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TAXONOMY AND ECOLOGY OF THE PHILO-
BRYIDAE AND LIMOPSIDAE (MOLLUSCA:
PELECYPODA)

MICHAEL J. S. TEVESZ

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TAXONOMY AND ECOLOGY OF THE PHILOBRYIDAE AND LIMOPSIDAE (MOLLUSCA: PELECYPODA)

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ABSTRACT

The Philobryidae (Eocene-Recent; order Arcoida) are redefined to include nine genera: *Adacnarca, Aupouria, Cosa, Cratis, Limarca, Limopsilla, Lissarca, Neocardia,* and *Philobrya.* Philobryids are generally small (2–10 mm), mytiliform, and have a ligament pit that lies between two series of interlocking denticles. Philobryids are most common and widely distributed in the Southern Hemisphere. They are epibyssate but also are efficient epifaunal crawlers.

The Limopsidae (Jurassic-Recent; order Arcoida) are redefined to include two genera: *Empleconia* and *Limopsis.* Limopsids are small (10–60 mm), ovate, and have a ligament pit that lies in a dorsal area above numerous teeth. Limopsids are endobyssate and are cosmopolitan at shelf depths.

Unlike the gill of other arcoids, the philobryid gill is composed of short, stubby filaments and has few ciliary junctures. These features of the philobryid gill represent adaptations for cleansing, strengthening the gill, and viviparity. Some philobryids have an anterior inhalant area. The presence of this feature in taxonomically remote pelecypod groups and in groups of Recent, highly specialized pelecypods shows that, contrary to prevalent opinion, its presence does not necessarily indicate primitiveness or taxonomic affinity.

Morphological, distributional, and temporal evidence suggests that limopsids probably arose from grammatodonts and in turn gave rise to glycymerids and philobryids. Neoteny may have played a role in philobryid and limopsid evolution.

1. INTRODUCTION

The pelecypod order Arcoida (Middle Ordovician-Recent) has a rich and continuous fossil history and is abundant and widespread in modern oceans. Most arcoids have a sturdy rhomboidal shell, numerous transverse hinge teeth, and an external ligament attached to a broad area above the dentition (dorsal area). Living arcoids have filibranchiate gills, a ventrally cleft foot, and are covered with a black or brown hairy periostracum. Although the taxonomy and ecology of six of the eight arcoid families are fairly well understood, two families, the Philobryidae and Limopsidae, are still poorly known.

The Philobryidae (Eocene-Recent) are small (2–15 mm), mytiliform pelecypods that are unique among arcoids in having in the adult form a ligament pit that lies between two rows of interlocking transverse denticles (Fig. 1). Unlike most arcoids, philobryids have an internal ligament, and
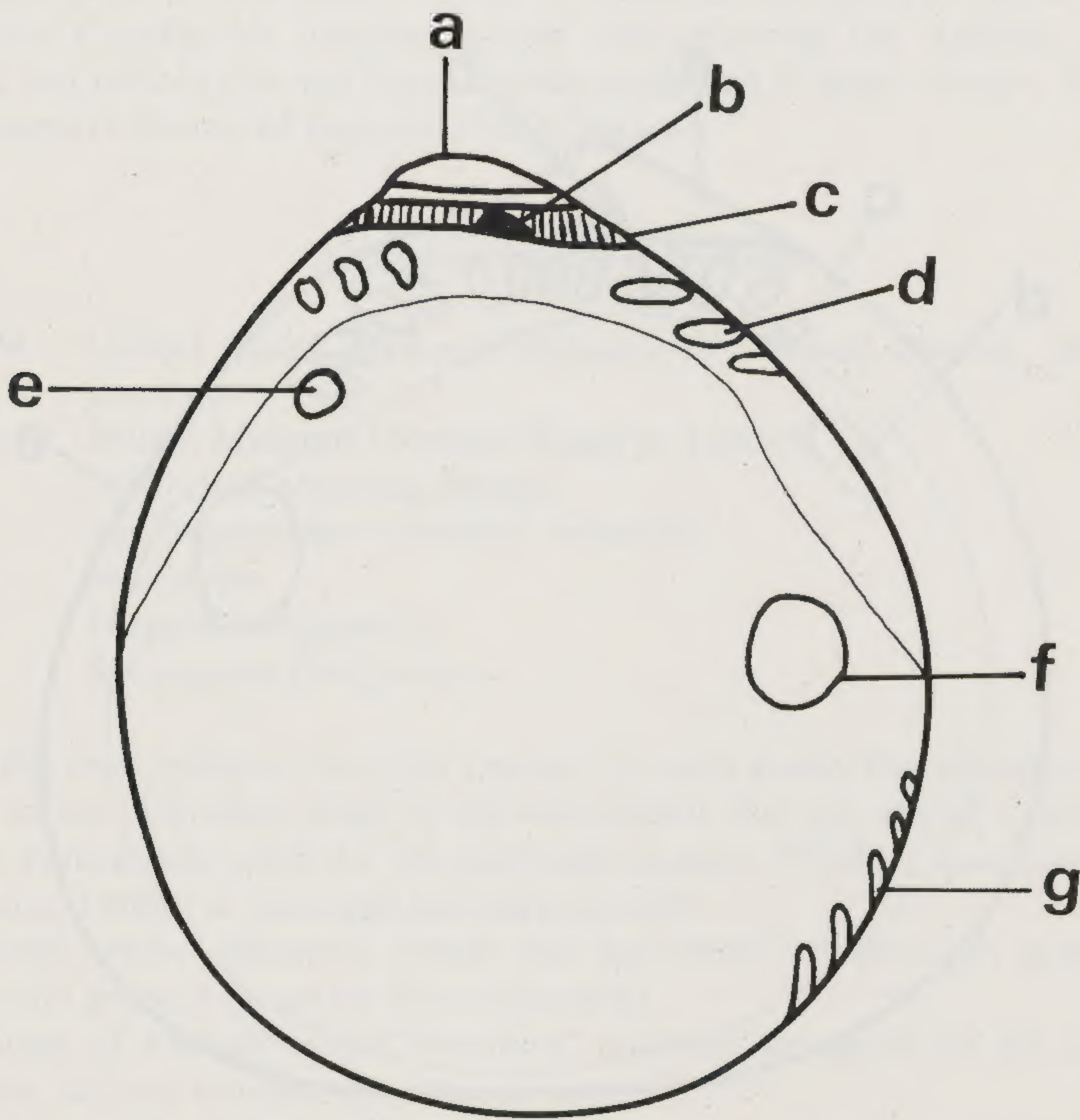
FIG. 1. Morphological features of the philobryid shell. a = prodissoconch, b = ligament pit, c = denticles, d = tooth, e = anterior adductor muscle scar, f = posterior adductor muscle scar, g = crenulation.

some genera lack teeth. Philobryids are epibyssate, exclusively marine, and occur from the intertidal zone to depths of over 1000 meters. There are 8 extant genera and more than 50 extant species. Most of these are found off Australia, New Zealand, and Antarctica. Other localities include South Africa, southern South America, Baja California (Mexico), the Caribbean, the Mediterranean, and scattered islands in the South Atlantic Ocean. Philobryids have a patchy distribution within their geographic range, and only about 10 species are known to be common. One extinct genus and about 12 extinct species have been described. The scanty fossil record of the family is confined to Australia and New Zealand.

The Limopsidae (Middle Jurassic-Recent) are small (10–55 mm), ovate, and unique among arcoids in having both a radially arrayed ligament in a pit and a smooth dorsal area (Fig. 2). Limopsids are endobyssate and are common at shelf depths throughout the world. There are 2 known extant genera and over 40 extant species. More than 30 extinct species have been described. The earliest limopsids are reported from Europe. Post-Jurassic fossil limopsids are found throughout the world.
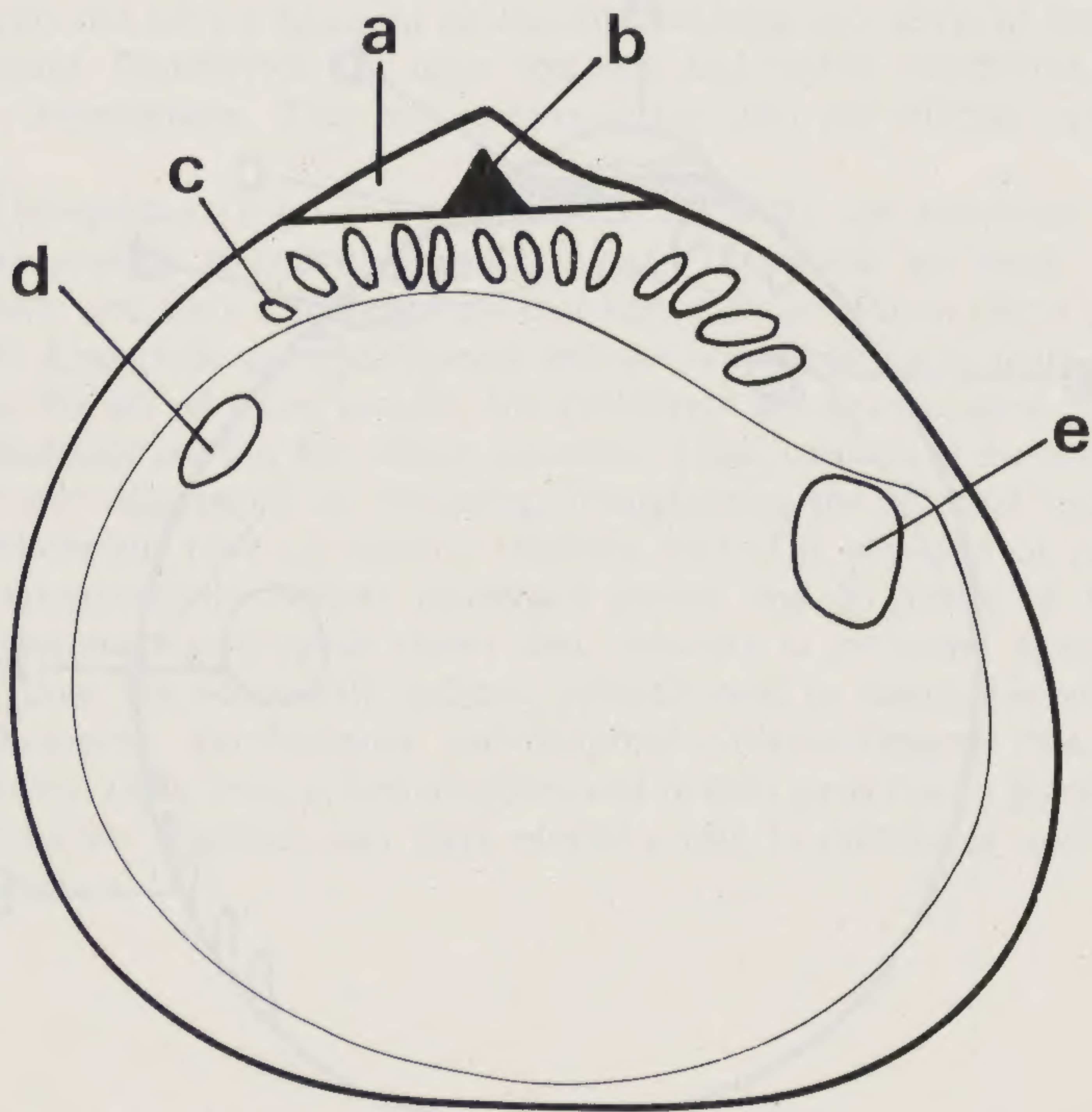
FIG. 2. Morphological features of the limopsid shell. a = dorsal area, b = ligament pit, c = tooth, d = anterior adductor muscle scar, e = posterior adductor muscle scar.

Except for species descriptions, the philobryid and limopsid literature is small. For philobryids, Bernard (1897), Thiele (1923), Dell (1964), Nicol (1966), Cox et al. (1969), and Bergmans (1970) briefly deal with aspects of supraspecific taxonomy. Pelseneer (1903), Clasing (1918), and Burne (1920) describe and diagram the anatomy of five different species. Cox et al. (1969) briefly summarize limopsid supraspecific taxonomy, and Dell (1964) comments on their variability and taxonomic problems. Nicol (1967) points out differences between the hard parts of *Limopsis* and *Glycymeris*. Pelseneer (1888; 1911) and Burne (1920) describe the soft parts of four different *Limopsis* species. No one has yet published observations on living limopsids or philobryids, nor looked at either family as a whole.

The purpose of this study is to revise the supraspecific taxonomy of both families and elucidate their autecology. First, the generic taxonomy of both families is revised. This revision consists of providing morphological definitions of both families and redescribing and discussing all valid genera in each family. Second, the life habits of these two families are described and analyzed. Much of the information in this second part comes from observing live individuals from both families. Third, information from the first two parts of this study is used to complete the supraspecific taxonomic revision. Criteria for morphologically characterizing the Arcoida are proposed and philobryids and limopsids are compared to these criteria. Then, the evolutionary history of both families is traced.

Abbreviations and Definitions

USNM   United States National Museum of Natural History, Washington, D.C.
BM   British Museum (Natural History), London
AM   Australian Museum, Sydney
SAM   South Australian Museum, Adelaide
M.   Monotypy
O.D.   Original Designation
S.D.   Subsequent Designation

In the description of the type species for each genus, the dimensions cited refer to an individual used in the description that the author considers to be an average-size adult for the particular species. Width is measured dorsoventrally. Length is measured anteroposteriorly.

Except where otherwise noted, the description of the type species for each valid genus is based on Recent material.

"Range of Morphological Variation" refers to the range for the genus as a whole, not just the type species.

2. Generic Revisions of the Families Philobryidae and Limopsidae

A redescription and discussion of each valid philobryid and limopsid genus is presented. A valid genus is here considered to be a form separated from all others by multiple, nongradational morphological differences. Because of their more conservative nature, hinge features are subjectively weighted more highly than features such as shell shape, color, and the nature of the inner margins.

Revision of the Genera of the Philobryidae

1) Morphological Definition

A member of the Philobryidae is here considered to be any bivalve that, as an adult, has both of the following features: 1) a ligament pit that lies between two rows of numerous, interlocking transverse denticles and 2) a filibranch gill with a posteriorly directed, ventral ciliary tract. The available generic and subgeneric names for the Philobryidae and their dispositions by recent workers are shown in Table 1. The valid philobryid genera sorted from these names are described and discussed below. Their geological and geographic ranges are given in Appendix A, and redescriptions of the junior subjective synonyms are given in Appendix B.

TABLE 1. Recent dispositions of philobryid generic and subgeneric names.

Dell (1964)

Valid genera. *Philobrya, Adacnarca, Lissarca, Verticipronus, Neoconcha* (= *Neocardia*).

Synonyms of *Philobrya. Philippiella, Stempellaria, Stempellia* (also name previously occupied).

Vokes (1967)

Nomenclaturally valid names listed under the heading "Philobryidae." *Adacnarca, Cosa, Cosatova, Cratis, Denticosa, Hochstetteria, Hochstetterina, Limarca, Limopsilla, Lissarcula, Micromytilus, Notomytilus, Philippiella, Philobrya, Stempelleria.*

Cox et al. (1969)

Valid genera. *Philobrya, Aupouria, Cosa, Cratis, Limarca.*

Synonyms of *Philobrya. Philippiella, Stempellaria, Stempellia* (also name previously occupied).

Subgenera of *Philobrya. Philobrya, Adacnarca, Neocardia, Micromytilus, Hochstetterina, Hochstetteria, Notomytilus.*

Bergmans (1970)

Valid genera. *Lissarca, Cratis.*

Synonym of *Lissarca: Austrosarepta;*
       of *Cratis: Denticosa.*

2) Valid Genera

Genus ADACNARCA

AUTHOR. Pelseneer, 1903, p. 24.

TYPE SPECIES. (M.) *Adacnarca nitens* Pelseneer, 1903, p. 24.

Described here from Pelseneer's (1903) original description and illustrations; also from examination of several nontype individuals from the USNM (Fig. 3).

Ligament pit short and triangular. Anterior series of denticles equal to 1/3× length and 1× width of posterior series. No teeth. Outer surface with numerous, fine, radial lines. Shape ovoid; slightly anteriorly reduced. Color white. This species seldom exceeds a length of 5 mm or a width of 6 mm. Although Pelseneer (1903) mentions that this species has an anterior adductor muscle, no other worker (including myself) has noticed this feature in *A. nitens*.

JUNIOR SYNONYM. *Hochstetterina* Thiele, 1934, p. 796.

TYPE SPECIES. (O.D.) *Hochstetteria crenella* Vélain, 1877, p. 131.

The following material was examined: 1) the original descriptions and illustrations of *A. nitens* and *H. crenella* and 2) several dozen of nontype *A. nitens* from the USMN. This comparison shows that these two species differ principally in shell shape and external ornamentation. *A. nitens* has a prominent anterior, is highly inflated, and is radially lined externally. *H. crenella* has a reduced but lobate anterior, is moderately inflated, and is concentrically lined externally.

For the Pelecypoda, Stanley (1970) shows that shell shape and external ornamentation are closely tied to life habits. Therefore, shell outline and external ornamentation alone are here considered insufficient reasons for separating *Adacnarca*, and *Hochstetterina* as distinct genera.

RANGE OF MORPHOLOGICAL VARIATION. Shell shape: submytiliform to ovate; strongly inflated to flat. External ornamentation: radial only to concentric only. Inner margins: prominently crenulated to smooth. Anterior denticle series: 1/3×–1× length of posterior series.

DIAGNOSTIC FEATURES. *Adacnarca* is edentulous and has a small, triangular ligamental pit.
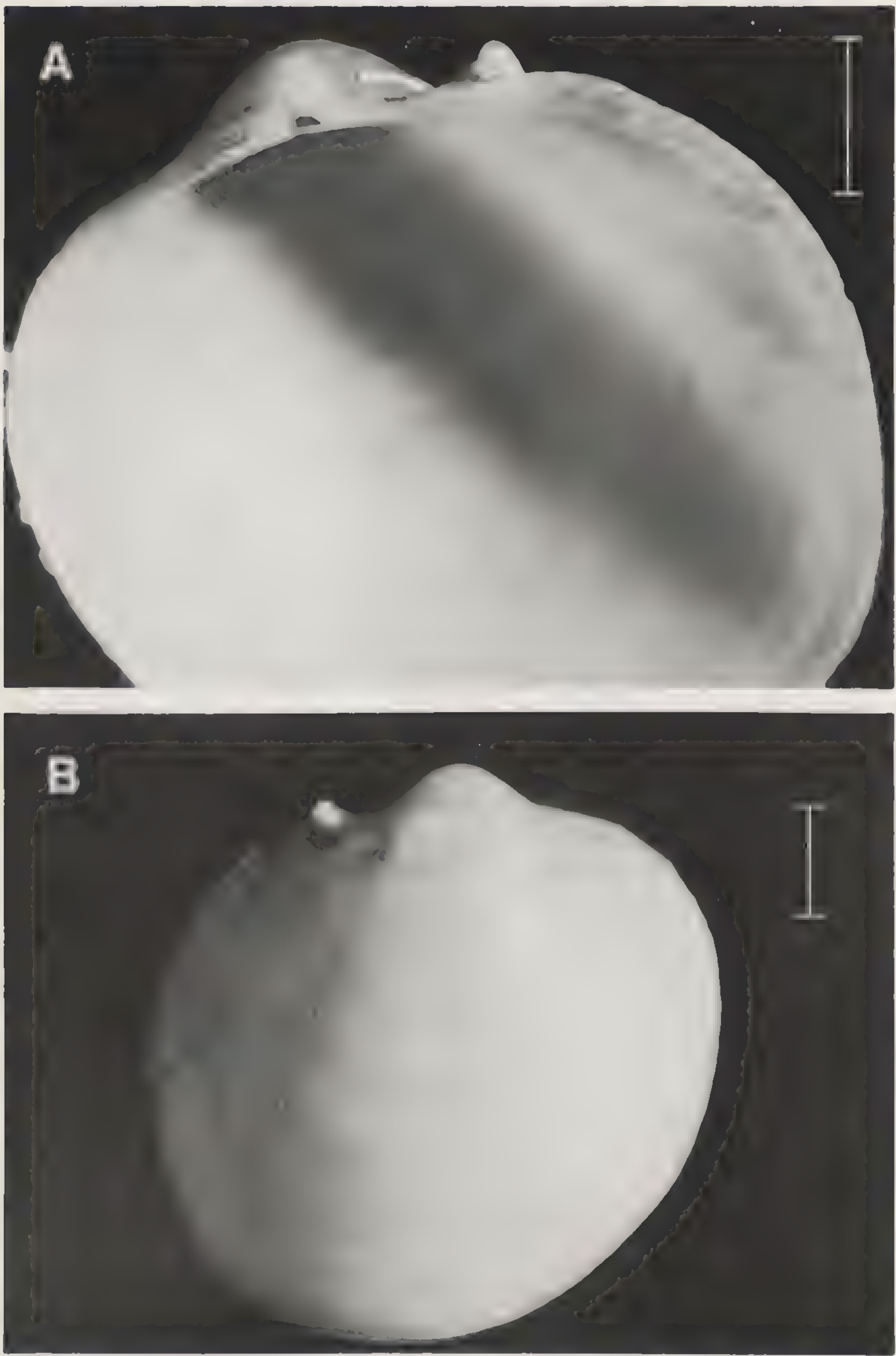
FIG. 3. *Adacnarca nitens* Pelseneer. USNM 613015; from Antarctica. *A*) Right valve, interior. *B*) Right valve, exterior. Scale = 1 mm.
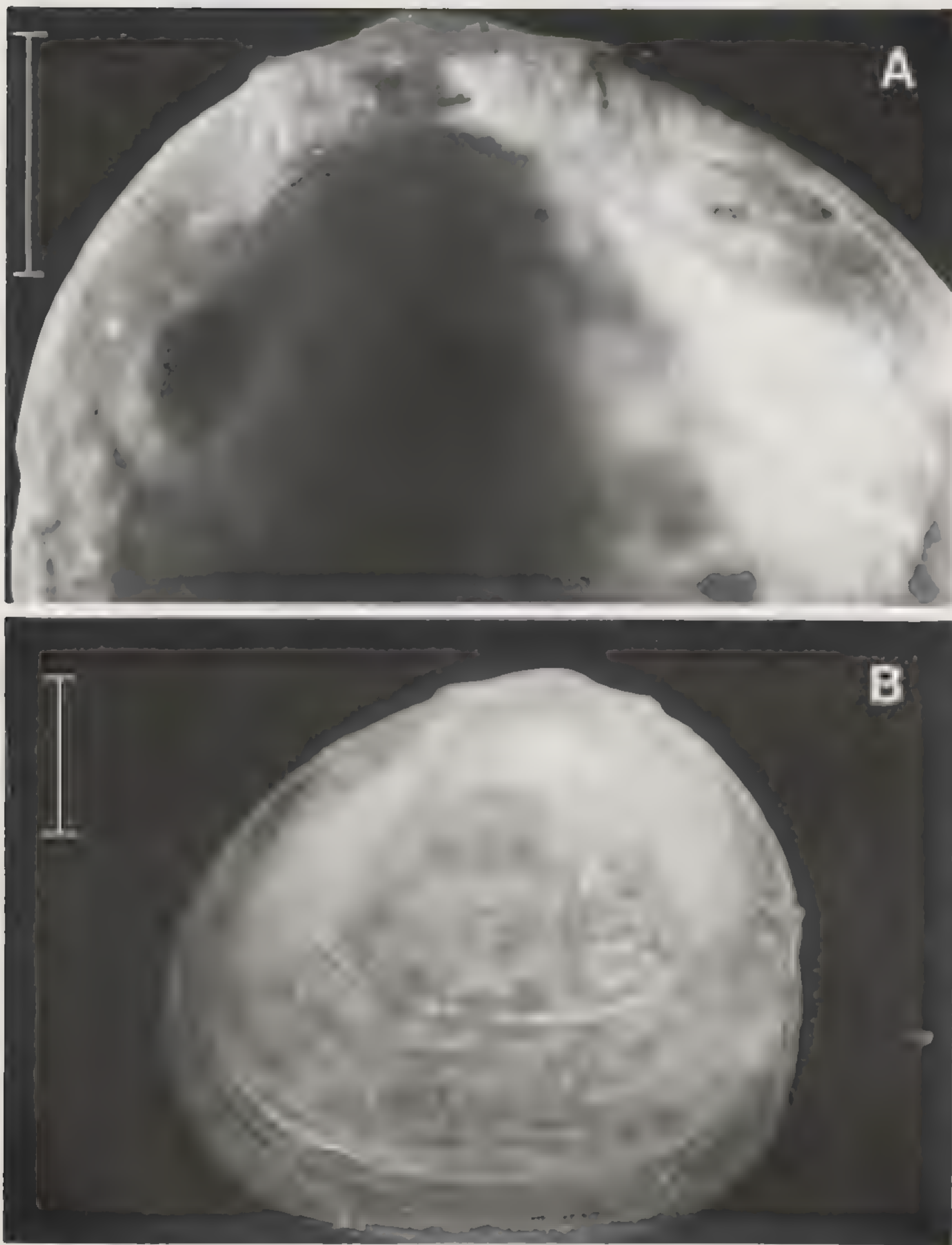
FIG. 4. *Aupouria parvula* Powell. Paratype; BM; from Three Kings Island, New Zealand. *A*) Right valve, interior. *B*) Right valve, exterior. Scale = 0.5 mm.

