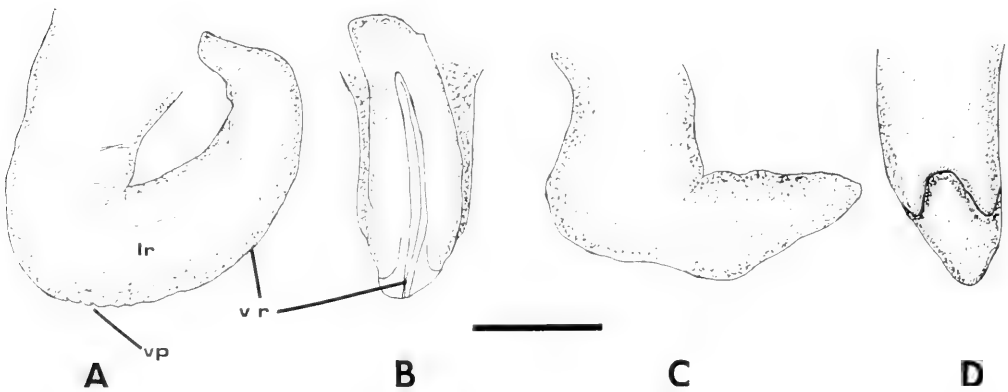


FIG. 6. Feet. A, lateral, and B, anterior view of foot of *Apiocardia obovale* (ANSP 316937). Scale bar = 4 mm. C, lateral, and D, anterior view of foot of *Cerastoderma edule*, specimen dissected live. Scale bar = 2 mm.

in *Clinocardium nuttallii* split in two, giving rise to left and right branches that separately enter the left and right caeca, respectively. In bivalves with stomach type IV of Purchon (1958, 1960a), the major typhlosole emerges from the midgut, traverses forward across the stomach floor and then curves to the left. Finally, the major typhlosole terminates within or close to the entrance of the left caecum. Purchon (1960a, b) considered the bivalve groups of stomach types I, II, III, and V to be monophyletic groups. However, Purchon (1960a, b) proposed that many bivalves with type IV stomachs — Sphaeridae, Lucinidae, Thyasiridae, Donacidae, *Chama multisquamosa* [Reeve, 1846] — were progenetically derived from bivalves with type V stomachs. Most of these forms are smaller in size than their closest relatives, the latter forms having type V stomachs. Purchon (1960a, b) therefore was of the opinion that the reversion to a type IV stomach in these bivalves is related to miniaturization. Purchon (1987a) distinguished these bivalves which secondarily evolved a

FIG. 7. Ventral view of foot of *Serripes groenlandicus* (USNM 600836), with prominent ventral papillae. Scale bar = 40 mm.

type IV stomach by erecting a new group for them, stomach type IVB. Purchon (1987a) considered only *C. multisquamosa,* the donacids, and the tellinids with type IVB stomachs to have evolved progenetically. Purchon (1987a) termed the stomachs of lucinids, thyasirids, and the pisidiid *Sphaerium corneum* (Linné, 1758) "secondarily simplified."

In the stomachs of *Trigoniocardia antillarum* and *Apiocardia obovale* (Sowerby, in Broderip & Sowerby, 1833) (Figs. 15J, K), the major typhlosole is as in type IV bivalve stomachs. The major typhlosole emerges from the combined midgut/style sac, traverses anteriorly across the stomach floor and then enters the left caecum, where it terminates. In *Lunulicardia retusa* (Linné, 1767) (Fig. 15L) and *Corculum cardissa* (Linné, 1758), the major typhlosole exits the midgut/style sac, and then

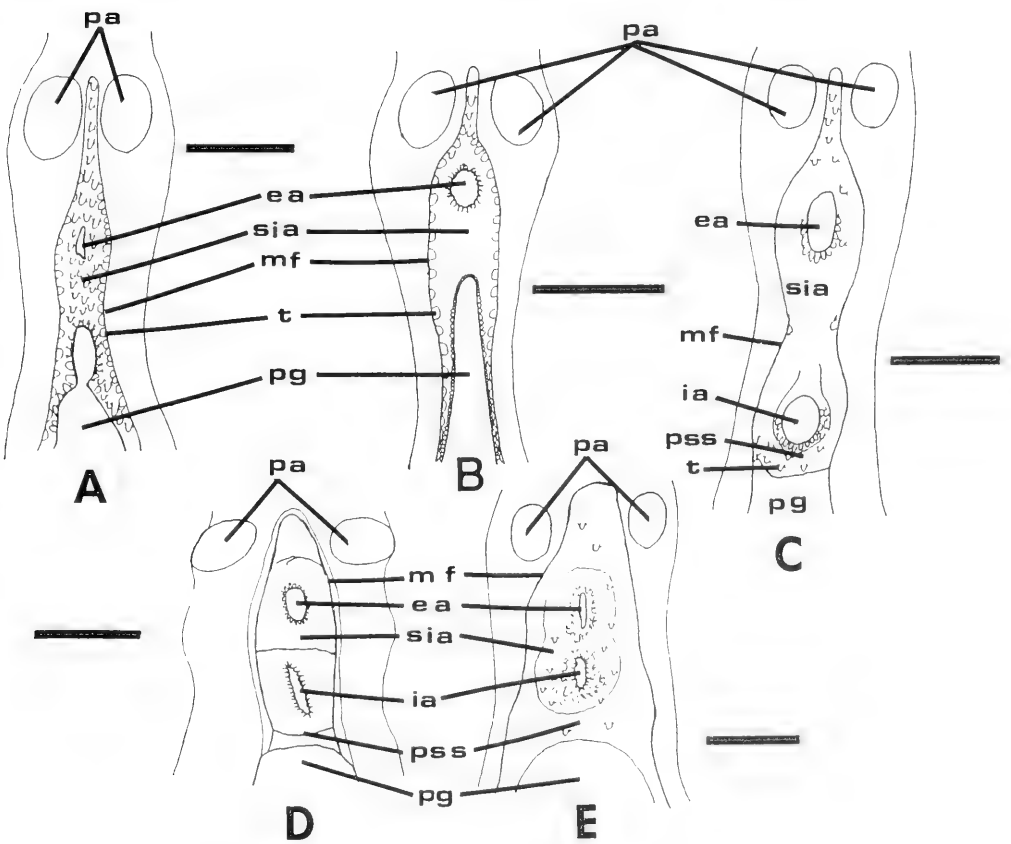


FIG. 8. Tentacles and siphons. A, *Papillicardium papillosum* (MNHN, unnumbered). Scale bar = 2 mm. B, *Ctenocardia symbolica* (ANSP 229873). Scale bar = 3 mm. C, *Serripes groenlandicus* (USNM 600836). Scale bar = 4 mm. D, *Hypanis* (*Monodacna*) *colorata* (USNM 769939). Scale bar = 2 mm. E, *Acanthocardia aculeata* (NHM Acc.2322). Scale bar = 10 mm.

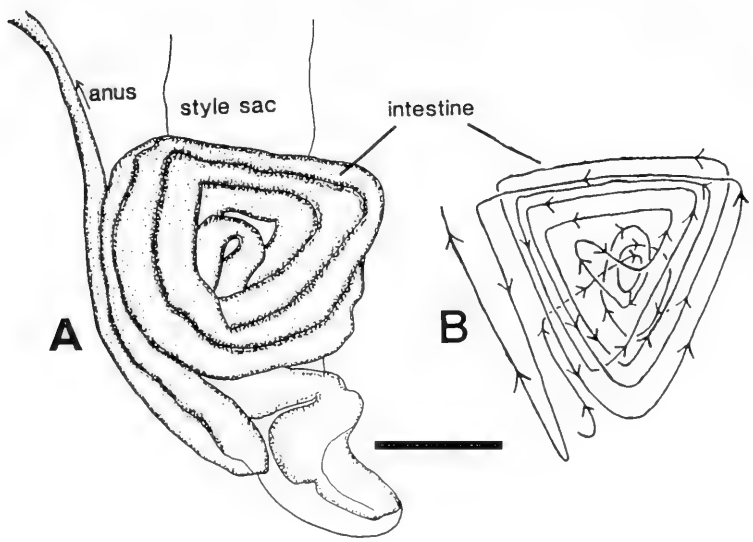


FIG. 9. Camera lucida drawing of intestine (A) of *Clinocardium nuttallii*, as seen from right side, and (B) diagram depicting pathway of intestine from exit of style sac/midgut to exit from visceral mass. Scale bar = 2 mm. From Schneider, 1994.

traverses anteriorly until it enters the right caecum, where it terminates. States: (0) T1 to RC, then LC, then spirals, (1) splits: T1r to RC, T1l to LC, (2) T1 to RC then LC, (3) T1 to LC, (4) T1 to RC.

15. Location of right caecum: (0) right side, (1) central.

16. Relative position of caeca. Starobogatov, in Kafanov & Popov, 1977, considered the relative position of the gastric caeca in erecting the five different cardiid stomach types. The caeca are "parallel" (i.e., a line connecting the midpoints of the caeca is perpendicular to a line from the esophagus to the style sac/midgut) in Cardiinae and Clinocardiinae, and not parallel in Lymnnocardiinae, Fraginae, and Protocardiinae (all subfamilies *sensu* Kafanov & Popov). From my dissections, I have found that the caeca are parallel in all ingroup taxa, except for *Lunulicardia retusa* (Fig. 11L, M). This character state is polymorphic for clinocardiines except for *Serripes groenlandicus* (Fig. 11E, F); caeca may be parallel or the right caecum may be more anterior. The caeca are not parallel in the cardiine *Acanthocardia aculeata* (Linné, 1767) (Fig. 11A), from which I have taken the anatomical data for the outgroup. States: (0) caeca parallel, (1) right caecum anterior to left caecum.

17. Tertiary typhlosole (T3). A typhlosole-like structure, just ventral of the posterior sorting area (SA3), is present in lymnocardiines and the clinocardiines *Ciliatocardium ciliatum* (Fabricius, 1780) (Fig. 11C, D) and *Serripes groenlandicus* (Fig. 11E, F). This structure is prominent in Graham's (1949) figure of the stomach of *Cerastoderma edule*, but is unlabeled and is not mentioned in the text. This structure is not mentioned in Kafanov & Popov (1977). States: (0) absent, (1) present.

18. Location of style sac: (0) posterior, (1) anterior.

19. Raised bar (rb). Some clinocardiines have a raised structure across the middle of the stomach floor. In *S. groenlandicus* (Fig. 11E, F), the raised bar is anterior to the caeca. In other clinocardiines, the raised bar is posterior of the caeca. States: (0) absent, (1) present.

20. Ridge (r). Graham (1949) discussed a ridge that runs transversely and obliquely across the anterior stomach floor, below the esophagus. This structure (labeled RCE by Graham) is found in lymnocardiines and tridacnines. States: (0) absent, (1) present.

21. Esophageal sorting area (SA7 or SAE). The esophageal sorting area is present in all cardiids except tridacnines. This has been noted by Purchon (1987a). States: (0) present, (1) absent.

G. Reproductive characters.

Data for characters 22 and 23 from Lovén (1848), Lacaze-Duthiers (1854), Grobben

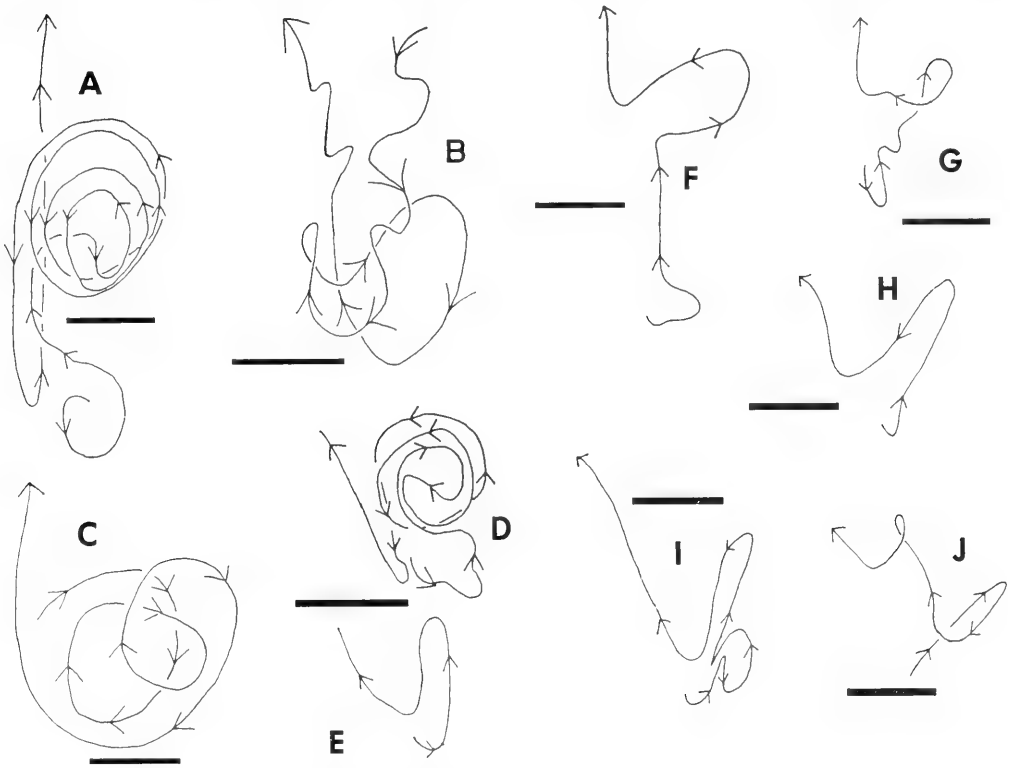


FIG. 10. Intestinal pathways. A, *Serripes groenlandicus* (USNM 600836). B, *Tridacna* (*Chametrachea*) *maxima* (ANSP A3276). C, *Parvicardium siculum* (AMNH 226511). D, *Apiocardia obovale* (ANSP 316937). E, *Trigoniocardia antillarum* (USNM 857540). F, *Lunulicardia retusa* (ANSP 302424). G, *Fragum fragum* (ANSP 289145). H, *Microfragum festivum* (AM C.164061). I, *Americardia media* (ANSP 297243). J, *Ctenocardia symbolica* (ANSP 229873). All scale bars = 2 mm, except for B (10 mm) and G (4 mm).

(1898), Johnstone (1899), Pelseneer (1911), Edmondson (1919), Stephenson (1934), Thorson (1936), Yonge (1936, 1981), Wada (1952, 1954), Matveeva (1953), Ockelmann (1959), Petersen (1958), LaBarbera (1975), Jameson (1976), Gwyther & Munro (1981), Gallucci & Gallucci (1982), Alcazar & Solis (1985), Braley (1985), Dolgov (1991) and Fitt (1991).

22. Larvae. In *Parvicardium exiguum* and *Cerastobyssum,* the eggs are attached singly to the bottom by means of a double mucous membrane (Lovén, 1848), similar to that of some species of *Macoma* and *Astarte* (Thorson, 1936). Presumably, these eggs are subsequently fertilized by sperm emitted into the water column. In *Goethemia,* fertilized larvae are brooded in pouches formed by folds of the ventral part of the mantle, and the young hatch when the shell length reaches about 1.2 mm (Matveeva, 1953; Fig. 12). In all other cardiids, both sperm and egg are emitted into the water column where fertilization takes place (Pelseneer 1911; Yonge, 1936). States: (0) fertilization in water column, (1) egg capsules, (2) brooded.

23. Sex: (0) dioecious: separate sexes throughout entire life history, (1) protandric: male stage preceeds female stage in life history, (2) monoecious: hermaphroditic through entire life history.

H. Other anatomical characters

24. Byssus (by; Figs. 2B, 13). Larval and early juvenile stage cardiids have a functional byssal gland (Pelseneer, 1911; Yonge, 1936). A functional byssal gland is present in the adults of fragines and *Chametrachea.* Other tridacnines have a functional byssal gland in older juveniles or sub-adults, until they are large enough to be held in place by their own weight. The loss of a functional byssus in

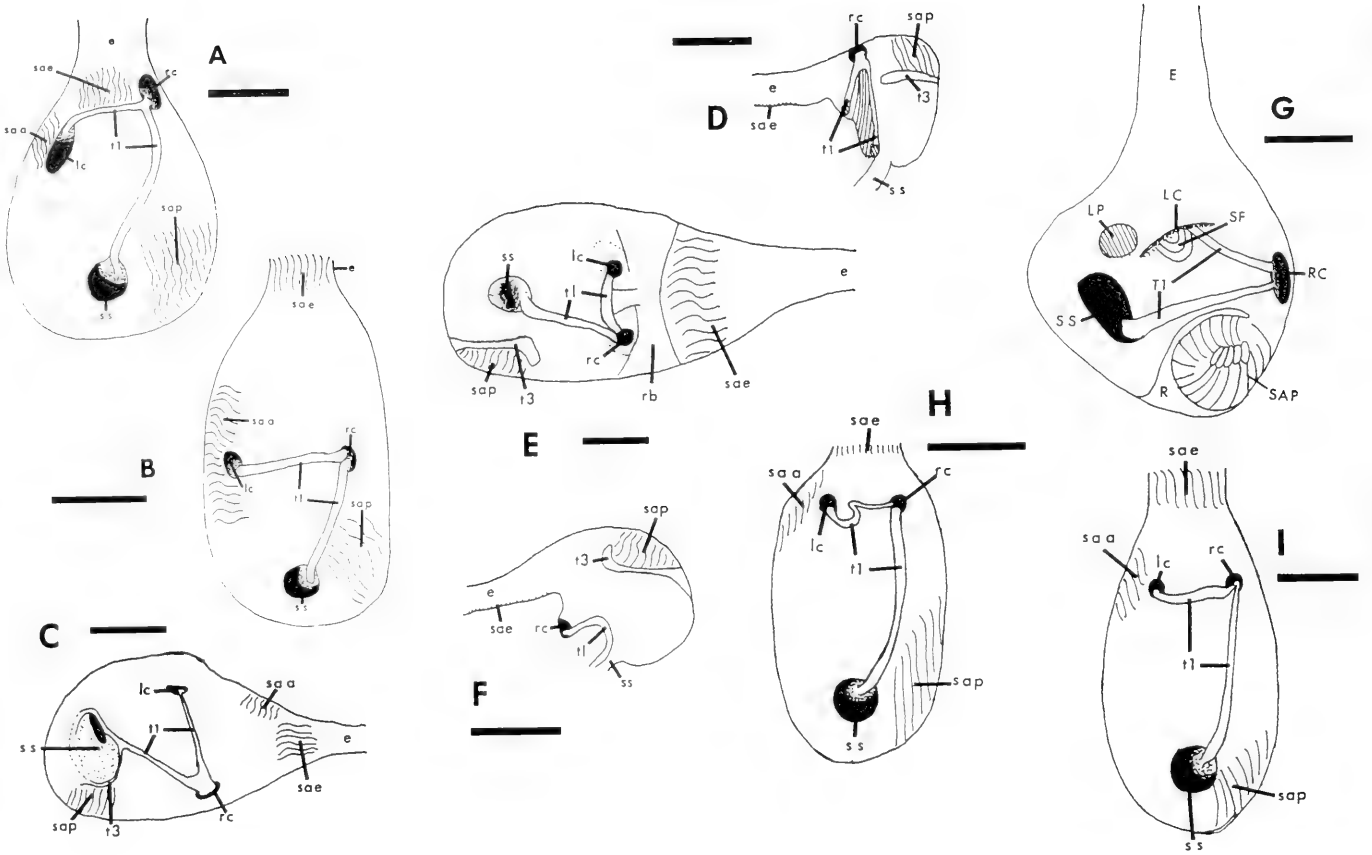


FIG. 11. Stomach morphology. All views of stomach are viewed from top of stomach looking downward. Stomach cut open at top along anterior-posterior axis. View distorted as in Purchon (1955, 1958, 1960a, 1987a) and Nakazima (1964a, b) so that structures on side and top of stomach appear to be on stomach floor in these two-dimensional drawings. Notably capacious stomachs are illustrated with additional views. The anterior sorting area (saa, or SA8) of *Serripes groenlandicus* is present, on the interior of the top of the stomach. A, *Acanthocardia aculeata* (NHM Acc.2322). Scale bar = 3 mm. B, *Maoricardium pseudolatum* (AM C.164058). Scale bar = 6 mm. C, D, *Ciliatocardium ciliatum* (USNM 604850). C, stomach floor as seen from top, scale bar = 2 mm; D, right side of stomach, scale bar = 4 mm. E, F, *Serripes groenlandicus* (USNM 600836). E, stomach floor as seen from top, scale bar = 2 mm; F, right side of stomach, scale bar = 5mm. G, *Tridacna* (*Chametrachea*) *maxima* (ANSP A3276). Scale bar = 2 mm. H, *Parvicardium siculum* (AMNH 226511). Scale bar = 1 mm. I, *Papillicardium papillosum* (MNHN, unnumbered). Scale bar = 1 mm.

