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ORIGINAL ARTICLE

Shell and hinge morphology of juvenile *Limopsis* (Bivalvia: Arcoida) – implications for limopsid evolution

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Abstract

Early ontogenetic shells of *Limopsis angusta*, *L. aurita*, *L. cristata*, *L. friedbergi* and *L. minuta* are described in detail and their morphogenetic traits discussed in a phylogenetic context. Prodissoconch length is found to range from 170–370 µm discounting the so-called prodissoconch 2 stage of authors. Reports of such a stage refer to the early postlarval 'interdissoconch'. Prodissoconch sizes are indicative of lecithotrophy but not of brooding. Limopsid-like prodissoconchs are rather common among pteriomorphs and at present of little use for phylogenetic interpretations, therefore. The early postlarval hinge is characterized by two tooth generations: an early one, (G1), representing the postlarval continuation of provincular teeth, and a late one, (G2), representing the independent adult dentition. This is a plesiomorphic trait for Pteriomorphia. The postlarval ligament is continuous with the larval resilium; it is neither co-functional with nor is it substituted by the typical duplivincular ligament as in other arcoids. Occasionally developed ridges, gutters or multiplication of ligament sublayers remain restricted to the primordial resilifer. It is concluded that the limopsid adult ligament represents a fusion of adult sublayer repetition within a retained larval resilium, a phenomenon best described as a heterochronic process. Comparisons with homologous characters of other arcoids support the view that Limopsidae evolved from parallelodontid arcoids and that they gave rise to Philobryidae but not to Glycymerididae.

Key words: *Limopsidae, Bivalvia, shell morphology, early ontogeny, morphogenesis, evolution*

Introduction

The Limopsidae is a small bivalve family with an almost worldwide distribution, absent only in the Arctic area. Reviews of their anatomy, shell microstructure and genetic analyses clearly relate this group to the Arcoida (Carter 1990; Giribet & Wheeler 2002; Giribet & Distel 2003; Oliver & Allen 1980; Waller 1978, 1980). However, their compressed, obliquely oval shell, lack of a duplivincular ligament, and the tendency to enlarging the posterior adductor muscle (Oliver 1981; Tevesz 1977) are unusual features among arcoids which have lead to different hypotheses concerning their phylogenetic relationships. According to Tevesz (1977), the family evolved by heterochrony from Grammatodontinae (Parallelodontidae) with the Bathonian (Middle Jurassic) *'Limopsis' minima* (Sowerby 1825) being the oldest representative presently known. According to Oliver (1981), *'L.' minima* more likely belongs to the Grammatodontinae and the Limopsidae could as well be derived from the Cucullaeidae. He does not disregard the possibility that Limopsidae evolved in the Jurassic but states that the first truly recognizable limopsids appear in the Albian (Lower Cretaceous). Alternative hypotheses of Carter (1990) and Neveskaya et al. (1971) also consider the possibility that limopsids evolved from Cyrtodontidae or Pichlerioidea.

Most authors agree that the Limopsidae gave rise to the Philobryidae (e.g., Carter 1990; Tevesz 1977). But, Tevesz (1977) also tentatively derives the Glycymerididae from Limopsidae (cf. Newell 1969) whereas Nicol (1950) and Carter (1990) consider it more likely that Glycymerididae evolved from Cucullaeidae (Arcoidea).

Much of this disagreement originates from our poor knowledge of the ontogeny and evolution

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of early shell features, especially of the limopsid hinge, where the assumed heterochronic changes should be observed best. The present contribution therefore focuses on the description of early shell characters of five, otherwise well known Atlantic species (Oliver & Allen 1980; Oliver 1981; Salas 1996; Warén 1980). The results are discussed in the light of published and new information concerning Philobryidae, Parallelodontidae and Arcidae (e.g., Bernard 1897; Dell 1964, 1990; Hayami & Kase 1993; Kiel 2004; Morton 1978; Prezant 1990) and a recently presented hypothesis on the evolution of early shell characters in pteriomorph bivalves (Malchus 2004a,b).

Material and methods

The invertebrate collection of the Swedish Museum of Natural History (SMNH) includes 243 catalogued lots of the five *Limopsis* species described here, each lot containing numerous small, articulated and single valves. Several lots of each species were examined and searched for specimens with well preserved larval shells. The selected lots are listed under each species in the systematic part with annotations on the collection sites. Detailed information on all lots can be retrieved from the 'Biodiversity Data portal' http://www.gbif.net/portal/index.jsp of the Global Biodiversity Information Facility (GBIF). Each search string 'Genus species' yields a single match which links to a list of data servers. The server link to 'GBIF-Sweden Provider' allows viewing as well as downloading the data in question. In the case of *Limopsis angusta* (1 record) also search for *Limopsis augusta* (11 records) (this is a misspelling, not yet corrected on the server). For the northern species, where our material constitutes a considerable addition to existing knowledge, we have given the distribution in more detail, under each species. Figured and complementary material is stored in the invertebrate collections of the Swedish Museum of Natural History (SMNH numbers).

The recent material was originally preserved in borax-buffered formalin and later transferred to 80% ethanol and usually dried. Only postlarval shells were available for study but were generally well preserved including prodissoconchs and remains of the resilia. The condition of the periostracum varies between species and localities. In *Limopsis cristata* Jeffreys 1876, it is generally better developed and remains across most of the valves except for specimens from the seamounts where it usually remains only along the ventral margin.

Additional material used for comparison are larval to adult shells of *L. marionensis* Smith 1885, *L. lilliei* Smith 1915, *L. enderbyensis* Powell 1958, and *L. knudseni* Dell 1990 and about 15 philobryid species from the southern oceans (collected by the British Antarctic Survey and the Alfred-Wegener-Institute) which form a part of an ongoing study of that family. In addition, early postlarval shells of two glycymeridids, *G. glycymeris* Linné 1758, and *G. violacescens* Lamarck 1819, were examined.

Species were examined under stereo microscope (*ca.* ×50). Small shells were selected, cleaned with commercial bleach and ultrasonicated, mounted on aluminium stubs sprayed with 3M non-permanent spray mount™ or on adhesive carbon pads, for study under a Hitachi S4300 scanning electron microscope. Length and height were measured of some larval shells of each species. The average error of measurements is ±5%.

Systematic part

Arcoida

Limopsoidea Dall 1895
Limopsidae Dall 1895

Family characters. After Tevesz 1977 and Oliver & Allen 1980. Shell orbicular to subtrigonal, equilateral to strongly drawn out posteriorly, commissure non-gaping, ligament with a generally short (in posteroventral direction) central triangular resilifer, taxodont dentition, and thick periostracum, often partly worn off, with bristles. Size commonly between 5–30 mm, but some species larger (e.g., *L. marionensis* up to *ca.* 60 mm).

Remarks. Oliver (1981) described the basic adult ligament as "amphidetic-alivincular (lamellar-fibrous-lamellar arrangement) within a ventrally extending resilifer". Adult specimens of some large species, e.g., *L. marionensis*, develop additional sublayers. This type has been termed 'multivincular' by Oliver (1981). In addition and unknown from recent species, the resilifer of Jurassic '*Limopsis*' *minima* (Sowerby 1825), has a series of grooves and ridges (Oliver 1981, fig. 9, appendix fig. 1). For this reason Oliver (1981) excluded this species from the Limopsidae (but see section on limopsid evolution, below).

Additional observations. All examined limopsids develop two generations of taxodont teeth. Generation 1 (G1) consists of small rectangular teeth of *ca.* 10 μm width which develop anteriorly and posteriorly of the resilifer on the early postlarval hinge area. These teeth generally disintegrate laterally and later also ventrally into tiny pustules and ultimately disappear (Figure 1A–C). The 'taxodont dentition'

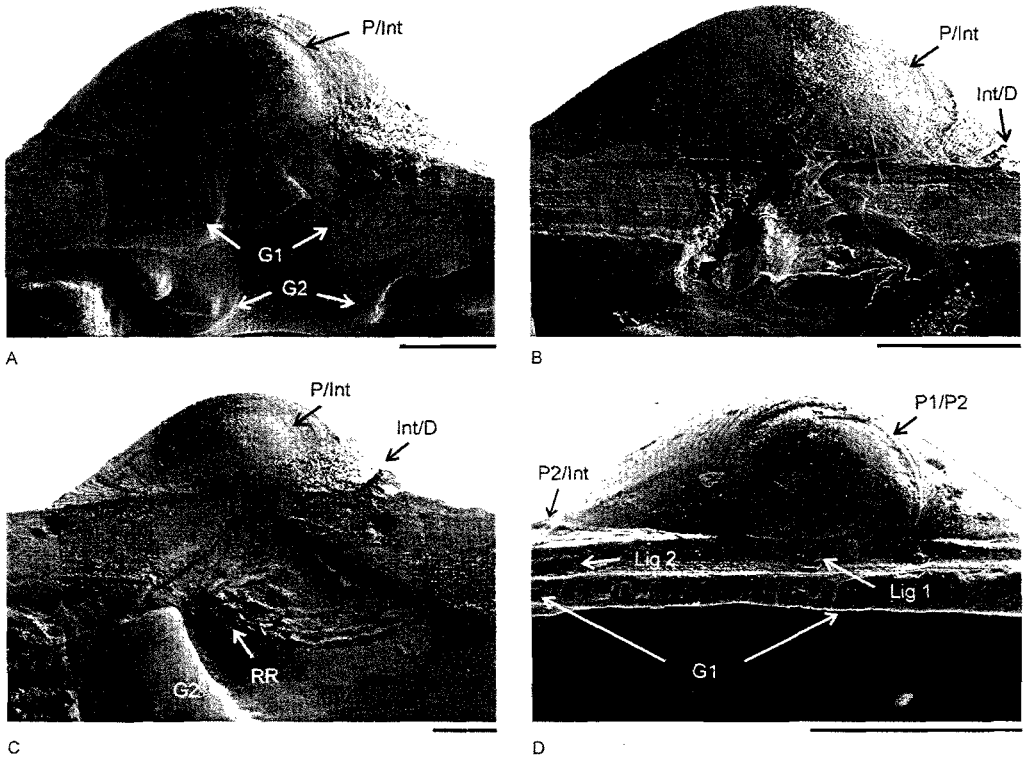

Figure 1. Early shell and hinge characters in Limopsidae and Parallelodontidae. All scale bars 100 µm. Abbreviations: G1, generation 1 teeth; G2, generation 2 teeth; Int/D, boundary between interdissoconch and dissoconch; Lig1, larval ligament (or resilifer = groove); Lig2, groove for second ligament (lamellar and fibrous); P1/P2, boundary between prodissoconch 1 and 2; P/Int, boundary between prodissoconch and interdissoconch; RR, resilifer ridge. (A) *L. cristata* (SMNH 72277, North Sea). Note growth tracks of postlarval G1 teeth and their ventral disintegration into pustules. (B) *L. minuta* (SMNH 37499, off western Norway). Note spongy ligament and its origination point below the larval hinge. (C) *L. minuta* (SMNH 72277). Note asymmetric resilifer ridge. (D) *Grammatodon* sp. (Bundesanstalt für Geowissenschaften und Rohstoffe, BGR 10870-5, Callovian, Poland). Note small prodissoconch 1 (< 100 µm) and well demarcated P2, presence of disjunct ligament (Lig 1, Lig 2), and G1 teeth; G2 teeth not visible at this magnification.

of authors refers to what we here call the second tooth generation (G2). G1 and G2 teeth are distinguished in shape, by the much smaller size of G1, and a distinct interspace between the two generations. However, this gap does not refer to the central, edentulous space between anterior and posterior G2 teeth. The 'series of ligamental pits' in the early dissoconch of '*Limopsis*' *azumana* Yokoyama 1910, mentioned by Tanabe (1990) are actually G1 teeth.