Genus AUPOURIA

AUTHOR. Powell, 1937, p. 164.

TYPE SPECIES. (O.D.) *Aupouria parvula* Powell, 1937, p. 164.

Described here from paratypes collected off Three Kings Island, New Zealand; located in the BM (Fig. 4).

Ligament pit shaped like an inverted *U* and located directly under umbo. Anterior and posterior series of denticles about the same length and width. Two prominent anterior teeth. Adductor muscle scars round, prominent and about the same size. Inner margins smooth. External surface with faint concentric markings. Prodissoconch prominently domed. Shape ovoid. Color white. Length = 2.2 mm. Width = 2.1 mm.

JUNIOR SYNONYMS. No other generic names have been proposed for forms resembling the type species.

RANGE OF MORPHOLOGICAL VARIATION. Too few available individuals to determine.

DIAGNOSTIC FEATURES. *Aupouria* is the only philobryid that has anterior but no posterior teeth.

Genus COSA

AUTHOR. Finlay, 1926, p. 449.

TYPE SPECIES. (O.D.) *Hochstetteria costata* Bernard, 1896a, p. 194.

Described here from syntypes, USNM 107763; collected from Stewart Island, New Zealand (Fig. 5).

Ligament pit short and triangular. Anterior series of denticles equal to 1/3× length and 1× width of posterior series. No teeth. Inner margins crenulated. Outer surface with about eleven raised radial ridges overlaid by a concentric pattern. Prodissoconch with prominent raised rim. Color light tannish. Mytiliform; greatly reduced anteriorly. Length = 2.5 mm. Width = 3.5 mm.

JUNIOR SYNONYMS. No other generic names have been proposed for forms resembling the type species.

RANGE OF MORPHOLOGICAL VARIATION. Shell shape: mytiliform to ovate. External ornamentation: radial to cancellate to concentric. Inner margins: crenulated to smooth. Color: white to tan.

DIAGNOSTIC FEATURES. *Cosa* is the only edentulous philobryid with all of the following features: highly prominent denticles, a prominent prodissoconch and a small, triangular ligament pit.
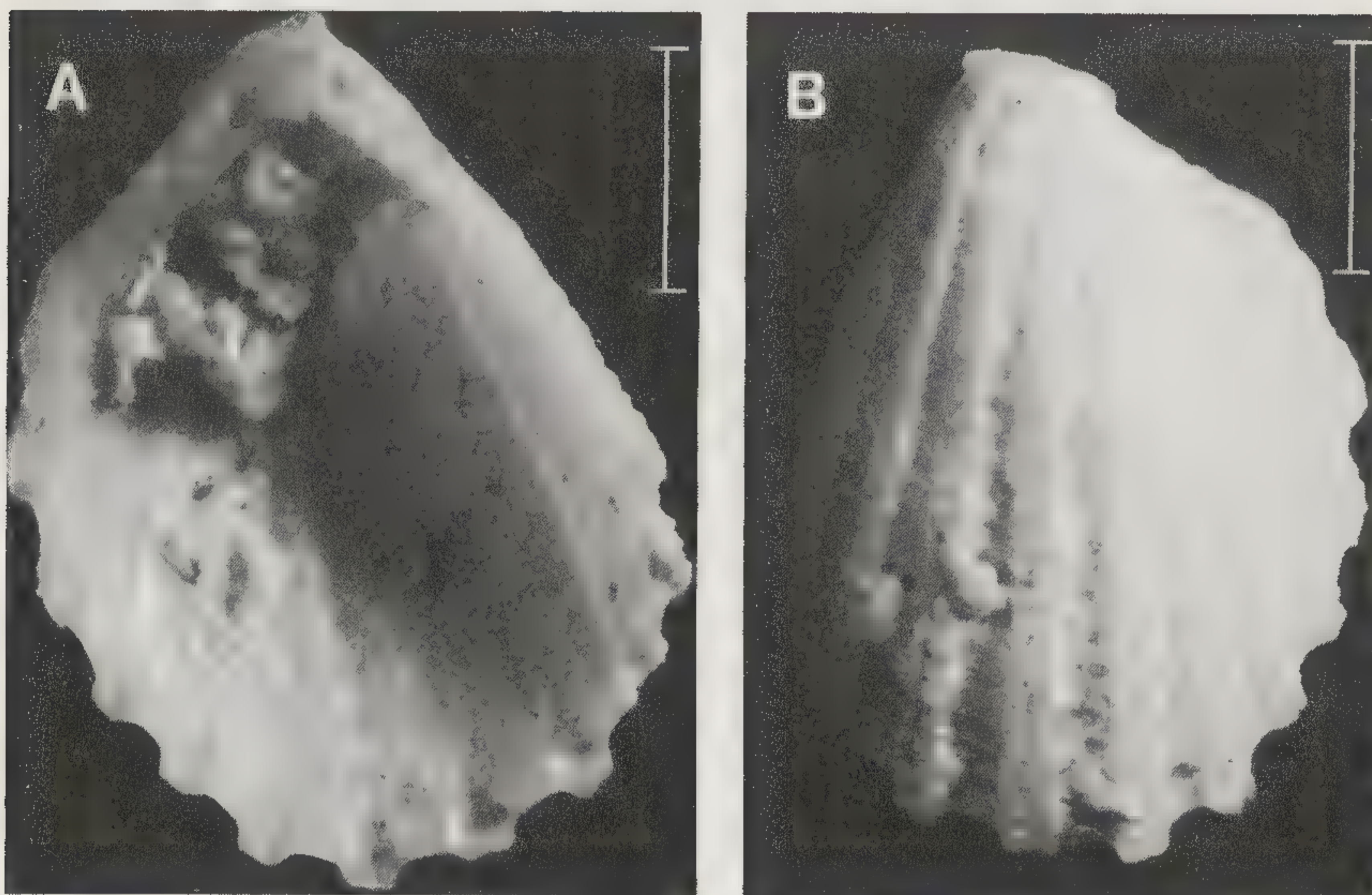
FIG. 5. *Cosa costata* (Bernard). Syntype; USNM 107763; from Stewart Island, New Zealand. *A*) Left valve, interior. *B*) Left valve, exterior. Scale = 1 mm.

Genus CRATIS

AUTHOR. Hedley, 1915, p. 698.

TYPE SPECIES. (O.D.) *Cratis progressa* Hedley, 1915, p. 698.

Described here from examination of syntypes; collected dead from 100 fms. off Port Macquarie, New South Wales, Australia; AM c37760 (Fig. 6).

Ligament pit strongly triangular and located directly under umbo. Anterior and posterior series of denticles about the same length and width. Two to three perpendicular anterior teeth; three oblique to horizontal posterior teeth. Inner margins crenulated; most strongly so posteroventrally. External surface with prominent cancellate ornamentation; beaded. Prodissoconch with a broad rim and prominent central boss. Shell shape submytiliform; margins rounded. Color white. Length = 3.2 mm. Width = 4 mm.

JUNIOR SYNONYMS.
 Denticosa Iredale, 1930, p. 385.

TYPE SPECIES. (O.D.) *Philobrya cuboides* Verco, 1907, p. 223.
 Cosatova Iredale, 1939, p. 304.

TYPE SPECIES. (O.D.) *Philobrya recapitula* Hedley, 1906, p. 471.
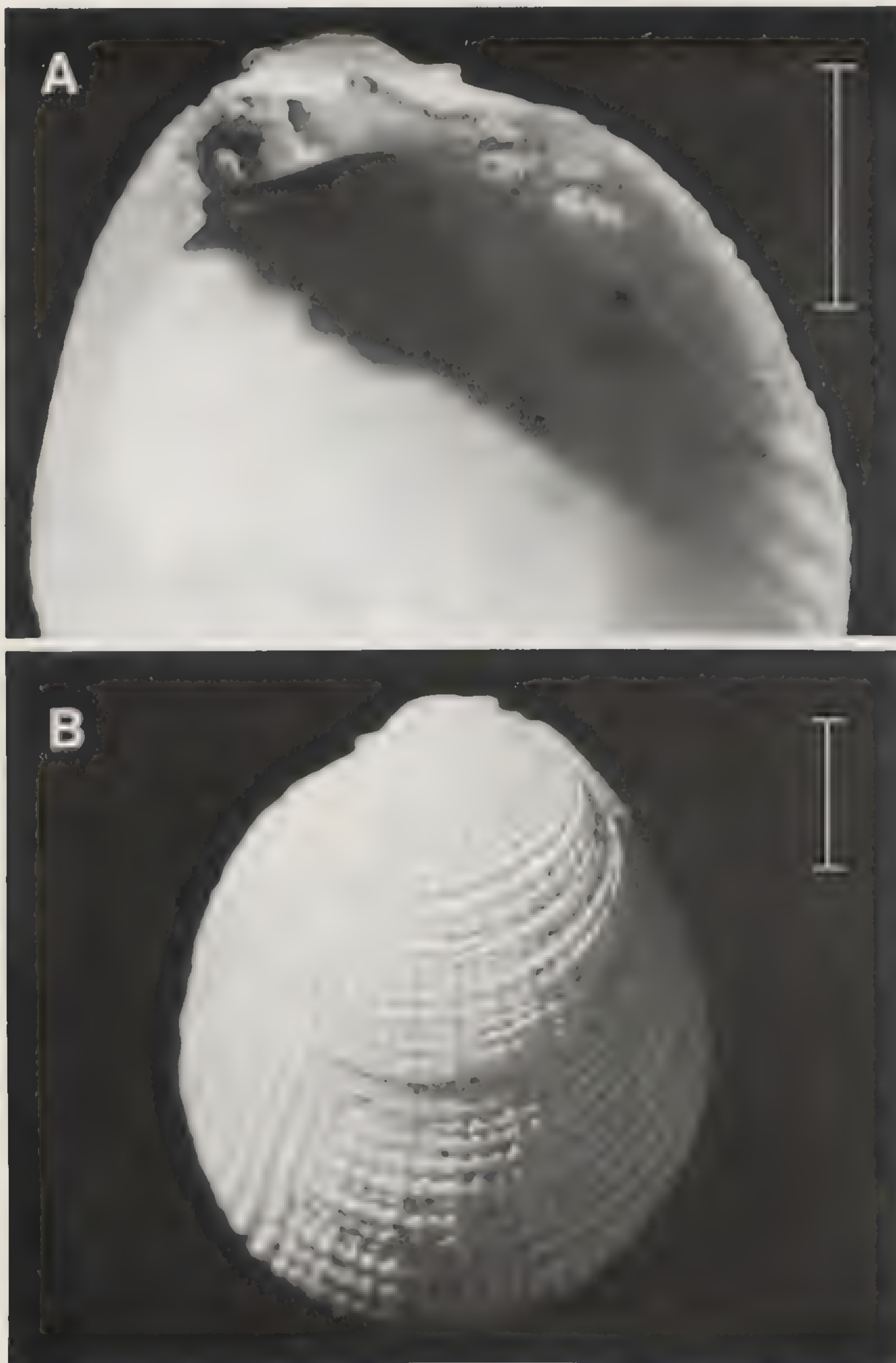
FIG. 6. *Cratis progressa* Hedley. Syntype; AM c37760; from 100 fms., off Port Macquarie, New South Wales, Australia. *A*) Right valve, interior. *B*) Right valve, exterior. Scale = 1 mm.

Iredale's descriptions of *Denticosa* (1930) and *Cosatova* (1939) fail to show how these supposedly distinct genera differ from *Cratis*. To discover these differences, several individuals of all three type species were compared. The examined holotype of *P. cuboides* is in the SAM; the examined syntypes of *P. recapitula* are in AM c19390. The principal differences among the type species of *Cratis*, *Cosatova*, and *Denticosa* are in tooth number and the shape of the anterior margin. *P. cuboides* has 1 to 2 anterior teeth and a rounded anterior margin. *P. recapitula* has 1 anterior tooth and a straight anterior margin. *C. progressa* has 2 to 3 anterior teeth and rounded anterior margin. Both of these features are quite variable intraspecifically within the Philobryidae. For example, some *Philobrya magellanica* (USNM 110735) have a deeply concave anterior margin while others in the same lot have a nearly straight anterior margin. Many other species in this family show a similar but less pronounced variation in the shape of this feature. The reason for this variation may be related to the epibyssate life habit of philobryids. Since their byssus emerges anteriorly, the anterior margin of the shell is in prolonged contact with the substratum. As in the byssate *Mytilus* and *Anomia*, shell shape may conform to the shape of the substratum upon which it rests. Tooth number can vary from valve to valve in these three species. For example, the left valve of most *C. progressa* has three anterior teeth, where the right valve has only two anterior teeth. In other dentate philobryids, tooth number may vary intraspecifically by as many as four per series (Nicol, 1966).

Since the principal differences among these type species are few and are manifest in features that are quite variable intraspecifically in philobryids, *Cosatova* and *Denticosa* are here considered generically indistinguishable from *Cratis*.

RANGE OF MORPHOLOGICAL VARIATION. Shell shape: anterior round and prominent to anterior straight and highly reduced. Dentition: 1–3 anterior teeth; 1–3 posterior teeth. Prodissoconch: flat to knobbed to prominently spiked. Denticles: anterior series $1\times$ to $1/4\times$ length of posterior series.

DIAGNOSTIC FEATURES. *Cratis* is the only philobryid that has all of the following features: a triangular ligament pit, anterior and posterior teeth, and a beaded external surface.

Genus LIMARCA

AUTHOR. Tate, 1886, p. 135.

TYPE SPECIES. (M.) *Limarca angustifrons* Tate, 1886, p. 135.

Described here from examination of the holotype; from Eocene deposits (borehole) near Adelaide, South Australia. SAM T1002 (Fig. 7).

Ligament pit straight and very long, extending posteriorly. Anterior series of denticles equal to $1\times$ width and $1/4\times$ length of posterior series. Three
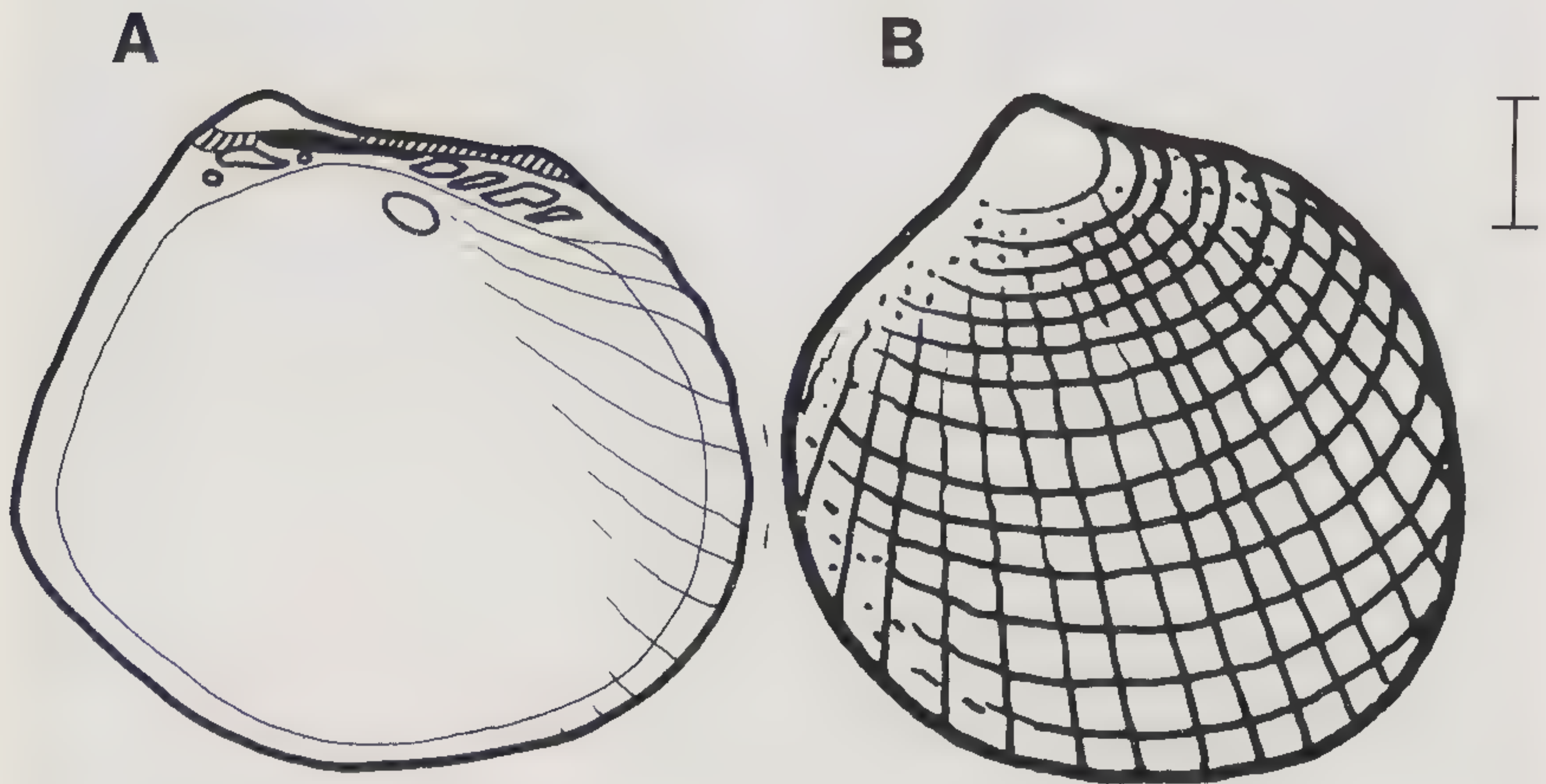
FIG. 7. *Limarca angustifrons* Tate. Drawn from holotype, SAM T 1002; from Adelaide. *A*) Right valve, interior. *B*) Left valve, exterior. Scale = 1 mm.

oblique anterior and four oblique posterior teeth. Inner margins crenulated. Outer surface with prominent cancellate ornamentation; beaded. Shape submytiliform. Prodissoconch with prominent central boss. Length = 5.5 mm. Width = 5.5 mm.

JUNIOR SYNONYMS. No other generic names have been proposed for forms resembling the type species.

RANGE OF MORPHOLOGICAL VARIATION. Too few available individuals to determine this.

DIAGNOSTIC FEATURES. *Limarca* is the only dentate philobryid with a long, straight ligament pit.

Genus LIMOPSILLA

AUTHOR. Thiele, 1923, p. 289.

TYPE SPECIES. (O.D.) *Limopsis pumilio* Smith, 1904, p. 43.

Described here from syntypes collected from Cape Colony, South Africa; located in the BM (Fig. 8).

