

PLANKTONIC GASTROPOD LARVAE FROM THE RED SEA: A SYNOPSIS

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ABSTRACT

Plankton hauls, which were taken during a Red-Sea-cruise of the research vessel METEOR in 1987, have been examined with regard to gastropods having a planktonic phase in their early ontogeny. Veligers of at least 75 different species could be recognized, most of which are described here. They can be attributed to 27 families, of which 24 belong to the subclass Caenogastropoda.

INTRODUCTION

The aim of this study is to contribute to systematics and biological oceanography. Zooplankton by definition cannot swim against or across currents and thus tracing the drift of such organisms is one way to reconstruct currents. Biological oceanography must rely on the taxonomic data provided by the specialists and therefore description of gastropod larvae, in particular the shells, constitutes the main part of this paper. Aquatic gastropods exhibit a variety of distribution patterns, which are also important for zoogeographical considerations. Different larval adaptations may be reflected by features of the early ontogenetic shell (protoconch). Larval anatomy is not reproducible in the post-metamorphic gastropod but the protoconch is usually preserved at least on the shell apices of juveniles. Consequently, shell morphology represents the main tool to relate larvae and post-larval adults. The number of described protoconchs from the apices of juvenile shells has increased much more in the last decades than the knowledge of the appropriate larvae.

Information on pelagic gastropod larvae world-wide is quite heterogeneous. The Atlantic Ocean has been examined to some extent in this respect. The main contributors have been Heinrich Simroth (1895, 1911), Marie Lebour (e.g. 1934a,b, 1936, 1937, 1945), Gunnar Thorson (1946), Rudolf Scheltema (e.g. 1966, 1971, 1972, 1979), Vera Fretter and Margaret Pilkington (1970),

Catherine Thiriot-Quiévreux (e.g. 1972, 1980a; 1974 and 1975 with Babio, 1982 with Scheltema) and Dan Laursen (1981). Catherine Thiriot-Quiévreux (e.g. 1967, 1969, 1980b) and Gotthard Richter and Gunnar Thorson (1975) described gastropod larvae from the Mediterranean Sea. The knowledge of Indo-Pacific gastropod veligers is very patchy. The most extensive study was conducted by Janet Taylor (1975) who described planktonic veligers of numerous gastropod species occurring around the Hawaiian Islands. Taylor's doctoral thesis was not published but frequently cited and larvae there from illustrated in Kay (1979). Data about Polynesian and western Pacific teleplanic gastropod larvae were presented by Scheltema and Williams (1983). Margaret Pilkington (e.g. 1974, 1976) to some extent described the planktonic gastropod larvae from off southern New Zealand. The Persian Gulf represents a studied area which is geographically closest to the Red Sea. Thorson (1940), however, mainly described hatchlings, in which a characteristic larval shell had not yet been secreted. There exist several embryogenetic studies of gastropods occurring in the northern Red Sea (Soliman 1991 and references therein), but planktonic veligers have not been described.

There is a fair amount of comprehensive papers on the gastropod fauna of the Red Sea (a.o. Issel 1869, Jickeli 1874, 1875, 1884, Sturany 1903, Moazzo 1939, Marcus 1959, Marstaller 1978, Couloumbel 1996), however, information on protoconchs is very scarce, and if existent, usually not suitable for modern taxonomy. Our identifications of veliger larvae are mainly based upon protoconchs of juvenile shells, which have been collected for many years in tropical regions around the world (including the Red Sea), and in some cases are based upon previous identifications made by others.

We are very grateful to master and crew of the research vessel METEOR and thank Prof. Dr. C. Hemleben (Tübingen) for close cooperation during the cruise. D. Lewandowski and K.-U. Seyboth (both Hamburg) prepared the drawings, which is greatly acknowledged. This study was carried out with financial support of the DEUTSCHE FORSCHUNGSGEMEINSCHAFT, grants Ba 675/14 and We 695/11.

METHODS AND MATERIALS

During the 1987 (section 5/5) Red-Sea-cruise of the R.V. METEOR, larvae of benthic and holopelagic gastropods were sampled at 29 stations (342 samples, 9.7.-7.8.1987). Samples were taken with various plankton gears from 0 to 960 m depth, i.e. with two types of multiple-opening-closing nets (Mocness, mesh size 0.33 mm; Hydrobios-net, 0.30 mm), and a neuston slide (mesh size 0.30 mm). More detailed information about stations, sampling devices and procedures can be found in the report (Nellen et al. 1996) of the METEOR expedition. Based upon the identification of larvae presented here, a qualitative and quantitative evaluation of collection data is now possible and in preparation.

Larvae of most species could be kept alive for a few days and observed with

the aid of a light microscope. The larvae were then fixed in ethanol or buffered formalin. The wet material was picked out, cleaned and dried at the INSTITUT FÜR HYDROBIOLOGIE UND FISCHEREIWISSENSCHAFT (Hamburg). Larval and juvenile specimens were mounted on stubs, sputtercoated with gold and then photographed using a SEM (scanning electron microscope) (CamScan). Voucher material is deposited at the INSTITUT FÜR PALÄONTOLOGIE of the FREIE UNIVERSITÄT BERLIN.

SYSTEMATICS AND DESCRIPTIONS

CLASSIFICATION

Veligers of the following **families** will be described:

Class GASTROPODA Cuvier, 1797

Subclass NERITIMORPHA Golikov & Starobogatov, 1975

Superfamily Neritoidea Rafinesque, 1815

Family **Neritidae** Rafinesque, 1815

Subclass CAENOGASTROPODA Cox, 1959

Order Cerithiimorpha Golikov & Starobogatov, 1975

Superfamily Cerithioidea Ferrussac, 1819

Family **Cerithiidae** Fleming, 1822

Family **Litiopidae** Gray, 1847

Order Discopoda Fischer, 1884

Superfamily Truncatelloidea Gray, 1840

Family **Rissoidae** Gray, 1847

Order Strombimorpha Bandel, 1991

Superfamily Stromboidea Rafinesque, 1815

Family **Strombidae** Rafinesque, 1815

Order Heteropoda Lamarck, 1812

Superfamily Carinarioidea Blainville, 1818

Family **Atlantidae** Rang, 1829

Family **Fiolidae** Rang, 1829

Order Ptenoglossa Gray, 1853

Superfamily Triphoroidea Gray, 1847

Family **Cerithiopsidae** H. & A. Adams, 1853

Family **Triphoridae** Gray, 1847

Superfamily Janthinoidea Lamarck, 1810

Family **Epitoniidae** Berry, 1910

Family **Janthinidae** Lamarck, 1810

Superfamily Eulimoidea Troschel, 1853

Family **Eulimidae** Troschel, 1853

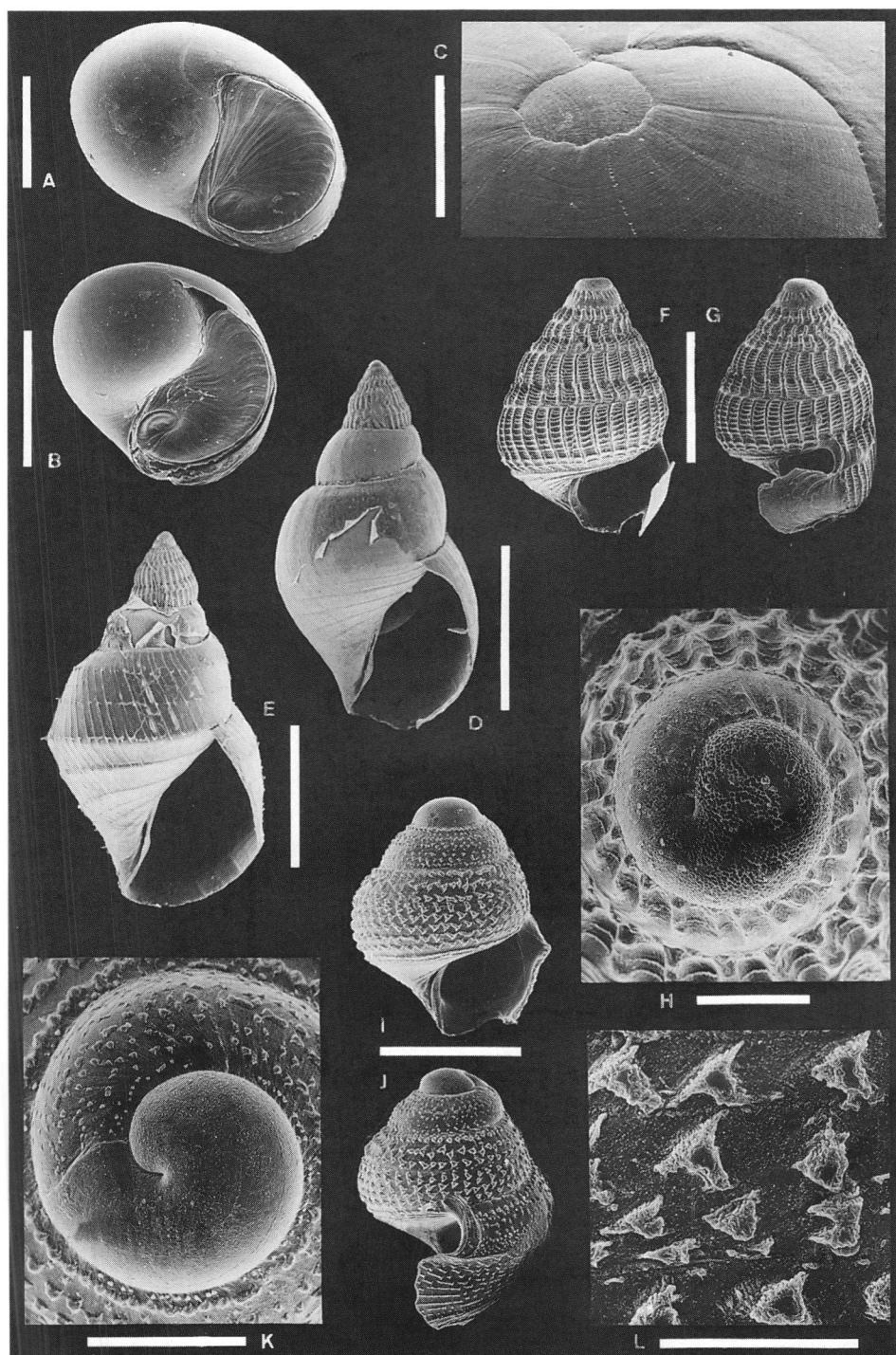
Order Neomesogastropoda Bandel, 1991

Suborder Simrothina Bandel & Riedel, 1994

- Superfamily Naticoidea Forbes, 1838
 - Family **Naticidae** Forbes, 1838
- Superfamily Cypraeoidea Rafinesque, 1815
 - Family **Cypraeidae** Rafinesque, 1815
 - Family **Ovulidae** Fleming, 1822
- Superfamily Lamellarioidea Orbigny, 1841
 - Family **Lamellariidae** Orbigny, 1841
- Suborder Trochelina Bandel & Riedel, 1994
- Superfamily Calyptraeoidea Lamarck, 1809
 - Family **Hipponicidae** Troschel, 1861
- Superfamily Cassoidea Latreille, 1825
 - Family **Cassidae** Latreille, 1825
 - Family **Personidae** Gray, 1854
 - Family **Ranellidae** Gray, 1854
- Order Neogastropoda Thiele, 1929
 - Superfamily Muricoidea Rafinesque, 1815
 - Family **Muricidae** Rafinesque, 1815
 - Family **Buccinidae** Rafinesque, 1815
 - Family **Columbellidae** Swainson, 1840
 - Family **Coralliophilidae** Chenu, 1859
 - Family **Mitridae** Swainson, 1831
 - Superfamily Conoidea Rafinesque, 1815
 - Family **Turridae** Swainson, 1840
- Subclass HETEROSTROPHA Fischer, 1885
- Order Allogastropoda Haszprunar, 1985
 - Superfamily Architectonicoidea Gray, 1840
 - Family **Architectonicidae** Gray, 1840
 - Superfamily Pyramidelloidea Gray, 1840
 - Family **Pyramidellidae** Gray, 1840

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Fig. 1. A: Egg-shaped veliger shell of a neritid species. Scale bar $\cong$ 0.2 mm. B: Globular veliger shell of a neritid species. Scale bar $\cong$ 0.3 mm. C: Typical suture of a neritid protoconch. Scale bar $\cong$ 0.1 mm. D: Juvenile shell of the pseudoplanktonic *Litiopa melanostoma* with preserved characteristic apex. Scale bar $\cong$ 1 mm. E: The juvenile shell of *Litiopa* sp. exhibits a protoconch, which cannot be differentiated from that of *L. melanostoma*. Scale bar $\cong$ 1 mm. F-G: Veliger shell of *Litiopa melanostoma* or *L. sp.*, respectively. Scale bar $\cong$ 0.3 mm. H: Initial whorls of the same specimen as in F-G. Scale bar $\cong$ 0.05 mm. I-J: Veliger shell of a rissoïd. Scale bar $\cong$ 0.3 mm. K: Ditto. The embryonic whorl exhibits spiral lirae. Scale bar $\cong$ 0.1 mm. L: Ditto. Close-up of larval ornamentation. Scale bar $\cong$ 0.05 mm.



DESCRIPTIONS

Neritidae

Fig. 1A-C

Generalized description: The larvae swim with the aid of a quadrilobated velum. The lobes are comparatively short, approximately matching the length of the conch. The velum is not lost by detachment but is resorbed when metamorphosis is triggered off. The larval shell is globular (Fig. 1B) to egg-shaped and in most species has a maximum diameter of about 0.5 to 0.6 mm, however, some protoconchs measure almost 0.8 mm across. The egg-shaped shells are usually broader than high (Fig. 1A). Intraspecific variation of maximum size occurs. The initial embryonic whorl measures (all species) 0.1 to 0.25 mm across.

The protoconchs are always smooth, the ornamentation confined to faint spiral striation and axial growth increments (Fig. 1C). The shell is transparent. Thus spatial arrangement and coloration of soft parts can easily be recognized, such as the green digestive gland in *Smaragdia* Issel, 1869. The same organ is brownish in larval *Nerita* Linné, 1758. A gill develops very late in larval ontogeny, in some species after metamorphosis. There is no special larval heart. Only part of the visceral mass is coiled, due to the dissolution of internal shell walls, which largely neutralizes spatial restrictions of tight spiral shell growth. Externally, the suture of the embryonic and early larval whorl(s) is characteristically covered by later whorls, creating a convolute protoconch. Therefore the number of whorls is difficult to estimate, but formation of up to 2.5 larval whorls has been observed. There is no umbilicus. The aperture is crescent-shaped, with the base comparatively broader. The outer apertural lip is thin and regularly rounded while the inner lip is thickened. In fully grown larvae the operculum seals perfectly the aperture of the protoconch. The nucleus lies excentric, situated at the left side of the operculum base. The size of the operculum increases in a spiral, featured by axial growth increments, which, however, are confined to the external side. Internally, a tooth-like projection reinforces the nucleus.