Affiliations. Tevesz (1977) recognizes *Empleconia* (Dall 1908) and *Limopsis* Sassi 1827, as valid genera whereas Oliver (1981) includes the type species of *Empleconia*, *E. vaginata* (Dall 1891) in his *Limopsis* sensu lato. *Oblimopa* Iredale 1939, and *Crenulilimopsis* Kuroda and Habe, 1971 (in: Kuroda et al. 1971) are treated as valid genera by Tanabe and Zushi (1988), but Tanabe (1990) considers *Crenulilimopsis* as a subgenus of *Limopsis*. *Nipponolimopsis* Habe 1951, (type species *Cyrilla decussata* Adams 1862) is more likely a philobryid genus based on its larval shell morphology (larval shell see Oliver 1981, figures 11–12; Okutani, 2000, figures Limopsidae 7-7, on adult shell). Another species, *N. azumana* (Yokoyama, 1910), was illustrated by Tanabe (1990, fig. 3) as *L. (Limopsis) azumana*.

Stratigraphic range. Middle Jurassic?, Lower Cretaceous to Recent.

Limopsis Sassi, 1827

Type species: *Arca aurita* Brocchi, 1814 (by monotypy), Tertiary, Italy.

Genus characters. Oliver (1981) distinguishes 13 morphological 'classes' within the genus which may or may not reflect monophyletic groupings. For shell morphology and anatomical features of species see Oliver and Allen (1980) and Oliver (1981).

Additional observations. The prodissoconch is D-shaped, equivalve, and almost equilateral (cf. Figure 5E). Most larval shells are moderately and rather evenly inflated and lack a steeply inclined shell lip towards the postlarval shell (Figure 1A–C), except for the antarctic *L. knudseni* of which the

larval shell is more tumid and has a lip. Some species possess an incipient, teardrop-shaped, dorsocentral elevation surrounded by a weak, narrow depression. In the following, we use the terms 'boss' and 'moat', respectively, for these structures (Figure 2C,J). Fine growth lines are present but often difficult to see. Radial ribs are generally lacking. However, there are between four and six, very low-profile radial ribs on the prodissoconch of *L. aurita* (Figure 2F). These hardly discernable structures are reminiscent of much better developed ribs or gutters in some philobryids (cf. Figure 5F). Shell lengths range from 170–370 μm and length/height ratios from 1.19 to 1.47.

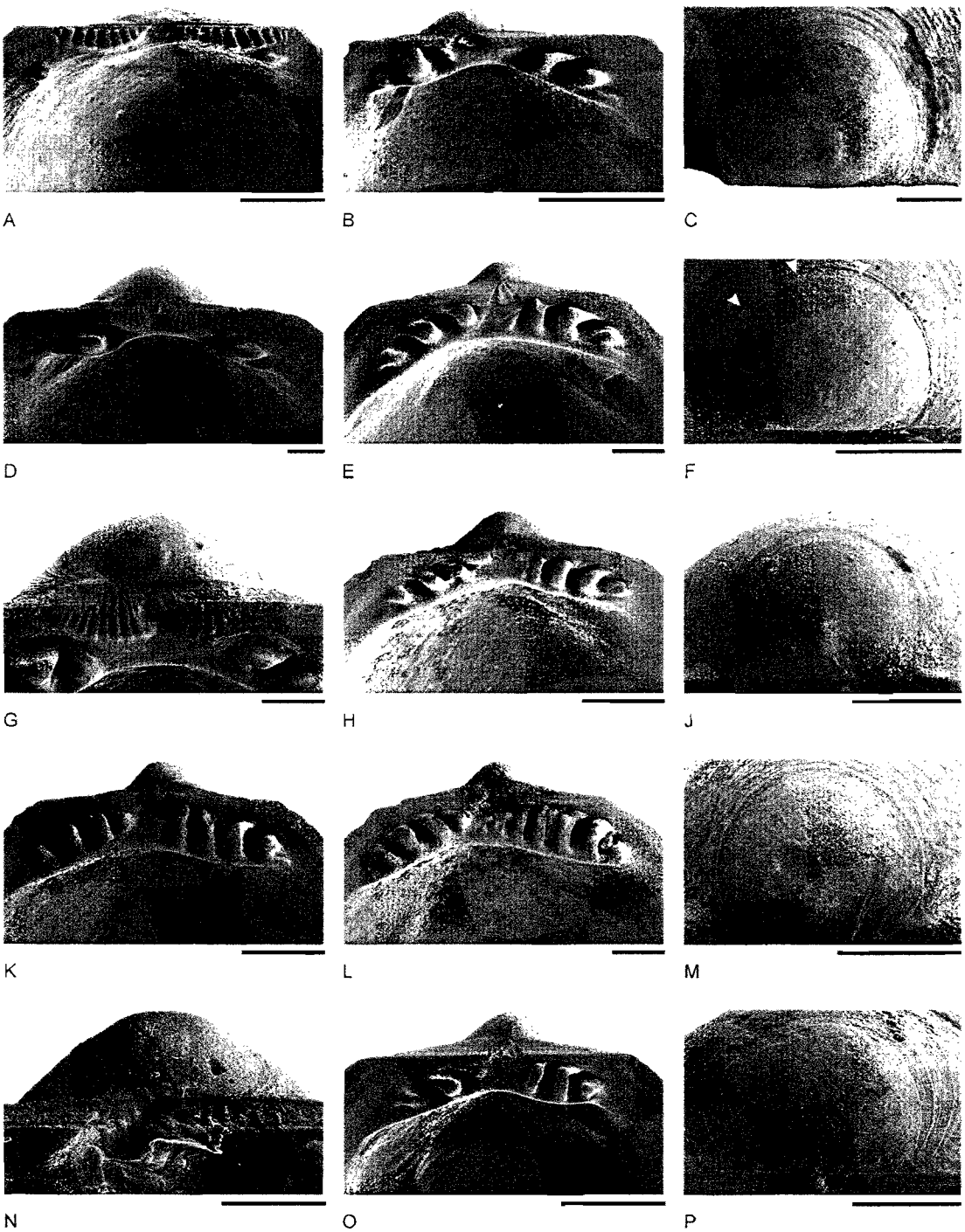

Figure 2. Larval shell and early postlarval hinge characters. Scale bars: left and right columns (except for figure K) 100 μm; centre column and figure K: 500 μm.(A–C): *L. angusta* (SMNH 36966, SW off Portugal). (D–F): *L. aurita* (SMNH 36966, SW off Portugal). (G–J): *L. cristata* (SMNH 72277, North Sea). (K–M): *L. friedbergi* (SMNH 37495, Italy, Lower Pleistocene). (N–P): *L. minuta* (SMNH 37499, off western Norway).

The prodissoconch is followed by a postlarval interdissoconch (Jørgensen 1946) with more or less dense growth lines and/or low ridges and no radial sculpture (but see remarks below). The prodissoconch-interdissoconch boundary is well defined whereas the transition from interdissoconch to dissoconch is not always clear (Figure 1C).

The interdissoconch to early dissoconch stage possesses both tooth generations simultaneously. Postlarval G1 teeth grow ventralwards and generally subparallel to each other cutting the ventral edge of the hinge area at a right angle (Figure 1A). However, instead of growing more or less parallel, the anterior and posterior teeth, which are separated by the resilium, may independently diverge in ventral direction (Figure 2G). In this case, there are two centres of divergence, one for the anterior and one for the posterior row of teeth.

The postlarval resilium emerges below and centrally or slightly behind the centre of the straight larval hinge and is continuous with the larval resilium (Figure 1A–C) (see Malchus 2004b, fig. 3, for positions and growth directions of ligaments). The rather thick basal part has a 'spongy' convoluted architecture with bundles of fibrous ligament (Figure 1B) which becomes densely packed towards the commissure plane. The lamellar ligament is not preserved in the examined specimens; it is unknown whether it fills the hollow spaces between the fibre bundles in living animals. The spongy ligament covers the entire surface of the resilifer. Lateral, purely lamellar sublayers have not been observed at this early postlarval stage, but it cannot be excluded that thin lamellar sheets, confined to the resilifer walls, were originally present.

Although the early ligament itself does not show the typical amphidetic-alivincular sublayer division, the resilifer may be divided by either one or two low, generally undulating, divergent ridges (Figure 1C). The lateral portions measure *ca.* 1/3 –1/4 the length of the central depression; the lateral portions are not necessarily of equal size.

Remarks. In contrast to other authors we think that the beginning of coarser concentric growth increments corresponds to the early post-metamorphic interdissoconch rather than prodissoconch 2 as interpreted by Tanabe and Zushi (1988) and Tanabe (1990). The dimensions given here for the larval shell should therefore be compared with the measurements for the prodissoconch 1 in their studies.

Our interpretation is based on two reasons. First, the surface of prodissoconch 2 (P2) has a smooth surface despite the presence of growth lines whereas the supposed P2 sculpture in *Limopsis* is coarse and often somewhat scaly (cf. Figure 1B and 1D). Second, the supposed P2 stage of lecithotrophic Crenellinae (Mytilidae), which present an analogous problem, is now known to be of post-metamorphic origin (Dinesen, pers. comm. 2002). Also, lecithotrophic Pectinoidea from Scandinavia and nordic seas (Dijkstra & Gofas 2004; Warén, unpubl.) show comparable prodissoconch characteristics with an abrupt initiation of interdissoconch growth. We therefore feel confident in our interpretation of these characters in *Limopsis*.

Limopsis angusta Jeffreys 1879
Figures 2A–C, 3A–B, 4E
1980 *Limopsis angusta* Jeffreys 1879: Warén, p. 72.
1879 *Limopsis minuta* var. *angusta* Jeffreys, Proceedings Zool. Soc., London, 585–6.
1996 *Limopsis angusta* Jeffreys 1879: Salas, p. 47, figs. 82–87.

Material examined. SMNH 36965 and 36966, off southwestern Portugal, Ampère Bank, 35.053N, 12.923W, in 300–325 and 225–280 m depth, respectively (Expedition: Seamount I 1987). The collection contains eight additional lots from off SW Portugal and two from the Alboran Sea, Spain (Expeditions Seamount I 1987, Balgim 1984, and P. Crovato, no date) (species depth range: 54–300 m) (www.gbif.net/portal/index.jsp: search for *Limopsis augusta* (misspelled) and *L. angusta*).

Species characters. According to Salas (1996, p. 47), the shell is usually notched for the exit of the byssus (cf. Figure 3B, arrow). The concentric and radial sculptures form a granular surface all over the shell. Towards the apical area, the shell is tinged brown.

Additional observations. The prodissoconch has an incipient dorsocentral boss with a shallow moat (Figure 2C). The length of four specimens ranges from 265 to 269 μm; the length/height ratio of two prodissoconchs is 1.19.

At a size of *ca.* 1 mm, the hinge has about eight well developed G1 teeth and one incipient G2 tooth on each side of the resilium; at a size of 3 mm, there are three posterior (anterior one incipient) and three anterior G2 teeth, with an edentulous gap below the ligament. The resilifer becomes divided by an anterior, low, wavy ridge. The inner shell surface has only very weak radial ridges, the internal shell margin is relatively narrow and smooth; the anterior muscle scar is situated ventrally to the ventral corner of the anterior hinge plate and has a short myophoral ridge (Figure 3B).