Ligament pit large, triangular, and located directly under umbo. Anterior and posterior series of denticles about the same length and width. Right valve with three anterior and four posterior teeth. Left valve with three anterior and five posterior teeth. Posterior adductor muscle scar slightly larger than anterior adductor muscle scar; both scars prominent and ovoid.
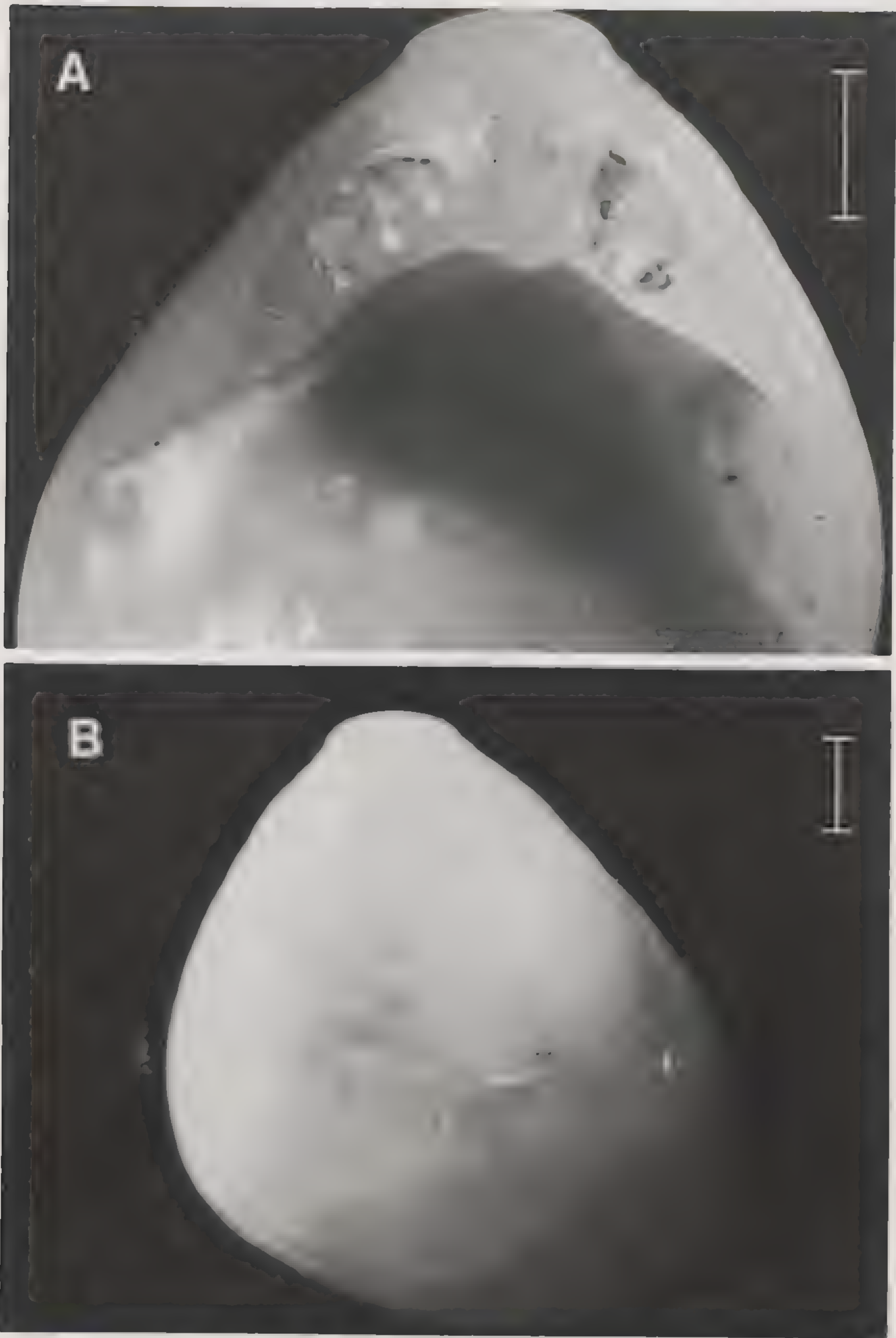
FIG. 8. *Limopsilla pumilio* (Smith). Syntype; BM; from South Africa. *A*) Left valve, interior. *B*) Left valve, exterior. Scale = 0.5 mm.

Inner surface with radial lines; inner margins smooth. Outer surface with concentric ridges. Faint saclike depression on central part of dorsal margin. Shape subtriangular; margins rounded. Color white. Length = 3.0 mm. Width = 3.3 mm.

JUNIOR SYNONYMS. No other generic names have been proposed for forms resembling the type species.

RANGE OF MORPHOLOGICAL VARIATION. Too few available individuals to determine.

DIAGNOSTIC FEATURES. *Limopsilla* is the only philobryid with both a saclike depression on the dorsal margin and a broad hinge area.

Genus LISSARCA

AUTHOR. Smith, 1877, p. 185.

TYPE SPECIES. (M.) *Arca* (*Lissarca*) *rubrofusca* Smith, 1877, p. 185.

Described here from syntypes collected from Kerguelen Island in the Indian Ocean, and located in the BM (Fig. 9).

Ligament pit triangular and located near umbo. Anterior series of denticles equal to 1× width and 3/4× length of posterior series. 4 anterior teeth; 4 posterior teeth. Inner margins prominently crenulated. Outer surface with fine concentric lines. Prodissoconch flat, smooth. Shape subelliptical. Color reddish. Length = 4 mm. Width = 2.5 mm.

JUNIOR SYNONYMS.
        Austrosarepta Hedley, 1899, p. 430.

TYPE SPECIES. (M.) *Austrosarepta picta* Hedley 1899, p. 430.
        Lissarcula Thiele, 1923, p. 290.

TYPE SPECIES. (M.) *Lissarcula australis* Thiele 1923, p. 290.
        Notolimopsis Maxwell, 1969, p. 167.

TYPE SPECIES. (O.D.) *Notolimopsis pulchra* Maxwell 1969, p. 167.

After examining the syntypes of *Lissarca rubrofusca*, the syntypes of *Austrosarepta picta* (AM c6378), Thiele's (1923) description of *Lissarcula australis*, and Maxwell's (1969) description and illustrations of *Notolimopsis pulchra*, it is clear that the main difference between these forms is tooth number. *L. rubrofusca* has 4 anterior and 4 posterior teeth; *A. picta* has 2 anterior and 3 posterior teeth; *L. australis* has 2 anterior and 2 posterior teeth; *N. pulchra* has 4 to 6 teeth in each series.

Tooth number variation has already been discussed for some philobryids, and at least one *Lissarca* species shows great variation in tooth number. Examination of the many *Lissarca notorcadensis* in the USNM confirms
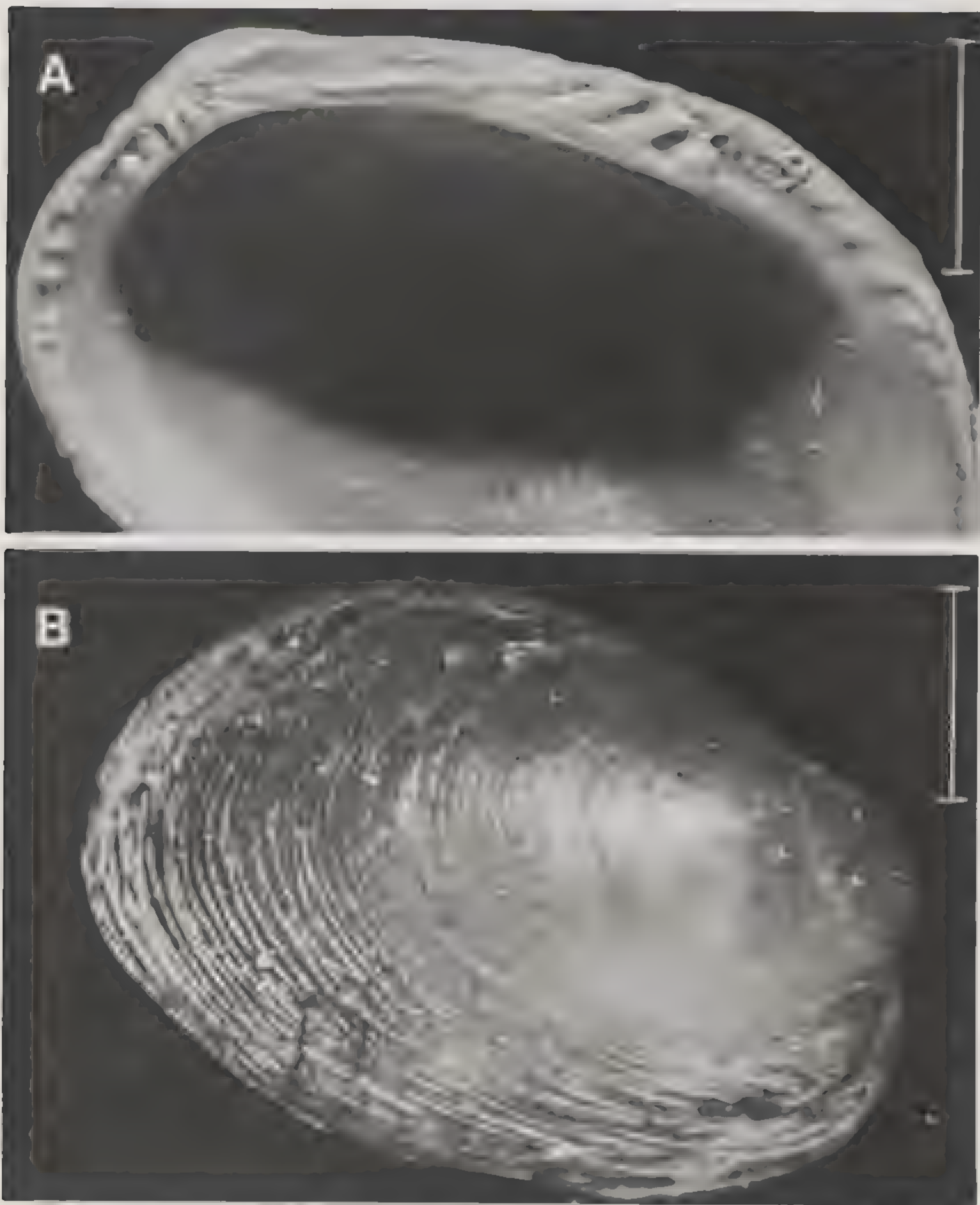
FIG. 9. *Lissarca rubrofusca* Smith. Syntype; BM; from Kerguelen Island. *A*) Right valve, interior. *B*) Right valve, exterior. Scale = 1 mm.

comments made by Nicol (1966) concerning the same material. He says that there may be as many as six teeth on either side (of the umbo) or as few as two. The present writer has observed that the larger individuals of this species usually have the most teeth. This large intraspecific variation in tooth number in certain species of *Lissarca* argues against a separation of *Lissarca, Austrosarepta, Lissarcula,* and *Notolimopsis* based on small differences in tooth number.

RANGE OF MORPHOLOGICAL VARIATION. Shell shape: subrhomboidal to subelliptical. Tooth number: 2 to 6 anterior teeth; 2 to 6 posterior teeth. Outer surface: smooth to prominent radial folds. Color: red to white.

DIAGNOSTIC FEATURES. *Lissarca* is the only philobryid with anterior and posterior teeth, and is always longer than it is wide.

Genus NEOCARDIA

AUTHOR. Sowerby, 1892, p. 63.

TYPE SPECIES. (M.) *Neocardia angulata* Sowerby, 1892, p. 63.

Described here from paratypes collected from South Africa and located in the BM (Fig. 10).

Ligament pit long and narrow, extending well posterior of the umbo. Anterior series of denticles about $1 \times$ width and $1/2 \times$ length of posterior series; both series tapering. 2 posterior teeth. Inner margins smooth. Outer surface uniformly covered with concentric ridges; prominent radial ridges posteriorly only. Prodissoconch with raised edges. Shape submytiliform. Color white. Length $= 4$ mm. Width $= 4.1$ mm.

JUNIOR SYNONYMS. No other generic names have been proposed for forms resembling the type species.

RANGE OF MORPHOLOGICAL VARIATION. External surface: smooth; with concentric lines only, varying to forms with cancellate ornamentation; with prominent radial ridges.

DIAGNOSTIC FEATURES. *Neocardia* is the only philobryid with posterior teeth only.

Genus PHILOBRYA

AUTHOR. Carpenter, 1872, Index p. 21.

TYPE SPECIES. (M.) *Bryophila setosa* Carpenter, 1864, p. 314.

Described here from syntypes, USNM 16187; collected from Cape St. Lucas, Mexico (Fig. 11).

Ligament pit narrow, elongate, and extending well posterior of the umbo; does not descend across the hinge. Anterior series of denticles equal to $1\ 1/2 \times$ width and $1/4 \times$ length of posterior series. No teeth. Inner margins smooth. External surface with faint concentric lines. Prodissoconch slightly domed. Shape mytiliform. Color tannish to white. Length $= 2.5$ mm. Width $= 3$ mm.

JUNIOR SYNONYMS.
        Hochstetteria Vélain, 1877, p. 129.
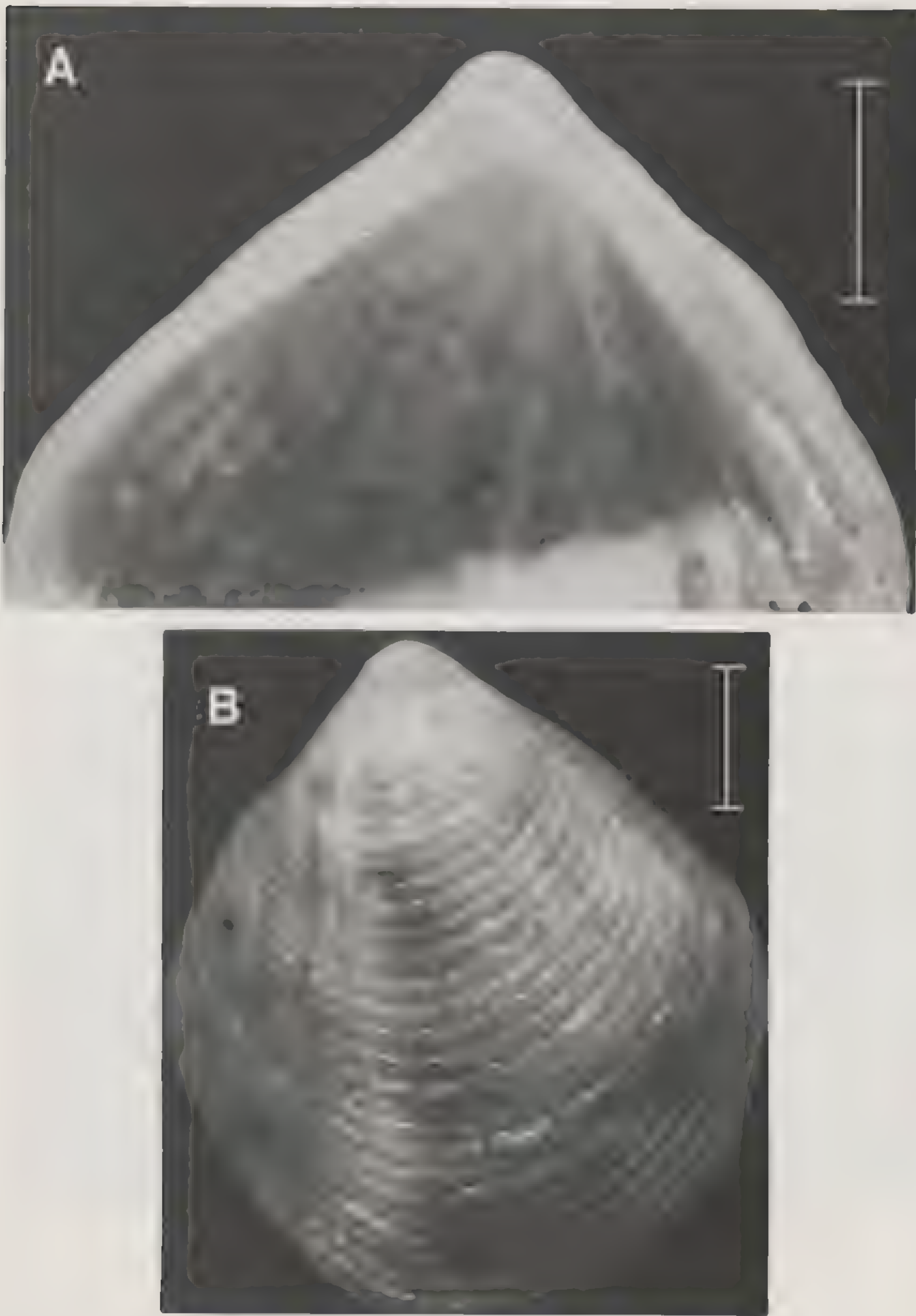
FIG. 10. *Neocardia angulata* Sowerby. Paratype; BM South Africa. *A*) Right valve, interior. *B*) Right valve, exterior. Scale = 1 mm.

FIG. 11. *Philobrya setosa* (Carpenter). Syntype; USNM 16187; from Cape St. Lucas, Baja California, Mexico. *A*) Left valve, interior. *B*) Left valve, exterior. Scale = 0.5 mm.

TYPE SPECIES. (S.D.-Kobelt, 1881) *Hochstetteria aviculoides* Vélain, 1877, p. 130.

Philippiella Pfeffer, 1886, p. 119.

TYPE SPECIES. (S.D.-Dell, 1964) *Philippiella quadrata* Pfeffer, 1886, p. 119.

Notomytilus Hedley, 1916, p. 20.

TYPE SPECIES. (O.D.) *Philippiella rubra* Hedley, 1940a, p. 207.

Stempelleria Clasing, 1918, p. 22.

TYPE SPECIES. (M.) *Avicula magellancia* Stempell, 1899, p. 230.

Micromytilus Cotton, 1931, p. 335.

TYPE SPECIES. (O.D.) *Myrinia crenatulifera* Tate, 1892, p. 131.

The original descriptions and illustrations of the five species listed above, along with the syntypes of *N. rubra* (AM c17723) and holotype of *M. crenatulifera* (SAM D13051) were compared to syntypes of *P. setosa*. The principal difference among these forms is the length and shape of the ligament pit. The pit of *N. rubra* descends sharply across the dorsal margin; the pit of *P. setosa* parallels the dorsal margin; the ligament pit is relatively long in *P. setosa* and relatively short in *M. crenatulifera*. The length and shape of the pit in the other species falls between these extremes.

Figure 12 shows that, for philobryids, a continuum of ligament pit lengths and curvatures exists between these extremes. Thus there are no natural discontinuities in these two aspects of this feature that could be used for separating genera.

RANGE OF MORPHOLOGICAL VARIATION. Shell shape: mytiliform to ovoid; umbos hooked to straight. Anterior denticle series: $1/3\times-1/6\times$ length of posterior series to $1\times-1\,1/2\times$ width of posterior series. Inner margins: smooth to crenulated. Ligament pit: straight to strongly curved; relatively short to relatively long.

DIAGNOSTIC FEATURES. *Philobrya* is the only edentulous philobryid with a nontriangular, somewhat elongate, ligament pit.

Revision of the Genera of the Limopsidae

1) Morphological Definition
A member of the Limopsidae is here considered to be any bivalve that has the following features:
   a) ligamental pit;
   b) radially arrayed, alternating fibrillar and lamellar ligamental material;
   c) small, mostly internal dorsal area that is smooth or that has oblique striations.
The available generic names for this family and their dispositions by recent writers are given in Table 2.
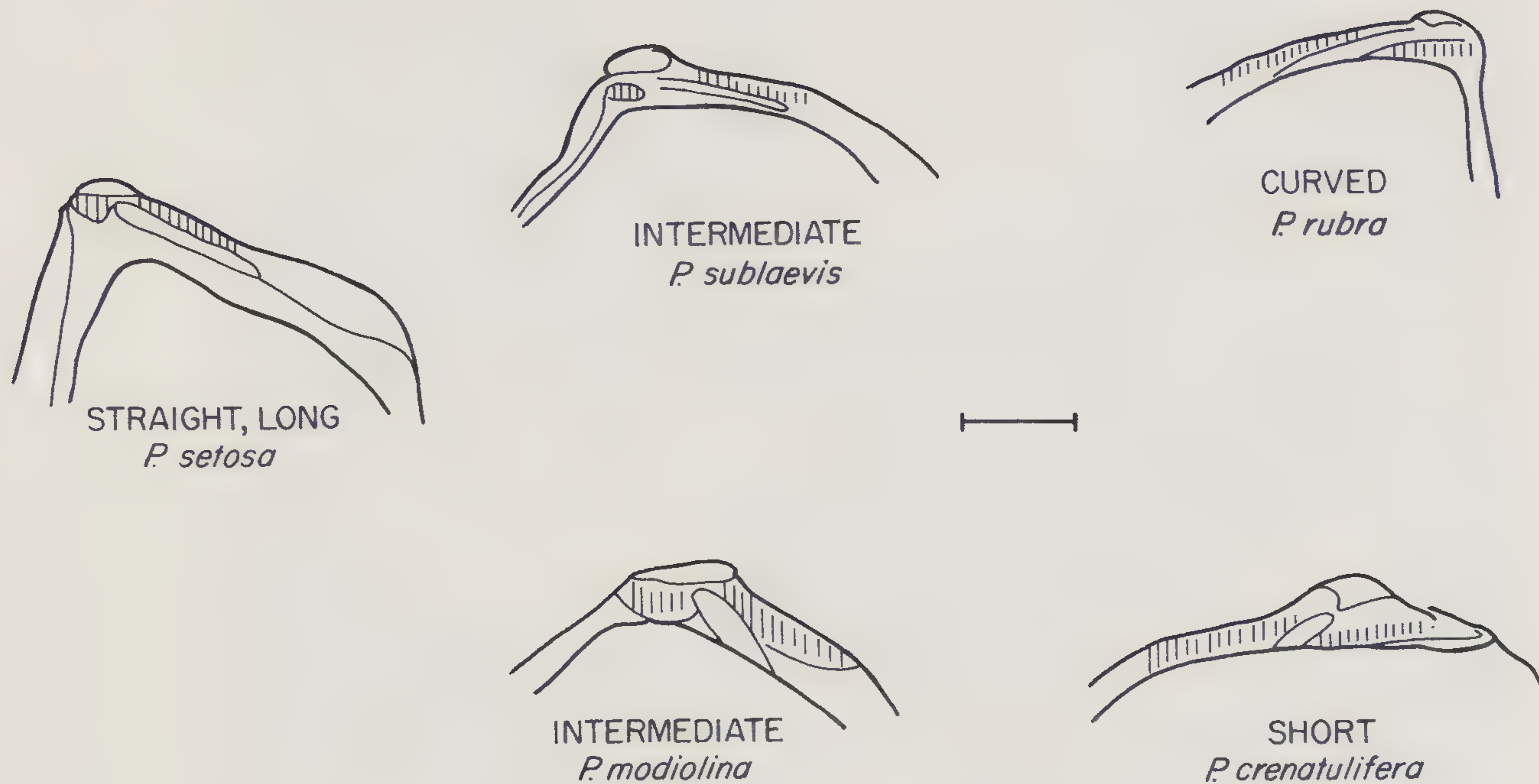
FIG. 12. Ligament pit variations in *Philobrya*. (After Bernard, 1897; Hedley, 1904a.) Scale = 2 mm.

TABLE 2. Recent dispositions of limopsid generic and subgeneric names.