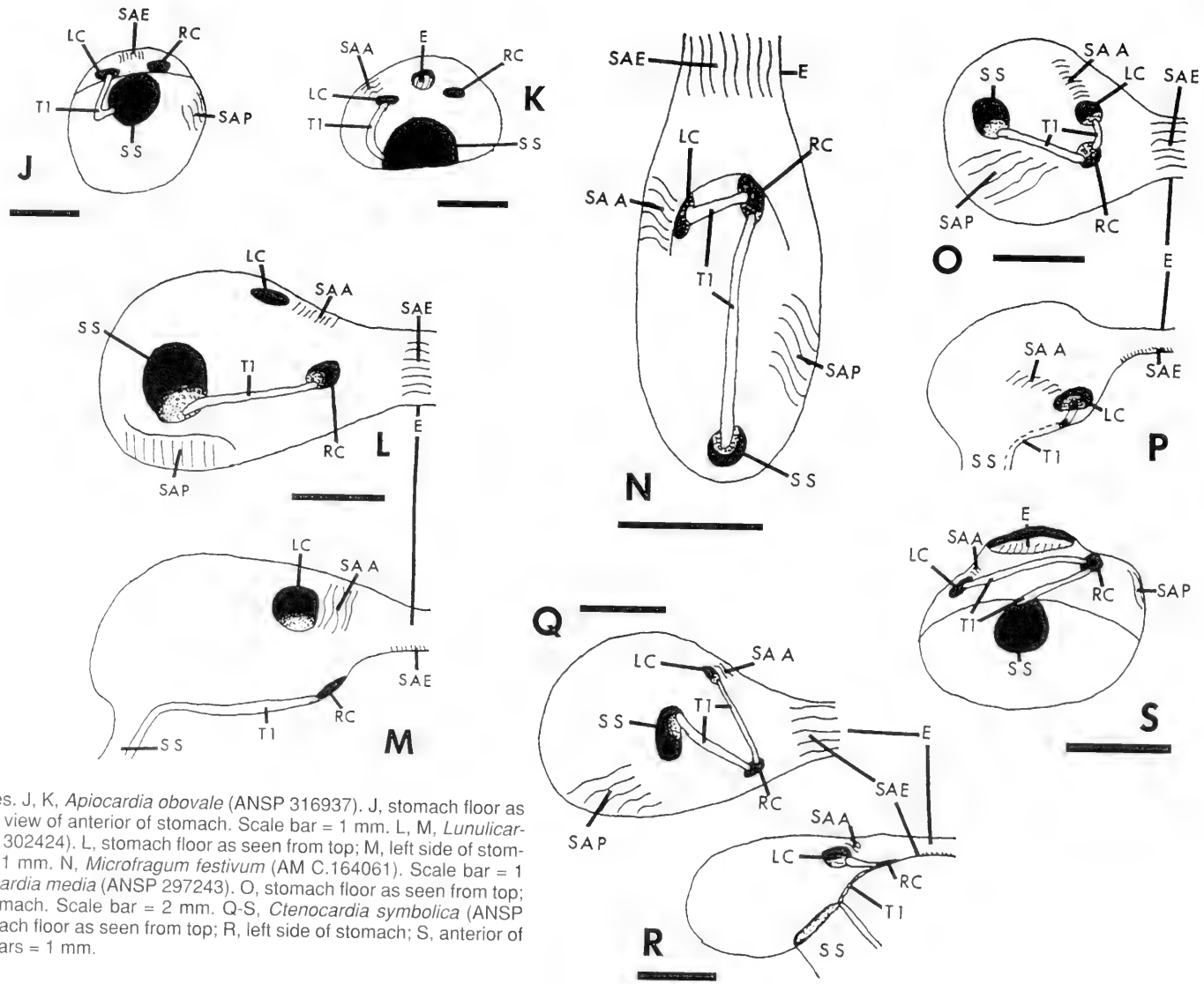


FIG. 11. Continues. J, K, *Apiocardia obovale* (ANSP 316937). J, stomach floor as seen from top; K, view of anterior of stomach. Scale bar = 1 mm. L, M, *Lunulicardia retusa* (ANSP 302424). L, stomach floor as seen from top; M, left side of stomach. Scale bar = 1 mm. N, *Microfragum festivum* (AM C.164061). Scale bar = 1 mm. O, P, *Americardia media* (ANSP 297243). O, stomach floor as seen from top; P, left side of stomach. Scale bar = 2 mm. Q-S, *Ctenocardia symbolica* (ANSP 229873). Q, stomach floor as seen from top; R, left side of stomach; S, anterior of stomach. Scale bars = 1 mm.

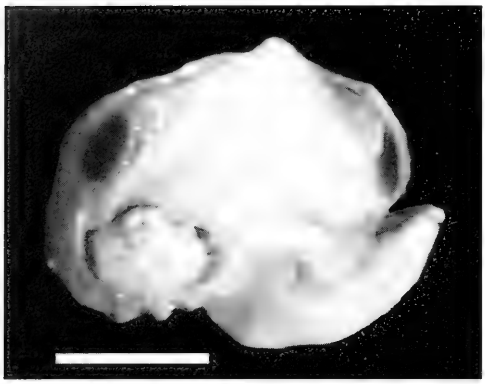


FIG. 12. *Goethemia elegantula* (SMNH 883) as seen from right side. Note brood pouch. Scale bar = 2 mm.

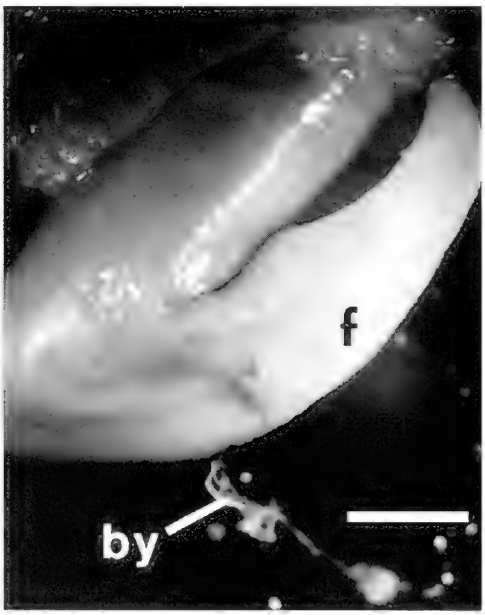


FIG. 13. Foot and byssal threads of *Fragum fragum* (ANSP 237102). Scale bar = 4 mm.

these forms is considered a secondary modification of a functional adult byssus (see Discussion). Petersen (1958), Yonge (1962), Petersen & Russell (1971), Lambiotte (1979), Yankson (1986), and Voskuil & Onverwagt (1989) discuss *Cerastoderma, Papillicardium, Parvicardium,* and *Cerastobyssum.* Pelseneer (1911) covers *Lunulicardia* and *Corculum,* and Kawaguti (1950), Savazzi (1985), and Severin & Cooper (1989) discuss *Corculum.* Rosewater (1965) and Yonge (1936, 1981) cover the tridacnines. States: (0) present in larval and early juvenile stage only, (1) present in later ontogeny, may be lost as adults.

25. Eyes. Most cardiids have simple, inverse eyes (Johnstone, 1899; Zugmayer, 1904; Weber, 1908; Pelseneer, 1911; Roche, 1925; Barber & Land, 1967; Barber & Wright, 1969). Tridacnines, except for *Hippopus* and *Tridacna* (*Persikima*) *tevoroa* Lucas et al., 1990, have hyaline organs (Yonge, 1936, 1981; Stasek, 1966; Kawaguti & Mabuchi, 1969; Fankboner, 1980; Wilkens, 1984, 1988, Lucas et al., 1991). *Hippopus* and *T. tevoroa* have neither simple inverse eyes nor hyaline organs. States: (0) absent, (1) simple inverse, (2) hyaline organs.

26. Mantle margins. The ventral, inner mantle folds of tridacnines are much larger than in other cardiids (Yonge, 1982; Morton, 1988). States: (0) small, (1) large.

B. Periostracum

27. Periostracal cilia (Fig. 14): (0) absent, (1) present.

C. Conchological characters

A. Shell exterior

28. Posterior margin. Discussed by Schneider (1995). (0) digitate, (1) crenulate, (2) smooth.

29. Beak gyry (Fig. 15). Most cardiids have slightly prosogyrous beaks or umbos (Wilson & Stevenson, 1977). Keen (1936) named *Clinocardium* for its strongly prosogyrous beaks. States: (0) weakly prosogyrous, (1) strongly prosogyrous. This character is coded as missing for the Recent tridacnines (see Discussion).

30. Shell shape (Fig. 16). Cardiids, like most bivalves, change the shape of their shell during ontogeny. Because of accretionary growth of bivalve shells, the shape at time 1 depends on the shape of the shell at time 0. This is a causal sequence and can be ordered under Alberch's (1985) criterion. Therefore, a character state tree can be constructed for shell shape. Although there have been several attempts to describe the ontogeny of bivalve shell shape (Raup, 1966; Løvtrup & Løvtrup, 1988; Checa, 1991; Johnston et al., 1991; Ackerly, 1992a, b), a rigorous method of converting morphometric information on bivalve ontogeny into cladistic character states

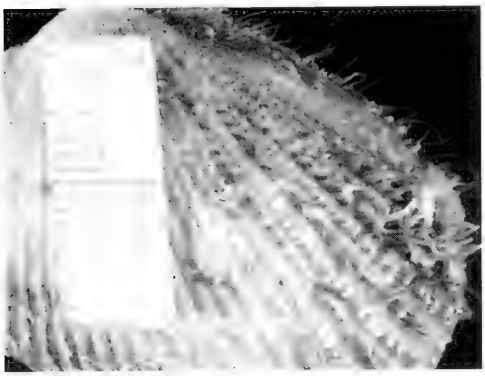


FIG. 14. Periostracal cilia of *Maoricardium pseudolatum* (AM C.164058). Scale indicated in figure.

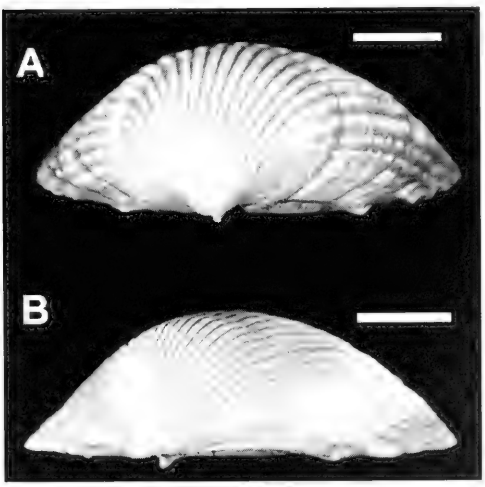


FIG. 15. Beak gyry. A, *Cerastoderma edule,* right valve (FMNH 278010), scale bar = 10 mm. B, *Clinocardium nuttallii,* right valve (FMNH 278016), scale bar = 20 mm.

has yet to be devised. In this study, the shell shapes exhibited by cardiids have been placed in six states, each of which can be described semi-quantitatively. Most cardiids go through at least two of the shell shape character states during ontogeny (hence the ability to construct character state trees; Table 3). *Maoricardium*'s and *Profulvia*'s shell shapes are terminal autapomorphies and are coded for the last ontogenetic state which fits on the character state tree. I follow the method proposed by Mabee & Humphries (1993) and consider the entire ontogenetic sequence as a single character state rather than coding the condition at each ontogenetic stage as a separate character. See Discussion for the coding of *Byssocardium, Hippopus, Chametrachea, Tridacna,* and *Persikima.* Shell shape can be determined by using the following key (Schneider, 1998, defines and illustrates the terms.) Schediform shell shape and oval shell shape are both preceded in ontogeny by circular shell shape (Schneider, 1998). The conchological component of the outgroup, *Schedocardia,* has a schediform shell shape. Therefore, schediform shell shape is considered the more basal state on the basis of outgroup comparison, not ontogeny. It should be noted that the "quadrate-short" shell shape of some fragines is not homologous to the "quadrate-short" shell shape of various taxa considered in Schneider (1995, 1998), because the ontogenetic pathway is vastly different.

Shell Shape Character Key

1. Apparent height (AH) > height (H) 2
   AH = H 3
2. Carina strong . . . . . trigonal
   (includes "triangular" of Schneider, 1998)
   Carina weak or absent . . . . . oval
3. H/length (L) > 1.0 . . . . . .quadrate-short
   1.0 > H/L > 0.9 4
   H/L < 0.9 . . . . . hypaniform
4. Post-hinge length (PHL) < (0.2) × L
   . . . . . schediform
   PHL > (0.2) × L . . . . . cerastiform

States: (0) schediform, (1) oval, (2) cerastiform, (3) hypaniform, (4) trigonal, (5) quadrate-short.

Character state tree:

Schneider (1998) discusses the next three characters.

31. Primary raised thread: (0) absent, (1) present.

32. Rib groove. On some eucardiids, there may be a faint depression running down the middle of the rib; this depression is homologous to a rib interspace in Cretaceous eucardiids. States: (0) absent, (1) present.

33. Cross-striae: (0) absent, (1) present.

34. Spine morphology (Figs. 17–21). *Sche-*

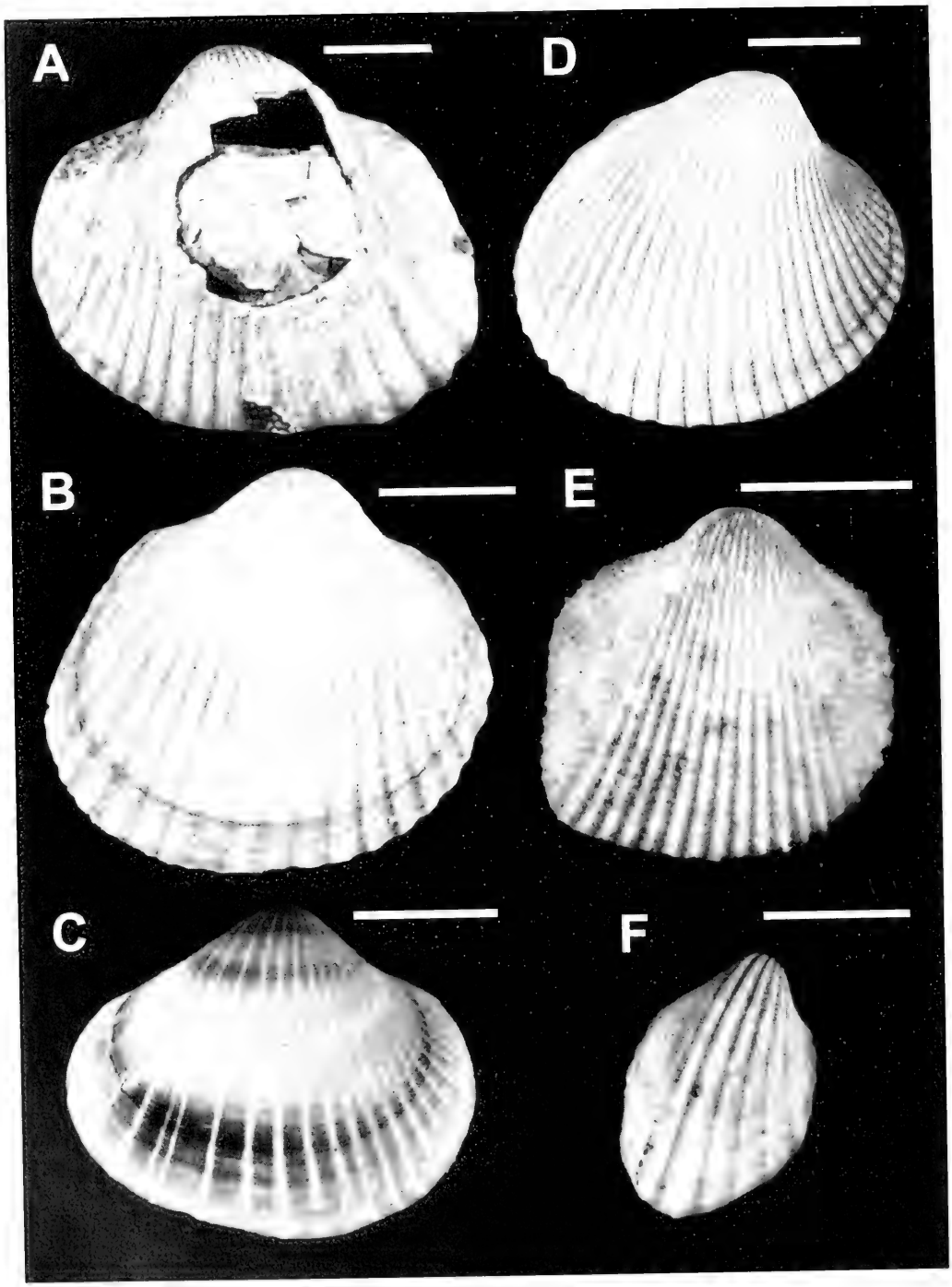


FIG. 16. Shell shape. A. *Acanthocardia (Schedocardia) hatchetigbeense*, left valve (USNM 645087 syntype); schediform. B. *Cerastoderma edule*, right valve (FMNH 278010); cerastiform. C. *Hypanis* (*Monodacna*) *colorata*, right valve (ANSP 338065); hypaniform. D. *Clinocardium nuttallii*, right valve (FMNH 278016); oval. E. *Ctenocardia symbolica*, right valve (ANSP 229980); quadrate-short. F. *Apiocardia obovale*, right valve (ANSP 317706); trigonal. A-C, E, F, scale bars = 10 mm; D, scale bar = 20 mm.

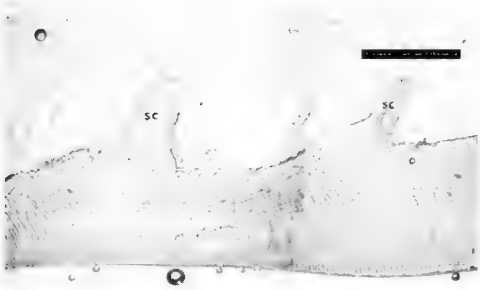


FIG. 17. Radial section through central portion of a rib of *Tridacna* (*Chametrachea*) *maxima* (FMNH 156836, right valve) to illustrate shell microstructure. Direction of ventral margin toward right, direction of umbo toward left. Note how scutes (sc) are microstructurally continuous with shell. Scale bar = 1 mm.

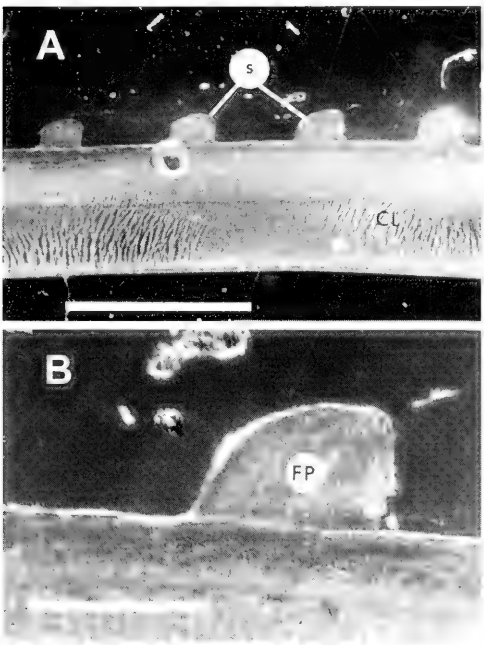


FIG. 18. Radial section through a portion of a rib of *Fragum fragum* (ANSP 288688, right valve). Note microstructural relationship of ornament to underlying shell and compare to *Granocardium kuemmeli* and *Profragum praecurrens* (Schneider, 1998: fig. 9). A, scale bar = 1 mm. B, detail of individual ornament, scale bar = 0.25 mm.