Early postlarval shells are posteriorly drawn out and rather convex, with an orthogyrate umbo,

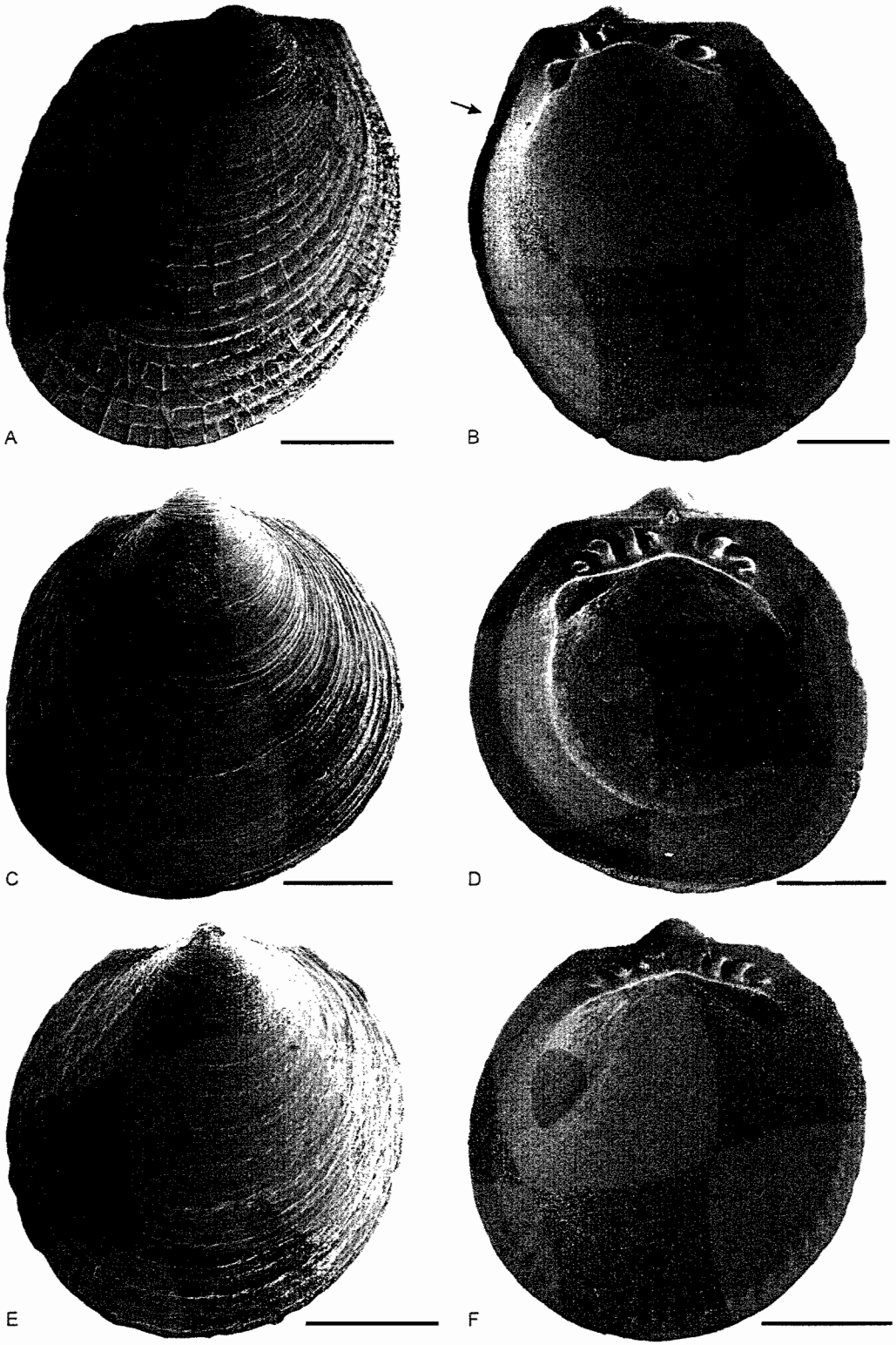

Figure 3. Adult shell characters. The position of adductor scars and myophoral ridge (where present) have been darkened. Scale bars: A–B and E–F, 1 mm; C–D, 500 μm. (A–B): *L. angusta*, RV (SMNH 36966, SW off Portugal). The arrow in Figure B points at the weak shell inflexion where the byssus emerges from between the valves. (C–D): *L. aurita*, RV (SMNH 36152, North Sea). (E–F): *L. cristata*, RV and LV (SMNH 72277, North Sea).

somewhat anterior to the midline of the hinge, and a posterior keel (Figure 3A). The growth crests are notched at the base of periostracal bristles (Figure 4E); the bristles themselves do not or only very weakly project beyond the shell margin. The central part of the shell has extremely weak radial

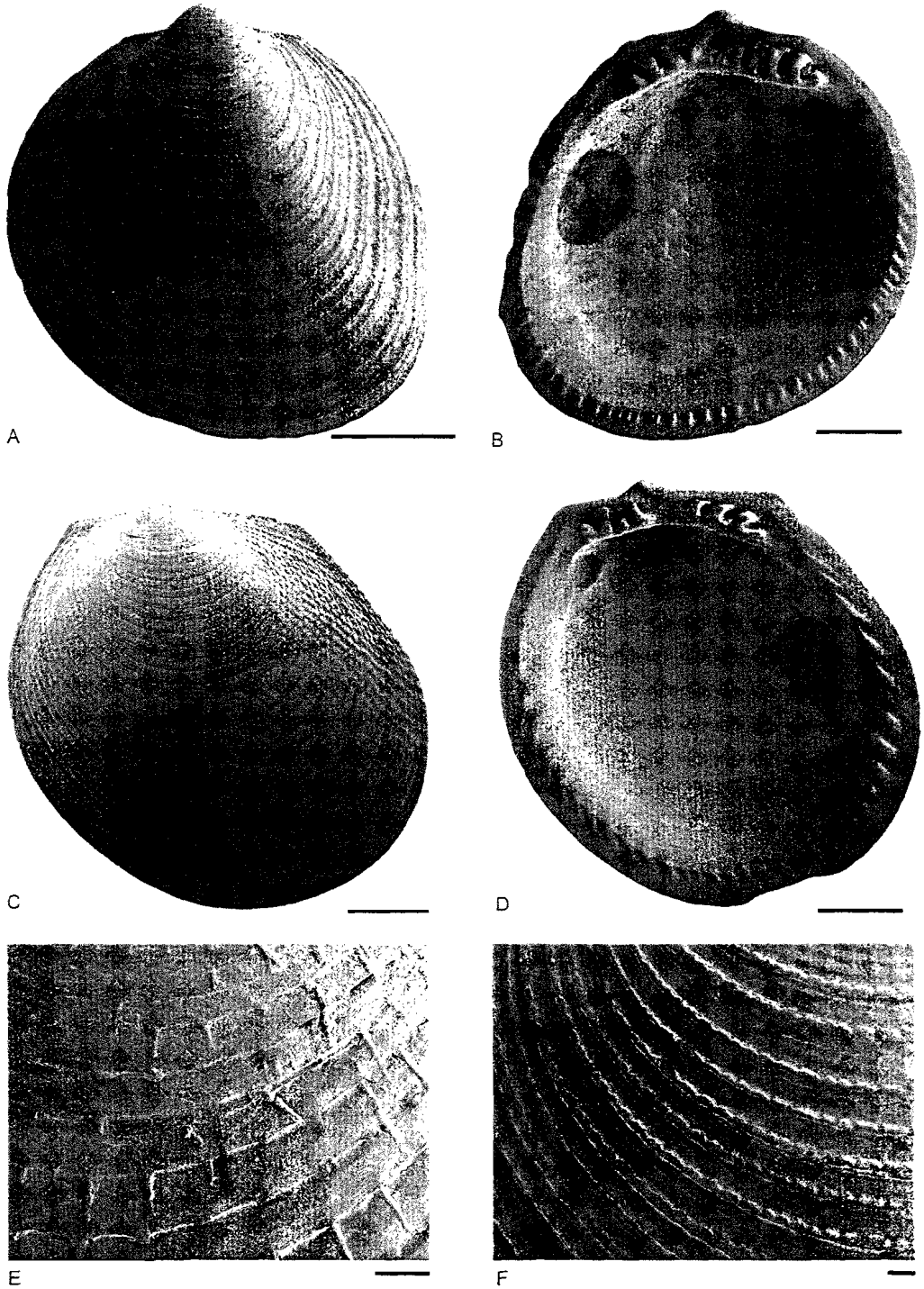

Figure 4. Adult shell characters. The position of adductor scars and myophoral ridge (where present) have been darkened. Scale bars: A–D, 1 mm; E–F, 100 µm. (A–B, F): *L. friedbergi*, A–B, LV (SMNH 37495, Italy, Lower Pleistocene); F, detail of sculpture. (C–D): *L. minuta*. LV and RV (SMNH 37499, North Sea). (E): *L. angusta* (SMNH 36966, SW off Portugal). Detail of sculpture.

ridges next to or below the bristles but seven to nine posterordorsal ridges are somewhat better developed.

Comparisons. The prodissoconch size is similar to that given for *L. tenella* Jeffreys, 1876, (240 µm) (Oliver & Allen 1980) but considerably larger than in most other compared species except *L. knudseni* with 367 µm. According to Salas (1996), *L. angusta* differs from *L. minuta* by its overall granular surface. This character is not convincingly developed in small specimens. However, *L. angusta* lacks the gutter-like impressions caused by bristles in other species. Radial elements are better developed on the central

part of the shell but posteriorly less developed than in *L. aurita* and *L. minuta*.

Limopsis aurita (Brocchi 1814)
Figures 2D–F, 3C–D
1814 *Arca aurita* Brocchi, p. 485, fig. 9a,b, pl. 13.
1980 *Limopsis aurita* (Brocchi 1814), Oliver and Allen, p. 78, figs 1–2.
1981 *Limopsis aurita* (Brocchi 1814), Oliver, p. 83, App. figs 8, 11–12.
1996 *Limopsis aurita* (Brocchi 1814), Salas, p. 47, figs 71–73.

Material examined. SMNH 36152, northern North Sea, Snorre B oil filed, 61.5N, 2.2E, 338 m depth (Expedition Akvaplan Niva, 1999); SMNH 36990, SW of Portugal, Seine Bank, 33.8N, 14.4W, 181 m depth (Expedition Seamount I, 1987). The collection contains 44 lots more from Iceland to off western Morocco obtained during expeditions Akvaplan Niva, 1993 and 2002; BIOFAR, 1988 and 1989; BIOICE, 1992; P. Crovato (lower Pleistocene, no date); J.G. Jeffreys (no date); Porcupine 1870, Zanclean (fossil; no date). Depth range: 117–1392m.

Species characters. For adult shell characters see Oliver and Allen (1980) and Oliver (1981), who placed *L. aurita* in morphological 'class 4' with ligament type A (primary ligament restricted to shallow resilifer, remainder of ligament area covered with periostracum).

Additional observations. The prodissoconch has four to six very weak radial ribs (Figure 2F, white triangles). Some specimens apparently have a weak dorsocentral boss and surrounding moat. The length of five specimens ranges from 182–200 μm and the length/height ratio of three specimens from 1.26–1.29.