Vokes (1967)

Nomenclaturally valid names listed under the heading "Limopsidae." *Aspalima, Aupouria, Austrosarepta, Circlimopa, Cnisma, Cosmetopsis, Cyrenolimopsis, Empleconia, Felicia, Glycilima, Limopsis, Limopsista, Lissarca, Loringella, Lunopsis, Nipponolimopsis, Oblimopa, Ovalarca, Pectunculina, Phrynelima, Senectidens, Vasconella, Versipella, Vetoarca.*

Cox et al. (1969)

Valid genera. *Empleconia, Limopsis, Hoferia, ·Lissarca, Nipponolimopsis,* ? *Nucunella, Pichleria,? Vasconella.*

Synonyms of *Limopsis (Limopsis). Trigonocoelia* (obj.), *Lunopsis, Cnisma, Limopsilla, ? Lissarcula, Loringella, Phrynelima, Glycilima.*

Synonyms of *Limopsis (Pectunculina). Cosmetopsis, Aspalima, Senectidens, Versipella, Limopsita, Circlimopa, Oblimopa.*

Synonyms of *Hoferia. Bittnerella, Elegantarca, Arcoptera.*

Synonym of *Lissarca. Austrosarepta.*

Synonym of *Vasconella. Boussacia.*

Subgenera of *Limopsis. Pectunculina, Limopsis.*

2) Valid Genera

Genus EMPLECONIA

AUTHOR. Dall, 1908, p. 393.

TYPE SPECIES. *Limopsis vaginata* Dall, 1891, p. 190.

Described here from examination of paratypes, USNM 122547, from the Bering Sea (Fig. 13).

Ligament pit approximately one-half of dorsal area. About 11 anterior and 7 posterior teeth. Posterior margin prominently infolded; forms declevity between closed valves. Adductor muscle scars ovoid and prominent. Inner margins smooth. External surface with numerous concentric lines. Shape subelliptical; anteriorly reduced; margins rounded. Covered with a brown, hairy periostracum. Length = 30 mm. Width = 28 mm.

JUNIOR SYNONYMS. No other generic names have been proposed for forms resembling the type species.

RANGE OF MORPHOLOGICAL VARIATION. Tooth number: 5 to 12 anterior and posterior teeth.

DIAGNOSTIC FEATURES. This is the only limopsid with a deeply infolded posterior margin.

FIG. 13. *Empleconia vaginata* (Dall). Paratype; USNM 122547; from 351 fms., Bering Sea. *A*) Right valve, interior. *B*) Right valve, exterior. Scale = 4 mm.

Genus LIMOPSIS

AUTHOR. Sasso, 1827, p. 476.

TYPE SPECIES. (O.D.) *Arca aurita* Brocchi, 1814.

Described here from Brocchi's (1814) original figures and nontype material, USNM 62848. Brocchi's material is from the Pliocene of Italy (Fig. 14).

Ligamental pit approximately 1/3 of dorsal area; dorsal smooth. Dentition consisting of about 15 small, transverse teeth arranged in an arcuate series below dorsal area. Anterior adductor muscle scar about 3/4× area of posterior scar. Both scars ovoid and prominent. Inner margins smooth. Exterior with numerous concentric lines. Shape ovoid; anteriorly reduced. Length = 12.5 mm. Width = 13 mm.

JUNIOR SYNONYMS. There are about seventeen available generic or subgeneric names based on species which resemble *L. aurita.* This proliferation of names for *Limopsis*-like forms stems from the following two related causes: 1) no one has outlined the range of morphologic variation in *Limopsis* and 2) few authors proposing these names bothered to compare their prospective genus with *Limopsis aurita.*

To see which, if any, of these *Limopsis*-like forms represent valid genera, the type species for each name was examined and briefly described (Appendix B). Inspection of these descriptions shows that all these forms possess the same principal morphological features. Thus, there are no major morphological discontinuities that can be used to separate these forms as discrete genera. Moreover, all these forms share the same principal features with *Limopsis aurita.* These other names are therefore considered to be junior subjective synonyms of *Limopsis.*

RANGE OF MORPHOLOGICAL VARIATION. Ligament pit: covers 1/6 to 3/4 of dorsal area. Tooth number: 7 to 28. Shell shape: subelliptical to subcircular to subtriangular; equilateral to anteriorly reduced. Inner margins: smooth to crenulated. External surface sculpture: cancellate to concentric to radial.

DIAGNOSTIC FEATURES. *Limopsis* is the only limopsid with a nonfolded posterior margin.

Reassignments

The genera mentioned below often are associated with the Philobryidae or Limopsidae (e.g. Cox et al., 1969; Vokes, 1967). These genera fail to satisfy the previously given morphological definitions of either family and are here reassigned.

Hoferia Bittner, 1894, p. 190 (Triassic).
Pichleria Bittner, 1894, p. 189 (Triassic).
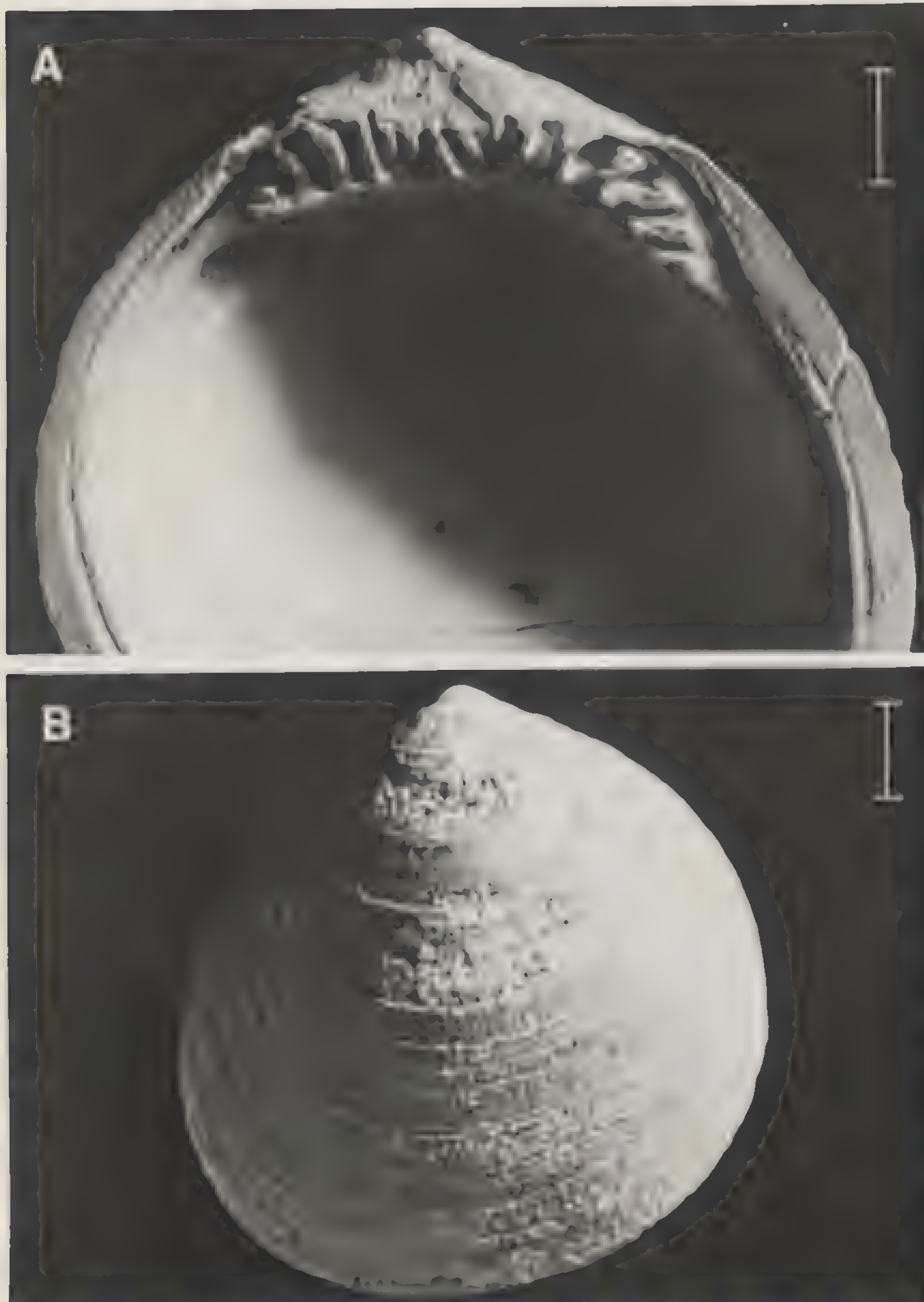
FIG. 14. *Limopsis aurita* (Brocchi). USNM 62848. *A*) Right valve, interior. *B*) Right valve, exterior. Scale = 2 mm.

These forms are placed in the parallelodontid subfamily Grammatodontinae (Arcoida) because they have a broad, external dorsal area, moderately large, oblique to parallel teeth, and are subquadrate. *Pichleria* has a feature on the dorsal area that possibly represents a ligament pit, yet is grammatodont-like in all other shell features. Its similarities to the limopsids are discussed later, and it is likely that this is a transitional form between limopsids and grammatodonts.

Vasconella Boussac, 1911, p. 42 (Eocene).
Deltaodon Barnard, 1962, p. 249 (Recent).

Because of its posteriorly elongate, external ligament, *Deltaodon* probably belongs to the Arcidae (Arcoida). *Vasconella* possibly lacks a ligamental pit and certainly lacks a limopsid-like dorsal area. Since it resembles *Deltaodon*, it too is assigned to the Arcidae.

Vetoarca Stephenson, 1947, p. 165 (Cretaceous).
Nucunella d'Orbigny, 1850, p. 66 (Tertiary).
Ovalarca Woodring, 1925, p. 52 (Miocene).

Vetoarca apparently lacks a dorsal area. It closely resembles certain members of the Noetiidae in shell shape and dentition, as does *Ovalarca*. *Nucunella* is problematic but probably also belongs to the Noetiidae (Arcoida).

Verticipronus Hedley, 1904b, p. 88 (Recent).

The external ligament and absence of denticles exclude this form from the Philobryidae. Dentition and shell shape are vaguely reminiscent of the Cyamiidae (Veneroida).

3. Ecology

Materials and Methods

Life habits of philobryids and limopsids were observed in the field and also studied in the laboratory with the animals placed on their native substrata in sea water regulated to the temperature at which they were collected. Particle transport in the mantle cavity was studied by removing one valve and corresponding mantle lobe.

Ecology of the Philobryidae

1) Habitat
Living specimens of *Philobrya modiolus, P. crenatulifera,* and *Lissarca rhomboidalis* were collected by the author at depths of 0 to 1 m in Pirates Bay at Eaglehawk Neck, Tasmania, during March, 1973. Pirates Bay is a small, narrow bay with a broad entrance located on the east side of the Neck.

There are no apparent restrictions to either water circulation within the bay or to water exchange with the adjacent Tasman Sea. Moreover, no large bodies of freshwater empty into the bay. Thus, water conditions within Pirates Bay are probably normal marine.

P. modiolus was found on both a wave-swept sandstone platform in the northern part of the bay and on a protected boulder-strewn beach in the northeast corner of the bay. *P. crenatulifera* and *L. rhomboidalis* were found only on the boulder-strewn beach. The philobryids are part of an intertidal, rocky shore biotic assemblage that includes littorinids, patelloids, siphonariids, thaids, mytilids, cirrepids, actiniarians, asteroids, and a variety of algae. The intertidal zonation of Pirates Bay is described by Guiler (1952).

2) Life Position and Locomotion

All three philobryid species live attached by a byssus to either brown or red algae. The animals are usually attached to the lower one-fourth of the plant and are oriented with the sagittal plane normal to the attachment surface and the posterior margin directed upward (Fig. 15). The byssus emerges anteriorly and the anterior and anterodorsal margin are in contact with the plant.
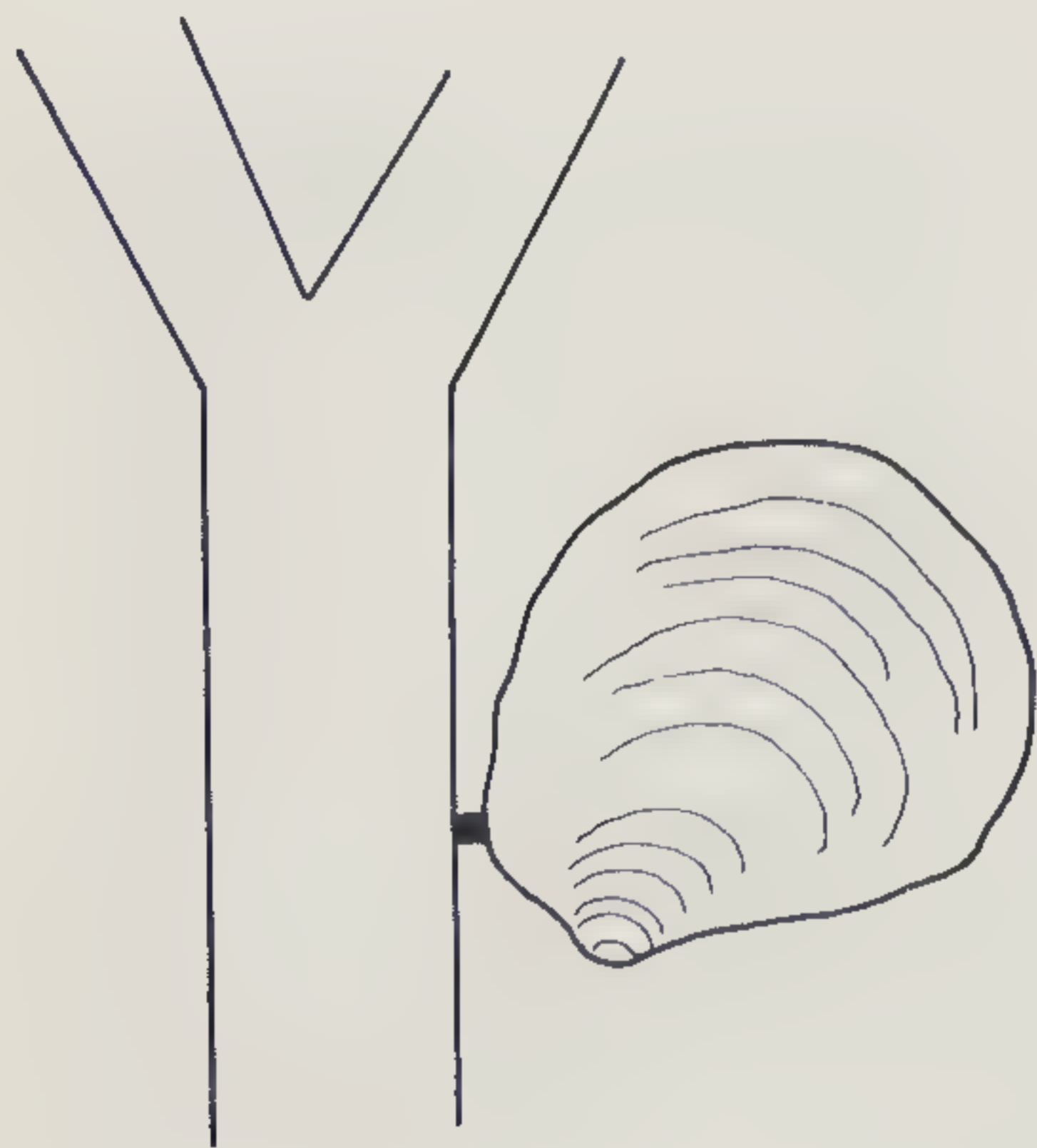
FIG. 15. Philobrya in life position.

In the laboratory, when detached and laid on either valve, all three species performed the following movements:

1) Valves open slowly about 15 to 20°; posterior tips of gills are protruded; water exchange between the mantle cavity and medium begins.

2) Foot is protruded anteriorly, then elongates anteriorly and posteriorly, forming a prominent toe and heel respectively. Extended toe-heel length approximately equals shell length.

3) Foot swings back and forth in sagittal plane; then descends downward until heel or toe adheres to substratum.

4) Foot pulls against bottom until shell rotates to a vertical position. Through this movement, the sagittal plane becomes normal to the substratum and the shell comes to rest on the anterior margin.

5) Foot reextends, reattaches, and pulls shell along to the attachment site. This movement is repeated several times.

The time interval for steps 1 to 5 may be as great as 20 minutes. After step 5 is completed, the animal may anchor itself by secreting several byssal threads.

3) Feeding and Cleansing

The mantle margins of the three species are unfused and water carrying food particles enters the mantle cavity both anteriorly and ventrally (Fig. 16). Particles accepted as food travel to the mouth by way of ciliary tracts on the gills and palps (Fig. 17). There is one major oralward tract on the gill. It is located subaxially and receives particles directly from the anterior and ventral inhalant currents and forms numerous ascending, parallel tracts that occur on the sides of filaments.
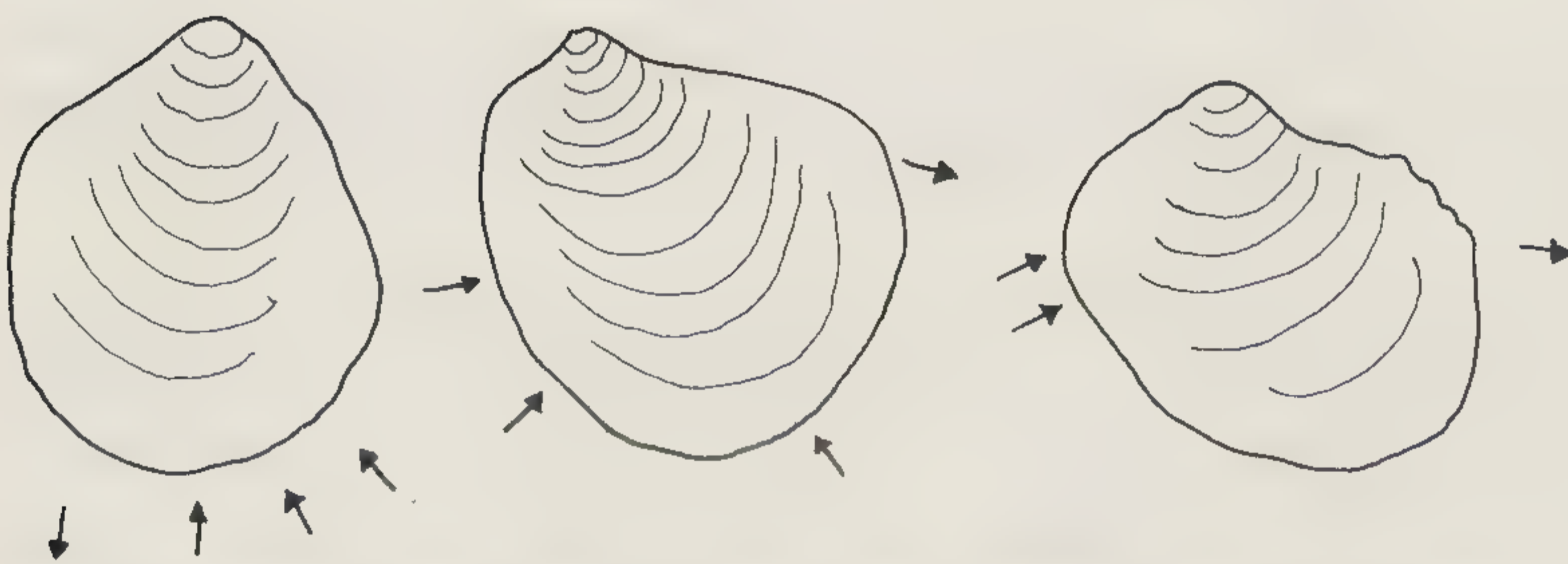
FIG. 16. Inhalant and exhalant areas. Left: *Philobrya modiolus*. Center: *P. crenatulifera*. Right: *Lissarca rhomboidalis*.

Particles rejected by the gill travel posteriorly along a tract located on the ventral edge of each demibranch. This tract receives particles from descending tracts and the palps, and it deposits these particles in a rotating, mucus-bound ball of particles located near the posteroventral tip of the gill. This ball is periodically expelled from the mantle cavity by rapidly closing the valves. The gill also has at least three ways of cleansing itself of unwanted particles without the aid of cilia. It may slough off particles by contracting violently, spread its filaments and allow particles to fall through, or it may push particles away with its posteroventral tip.
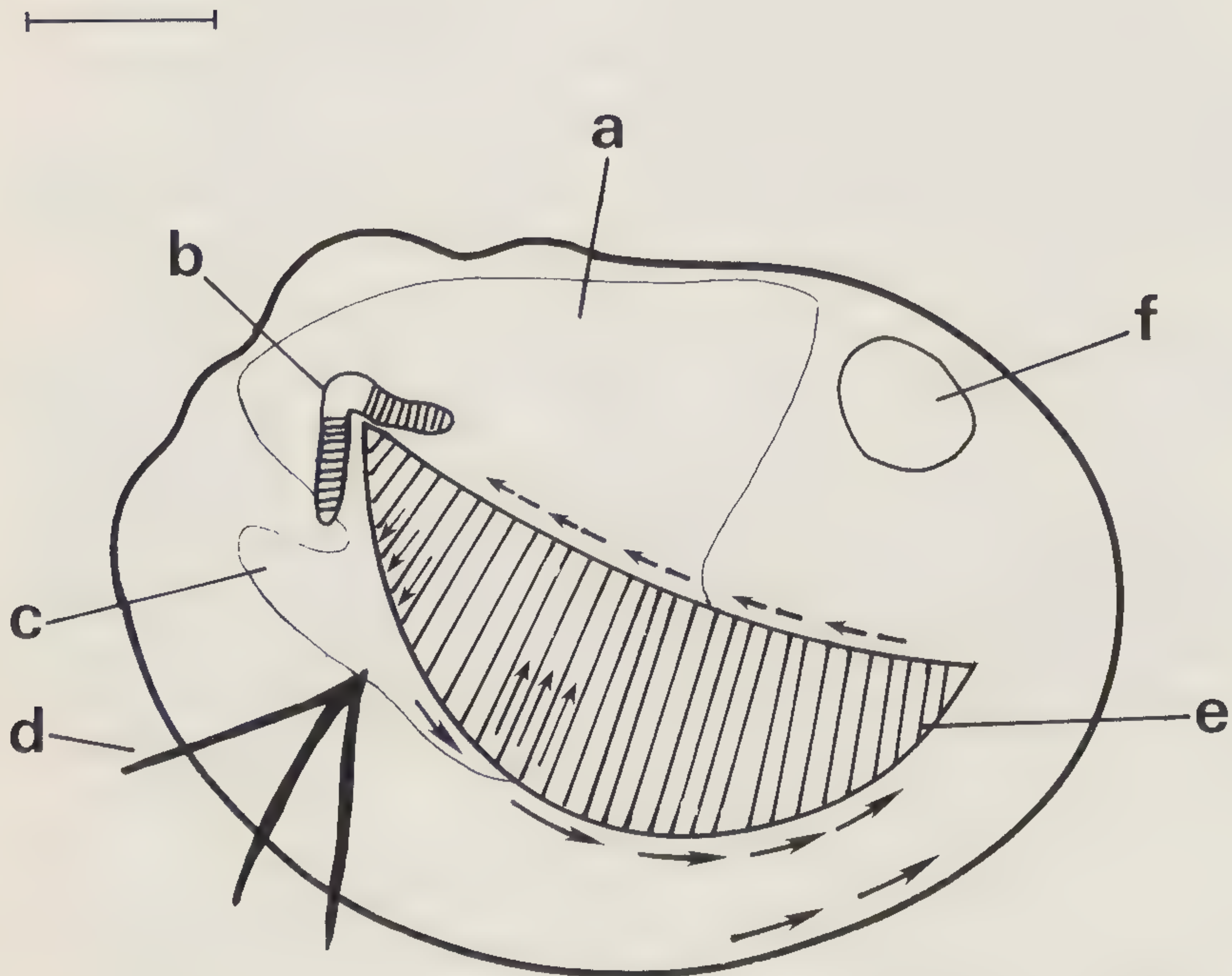
FIG. 17. Philobryid ciliary tracts. *Lissarca* is figured. a = visceral mass, b = palps, c = foot, d = byssus, e = gill, f = posterior adductor muscle. Arrows show directions of ciliary tracts. Scale = 1 mm.

