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The Conch of *Limacina* and *Peraclis* (Pteropoda) and a Model for the Evolution of Planktonic Gastropods

By

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With 25 figures and 2 tables in the text

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Abstract: Pteropod shell morphologies can be explained by neotenic extension of larval features observed in benthic forms, such as the sinistral coiling of *Architectonacea* and the ornamentation patterns of *Tonnacea*, into the adult shell of permanently planktonic living snails. Presented models suggest derivation of pteropods from primitive prosobranch mesogastropods of the Late Paleozoic, rather than from opisthobranchs.

Key words: Pteropoda, Holocene, shell, ultrastructure, ornamentation, coiling, ontogeny, phylogeny, benthic, taxa.

Zusammenfassung: Die morphologische Analyse der frühontogenetischen Gastropoden-Schale liefert uns Daten, die zur Deutung der Evolution herangezogen werden können. Limacinide Pteropoden besitzen eine Primärschale ohne Anwachsstreifen. Sie entsteht, wenn der Weichkörper mit der Schale am Schalenbildungsgewebe des Mantels verbunden ist. Die Sekundärschale entspricht jener, die von marinen Gastropoden mit freier Larvalphase während ihrer planktonischen Entwicklung ausgeschieden wird. Im Gegensatz zu letzterer ändert sich der Baustil bei Limacinidenschalen nicht, nachdem die Metamorphose des Weichkörpers vollzogen wurde. Der Ursprung der Limaciniden wird in marinen Gastropoden gesehen, die wie die Architectoniden ein normales Primärgehäuse, ein linksgewundenes Larvalgehäuse und ein rechtsgewundenes Adultgehäuse besaßen. Beim Übergang zum vollständig planktonischen Leben wurde das rechtsgewundene Adultgehäuse als überflüssig aufgegeben und das linksgewundene Larvalgehäuse zum endgültigen Gehäuse auch nach der Weichkörpermetamorphose weitergebaut.

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Peraclis legt von außen auf die Schale eine Skulptur, die aus einem hexagonalen Netzwerk besteht. Ähnliche Abscheidungen von außen an und auf die Schale sind bei planktonischen Tonnaceenlarven zu beobachten. Ähnliche Langzeit-Veligerlarven eines benthischen Prosobranchiers können gut die Vorfahren der Peraclididae gewesen sein und dienen hier als Modell zur Entstehung dieser völlig planktonischen Schnecken. Limacinidae wie Peraclididae können in den vorgestellten Modellen von prosobranchiaten Vorfahren abgeleitet werden, die ihrerseits mit primitiven Mesogastropoden des späten Paläozoikums in Verbindung stehen.

Introduction

Ever since the Late Cambrian gastropods play an important role in epicontinental faunas. The evolutionary interpretation of our data concerning shell morphology, distribution and phylogeny, however, is hampered by the incoherence of data collected by paleontologists and by malacologists dealing with Recent faunas. This can be demonstrated by the Treatise on Invertebrate Paleontology (BROOKES KNIGHT et al., 1960) which deals with Archaeogastropods only, while higher developed gastropods groups are not yet covered. Moreover most archaeogastropod taxa became "extinct" mainly due to the inadequate knowledge of modern taxa. A well preserved gastropod shell exhibits its entire ontogeny, which is commonly very complex.

Between the embryonic development inside the egg capsule and the adult benthic life on the sea floor, many marine gastropods pass through a planktonic veliger stage. At this stage, the snail can "sail" through the sea carried by currents to distant places which the adult could never reach. In primitive marine gastropods, like the archaeogastropods, the sail or velum is used only for locomotion. Their veligers rely on the egg-yolk as the only source of energy. Therefore planktonic life is, limited to a few days. In the more highly organized planktotrophic gastropods (neritaceans, the meso- and neogastropods, opisthobranchs and pulmonates), the velum has been improved to facilitate food collection from the seawater while swimming. In a food groove bordering the ciliated rim of the velum, minute organisms (mainly nanno- and microplanktonic cells) are transported into the mouth and provide energy for a larval life of up to several weeks.

Veligers of higher gastropods secrete during their planktonic stage a shell which is specific to this phase of life and differs in composition, morphology (Fig. 1), and sculpture from the conch formed within the egg capsule (embryonic shell) and the conch secreted by the benthic adult (adult shell). Shortly before the pelagic phase ends, the veliger stops its typical ciliary feeding in order to undergo reorganization for the benthic life style. The foot, which had been responsible mainly for manipulating the shell lid (operculum) in the veliger, now increases in size to become the main organ for locomotion. The mouth enlarges to form a snout and develops a rasping and biting organ, the radula. For a short period these snails have

the ability both to crawl with their foot and to swim with their velum (pediveliger). This helps them to find an appropriate place for their future adult life. Thereafter, the young adult loses all structures formerly needed for swimming. At the same time, the shape and composition of the shell as well as the kind of food utilized change drastically.

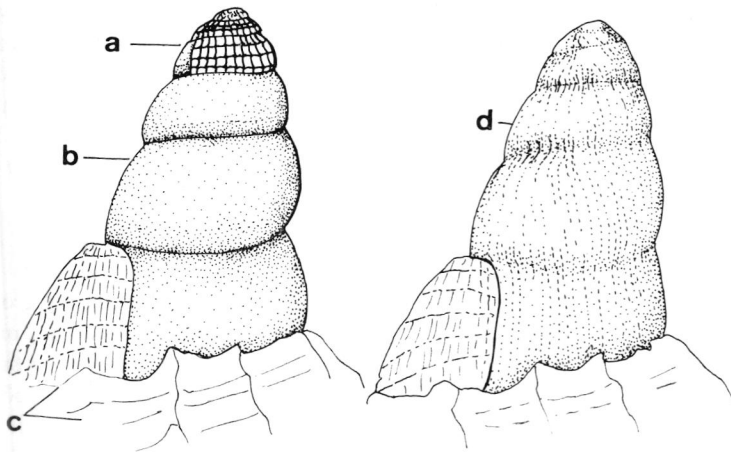


Fig. 1. Early conch of a prosobranch gastropod (*Cymatium*, *Tonnacea*): a: embryonic first whorl (primary shell); b: larval whorl secreted by the veliger (secondary shell); c: shell produced by the adult (tertiary shell). The long-term veliger (d) can secrete an additional cover on top of the embryonic and larval whorl.