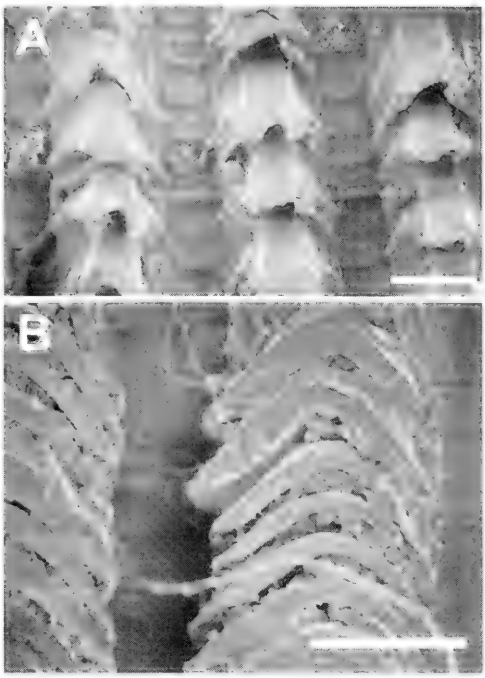


FIG. 19. External ornament of A, *Ctenocardia symbolica* (ANSP 229980, right valve), scale bar = 0.4 mm; and B, *Americardia media* (ANSP 54280, right valve), scale bar = 1 mm.

docardia (the conchological component of the outgroup) has simple spines (state 1); tridacnines and *Goethemia* have scutes (sc; state 2) (Schneider, 1998). Fraginae have poorly organized fibrous prisms (FP) microstructurally discontinuous with the underlying shell (state 3). *Maoricardium* and *Plagiocardium* (state 4) have complex spines in which the core of the spine is poorly organized fibrous prisms microstructurally discontinuous with the shell (i.e., state 3) and the outer portion of the spine is simple (state 1). Taxa lacking spines are assigned state 0.

35. Lunule flap (1f; Figs. 22A, H, 23A, H). On some cardiids, the inner shell layer may be raised just anterior to the beak; on a few forms, this structure may be reflected over the lunule and touch the beak. Although this structure has been noted numerous times in species descriptions, its phylogenetic utility was not recognized until Kafanov & Popov (1977) and Kafanov (1980) used it as one of the characters differentiating Clinocardiinae from Cardiinae. On most cardiines, the lunule flap touches the beak and is frequently reflected over the lunule. This state is unknown on clinocardiines. On clinocardiines, the lunule flap may be raised or may block the beak, but never touches it. Tridacnines are scored missing for this character, for the

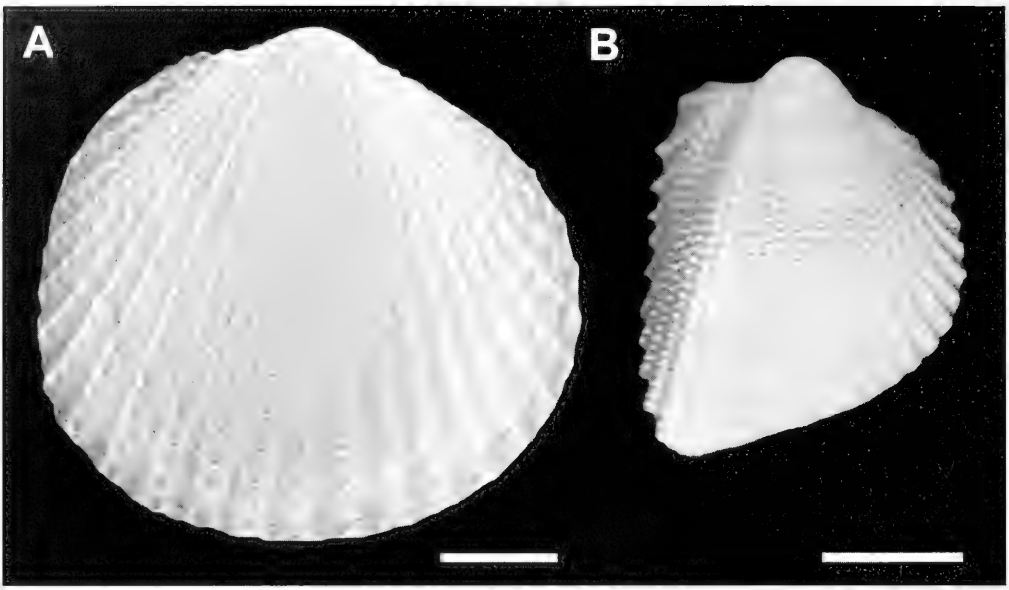


FIG. 20. External ornament of A. *Papillicardium papillosum*, right valve (ANSP 54266), scale bar = 2 mm; and B, *Fragum fragum*, right valve (ANSP 288688), scale bar = 10 mm.

lunule flap is a structure of the anterior part of the shell, which is missing in tridacnines (except for *Goniocardium*).

The terminology for this morphological structure in cardiid bivalves has never been standardized. It is here designated the lunule flap. States: (0) absent, (1) raised, does not block beak, (2) blocks beak, (3) touches beak.

36. Byssal gape (bg; Schneider, 1998; Figs. 25, 27–30). Except for *Goniocardium,* all tridacnines have a byssal gape sometime during ontogeny. This character is not redundant on the presence of a byssus (character 24), for fragines have a functional byssus but do not have a byssal gape. States: (0) absent, (1) present.

37. Riblets (rbl; Figs. 26-30). As defined by Rosewater (1965), riblets are secondary radial folds that occur on top of (1) primary radial folds and (2) between primary radial folds. The terms "primary" and "secondary" here are not used in a phylogenetic sense, but in a morphological one: the primary folds are more pronounced than the secondary ones. Riblets are found on the extant taxa of tridacnines. States: (0) absent, (1) present.

38. Pseudocarina (ps; Figs. 24, 25) Except for *Goniocardium*, tridacnines have a break in the slope of the shell that begins at the umbo and continues down that portion of the shell that is furthest from the hinge and ligament. This portion of the shell would be ventral in life condition, bearing the byssal gape. (Stasek [1962] called this portion of the shell the ventral margin. Rosewater [1965] called this portion of the shell "posterior.") In *Avicularium* and *Byssocardium,* this slope break is strong throughout ontogeny (state 1): about 80° on *Avicularium,* and 90° on *Byssocardium.* On other tridacnines, this slope break decreases in strength through ontogeny. *Hippopus* has a slope break comparable to that of *Avicularium* and *Byssocardium* until late in ontogeny, when the angle decreases to about 60° (state 2). *Chametrachea* (state 3), *Tridacna* (*Tridacna*) (state 4), and *Persikima* (state 5) have sequentially weaker slope breaks and earlier onset of the decrease in strength of the slope break. Therefore, this character can be linearly ordered on the basis of ontogeny. This character satisfies Alberch's (1985) criterion, because the angle of the pseudocarina at time 1 would depend upon the angle of the pseudocarina at time 0. Taxa lacking a pseudocarina are scored absent (state 0), which is considered primitive on the basis of outgroup comparison.

This structure is herein called the pseudocarina. It should not be called a carina, for a true carina refers to a change in the angle on the surface of a shell, demarcating the posterior slope of the shell from the central slope. A

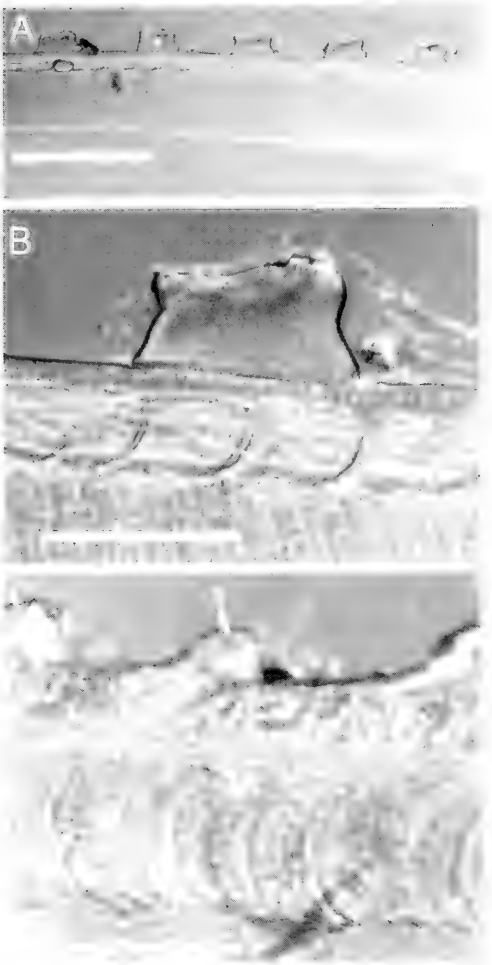


FIG. 21. Microstructure of ornament of *Maoricardium pseudolatum* (ANSP A103, right valve). A, B, radial section through central portion of ornament. Note that ornament is microstructurally discontinuous with underlying shell. C, radial section through side of ornament. Note that ornament is microstructurally continuous with underlying shell. A, scale bar = 2 mm; B, scale bar = 0.5 mm; C, scale bar = 0.2 mm.

carina is prominent in fragines (Kafanov & Popov, 1977), especially *Corculum.* Keen (1980) referred to the fragine carina as an umbonal ridge. Voskuil & Onverwagt (1989) referred to this structure on *Ctenocardia* and *Parvicardium* as an umbonal keel. Because the slope break on tridacnines does not demarcate the posterior slope from the central slope, it is not homologous to the carina.

B. Muscle scars

39. Dorsoumbonal scar. This muscle scar indicates the attachment point of the pedal elevator muscle, which is present in virtually all cardiids (Pelseneer, 1911; Cox, 1969; Kafanov, 1980). In some clinocardiines, the scar is more deeply impressed into the shell and more darkly colored than in other cardiids. Because the pedal elevator muscle is more firmly attached in these forms, it takes greater effort to remove an animal for dissection. Furthermore, when the pedal elevator muscle is separated from the dorsoumbonal muscle scar, there is an audible ripping sound. States: (0) weak, (1) strong.

40. Adductor muscle scars (Fig. 32): (0) anterior and posterior adductor muscle scars roughly equal in size and equally distant from shell margin, (1) anterior adductor muscle scar smaller, much closer to shell margin; posterior adductor muscle scar larger, located further from shell margin, (2) anterior muscle scar absent, posterior adductor muscle scar large and located in central portion of shell.

C. Ligament groove and nymph

41. Ligament groove on right valve (Fig. 22). On the right valves of *Clinocardium, Keenocardium, Fuscocardium, Serripes* and *Yagudinella,* the ligament (lg) groove is continuous with the posterior lateral socket (pls). On all other cardiids, the ligament groove terminates anterior of the posterior lateral socket. States: (0) not continuous with posterior lateral socket, (1) continuous with posterior lateral socket.

42. Nymph (n; Figs. 22, 23): (0) not located immediately dorsal to cardinal teeth, (1) located immediately dorsal to cardinal teeth.

D. Hinge (Figs. 22, 23). Tridacnines, excluding *Goniocardium,* plus the lymnocardiines *Hypanis* and *Didacna,* have no anterior lateral teeth and are therefore scored missing (?) for characters 44–47. *Hypanis* and *Didacna* lack posterior laterals, and are scored missing for character 48. *Byssocardium* and the extant tridacnines lack the anterior cardinal tooth and are scored missing for character 49.

43. Posterior umbonal buttress (pub). On some cardiids, the hinge plate is raised just posterior of the beak, blocking the beak. States: (0) absent, (1) present.

44. Right anterior ventral lateral tooth (vlt) (0) does not continue into umbo, (1) does continue into umbo. Dall (1903) noticed that for some cardiids "the teeth often . . . seem to

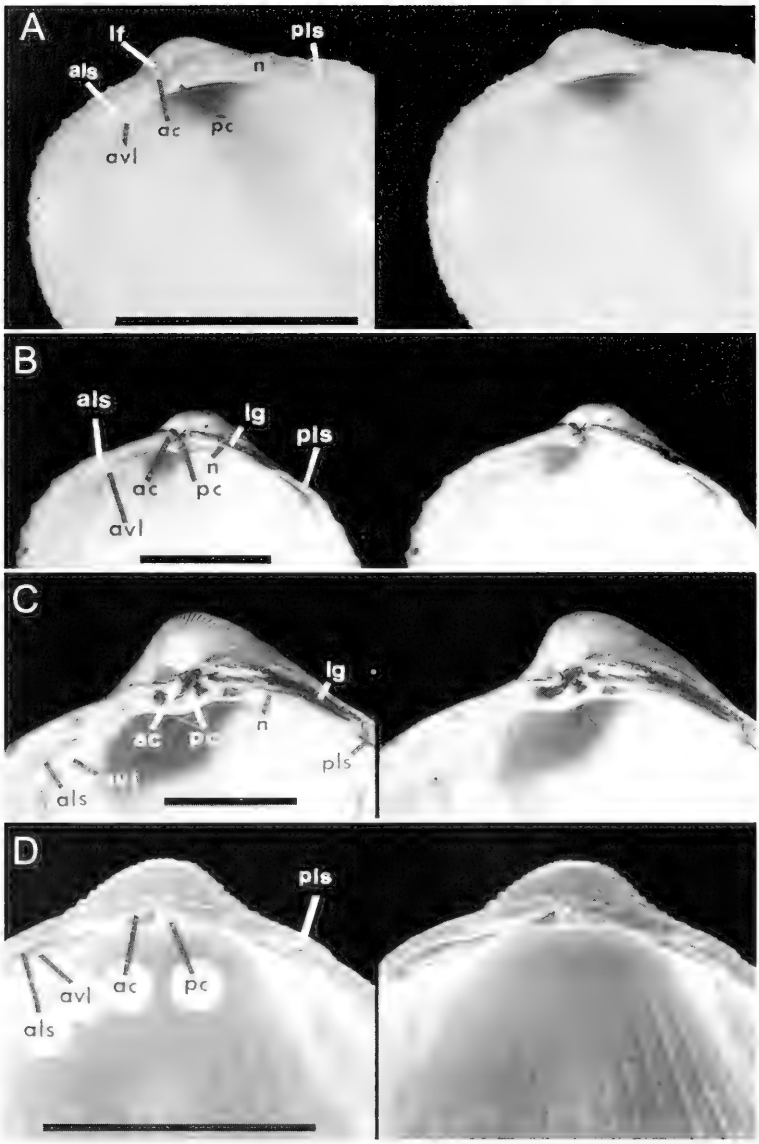


FIG. 22. Right hinges, stereo pairs. A, *Maoricardium pseudolatum* (ANSP A103), scale bar = 20 mm. Left pls moderate, ac shape 1, pc shape 1. B, *Ciliatocardium ciliatum* (ANSP 54269), scale bar = 20 mm. Left pls moderate, ac shape 1, pc shape 1. C, *Clinocardium nuttallii* (FMNH 278016), scale bar = 20 mm. Left pls moderate, ac shape 2, pc shape 1. D, *Papillicardium papillosum* (ANSP 54266), scale bar = 10 mm. Left pls absent, ac shape 3, pc shape 1. E, *Parvicardium exiguum* (ANSP 54289), scale bar = 1 mm. Left pls small, ac shape 3, pc shape 2. F, *Trigoniocardia antillarum* (ANSP 283822), scale bar = 3 mm. Left pls large, ac shape 3, pc shape 3. G, *Goniacardia callopleura* (ANSP 3445), scale bar = 3 mm. Left pls large, ac shape 3, pc shape 3. H, *Fragum fragum* (ANSP 288688), scale bar = 10 mm. Left pls large, ac shape 3, pc shape 3. I, *Ctenocardia symbolica* (ANSP 229980), scale bar = 5 mm (Fig. 22), = 2 mm (Fig. 23). Left pls moderate, ac shape 3, pc shape 3. J, *Americardia media* (ANSP 54280), scale bar = 10 mm (Fig. 22), = 5 mm (Fig. 23). Left pls moderate, ac shape 3, pc shape 3. K, *Corculum cardissa* (ANSP 231526), scale bar = 10 mm. Left pls absent, ac shape 4, pc shape 5. L, *Cerastoderma edule* (FMNH 278010), scale bar = 17 mm. Left pls moderate, ac shape 3, pc shape 1. M, *Hypanis* (*Monodacna*) *colorata* (ANSP 338065), scale bar = 10 mm. No posterior laterals (left pls coded as missing, "?"), ac shape 3, pc shape 1. N, *Goethemia elegantula* (SMNH 883), scale bar = 1 mm. Left pls absent, ac shape 3, pc shape 1. O, *Avicularium aviculare* (ANSP 6279), scale bar = 10 mm. Left pls small, ac missing (coded "?"), pc shape 2. P, *Byssocardium emarginatum* (IRSNB I. G. 10591), scale bar = 13 mm. Left pls small, ac missing, pc shape 2. Q, *Tridacna* (*Chametrachea*) *maxima* (ANSP 252683), scale bar = 90 mm. Left pls absent, ac missing, pc shape 2.

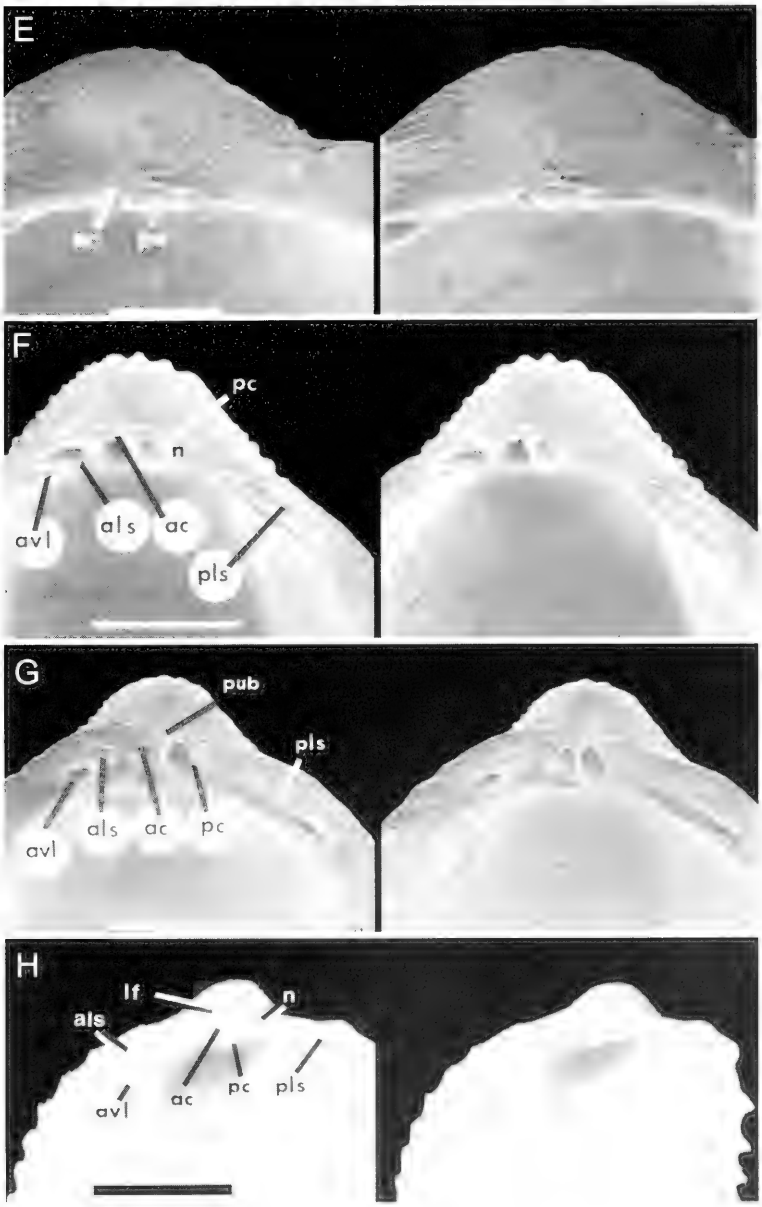


FIG. 22. Continued.

spring from the umbonal cavity rather than from a hinge plate . . ."