The philobryid gill is remarkable because it is composed of short, stubby filaments connected by a few strong interfilamentary junctures. Contrastingly, the gills of other arcoids, including limopsids, are composed of long, slender filaments interconnected by numerous, relatively weak ciliary junctures. Philobryids are viviparous and the young are frequently seen resting on the gills.

Particles rejected by the gills and palps are ultimately dumped onto the mantle where they are carried posteroventrally by cilia and expelled by rapid valve closure.

Ecology of the Limopsidae

1) Habitat

Five *Limopsis loringi* were dredged during 15 February to 3 March 1973, off Malabar and Port Jackson Heads, New South Wales, at depths of 63-70 m on a gravelly sand substratum. The water temperature and dissolved oxygen

content on the bottom were 15.5°C and 6.4 mg/l to 6.8 mg/l, respectively. Associated live molluscs include the pelecypods *Placimen*, *Neotrigonia*, and *Talabrica* and the gastropods *Chicoreus*, *Gazameda*, and *Conus*.

Three *L. soboles* were dredged during 1 to 30 April 1973, between Magnetic Island and Keeper Reef, Australia (lee side of the Great Barrier Reef), at depths of 42 to 48 m on a gravelly carbonate substratum. Associated live molluscs include the pelecypods *Amusium*, *Glycymeris*, and *Pratulum* and the gastropods *Murex*, *Conus*, and *Colus*. Both *Limopsis* species were always found associated with a gravelly hash composed of broken sabellid (polychaete) tubes.

2) Life Position and Locomotion

In the laboratory, both species performed the following sequence of movements:

1) Valves open 5 to 10°.
2) Foot emerges ventrally and slowly moves in the sagittal plane.
3) Foot rotates downward and buries its ventral edge in the sediment.
4) Anteroventral part of the shell is pulled into the sediment by periodic thrusting and retracting of foot.
5) Burrowing activity ceases when the shell is almost completely buried in the sediment. In the attained life position, the shell lies downward with the posterior margin barely protruding above the substratum (Fig. 18).
6) Three to four byssal threads are secreted from a duct in the anterior part of the ventral cleft of the foot.

Members of this species are slow burrowers and usually take over 45 minutes to complete steps 1 to 6.
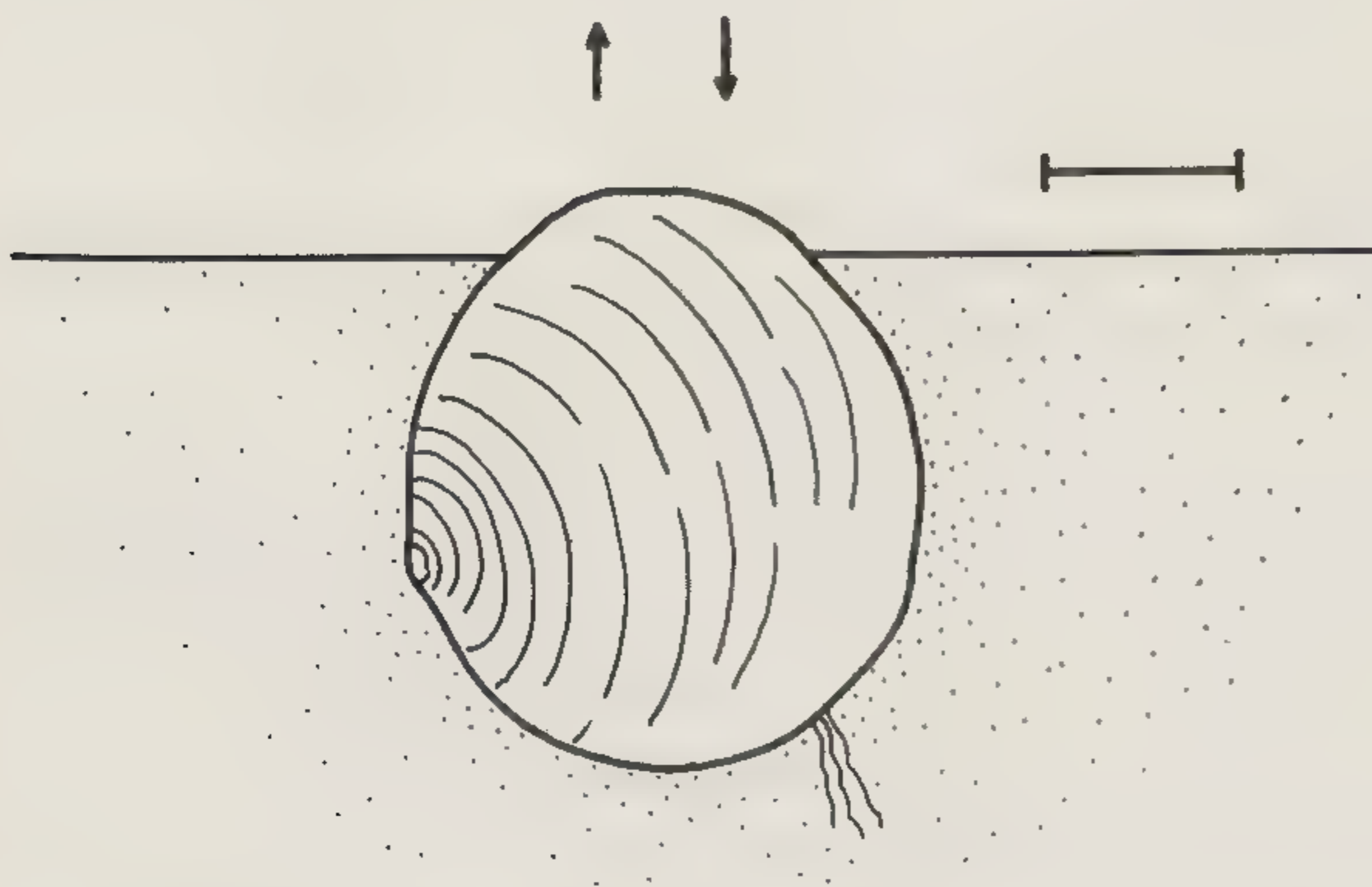
FIG. 18. *Limopsis* life position. Arrows show inhalant and exhalant areas. Scale = 5 mm.

3) Feeding and Cleansing

Limopsis has discrete, posteriorly located inhalant and exhalant apertures which are both formed by local pressing together of the unfused mantle margins. As is the case with the philobryids, particles are drawn in with water by the inhalant current and are sorted by the gills and palps (Fig. 19). There are two major kinds of oralward tracts on the gill. One is located on the dorsal outer surface of each demibranch and the other is located beneath the gill axis. Particles reach these tracts directly from the inhalant current and from numerous parallel, ascending tracts on each surface of the demibranchs.
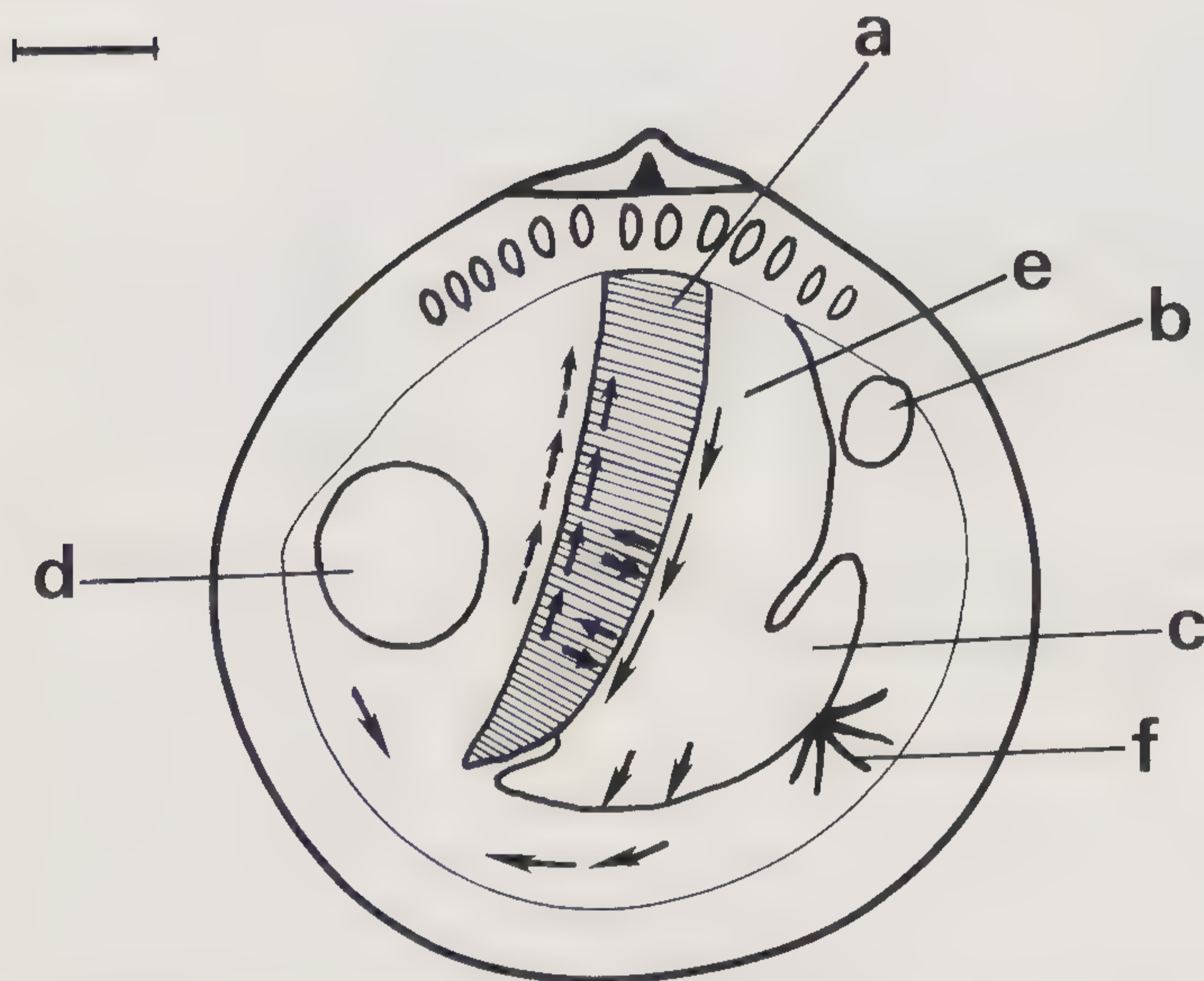
FIG. 19. *Limopsis* ciliary tracts. *a* = gill, *b* = anterior adductor muscle, *c* = foot, *d* = posterior adductor muscle, *e* = visceral mass, *f* = byssus. Arrows show directions of ciliary tracts. Scale = 5 mm.

Particles accepted by the gill pass directly to the distal portion of the palps, the inner surface of which contains approximately twelve ridges. From here accepted particles travel to a proximal, smooth portion and, from there, to the mouth. Almost all particles reaching the smooth portion reach the mouth.

Particles rejected by the gills travel posteriorly down a tract which runs along the ventral edge of each demibranch. This tract receives particles mostly from a series of parallel, descending tracts. The ventral tract deposits its particles near the posteroventral margin where they are periodically expelled by rapid valve closure.

Particles rejected by the ridged portion of the palps often travel to the sixth ridge (counting from the gill), change direction by 90°, then move to the edge of the palp and drop off onto the mantle or foot. Most particles falling onto the mantle are carried posteriorly and ventrally, and are eventually expelled. Most of the particles reach the mantle by way of the gill or foot, but some come there directly from the inhalant current.

The posterior part of the foot has a few weak ciliary tracts. These run posteriorly, and dump particles onto the mantle. Most of the particles reach the foot by way of the gills.

Functions and Implications

Philobryids have the following four features that are either uncommon or absent in most bivalve groups:
1) a ventral, posteriorly directed, gill ciliary tract;
2) a gill with short, stubby filaments and few interfilamentary junctures;
3) an anterior inhalant area;
4) the ability for efficient epifaunal crawling.

The gill tract developed in philobryids and other arcoids (including limopsids) probably in response to a need for an additional mode of mantle cavity cleansing.

Most pelecypods have a basic set of ciliary rejectory tracts that aid in cleansing the mantle cavity. This set usually includes ventrally directed gill tracts, laterally directed palp tracts and posteriorly directed foot and mantle tracts. The tracts alone are probably not sufficient for rapid, thorough cleansing because almost all pelecypods have developed one or more of the following additional means of cleansing the mantle cavity:

1) Partially sealed mantle cavity.

This serves as a cleansing function by closing off avenues of particle entrance to the mantle cavity. It is characteristic of many protobranchiate and eulamellibranchiate bivalves.

2) Rapid flushing system.

    a) Bivalves with an extensively fused mantle cavity can build up relatively high water pressures within the cavity. When released, the rapid flow helps clean out the mantle cavity.

    b) Bivalves with an enlarged, centralized posterior adductor and a localized, springy internal ligament can clap their valves together rapidly and repeatedly. This action produces strong cleansing currents (Yonge, 1936) and is characteristic of many pterioids and other monomyarian bivalves.

3) Elevated inhalant current or permanent inhalant aperture, or both.

    a) Elevation helps keep the current away from unwanted particles from the substratum. Elevation may be accomplished through siphonal formation or living with the posterior margin well above the substratum (e.g., *Atrina*).

b) A permanent inhalant aperture localizes the inhalant current and diminishes the area through which unwanted particles could enter. These apertures are formed by mantle fusion and are characteristic of most eulamellibranchs and protobranchs.

4) Preintake particle selectors.

The palp probiscides of the protobranchs serve this function (Yonge, 1939). Marginal tentacles on the mantle and siphons do not necessarily serve this function (personal observation).

Philobryids and other arcoids probably did not develop any of these additional cleansing features because they lack the necessary morphological matériel. For example, arcoids are probably incapable of developing cleansing features that necessitate mantle fusion [1, 2a, 3a (siphons), 3b] because of the generally assumed pumping inefficiency of the filibranch gill. To maintain water flow in a partially enclosed volume (= mantle cavity after fusion), it is necessary to have an efficient pumping device.

Although some filibranchs are capable of forming a localized inhalant area by pressing together parts of the mantle (Yonge, 1955), this is probably not very efficient in excluding unwanted particles because the apertures formed are only temporary. This inefficiency may be inferred by noting that in many filibranchs, water enters the mantle cavity in a variety of places (Yonge, 1953). Feature 2b would be difficult to develop in arcoids because they have an external, nonspringy ligament, and feature 4 is ruled out because arcoids are filter feeders, and proboscides are only useful to deposit feeders. Feature 3a would be difficult to implement because many arcoids have inhalant areas at opposite ends of the shell. Elevating one would lower the other.

Thus, in order to develop an additional means of cleansing, it seems a reasonable path left to arcoids was modifying existing ciliary mechanisms. One way of doing this would be to reverse the direction of the ventral tract. In most bivalves (and presumably in the ancestors of the arcoids), this tract runs anteriorly and deposits particles near the mouth. Reversing this tract so it runs posteriorly would effectively add to the extant cleansing mechanism because it would deposit unwanted particles near the posteroventral margin where they could easily be expelled through rapid valve closure.

Reversing this tract was probably simply effected by the arcoids. Purchon (1956) reports that the ventral gill tract in *Anadara granosa* runs anteriorly. Lim (1966) reports in a later study of the same species that the tract runs posteriorly, as expected. Assuming neither of these workers is in error in observing this obvious feature, this means that some arcoids have the ability, by either volition or mutation, to at least temporarily change the direction of this tract. Since the tract is reversible it probably would have been relatively easy for arcoids to change its average direction from anterior to posterior, and thus provide themselves with an additional means of mantle cavity cleansing.

The structure of the philobryid gill can be interpreted as an adaptation for strengthening the gill filaments and viviparity. In contrast to the philobryid gill, the ordinary filibranch gill is comparatively fragile. For example, sand-sized abrasive particles that become wedged between the demibranchs of the ordinary gill are sometimes capable of breaking the ciliary junctures and tearing off pieces of filaments (personal observation). By having shorter, thicker filaments, the philobryid gill is less prone to tearing. Also, reducing the number of junctures and reinforcing existing junctures makes the probability of ciliary rupture less likely. This tougher structure with fewer junctures permits pushing and spreading movements which would certainly damage the ordinary gill.

A strongly constructed gill would be advantageous to philobryids because they are viviparous. There are often 10 to 25 young, brooded to a relatively large size (sometimes 1/15 adult shell length), and each one has at least two sharp corners that could possibly damage the ordinary filibranch gill. In addition to cleansing, the separating and pushing movements that the gill structure allows could also be used for getting the young off the gills and out of the shell.

The presence of an anterior inhalant area in philobryids is remarkable because Yonge (1939) considers an anterior inhalant area to be a primitive feature in pelecypods. Also, recent writers (e.g. Allen, 1968) have interpreted the presence of this feature in certain living pelecypods as indicating both primitiveness and taxonomic affinity.

It is here contended that, while pelecypods may have passed through an evolutionary grade where the inhalant current was anterior, the presence of such a current in any particular pelecypod does not necessarily indicate primitiveness or taxonomic affinity. The taxonomic distribution of this feature indicates this.

Members of the following groups are known to have an anterior inhalant area: Nuculidae, Solemyidae (Yonge, 1939), Lucinacea (Allen, 1958), Erycinacea (Popham, 1940), Crassatellacea, Carditidae (Allen, 1968), Arcidae, Glycymeridae (Atkins, 1936), and Philobryidae. Also, Stasek (1963) mentions that this feature is present in the early postlarval stage of several pelecypods. Because this feature is present in taxonomically remote groups (e.g. Solemyidae and Crassatellacea), it is not necessarily an indicator of taxonomic affinity. The absence of this feature in post-Paleozoic ancestral groups and its presence in relatively recently evolved descendant groups (e.g. limopsids-philobryids) suggests that it represents an adaptation developed within the descendant group. Therefore, the feature is not necessarily an indication of descent from some primitive ancestor and a pelecypod that has it is not necessarily primitive.

Besides philobryids, only members of a few pelecypod groups such as the Mytilidae, Limidae (Young, 1953), Anomiidae (Yonge, 1957), and Erycinacea (Popham, 1940) crawl effectively epifaunally as adults. These bivalves usually crawl either by anchoring the foot to the substratum and drawing the shell up to the anchorage site by contracting the pedal muscles or by pedal locomotory waves.

Philobryids, anomiids, and erycinaceans are relatively rapid crawlers because the bond between the foot and substratum (often suction) can be easily and rapidly broken after the shell draws up to the anchorage site. Thus crawling is easy and members of these groups are very active and can crawl for extended periods of time.

Crawling is more laborious for limids, mytilids, and other larger bivalves because each step often requires making and breaking a byssal bond with the substratum. Possibly for this reason, these forms are usually not active crawlers and spend most their time byssally attached to the substratum.

The most active epifaunal crawlers are often small. *Enigmonia aenigmatica*, the mobile anomiid, seldom gets longer or wider than 4 cm. Erycinaceans and philobryids usually do not exceed 1.5 cm and are usually much smaller. Small size is probably advantageous for this kind of crawling, because as the animal gets larger the area available for anchorage (the surface of the foot) increases by a power of two while shell volume increases by a power of three (Thompson, 1942). Therefore, as the animal becomes larger, the shell often becomes too bulky and heavy for the foot to effectively move it epifaunally.

4. HIGHER TAXONOMY

Ordinal Affinities

While all recent workers place the Limopsidae in the Order Arcoida, the ordinal affinities of the Philobryidae are still controversial. Although most workers consider philobryids to be arcoids, Nicol (1966) asserts that they are mytilaceans and supports this contention by pointing out that both philobryids and mytilaceans have similar hinge ligaments, shell shapes, and anterior adductor musculature.

However, this evidence is not conclusive. In the first place, the ligament evidence is incorrect. All philobryids have an internal ligament, while most mytilaceans have an external ligament. Secondly, the evidence regarding shell shape and adductor musculature is ambiguous since many other non-mytilacean groups (e.g. Ambonychiidae, Myalinidae, Pteriidae) also have anteriorly reduced shells and reduced anterior adductors. In many cases, anterior reduction of the shell has been interpreted as being an adaptation for epifaunal stability that occurs in taxonomically diverse groups (Stanley, 1970). In addition, reduction of the anterior adductor often occurs along with anterior reduction of the shell.

There are other striking differences between philobryids and mytilaceans. For example, the inner shell layer in philobryids is crossed-lamellar while it is nacreous in mytilids; the philobryid foot is broad and pointed at both

ends, while the mytilacean foot is finger-shaped; the ventral-most gill ciliary tract is posteriorly directed in philobryids and anteriorly directed in mytilaceans. Also unlike most mytilaceans, several philobryids have true hinge teeth.