Many members of the pteropod genera *Peraclis* and *Limacina* also hatch from egg capsules as veligers that swim in the sea like the veligers of other higher gastropods, feeding with their velum and a mouth not yet equipped with a radula. However, in contrast to other snails, they remain planktonic. Thus they do not undergo the drastic change from a pelagic to a benthic life. This difference should be reflected in the shell built during larval and adult life. Both genera have species with left-coiling (sinistral) conches. In the case of *Peraclis*, we also observe a typical sculpture on the adult shell. These features are not restricted to pteropods with coiled shells, but may also be found in the larval shells of higher gastropods, which have larval stages of much longer duration than usual. In the Architectonicacea and the Tonnacea whose planktonic stage may last for several months, we find veliger larvae that have a sinistral shell in the first and produce a special secondary conch in the second "superfamily".

In this study we compare Limacinidae and Peraclididae with larvae of Tonnacea and Architectonicacea and present a model for a possible evolutionary pathway that might have led from benthic ancestors with planktonic larva to fully planktonic gastropods.

Method and Material

Field observations and culture procedures were mainly carried out at the marine Stations of Santa Marta (Colombia), Bermuda and Banyuls-Sur-Mer, France. For special culturing procedures of tonnageans and architectonids see (BANDEL 1975). Additional material was obtained by plankton tows off Bermuda, sediment traps off Bermuda and Barbados (water depth 3200 m) and sediment samples from various depths (3—15 m) of Fuertaventura (Canary Islands), Port Sudan (Red Sea), Santa Marta (Colombia). Fossil architectonids had been collected by the senior author in Big Brazos River Formation (Eocene), Louisiana (U.S.A.). The SEM micrographs were taken with a Stereoscan 250. The species names are used in accordance with ABBOTT (1974).

Limacinidae

Limacinids are representatives of a family of the thecosomate pteropods with small, left-coiling shells (1—5 mm). These snails have a transformed foot that can not be utilized for crawling on hard substrates. The posterior part is attached to the operculum and the anterior foot parts are modified into a pair of wings (balancers) which are used for swimming, much as a butterfly moves through the air. The wings are separate and merge at the head, in a position near or at the level of the mouth. They form a kind of funnel with a lip-like part of the foot, to the outside of which the operculum

Fig. 2. Apical end of the primary conch of *Limacina inflata* with a shallow concavity reflecting the area of tissue attachment on the inside of the shell. x 640.

Fig. 3. The primary conch of *L. inflata* is almost planispirally coiled and lacks growth lines. It is formed while conch margin and shell secreting epithelia are still attached to each other. x 560.

Fig. 4. Conch of juvenile *L. trochiformis*. The change from embryonic (primary) to larval shell is well marked, while no change can be seen at the transition from larval to adult shell. x 290.

Fig. 5. An adult *L. inflata* in apical view shows the same style of sculpture throughout with exception of the primary conch. Metamorphosis of the soft body is not reflected by a change in shell ornamentation. x 40.

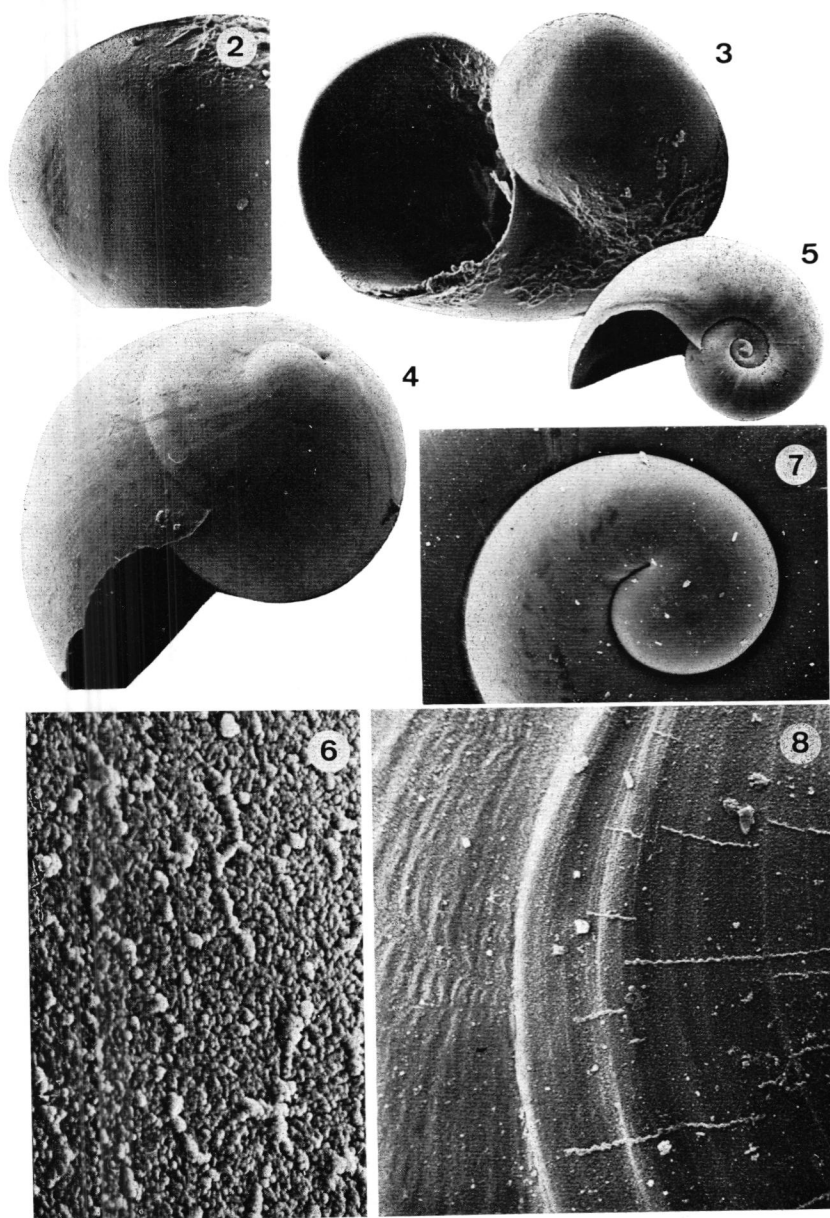
Fig. 6. The sculpture of the primary conch of *L. lesueurii* consists of a delicate network of ridges. x 11,500.

Fig. 7. The transition from embryonic (= primary) conch to the conch produced by the free swimming veliger larva in *L. lesueurii* is documented by a change in ornamentation (see Fig. 8) and growth lines. x 275.