At a shell size of 1 mm the hinge has about ten well developed G1 teeth on each side of the resilifer, with the central teeth being largest and slightly diverging ventrally; the terminal teeth disintegrate into pustules. On each side of the ligament pit there is a single well developed G2 tooth in the right and two teeth in the left valve (Figure 2D). At a size of *ca.* 9–14 mm the shell possesses 5–7 posterior and 8–9 anterior G2 teeth. The anterior G2 teeth extend below the resilifer but leave a gap between the anterior and posterior rows of teeth. The anterior adductor scar is situated below the ventral corner of the anterior G2 teeth (Figure 3D). The incremental growth crests of the outer shell surface are ventrally notched and their dorsal surfaces have gutter-like impressions. Towards the dorsal margin the ends of the valves have a weak sculpture of radial ridges (Figure 3C).

Comparisons. The prodissoconch size measured by us compares reasonably well with the 170 μm reported by Oliver and Allen (1980) for this species. According to Salas (1996, p. 47), the species is easily recognised by its smooth inner shell margin at all growth stages (cf. Figure 3D). The external sculpture is generally more irregular in *L. aurita* than in *L. minuta*, but in small specimens (*ca.* 2mm) of both species the periostracum bristles cause similar gutter-like impressions. If, in addition, internal marginal crenulations are missing or very few in *L. minuta*, distinction from *L. aurita* may be difficult.

Limopsis cristata Jeffreys 1876
Figures 1A, 2G–J, 3E–F, 5B,E
1876 *Limopsis cristata* Jeffreys 1876, pp. 434–5.
1980 *Limopsis cristata* Jeffreys 1876: Warén, 1980, p. 42, pl. 7, figs 5–6.
1981 *Limopsis cristata* Jeffreys 1876: Oliver, p. 83.
1996 *Limopsis cristata* Jeffreys 1876: Salas, p. 48, figs. 78–81.

Material examined. SMNH 36577, northern North Sea Snorre TLP oil field, 61.4N-2.2E; 303 m (Akvaplan Niva, 1999); SMNH 37698 and 40818, northern North Sea, Statfjord nord oil field, 61.4N-1.9E, 262 m and 61.4N-2E, 278 m, respectively (Akvaplan Niva, 1999); SMNH 48692, northern North Sea, Togi oil platform, 60.6N-3.6E, 304 m (Akvaplan Niva, 2001); SMNH 72277, northern North Sea Troll West oil platform, 60.8N-3.5E, 324 m (Akvaplan Niva, 1995). The collection contains a total of 136 lots collected during numerous expeditions from Iceland, Faroes to the Norwegian coast, also in fjords from 60°N and a depth of 90–800 m, north to 72°N and east to 26°E, in 200–400 m. Depth range: 93–1162 m.

Species characters. For adult shells see Oliver and Allen (1980) and Oliver (1981), who placed the species in his morphological 'class 5' with ligament type C (exclusively fibrous resilium in restricted, narrow resilifer, and transitional or lamellar sublayer covering remainder of hinge area).

Additional observations. The prodissoconch has a knobby dorsocentral boss with a shallow moat (Figure 2J). The prodissoconch length of four speci-

mens ranges from 175–186 and the length/height ratio from 1.27–1.39.

The hinge of small specimens (< 3 mm) has well developed G1 teeth which are arranged in two radial series, one on each side of the ligament pit (Figures 1A, 2G). With age, the teeth disintegrate into pustules. The anterior G2 row has generally one or two teeth more than the posterior series (e.g., anterior 4 – posterior 3 teeth at a length of 2.4 mm, Figure 2H, and anterior 7 – posterior 5 teeth at a length of 6 mm). The ligament occupies a small, rather symmetric triangular resilifer without subdivisions. The internal ribs are rather well developed and the crenulation of the inner shell margin covers almost the whole circumference at a size of *ca.* 3 mm. External radial ribs are regularly interrupted by the concentric sculpture; however, they appear as being continuous at lower magnification through their linear arrangement. These ribs are present all over the shell, with wide interspaces (Figure 3E). The periostracum bristles are flattened at their base and the external face is concave. They detach from the shell at commarginal growth crests and function as stiffening rods of a thin, transparent periostracum; both periostracum lamellae and bristles extend beyond the shell margin. Rib-related bristles emerge from the ventral face of growth steps, where they leave a notch.

Comparisons. According to Salas (1996), p. 48), *L. cristata* is smaller than the sympatric *L. minuta*, has a more circular outline and periostracal hair along radial lines. We add that *L. cristata* lacks gutters in the shell below the bristles and that ribs in *L. minuta* are restricted to the flanks (cf. Figure 3E and 4C).

Limopsis friedbergi Glibert & van de Poel 1965
Figures 2K–M, 4A–B, F
1965 *Limopsis anomala friedbergi* n. nov. Glibert & van de Poel, 1965, pp. 74–5.
1836 *Pectunculus pygmaeus* Philippi, 1836: p. 63, plate 5, fig. 3 (not Lamarck 1819).
1996 *Limopsis friedbergi* Glibert & van de Poel, 1965: Salas, p. 48, figs. 88–90.

Material examined. SMNH 37495, Italy, Reggio di Calabria, Archi (lower Pleistocene) (expedition P. Crovato, no date). Most shells are quite worn and there are only traces left of the ligament. The collection contains four more lots with recent material from off southwest Portugal (expedition Seamount I, 1987). Depth range: 235–255 m.

Species characters. The prodissoconch is not well preserved but seems to have an incipient dorsocentral boss (Figure 2M). The length of one prodissoconch is 171 µm with a length/height ratio of 1.26.

At 3–4 mm size G1 teeth are reduced to tiny pustules, and the left valve has five G2 teeth on each side, the anteriormost ones being knob-like. A sixth and seventh tooth may develop in the edentulous space between the two rows (present at 4.7 mm size). These teeth belong to the anterior tooth row (Figure 2K–L). The right valve has four to five anterior and four posterior teeth; one additional tooth is situated below the anterior part of resilifer. The resilifer is symmetric and apparently without divisions. The internal margin is broad with strong crenulations except for the anterodorsal margin. The posterior adductor muscle is three times the diameter of the anterior one (Figure 4B) which has a weak scar only on an indistinctly set off myophore next to the anterior G2 tooth plate.

The shell is posteriorly drawn out, oblique-quadrangular-to-oval, and has a steep posterior flank and weak posteroventral sulcus. Growth crests, low radial ribs and depressions (supposedly bristle imprints) together produce a fine cancellate sculpture; ribs are more pronounced on the posterior flank. The umbo is orthogyrate and almost central with respect to the hinge line (Figure 4A–B).

Comparisons. According to Salas (1996), p. 48), the species differs from *L. cristata*, *L. angusta*, *L. minuta* and *L. aurita* by the regularly crenulated inner shell margin and convex shell. According to our material, crenulations are similarly developed in *L. minuta* but *L. friedbergi* differs by its posterior sulcus and the dense, somewhat nodular, cancellate sculpture (Figure 4A, F).

Limopsis minuta (Philippi 1836)
Figures 1B–C, 2N–P, 4C–D
1836 *Pectunculus minutus* Philippi 1836, p. 63, pl. 5, fig. 5.
1980 *Limopsis minuta* (Philippi 1836): Oliver and Allen, p. 96.
1981 *Limopsis minuta* (Philippi 1836): Oliver, p. 86, app. fig. 15.
1996 *Limopsis minuta* (Philippi 1836): Salas, p. 47, figs. 74–77.

Material examined. SMNH 36973, southwest off Portugal, Josephine Bank, 36.7N–14.2W, 200 m (expedition Seamount I, 1987); SMNH 37498, northern North Sea, Tordis oil platform, 61.3N–2.1E, 196m (expedition Akvaplan Niva, 1993);

SMNH 37499, off western Norway, Haltenbanken Åsgard oil field, 65.1N–7E, 300m (expedition Akvaplan Niva, 1996). The collection contains 44 lots with material from the Faroes to off the Morrocan-Iberian coasts and some samples from the Italian lower Pleistocene. In Scandinavia, the species was recorded from off the Norwegian coast, between 61N–65N in 130–400 m (including a single coastal record from off Korsfjorden, 60.07N–4.53E, and south of the Faroes together with *L. aurita*. The species is not known from Iceland. Depth range: 129–1110m.

Species characters. – The species belongs to morphological 'class 7' (Oliver 1981) with ligament type A (cf. *L. aurita*).

Additional observations. The prodissoconch has a very weak dorsocentral boss with a moat (Figure 2P). The length of three specimens ranges from 177–180 μm, the length/height ratio of one specimen is 1.31.

The hinge has weakly developed G1 teeth even in young postlarval shells of 2.2 mm size, forming only centrally rectangular ridges but irregular pustules along most of the ventral hinge border (Figure 1B–C); in addition, two anterior and three posterior G2 teeth are developed. At 5 mm size there are three to four anterior and four posterior G2 teeth (Figures 2O, 4D; hinge of Figure 4D from a slightly larger shell than 2O). The resilifer of larger specimens is asymmetric, directed slightly backwards with a single ridge separating the anterior flank from the rest whereas younger specimens apparently lack this division (cf. Figure 1B and 1C). Internal ribs are present, the margin is broad and smooth in specimens of *ca.* 2.5 mm but distinctly crenulate at 5 mm size. The anterior adductor scar rests on a weak myophore below the ventral corner of anterior G2 (Figure 4D).

Specimens of 2–5 mm size possess anterodorsal and posterodorsal ribs; bristles emerge from slit-like notches all over the shell, the notches cause undulation of the overlying growth lamellae but without producing a true rib pattern (Figure 4C). Under lower magnifications, these undulations appear to be short radial gutters, but this is an optical effect.

Comparisons. L. minuta differs from *L cristata* by lacking radial ribs on most of the shell, by having less developed G1 teeth, and by an oblique resilifer in adult specimens. This latter difference is correlated with the reduced anterior hinge length and a more anterior position of the umbo with respect to hinge length.

Character distribution and evolution

Prodissoconch

The prodissoconchs of Limopsidae show very little variation in shape (outline and convexity) and sculpture, except for weak, boss-like elevations and/or irregular discontinuous ribs in some species of *Limopsis, Crenulilimopsis* and *Oblimopa* (Oliver & Allen 1980; Tanabe & Zushi 1988; Tanabe 1990; this study). *L. knudseni* is the only species known to us with a more tumid prodissoconch which terminates with a thicker, vertical shell lip. Similarly, prodissoconch size varies within a relatively narrow range (170–370 μm), especially compared to the supposedly closely related Philobryidae (350–1200 μm) (cf. Figure 5E,F). Prodissoconch size and morphology suggest that limopsids have lecithotrophic larval development which is consistent with egg diametres of >100–200 μm reported by Oliver and Allen (1980) for four Atlantic species.

Despite this homogeneity, the limopsid larval shell currently adds little to resolve phylogenetic questions. As far as is known, Jurassic and Cretaceous Parallelodontidae, Cretaceous and recent Striarcinae (Noetiidae), recent *Arca* (Arcinae) and recent *Anadara* (Anadarinae) have typical planktotrophic larval shells with a small P1 and a relatively large and well demarcated P2 (Kiel 2004; La Perna 1998; Loosanoff et al. 1966; Lutz & Jablonski 1978; Lutz et al. 1982; NM, observations on Jurassic *Grammatodon*, *Cosmetodon*, and recent *Striarca*; Figure 1D). It therefore appears that the limopsid ancestor was planktotrophic. One may also assume that limopsids lost planktotrophy before the Pliocene, but this date cannot presently be specified further.