This writer feels that both limopsids and philobryids belong to the Order Arcoida because members of both families possess the following combination of features which, it seems, are found together only in arcoids: 1) a dentition with numerous anterior and posterior teeth; 2) a ligament consisting of alternating sheets of fibrillar and lamellar material; 3) a broad foot with a prominent ventral groove; and 4) filibranchiate gills with a posteriorly directed ventral ciliary tract.

This list of features comes from examining scores of individuals from all arcoid families except the Philobryidae and Limopsidae and listing common features not found in most other bivalves. Features 1 and 2 are or were once present in all examined arcoids. Features 3 and 4 are present in all examined living arcoids. All these features are present together in many members of the Philobryidae and all members of the Limopsidae. No nonarcoid bivalves possess more than two of these features.

Although these features set philobryids and limopsids apart from all nonarcoid bivalves, two other nonarcoid groups, the limids and nucinellids, are frequently confused with philobryids. The dentition and adductor musculature of nucinellids are superficially similar to the same features in philobryids. Nevertheless, the corresponding features occupy a posterior position in philobryids and an anterior position in nucinellids. Moreover, Allen and Sanders (1969) show that living nucinellids have protobranchiate gills.

Although small limids resemble philobryids in shell shape and some hinge features, there are two obvious ways in which small limids may be distinguished from philobryids. First, there are seldom more than 10 denticles on the limid hinge while there are seldom fewer than 30 on the philobryid hinge. Secondly, the soft parts of limids are characterized by numerous, long tentacles on the mantle margin.

There is no danger of confusing limopsids with any nonarcoid group.

Evolution

Various views of arcoid phylogeny are illustrated in Figure 20. How do philobryids and limopsids fit into the picture?
1) Limopsid Origins
Three Jurassic species are the oldest limopsids known to the writer. The oldest of these is *Limopsis minimus* (Sowerby) [= *L. oolithica* (Buvignier); = *Pectunculus minimus* Buvignier], which is reported from the Middle Jurassic (Bathonian) of England and southern Europe (Sowerby, 1825; Gürich, 1934). According to Sowerby's (1825) original description and figures, this species has 4 to 5 anterior and posterior teeth, an anteroposteriorly elongate
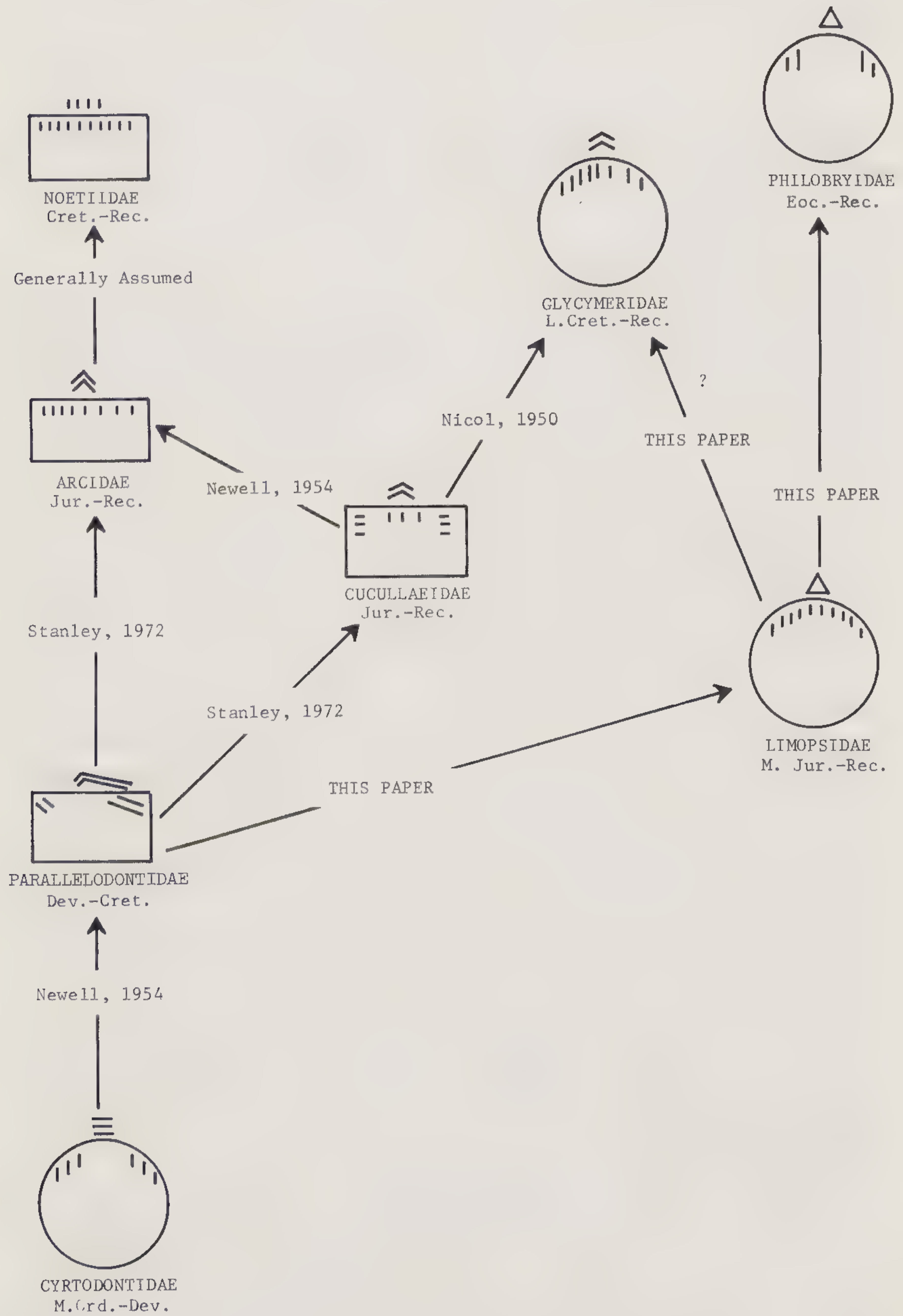
Fig. 20   Summary of arcoid phylogeny.

<u>Addendum</u>

Tevesz, M.J.S. 1977. Taxonomy and ecology of the Philobryidae and Limopsidae
    (Mollusca: Pelycypoda), Postilla Number 171, Peabody Museum of Natural
    History, Yale University, New Haven, CT.

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Page 40. Add the legend: Fig. 20. Summary of arcoid phylogeny.

shell, and a smooth outer surface. Although Sowerby neither mentions nor figures a ligament pit, Arkell (1929–36), after examining specimens and comparing them to Recent limopsids, says that it has a ligament pit and unequivocally considers it a true limopsid.

The other two species are from the Upper Jurassic. One is *Limopsis corallensis* (Buvignier), which occurs in England and France (Arkell, 1929–36). It has an anteroposteriorly elongate shell, ligament pit, about 14 teeth, a concentrically lined outer surface, and a dorsal area with oblique striations. The other is *Limopsis* sp. Pickering, which, according to Arkell (1929–1936), has an anteriorly reduced, dorsoventrally elongate shell and is known only from the Oxfordian of England. Arkell thinks it is possible that the individuals he previously called *L. corallensis* may belong to this species.

The origins of the Limopsidae can probably be traced to the parallelodontid subfamily Grammatodontinae (Triassic-Cretaceous; -Eocene? -Recent?) because early limopsids look more like certain grammatodonts than any other pre-Middle Jurassic arcoids.

Grammatodonts generally have a rounded, subquadrate shell that is slightly longer than wide and their dentition consists of about 4 or 5 shorter, oblique anterior teeth and about 4 or 5 longer, oblique posterior teeth. The dorsal area is often grooved and the adductor muscle scars are about the same size.

By comparison, two of the earliest limopsids, *L. minimus* and *L. corallensis*, resemble grammatodonts because they have anteroposteriorly elongate shells with rounded margins. In addition, *L. corallensis* has nearly equal sized muscle scars and a striated dorsal area. Moreover, there are two Triassic grammatodonts, *Hoferia* and *Pichleria*, which especially resemble early limopsids. The dentition of these grammatodonts, like the limopsid dentition, consists of small, equally spaced teeth. Also, *Hoferia* like early limopsids, has external concentric markings, is ovate, and is known from Europe (Bittner, 1894). These similarities between limopsids and grammatodonts are shown in Figure 21.

Stanley (1970) shows that modern free-burrowing arcids have a shell length/height ratio of less than 1.35, while modern epibyssate forms have the ratio greater than 1.35. Applying the same statistic to grammatodonts, it is possible to infer that while many were probably epifaunal, some, including *Hoferia* and *Pichleria*, like *Limopsis*, were probably infaunal.

No other pre-Middle Jurassic arcoids share nearly as many similarities with the earliest limopsids, or even limopsids in general, as do these grammatodonts.

The main morphological difference between grammatodonts and limopsids is that all limopsids have a ligament pit and most have a smooth dorsal area, whereas most grammotodonts lack a ligament pit and have oblique grooves on the dorsal area. This difference chiefly means the grammatodont ligament covered more of the dorsal area than the limopsid ligament. This
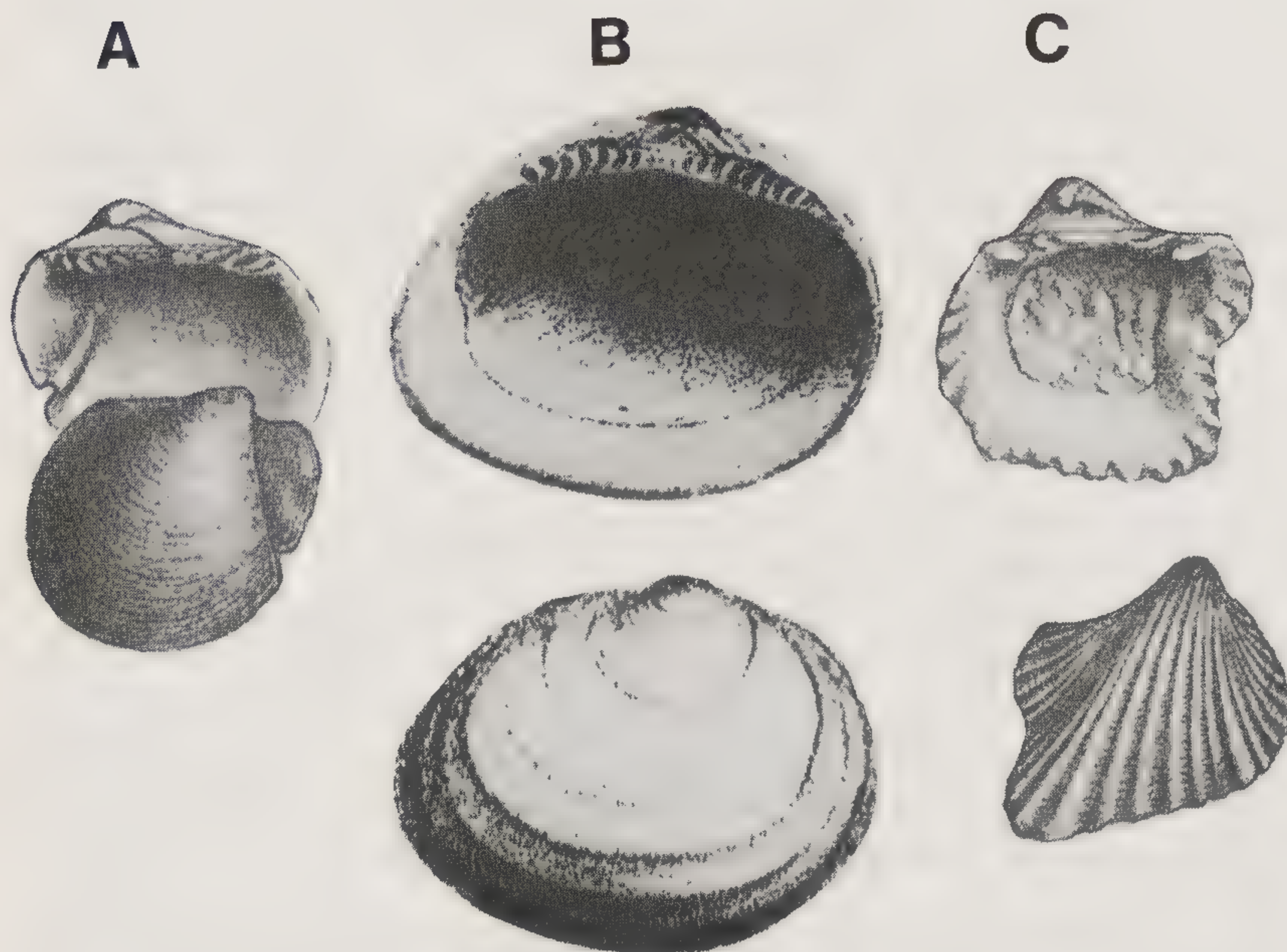
FIG. 21. *Limopsis* and limopsid-like grammatodonts. *A*) *Hoferia*; *B*) *Limopsis*; *C*) *Pichleria*.

point may be illustrated by comparing the ligaments of both groups. The limopsid ligament consists of a radially arrayed pattern of fibrillar and lamellar material (Newell, 1938; personal observation) and it can be inferred that the composition and arrangement of ligamental material in grammatodonts was similar, because the dorsal area of most well-preserved grammatodonts is marked with oblique grooves. This pattern, in modern arcoids, reflects the composition and arrangement of ligamental material. The grooves mark the insertion sites of lamellar material while the spaces mark the location of fibrillar material. Oblique grooves are produced on the dorsal area when this material is radially arrayed. Since the pattern is etched into the shell, these marks are usually preserved long after the ligament disintegrates. In limopsids, the ligament is usually entirely confined to the pit and is often composed of comparatively few sheets of material. Judging from the chevrons, the grammatodont ligament covered the entire dorsal area.

2) Philobryid Origins
Three lines of evidence suggest the ancestry of the Philobryidae may be traced to the Limopsidae. The first is the overall morphological similarity between members of the two families. This similarity can be most con-
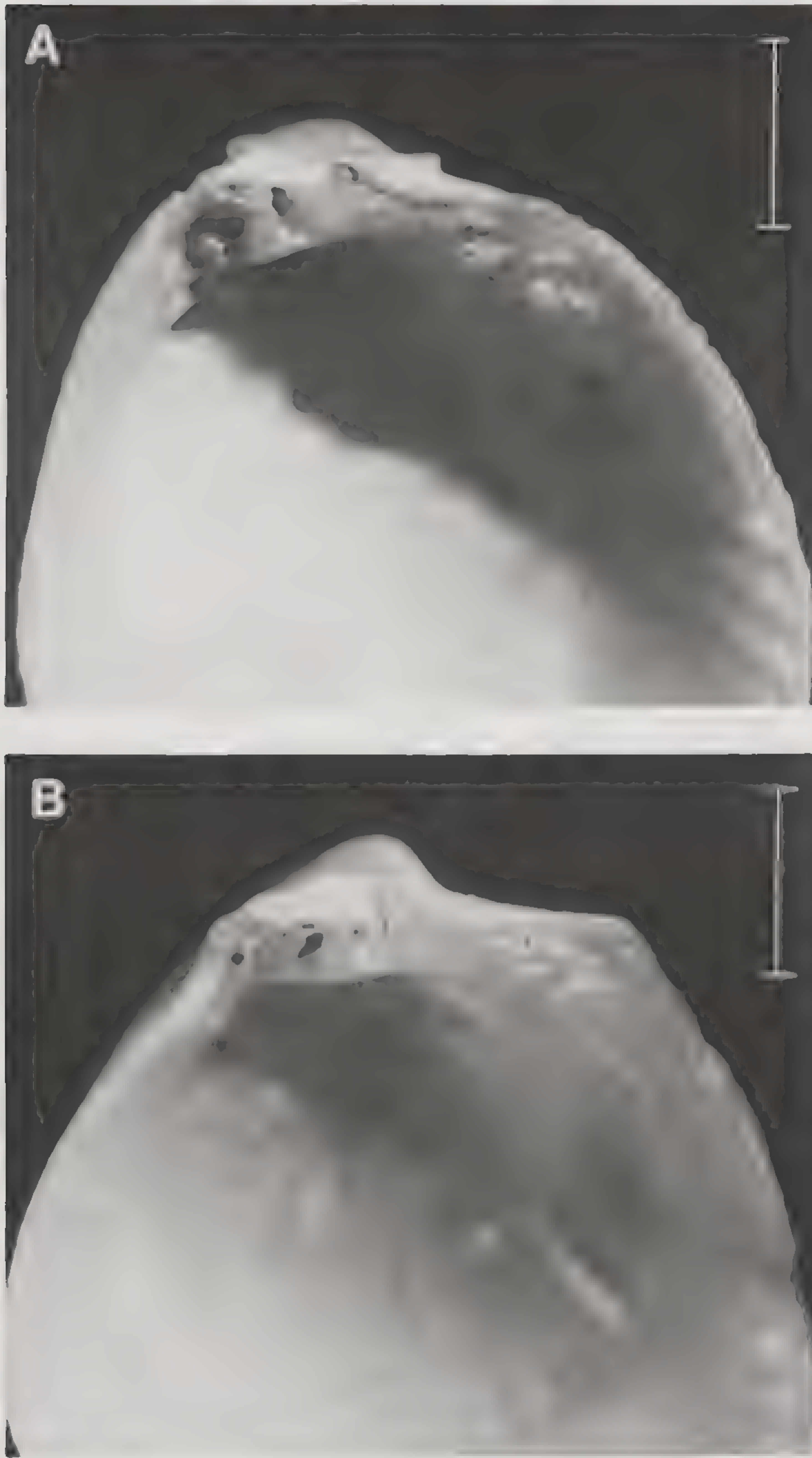
FIG. 22. Philobryid and limopsid similar in overall shell features. *A*) *Cratis progressa; B*) *Limopsis antillensis.* Scale = 1 mm.

vincingly illustrated by comparing *Cratis progressa* (Recent) with *Limopsis antillensis* (Recent). Both these species have a dentition consisting of 2 to 4 anterior teeth and 3 to 6 posterior teeth, a similar anteriorly reduced outline, and a cancellate external surface (Fig. 22). Moreover, *Limarca* (Eocene), one of the first known philobryids, also shows these similarities with *Limopsis antillensis* and other philobryids such as *Lissarca* and *Limopsilla* resemble limopsids in general. Like limopsids, these genera have a dentition consisting of small, transverse anterior and posterior teeth and all have an anteriorly reduced shell. Moreover, adult limopsids and philobryids have a ligament pit which contains radially arrayed ligamental material. No other arcoids show as many similarities to philobryids as do limopsids.

The principal differences between limopsids and philobryids in no way discredit arguments, based on overall similarity, that suggest their ancestor-descendant relationship. The principal differences in external features are the presence of denticles in philobryids and the presence of a dorsal area in limopsids.

No other adult arcoids have denticles; moreover, only two adult arcoid features even remotely resemble denticles. These are the transverse striations on the dorsal area of certain noetiids and arcoid teeth in general. These striations in noetiids are sites of ligament insertion, and, unlike denticles, do not interlock. Ligamental insertion in philobryids takes place only within the ligament pit and not on the surface where denticles are located. Moreover, ligamental insertion in philobryids does not produce transverse striations.

Teeth are the only other arcoid feature with which denticles could possibly be homologous. However, this relationship is unlikely, because arcoid teeth are located below the ligament, while denticles are located lateral to the ligament. Secondly, denticles are located well above and separate from the teeth in philobryids.

Where do denticles come from? Bernard's (1896b) illustrations of young arcoids show that many possess denticles. These denticles apparently serve as articulating aids prior to the development of teeth. Also, similar denticlelike features are present in the early growth stages of several non-arcoid pelecypods (Cox et al., 1969). This strongly suggests that philobryid denticles represent juvenile features retained by the adult (neotenous features). Since early limopsid growth stages have denticles, their presence in adult philobryids does not obstruct the proposed phylogenetic relationship of these two families.

Philobryid denticles are interlocking and hence serve an articulating function. Since they are located above the teeth, they still interlock when the valves open widely (15 to 20°) and the teeth no longer interlock. In life, philobryids often open the shell to this angle before crawling commences. One reason for this wide opening may be to allow the foot freedom of movement before and during locomotory activity. Thus, denticles can serve to articulate the shell when the teeth cannot, and the presence of denticles may

have allowed some philobryids to lose their regular dentition without suffering a loss of articulating ability.

The second principal difference in shell features, the presence of a dorsal area in limopsids and its absence in philobryids, may be more apparent than real. The surface containing denticles possibly represents a dorsal area, since it is a discrete surface located above the dentition and adjacent to the ligament pit. Unlike the dorsal area of most limopsids, it is parallel to the sagittal plane and very small. Nevertheless, some limopsids, including *L. nipponica*, also have a small dorsal area that is nearly parallel to the sagittal plane.

The major differences in the soft parts of philobryids and limopsids are the sturdy gill and highly reduced or absent anterior adductor muscle of the former. The philobryid-like gill is unique within the Arcoida and therefore represents a feature evolved entirely within the Philobryidae. As such, the philobryid gill does not suggest relationships with nonlimopsid arcoids. As pointed out earlier, a reduced or absent anterior adductor muscle characterizes a wide variety of bivalves. It often occurs along with anterior reduction of the shell, which can be an adaptation for epifaunal stability (Stanley, 1970).

Thus, this first line of evidence shows that there are several close similarities between philobryids and limopsids and also shows that their principal differences do not necessarily indicate other origins for philobryids. Furthermore, it suggests that limopsids have all the morphological matériel necessary to produce the philobryid form.

The second line of evidence comes from the spatial and temporal relationships of the two families. Limopsids, which first appear in the Jurassic, well predate philobryids, which first appear in the Eocene. Moreover, limopsids occur in Eocene and pre-Eocene sediments in the Australia-New Zealand region, where philobryids first appear (Flemming, 1966). This suggests that limopsids had the potential in space and time to give rise to the philobryids.

The third line of evidence follows from analogous morphological-life habit transitions in other groups. The types of changes necessary to produce a philobryid-like form from a limopsid-like form have occurred previously within several other pelecypod orders. These changes produce an anteriorly flattened, alobate form from an anteriorly rounded, lobate form. Such changes also accompany a transition from an endobyssate to epibyssate life habit.

These types of changes and their significance were first brought to light and discussed by Stanley (1972). He feels that such morphological and life habit changes have occurred in groups such as the Pterioida, Modiomorphoida, and early Heterodonta. For evidence, he points out that some of the earliest known members of these groups have some of the following features: a reduced, lobate anterior, an elongate shell, a broad byssal sinus, and the absence of appreciable ventral flattening. He also shows, through recent

analogies, that these features occur in endobyssate pelecypods. Then, he mentions that some of the forms evolved later in these groups have a flattened, alobate anterior. Based on recent analogies and considerations of physical stability, he suggests that these features are adaptive to an epibyssate life habit. This suggests that many epibyssate stocks arose from endobyssate stocks.