45. Right anterior ventral lateral tooth: (0) does not insert into anterior lateral socket, (1) inserts into anterior lateral socket.

46. Left anterior lateral (al) (0) not horizontal, (1) horizontal.

47. Left anterior lateral socket (als): (0) absent or small, (1) large.

48. Left posterior lateral socket (pls): (0) absent or small, (1) moderate, (2) large.

49. Right anterior cardinal (ac) shape: states 0 to 4.

50. Right posterior cardinal socket angle:

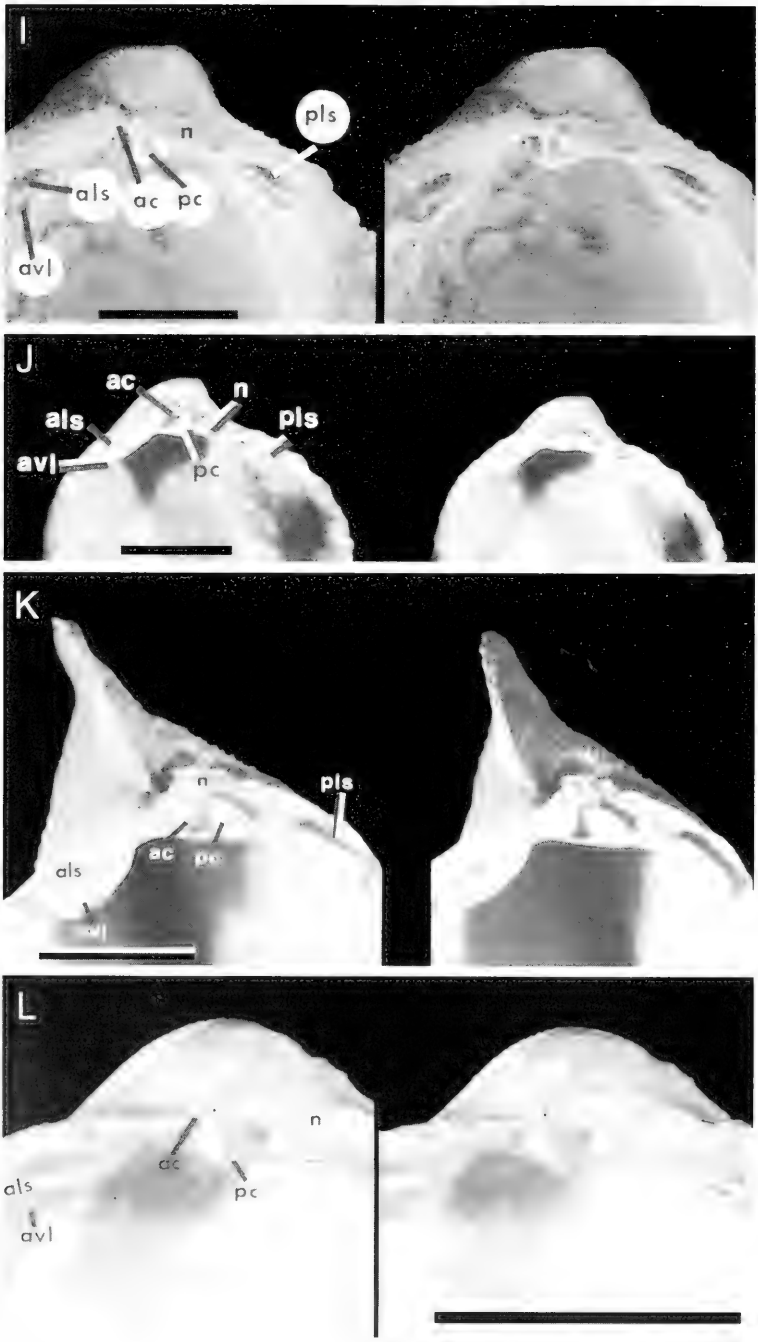
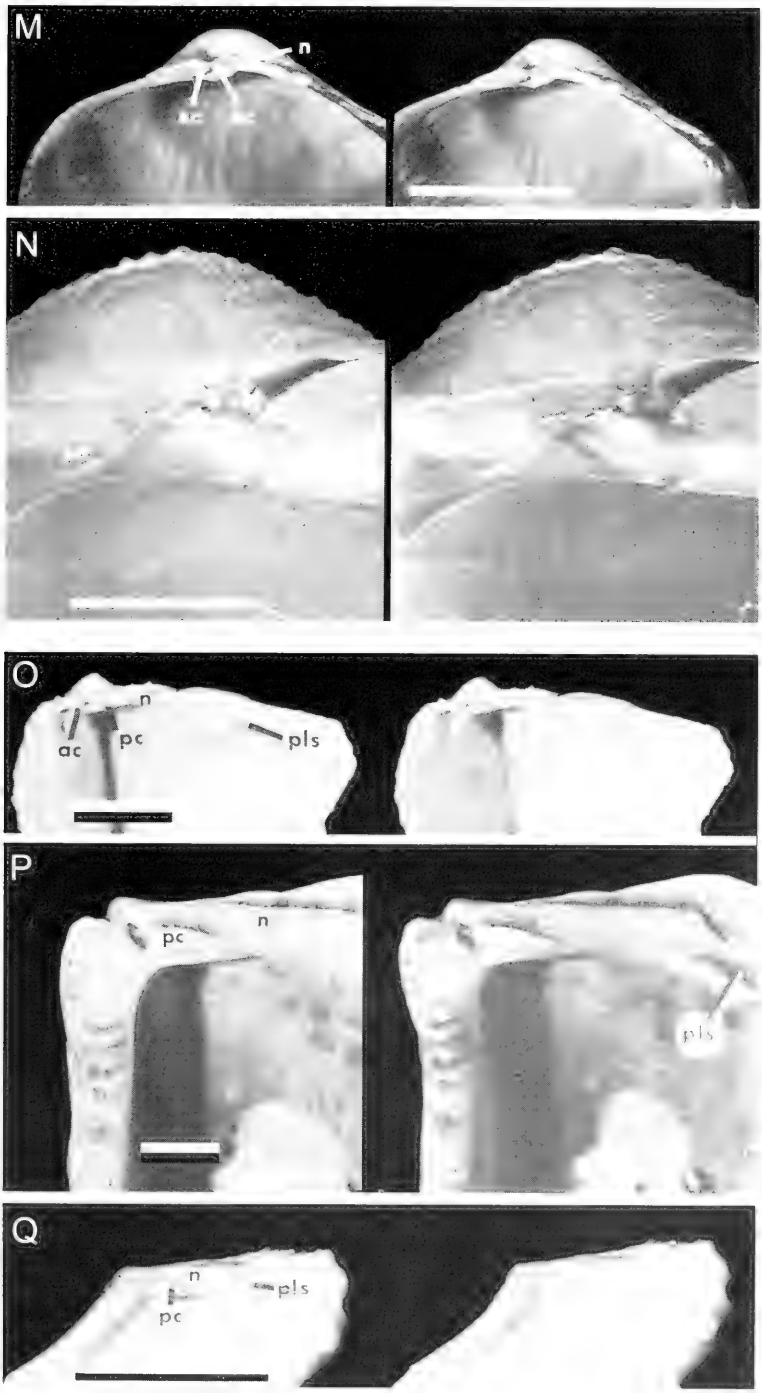


FIG. 22. Continued.



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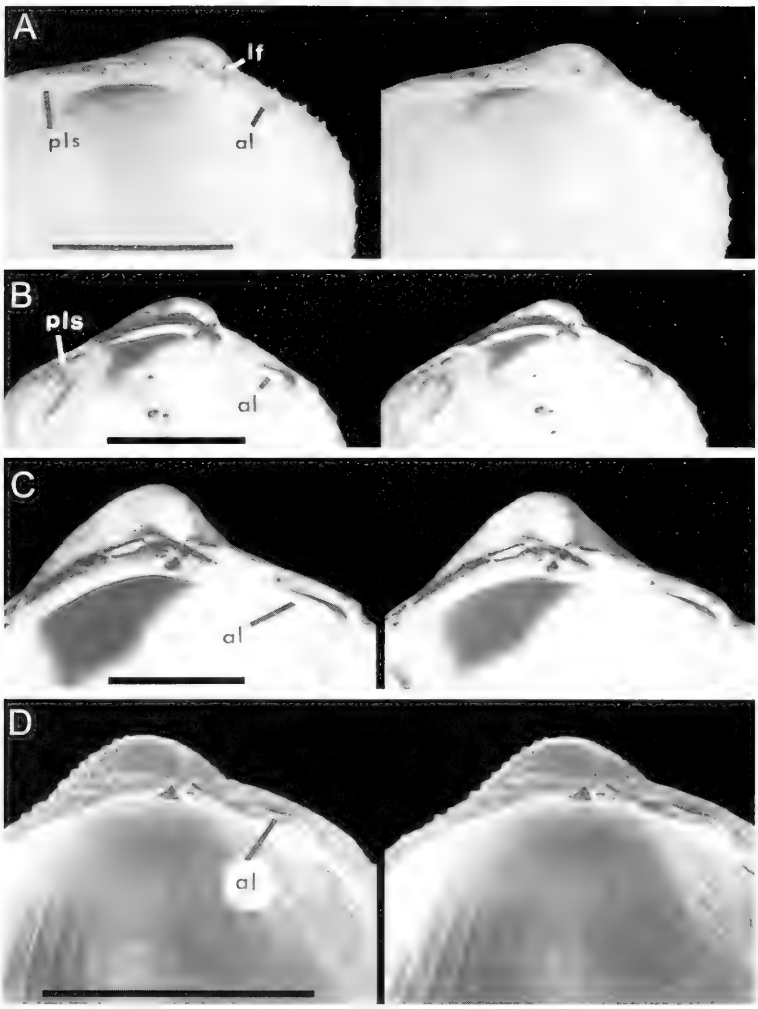

FIG. 23. Left hinges, stereo pairs. For explanation, see caption to Figure 22.

(0) high (>40° from horizontal), (1) low (<40 from horizontal).

51. Right posterior cardinal (pc) shape: states 0 to 5

RESULTS

PAUP 3.1.1 found 28 most parsimonious trees of length 162 steps (CI = 0.605, RI = 0.805). The majority-rule consensus tree is presented in Figure 33. Syanapomorphies for internal nodes of tree number 15 are presented in Figure 34 and Table 2. A suggested taxonomy of the ingroup is presented in Table 3. The taxonomies of Keen (1969a, b, 1980) and Popov (1977; Kafanov & Popov, 1977) are presented in Appendices 4 and 5.

The ingroup has a topology of (*Plagiocardium* (*Maoricardium* + and all other taxa)). *Plagiocardium* was found to be a member of the Fraginae by Kafanov & Popov (1977) and Schneider (1992). Clinocardiinae contains the same taxa included in the group by Kafanov (1980). Kafanov considered *Fuscocardium* a subgenus of *Clinocardium,* and the genus *Keenocardium* the closest relative of these two taxa. Along with *Ciliatocardium,* Kafanov

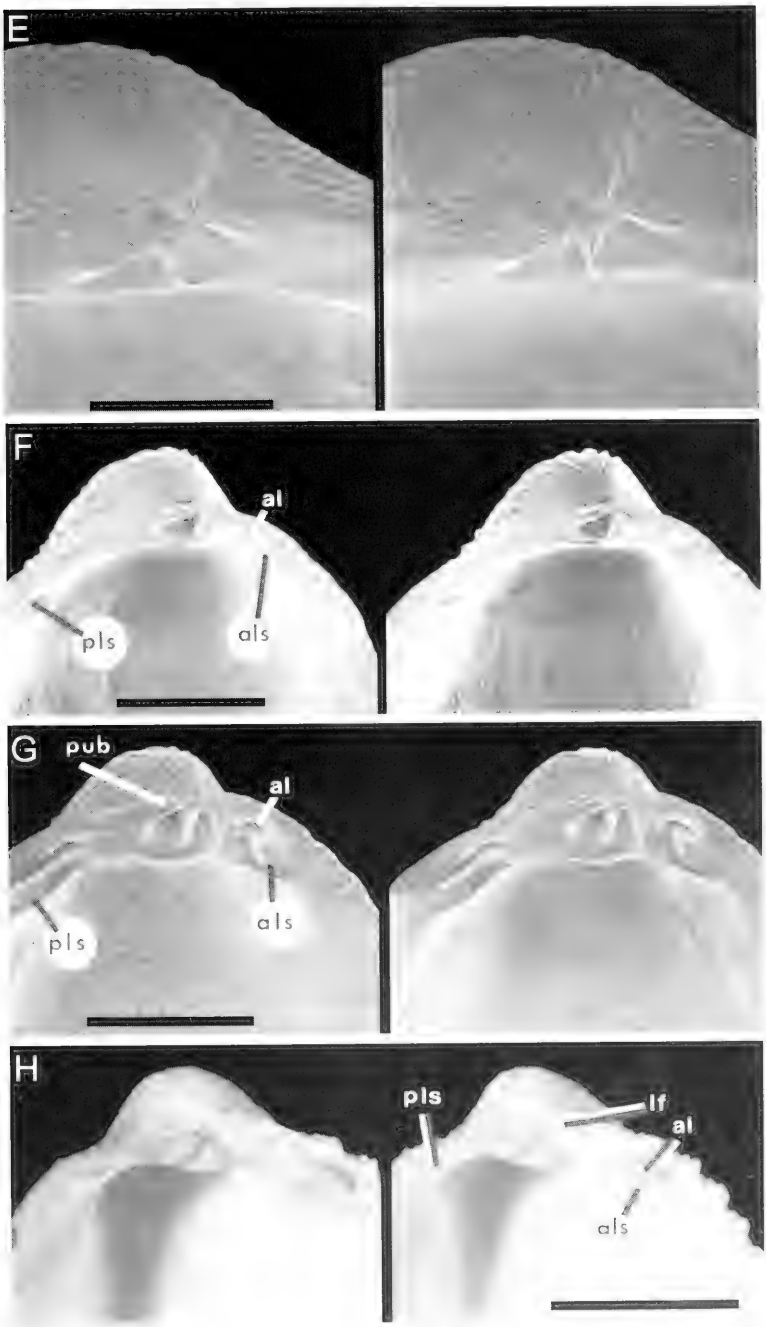

FIG. 23. Continued.

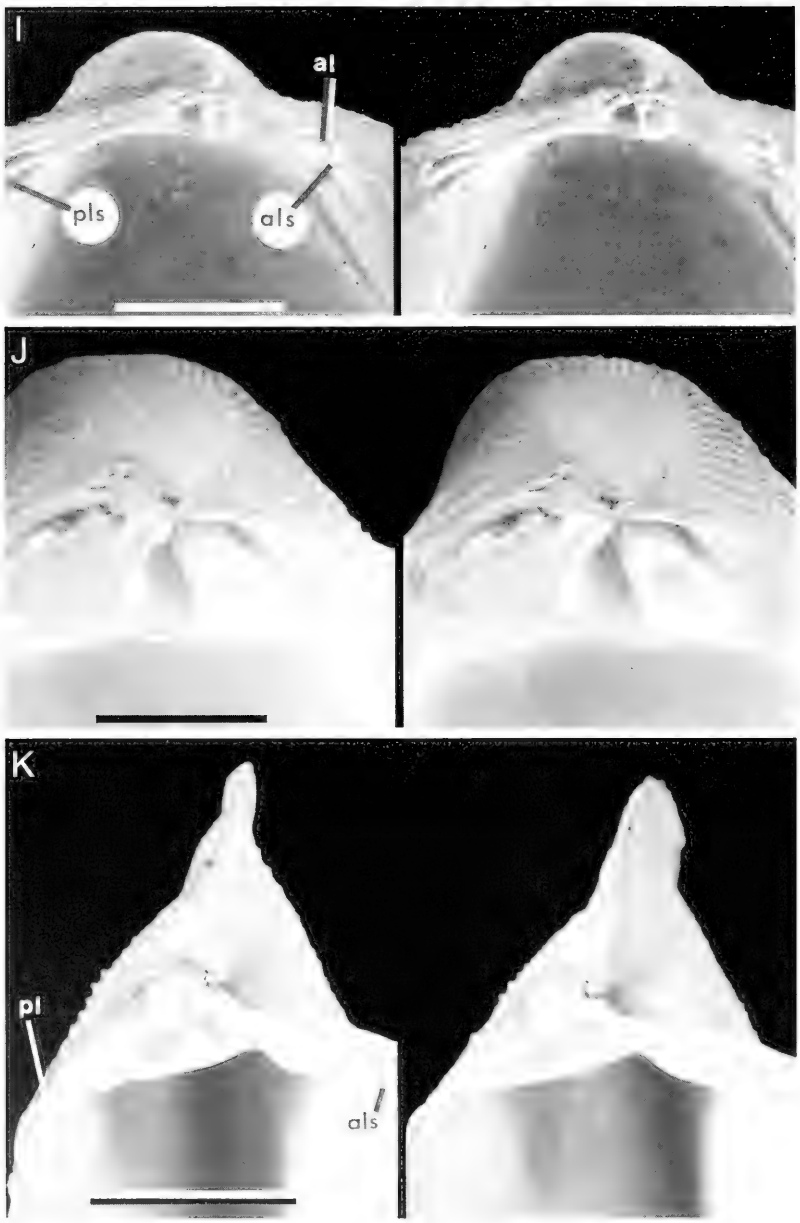

FIG. 23. Continued.

placed these taxa in the tribe Clinocardiini. In the present analysis, *Ciliatocardium* is most closely related to *Profulvia,* the only genus that Kafanov (1980) placed in the tribe Profulviini. Kafanov (1980) placed *Serripes* and *Yagudinella* in the tribe Serripedini.

Goethemia is the sister group to Lymnocardiinae + Tridacninae, and these three taxa together are the sister group to Fraginae. Lymnocardiinae *sensu* Kafanov & Popov (1977) (i.e., including *Cerastoderma*), Tridacninae, and Fraginae are monophyletic groups. Cerastodermatiinae *sensu* Nordsieck (1969) and Voskuil & Onverwagt (1989) would be a para-

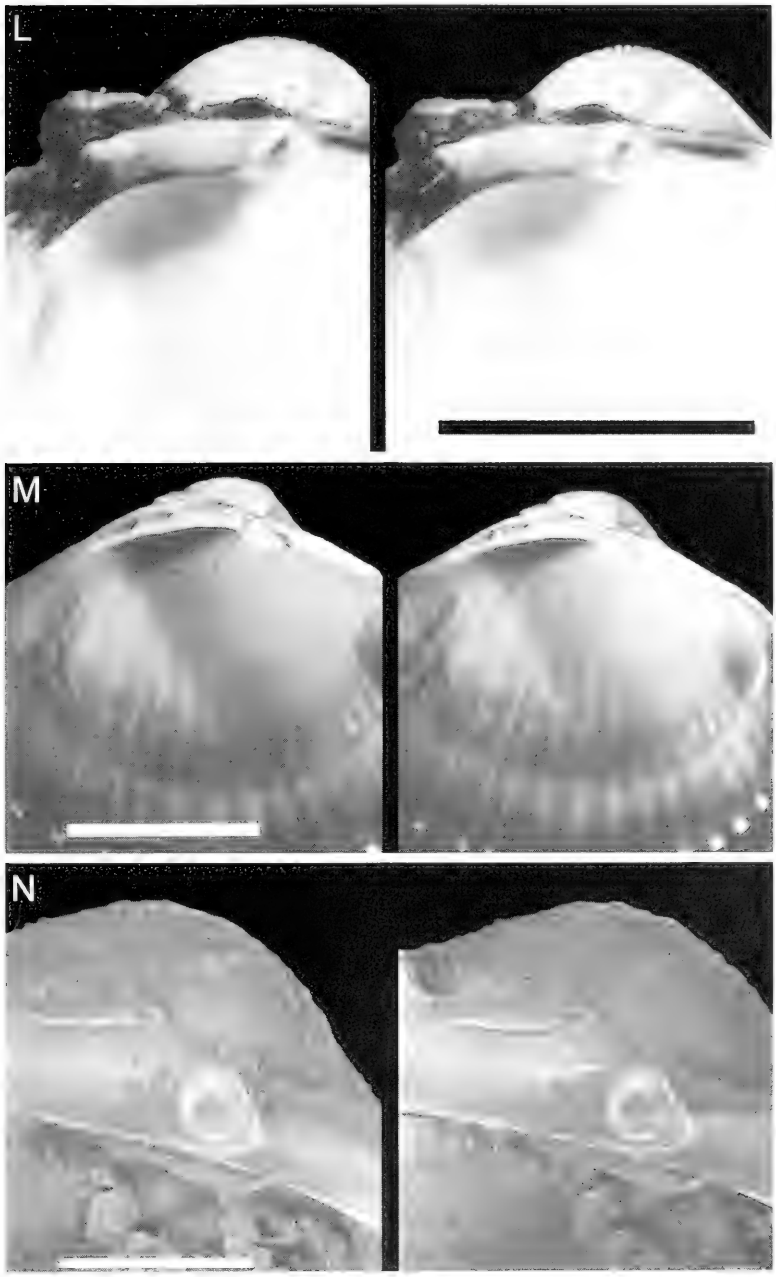

FIG. 23. Continued.

phyletic group, specifically a grade containing basal fragines (*Parvicardium, Papillicardium,* and *Cerastobyssum*), the sister taxon to Lymnocardiinae + Tridacninae (*Goethemia*), and a basal lymnocardiine (*Cerastoderma*).