Neogene to Recent species of *Asperarca*, several species of Recent *Barbatia (Acar)*, *B. (Calloarca)* (cf. La Perna 1998, for a brief review and literature) as well as Recent *Glycymeris glycymeris*, *G. violacescens* (this study) and Pliocene (and still existing) *G. rotunda* (Dunker, 1882; Tanabe & Zushi 1988) have lecithotrophic prodissoconchs of similar size as in limopsids. However, in contrast to the studied limopsids, *Asperarca* and *Barbatia* have sculptured prodissoconchs and a less convex anteroventral border. *Glycymeris violacescens* has well demarcated P1 and P2 stages (of 146 μm and 209 μm length, respectively, the P1 size still suggesting lecithotrophy; cf. Figure 5D). Interestingly, the prodissoconchs of *G. glycymeris* and *G. rotunda* are limopsid-like in all basic characters including outline, symmetry, lack of sculpture, and lack of a P2 stage. However, this is also true for numerous lecithotrophic pectinids, limids and mytilids (e.g., Dijkstra & Gofas 2004; Linse & Page 2003; Salas &

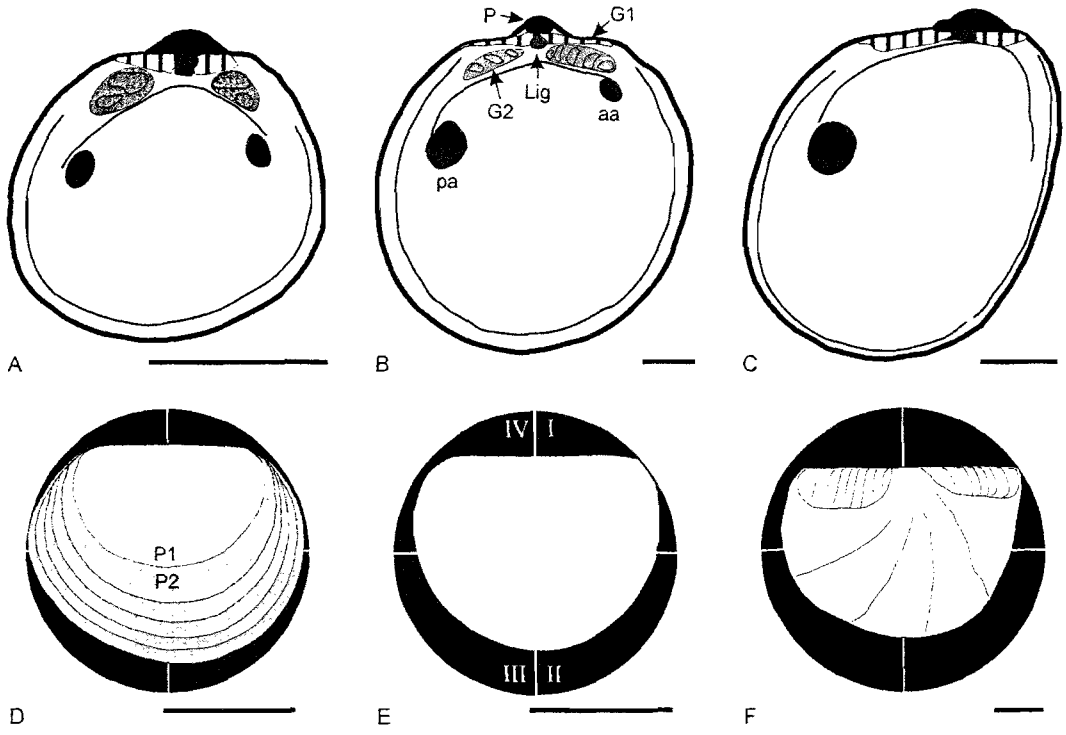

Figure 5. Schematic drawing of basic internal features of postlarval *Glycymeris*, *Limopsis* and *Philobrya* (A–C) and outline of corresponding prodissoconchs (D–F). All shells are left valves. Each prodissoconch (D–F) is superimposed on a black circular background; circle and prodissoconch midpoints coincide; circles have the minimum size at which the shell becomes enclosed; circle quadrants (I to IV) are marked by a white cross. Abbreviations: aa, anterior adductor scar; Lig, ligament pit of first ligament (shaded); G1, position of tooth generation 1 (vertically barred area); G2, position of tooth generation 2 (shaded hinge area); P, prodissoconch; pa, posterior adductor scar. Scale bars: A–C, 500 μm; D–F, 100 μm. Note that *Limopsis* (B) has a larger posterior adductor and reduced anterior adductor in a more dorsal position with respect to *Glycymeris* (A). The anterior adductor and G2 dentition are completely reduced in *Philobrya* (C). The figured *Glycymeris* prodissoconch (D) has both P1 and P2 stages in contrast to *Limopsis* (E) and *Philobrya* (F). The *Limopsis* prodissoconch (E) is rather symmetric and *Philobrya* (F) has a sharp angle between straight hinge and posterior border (quadrant I and II). Many *Philobrya* prodissoconchs have well developed 'wings' and some have few and weak radial elements (gutters in this case). Figures A, D: after *Glycymeris violacescens* (length of postlarval shell, 900 μm; P1, 146 μm and P2, 209 μm). Figures B, E: after *Limopsis cristata* (length of postlarval shell, 3mm; prodissoconch, 175 μm). Figures C, F: after *Philobrya wandelensis* Lamy 1906 (length of postlarval shell 1.9mm; prodissoconch 479 μm). Note: the characteristic pitted prodissoconch surface of this species is not shown.

Gofas 1997; NM, observations on *Crenella magellanica* Linse 2002) which indicates multiple convergent evolution of this shell type. Thus, prodissoconch similarities presently provide no evidence for or against common ancestry of glycymeridids and limopsids. *Asperarca* and *Barbatia* evolved in the Tertiary (? Neogene) and can therefore not be ancestral to Limopsidae, if the known fossil record is complete.

It may be of phylogenetic significance that some *Philobrya* species show a similar radial segmentation (here fine ribs or gutters) of the prodissoconch surface and/or incipient posterodorsal boss as limopsids. However, philobryid prodissoconchs are distinct by their size, asymmetry, convexity, and generally a steep shell lip, characters that are probably a result of brooding (cf. Figure 5E,F). In some philobryids, the incipient boss is replaced by a large conical elevation, especially well developed in *Cosa* and *Cratis*, and(or) the weak radial lines are replaced by stronger ribs (antimarginal) and(or) reticulate or pitted sculptures (see, e.g., Hayami & Kase 1993). These again are convergent features which, in variable combinations, are also found in Arcidae, Pectinidae, and Limidae (cf. Moran 2004, on *Barbatia*; La Perna 1998, on *Asperarca*; Salas 1994, on *Notolimea*; Hayami & Kase 1993, on *Chlamydiella* and *Limatula*). None of the characters is therefore conclusive for close phylogenetic relatedness of limopsids and philobryids.

Brooding

Oliver and Allen (1980), p. 116) noted that limopsids are 'characterized by lecithotrophic development with short-lived non-feeding larvae' which may have lead readers to assume that limopsids are brooding. However, this interpretation is neither supported by prodissoconch characteristics nor by direct observations. Limopsid prodissoconchs are quite distinct from arcoids that are known to brood such as some *Barbatia* species and the

Philobryidae (cf., Moran 2004; Hain & Arnaud 1992; Hayami & Kase 1993; see comparisons above). Comparisons with non-arcoid pteriomorphs also reveal that species with limopsid-like, lecithotrophic prodissoconchs comprise intramaternal and extramaternal brooders as well as non-brooders (cf., Linse & Page 2003, on Limidae; Salas & Gofas 1997, on Mytilidae; Dinesen, pers. comm. 2002, on *Crenella decussata* (Montagu 1808), an extramaternal brooder). The nuculoid *Ennucula delphinodonta* (Mighels & Adams 1842) presents another case of extramaternal brood protection (within a brood chamber made of mud) (Drew 1901) in which the larval shell is quite bulging and shows a strongly pitted surface, however. In addition to this, Warén has examined large quantities of living limopsids, directly taken from bottom samples and never seen any indication of brooding. We therefore presently assume that limopsids are lecithotrophic non-brooders. This could represent an intermediate evolutionary grade between the supposedly planktotrophic ancestor of the Limopsidae and the brooding Philobryidae.

Hinge teeth

The development of two tooth generations (G1, G2) in Limopsidae (Figure 1C) and some Philobryidae is a plesiomorphic character for Arcoida and Pteriomorphia in general (e.g., Bernard 1898; Ockelmann 1995; Prezant 1990; Tanabe & Zushi 1988). However, differences occur in the arrangement, shape, and number of G2 teeth. The number is highest in most of the potential limopsid ancestors (except Pichleriidae) and is most reduced in Philobryidae with *Philobrya* lacking G2 teeth altogether (cf., Tevesz 1977; cf. Figure 5A–C). The intermediate number of teeth in Limopsidae may therefore reflect an evolutionary grade between their ancestor and the Philobryidae. A similar complete loss of G2 teeth appears to occur in *Arca noae* (Arcinae) (observations by NM) where (after removal of the ligament) adult teeth can be traced back over the entire hinge area and the central, ontogenetically oldest teeth originate below the umbo (cf. Bernard 1898, 101, fig. 9). These teeth have all characteristics of postlarval G1 teeth (e.g., proximity to larval hinge, taxodont-like shape, size, constancy of size) as is also true of numerous non-arcoid pteriomorphs (see, e.g., Bernard 1896, 441, fig. 13; Bernard 1898, pl. 8, fig. 9, pl. 9, fig. 9; Malchus 2000; Salas 1994). These observations strongly suggest that the loss of G2 teeth is another multiple convergent character in pteriomorphs, apparently also within the Arcoida.

Ligament

The ancestral adult ligament of Pteriomorphia forms independently and spatially separate from the larval/early postlarval resilium (disjunct ligament; Waller 1978, 1990). In arcoids, this leads to the development of a time series of lamellar sublayers which insert into narrow grooves on the ligament area which is generally covered by a fibrous sublayer (details in Carter 1990; Malchus 2004b). The adult ligament of limopsids differs principally in being an extension of the larval/early postlarval resilium (Figure 1A–C) which remains confined to the extended larval resilifer. From this point of view, the limopsid ligament is homologous with the larval ligament rather than with the ancestral duplivincular type. However, the Jurassic '*L.*' *minima* developed ligament grooves within the resilifer, and the recent *L. marionensis* develops sublayer repeats (without grooves) which are as well restricted to the resilifer. This indicates that the genetic information for sublayer repetition is still latently present in these taxa (cf. Malchus 2004b). The limopsid ligament, therefore, apparently evolved by merging two plesiomorphic, but originally successive ontogenetic features, that is, sublayer repetition, which is an adult trait, within a postlarvally retained resilifer. This phenomenon is best described as a heterochronic process.

The Philobryidae possess the same type of ligament as limopsids (Figure 5C), except that they lack sublayer repeats or grooves (Prezant 1990; own observations), and Morton (1978, fig. 14b) suggested a heterochronic origin for it. However, he did not suggest its homology with the larval ligament as is argued here. In fact, paedomorphic retention of the larval resilium occurred repeatedly in ancestrally duplivincular Pectinoida, Limoida, and possibly Pichleriidae as well as in multivincular taxa such as Ostreoidea and Pterioida (Malchus 2004b). In contrast, Parallelodontidae, Cucullaeidae, Glycymerididae, and Arcidae maintain the typical disjunct ligament type (Figure 1D). However, in Arcidae, as well as the secondarily multivincular Noetiidae, the fibrous sublayers of the opposing valves are separated by a lamellar bridge whereas they are continuous between valves in all other arcoids (Carter 1990; NM, observations on *Striarca*, Noetiidae). As Noetiidae preserve the lamellar bridge despite the probably paedomorphic origin of their ligament, the absence of such a bridge in Limopsidae and Philobryidae may be an inherited trait rather than a consequence of heterochrony.