A limopsid-philobryid transition would parallel this widespread, well-documented type of morphological and life habit transition. Limopsids have some of the features characteristic of the endobyssate grade of evolution. These are a reduced but lobate anterior, the absence of ventral flattening, and, in some cases, a broad byssal sinus. Moreover, limopsids are here observed to be endobyssate. On the other hand, many philobryids show features characteristic of the epibyssate grade of evolution, such as a flattened, alobate anterior. Also, philobryids are here observed to be epibyssate.

Thus, this third line of evidence shows that the major morphological and life habit changes that would occur in evolving a philobryid from a limopsid have occurred several times in other pelecypod lines. This evidence suggests that a limopsid-philobryid transition would not be unusual, and furthermore, would be feasible within the limits of their respective morphologies and ways of life.

In short, philobryids look more like limopsids than any other arcoids. Moreover, the morphological-life habit transition that would be required in evolving a philobryid from a limopsid has several precedents. For these reasons, limopsids are here considered the most probable ancestors of philobryids.

3) Mechanisms

The importance of neoteny in pelecypod evolution has been recently stressed. Yonge (1962) suggests the byssus in adult pelecypods is a neotenous feature and Stasek (1963) and Ockelman (1964) suggest neotenous origins for, respectively, erycinaceans and the venerid *Turtonia*. Stanley (1972) summarizes recent bivalve literature concerning neoteny and invokes neoteny as a mechanism in major life habit transitions in the Pelecypoda.

Certain morphological features of philobryids and limopsids suggest that neoteny was a factor in the evolution of both these families. Besides denticles, Bernard (1896b) shows that the juveniles of several arcoid genera (e.g. *Arca, Glycymeris, Cucullaea*) have a ligament pit that later disappears in the adult (Fig. 23). Many erycinaceans and *Turtonia* are small (2 mm– 10 mm) and byssate. Philobryids have all these features characteristic of juvenile and neotenous pelecypods. Limopsids have a byssus and ligament pit. Moreover, the earliest known limopsid, *Limopsis minimus*, is a small species (less than 10 mm long).

Since adult philobryids and limopsids have features of juvenile arcoids and also share features with presumably neotenous groups, it is conceivable that neoteny was a mechanism in the evolution of both these families.

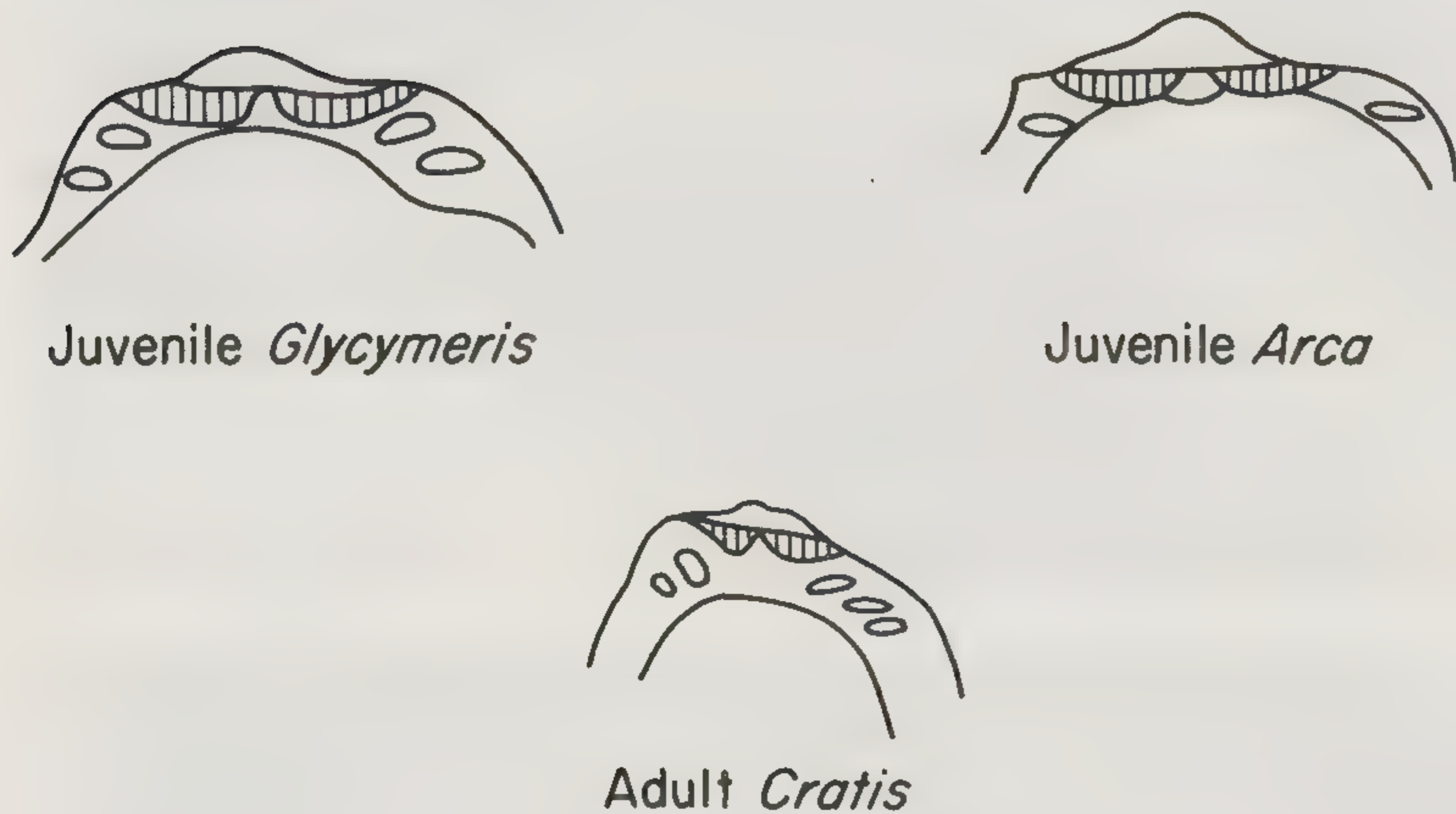Juvenile *Glycymeris*   Juvenile *Arca*

Adult *Cratis*

FIG. 23. Arcoid denticles. (After Bernard, 1896b; Hedley, 1915.)

4) Other Limopsid Offshoots

Two pieces of evidence suggest limopsids may be considered as possible ancestors of Glycymeridae (Lower Cretaceous-Recent). The first is the truly striking similarities between limopsids and glycymerids, which are especially evident in their dentitions and shell shapes. Members of both families characteristically have numerous transverse, evenly spaced, arcuately arrayed hinge teeth and ovoid, approximately equilateral shells (Fig. 24). The shape and arrangement of the soft parts are very similar in *Limopsis* and *Glycymeris* (Pelseneer, 1911), and their mantle, foot, and gill ciliary tracts are almost identical (Atkins, 1936; personal observation).

The main difference is that the limopsid dorsal area is marked by a pit, whereas the dorsal area in glycymerids is marked by chevron grooves. The preceding discussion about the significance of this difference, applied to grammatodonts, also applies here. Also, a ligament pit is present in juvenile glycymerids (Bernard, 1896b).

The second piece of evidence for this relationship is *Limopsis corallensis*, a morphological intermediate between limopsids and glycymerids. Buvignier's (1842) figures of this species show that, like most glycymerids, *L. corallensis* is nearly equilateral, anteroposteriorly elongate, and has two nearly equal-sized adductor muscle scars. In addition, *L. corallensis*, like the first undoubted glycymerid, *Glycymeris marulensis* (Leymerie), is known only from Europe (Arkell, 1929–1937; Nicol, 1950). Although Cossmann (1924) reports two Jurassic species of *Limopsis* (*minimus* and *oblongus*) that he refers to the genus *Pectunculus* (now called *Glycymeris*), this writer thinks both these forms are *Limopsis minimus*. Although they seem to lack a ligament pit, this is probably a result of their poor preservation.
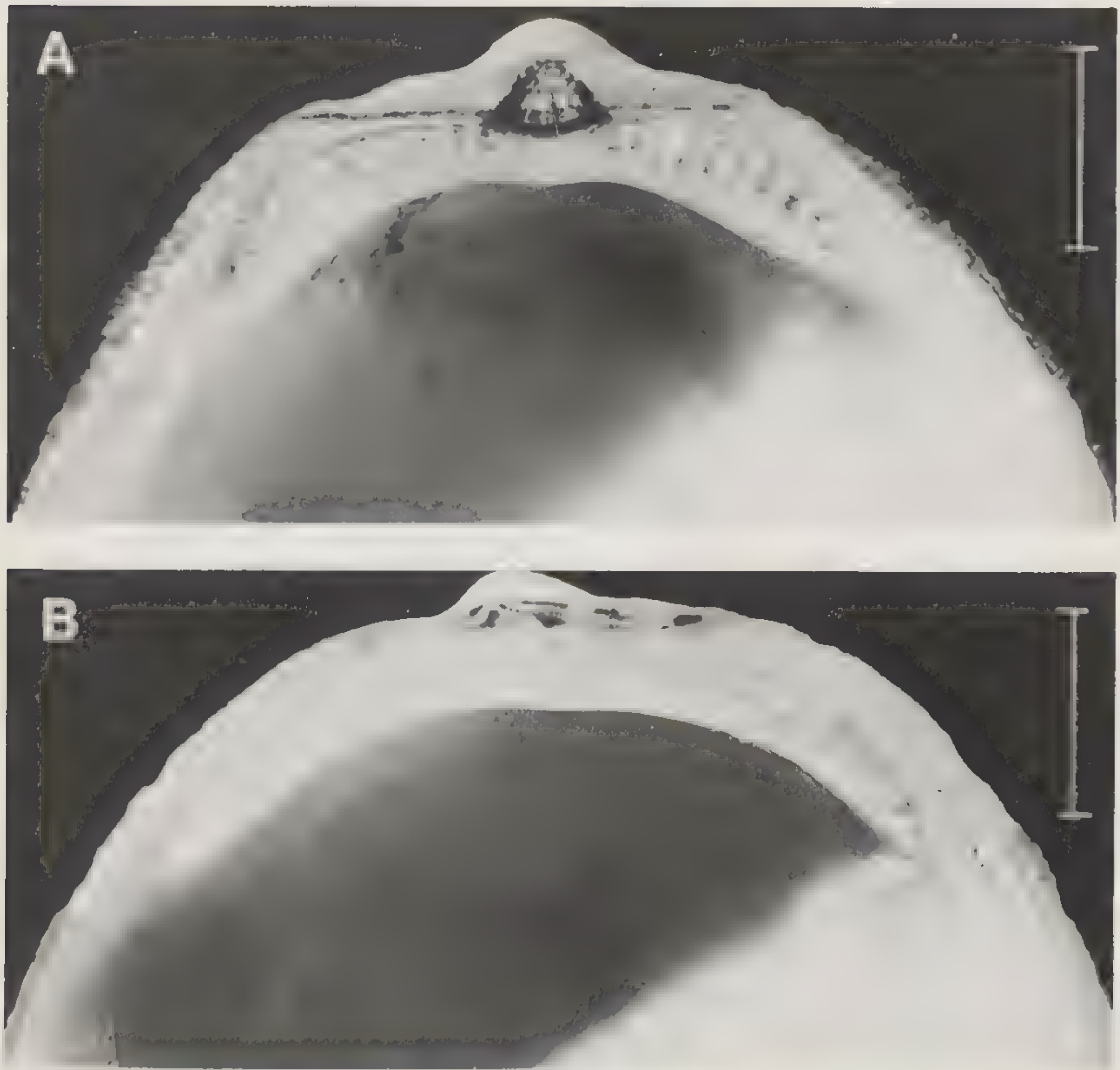
FIG. 24. Limopsid and glycymerid similar in overall shell features. *A*) *Limopsis* sp.; *B*) *Glycymeris pilosus*.

Most importantly, however, the dorsal area of *L. corallensis* is apparently marked both by a ligament pit and oblique grooves. Arkell (1929–1937) also notes the presence of these grooves in *L. corallensis* when he mentions that the cardinal area (= dorsal area) is "finely striated." Thus, the hinge of *L. corallensis* combines the characteristics of both limopsids and glycymerids. This is important because it suggests that not all limopsids lost the oblique grooves of their grammatodont ancestors and hence did not have to redevelop them in giving rise to glycymerids.

These ideas about limopsid-glycymerid relationships are contrary to those of Nicol (1950), who has made the only extensive attempt so far to trace glycymerid ancestry. Nicol believes that glycymerids arose from cucullaeids. For his evidence, Nicol shows how the dentition, dorsal area, ligament, shell shape, umbonal position, ornamentation, and adductor musculature of certain glycymerids resembles corresponding features in certain cucullaeids.

He then relates that glycymerids are first known from the Lower Cretaceous of France, and that there are late Jurassic and Lower Cretaceous cucullaeids from roughly the same area. Because of this evidence, he ". . . is certain that the ancestor of the Glycymeridae was a species belonging to the genus *Idonearca* of the family Cucullaeidae."

This evidence is not convincing because limopsids share most of these morphological, spatial, and temporal similarities with glycymerids. Nicol's conclusions can therefore be challenged by showing several similarities between glycymerids and limopsids that are not common to glycymerids and cucullaeids. This can be done first by using Nicol's own words. On page 95, he outlines the morphological changes necessary to derive a glycymerid from a cucullaeid, using for his reference points *Idonearca* and *Glycymerita*. He feels the following changes are among those necessary to derive the latter from the former:

1. The outline changed from quadrate or subrhomboidal to subquadrate with an arched dorsal margin and a more symmetrically rounded outline. The posterior truncation and constriction became less pronounced, and the convexity became less in *Glycymerita* than in the ancestral cucullaeid.

2. With the rounding of the dorsal border the ligamental area decreased in length in *Glycymerita*, and the hinge plate became more arched and weaker.

3. The central teeth changed little, although they appear to have become shorter in *Glycymerita*. The most pronounced change occurred in the modification of the side teeth. The ancestral cucullaeid had long side teeth arranged almost one above the other, all of them parallel or nearly parallel to the dorsal margin. Usually the distal side teeth of *Idonearca* are slightly divergent ventrally. The side teeth in *Glycymerita* became much shortened and arranged in a converging arc instead of being arranged one above the other. This shortening of the side teeth became necessary because the hinge plate became arched and weaker.

These very points show similarities which are common to glycymerids and limopsids, but which are not common to glycymerids and cucullaeids, because none of these changes is necessary if glycymerids arose from limopsids.

However, the best way of showing similarities which are common to glycymerids and limopsids, but which are not common to glycymerids and cucullaeids, is to compare the limopsid and cucullaeid forms that are thought to be ancestral to the glycymerids. Using these antecedent forms minimizes the possibility that the comparisons are biased by convergence.

L. corallensis, the writer's choice, an *Idonearca*, Nicol's choice, and a Cretaceous glycymerid are illustrated in Figure 25. Nicol mentions that members of a group of species such as *I. gabrielis*, *I. forbesi*, and *I. moreana*
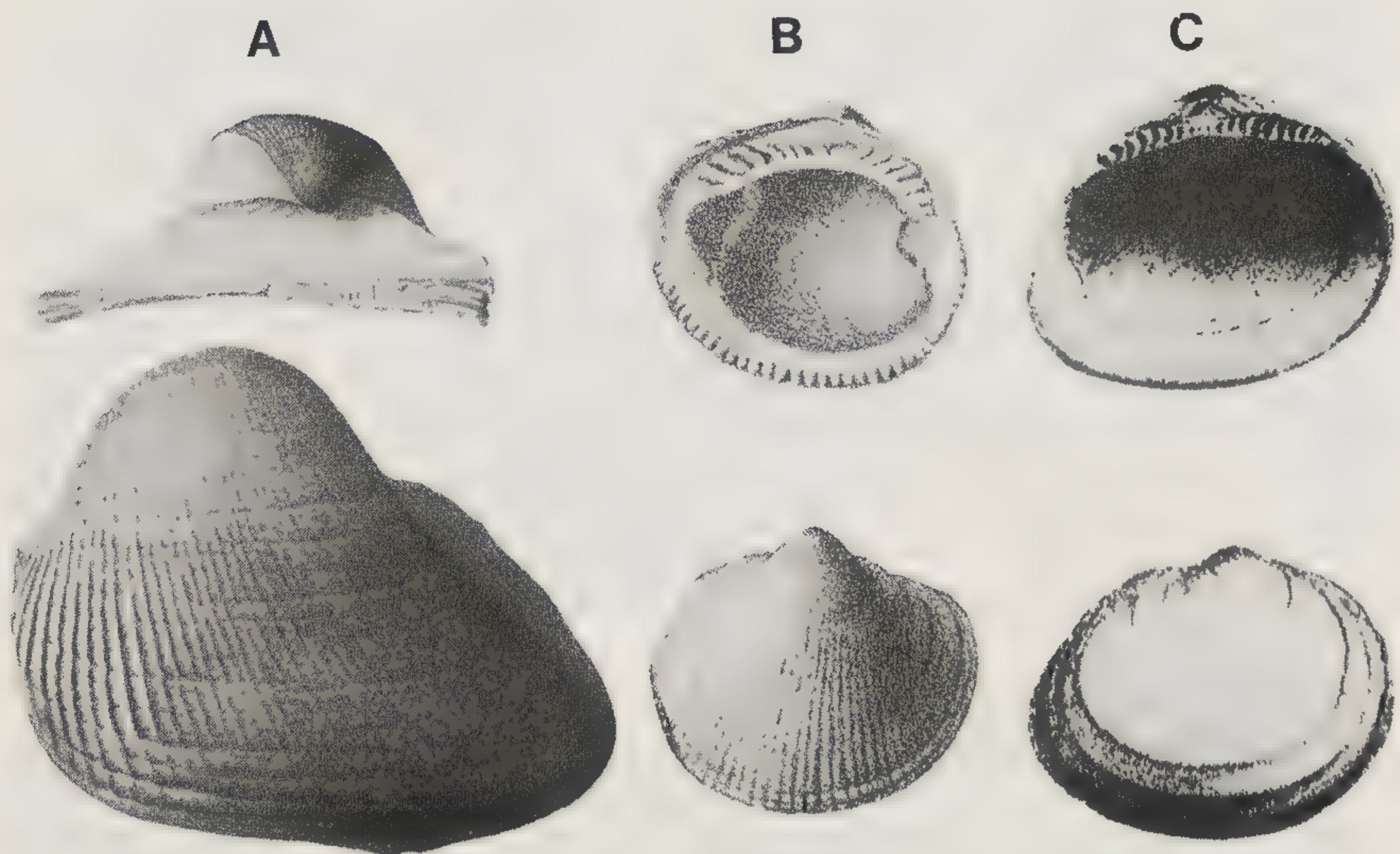
FIG. 25. Mesozoic limopsids, cucullaeids, and glycymerids—a comparison. *A*) *Idonearca forbesi; B*) *Glycymeris sublaevis; C*) *Limopsis corallensis.*

could have given rise to the glycymerids. *I. forbesi* is illustrated here. It might be argued that this comparison is unfair because Nicol states that it is the dentition of young rather than adult cucullaeids that resembles the dentition of glycymerids. However, he offers no evidence to show that this is true for *Idonearca.*

Whatever the case, Figure 25 shows that the glycymerid generally looks more like *Limopsis corallensis* than *Idonearca forbesi*, especially in dentition and shell shape.

Much more work needs to be done to firmly establish the ancestry of the glycymerids, and the possibility of the group's having arisen from cucullaeids can by no means be ruled out. Rather, the point being made here is that, based on what is known from the available literature, a reasonable case may be made for limopsids as possible glycymerid ancestors.

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APPENDIX A
Geological and Geographical Ranges of Valid Genera
Fleming, 1966; Cox et al., 1969)

	Geological Range	Geographical Range
Philobryidae		
Adacnarca	Recent	Antarctica
Aupouria	Pliocene-Recent	New Zealand
Cosa	Pliocene-Recent	Australia; New Zealand; Caribbean; Western North America
Cratis	Miocene-Recent	Australia; New Zealand; Caribbean
Limarca	Eocene	South Australia
Limopsilla	Recent	South Africa
Lissarca	Miocene-Recent	Antarctica; Australia; New Zealand
Neocardia	Recent	South Africa
Philobrya	Miocene-Recent	Western North America; Central America; Antarctica; Southern South America; South Pacific; South Atlantic; Australia; New Zealand; Mediterranean; Indian Ocean
Limopsidae		
Limopsis	Middle Jurassic-Recent	Cosmopolitan
Empleconia	Recent	North Pacific; Bering Sea

APPENDIX B
Descriptions of junior subjective synonyms

I. Philobryidae

AUSTROSAREPTA Hedley, 1899, p. 430

TYPE SPECIES. (M.) *Austrosarepta picta* Hedley, 1899, p. 430.