Complementary literature: Robertson 1971, Scheltema 1971, Laursen 1981, Bandel 1982, 1991, 1992.

Remarks: Neritid larvae are very common in the plankton of the Red Sea. The larval shells of this family may be confused with naticoid protoconchs, which are also more-or-less globular, tightly coiled, in many cases have no prominent ornamentation and bear a spirally growing operculum with excentric nucleus (see under Naticidae). However, convergence is very superficial. The dissolution of internal shell walls occurs only in Neritoidea and the convolute coiling of the larval whorls is also characteristic. Moreover, sculptural details of embryonic and larval shells are different and naticoid protoconchs are larger in most species.

There are several neritid freshwater species, which also produce planktonic

offspring. Size and shape of their protoconchs are within the range of their fully marine counterparts, but possibly may be differentiated by the axial ridges on the larval whorls. This character, however is not yet fully checked. Larval shells with axial ridges could not be recognized in the plankton of the Red Sea. The protoconchs of all planktonic Neritoidea have a very similar morphology and specific or even generic attribution of larval shells in most cases will be very difficult, sometimes even impossible.

?Cerithiidae

Fig. 2

Generalized description: A smooth larval shell with a total height of 0.4 mm may represent a species of *Bittium* Leach, 1847 (but see remarks). The embryonic whorl measures almost 0.1 mm across. Three larval whorls were formed, having a maximum diameter of 0.25 mm. The outer lip of the aperture is shaped to a large beak and two deep notches respectively, from which the two velar lobes of the swimming larva project.

Complementary literature: Lebour 1945, Thiriot-Quiévreux 1969, Thiriot-Quiévreux & Babio 1975, Richter & Thorson 1975, Thiriot-Quiévreux & Scheltema 1982, Bandel 1991b, Bandel & El-Nakhal 1993, Houbbrick 1993.

Remarks: Some larval shells of cerithiids closely resemble those of certain rissoids. In this case the protoconch of the presumed *Bittium* is very similar to that of *Rissoina* d'Orbigny, 1840 (Thiriot-Quiévreux 1980a,b). More detailed investigations are needed to distinguish larvae of these two families, but some traits can already be used which point in the one or the other direction. Most rissoid larval shells are more globular than those of cerithiids. The ornamentation of rissoids may be more complex as in cerithiids, in which spiral keels and axial keels or derivate compose the sculpture (e.g. Houbbrick 1987). Cerithiids usually have an embryonic shell which is more-or-less "beaten" (Bandel 1975) whereas in rissoids also other ornamentations occur such as spiral lirae (Fig. 1K) or a zigzag pattern.

Some Vermetidae may also show protoconchs (Kay 1979), which are difficult to distinguish from the one described here. Certain larval cerithiids may be confused with cerithiopsids. The latter are usually larger and more turritiform. The embryonic shells of cerithiopsids are usually larger and in many species are heavily sculptured with tubercles, which is not known from cerithiids. Thus mainly shells of young larvae of cerithiopsids without characteristic ornamentation can be confused with a few cerithiids. The living larvae of both groups can easily be distinguished (see below).

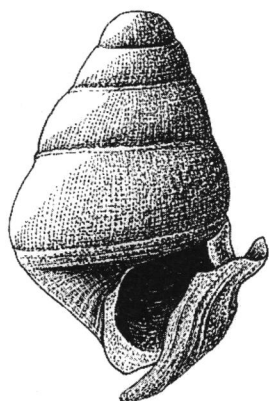


Fig. 2. Veliger shell of a cerithiid species.
Height $\approx$ 0.4 mm.

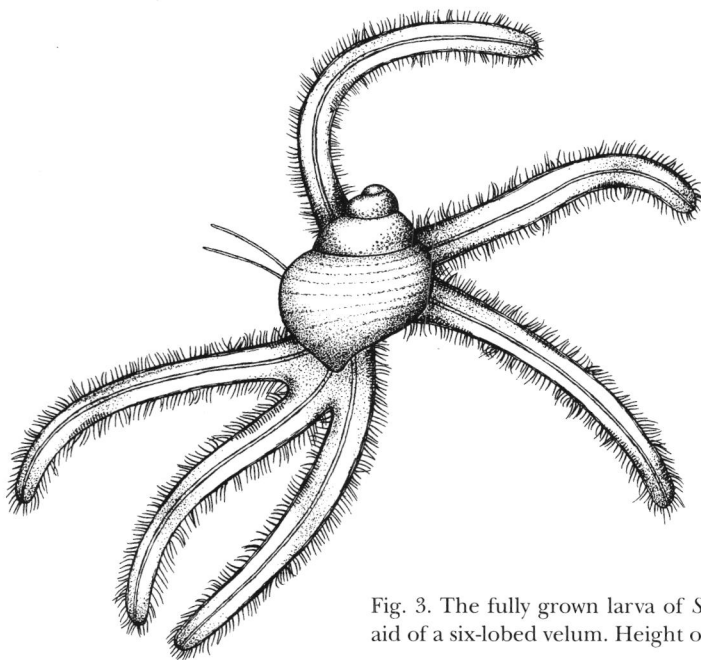


Fig. 3. The fully grown larva of *Strombus* sp. swims with the aid of a six-lobed velum. Height of shell $\approx$ 0.95 mm.

Litiopidae

Fig. 1E-H

Generalized description: Litiopid veligers show a characteristic, asymmetric, bi-lobed velum. Larval conchs are densely ornamented, yellow-brownish in colour, and represent the genus *Litiopa* Rang, 1829. One embryonic and four larval whorls compose the protoconch, which is almost 0.6 mm high and 0.4 mm wide (Fig. 1F). The embryonic shell measures 0.1 mm across and shows the simple

"beaten" appearance, which is known from numerous gastropod taxa. The upper flanks of larval whorls are set with axial ribs, which increase in number from 22 to 28 per whorl, and which are interrupted in alignment by a subsutural, constrictive, spiral ridge. The axial ribs are interconnected (not crossed) by several spiral lirae, about 15 on the latest whorl. The lower flanks of larval whorls are sculptured by five to six spiral ridges. The aperture of the larval conch is subovate, with deep sinusigeral notches (Fig. 1G). The sinusigeral beak is almost 0.2 mm long and smooth except for growth lines. The operculum is multispiral, with a central nucleus.

Complementary literature: Robertson 1971, Bandel 1976a, Okutani et al. 1983, Houbrick 1987.

Remarks: The larval conch characters described here correspond in detail with those of *Litiopa melanostoma* Rang, 1829, documented by Robertson (1971). In the plankton hauls, juvenile *L. melanostoma* could actually be recognized (Fig. 1D), showing exactly the same protoconch. However, a second species with angulated teleoconch whorls (Fig. 1E) shows also identical pre-metamorphic whorls. Thus it must be concluded that species of *Litiopa* probably cannot be differentiated with the aid of the protoconch. Generic distinction between *Litiopa* and *Alaba* H. & A. Adams, 1853 can be made using characters of the early shell. The larval conch of *Alaba* for the most part lacks spiral crests, which connect axial riblets in *Litiopa*, and is also smaller, due to the lower number of larval whorls (Robertson 1971, Jung 1975, Houbrick 1987).