Fig. 8. Larval and adult sculpture of the conch of *L. lesueurii* consist of shell portions with delicate ridges interrupted by a zone only showing growth lines and concentric folds. x 1350.

is attached. This organization of the wings places the Limacinidae into the Euthecosomata (TESCH, 1946).

Traditionally *Limacina* is the only genus recognized within this family. However, for reasons discussed below, RICHTER (1976) and RAMPAL (1975) suggested to split this genus into three. TESCH (1946) described seven extant species in this genus which are still recognized in more recent publications.



Figs. 2—8 (Legend see p. 90)

Four of these were studied by us; data on the three remaining (arctic) species have been extracted from studies by LEBOUR (1932), BOLTOVSKOY (1974), and VAN DER SPOEL (1976), (see Table 1).

In all cases, a primary shell can be differentiated from the secondary shell. With the exception of *L. inflata* (Fig. 2), which is smooth throughout, the primary shell shows a network (mesh size $5\ \mu\text{m}$) of fine ridges. In the case of *L. helicoides* ridges are coarse (VAN DER SPOEL, 1976, pl. 1, Fig. 4).

In all species the primary shell, which forms while the gland cells of the embryo are still fully attached to the shell, is characterized by the total absence of growth lines. Growth lines appear as soon as the gland cells become detached from the rim of the primary shell, and the body tissue attaches itself with the retractor muscle to the apical part of the conch. This change is reflected by a shallow groove forming on the outside of the internal muscular attachment as seen in *L. inflata* (Figs. 2, 3); but as mineralization sets in after the gland tissue has become detached from the shell, this deformation is restricted to the earliest stages in which the shell was still purely organic.

The adult conch of *L. trochiformis* measures about 1 mm in length and resembles a miniature of the freshwater snail, *Physa*. The primary shell shows the typical delicate network, and the secondary shell is covered with spiral ridges and shows growth lines (Fig. ▲). BOLTOVSKOY (1974) had noted the sculpture of the primary shell, but missed that of the secondary shell. There is no change in morphology or sculpture in the secondary shell that would reflect the time of metamorphosis of the veliger to the wing-supported adult. According to WELLS (1976), this change should occur at a time when the shell measures 0.25 mm. In Bermuda we observed metamorphosis at 2.2–2.5 whorls.

L. inflata is a very common species with a tiny, almost planispirally coiled shell showing 3–3.5 whorls. The aperture of the adult has the outer lip drawn out to form a tooth-like projection. This projection develops only in adult individuals, after completion of the second whorl. From there onward it can be traced by the growth lines (Fig. 5). An operculum is present throughout life. The primary conch composes the first three-quarters of the whorl and exhibits a smooth surface. The secondary shell is also smooth, with the exception of growth lines. During metamorphosis, observed by THIRIOT-QUIEVREUX (1969), no change in the production of the secondary shell is seen. Metamorphosis occurs during the secretion of the second whorl, as observed during our stay at the Bermuda Biological Station in early 1983. The apertural projection, that develops during the terminal growth stage, is ornamented by tuberculate ridges.

The adult shell of *L. lesueuri* measures a little more than 1 mm in length and is shaped like a minute *Helix* with four whorls. The primary shell consists of half a whorl only and shows a delicate network pattern which

BOLTOVSKOY (1974) described as a granular ornamentation. It is followed by a secondary shell with growth lines and some very fine discontinuous ridges (Figs. 6—8). Again, no difference between larval and adult shells can be noted. Metamorphosis in individuals from Bermuda occurred during secretion of the second whorl.

L. bulimoides measures about 2 mm in length and resembles the common *Lymnaea stagnalis* (LINNÉ) in shape. Metamorphosis has been observed to occur in specimens from Bermuda after completion of two-and-a-half

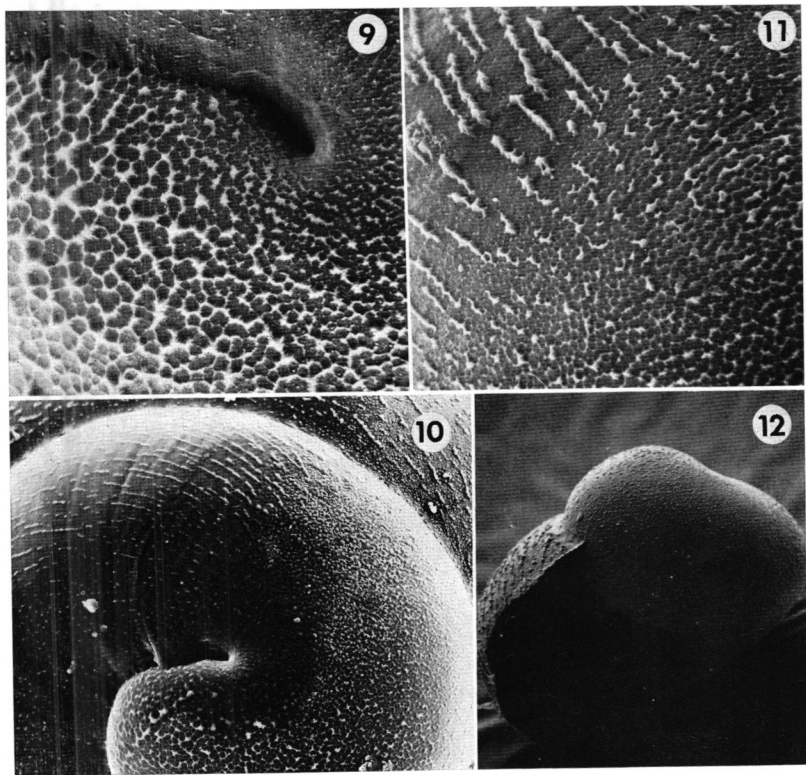


Fig. 9. The primary conch of *L. bulimoides* is covered by a network of grooves and ridges. x 1875.

Fig. 10. The transition between primary shell (right) and secondary shell (left) is shown in the case of *L. bulimoides*. The first growth lines occur together with the change in ornamentation. x 640.

Fig. 11. The transition from primary to secondary (embryonic to larval) shell in *L. bulimoides* is marked by a change in ornamentation and the begin of growth lines. x 1950.

Fig. 12. The primary conch of *L. bulimoides* is nearly planispirally coiled, while the following whorls show a left handed trochospiral coiling. x 350.

whorls. A slight dextral coiling characterizes the primary conch while the following secondary shell (five to six whorls) is definitely sinistrally coiled. It is covered by a typical network sculpture of fine transverse ribs and tubercular rows (Figs. 9—12). There is no change from larval to adult life, not even a gradational one, as BOLTOVSKOY (1974) reports.