Origin and evolution of Limopsidae

The present review of larval shell types and early postlarval hinge characteristics suggests that limopsids derive from a taxon with planktotrophic development, a postlarval duplivincular ligament without lamellar bridge, and well developed and numerous G2 teeth. This combination of characters excludes the Arcidae and Noetiidae as potential ancestors because they possess a lamellar ligament bridge. In addition, we exclude Cucullaeidae and Glycymerididae because they differ in shell microstructural details from all other arcoids (Carter 1990). In contrast, the Jurassic '*L.*' *minima* is morphologically transitional between Parallelodontidae and Limopsidae (cf. Tevesz 1977), it has a triangular adult resilium which seems to be continuous with the larval ligament, and its resilifer has resilial grooves and ridges. These ligament characters distinguish '*L.*' *minima* from typical duplivincular arcoids, and the retention of the larval resilifer shows that it had already passed through heterochrony. In this respect, '*L.*' *minima* is more similar to Limopsidae than Parallelodontidae and may represent the 'connecting link' between the two families as is hypothesized by Tevesz (1977).

Our data on hinge and ligament development are also consistent with the widely accepted view that the Limopsidae gave rise to the Philobryidae. In contrast, the hypothesis that Glycymerididae evolved from Limopsidae is not supported because this would imply the reversion from the heterochronically fused limopsid ligament into the ancestral duplivincular condition. It presently appears more likely, therefore, that glycymeridids evolved directly from a duplivincular taxon which may belong to the Cucullaeidae as is suggested by Nicol (1950) and which would be supported by shell microstructural similarities as outlined by Carter (1990). However, except for the placement of the Jurassic '*L.*' *minima* in the limopsids, our morphogenetic interpretation alone is also consistent with the idea that limopsids derive from a glycymeridid or that the two are sister taxa. What would speak for this interpretation is the very close overall shell similarity especially between young glycymeridids (which still lack the duplivincular ligament) and limopsids (cf. Figure 5A–B). This question can probably only be resolved by a comprehensive genetic analysis of arcoid relationships.

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References

Adams A. 1862. Descriptions of some new species of *Limopsis* from the Cumingian collection. Proceedings of the Zoological Society London 1862:229–31.

Bernard F. 1896. Troisième note sur le développement et la morphologie de la coquille chez les lamellibranches (Anisomyaires). Bulletin de la Société géologique de France 24: 412–49.

Bernard F. 1897. tudes comparatives sur la coquille des Lamellibranches. Les genres *Philobrya et Hochstetteria*. Journal de Conchyliologie 1:1–47.

Bernard F. 1898. Recherches ontogenetiques et morphologiques sur la coquille des lamellibranches, 1 partie: taxodontes et anisomyaires. Annales des Sciences naturelles. Zoologie et Paléontologie 8:1–208.

Brocchi G. 1814. Conchiologia fossile subapennina con osservazioni geologiche sugli Apennini e sul suolo subjacente. 2 volumes. Milan: 712 pp.

Carter JG. 1990. Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorphia and Isofilibranchia (Bivalvia: Mollusca). In: Carter JG, editor. Skeletal Biomineralisation: Patterns, Processes and Evolutionary Trends. New York: van Nostrand Reinhold. p 135–296.

Dall WH. 1891. Scientific results of the explorations by the U.S. Fish Commission steamer Albatross. Proceedings of the U.S. National Museum 14:173–91.

Dall WH. 1895. Contributions to the Tertiary fauna of Florida, with especial reference to the silex-beds of Tampa, and the Pliocene beds of the Caloosahatchie River, including in many cases a complete generic revision of the generic groups treated of and their American Tertiary species. Transactions of the Wagner Free Institute of Philadelphia 3:483–565.

Dall WH. 1908. Mollusca and Brachiopoda. Bulletin of the Museum of Comparative Zoology. Harvard University 43:205–487.

Dell RK. 1964. Antarctic and subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. Discovery Reports 33: 93–250.

Dell RK. 1990. Antarctic Bivalvia with special reference to the fauna of the Ross Sea. Bulletin of the Royal Society of New Zealand 27:1–312.

Dijkstra HH, Gofas S. 2004. Pectinoidea (Bivalvia: Propeamussiidae and Pectinidae) from some northeastern Atlantic seamounts. Sarsia 89:33–78.

Drew GA. 1901. The life history of *Nucula delphinodonta* (Mighels & Adams). Quarterly Journal of Microscopical Science 44:313–91.

Dunker WR. 1882. Index molluscorum maris japonici conscriptus et tabulis iconum XVI illustratis. Casselis: Fischer. 301 pages.

Giribet G, Wheeler W. 2002. On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data. Invertebrate Biology 121:271–324.

Giribet G, Distel D. 2003. Bivalve phylogeny and molecular data. In: Lydeard C, Lindberg DR, editors. Molecular Systematics and Phylogeography of Mollusks. Washington, DC: Smithsonian Institution. p 45–90.

Glibert M, van de Poel L. 1965. Les Bivalvia fossiles du Cénozoique étranger des collections de l'Institut royal des Sciences naturelles de Belgique, I, Palaeotaxodontida et Eutaxodontida. Mémoires de l'Institut royal des Sciences naturelles de Belgique. 77:1–112.

Habe T. 1951. Genera of Japanese Shells. Pelecypoda and Scaphopoda. Kyoto: 326 pages.

Hain S, Arnaud PM. 1992. Notes on the reproduction of high-Antarctic molluscs from the Weddell Sea. Polar Biology 12:303–12.

Hayami I, Kase T. 1993. Submarine cave Bivalvia from the Ryukyu Islands: Systematics and evolutionary significance. National Science Museum Tokyo, Bulletin 35:1–133.

Iredale T. 1939. Mollusca. Part 1. Great Barrier Reef Expedition, 1928–29. Scientific Reports 5:209–425.

Jeffreys JG. 1876. New and peculiar Mollusca of the *Pecten*, *Mytilus* and *Arca* families procured in the "Valorous" Expedition. Annals and Magazine of Natural History, ser. 4 18:434–5.

Jeffreys JG. 1879. On the Mollusca procured during the Lightning and Porcupine expeditions (part 2). Proceedings of the Zoological Society of London 1879:553–88.

Jørgensen CB. 1946. Lamellibranchia. In: Thorson G, editor. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the sound (Øresund), with a section on lamellibranch larvae by C. Barker Jørgensen. Meddelelser fra Kommissionen for Danmarks Fiskeriog Havundersøgelser, serie: Plankton, 4: 277–311.

Kiel S. 2004. Presence of a posterodorsal ridge in Jurassic to Recent larval shells of arcoidean bivalves. Journal of Molluscan Studies 70:302–304.

Kuroda T, Habe T, Oyama K. 1971. The Sea Shells of Sagami Bay. Tokyo: Maruzen Co. Ltd. 741+51 pages.

Lamarck J.-B. M. de 1819. Histoire naturelle des animaux sans vertebras, Vol. 6 (1): 343 pages.[Published by the author].

Lamy ME. 1906. Lamellibranches recueillis par l'expédition antarctique française du Dr. Charcot. Bulletin du Muséum d'Histoire Naturelle 1:44–52.

La Perna R. 1998. On *Asperarca* Sacco, 1898 (Bivalvia, Arcidae) and two new Mediterranean species. Bollettino Malacologico 33:11–18.

Linné C von. 1758. Systema Naturae. Editio decima. 1. Regnum Animale. Holmiae: 824+III pages.

Linse K. 2002. The Shelled Magellanic Mollusca: With special reference to biogeographic relations in the southern ocean. Ruggell/Lichtenstein: Gantner, 252 pages.

Linse K, Page TJ. 2003. Evidence of brooding in southern ocean limid bivalves. Journal of Molluscan Studies 69:290–3.

Loosanoff VL, Davis HC, Chanley PE. 1966. Dimensions and shapes of larvae of some marine mollusks. Malacologia 4:351–435.

Lutz RA, Jablonski D. 1978. 24 Larval bivalve shell morphometry: A new paleoclimatic tool? Science 202:51–3.

Lutz RA, Goodsell JG, Castagna M, Chapman S, Newell C, Hidu H, Mann R, Jablonski D, Kennedy V, Siddall SE, Goldberg R, Beattie H, Falmagne C, Chestnut A, Partridge A. 1982. Preliminary observations on the usefulness of hinge structures for identification of bivalve larvae. Journal of Shellfish Research 2:65–70.

Malchus N. 2000. Early shell stages of the Middle Jurassic bivalves *Camptochlamys* (Pectinidae) and *Atreta* (Dimyidae) from Poland. Journal of Molluscan Studies 66:577–81.

Malchus N. 2004a. Shell ontogeny of Jurassic bakevelliid bivalves and its bearing on bivalve phylogeny. Acta Palaeontologica Polonica 49:85–110.

Malchus N. 2004b. Constraints in the ligament ontogeny and evolution of pteriomorphian Bivalvia. Palaeontology 47:1539–74.

Mighels JW, Adams CB. 1842. Descriptions of twenty-four new species of New England shells. Boston Journal of Natural History 4:37–54.

Montagu G. 1808. Supplement to Testacea Britannica. With additional plates. London: White and Exeter: Woolmer, V+183+[5] pages.

Moran AL. 2004. The unusual prodissoconch and larval development of *Barbatia baylei* (Bartsch,1931) (Mollusca: Bivalvia: Arcidae). Veliger 47:47–52.

Morton B. 1978. The biology and functional morphology of *Philobrya munita* (Bivalvia: Philobryidae). Journal of Zoology. London 185:173–196.

Neveskaya LA, Scarlato OA, Starobogatov YI, Eberzin AG. 1971. New ideas on bivalve systematics. Paleontological Journal 1971:141–55.

Newell ND. 1969. Superfamily Limopsacea Dall, 1895. In: Moore RC, editor. Treatise on Invertebrate Paleontology, part N, vol. 1, Mollusca 6, Bivalvia. Lawrence, KS: University of Kansas. p N264–N270.

Nicol D. 1950. Origin of the pelecypod family Glycymeridae. Journal of Paleontology 24:89–98.

Ockelmann KW. 1995. Ontogenetic characters of mytilaceans. Phuket marine biological Centre special publication 15:85–88.

Okutani T. 2000. Marine Mollusks in Japan. Tokyo: Tokai University Press, 1174 pages.

Oliver PG. 1981. The functional morphology and evolution of recent Limopsidae (Bivalvia, Arcoidea). Malacologia 21: 61–93.

Oliver PG, Allen JA. 1980. The functional and adaptive morphology of the deep-sea species of the Arcacea (Mollusca: Bivalvia) from the Atlantic. Philosophical Transactions of the Royal Society London, B (Zoology) 291:46–76.

Philippi R.A. 1836. Enumeratio molluscorum Siciliae cum viventum tum in tellure tertiaria fossilium. Berolini, 267 pages.

Powell AWB. 1958. Mollusca from the Victoria-Ross quadrants of Antarctica. B.A.N.Z. Antarctic Research Expedition 1929–1931 under the command of Douglas Mawson, Report series B (Zoology and Botany) vol. 6, pt. 9:167–215.

Prezant RS. 1990. Shell and hinge ontogeny of the Antarctic bivalve *Lissarca notorcadensis*. Journal of the Marine Biological Association of the United Kingdom 70:841–55.

Salas C. 1994. *Notolimea clandestina* a new species of neotenous bivalve (Bivalvia: Limidae) endemic to the Strait of Gibraltar. Journal of Molluscan Studies 60:249–54.

Salas C. 1996. Bivalves from off the southern Iberian peninsula collected by the Balgim and Fauna 1 expeditions. Haliotis 25:33–100.