Rissoidae

Fig. 1I-L

Generalized description: Only one type of rissoid larval shell could be recognized. One embryonic and two and a quarter larval whorls compose a protoconch with a height of 0.51 mm and a maximum diameter of 0.42 mm. The embryonic shell measures 0.16 mm across and is set with granules and three spiral lirae (Fig. 1K). The transition to the larval shell is clearly demarcated. The larval whorls are ornamented with tubercles, which are roughly triangular in shape. The larval aperture is of the sinusigera-type (Fig. 1J).

The living veliger could not be observed but the velum of rissoids is usually bilobate.

Complementary literature: Lebour 1934a, Thiriot-Quiévreux 1969, 1980a,b, Fretter & Pilkington 1970, Thiriot-Quiévreux & Babio 1975, Richter & Thorson 1975, Bouchet & Warén 1993.

Remarks: Some diagnostic differences between rissoid and cerithiid larval shells have been pointed out above. Certain littorinid protoconchs are also very similar. They range in the same size and have a similar outline, usually with sinusigera aperture.

Strombidae

Fig. 3, Fig. 4A-D

Generalized description: The larvae swim with a six-lobed velum (Fig. 3). Each velar lobe is almost twice as long as the conch. The larval conchs have a spherical, smooth appearance, and a more-or-less transparent shell. Two species can be distinguished.

The conch of species 1 (Fig. 4A-C) consists of one embryonic and three and a half larval whorls, which amount to a width of almost 1 mm and a height of 1.1 mm. The embryonic shell measures around 0.16 mm across and is ornamented with irregularly fused aragonitic granules. There is no significant sculptural change at the transition to the first larval whorl, which is densely covered by granules. The transition to the second larval whorl is characterized by the onset of faint spiral lirae and decrease of granular ornamentation. The spiral lirae become the dominant sculpture of the two youngest larval whorls. The aperture is subovate and shows a distinct siphonal notch. The operculum seals tightly the aperture, including the siphonal notch, which is covered by a basal opercular projection (Fig. 4B). The nucleus of the operculum lies close to the anterior (basal) part of the columella and shows remains of spiral growth, whereas later growth increments are concentric.

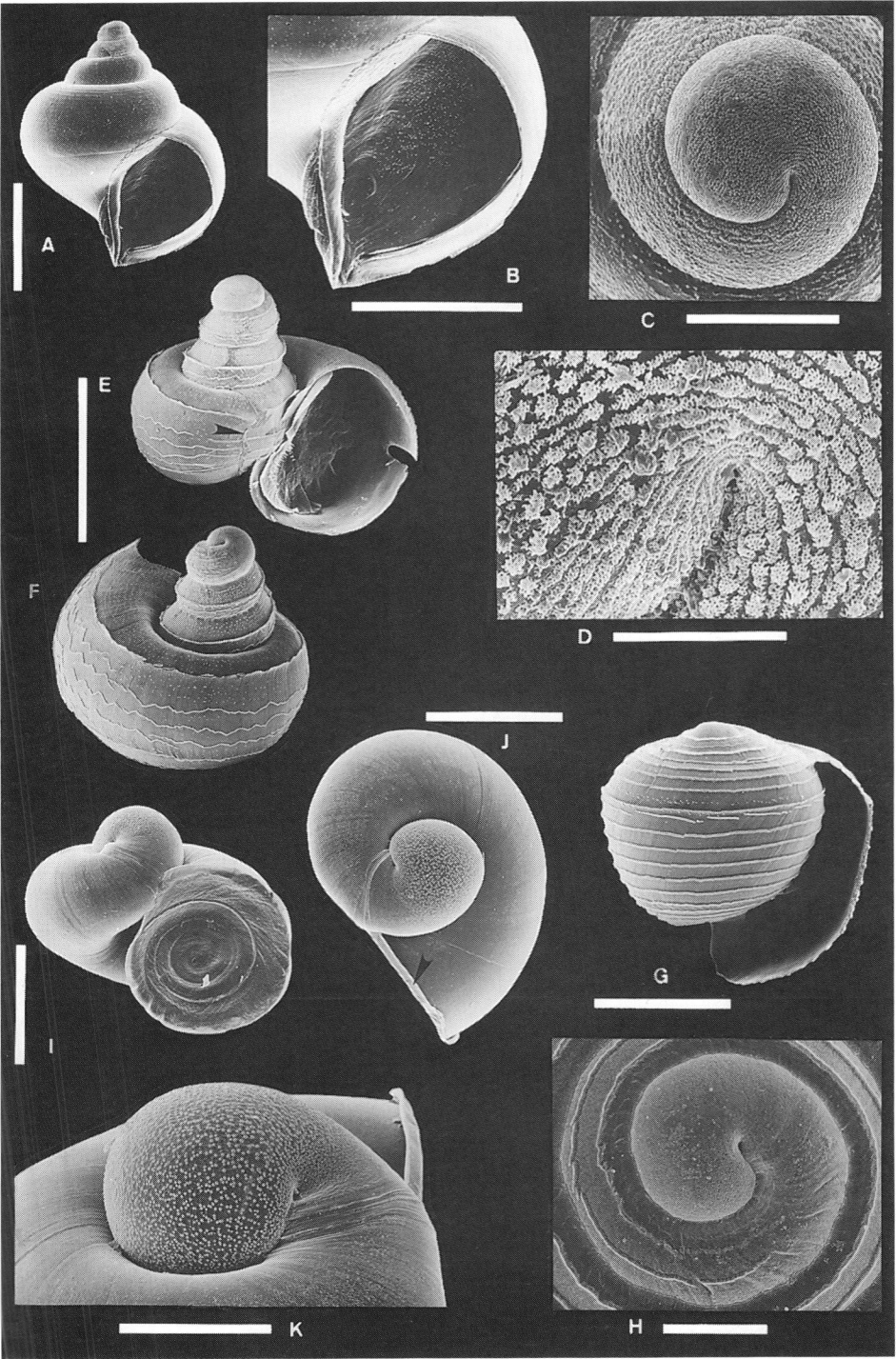
The larval conch of species 2 is composed of one and a quarter embryonic and two and a half larval whorls. The conch is about 0.85 mm wide at maximum, and 0.95 mm high. The embryonic shell measures almost 0.2 mm across. Ornamentation of embryonic shell is similar to that in species 1, but granules are larger and more complex in structure (Fig. 4D). Development of sculpture is the same as in species 1. The aperture shows the same characteristic features as in the other species, but the operculum is different. The nuclear part of it is formed to a semi-circular groove.

Complementary literature: Gohar & Eisawy 1967, Mienis 1971, Eisawy & Sorial 1968, 1976, Bandel 1976b.

Remarks: Strombid larvae were fairly common in the plankton hauls. The larval conchs (as far as known) are all very similar in size and shape (compare e.g. Lebour 1945: unidentified veliger D; Kay 1979). Seraphidae which occur in the Red Sea, such as *Terebellum* Röding, 1798, have a different type of protoconch

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Fig. 4. A: Veliger shell of *Strombus* sp. 1. Scale bar $\cong$ 0.5 mm. B: Ditto. The magnification of the aperture exhibits a basal process of the operculum. Scale bar $\cong$ 0.4 mm. C: Ditto. Close-up of nuclear whorl. Scale bar $\cong$ 0.1 mm. D: Magnification of the ornamentation of the embryonic shell of *Strombus* sp. 2. Scale bar $\cong$ 0.025 mm. E-F: Juvenile of *Atlanta turriculata*. Arrow points at transition from larval to juvenile shell. Scale bar $\cong$ 0.3 mm. G: Veliger shell of *Atlanta helicinoides*. Scale bar $\cong$ 0.2 mm. H: Ditto. Close-up of initial whorls. The transition to the larval shell is characterized by the onset of spiral ridges. Scale bar $\cong$ 0.05 mm. I-J: Shell of *Firoloida demarestia*, which is lost during metamorphosis. Arrow points at bent operculum. Scale bars $\cong$ 0.2 mm. K: Ditto. The larval whorl is oblique to the embryonic whorl. Scale bar $\cong$ 0.1 mm.