Development of Limacinidae

Five species of limacinids have a free-swimming veliger stage hatching from a free-floating egg mass (VAN DER SPOEL, 1967, and LALLI & WELLS, 1978). The size of the eggs usually is 0.1 mm in diameter. LALLI & WELLS (1978) observed *L. retroversa* producing a floating gelatinous egg mass from which normal veligers hatched. VAN DER SPOEL (1967) reported individuals with egg masses that held eggs of 0.08 mm in diameter. From these larvae hatched after two days, before having developed a shell. The primary shell was formed during the following days by the free-swimming embryo. LEBOUR (1932) had noted that it is at this stage that the shell gets its first sinistral twist while the animal inside remains dextrally organized. The fully functional shell reaches a size of 0.13 mm after completion of the operculum.

Table 1.

Species	primary shell (mm)	Width of embryonic shell (mm)	larval shell (mm)
<i>Limacina helicina</i> (PHIPPS)	0.06	0.12	0.3
<i>Limacina retroversa</i> (FLEMING)	0.04	0.11—0.13	0.35—0.4
<i>Limacina trochiformis</i> (D'ORBIGNY)	0.04	0.06	0.25
<i>Limacina inflata</i> (D'ORBIGNY)	0.03—0.04	0.07—0.08	0.2—0.4
<i>Limacina lesueurii</i> (D'ORBIGNY)	0.05	0.11	0.4
<i>Limacina bulimoides</i> (D'ORBIGNY)	0.05—0.06	0.09—0.11	0.3
<i>Limacina helicoides</i> JEFFREYS	0.09	0.15	0.5

Both, *L. inflata* and *L. helicoides* have developed brood protection, but quite differently. In the case of *L. inflata*, about 50 embryos of various developmental stages, including the early veliger stage, are found within the mantle cavity of the mother (LALLI & WELLS, 1978). Here, the eggs (diameter smaller than 0.1 mm) develop from non-shelled embryos into fully developed veliger larvae, while the tissues of the mantle cavity probably provide some kind of food through secretion. Thus, small egg size and the lack of yolk needed during embryonic development are compensated for until the animal has formed a protective and functional shell. The small size of the primary shell reflects this course of early ontogeny. A similar shell size in *L. trochiformis* remains to be explained.

In the case of *L. helicoides*, the eggs are retained within the mucus gland of the female. Here they develop inside their egg capsules until they hatch and are released into the mantle cavity, where they spend their whole larval life, supplied with food by the mother. After completion of metamorphosis the young animals are released, looking like miniature versions of their progenitors (TESCH, 1946).

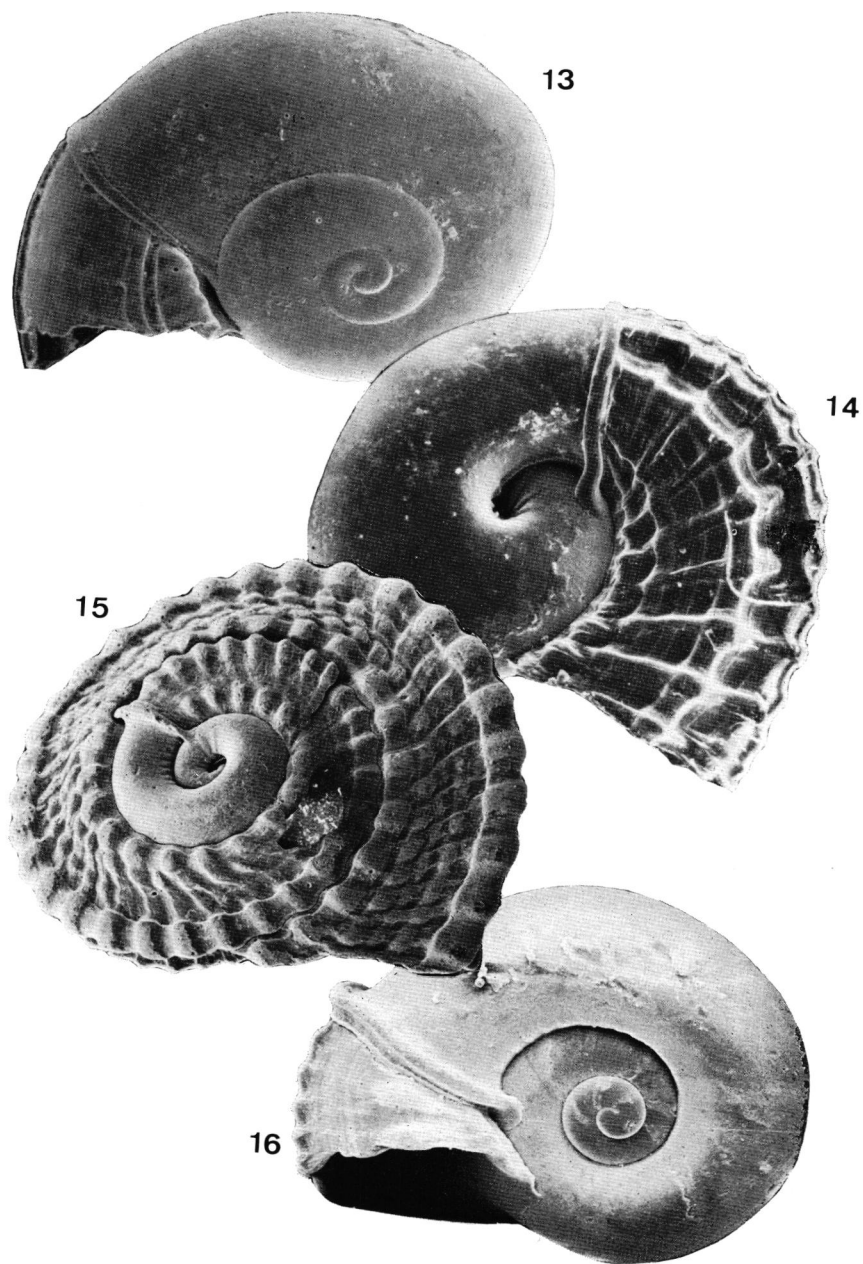
Developmental stages in different *Limacina* species are clearly related to the size of the eggs; smaller than 0.1 mm develop into larvae that hatch before a veliger can be formed. While in some populations of *L. retroversa* this development occurs in the open water, the eggs of others are larger and the energy supply (yolk content) of the eggs is sufficient to allow development of a fully functional veliger before the egg capsules disintegrate. The discriminating size lies at 0.1 mm egg diameter. *L. inflata* eggs are smaller, but this species has developed a special way of brood protection that allows the mother animal to retain the larvae until they have developed into full veligers. Probably this provides a great flexibility in producing off-springs in populations living in different environments. *L. helicoides* has eliminated the veliger stage requiring external food sources (mainly minute phytoplankton) and provides the larvae with food until they have developed sufficiently to feed on the same food (organisms) as utilized by adults. The larvae of his species is free and not retained in the egg. Therefore, an embryonic shell is differentiated from a larval shell. However, this is also the only species of *Limacina*, in which a larval (secondary) shell is followed by a tertiary shell differing in sculpture (not gross morphology) and reflecting the time of hatching from the mantle cavity (VAN DER SPOEL, 1976).