Papillicardium is the sister taxon to the remaining fragines. *Papillicardium* should be considered a genus as opposed to a subgenus of *Parvicardium.*

All the most parsimonious trees support a

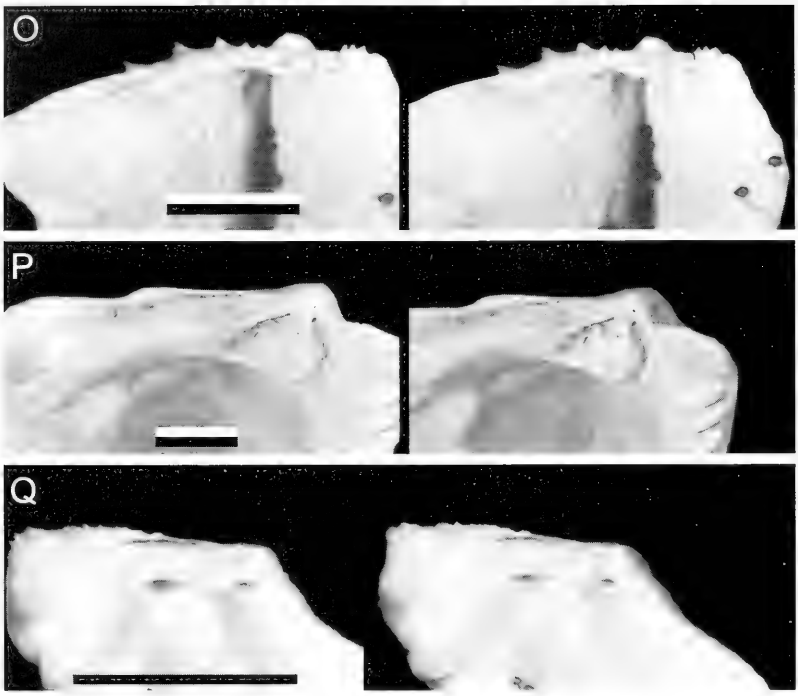

FIG. 23. Continued.

monophyletic group of *Trigoniocardia, Apiocardia,* and *Goniacardia* (the "*Trigoniocardia*-group"). *Apiocardia* and *Goniacardia* are considered subgenera of *Trigoniocardia* by Olsson (1961), Keen (1969a, 1980), Woodring (1982), and Vokes (1989).

All the trees support a clade of (*Microfragum* + (*Ctenocardia* + *Americardia*)), which can informally be referred to as the *Ctenocardia*-group. *Microfragum,* erected as a genus by Habe (1951), was considered a subgenus of *Ctenocardia* by Keen (1969a, 1980). On the basis of the hinge, Wilson & Stevenson (1977) considered *Microfragum* a subgenus of *Fragum. Americardia* was erected as a subgenus of *Trigoniocardia* by Stewart (1930), who was followed by Clench & Smith (1944), Keen (1951, 1969a, 1980), Olsson (1961), Glibert & van de Poel (1970), and Popov (1977). Woodring (1982) and Vokes (1989) raised *Americardia* to genus. Voskuil & Onverwagt (1989) synonomized *Americardia* with *Ctenocardia.*

All most parsimonious trees support a sister taxon relationship of *Lunulicardia* and *Corculum,* which agrees with Popov's (1977) treatment of *Lunulicardia* as a subgenus of *Corculum.* Keen (1969a, 1980) had considered *Lunulicardia* a subgenus of *Fragum.* In the present analysis, *Fragum* is one branch of a trichotomy with the *Ctenocardia*-group and *Lunulicardia* + *Corculum.*

DISCUSSION

Plagiocardium and *Maoricardium*

Plagiocardium and *Maoricardium* display several features that seem to be intermediate in morphology between basal eucardiids (subfamilies Profraginae, Trachycardiinae and Cardiinae; see Schneider [1993a, 1995] for a definition of eucardiids) and the more derived eucardiids (the remainder of the ingroup). *Cardium ciliatum* Fabricius, 1780, the type species of *Ciliatocardium,* was named for the presence of periostracal cilia (27:1). Since Reeve (1844), periostracal cilia have been known from what are now considered the Recent species of *Maoricardium.* To my knowledge, the possibility that the periostracal cilia

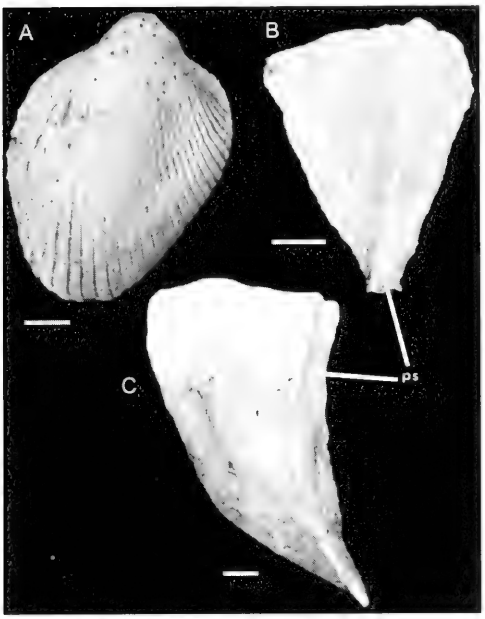

FIG. 24. External views of right valves of extinct tridacnines. A, *Goniocardium rachitis* (ANSP 12429). B, *Avicularium aviculare* (ANSP 6279). C, *Byssocardium emarginatum* (IRSNB I. G. 10591). Scale bars = 5 mm. All have trigonal shell shape, which is considered derived from trigonal shell shape (see shell shape key in Schneider, 1998).

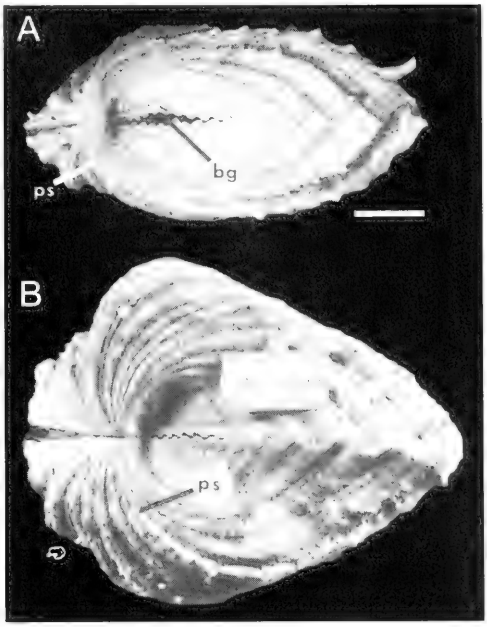

FIG. 25. *Hippopus hippopus*. A, juvenile (USNM 63793) with byssal gape, scale bar = 10 mm. B, adult (USNM 621313) with no byssal gape, scale indicated in figure.

of these two taxa are homologous has not previously been suggested. Clinocardiines have the same shape right posterior cardinal (51:1) as *Plagiocardium* and *Maoricardium*. The basal clinocardiines, *Ciliatocardium* and *Profulvia,* have the same shape right anterior cardinal (49:1) as *Plagiocardium* and *Maoricardium*. Kafanov & Popov (1977) were uncertain of how the subfamily Clinocardiinae was related to other cardiids. Kafanov & Savitskiy (1982) suggested that clinocardiines were derived from trachycardiines, for the earliest member of the subfamily (*Ciliatocardium asagaiense* [Makiyama, 1934], Early Oligocene of Sakhalin and Japan) has rudimentary ornament on the radial ribs. However, *Plagiocardium* and *Maoricardium* also have ornament on the radial ribs.

According to the results, the characters shared by *Plagiocardium* and *Maoricardium* on one hand, and Clinocardiinae on the other, are either symplesiomorphic (shape of cardinal teeth, shell shape) or homoplastic (periostracal cilia). Postulating that the periostracal cilia of *Maoricardium* and clinocardiines are homologous (i.e., symplesiomorphic, having been derived only once and subsequently lost twice) would add one step to the most parsimonious trees.

The ornamental microstructure of basal eucardiids is simple knobs, comprised of branching crossed lamellae grading into fibrous prisms, in microstructural continuity with the rest of the shell (Schneider, 1998). The ornamental microstructure of members of the subfamily Fraginae consists of poorly organized fibrous prisms that are microstructurally discontinuous with the shell (Fig. 18). In *Plagiocardium* and *Maoricardium,* the core of a spine is the poorly organized fibrous prisms that are microstructurally discontinuous with the shell (Fig. 21). However, the outer portion of the spine is somewhat more organized fibrous prisms, which are not microstructurally discontinuous with the branching crossed lamellae of the shell. This microstructure appears to be that of simple spines (Schneider, 1998: fig. 9). According to the results of the cladistic analysis, *Plagiocardium, Maoricardium* and Fraginae independently evolve this discontinuity. Postulating that this shell-spine discontinuity is homologous between *Plagiocardium* + *Maori-*

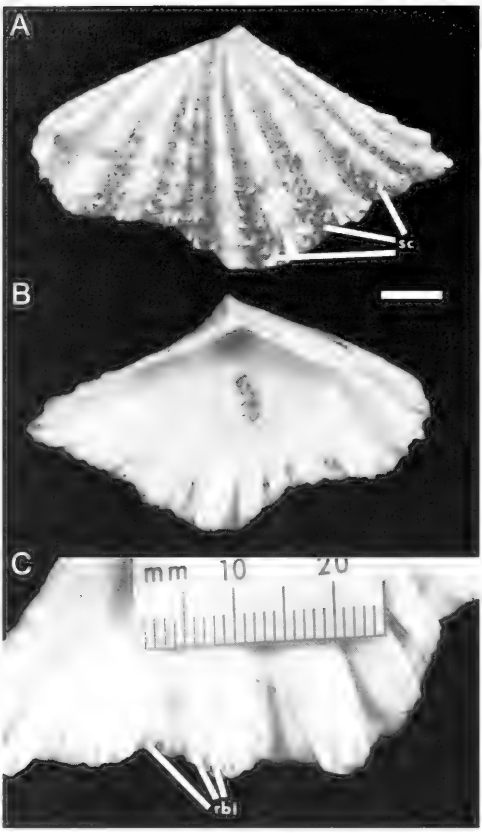

FIG. 26. *Hippopus hippopus*. A-C, juvenile (USNM 63793), right valve. A, external. Note scutes on "riblets". B, internal. Scale = 10 mm. Note expression of "riblets" at ventral margin. C, detail of B, scale indicated in figure.

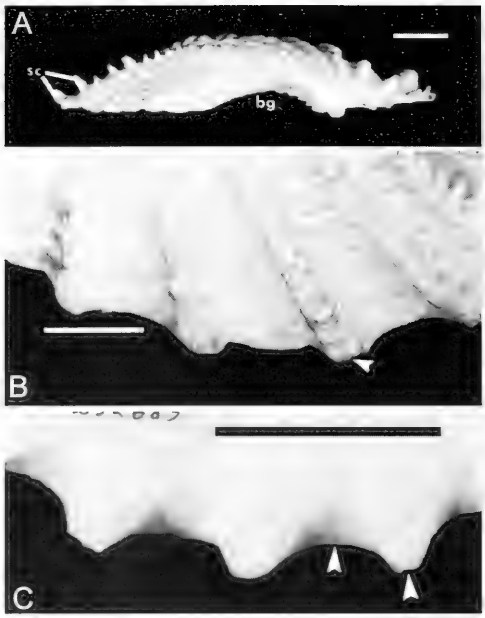

FIG. 27. *Tridacna* (*Chametrachea*) *maxima*. A-C, juvenile (ANSP 252683), right valve. A. View of byssal gape. B. Ventral margin. Note scutes and expression of "riblets" (indicated by arrow) at ventral margin. C. Internal view of ventral margin. Note expression of "riblets", indicated by arrows. Scale bars = 10 mm.

cardium on one hand, and Fraginae on the other, would add one step to the most parsimonious trees.

Given the foregoing, the phylogenetic relationships of *Plagiocardium* and *Maoricardium* are uncertain, and the naming of new subfamilies is strongly discouraged at this time. It is altogether possible that *Plagiocardium* and/or *Maoricardium* are paraphyletic, and species assigned to these taxa in the literature are actually basal members of other subfamilies.

Morphological Evolution of Clinocardiinae

Much of the morphological evolution of the Clinocardiinae involves modification of the foot, its musculature, and the attachment of these muscles to the shell. These characters are (1) ventral papillae on the foot (8:1), (2) the strength of the dorsoumbonal muscle scar (39:1), which is the attachment site of the pedal elevator muscle (Pelseneer, 1911; Cox, 1969), and (3) the degree of umbonal prosogyry (29:1). Increase in prosogyry results in an increase of the length of the pedal elevator muscles. These characters are independent since they do not have the same distribution among clinocardiines. Ventral papillae are present on all clinocardiines. Kafanov (1980) stated that papillae are absent on *Keenocardium*. However, I have detected microscopic appendages on *Keenocardium*. *Trigoniocardia* + *Apiocardia* + *Goniacardia* independently derives ventral papillae. The dorsoumbonal muscle scar is weak in the primtive clinocardiine *Ciliatocardium* (state unknown in its sister taxon *Profulvia*).

Systematics and Evolution of Giant Clams (Tridacninae)

The giant clams form a monophyletic group within the family Cardiidae and therefore

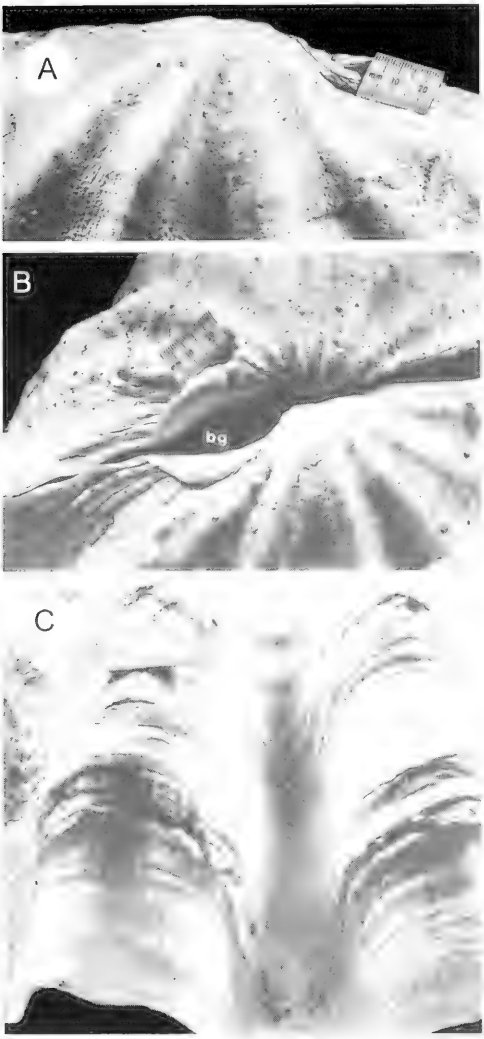

FIG. 28. *Tridacna gigas*. A-C, adult (USNM 602502). A, umbo of right valve. Note "riblets", manifested as radial striations running from the umbo towards the ventral margin. B, detail of narrow byssal gape. C, ventral margin of right valve. Note faint expression of "riblets". Scales indicated in figure.

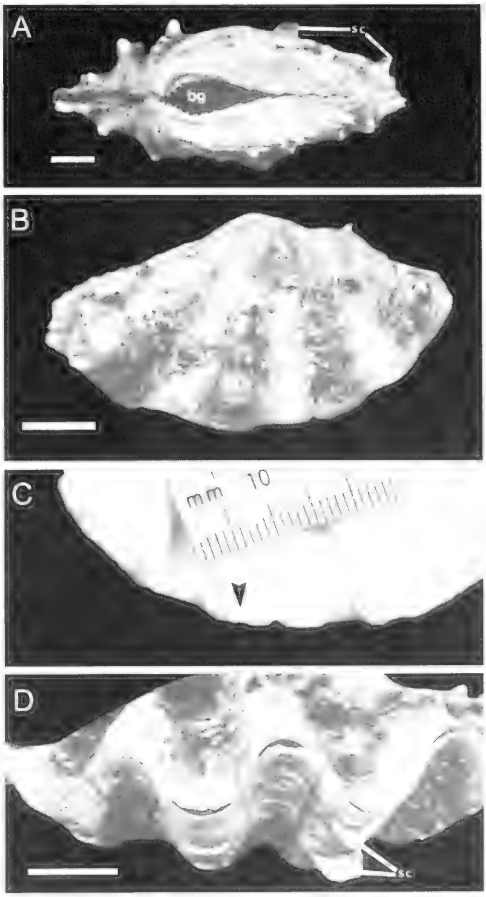

FIG. 29. *Tridacna gigas*. A-D, juvenile (USNM 686575). A, view of large byssal gape (compare with Fig. 31B) and scutes. B, external view of right valve. C. Internal view of ventral margin (same specimen as in B). Note expression of "riblets" as crenulations at margin, indicated by arrow. D. Commissure. Note scutes and "riblets". A, B, D, scale bar = 10 mm; C, scale indicated in figure.

should be considered a subfamily (Tridacninae) of Cardiidae. Keeping the giant clams as a separate family (Fischer, 1887; Ridewood, 1903; Zittel, 1927; Thiele, 1934; Yonge, 1936, 1953a, b, 1981, 1982), or even superfamily (Kafanov & Popov, 1977; Scarlato & Starobogatov, 1979; Purchon, 1987a, b; Keen, 1969b; and *The Zoological Record*) makes the Cardiidae a paraphyletic group. Lamarck (1809) was the first to recognize a close relationship between cardiids and giant clams. Noting the similarities of the hinge, Yonge (1936) thought that the giant clams were derived from a *Cerastoderma*-like form. The results of the cladistic analysis indicate a sister taxa relationship between Tridacninae and Lymnocardiinae. Because *Cerastoderma* is the least derived lymnocardiine, Yonge's view is upheld.