(see Jung 1974). The two strombid larval conchs possibly represent *Strombus gibberulus* Linné, 1758 (*S. gibberulus albus* Mörch, 1850) and *Strombus fasciatus* Born, 1778, which are very common in the Red Sea and are known to have planktonic development (Eisawy & Sorial 1976). However, the attribution is more-or-less tentative and a species like *Strombus plicatus* Röding, 1798, which has a wide Indo-Pacific distribution, must also be taken into taxonomic considerations.

Atlantidae

Fig. 4E-H, Fig. 5

Generalized description: Several species of the genus *Atlanta* Lesueur, 1817 could be recognized. Most common were *A. turriculata* Orbigny, 1836 and *A. helicinoides* Souleyet, 1852, which are briefly described here. Larval (and adult) conchs of (e.g.) *A. plana* Richter, 1972 and *A. inflata* Souleyet, 1852 also occur in the plankton hauls, but differ from *A. helicinoides* only in detail. Almost all larval conchs of atlantids have already been described and figured in the literature (see remarks).

Larvae were observed to swim with a six-lobed velum. The velar lobes are not much longer than the largest dimension of the larval conch. The name of *Atlanta turriculata* was coined in respect of the protoconch, which actually is turriculated (Fig. 5). The larval conch is composed of one embryonic and two and a half larval whorls, which amount to a height of almost 0.4 mm and a width of little more than 0.2 mm. The embryonic shell measures nearly 0.1 mm across and is ornamented with minute aragonitic granules. The outer lip of the aperture of the embryonic whorl is sinus-shaped. The larval (and juvenile) whorls show a prominent spiral ridge dividing off a sutural ramp, and several spiral lirae forming a zigzag pattern. The spiral lirae are pronounced mainly on the lower flanks of the whorls and may be interrupted or somewhat disintegrated. The spiral sculpture continues on the juvenile shell (Fig. 4E-F, Fig. 5) but is reduced in later ontogeny. Apart from spiral ornamentation, early stage whorls are set with tubercles, which are significantly larger than embryonic granules. The aperture of the larval conch is subovate with basal angularity and the outer lip shows a prominent beak (Fig. 4E arrow, Fig. 5). The operculum coils left – the nucleus remaining at the lower part of the columellar side – and is set with several rows of organic tines (Fig. 4E).

The larvae of *Atlanta helicinoides* form a shell of almost three and a half whorls (excluding embryonic portion), which measure about 0.38 mm in height and around 0.4 mm in width (Fig. 4G). The embryonic whorl (Fig. 4H) matches in diameter and ornamentation that of *A. turriculata*. The larval (and early juvenile) whorls are set with several spiral ridges, which increase in number to about twenty on the terminating whorl. The aperture is comparatively high and narrow, almost sausage-shaped. The outer apertural lip shows a prominent beak (broken in the figured specimen).

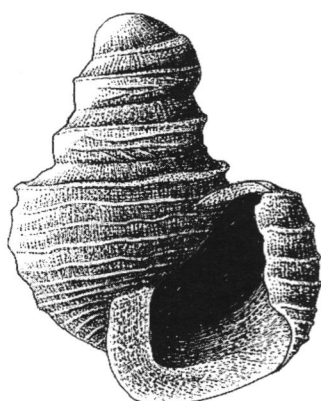


Fig. 5. The veliger shell of *Atlanta turriculata* differs significantly from the planispiral teleoconch. Height ≈ 0.4 mm.

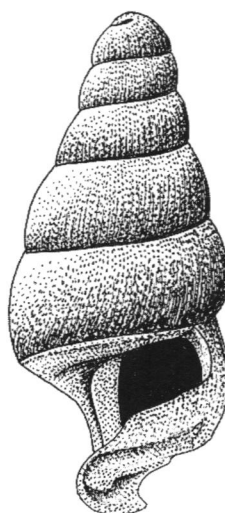


Fig. 6. Six-whorled cerithiopsid veliger shell. Height ≈ 0.73 mm.

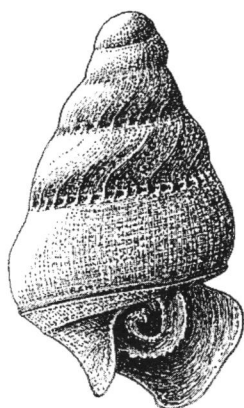


Fig. 7. The aperture of this cerithiopsid larva exhibits the multispiral operculum. Height of the conch ≈ 0.7 mm.

Complementary literature: Thiriot-Quévéreux 1973, Richter 1974, Bandel & Hemleben 1987, Seapy 1990.

Remarks: Heteropod gastropods, i.e. Atlantidae, include several species with circum-tropical distribution. Species like *A. helicinoides* have been caught in the Atlantic as well as in the Indo-Pacific. Larvae and adults of atlantids commonly occur in the same plankton hauls and, moreover, the protoconchs of adults are usually not much corroded. Thus specific attribution of larval conchs is comparatively easy and actually most species have been examined in this respect (see references and references therein). Even adults are usually small enough to be examined under the SEM, providing the possibility to document perfectly the correlation of protoconchs and teleoconchs.

Firolidae

Fig. 4I-K

Generalized description: Larval conchs could be attributed to *Firoloida demarestia* Lesueur, 1817, the single known species of the genus. The living larva could not be observed. A four-lobed veliger, with length of each lobus equal to the largest dimension of the larval conch was figured by Thiriot-Quévèreux (1973).

There is one embryonic and one larval whorl, which measure about 0.45 mm in width and 0.35 mm in height (Fig. 4I-J). The embryonic whorl has a maximum diameter of 0.2 mm. The coiling axis is oblique to that of the larval whorl (Fig. 4K). The bulbous embryonic portion is densely covered by minute aragonitic granules, whereas the larval whorl is smooth, except for growth increments. The aperture is circular and measures about 0.25 mm in diameter. The operculum shows perfect spiral growth, with the nucleus almost in the centre (Fig. 4I). It is unusually large, which can be recognized by the opercular margins enveloping the apertural lips (Fig. 4J arrow).

Complementary literature: Owre 1964, Thiriot-Quévèreux 1972, Bandel & Hemleben 1987.

Remarks: The larvae of *Firoloida demarestia* were among the rarest in the plankton hauls of the Red Sea. There are marked differences to atlantid larval shells such as the larger embryonic shell, the lower number of larval whorls, the rounded aperture, etc. On the other hand the early larval shell reflects close relationship to *Pterotrachea* Forsskål, 1775. Size of the protoconch, round aperture and number of whorls are similar in the two genera, but the embryonic shell coiling oblique to the larval whorl represents a character, which appears to be autapomorphic for *Firoloida*. Phylogenetic implications of heteropod shell characters have been discussed by Bandel and Hemleben (1987).

Cerithiopsidae

Figs. 6-7

Generalized description: Larvae of three different species could be observed to swim with the aid of a bilobed velum, the left lobe being much smaller than the right one. The larval shell of one species (Fig. 6) consists of one embryonic whorl measuring about 0.1 mm across, and almost five larval whorls, which amount to a maximum diameter of 0.32 mm. The larval conch has a total height of 0.73 mm. The embryonic shell is almost smooth except for some minute tubercles. The tubercles are set more or less densely on the larval whorls and may form short spiral and axial rows. The last whorl exhibits a sutural carina. The outer lip of the aperture shows a deep posterior sinus and a large beak.