Comparison with other gastropods

The planktonic limacinids are not very different from representatives of other marine gastropod families with respect to their developmental strategies. For example, the intertidal littorinids have numerous species that shed free-floating egg capsules from which veligers hatch. *Littorina angulifera* (LAMARCK) normally retains the hatched young for some time in the shelter of its mantle cavity before releasing them into the sea as free-swimming veligers, but if necessary, the egg capsules can also be shed directly into the sea. *Littorina saxatilis* (OLIVI) holds the egg masses within its mantle cavity until the young hatch, resembling miniature adults. *Littorina obtusata* (LINNÉ) glues the yolk-rich egg masses to algae on which advanced veligers develop, fed by yolk reserves. They grow into metamorphosed young animals which hatch from the egg mass as miniature adults (BANDEL, 1974, 1976).

The main difference between benthic marine gastropods and *Limacina* species is in the mode of life after metamorphosis. The free-swimming larval stage of *Limacina* is succeeded by free-swimming juveniles and

adults, while in normal benthic gastropods the veliger changes from free-swimming to benthic life with associated changes in the mode of breathing, feeding, excretion, locomotion and in function of the shell. A



Figs. 13—16 (Legend see p. 97)

light shell is replaced by a solid one, which is no longer carried below the animal, but above it or dragged behind. It withstands active attack and does not just serve as refuge, closed by the operculum, or for sinking out of the reach of predators.

All these changes are of no value to a *Limacina*, in which the function of the shell is basically the same in the adult as in the larval stage. A change in life style is no longer needed and thus not retained. The metamorphosis of the soft body is thus no longer reflected in the morphology of the shell.

Architectonicid larvae

Species of the architectonicids, a family of the lower mesogastropoda, that have a free larval stage in the course of their ontogeny show (1) a planispirally coiled primary shell; (2) a low trochospiral, sinistrally coiled larval shell (secondary shell); and (3) a low, trochospiral, dextrally coiled adult shell (tertiary shell). The change from left-coiling to right-coiling is not drastic as the architectonicid trochospire is very low (Figs. 13—14). This type of shell coiling has been referred to as "hyperstrophic" in general literature of gastropods (see ABBOTT, 1974).

Architectonicids, during adult life, feed on coelenterates. *Architectonica nobilis* RÖDING, for example, extends a proboscis, penetrates the body wall of an actinian with its tip and, with the aid of the hooked teeth of the radula, feeds on the interior tissue until the prey dies (BANDEL 1976). The shape of the teeth in architectonicids is very similar to that found in pteropods; also, the number of teeth in each row of the radula is not restricted to seven, as in other mesogastropods, but may be less (in *Philippia*) or more (in *Architectonica*), just as seen in the different genera of the pteropods.

The gelatinous spawn of the architectonicids consists of egg capsules connected by a thread, very much like in some pyramidellids and marine

Fig. 13. The larval conch of *Architectonica nobilis* from the Caribbean Sea (Santa Marta, Colombia) shows a left-handed trochospiral coiling, while the adult conch turns into a right-handed coil. Larval and adult sculpture are very different from each other and mark the transition from planktonic to benthic life; sediment sample from turtle gras. x 45.

Fig. 14. The left-handed coil of the larval conch of *Architectonica* is followed by the right-handed coil of the adult conch. Thus, the apex is composed of a reversed larval conch. (Sediment sample from turtle gras, Santa Marta, Colombia, Caribbean Sea). x 80.

Fig. 15. Fossil architectonicid conch from the Eocene of Louisiana (Big Brazos River) with sinistral larval conch in the apex of the dextral adult conch. x 45.

Fig. 16. Fossil architectonicid from the Eocene of Louisiana (Big Brazos River) showing the apex of the larval conch, which will become the umbilicus of the adult. x 75.

pulmonates (BANDEL, 1976). From the spawn of one female of *A. nobilis* 30 000 to 150 000 veligers hatch with a planispirally coiled, smooth shell consisting of almost one complete whorl 0.14 mm in diameter (BANDEL, 1975). The embryonic shell is also the primary shell, formed by the gland cells of the mantle during close contact between cells and shell. Upon hatching this shell is already fully functional, allowing the veliger to withdraw into it and to tightly close the aperture with an operculum secreted and held by the foot.

The veligers of many species of the architectonicids remain planktonic for many weeks, in several species even for months, during which time they feed on phytoplankton (ROBERTSON et al., 1970).

Philippia krebsii (MÖRCH) produces an early ontogenetic shell very similar to that of *A. nobilis*. It remains in the planktonic phase for up to six months, while its larval conch (secondary shell) grows to full size within a few weeks (SCHELTEMA, 1971).

The long larval life of the architectonicids is not a newly developed evolutionary feature. This can be demonstrated in architectonicid specimens having the same shape regardless of whether they are Recent or Eocene in age (e.g. Eocene deposits of Louisiana, Big Brazos River) (Figs. 15—16). Their larval shells are always sinistral and resemble *Limacina* in this respect. They also grow to a size similar to that of many limacinid species with 1—1.6 mm and 2.5 to 3 whorls.