Much of the evolutionary history of giant clams had been understood by the middle of the twentieth century. A step backwards in our

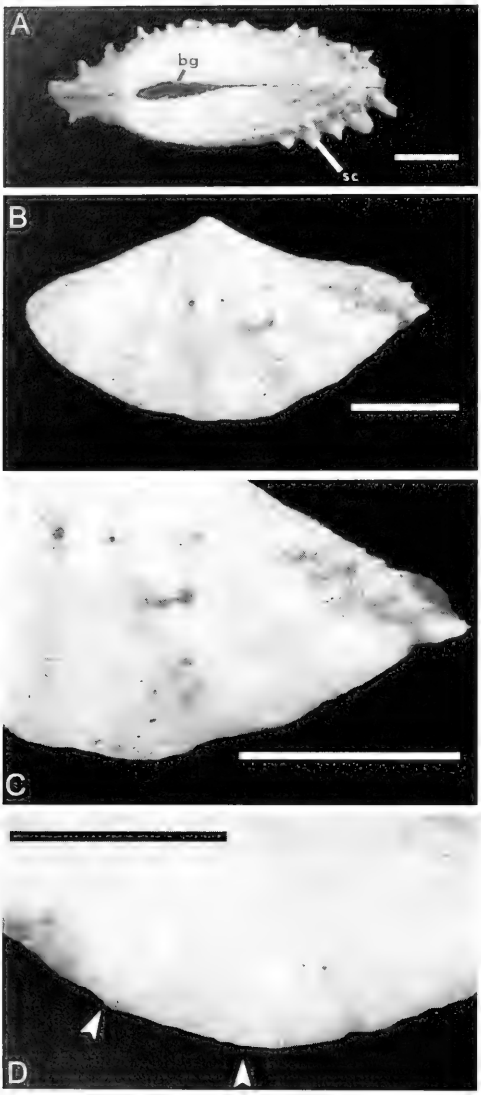

FIG. 30. *Tridacna (Persikima) derasa.* A-D, juvenile (USNM 845538). A, view of byssal gape; note prominent scutes. B, C, external view of right valve. Note weak expression of "riblets" on shell exterior. D, Internal view of ventral margin (same specimen as in B and C). Note weak expression of "riblets" as crenulations along interior ventral margin, indicated by arrows. Scale bars = 10 mm.

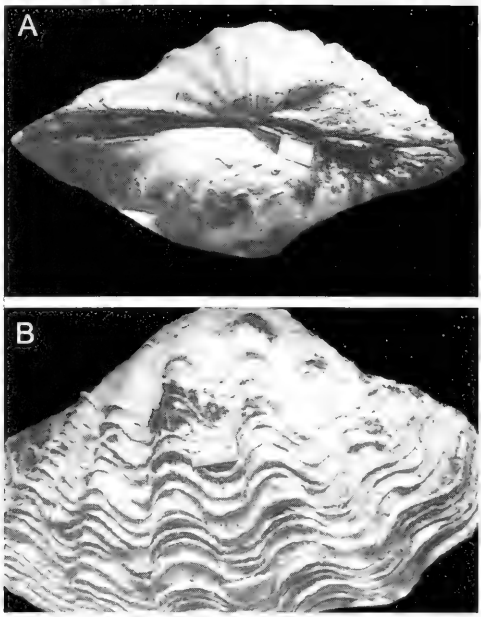

FIG. 31. *Tridacna derasa.* Adult (USNM 654256), A, B, scales indicated in figures. A, dorsal view. Note absence of byssal gape. B, external view of right valve. Note that "riblets" are not detectable on A and B.

understanding of giant clam evolution was taken when a presumably Miocene *Chametrachea* was described as coming from Cretaceous sediments. Collignon (1949) described *Tridacna besairiei* from the Maastrichtian of Madagascar. Collignon received the fossil in a box of specimens from H. Besairie. The other fossils in the box were from the Maastrichtian (later redescribed as Danian [Collignon, 1968]) zone G à *Tripylus* de Antonibe, Madagascar, and the box was labeled accordingly. Collignon (1949) took Besairie's word that *T. besairiei* was from Antonibe and noted that the nearest Miocene sediments were 150 kilometers from Antonibe. The distance from Antonibe to Miocene outcrops is irrelevant, for Besairie collected specimens from all over Madagascar, and specimens from different localities and strata may have been accidentally mixed. There is no evidence that *T. besairiei* comes from Danian sediments. Unfortunately, subsequent authors (Stasek, 1962; Rosewater, 1965; Keen, 1969b; Sepkoski, 1992) gave at least some creedence to Collignon's (1949, 1968) claim of a Maastrichtian/Danian *Tridacna.* Acceptance of a moderately derived *Tridacna* approximately 15 million years older than the more primitive forms *Goniocardium, Avicularium,* and *Byssocardium* obfuscated the actual tempo and mode of tridacnine evolution, and the correspondence between the

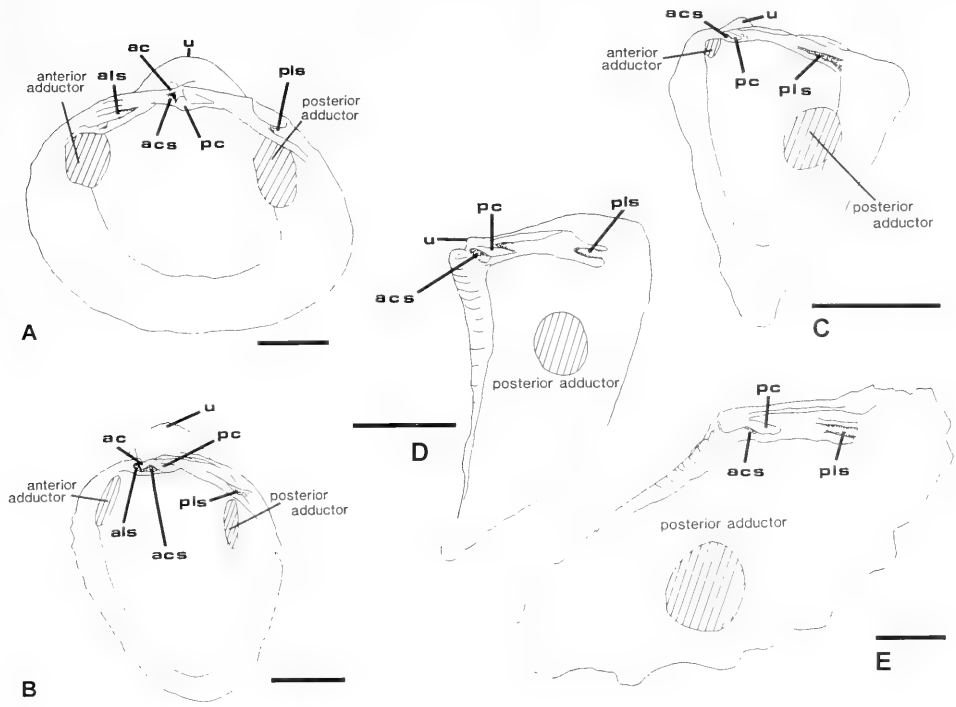

FIG. 32. Camera lucida drawings of interior of right valves of *Cerastoderma edule* and several tridacnines, to show morphology of hinge and adductor muscle scars. A, *Cerastoderma edule* (FMNH 278010). B, *Goniocardium rachitis* (ANSP 12429). C, *Avicularium aviculare* (ANSP 6279). D, *Byssocardium emarginatum* (IRSNB I. G. 10591). E, *Tridacna* (*Chametrachea*) *maxima* (ANSP 252683). A–C, E, scale bars = 10 mm; D, scale bar = 15 mm.

actual fossil record and morphological evolution has not been appreciated.

The three most basal giant clams are the extinct taxa *Goniocardium* Vasseur, 1880, *Avicularium* Gray, 1853 (= *Lithocardium* Woodward, 1854), and *Byssocardium* Munier-Chalmas, 1882. All three taxa originated in the Middle Eocene (Keen, 1969b). These taxa were erected as genera of Cardiidae (note the generic names) and comprised species that had been described under *Cardium* (Lamarck, 1819; Deshayes, 1829; Bronn, 1831; Michelotti, 1861), not *Tridacna.* However, many workers recognized that the species of *Avicularium* and *Byssocardium* were either allied to the tridacnine *Hippopus* (Sowerby, 1823; Gray, 1853) or transitional from cardiids to giant clams (Tournauer, 1882; Fischer, 1887; Grobben, 1898; Anthony, 1904, 1920; Thiele, 1934; Yonge, 1936; Dechaseaux, 1952). Deshayes (1829) criticized Sowerby for suggesting that *Cardium avicularium* (Lamarck, 1805) was related to *Hippopus* on the basis of the position of the muscle scars. Deshayes called the similarity of the muscle scars between these two taxa an "analogie trompeuse" ("false analogy"). Grobben (1898) was the first to recognize an (*Avicularium* (*Byssocardium* (Recent tridacnines))) pattern of relationships and to discuss the morphological evolution of the adductor muscle scars and byssal gape. Cossmann (1886, 1905, 1921; Cossmann & Pissarro, 1904) considered *Avicularium* and *Byssocardium* to be cardiids. Keen (1937) transferred *Avicularium* and *Byssocardium* to Tridacnidae.

The relationship of the species of *Goniocardium* to giant clams took longer to be recognized. The species of *Goniocardium* were considered cardiids by Deshayes (1829), Vasseur (1881), and Cossmann (1886, 1905, 1921; Cossmann & Pissarro, 1904). Cossmann (1886) and Koenen (1893) placed species of *Goniocardium* in *Fragum.* (The Early Oligocene species *Cardium* (*Fragum*) *reniforme* Koenen, 1893, is a *Goniocardium;* this is the first atribution of an Oligocene species to *Goniocardium.*) Dall (1903) was

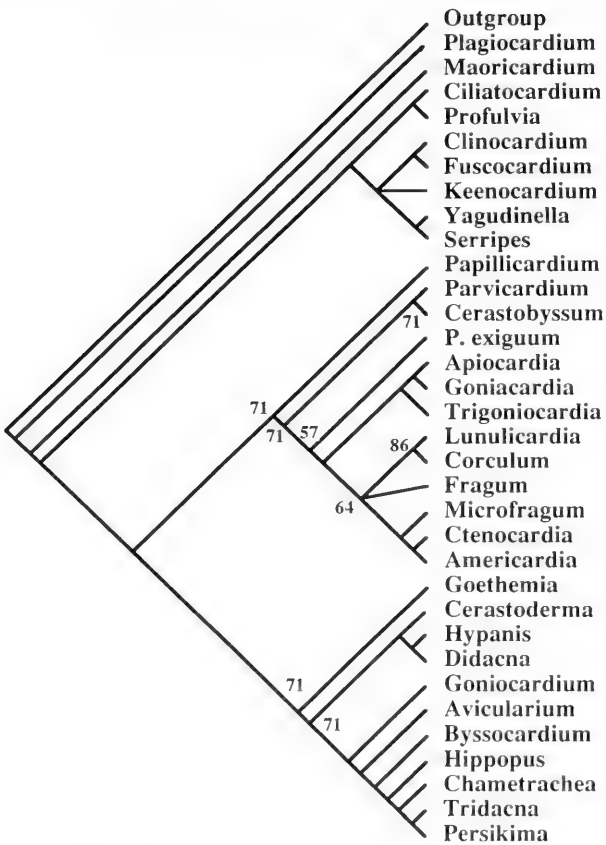

FIG. 33. Majority-rule tree of 28 most parsimonious trees. Numbers indicate percentage of trees which support that node. Unnumbered nodes supported by all 28 trees.

the first to suggest that *Goniocardium* was related to *Avicularium* and *Byssocardium,* but put all three taxa in Cardiidae. Dall did not discuss the possibility that these forms were related to tridacnids. Keen (1937) was unsure of the affinities of *Goniocardium,* suggesting a relationship to the lymnocardiine *Prosodacna.* Stasek (1962) was the first worker to realize that *Goniocardium* was morphologically intermediate between cardiids and the basal giant clams *Avicularium* and *Byssocardium.* Rosewater (1965) and Keen (1969b) followed Stasek (1962) and transferred *Goniocardium* to Tridacnidae.

In general, *Cerastoderma* has the typical cardiid hinge and muscle scar arrangement (Fig. 32A). The right valve has both anterior and posterior lateral teeth, and anterior and posterior lateral sockets. There are both anterior and posterior cardinal teeth, with anterior and posterior cardinal sockets. *Goniocardium*'s shell shape (Figs. 24A, 32B) is not unlike that of a typical cockle. However, the anterior part of the hinge is almost entirely lost. A small knob is all that remains of the anterior laterals (*contra* Keen, 1969b), and the anterior lateral socket is continuous with the anterior cardinal socket. The anterior adductor muscle is positioned more anteriorly, closer to the margin of the shell and the posterior adductor muscle is positioned slightly more forward than in *Cerastoderma. Avicularium* (Fig. 32C; Yonge, 1953b, 1981) loses the remnants of the anterior laterals and anterior lateral socket. The posterior adductor scar is enlarged and is more centrally located than in *Goniocardium.* Also, the anterior adductor scar is smaller and more anteriorly located than in *Goniocardium.* In *Byssocardium,* the anterior cardinal tooth is lost, as is the anterior adductor (Fig. 32D). The posterior adductor is larger than in *Avicularium,* and it is centrally

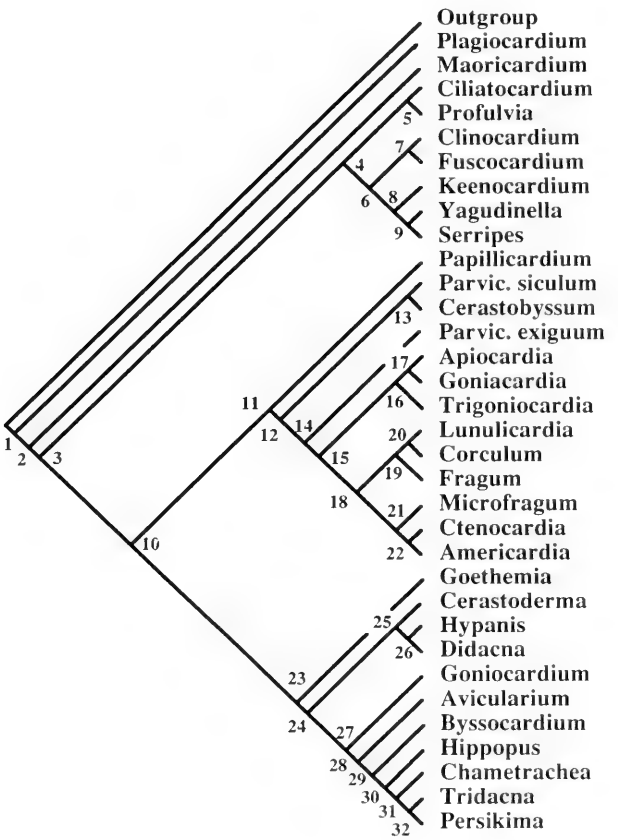

FIG. 34. Tree number 15 (of 28). Synapomorphies for each numbered node indicated in Table 2.

TABLE 3. Shell shape character states detected during ontogeny of species considered in the present analysis. Shell shapes are listed in order of ontogenetic appearance.

Schedocardia hatchetigbeense: circular, schediform (Schneider, 1998).
Plagiocardium granulosum: circular, oval (Schneider, 1998)
Maoricardium pseudolatum: circular, oval, unnamed autapomorphic state
Ciliatocardium ciliatum, Clinocardium nuttallii, Clinocardium (*Fuscocardium*) *braunsi, Clinocardium* (*Keenocardium*) *blandum, Yagudinella notabile, Serripes groenlandicus, Papillicardium papillosum:* circular, oval
Profulvia harrimani: circular, oval, unnamed autapomorphic state
Parvicardium (*Parvicardium*) *siculum, P.* (*P.*) *exiguum, P.* (*Cerastobyssum*) *hauniense, Trigoniocardia* (*Trigoniocardia*) *antillarum, T.* (*Apiocardia*) *obovale, T.* (*Goniacardia*) *callopleura, Goniocardium rachitis:* oval, trigonal
Lunulicardia retusa, Corculum cardissa, Fragum fragum, Avicularium aviculare, Byssocardium emarginatum: trigonal
Microfragum festivum, Ctenocardia (*Ctenocardia*) *symbolica, C.* (*Americardia*) *media:* trigonal, quadrate-short
Goethemia elegantula, Cerastoderma edule: oval, cerastiform
Monodacna (*Hypanis*) *colorata:* oval, cerastiform, hypaniform
Hippopus hippopus, Tridacna (*Chametrachea*) *maxima, Tridacna* (*Tridacna*) *gigas, Tridacna* (*Persikima*) *derasa:* trigonal, unnamed terminal autapomorphy

TABLE 4. Suggested taxonomy of the taxa *Plagiocardium, Maoricardium,* Clinocardiinae, Fraginae, *Goethemia,* Lymnocardiinae, and Tridacninae, based on the present phylogenetic analysis. Stratigraphic ranges from J. J. Sepkoski Jr.'s unpublished compendium of stratigraphic ranges of marine invertebrates, except where indicated. Abbreviations of stratigraphic units from Harland et al. (1990).

Family Cardiidae	Stratigraphic Range
No subfamilial designation	
Plagiocardium	Dan-Mio
Maoricardium	Cht-Hol
Goethemia	Ple-Hol (herein)
Subfamily Clinocardiinae	
Clinocardium	
(*Clinocardium*)	Cht-Hol
(*Fuscocardium*)	Srv-Ple (Kafanov, 1980)
(*Keenocardium*)	Cht-Hol
Ciliatocardium	Rup-Hol
Profulvia	Oli-Ple (Keen, 1980; Kafanov, 1980; Akamatsu & Suzuki, 1990)
Serripes	Rup-Hol
Yagudinella	Srv-Hol (Kafanov, 1980)
Subfamily Fraginae	
Papillicardium	Eoc-Hol
Parvicardium	
(*Parvicardium*)	Ypr-Hol
(*Cerastobyssum*)	Hol (herein)
Trigoniocardia	
(*Trigoniocardia*)	Cht-Hol
(*Apiocardia*)	Pli-Hol
(*Goniacardia*)	Mio-Zan (herein)
Corculum	Pia-Hol (Paulay, 1996)
Lunulicardia	Ple-Hol
Fragum	Mio-Hol (Keen, 1980)
Ctenocardia	
(*Ctenocardia*)	Mio-Hol
(*Americardia*)	Mio-Hol (Keen, 1980)
(*Microfragum*)	Ple-Hol (herein)
Subfamily Lymnocardiinae	
Cerastoderma	Rup-Hol (Keen, 1980)
Hypanis (*Monodacna*)	Zan-Hol (Keen, 1969a)
Didacna (*Didacna*)	Hol (Keen, 1969a)
Subfamily Tridacninae	
Tridacna	
(*Tridacna*)	Aqu-Hol (Rosewater, 1965; Keen, 1969b)
(*Chametrachea*)	Tor-Hol (Rosewater, 1965)
(*Persikima*)	U. Mio.-Hol (Beets, 1986)
Avicularium	Lut-Rup
Byssocardium	Lut-Bur
Goniocardium	Lut-Rup (herein)
Hippopus	Aqu-Hol (Rosewater, 1965)

located. The hinge and arrangement of the muscle scars in Recent giant clams is similar to that of *Byssocardium.*

Early in ontogeny, modern giant clams do have both anterior and posterior adductor muscles and are trigonal in shape (LaBarbera, 1974, 1975; Jameson, 1976; Rosewater, 1981; Fig. 35). Juveniles of *Tridacna* (*Chametrachea*) *maxima* (Röding, 1798) and *T.* (*C.*) *squamosa* Lamarck, 1819, have hinges with anterior lateral and anterior cardinal teeth, which are lost during ontogeny (LaBarbera, 1975). During ontogeny, the anterior adductor muscle becomes smaller and

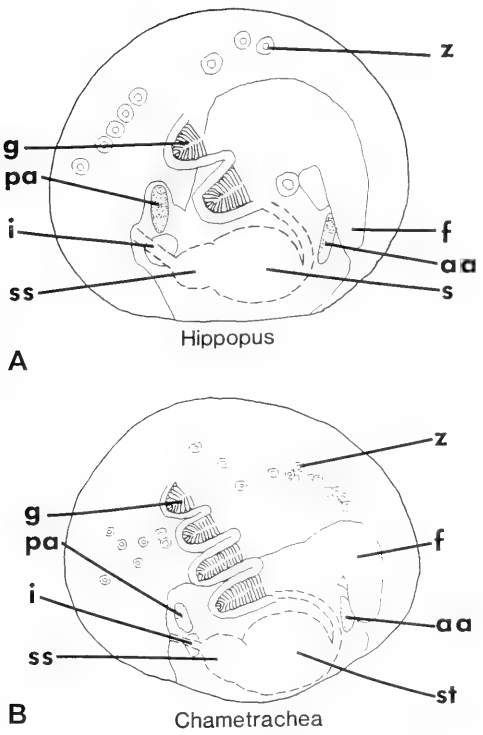

FIG. 35. Tridacnine juveniles. A, 27-day juvenile of *Hippopus hippopus.* Scale bar equals 50 microns. B, 47-day juvenile of *Tridacna* (*Chametrachea*) *maxima.* Scale bar equals 100 microns. From Jameson (1976).

more anterior until it is lost entirely, and the posterior adductor becomes larger and more centrally located. Likewise, through ontogeny, the posterior retractor becomes larger and situated more towards the middle of the shell.