The protoconch of a second species shows a similar general shape but in especially the ornamentation is very different and characteristic for the genus *Ce-*

rithiopsis Forbes & Hanley, 1850. The one-whorled embryonic shell measures about 0.15 mm across and is densely ornamented with flatworm-shaped tubercles, which are maximally 10 μ m long and 4 μ m wide, and composed of minute aragonitic filaments. The transition to the first larval whorl is clearly demarcated by the abrupt sculptural change. The upper flank of the three larval whorls are set with orthocline ribs except for a subsutural strip, which is densely covered by aragonitic filaments of more-or-less spiral orientation. The smooth lower flank and the ornamented upper flank of the larval whorls are separated by a spiral ridge, which is set with aragonitic granules. The larval aperture shows a basal siphonal canal and an outer lip with a pronounced, broad beak. The protoconch has a total height of 0.63 mm and a maximum width of 0.32 mm.

The larval conch of a third species (Fig. 7) is about 0.7 mm high and has a maximum diameter of little more than 0.4 mm. The larval whorls, except for the final one, are characteristically sculptured by prosocline ribs. The larval aperture shows a prominent beak.

Complementary literature: Thiriot-Quiévreux 1969, 1980a,b, Richter & Thorson 1975.

Remarks: Cerithiopsid larvae may be confused with some cerithiids, in which, however, the protoconchs are usually smaller and the number of larval whorls is lower. The embryonic shell in some cerithiopsids is as small as in certain cerithiids, but in most cases is larger. Additionally, the nuclear whorl of many cerithiopsids is ornamented with tubercles, while this feature is not known from planktonic cerithiid veligers.

Triphoridae

Fig. 8, Fig. 9A-C

Generalized description: Larvae of several species were observed to swim with an asymmetric bilobed velum. In contrast to the observed cerithiopsid larvae, in triphorids the right velar lobe is significantly smaller than the left one (Fig. 8). The small velar lobe is usually in front of the aperture while the large lobe shades the larval conch.

One protoconch is described, which in its general features is more-or-less characteristic of the planktonic veligers of the whole family. The whorls of triphorids coil sinistral (but see remarks) and form a more-or-less turreted conch. The protoconch is composed of one embryonic and 3.5 larval whorls, with a total height of almost 0.55 mm and a maximum diameter of 0.4 mm. The nuclear whorl measures 0.16 mm across and is ornamented with tubercles (Fig. 9B-C). The larval whorls are sculptured by about 25 axial riblets each, which are crossed by a spiral ridge producing a pattern of rectangles (Fig. 9A). A sutural ridge divides the upper ornamented flank of the whorl, from the lower flank, which is not sculptured. The larval aperture is nearly circular and shows a posterior but no basal sinus.

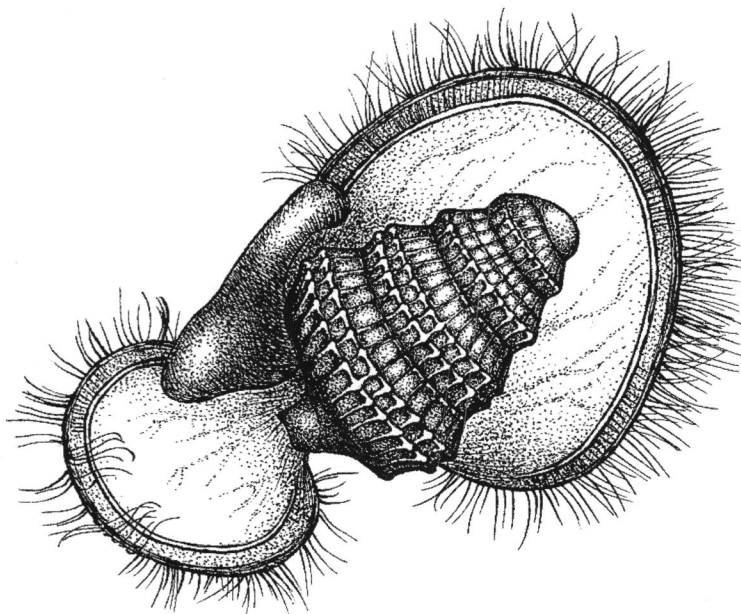


Fig. 8. Triphorid larvae swim with the aid of an asymmetric bilobed velum. Height of the sinistral conch ≈ 0.65 mm.

Complementary literature: Lebour 1945, Richter & Thorson 1975, Thiriot-Quiévreux & Scheltema 1982, Marshall 1983.

Remarks: The larvae of triphorids cannot be confused with those of any other group when restricting the family to the sinistral species. Mainly based upon radula characters, dextrally coiled triphorids (Metaxiinae) have been recognized (e.g. Marshall 1977, Bouchet 1985), which, however, may also be interpreted to represent members of a derived cerithiopsid group, which could have given rise to the sinistrally coiled triphorids. The ornamentation of larval whorls with spiral and axial ribs is typical for most triphorids. The height of triphorid protoconchs varies interspecifically from about 0.5 to 1 mm, which is about the same as in cerithiopsids. Additionally, the diameters of the embryonic shells are within the same range of about 0.1 to 0.2 mm in both groups. In triphorids as well as in cerithiopsids the embryonic whorl is usually sculptured by tubercles. The asymmetric bilobed velum appears to occur throughout both families but is not confined to the Triphoroidea (see e.g. Litiopidae).

The larvae as well as the feeding and reproductive ecology suggest that Cerithiopsidae and Triphoridae are closely related. Thus separation at the superfamily level as proposed by some authors (e.g. Vaught 1989) cannot be supported here.

Epitoniidae

Fig. 9D-F

Generalized description: Larvae of three species of epitoniids could be observed to swim with the aid of an asymmetric bilobed velum. As usual in planktonic species the embryos hatch with a one-whorled shell, to which in epitoniids 2-4 whorls are added during larval life. The pediveliger shows a deep pallial cavity, which extends almost over a whole whorl and shows a large gill. The hypobranchial gland can easily be recognized by its almost black colour. The larval heart has already ceased to work prior to metamorphosis.

Two of the three protoconchs, which are introduced here, are composed of one embryonic and 3.5 larval whorls. One larval conch has a height of about 0.73 mm and a maximum diameter of 0.47 mm (Fig. 9D). The embryonic shell measures 0.11 mm across and shows no ornamentation (Fig. 9F). The larval whorls are characteristically sculptured by axial threads, about 70 on the last whorl. Each thread shows tiny indentations (Fig. 9E). The larval aperture is holostome and about egg-shaped. The protoconch of the second species is very similar, i.e. the embryonic shell shows no differences, the number of larval whorls is equal and the ornamentation differs only in details, which could also represent intraspecific variation. However, the larval conch is slenderer and significantly smaller. It has a height of about 0.56 mm and a maximum diameter of 0.33 mm.

The third species shows one smooth embryonic whorl measuring 0.13 mm across and three and a quarter larval whorls. The total height amounts to 0.63 mm and the maximum diameter is 0.43 mm. The larval whorls show a slight sutural angulation. The ornamentation differs from that of the other two species by the higher number of indentations of the axial threads. The indentations are also more pronounced and thus produce regularly interrupted spiral lirae (compare Fig. 9J-K).