Any prosobranch with an architectonicid-like coiled larval shell and with a long larval stage could have developed into a planktonic gastropod similar to *Limacina* by using the frontal and lateral portions of the foot as wings to substitute for the velum and the foot cilia to substitute for the velum food groove. During development of the radula and sexual maturation the position of the intestine remains more or less the same as in the veliger. A *Limacina* has its anal opening on the left side with the mouth pointing upwards, the foot towards the observer, and the conch hanging downwards. This is the same position as in any prosobranch veliger feeding on phytoplankton. Regarding the shell, the formation of a tertiary shell could be abolished and the conch could continue throughout life like the larval types. This had already been noted by LEBOUR (1932) in the case *L. retroversa*. She wrote that the snail, after metamorphosis, retains the larval shell as a base for the adult shell, but here observations were not followed up by later authors.

Flexibility to ontogenetic changes with respect to construction, morphology and sculpture of the shell are common among closely related species of molluscs. Species that pass their embryonic phase within the egg capsule change the morphology of the early shell and produce only a simple embryonic or primary shell. However, if a plankton-feeding, free larval stage is present, individuals produce a sculptured embryonic shell and a differently shaped and sculptured larval shell (BANDEL, 1975). *Limacina* may

represent a similar case, with the exception that the adult and larval shells fuse into a single stage, rather than the embryonic and larval shells.

Limacinidae may thus represent prosobranch gastropods that have developed from benthic ancestors with an extended larval phase. During this stage, a sinistrally coiled shell may have been present, as is the case in Architectonicidae; but they may have also been comparable to other groups such as the Mathildidae or the Pyramidellidae. TESCH (1946) described "*Agadina*" conchs, probably architectonicid larval shells, which had been included with the Limacinidae. He noticed that the main difference between these conchs and those of the limacinids is not in their shell size, morphology, or composition, but in their soft parts, which are always organized as veligers. RICHTER (1973) thought that the adult conch of *L. trochiformis* or *L. bulimoides* showed nothing indicative of the special way of life of its carried and could not be distinguished from benthic snails. But like the "*Agadina*"-architectonicid larval shell, limacinids have a primary embryonic shell and a secondary larval shell, but never the tertiary adult shell present in adult benthic snails. This clearly differentiates limacinid conches from similar benthic gastropods.

Paraclididae

The family Paraclididae consists of a single genus with five species (RAMPAL, 1975). Characteristic is a delicate shell with a sinistral coil and lymnaeid shape, up to 5 mm in length. In contrast to those of *Limacina*, the wings (or fins) of *Peraclis* are fused into a single structure, which is close to the head but forms no ciliated edge acting as a food groove. Also in contrast to Limacinids, the mouth extends into a short proboscis and the anal opening is situated on the left side of the mantle cavity and the gills on the right side, similar to *Bulla* (RAMPAL, 1975). Due to the presence of ctenidia and a uniform wing, *Peraclis* is considered to be a member of the Pseudothecosomata.

We have studied the shell of *P. reticulata* (D'ORBIGNY). For comparison, data on *P. bispinosa* PELSENER (BOLTOVSKOY, 1974), *P. moluccensis* (TESCH) (BOLTOVSKOY, 1974, VAN DER SPOEL, 1976) and *P. apicifulva* MEISENHEIMER (ALMOGI-LABIN & REISS, 1977) can also be used.

The primary shell of *P. reticulata* (Fig. 17) is sculptured with a network of fine ridges, usually covering only the posterior portion of the shell and disappearing near its margin. In the case of *P. moluccensis*, this sculpture is strong, in *P. reticulata* more delicate, and in *P. bispinosa*, according to BOLTOVSKOY (1974), almost absent. The primary shell (embryonic conch) of *P. reticulata* measures only 20–30 μm in width and 60 μm in maximum diameter and consists of two-thirds of a whorl. The mesh width of the sculptures is 1 μm and thus about five to six times smaller than that of *Limacina*.

The larval shell of *P. reticulata* is smooth except for growth lines (Figs. 17—20). After the conch has grown to at least 1.5 whorls, a sculptural feature is added to the outside of the shell. It consists of a regular network of ridges either in a zigzag pattern or as a more or less regular hexagonal network (Figs. 18—21). Contrary to the suggestion by ABBOTT (1974), this sculpture consists of aragonitic crystallites arranged perpendicularly to the surface of growth. Where the ridges bend or cross, perpendicular spines project

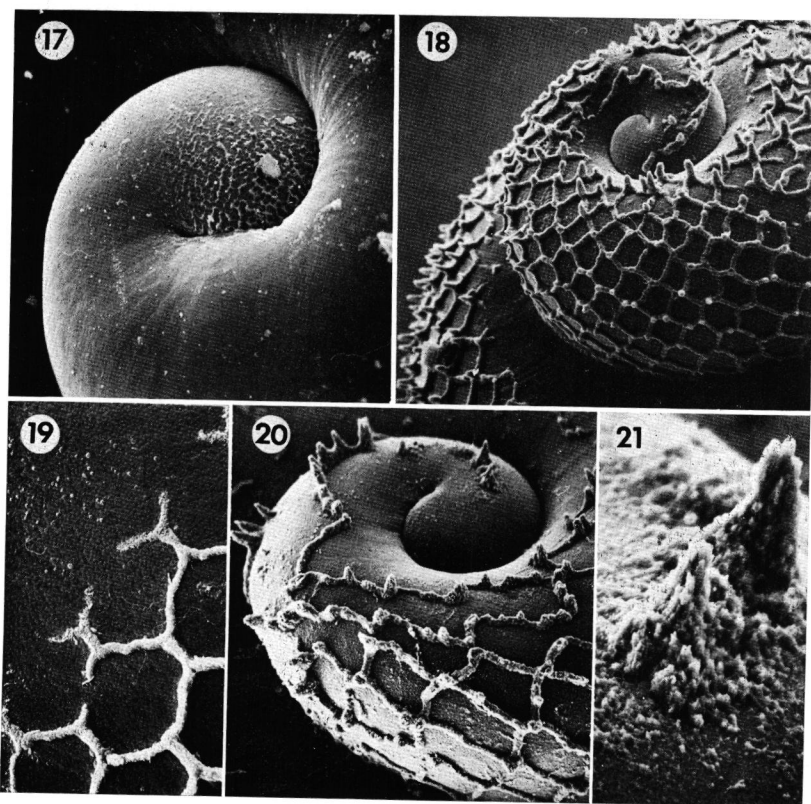


Fig. 17. The embryonic (= primary) conch of *Peraclis reticulata* shows a sculpture of grooves and ridges. The onset of larval (= secondary) shell is marked by growth lines. x 1050.

Fig. 18. Embryonic, larval and adult conch become covered by secondary shell deposits forming a characteristic hexagonal network of ridges. x 240.