In dimyarian bivalves, including cardiids, length is measured along a line parallel to the line that goes through the midpoint of the adductor muscles (Keen, 1980). Length is measured from the anteriormost point of the shell to the posteriormost shell point along that line (Schneider, 1995, 1998). Because it takes two points to constitute a line, then *Byssocardium* and Recent giant clams have no length. The anterior adductor muscle, along with the rest of the anterior portion of the shell, is absent. Lacking length, at least in the sense homologous to other cardiids, the shells of the giant clams cannot be measured and placed in the shell shape character-state tree (character 31). However, since their juvenile shells do have both adductor muscles, the shape of their juvenile shells can be entered in the shell shape character state tree. Then, as with *Maoricardium* and *Profulvia,* their terminal adult shell shape can be considered as an uncoded autapomorphy. Because extant giant clams lack a length measure, it was decided to code character 1, labial palp length, as missing.

Stasek (1962) reviewed the controversy regarding the ontogeny and morphology of giant clams. Vaillant (1865) proposed the idea that the animal has rotated relative to the mantle and shell and was followed by Dall (1895), Grobben (1898), and Keen (1969b). The concept of rotation was rejected by Lacaze-Duthiers (1902), Anthony (1904, 1920), Pelseneer (1911), and Boutan (1919). Instead, these authors felt that the tridacnid form was a result of differential growth: a tremendous rate of growth of the posterior portions of the animal and shell, and essentially no growth (or even negative growth; i.e., shell resorption) of the anterior portion of the shell. However, Yonge (1936) proposed that in the evolution of giant clams, the shell and mantle had rotated about the animal. Most later studies (Mansour, 1946; Yonge, 1953b, 1981; Purchon, 1955; Rosewater, 1965; Seilacher, 1990; Janssen, 1992; Schneider, 1992) accepted Yonge's thesis. Only Stasek (1962) and LaBarbera (1975) supported the concept of differential growth as responsible for the ontogenetic and evolutionary patterns of giant clams.

From character analysis, ontogeny, and subsequent phylogenetic analysis, it appears that the evolution of giant clam form does not involve rotation, but differential growth. Specifically, giant clams seem to lack almost the entire front half of the shell (the anterior anatomical features, such as the mouth, labial palps, and ctenidia remain essentially the same as in *Cerastoderma;* Yonge, 1953b). In the evolution of giant clams, the posterior part of the shell grew in an increasingly rapid pace relative to the front half of the shell, which essentially stops growing after the settlement of the planktotrophic larva. Stasek (1962) plotted the relative proportions of homologous regions of the mantle/shell of the *Clinocardium nuttallii* (Conrad, 1837) and *Tridacna* (*Chametrachea*) *maxima* (Fig. 36). The anterior shell region is absent on *T. maxima.* Because the Recent giant clams lack the anterior portion of the shell, they are coded as missing (?) for degree of umbonal prosogyry (character 29), for

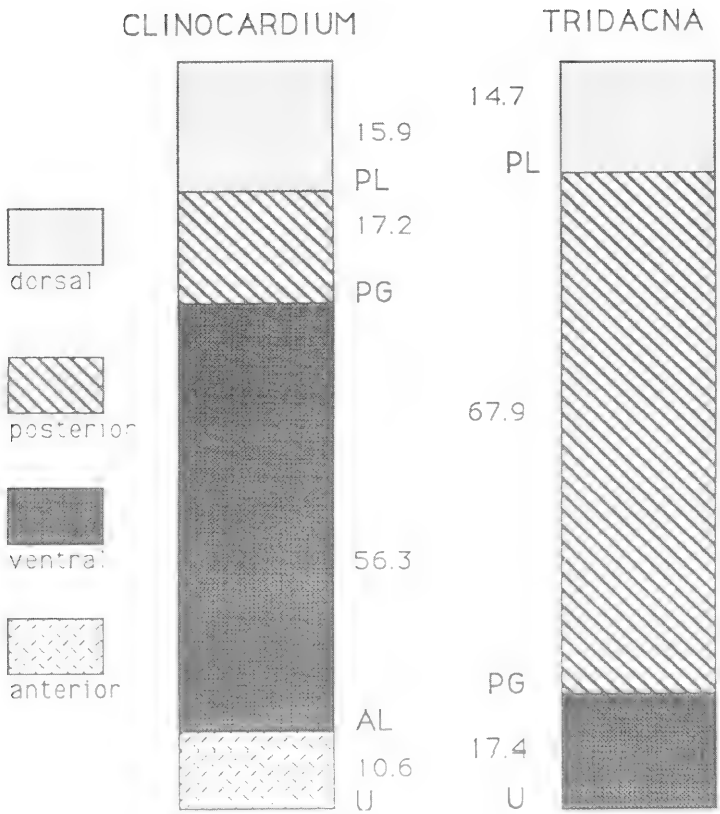

FIG. 36. Relative proportions of homologous regions of mantle/shell and relative distribution of marginal increments about the perimeter of *Clinocardium nuttallii* and *Tridacna* (*Chametrachea*) *maxima*. Numbers indicate percent of total perimeter for a particular region. From Stasek (1962).

there is no anterior direction into which the beaks can be pointing.

In regards to the hinge and the adductor and pedal retractor muscles, the evolution of giant clams is a case of peramorphosis. The ontogeny of these structures in the juveniles of modern giant clams recapitulates the states of these characters in concordance with the pattern of phylogenetic relationships of the group: (*Goniocardium* (*Avicularium* (*Byssocardium* (*Hippopus* (*Tridacna*))))). Yonge (1936, 1981) had thought that it was impossible for the ontogeny of giant clams to recapitulate their phylogeny.

In contrast to the peramorphosis of the shell and of the adductor and retractor muscles, the byssus of giant clams is paedomorphically retained late into ontogeny. The byssus, present in all or most larval cardiids (Pelseneer, 1911; Yonge, 1936), is retained throughout adulthood in *Chametrachea* (Rosewater, 1965; Yonge, 1953b, 1981; Lucas et al., 1991; pers. obs.). Other tridacnines are byssally attached early in ontogeny but later become free-living and the byssus is lost (Rosewater, 1965; Yonge, 1953b, 1981; Lucas et al., 1991). Because of the tremendous increase in both growth rate and size attributable to photosymbionts, it is difficult to ascertain the result of the paedomorphic processes responsible for the retention of the byssus in tridacnines. It should be noted that *Avicularium* and *Byssocardium* have byssal gapes (Schneider, 1998), but these shells are not notably large. The tremendous size increase in tridacnines may not have occurred until the Miocene origination of the Recent taxa. Ironically, this size increase is thought to be responsible for the subsequent *loss* of the byssus and byssal gapes in the adults of *Tridacna, Persikima, Hippopus,* and

very large specimens of *T.* (*Chametrachea*) *squamosa,* for these large clams are held in place simply by their bulk (Rosewater, 1965; Yonge, 1953b, 1981; Lucas et al., 1991).

Goniocardium lacks a byssal gape (Schneider, 1998). A narrow byssal gape is present throughout ontogeny in *Avicularium;* a wider byssal gape is present throughout ontogeny in the more derived *Byssocardium* and *Chametrachea* (Schneider, 1998; Fig. 27A). The closing of the byssal gape throughout post-juvenile ontogeny can be seen in the shells of *Hippopus, Tridacna,* and to a lesser degree, *Persikima* (Rosewater, 1965; Yonge, 1981; Figs. 25, 29, 30). The closing of the byssal gape (and subsequent loss of byssus) is a peramorphic superimposition onto the paedomorphic retention of the byssus into post-larval development. Heterochrony resulting in pre-displacement is responsible for the closing of the byssal gape, for the descendant adult morphology has developed beyond that of its ancestor (McNamara, 1986).

Independently, fragines also paedomorphically retain the byssus into adulthood. In this instance, heterochrony results in post-displacement, for an ancestral juvenile character (functional byssus) is present in the adult, without the size increase found in neoteny. In the present analysis, it is hypothesized that Fraginae and Tridacninae independently derived a functional byssus in the adult.

Morton (1988) noted that the foot is reduced in cemented or unusually inactive bivalves. The tridacnines are sedentary non-burrowers (Rosewater, 1965; Yonge, 1981): *Chametrachea* byssally attaches to, or bores into, hard substrata. *Tridacna* and *Perskima* are likewise byssally attached to hard substrata early in life; late in ontogeny the byssal apparatus is lost and they are epifaunal on hard substrata. *Hippopus* is epifaunal on sandy surfaces. The fragine clades *Parvicardium* + *Cerastobyssum* and *Corculum* independently lose the ventral ridge. Fragines, especially *Corculum,* are the most superficial burrowers of the non-tridacnine cardiids (Stanley, 1970; Savazzi, 1985; Severin & Cooper, 1989).

In the evolution of Cenozoic eucardiids from their Cretaceous ancestor, adjacent ribs fused together, forming one wide rib (Schneider, 1993a, 1998). A single rib on a Cenozoic eucardiid is homologous to two ribs on a Cretaceous eucardiid. The Maastrichtian *Perucardia* displays an intermediate condition. The anterior and posterior slopes of the shell of *Perucardia* have ribs as on Cretaceous eucardiids, whereas the central slope has the fused ribs of Cenozoic eucardiids.

Study of the ontogeny and phylogenetic relationships of tridacnines indicates that rib reduction in this group has proceeded by a process which can be called rib suppression. The radial ribs of *Goniocardium, Avicularium,* and *Byssocardium* are all of the same strength and width over the entire surface of the shell. Each rib will bear only one row of scutes (Fig. 24). On the most basal living tridacnine, *Hippopus,* the "primary" ribs (terminology of Rosewater, 1965) are homologous to several radial ribs, and indeed they may bear multiple rows of scutes (Fig. 25). Rosewater termed these multiple "secondary" ribs as "riblets." Riblets are also present in between the primary ribs. On *Chametrachea,* the riblets are apparent throughout ontogeny (Rosewater, 1965; Fig. 26). The underside of the "primary" ribs of *Hippopus* and *Chametrachea* has several marginal serrations (Figs. 25, 26); each marginal serration corresponds to a riblet and is homologous to one rib on *Goniocardium, Avicularium,* and *Byssocardium.* On the more derived *Tridacna* and *Persikima,* the riblets are readily apparent only early in ontogeny (Figs. 28–31). Only the riblets of *Hippopus* bear scutes (Fig. 25). Rosewater's "riblets" are homologous to radial ribs, whilst his "primary" ribs are secondary undulations in the commissure superimposed over the primitive and suppressed cardiid radial rib pattern.

Photosymbiosis in Cardiids

All species of tridacnines are known to harbor photosymbiotic dinoflagellate algae (zooxanthellae) in their tissues (Trench et al., 1981; Alcazar et al., 1987; Lucas et al., 1991). Photosymbiotic dinoflagellates have also been found in the fragines *Corculum cardissa* (Linné, 1758), *Lunulicardia retusa* (Linné, 1767), *Fragum fragum* (Linné, 1758), *F. unedo* (Linné, 1758), *F. mundum* (Reeve, 1845), *F. loochooanum* Kira, 1962, and two undescribed species of *Fragum* (Kawaguti, 1950, 1968, 1983; Trench et al., 1981; Umeshita & Yamasu, 1985; Yamasu, 1988a, b; Severin & Cooper, 1989; Paulay, 1996.; pers. obs.). These photosymbionts transfer excess carbon from photosynthesis to the host's tissues (Trench et al., 1981; Fisher et al., 1985, Klumpp et al., 1992).

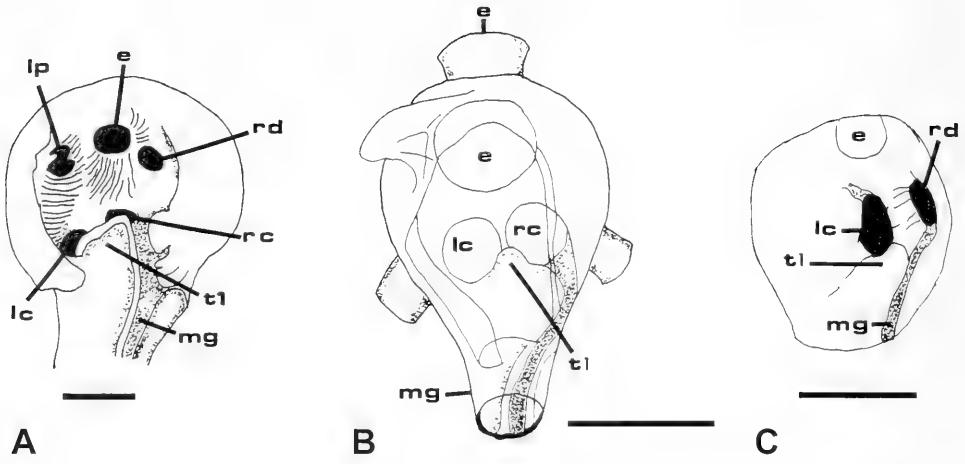

FIG. 37. Representative stomachs of lucinoids. A, *Diplodonta semiaspera* (Ungulinidae). B, *Thyasira flexuosa* (Thyasiridae). C, *Loripes lucinalis* (Lucinidae). Note following structures: GT, major typhlosole; LC, left caecum; RC, right caecum. Lucinids lack a right caecum. All scales = 1 mm. From Allen (1958).

Bivalves of the families Lucinidae and Solemyidae (as well as members of several other families) have chemautotrophic bacteria in their tissues (Reid, 1990); this phenomenon is known as chemosymbiosis. Lucinids reduce and/or lose many of the structures in their digestive system (Allen, 1958; Reid, 1990; CoBabe, 1991; Fig. 37). The stomach and the gut are reduced or even lost, and the labial palps and the outer demibranch are lost. Simplification of the stomach involves reduction from the typical type V stomach to a type IVb stomach (Purchon, 1960a, 1987a). In type V stomachs, the major typhlosole emerges from the midgut, enters the right caecum, then re-emerges and traverses across the floor of the stomach, before finally entering the left caecum. In a type IV stomach, the major typhlosole simply emerges from the midgut, crosses the floor of the stomach and enters the left caecum. The major typhlosole does not enter the right caecum.

Solemyids reduce or lose the gut (Morse, 1913; Yonge, 1939; Owen, 1961; Reid 1980, 1990; Reid & Bernard, 1980; Kuznetsov & Shileiko, 1984), as well as the esophagus (Reid & Bernard, 1980; Reid, 1990). In both lucinids and solemyoids, the chemosymbionts provide all or most of the nutrition for the clam (Conway et al., 1989; Conway & McDowell Capuzzo, 1991; Fisher & Childress, 1986; Reid, 1990; Krueger et al., 1992).

Primitively, eucardiids have a very long and complex gut, as seen in *Acanthocardia, Maoricardium,* and the Clinocardiinae (Figs. 9, 10A). This type of gut (13:3) exits from the style sac and loops eleven times before exiting the visceral mass and terminating at the anus. *Acanthocardia, Maoricardium* and the Clinocardiinae have the typical cardiid type V stomach (Graham, 1949; Purchon, 1960a, 1987a; Nakazima, 1964b; Fig. 11). The major typhlosole emerges from the midgut, going first to the right caecum and then to the left caecum.

Clinocardiines have always been restricted to the cool temperate and arctic waters of the northern hemisphere, especially from Oregon north to Alaska (Kafanov, 1980), a zone of upwelling (Berger, 1989). High latitude and otherwise cool waters generally have higher productivity than warmer, low latitude waters (Berger, 1989). Therefore, it is not unexpected to find that the clinocardiine digestive system, is at least as complex, or even more complex, than those of *Acanthocardia* (North Atlantic and Mediterranean) and *Maoricardium* (Indo-Pacific), which live in areas of lower productivity. Modifications of the clinocardiine digestive tract include the presence of (1) an additional typhlosole on the right posterior portion of the stomach (17:1) in *Ciliatocardium* and *Serripes,* (2) a raised bar running across the middle of the stomach (19:1) in *Clinocardium, Keenocardium,* and *Serripes,* and (3) a food groove on the outer demibranch of *Serripes groenlandicus* (Fig. 5B). The other Recent species of *Serripes, S.*

laperousii (Deshayes, 1839), lacks a food groove on the outer demibranch (pers. obs.).

Papillicardium is the most basal fragine and has a gut and stomach similar to that of *Maoricardium.* However, the labial palps are reduced (1:0), as in the chemosymbiont-bearing lucinoideans and solemyoideans. *Parvicardium siculum* (Figs. 10C, 11H) has a similar stomach but has reduced the gut. Neither *Cerastobyssum* (the sister taxon to *P. siculum*) nor *P. exiguum* have reduced guts.

In *Apiocardia* and *Trigoniocardia,* the stomach has been simplified from a type V stomach to a type IV stomach. The midgut/style sac opening is not located posteriorly, but anteriorly. The major typhlosole goes directly from the midgut/style sac opening to the left caecum. This is the first report of a type IV stomach in Cardiidae. *Apiocardia* undergoes a reversal to the primitive states of a complex gut (13:4) and large labial palps (1:1). *Lunulicardia* also undergoes reversals of digestive characters: large labial palps (1:1) and a posteriorly located midgut/style sac opening (18:0). *Lunulicardia* and *Corculum* have a simplified stomach, but not as in *Apiocardia* and *Trigoniocardia*. The major typhlosole enters only one caecum, but it is the right caecum, not the left caecum. Functionally, the stomach of *Lunulicardia* and *Corculum* is a type IV stomach, although it does not adhere to Purchon's (1960a, 1987a) definition of a type IV stomach. *Fragum* and the *Ctenocardia*-group have a type V stomach, although the style sac is located anteriorly. Other simplifications of the digestive system of these cardiids are the reduction of the crystalline style and style sac of *Corculum* and the loss of ridges on the labial palps of *Microfragum* (Fig. 3B).

Reduction of digestive structures is often indicative of symbiosis with microorganisms. Bernard (1980) and Kuznetsov & Shileiko (1984) have inferred symbiosis in some solemyids and nucinellids because these bivalves are gutless (reviewed by Reid, 1990). Of the fragines that significantly simplify their digestive system, only *Microfragum, Fragum, Lunulicardia* and *Corculum* have been the subject of any sort of anatomical investigation previous to Schneider (1992) and this study (Pelseneer, 1911; Kawaguti, 1950, 1968, 1983; Kratzing & Ladd, 1967; Matsuno, 1988; Severin & Cooper, 1989; Janssen, 1991, 1992; Ohno et al., 1995). It is not that *Apiocardia, Trigoniocardia, Americardia,* and *Ctenocardia* have been found to lack photosymbionts; it is that no one has ever examined the soft parts of species of these taxa. Based on the reduction of the stomach and intestine, it is predicted that all or most of the species of these four taxa harbor photosymbiotic dinoflagellates in their tissues. However, Ohno et al. (1995) report that *Microfragum festivum* (Deshayes, 1854) lacks photosymbionts.