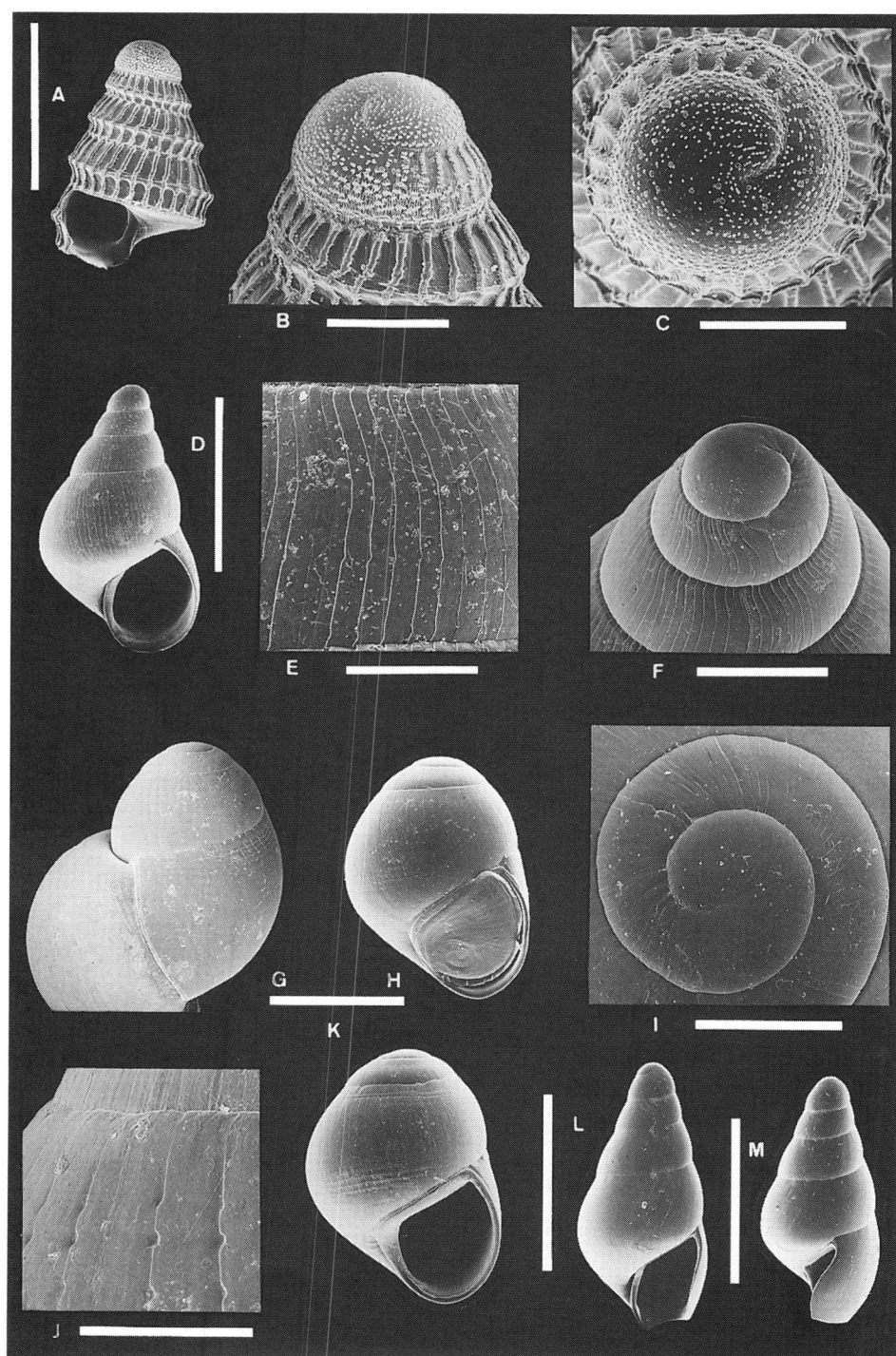
Complementary literature: Robertson 1980, 1994, McDermott 1981.

Remarks: Larval shells of Epitoniidae are quite characteristic and probably can only be confused with those of certain janthinids. The protoconchs introduced here are like those known from species of the genus *Epitonium* Röding, 1798. However, very little is known about characteristic sculptural elements of the more than sixty genera, which are included in the family.

Janthinidae

Fig. 9G-K

Generalized description: The larvae of *Janthina exigua* Lamarck, 1816 were observed right after hatching. The young veligers are one-whorled and swim with the aid of two velar lobes, which are more-or-less symmetric. The yolk reserves



are minute, indicating that the veligers have to feed on plankton prior to metamorphosis. The hypobranchial gland has already a deep purple colour. The operculum is functional.

During larval life little more than two and a half whorls are added. The total height of the egg-shaped protoconch varies around 0.55 mm, the maximum diameter around 0.45 mm (Fig. 9G,H,K). The embryonic shell is smooth and measures 0.12-0.13 mm across (Fig. 9I). The larval whorls show axial threads, each with several indentations, which are more-or-less angulated, somewhat trapezoidal (Fig. 9J). The indentations may be interconnected by faint or sometimes distinct spiral striae (Fig. 9K). The larval aperture is holostome and about crescent-shaped. The operculum is multispiral and shows a more-or-less basal nucleus (Fig. 9H). It is fully functional in the late veliger and is not lost during metamorphosis, but in the juvenile.

Complementary literature: Laursen 1953, Robertson 1971.

Remarks: *Janthina exigua* was common in the neuston of the Red Sea. Other species of the genus such as *J. janthina* (Linné, 1758) or *J. globosa* Swainson, 1822 should also be expected to occur in the Red Sea, however, they were not found in the neuston samples. The protoconch of *J. exigua* shows considerable intra-specific variability, i.e. with regard to the sculpture (compare Figs. 9H and 9K). It can, however, be distinguished from those of the other known *Janthina* species. *J. janthina* with 0.1-0.23 mm has a wide range of embryonic shell diameter (Wilson & Wilson 1956), which may be connected with the ovoviviparity of this species (Robertson 1971, Kay 1979). Moreover, in *J. janthina* three larval whorls are formed, the protoconch is larger and more distinctly sculptured (Robertson 1971) than in *J. exigua*. The protoconch of *J. pallida* has the same number of larval whorls as is formed in *J. exigua* (about 2.5), but is smaller, the ornamentation more prominent and the columellar lip of the larval aperture is more rounded (see Robertson 1971).

←

Fig. 9. A: Sinistral veliger shell of a triphorid. Scale bar $\cong$ 0.4 mm. B: Ditto. Magnification of transition from embryonic to larval shell. Scale bar $\cong$ 0.1 mm. C: Ditto. Apical view of initial whorls. Scale bar $\cong$ 0.1 mm. D: Veliger shell of epitoniid. Scale bar $\cong$ 0.5 mm. E: Ditto. Close-up of larval ornamentation. Scale bar $\cong$ 0.05 mm. F: Ditto. Oblique view of initial whorls. Scale bar $\cong$ 0.1 mm. G: Juvenile shell of *Janthina exigua* with protoconch. Scale bar $\cong$ 0.3 mm. H: Veliger shell of *J. exigua*. Scale bar $\cong$ 0.3 mm. I: Ditto. Magnification of initial whorls. The transition from embryonic to larval shell is demarcated by the onset of growth increments. Scale bar $\cong$ 0.1 mm. J: Ditto. Close-up of larval shell sculpture. Scale bar $\cong$ 0.05 mm. K: Ditto. Differences in size and ornamentation to specimen in H are intraspecific. Scale bar $\cong$ 0.3 mm. L-M: Eulimid protoconchs lack characteristic ornamentation. Scale bars $\cong$ 0.5 mm.