Salas C, Gofas S. 1997. Brooding and non-brooding *Dacrydium* (Bivalvia: Mytilidae): A review of the Atlantic species. Journal of Molluscan Studies 63:261–83.

Sassi A. 1827. Saggio geologico sopra il Bacino terziario di Albenga. Giornale ligustico di scienze. lettere ed arti 1:467–84.

Smith EA. 1885. Report on the Lamellibranchiata collected by H.M.S. Challenger, during the years 1873–1876. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–1876. Zoology 13(25):1–341.

Smith EA. 1915. Mollusca. Part 1. Gastropoda prosobranchia, Scaphopoda, and Pelecypoda. British Antarctic ("Terra Nova") Expedition 1910. Natural History Report Zoology 2(4): 61–112.

Sowerby G de C. 1825 (in 1823–25). The Mineral Conchology of Great Britain 5. London: J. Sowerby. 545 pages.

Tanabe K. 1990. Early life history of two Middle Pleistocene species of *Limopsis* (Arcoida: Bivalvia). Transactions and Proceedings of the Palaeontological Society of Japan 160: 631–40.

Tanabe K, Zushi Y. 1988. Larval paleoecology of five bivalve species from the Upper Pliocene of Southwest Japan. Transactions and Proceedings of the Palaeontological Society of Japan 150:491–500.

Tevesz MJS. 1977. Taxonomy and ecology of the Philobryidae and Limopsidae (Mollusca: Pelecypoda). Postilla 171:1–64.

Waller TR. 1978. Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia). Philosophical Transactions of the Royal Society London, B (Zoology) 284:345–65.

Waller TR. 1980. Scanning electron microscopy of shell and mantle in the Order Arcoida (Mollusca: Bivalvia). Smithsonian Contributions to Zoology 313:1–58.

Waller TR. 1990. The evolution of ligament systems in the Bivalvia. In: Morton B, editor. The Bivalvia – Proceedings of a memorial symposium in honor of Sir Charles Maurice Yonge. Hong Kong University Press, Hong Kong. p 49–71.

Warén A. 1980. Marine mollusca described by John Gwyn Jeffreys. Conchological Society of Great Britain and Ireland. special publication 1:1–60.

Yokoyama M. 1910. On species of *Limopsis* found in the Neogene of Koshiba. Journal of the Geological Society Tokyo 17:1–5.

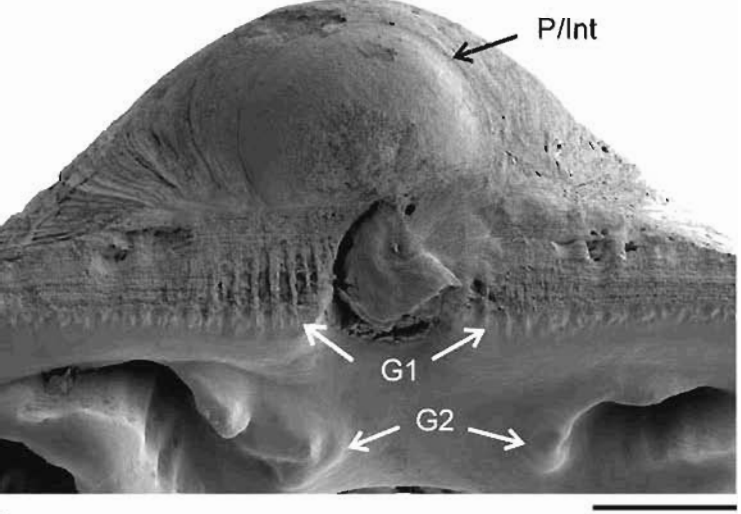
Editorial responsibility: Christoffer Schander

Addendum

La Perna (2000) recently described L. tenuis Seguenza, 1876, from the Pleistocene to Recent Mediterranean, and compared the species with L. angusta, L. friedbergi, and L. minuta including figures of early ontogenetic to adult shells of these species. In the present context, it is worth noting that we coincide in the recognition of an interdissoconch rather than P2 shell stage, the origin of G1 dentition, and a heterochronic hinge tooth development in Philobryidae. Larval shell sizes of 230–240 micrometres of L. tenuis are similar to those of L. angusta measured here, which would be consistent with La Perna's view of a close (sister-taxon?) relationship between the two species.

Reference

Perna L. 2000. Limopsis tenuis Seguenza, 1876, a poorly known Mediterranean bivalve (Arcoida: Limopsidae). Journal of Conchology 37:39–47.



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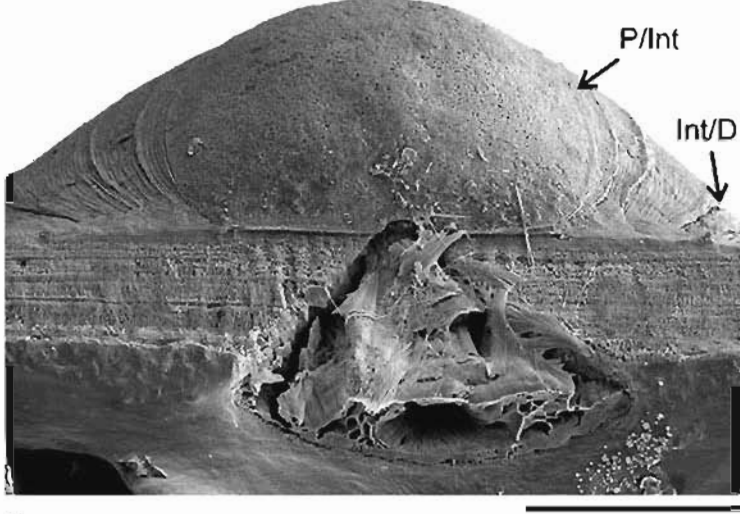

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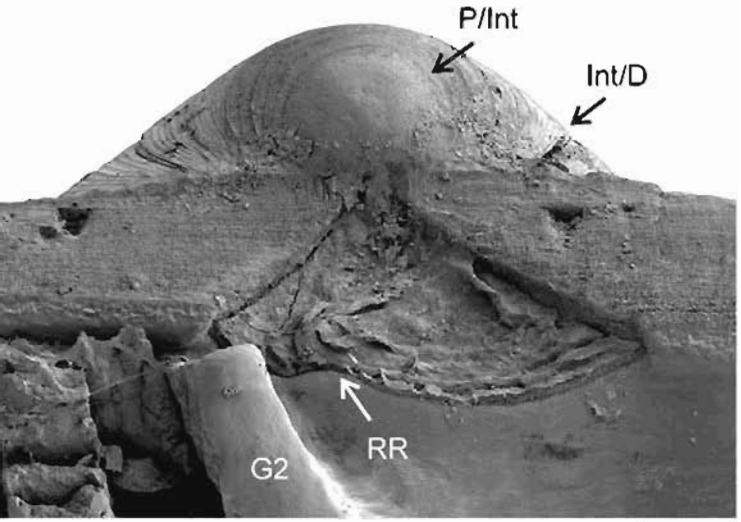

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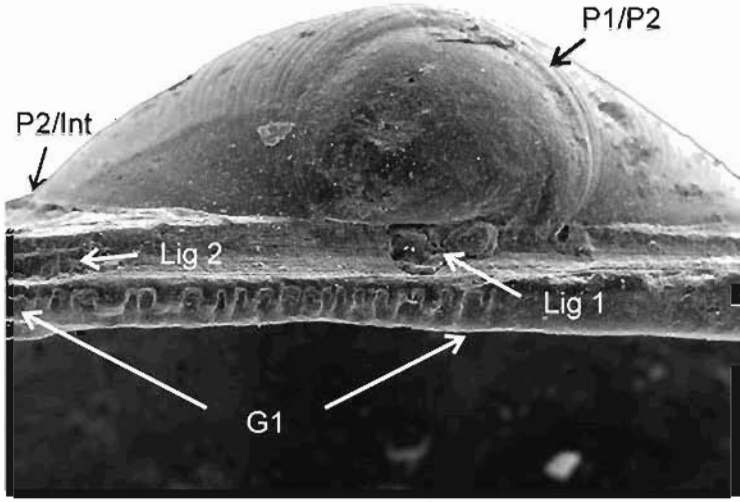

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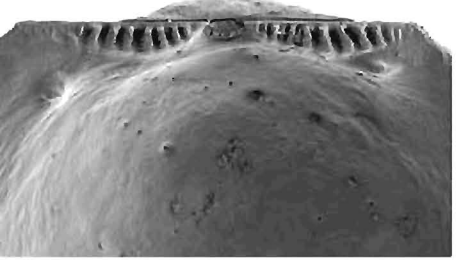

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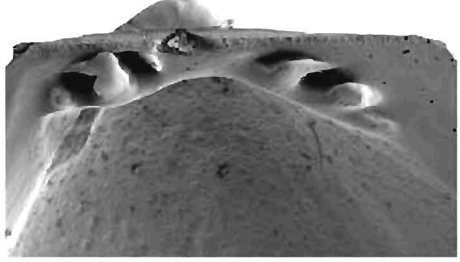

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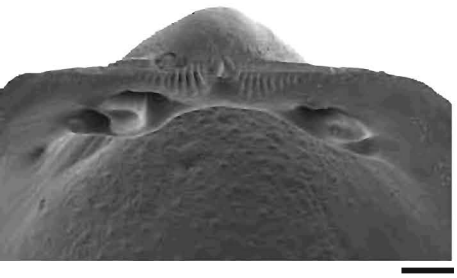

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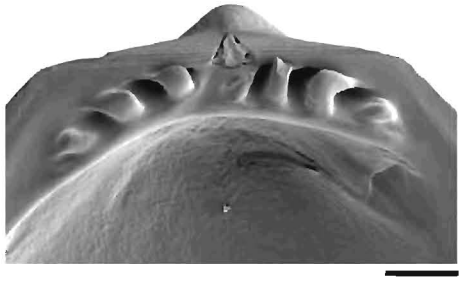

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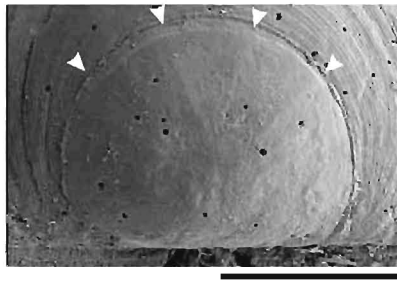

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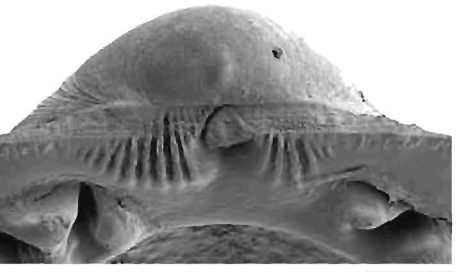

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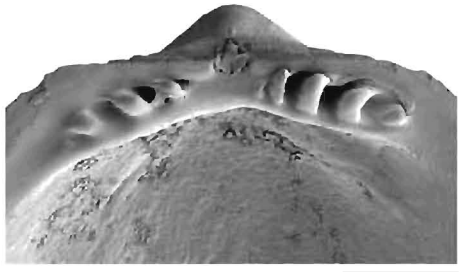

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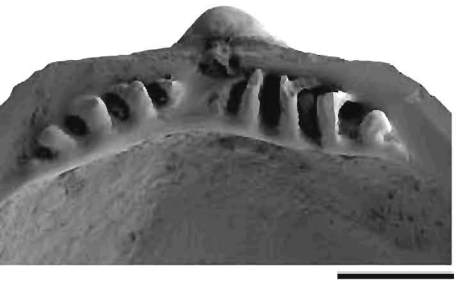