Giant clams, which are well known for bearing symbiotic dinoflagellates in their tissues (Brock, 1888; Bochsma, 1924; Yonge, 1936, 1981; Rosewater, 1965; Trench et al., 1981; Klumpp et al., 1992; numerous others), have a fully functional digestive system (Trench, 1974; Morton, 1978; Reid et al., 1984). Tridacnines do not simplify the stomach, except for the loss of the esophageal sorting area (21:1). However, the stomach of giant clams does have a ridge (20:1), and the major typhlosole forms a tight spiral on the floor of the stomach (14:0). The gut is somewhat reduced (13:2); however, this character state is shared with lymnocardiines and should not be interpreted as having been derived as a result of the acquisition of zooxanthellae. Additionally, the largest species of giant clam, *Tridacna gigas,* develops a food groove on its outer demibranch (4:1). The clinocardiine *Serripes groenlandicus* is the only other cardiid known to have a food groove on its outer demibranch. Furthermore, Yonge (1932, 1936) reported that the crystalline style and style sac is unusually large in *Tridacna* (*Persikima*) *derasa.*

Tridacnines include the largest and fastest-growing Recent bivalves (Bonham, 1965; Yonge, 1981; Klumpp et al., 1992). Bonham suggested that the shell of *Tridacna gigas* (the largest of the giant clams; Rosewater, 1965) increases in thickness by 1 cm annually. Yonge (1981) reported that a specimen of *T. gigas* grew to a length of 55 cm in about six years. Klumpp et al. (1992) reported that *T. gigas* grew from 1.7 cm to 19 cm in 28 months. It has been found that photosymbionts can potentially satisfy all the respiratory requirements of giant clams (Gwyther & Munro, 1981; Fisher et al., 1985; Klumpp et al., 1992). The photosymbionts augment a fully functional digestive system; hence the spectacular growth rates and size of giant clams.

The present results indicate that symbiosis with dinoflagellate algae evolved separately in Tridacninae and Fraginae. Kawaguti (1983) had suggested that photosymbiosis evolved only once. If Tridacninae and Fraginae are posited as sister taxa, tree length increases by five steps. It is felt that the present results

reject the hypothesis that symbiosis with dinoflagellate algae evolved only once in cardiids.

Goethemia independently simplifies its gut (13:0). Given its subarctic distribution (Clench & Smith, 1944; Voskuil & Onverwagt, 1989), it is unlikely to bear photosymbionts. *Goethemia* never is larger than 14 mm, and the simplification of the gut may simply be a consequence of the increase of the surface area/volume ratio (Reid & Bernard, 1980).

Some populations of the clinocardiine *Clinocardium nuttallii* from Oregon and Washington have a very different sort of alga in their tissues. Cooke (1975) and Hartmann & Pratt (1976) independently reported the presence of a zoochlorella of the form genus *Chlorella* in the tissues of *C. nuttallii*. Hartmann & Pratt (1976) and Jones & Jacobs (1992) reported that algae are absent in small, young, infaunal individuals. Larger and older semi-infaunal clams contain algae only in tissues exposed to sunlight (Jones & Jacobs, 1992). Finally, the oldest, largest, epifaunal clams have algae throughout the mantle and foot tissues. This is in contrast to the dinoflagellate algae in tridacnines, which are ingested by the clams during the veliger stage or early juvenile stage (LaBarbera, 1975; Jameson, 1976; Fitt & Trench, 1981). Hartman & Pratt considered the zoochlorella to be parasitic on *C. nuttallii*, but Jones & Jacobs suggested that *C. nuttallii* is at an intermediate stage of evolving a symbiotic relationship with the zoochlorella. If this is true, then *C. nuttallii* has not yet reached the stage at which reduction of the digestive system occurs (this stage was never reached in tridacnines). The amount of carbon, if any, that the zoochlorellae contribute to *C. nuttallii* is still unknown.

Phylogeny and the Fossil Record

The results of the phylogenetic analysis are broadly concordant with the fossil record (Fig. 38). *Plagiocardium* appears in the Paleocene (Keen, 1980). The oldest known clinocardiines are Early Oligocene (Kafanov, 1980; Kafanov & Savitskiy, 1982). *Papillicardium*, the most basal fragine, originates in the Eocene (Keen, 1980; Schneider, 1993a, 1998). *Parvicardium* also originates in the Eocene (Keen, 1980; Schneider 1993a, 1998).

Goethemia as the sister taxon to Tridacninae + Lymnocardiinae is the only notable stratigraphic anomaly (within a particular clade, a case of a more derived taxon appearing before a less derived taxon) in the present phylogenetic analysis. *Goethemia*'s fossil record dates from the earliest Pleistocene, whereas the three extinct tridacnine taxa are known from the Middle Eocene, and the extant tridacnine taxa are known from Miocene fossils. The oldest lymnocardiine fossils are Early Oligocene (Keen, 1969a, 1980). *Goethemia* is known from its Recent type species, *Cardium elegantulum* Möller, 1842 (*ex* Beck MS). I would also place *Cardium strigilliferum* Wood, 1853, from the lowermost Pleistocene Red Crag of England, in *Goethemia*. If the results of the present phylogenetic analysis are accepted, then *Goethemia* would be hypothesized to have originated in the Eocene.

A minor stratigraphic anomaly is *Microfragum*. *Microfragum*'s fossil record consists only of Pleistocene specimens of *Cardium ebaranum* (discussed in Materials and Methods). If we were to accept the results of the ordered analysis, *Microfragum* is the sister taxon to *Ctenocardia* + *Americardia*, and *Microfragum* is postulated to have originated in the Miocene.

Valentine (1989) found that 77% of Recent bivalve and gastropod species of the California Province are known from Pleistocene fossils. Those forms that have yet to be found as fossil are fragile, minute, and rare, although rare forms are found as new studies are conducted. *Goethemia* and *Microfragum* fulfill all three of these criteria: they are small (*Goethemia* no larger than 14 mm long; *Microfragum* less than 15 mm high), fragile, and rare (Clench & Smith, 1944; Keen, 1980; Voskuil & Onverwagt, 1989). Additionally, *Goethemia* lives in an area (boreal Atlantic Ocean: Massachusetts north to Baffin Bay, west Greenland, Iceland, northern and western Norway, Spitsbergen, Barents Sea; Fischer-Piette, 1977) for which there was virtually no net marine sedimentation during the Cenozoic until the Pliocene. To my knowledge, *Goethemia* is absent from the few Pliocene and Pleistocene localities in New England, eastern Canada, Greenland, and Iceland. Given its low preservation potential, *Goethemia*'s absence from the fossil record, from a cladisticially postulated Eocene origin until the Pliocene, is plausible. The phylogenetic position of *Goethemia* as the sister taxon to Tridacninae + Lymnocardiinae should not be rejected simply on the basis of the fossil record.

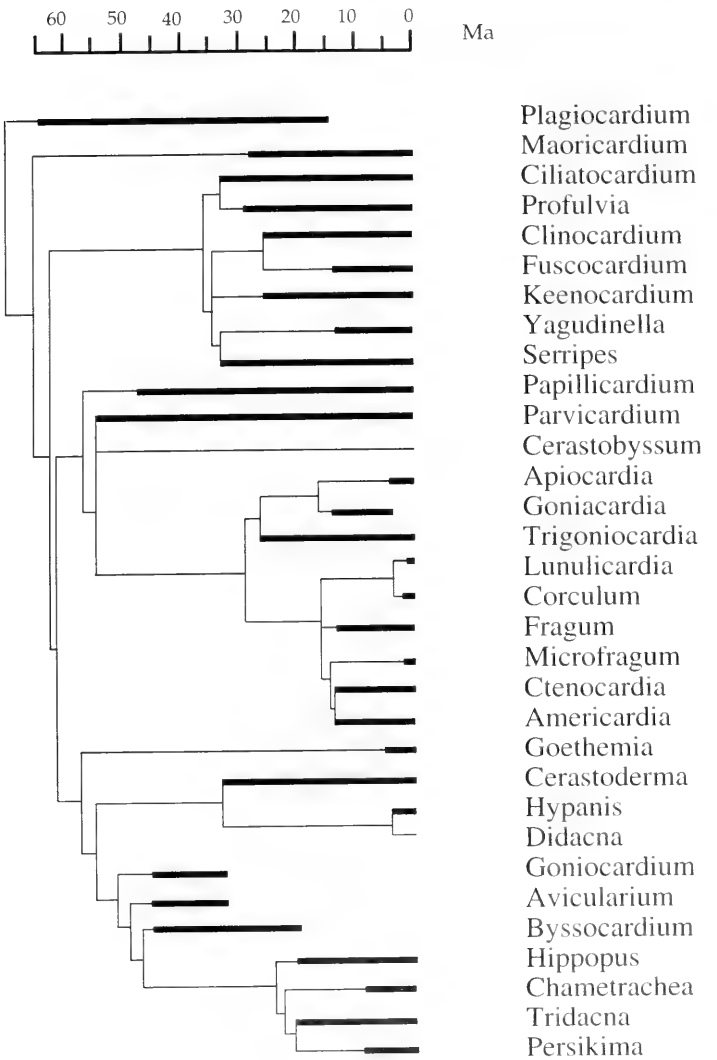

FIG. 38. Phylogenetic results of the ordered analysis plotted against the fossil record. Time scale from Harland et al. (1990). Stratigraphic ranges from Table 3. *Parvicardium* is represented only once, with earliest species known from the Eocene (see text; Schneider 1998). Taxa with no fossil record indicated by narrow horizontal line at 0 Ma.

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APPENDIX 1

Material examined. Number of specimens examined indicated in parentheses.

Acanthocardia aculeata (Linné, 1758). USNM 304723 (4); ANSP 54235 (12); UNC 15376 (2). Anatomical: NHM Acc. 2322 (1).

Acanthocardia (*Schedocardia*) *hatchetigbeense* (Aldrich, 1886). USNM 645087 (1, syntype), 638802 (1, syntype); ANSP 5420 (1), 8687 (1), 8756 (3).

Plagiocardium granulosum (Lamarck, 1805). ANSP 6268 (14), 7663 (1).

Maoricardium pseudolatum Voskuil & Onverwagt, 1991. ANSP A103 (55); AM C.164058 (3). Anatomical: AM C.164058 (3).

Ciliatocardium ciliatum (Fabricius, 1780). ANSP 54269 (12), FMNH 278012 (1). Anatomical: USNM 600831 (4), 604850 (3), 796257 (11); ANSP 64388 (1); FMNH 278012 (1).

Profulvia harrimani (Dall, 1904). USNM 164867 (1) (holotype); UCMP A-22582 (1).

Clinocardium nuttallii (Conrad, 1837). Shell: YPM 10148 (1), 10149 (1). Shell and anatomy: FMNH 49126 (1), 278015 (2), 278016 (1).

Clinocardium (*Fuscocardium*) *braunsi* (Tokunaga, 1906). Data from Oyama (1973).

Clinocardium (*Keenocardium*) *blandum* (Gould, 1850). USNM 3899 (1), 304266 (1); FMNH 12851 (2); ANSP 85407 (2). Anatomical: FMNH 12581 (2). Misidentified as *Clinocardium* (*Keenocardium*) *californiense* (Deshayes, 1839) by Schneider (1993b).

Serripes groenlandicus (Mohr, 1786). ANSP 64421 (11), FMNH 278013 (2); YPM 49159 (1). Anatomical: USNM 600836 (1), 604849 (2), 796460 (2); FMNH 278013 (2).

Yagudinella notabile (Sowerby, 1915). FMNH 278014 (1).

Papillicardium papillosum (Poli, 1795). AMNH 29980 (3), 29981 (4); ANSP 54098 (1), 54266 (13). Anatomical: MNHN, unnumbered specimens (18).

Parvicardium siculum (Sowerby, 1841). ANSP 54123 (1), 54266 (1), 54288 (1), 54289 (9); AMNH 226511 (1). Anatomical: AMNH 226511 (1), 226512 (3).

Parvicardium exiguum (Gmelin, 1791). ANSP 54121 (4), 209588 (1); USNM 171808 (1); NHM 1964269W (50). Anatomical: NHM 1964269W (50).

Parvicardium (*Cerastobyssum*) *hauniense* Petersen & Russell, 1971. Conchological and anatomical: ZM, unnumbered specimens (3).

Trigoniocardia antillarum (Orbigny, in Ramon de la Sagra, 1842). ANSP 54283 (60), 283822 (22); USNM 429926 (2). Anatomical: USNM 857540 (2).

Trigoniocardia (*Apiocardia*) *obovale* (Sowerby, 1833). AMNH 78213 (19), 72589 (11), 78218 (9); ANSP 317706 (51). Anatomical: ANSP 316937 (2); 81974 (1).

Trigoniocardia (*Goniacardia*) *callopleura* Gabb, 1881. ANSP 3439 (2, syntypes), 3445 (2).

Lunulicardia retusa (Linné, 1767). AMNH 30073 (21); ANSP 12527 (4), 302424 (12), 319313 (2); USNM 631219 (2); YPM 9676 (1). Anatomical: ANSP 302424 (1).

Corculum cardissa (Linné, 1758). ANSP 231526 (40); UNC 8291 (1); USNM 636206 (2). Anatomical: ANSP 200771 (1); USNM 661032 (1).

Fragum fragum (Linné, 1758). ANSP 288688 (68); USNM 674681 (2). Anatomical: ANSP 289145 (9); USNM 746995 (1), 747674 (1), 766795 (1), 849695 (1).

Ctenocardia symbolica Iredale, 1929. ANSP 229980 (10); USNM 236040 (2). Anatomical: ANSP 229873 (2).

Ctenocardia (*Americardia*) *media* (Linné, 1758). ANSP 54280 (14); PRI 26699 (2), 33068 (1); USNM 92089 (2), 36431 (2). Anatomical: NHM Acc. No. 2270 (6); ANSP 297243 (2); USNM 801849 (1), 801850 (1), 804669 (1), 847861 (1).

Microfragum festivum (Deshayes, 1854). ANSP 54263 (4). Conchological and anatomical: AM C.164061 (4), C.164062 (10).

Goethemia elegantula (Möller, 1842, *ex* Beck MS). Conchological and anatomical: SMNH 883 (6), 1482 (6); NHM 196284W (6); ZM, unnumbered specimens (3).

Cerastoderma edule (Linné, 1758). ANSP 54252 (15); FMNH 278010 (2); YPM 9672 (1). Conchological and anatomical: NHM 1964273W (17); FMNH 278010 (2), 278017 (2); UMMZ, unnumbered specimens (3).

Hypanis (*Monodacna*) *colorata* (Eichwald, 1829). ANSP 338065 (25). Anatomical: USNM 769939 (2).

Didacna trigonoides (Pallas, 1771). ANSP 54193 (4). Anatomical: NHM 1862.11.19.33 (2).

Goniocardium rachitis (Deshayes, 1829). ANSP 12429 (6); FMNH PE 3624 (2).

Avicularium avicularium (Lamarck, 1805). ANSP 6279 (3).

Byssocardium emarginatum (Deshayes, 1829). IRSNB I. G. 10591 (4).

Hippopus hippopus (Linné, 1758). FMNH 2635 (1), 164189 (1); USNM 63793 (6). Anatomical: UMMZ, 265468 (1).

Tridacna (*Chametrachea*) *maxima* Röding, 1798. FMNH 156836 (2); ANSP 252683 (2), 269769 (1). Anatomical: ANSP A3276 (1); UMMZ 265463 (1).

Tridacna gigas (Linné, 1758). USNM 602502 (2), 686575 (4). Anatomical: UMMZ 265466 (1).

Tridacna (*Persikima*) *derasa* Röding, 1798. USNM 654256 (4), 845538 (40). Anatomical: UMMZ 265467 (1).

APPENDIX 2

Abbreviations of Repositories

AM: Australian Museum, Sydney, Australia.
AMNH: American Museum of Natural History, New York, New York, USA
ANSP: Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA.
FMNH: Field Museum of Natural History, Chicago, Illinois, USA.
GSI: Geological Survey of India, Calcutta, India.
IRSNB: Institut Royal des Sciences Natuelles de Belgique, Brussels, Belgium.
MACSRI: Mahrashtra Association form the Cultivation of Science, Research Institute, Pune, India.
MNHN: Museum National d'Histoire Naturelle, Paris, France.
NHM: The Natural History Museum. London, United Kingdom.
PRI: Paleontological Research Institution, Ithaca, New York, USA.
SMNH: Swedish Museum of Natural History, Stockholm, Sweden.
UCMP: University of California Museum of Paleontology, Berkeley, California, USA.
UMMZ: University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA.
UNC: University of North Carolina, Department of Geology, Chapel Hill, North Carolina, USA.
USNM: United States National Museum, Washington, D.C., USA.
YPM: Yale Peabody Museum, New Haven, Connecticut, USA.
ZM: Zoologisk Museum, Copenhagen, Denmark.

APPENDIX 3

List of Abbreviations

aa	anterior adductor
ac	anterior cardinal
acs	anterior cardinal socket
al	anterior lateral
alid	ascending lamella of inner demibranch

alod	ascending lamella of outer demibranch
als	anterior lateral socket
avl	anterior ventral lateral
bcl	branching crossed-lamellae
bg	byssal gape
by	byssus
cs	cross-striae
dlid	descending lamella of inner demibranch
dlod	descending lamella of outer demibranch
e	esophagus
ea	excurrent aperture
f	foot
fg	food groove
fp	fibrous prisms
g	gill
i	intestine
ia	incurrent aperture
id	inner demibranch
ip	inner palp
lc	left caecum
lf	lunule flap
lg	ligament
lp	labial palp
lpo	left pouch
lr	lateral ridge
n	nymph
od	outer demibranch
og	oral groove
op	outer palp
pa	posterior adductor
pc	posterior cardinal
pci	periostracal cilia
pcs	posterior cardinal socket
pf	periostracal frill
pg	pedal gape
pl	posterior lateral
pls	posterior lateral socket
ps	pseudocarina
pss	perisiphonal suture
r	ridge
rb	raised bar
rbl	riblet
rc	right caecum
rd	right duct
rr	rib
s	spine
sa	supra-axial extension of demibranch
saa	anterior sorting area (SA8)
sae	sorting area of esophagus (SA7)
sap	posterior sorting area (SA3)
sc	scute
sf	spiral fold
sia	siphonal area
ss	style sac
st	stomach
t	tentacle
t1	major typhlosole
t3	tertiary typhlosole
u	umbo
v	valvule
vm	visceral mass
vp	ventral papillae
vr	ventral ridge
z	zooxanthellae

APPENDIX 4

Taxonomy of taxa considered herein by Keen (1980); family Lymnocardiidae and superfamily Tridacnacea from Keen (1969a, b).

Superfamily Cardiacea
Family Cardiidae
- Subfamily Cardiinae
  - *Parvicardium*
  - *Plagiocardium*
    - (*Plagiocardium*)
    - (*Maoricardium*)
    - (*Papillicardium*)
- Subfamily Fraginae
  - *Fragum*
    - (*Fragum*)
    - (*Lunulicardia*)
  - *Corculum*
  - *Ctenocardia*
    - (*Ctenocardia*)
    - (*Afrocardium*)
    - (*Microfragum*)
  - *Trigoniocardia*
    - (*Trigoniocardia*)
    - (*Americardia*)
    - (*Apiocardia*)
- Subfamily Laevicardiinae
  - *Cerastoderma*
  - *Clinocardium*
    - (*Clinocardium*)
    - (*Ciliatocardium*)
    - (*Fuscocardium*)
    - ? (*Keenocardium*)
  - *Serripes* (= *Yagudinella*)
  - *Laevicardium* (*Profulvia*)

Family Lymnocardiidae
- *Hypanis* (*Monodacna*)
- *Didacna*

Superfamily Tridacnacea
Family Tridacnidae
- *Tridacna*
  - (*Tridacna*)
  - (*Chametrachea*)
  - (*Persikima*)

Avicularium
Byssocardium
Goniocardium
Hippopus
Sawkinsia

APPENDIX 5

Taxonomy of taxa considered herein by Popov (1977), with emendations on Clinocardiinae and Lymnocardiinae from Kafanov & Popov (1977) and Kafanov (1980).

Superfamily Cardioidea
Family Cardiidae
Subfamily Clinocardiinae
Clinocardium
(*Clinocardium*)
(*Fuscocardium*)
Ciliatocardium
Keenocardium
Profulvia
Serripes
Yagudinella
Subfamily Fraginae
Fragum
(*Fragum*)
(*Ctenocardia*)
Corculum
(*Corculum*)
(*Lunulicardia*)
Trigoniocardia
(*Trigoniocardia*)
(*Americardia*)
Plagiocardium
Maoricardium
Parvicardium (= *Papillicardium*)
Subfamily Lymnocardiinae
Cerastoderma
Didacna
Monodacna
Superfamily Tridacnoidea

MALACOLOGIA, 1998, 40(1–2): 375–391

INDEX

Taxa in **bold** are new; pages in *italic* indicate figures of taxa.

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VOL. 40, NO. 1-2 MALACOLOGIA 1998

CONTENTS