Fig. 19. Secondary sculpture growing towards the aperture. (*P. reticulata*). x 600.

Fig. 20. Secondary sculpture in its growth towards the apex, here covering part of the embryonic conch. (*P. reticulata*). x 510.

Fig. 21. Secondary sculpture of *P. reticulata* in close-up shows composition of minute aragonitic needles and spherulites. x 3000.

from the surface of the conch. This sculpture is not restricted to the larval shell as the description and illustration of BOLTOVSKOY (1974) suggests, but is secreted onto the larval as well as the embryonic shell. Such patterns as described here for *P. reticulata* are also present on the conch of *P. bispinosa* and *P. moluccensis* (BOLTOVSKOY, 1974). In *P. apicifulva*, however, the shell is covered with longitudinal, wavy protrusions of organic composition (ALMOGI-LABIN & REISS, 1977).

A very similar pattern of hexagonally mineralized ridge work decorating the shell and originating after formation of the primary shell, is found in the archaeogastropod group *Calliostoma* (BANDEL, 1982).

Tonnacean larvae

Many species of different genera of tonnaceans produce larvae having an extended planktonic phase. All mature tonnaceans prefer to live in shallow, warm water and hunt large animal prey. Many species feed on various echinoderms, others on worms and molluscs. Several species are cosmopolitan owing to their free-swimming larval stage.

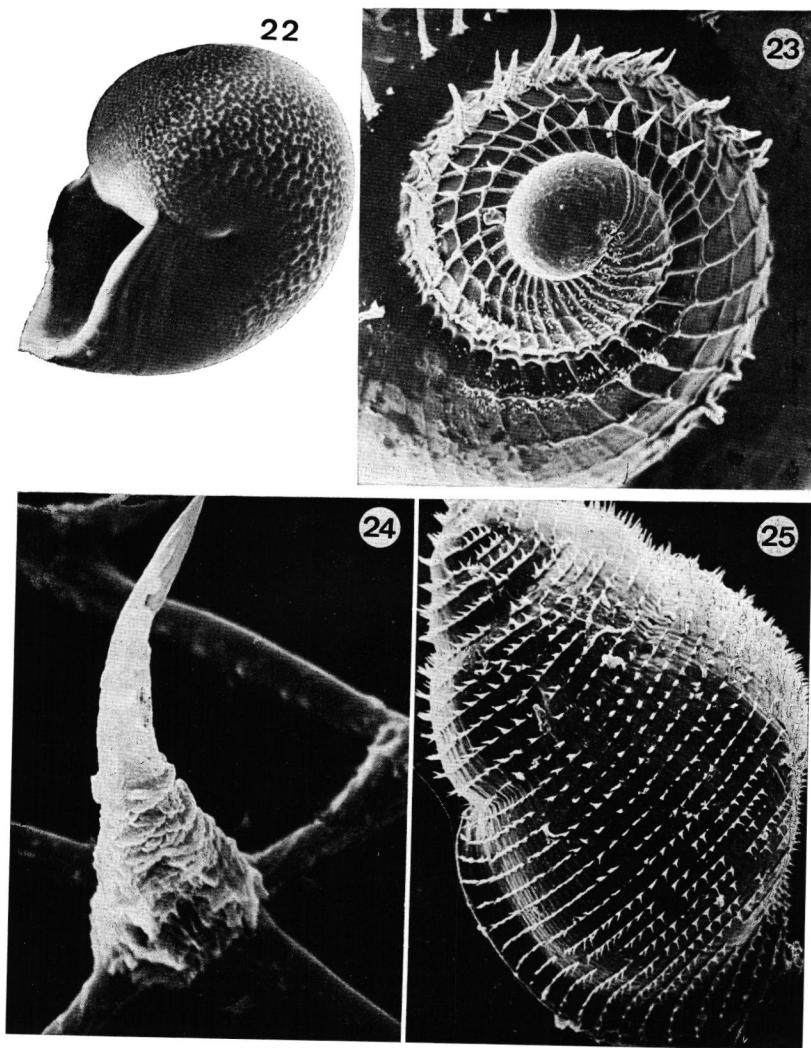
From the spawn, which in many cases is brooded by the female, veligers hatch with a complete primary shell (Fig. 22). They usually show a characteristic ornamentation (BANDEL, 1975). After hatching, the larva feeds on phytoplankton (D'ASARO, 1969) and shell formation continues, but with different sculptures and a different morphology. In many members of the tonnaceans, the sculpture consists of spiral ribs crossed by radial ribs to form a pattern of rectangles. This larval secondary shell is weakly mineralized and is characterized by 1 to 1.5 whorls (Fig. 23). Later, the larva continues to increase its conch by secreting organic material only, which does not become mineralized. During this stage, not only the apertural edge continues to grow, but organic shell layers may also be deposited on top of the formerly secreted shell, e.g. in species of the genera *Cymatium*, *Distorsio*, *Charonia*, and *Tonna*. This additional shell material may be smooth or it may show a regular pattern of thorns (Figs. 24—25) or crests. D'ASARO (1969) has shown that veligers of *Distorsio* form conspicuous lines of cells on the mantle edge and on the skirt of the foot. These cells are associated with the formation of a keel, on the outside of the veliger conch posterior to the aperture.

After completion of the larval shell the animal can remain free-swimming and fully active for more than four months, as demonstrated in experiments (SCHELTEMA, 1971). The larva swims with a large 4-lobed velum and a rudder-like, thin propodium. Usually, the creeping foot is not yet fully developed, but short and serves mainly to carry the operculum. Larvae of the shallow water tonnaceans have been noted midway across the ocean (THORSON, 1961). Estimates of SCHELTEMA (1972) suggest that *Cymatium parthenopeum* (VON SALIS) larvae can swim for almost a year.

Such a veliger can this easily cross the Atlantic Ocean via equatorial currents.

In all species listed here, the shell which has been formed after metamorphosis (adult shell) has no resemblance to that of the larva at all (Table 2).

It is not known why some of these species produce spiny shells and others remain smooth; the type of shell is not related to the time spent as a veliger.



Figs. 22—25 (Legend see p. 103)

Table 2.