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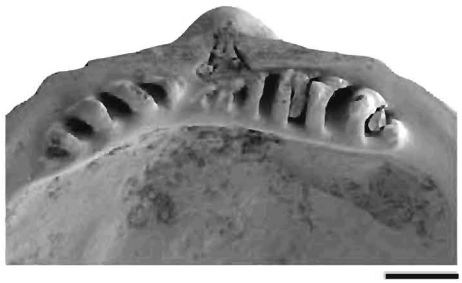

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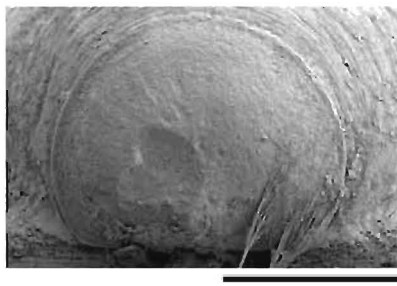

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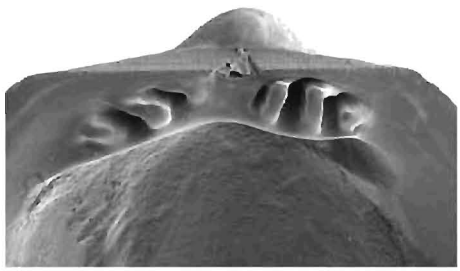

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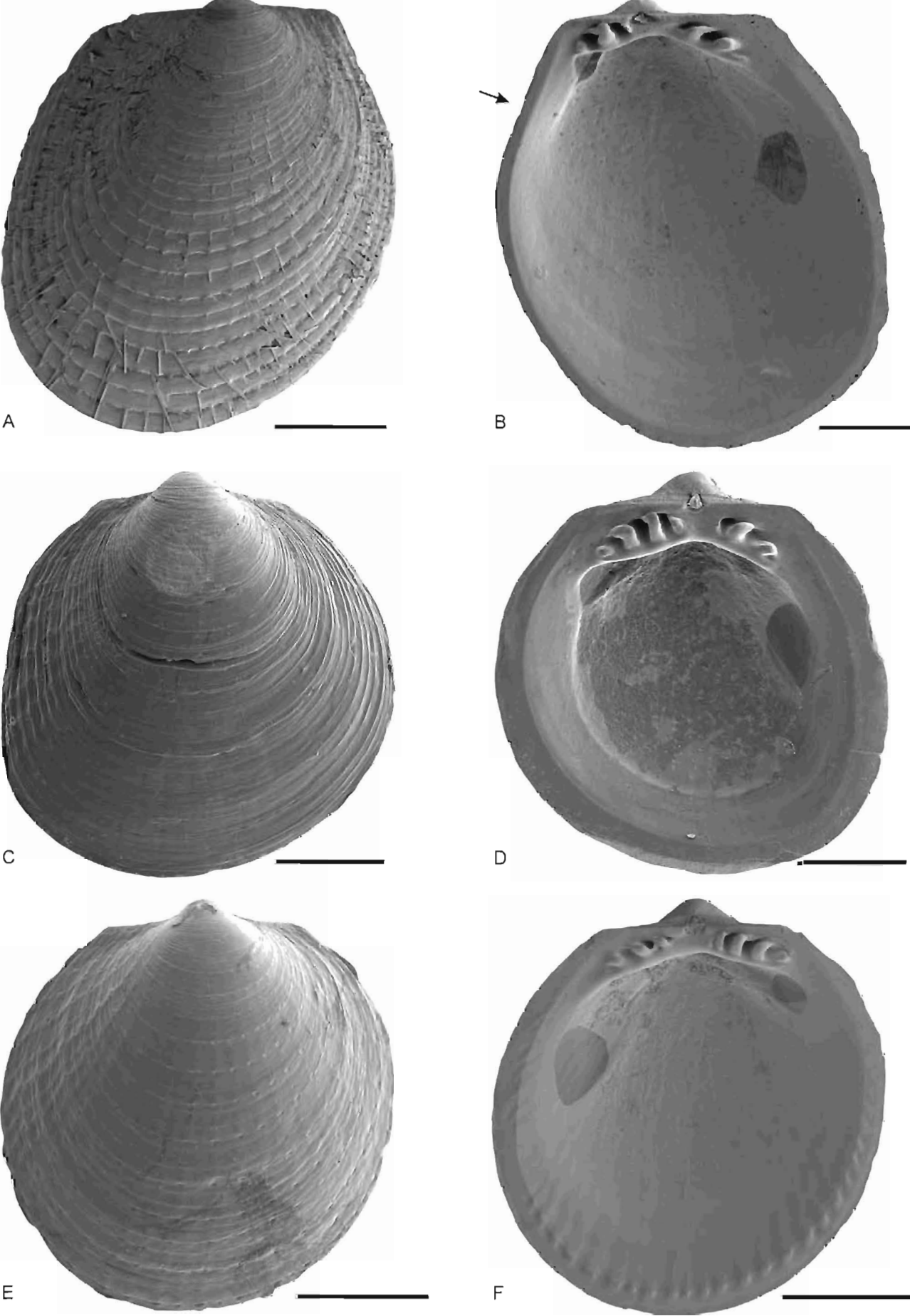
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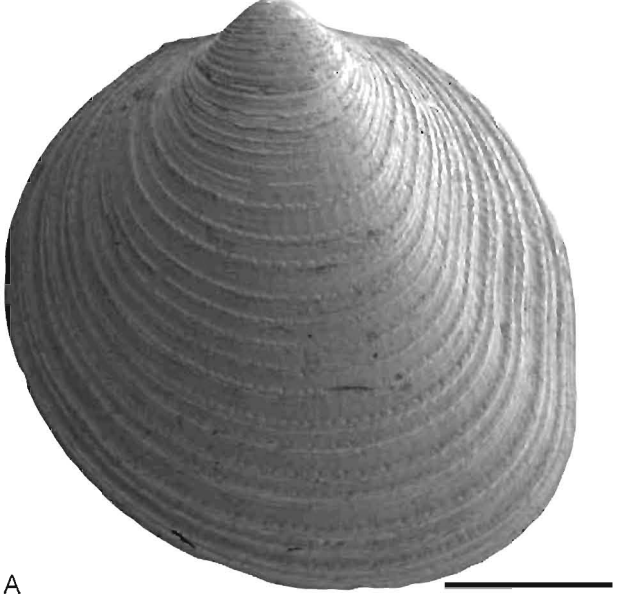

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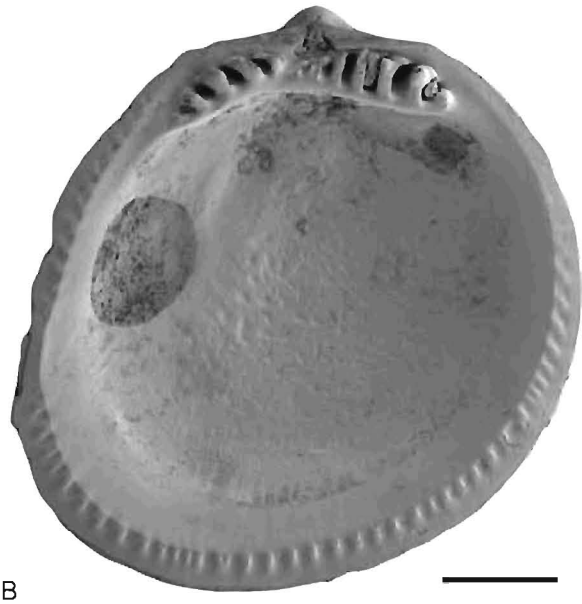

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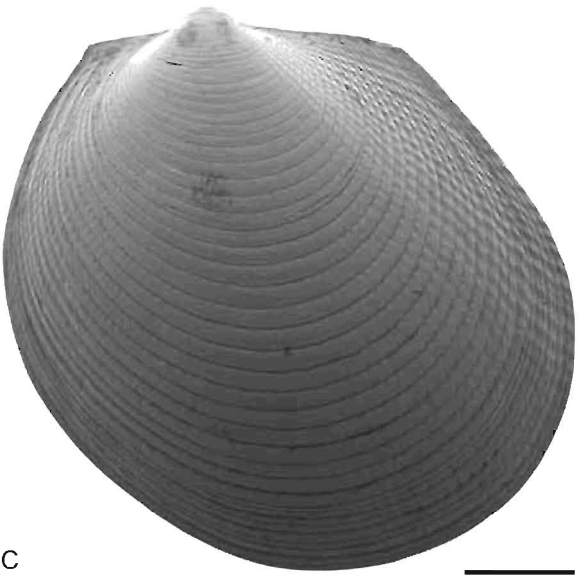

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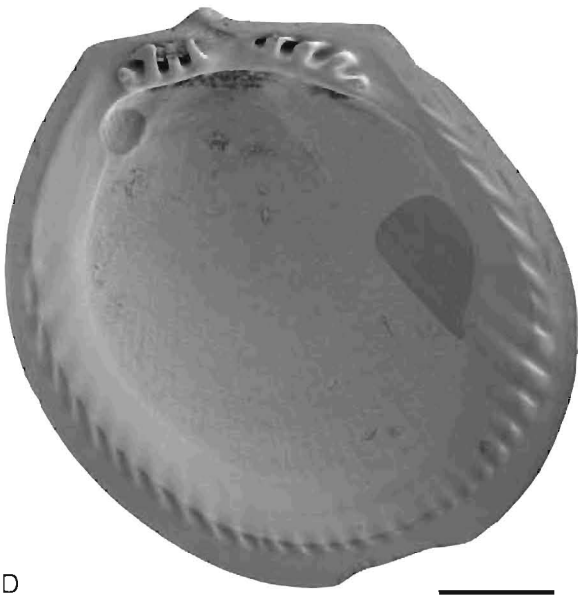

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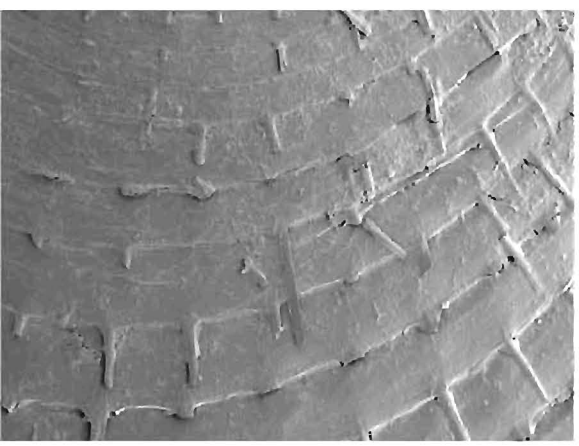

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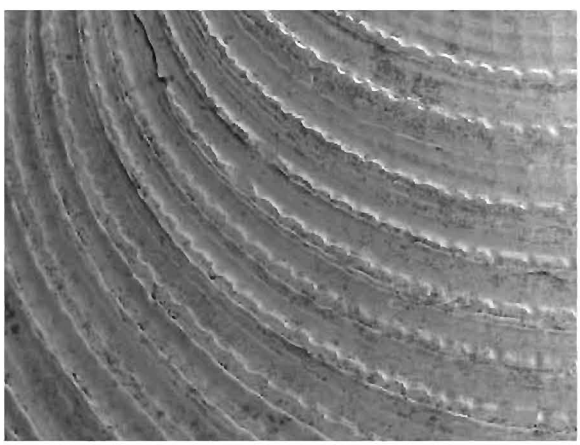

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