Described here from examination of syntypes, AM c6378; collected from Middle Harbor, Sydney; also nontype material, USNM 162148 (Fig. 26).
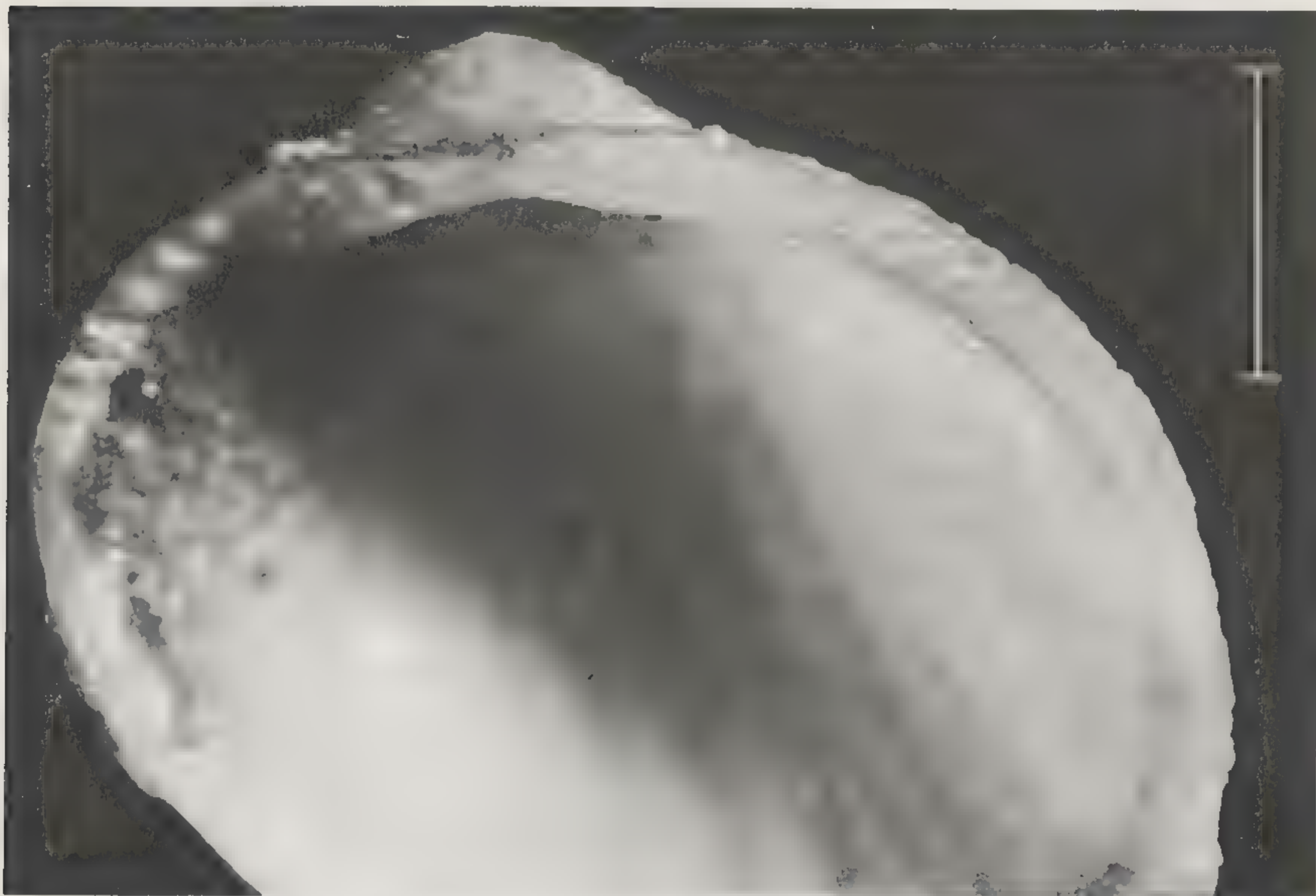
FIG. 26. *Lissarca picta* (Hedley). USNM 162148; from Sydney Harbor. Right valve, interior. Scale = 0.5 mm.

Ligament pit short and triangular. Anterior and posterior series of denticles about the same length and width. Two anterior and three posterior teeth. Margins mostly smooth; sharp folds descending obliquely from the umbo to the posterior margin. External surface concentrically lined. Color reddish brown; mottled. Shape subelliptical. Length = 2.5 mm. Width = 2 mm.

COSATOVA Iredale, 1939, p. 304

TYPE SPECIES. (O.D.) *Philobrya recapitula* Hedley, 1906, p. 471.

Described here from examination of syntypes, AM c19390; collected from 17 to 20 fms., Masthead Island, Queensland, Australia.

Ligament pit short and triangular. Anterior series of denticles about 1/2×
length and 1× width of posterior series. One anterior and three posterior
teeth. External surface with cancellate ornamentation; beaded. Portions of
the inner margins are crenulated. Prodissoconch with a central spike. Shape
mytiliform; anterior margin straight. Color white.. Length = 2 mm. Width
= 3 mm.

DENTICOSA Iredale, 1930, p. 385
TYPE SPECIES. (O.D.) *Philobrya cuboides* Verco, 1907, p. 223.

Described here from examination of holotype from the SAM; collected
from the Backstairs Passage, Australia (20 fms.).
Ligament pit short and triangular. Anterior and posterior series of den-
ticles about the same length and width. 2 anterior and 3 posterior teeth.
Inner margins crenulated. External surface with cancellate ornamentation;
beaded; anterior reduced; shape submytiliform. Length = 2.2 mm. Width
= 2.8 mm.

HOCHSTETTERIA Vélain, 1877, p. 129
TYPE SPECIES. (S.D., Kobelt, 1881) *Hochstetteria aviculoides* Vélain, 1877,
p. 130.

Described here from Vélain (1877). This species was first identified from
specimens collected from Ile Saint-Paul, Indian Ocean.
Ligament pit large and triangular. Anterior denticle series 1/3× length
and 1× width of posterior series. No teeth. Shape mytiliform. Inner mar-
gins crenulated. Length = 2 mm. Width = 3 mm.

HOCHSTETTERINA Thiele, 1934, p. 769.
TYPE SPECIES. (M.) *Hochstetteria crenella* Vélain, 1877, p. 131.

Described here from Vélain (1877). This species was first reported from
Ile Saint-Paul and Amsterdam, both in the Indian Ocean.
Ligament pit triangular. Anterior series of denticles 1/2× length and 1×
width of posterior series. No teeth. Inner margins crenulated. External sur-
face with concentric lines. Shape modioliform. Length = 1 mm. Width
= 1 mm.

LISSARCULA Thiele, 1923, p. 290
TYPE SPECIES. (O.D.) *Lissarcula australia* Thiele, 1923, p. 290.

Described here from Thiele (1923). First identified from the Torres Strait
and Dirk Hartog Island, Australia.
Two anterior and two posterior teeth. Predominantly concentrically orna-
mented. Surface of inner margins uneven. Length = 2 mm. Width =
2.2 mm.

MICROMYTILUS Cotton, 1931, p. 335
TYPE SPECIES. (O.D.) *Myrina crenatulifera* Tate, 1892, p. 131.

Described here from examination of holotype, SAM D31051; collected from MacDonnell Bay, Australia, in shell sand.

Ligament pit rather short, not triangular; descends across hinge. Anterior denticles $1/3\times$ length and $1\times$ width of posterior series. Both series tapering. Posterior inner margins strongly crenulated. External surface with concentric markings. Color brownish red. Submytiliform. Length $= 2$ mm. Width $= 2$ mm.

NOTOLIMOPSIS Maxwell, 1969, p. 167
TYPE SPECIES. (O.D.) *Notolimopsis pulchra* Maxwell, p. 167.

Described here from Maxwell (1969); holotype collected from the Lower Miocene of New Zealand.

Ligament pit short and triangular. Anterior and posterior series of denticles about the same length and width. Four to six anterior and posterior teeth. Inner margins smooth. External ornamentation predominantly concentric. Length $= 3.5$ mm. Width $= 3.1$ mm.

NOTOMYTILUS Hedley, 1916, p. 20
TYPE SPECIES. (O.D.) *Philippiella rubra* Hedley, 1904a, p. 207.

Described here from examination of syntypes, AM c17723; collected from Eaglehawk Neck, Tasmania, Australia, in shell sand; also nontype material, USNM 348938 (Fig. 27).
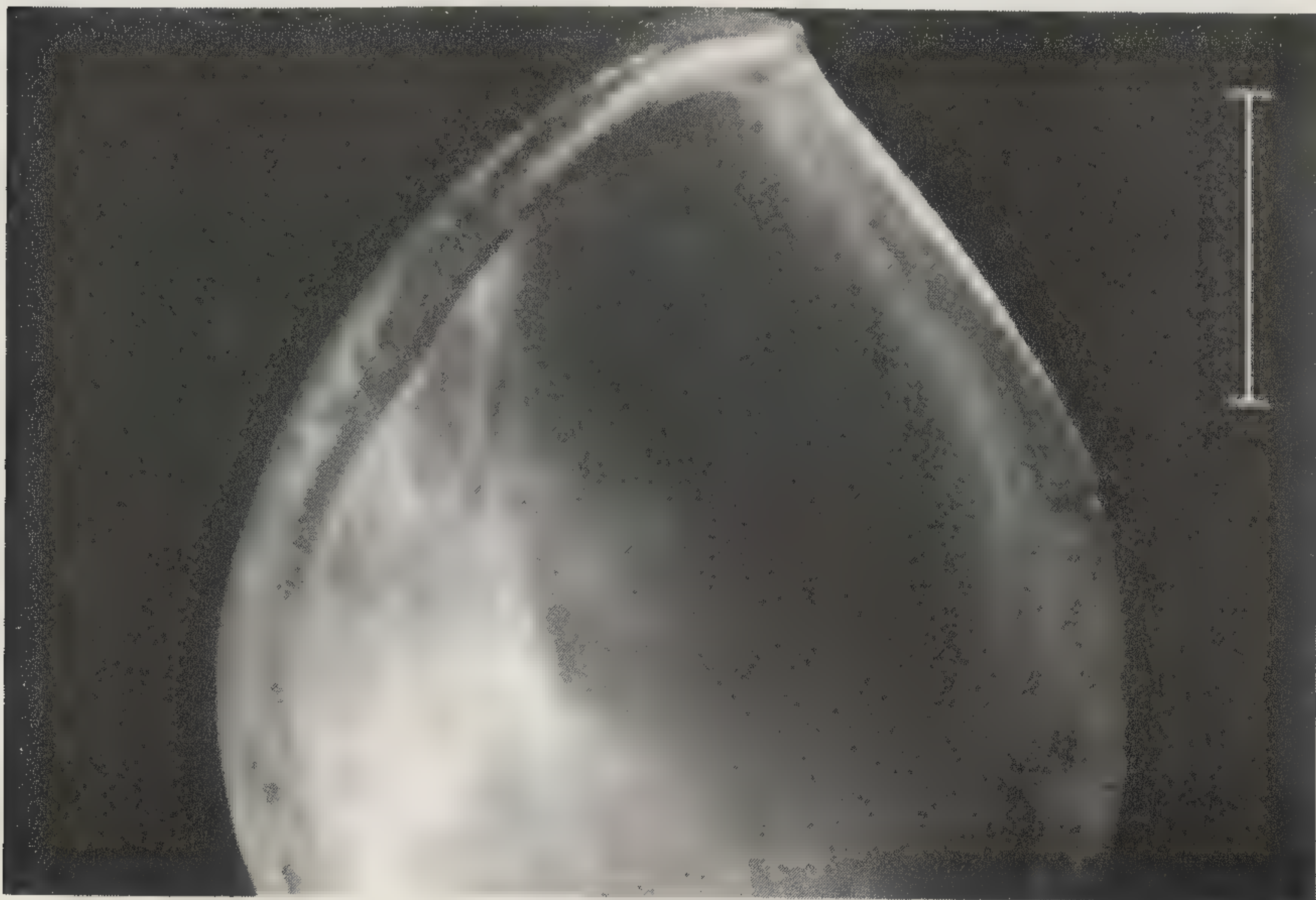

FIG. 27. *Philobrya rubra* (Hedley). USNM 348938; from Victoria, Australia. Left valve, interior. Scale $= 1$ mm.

Ligament pit elongate posteriorly, sharply descending across hinge. Anterior denticles 1/2× length and 1× width of posterior series; both series tapering. No teeth. Inner margins prominently crenulated posteriorly. External surface concentrically lined. Color reddish. Shape mytiliform; anterior margin concave. Length = 2.9 mm. Width = 3.8 mm.

PHILIPPIELLA Pfeffer, 1886, p. 119

TYPE SPECIES. (S.D.; Dell, 1964) *Philippiella quadrata* Pfeffer, 1886, p. 119.

Described here from Pfeffer (1886) and Dell (1964). First identified from South Georgia, South Atlantic Ocean.

Ligament pit elongate posteriorly. No teeth. Two adductor muscle scars. Mytiliform. Prodissoconch apparently punctate.

STEMPELLERIA Clasing, 1918, p. 22

TYPE SPECIES. (M.) *Avicula magellanica* Stempell, 1899, p. 230.

Described here from Stempell (1899) and nontype material, USNM 110735; first identified from southern South America (Fig. 28).

Ligament pit straight, extending posteriorly. Anterior denticle series 1/3× length and 1× width of posterior series. Inner margins smooth. External surface with radial and concentric markings; markings rather faint. No teeth. Shape submytiliform. Periostracum extending about 2 mm over edge of shell. Length = 9 mm. Width = 9 mm.

II. Limopsidae

The forms described in this section, like *Limopsis aurita,* generally have the following principal features:

1) a triangular ligament pit situated in a dorsal area.

2) two adductor muscle scars, usually with the anterior scar smaller than the posterior scar.

3) numerous small, transverse teeth arrayed in an arcuate pattern under the hinge.

4) an anteriorly reduced shell with rounded margins.

Additional morphological information is provided here for each name.

ASPALIMA Iredale, 1929, p. 160

TYPE SPECIES. (O.D.) *Limopsis erectus* Hedley and Petterd, 1906, p. 224.

Described here from examination of syntype, AM c32046; collected off Sydney.

11 teeth, all in one series. Ligament pit comprises 1/4 of dorsal area. Shell outline ovate. External ornamentation concentric.

CIRCLIMOPA Iredale, 1939, p. 243

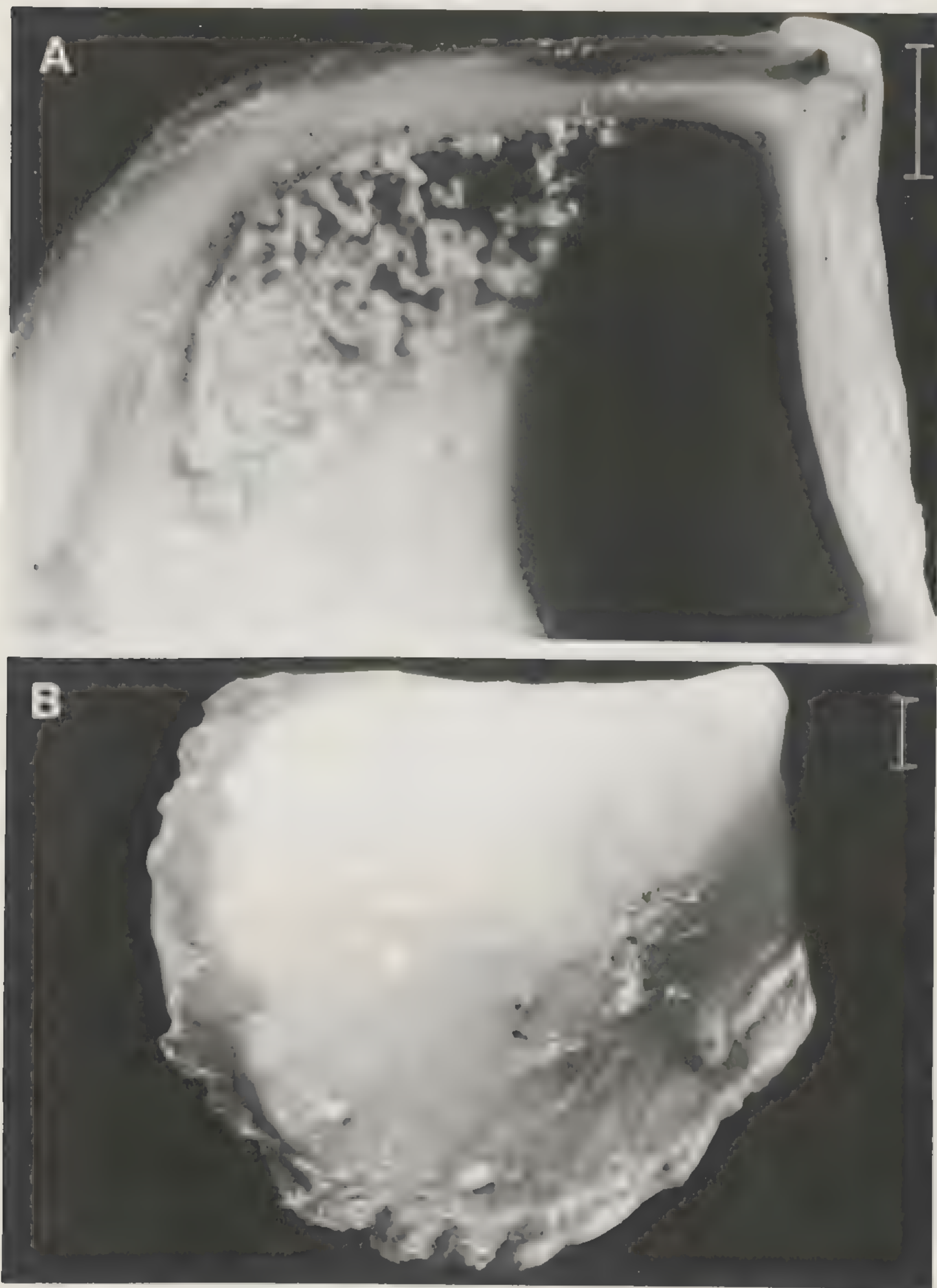TYPE SPECIES. (O.D.) *Circlimopa woodwardi mutanda* Iredale, 1939, p. 243.

FIG. 28. *Philobrya magellanica* (Stempell). USNM 110735; from the Straits of Magellan. *A*) Left valve, interior. *B*) Left valve, exterior. Scale = 1 mm.

Described here from examination of syntypes, AM c60262; collected from Low Isles, Queensland, Australia.

Approximately 24 teeth in a continuous series. Ligament pit comprises about 1/5 of dorsal area. Ornamentation predominantly radial. Shape subcircular.

CNISMA Mayer, 1868, p. 27
TYPE SPECIES. (M.) *nuculatus* Lamarck, 1805, p. 217.

Described here from Lamarck (1805) and Deshayes (1824).

6 posterior and 4 anterior teeth. Ligament pit comprises about 1/5 of dorsal area. External surface with cancellate ornamentation; apparently beaded. Shell greatly reduced anteriorly.

COSMETOPSIS Rovereto, 1898, p. 162
TYPE SPECIES. *retifera* Semper.

Described here from Rovereto (1898).

Concentric external ornamentation. Shape ovoid.

CYRENOLIMOPSIS, Habe 1953, p. 207
TYPE SPECIES. (O.D.) *adamsiana* Yokoyama, 1920, p. 175.

Described here from Habe (1953).

Shape subtriangular. Ornamentation concentric.

FELICIA Mabille and Rochebrune, 1889, p. 115
TYPE SPECIES. (O.D.) *Felicia jousseaumi* Mabille and Rochebrune, 1889, p. 115.

Described here from Mabille and Rochebrune (1889) and from nontype material from the USNM. (Fig. 29).

Nicol (1966) and other writers consider *F. jousseaumi* to be a junior subjective synonym of *Limopsis marionensis*, and the present writer agrees. Although Mabille and Rochebrune (1889) do not mention a ligament pit, it is likely that the absence of this feature in their material is due to poor preservation. *L. marionensis* is the largest known living limopsis and this writer has seen one individual of this species over 60 mm long. This species usually has about 10 to 25 teeth, a ligament pit that extends over about 2/3 of the dorsal area, and is subelliptical in shape.

GLYCILIMA Iredale, 1931, p. 204
TYPE SPECIES. (O.D.) *Glycilima paradoxa* Iredale, 1931, p. 204.

Described here from examination of lectotype, AM c62324, collected from 100 fms., 16 mi. east of Wollongong, New South Wales, Australia.

9 teeth in a single series. Ligament pit comprises most of dorsal area. Ornamentation predominantly concentric.

FIG. 29. *Limopsis marionensis* Smith. USNM 653091; from Antarctica. Right valve, exterior. Scale = 10 mm.

LIMOPSISTA Finlay and Marwick, 1937, p. 24

TYPE SPECIES. (O.D.) *Limopsis (Limopsista) microps* Finlay and Marwick, 1937, p. 24.

Described here from Finlay and Marwick (1937). Holotype located in the New Zealand Geological Survey Collection; from the Danian of New Zealand.

Approximately 10 anterior and 10 posterior teeth. Ligament pit comprises about 1/3 of dorsal area. Shape ovoid. Ornamenation concentric.

LORINGELLA Iredale, 1929, p. 160

TYPE SPECIES. (O.D.) *Limopsis loringi* Angas, 1873.

Described here from Angas (1873) and from AM c11329.

Approximately 17 teeth. Ligament pit about 1/3 of dorsal area. External ornamentation concentric. Small individuals subcircular. Large individuals always wider than long.

LUNOPSIS d'Orbigny, 1850, p. 243
TYPE SPECIES. (O.D.) *hoeninghausii* Müller, 1847.

Described here from Müller (1847).
Concentric external ornamentation, with radial elements as well. Ovate.

NIPPONOLIMOPSIS Habe, 1951, p. 45
TYPE SPECIES. (O.D.) *Limopsis nipponica* Yokoyama.

Described here from Habe (1951).
4 posterior lateral teeth and 3 perpendicular anterior teeth. Ligament pit comprises about 1/4 of dorsal area. External surface with a cancellate pattern; apparently beaded. Shell greatly reduced anteriorly.

OBLIMOPA Iredale, 1939, p. 242
TYPE SPECIES. (O.D.) *Oblimopa macgillivrayi actaviva* Iredale, 1939, p. 242.

Described here from examination of syntype, AM c60261; from the Low Isles, Queensland, Australia.
Approximately 8 anterior and 12 posterior teeth. Ligament pit comprises about 1/2 of dorsal area. Shell shape ovate.

PECTUNCULINA d'Orbigny, 1844, p. 182
TYPE SPECIES. (O.D.) *Pectunculus scalaris* Sowerby, 1825, p. 113.

Described here from Sowerby (1825).
27 teeth. Ligament pit comprises about 1/3 of dorsal area. Shell wider than long, with rounded margins, and covered externally with about 25 prominent radial ridges.

PHRYNELIMA Iredale, 1929, p. 160
TYPE SPECIES. (O.D.) *Limopsis brazieri* Angas, 1871, p. 21.

Described here from Angas (1871).
Shell shape ovate. External ornamentation concentric.

SENECTIDENS Iredale, 1931, p. 204
TYPE SPECIES. (O.D.) *Senectidens dannevigi* Iredale, 1931, p. 204.

Described here from examination of lectotype, AM E4832; collected from 30 fms. off Gabo Island, New South Wales, Australia.
Approximately 21 teeth, all in one series; teeth very faint under ligament pit. Two anterior teeth are parallel rather than transverse. Ligament pit comprises about 1/2 of dorsal area. External ornamentation concentric.

VERSIPELLA Iredale, 1931, p. 203
TYPE SPECIES. (O.D.) *Versipella soboles* Iredale, 1931, p. 203.

Described here from examination of syntypes, AM c24366; collected from east of Sydney Heads, New South Wales, Australia.

Approximately 20 teeth, all in a single series. Ligament pit comprises about 1/3 of dorsal area. Concentric external ornamentation. Shell outline subelliptical.

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