Species	embryonic shell (mm)	larval shell (mm)	no. of whorls
<i>Tonna galea</i> (LINNÉ)	0.5	3.5	4.0
<i>Phalium granulatum</i> (BORN)	0.2	2.6	4.3
<i>Malea pomum</i> SCHUBERT & WAGNER	0.45	3.7	3.5
<i>Casmaria cernica</i> SOWERBY	0.22	2.1	2.5
<i>Bursa granulatis</i> RÖDING	0.25	2.5	3.7
<i>Cymatium nicobaricum</i> (RÖDING)	0.8	3.4	5.0
<i>Charonia nobilis</i> CONRAD	0.6	4.5	4.0

Conclusions and Model

Since the Late Paleozoic, prosobranch larvae like those of the Recent Architectonicacea or Tonnacea grow to large sizes, remain free-swimming for a considerable portion of their ontogeny and exhibit completely different shells during this phase compared to the adult. Member of both superfamilies may serve as a model for the evolution of planktonic gastropods, e.g. the Limacinidae and the Peraclididae. Sinistral or dextral coiling is not a very important characteristic, as this feature is rather variable in some species and occurs as a non-lethal mutation in many gastropods. It seems that the sinistral coil is more convenient for free-swimming gastropods, while the dextral coil is more advantageous to the benthic snails. The reason for this is yet unknown.

The architectonicids have developed an ontogeny with left-coiling larval and right-coiling adult conchs. This enables them to combine the possible benefits of left coiling in free-swimming life with those of right coiling during benthic life. In transition to a limacinid-like ontogeny the larval-

Fig. 22. The embryonic conch of *Cymatium* shows a regular groove and ridge sculpture abruptly ending with the onset of shell produced by the plankton feeding veliger. Hatched from egg capsule, Caribbean Sea, Santa Marta, Colombia. x 150.

Fig. 23. The embryonic stage of a *Bursa* from the Red Sea (Sudanese Coast, Port Sudan) is sculptured like that illustrated in Fig. 21, while the larval conch is sculptured completely differently. Spines on top of this sculpture have been deposited from outside during a much later stage in larval life (see Figs. 23 and 24); lagoonal sediment. x 50.

Fig. 24. Detail of 22 of a spine that has been secreted from the outside on top of the larval sculpture from t outside. x 900.

Fig. 25. The outgrown conch of a larval *Cymatium*; Canary Islands. The embryonic and early larval shell is covered from the outside by later organic shell deposits and, thus, totally hidden by them. From sediment sample collected off-shore at 3 m water depth; Fuerteventura. x 35.

stage shell coiling was simply continued and possibly advantageous for animals remaining free swimmers throughout life.

In the tonnaceans an extended planktonic larva has evolved with a special mode of larval shell construction. This shell can be reinforced from the outside, as is also seen in *Peraclis* and it is right-coiling, as in the adult. Mutation provides left-coiling larvae, which perhaps will not survive to the benthic stage, but could be better adapted for a continued planktonic existence. Selection would thus perhaps favour the sinistral individual, if the construction of the adult-like benthic shell is discontinued and the animal remains free-swimming throughout ontogeny.

In our model we dwell on the selective benefits of left-versus right-coiling during the pelagic life. But there are also benthic species that are left-coiling during adult life. By looking more closely at these, it becomes apparent that they are adapted to special substrates. For example, the left-coiling triphorids live in sponges, while their right-coiling close relatives, the cerithiopsids, live in various environments.

Anatomically, *Peraclis* and *Limacina* resemble very closely a phytoplankton-feeding prosobranch veliger. The anus is on the left side, the mouth is central, the intestine makes a turn to the right before going to the left. The mantle cavity lies dorsal of the head, and an operculum is present on a foot which can manipulate it, but cannot creep.

Differences in the body organization of *Limacina* and *Peraclis* indicate that these two genera are not closely related (TESCH, 1946): The position of the operculum attachment suggests that the fins have developed from different parts of the foot. This is also stressed by the ciliated food groove on the fins present in *Limacina*, a feature absent in *Peraclis*. The latter feeds with the help of a radula-armed snout, while *Limacina* has no proboscis.

There is no need to derive pteropods from opisthobranchs (VAN DER SPOEL, 1967, RAMPAL, 1975). If we agree on the development of pteropods from larval forms of ancestors with long-living larvae, then the prosobranch larva provides the organization of the shell and body alike. The differences regarding the shell in *Peraclis* and *Limacina* suggest that their ancestors already differed in this respect, as do long-living larvae in Architectonicacea and Tonnacea.

BOLTOVSKOY (1974) noted that the primary conches of *Peraclis* and *Limacina* are similar in shape, dimension, and sculpture. This can be confirmed here only in a very general way, because the dimensions are quite different. BOLTOVSKOY also suggested that these characteristics are useless. On that point we have to disagree. Size, sculpture and composition of the primary shell are quite valuable systematic tools, as BANDEL (1975) has demonstrated. A comparison of the features of pteropod shells suggests relationship with simple mesogastropods, like Rissoacea, Littorinacea, and Cerithiacea (s.l.), taxa known to have existed since Late Paleozoic time.

Morphology and sculpture of the larval shell also point in this direction. An answer will not be derived from the recent fauna alone, but evidence from fossil species has to be taken into account. It is an interesting idea that new species exploiting completely new food sources and a different environment may arise from a larval stage of some benthic species with a specialized biology. The opportunity appeared when a plankton-feeding larva had evolved. We know that this stage in gastropod evolution had been reached somewhere in the Paleozoic.

Summary

The morphological analysis of early ontogenetic gastropod shells provides us with data which can be used to trace pathways of their evolution.

Limacinid pteropods exhibit a primary shell without growth lines. The secondary shell is formed during larval and adult life in contrast to benthic marine gastropods with free larval life, where the secondary shell is formed by the larva only. The secondary shell is not only attached to the shell secreting epithelium during shell formation. Metamorphosis of the soft body is not reflected in the morphology of the shell. A model for the origin of the limacinid conch is seen in recent architectonicids where, during ontogeny, a planispirally coiled primary shell is followed by a sinistral larval conch (secondary shell) and a dextral tertiary adult conch. It is suggested that the sinistral larval conch also continued to be formed after metamorphosis when the snail remained free swimming and a tertiary shell became disadvantageous.

Peraclis produces a secondary sculpture of hexagonal ridge patterns secreted onto its conch from the outside. Similar additional shell material to the larval conch can be observed in several tonnacian species. Long term larvae of prosobranchs similar to those of the tonnacians can serve as model for the formation of free swimming peracids from benthic ancestors. According to the models presented peracidian and limacinid pteropods can be derived from a prosobranch phylogenetic ancestor, connected with primitive Late Paleozoic mesogastropods.

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