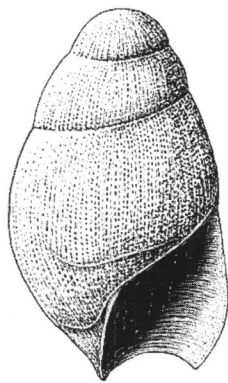


Fig. 10. Eulimid protoconchs lack significant ornamentation. Height ≈ 0.65 mm.

Eulimidae

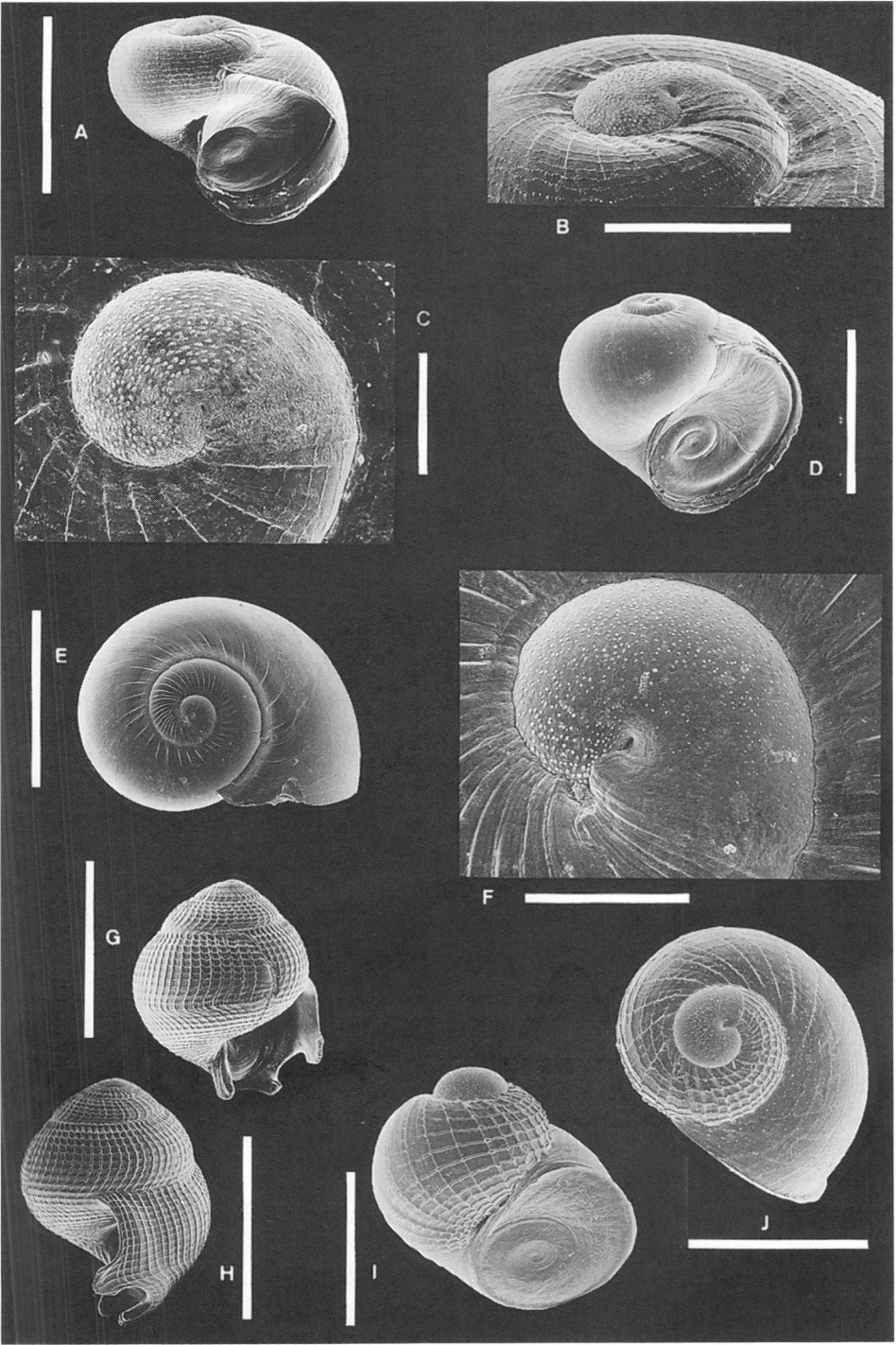
Fig. 9L-M, Fig. 10

Generalized description: Eulimid larvae swim with the aid of a bilobed velum, which is more-or-less asymmetric. Larval shells of eulimids are all characterized by the lack of ornamentation. Protoconchs of two different species are introduced here. One protoconch is composed of one embryonic whorl measuring about 0.12 mm across, and three and three quarter larval whorls, which have a maximum diameter of 0.38 mm. The total height of the protoconch is about 0.68 mm. The larval aperture is channelled and the outer lip is waved (Fig. 9L-M). The second species (Fig. 10), with a height of 0.65 mm and a maximum diameter of 0.39 mm has almost the same size as the first species, however, only two and three quarter larval whorls had been formed and the embryonic shell is larger (0.14 mm). The aperture shows the same features as described for the other species.

Complementary literature: Lebour 1935, Thiriot-Quiévreux 1969, Warén et al. 1994.

Remarks: Eulimid larvae were fairly common in the plankton of the Red Sea. Planktonic veligers of several more species will have to be described and probably not all can be distinguished by shell characters. In eulimids, the examination of living larvae is thus more essential than in most other groups. Usually the soft parts of the veligers provide sufficient diagnostic features.

→
Fig. 11. A: Naticid larvae seal their aperture with a characteristic operculum (compare D). Scale bar ≈ 0.5 mm. B: Ditto. The larval whorls of this species show spiral and axial sculpture. Scale bar ≈ 0.2 mm. C: Dito. The embryonic shell is clearly demarcated. Scale bar ≈ 0.1 mm. D: The shape of the naticid veliger shell resembles that of the teleoconch. Scale bar ≈ 0.5 mm. E: Ditto. The apical view exhibits the development of axial sculpture. Scale bar ≈ 0.4 mm. F: Ditto. The aperture of the embryonic shell shows a varix. Scale bar ≈ 0.05 mm. G-H: The larval whorls of *Cypraea* sp. show a pattern of rectangles. Scale bars ≈ 1 mm. I-J: Veliger shell of the limpet *Hipponix conicus*. Scale bars ≈ 0.3 mm.



Naticidae

Fig. 11A-F

Generalized description: Naticid veligers could be observed to swim with a quadri-lobate velum, each lobus having about two times the length of the conch. The pediveligers may already enter the sediment, thus testing the substrate before metamorphosis begins.

Two different larval shells of uncertain generic attribution are described here (see remarks). Both larval conchs have a more-or-less spherical outline, the shell having a whitish, nearly transparent appearance. Type 1 (Fig. 11A-C) is almost 0.7 mm wide and 0.6 mm high. The embryonic whorl measures about 0.25 mm across and is densely ornamented with spiral rows of tubercles. Only one and a quarter larval whorls have been built. Sculptural elements are delicate but distinct spiral ridges, and axial ribs, which are marked on the early larval shell and can hardly be recognized on the last half whorl. Thus the early larval shell appears somewhat cancellated. The aperture is relatively large and of more-or-less spherical outline, with angularity at the sutural portion. The operculum grows in a spiral, the nucleus lying central in the young larva and shifted only little to the left in the late larva. The umbilicus is pronounced.

Type 2 is characterized by a relatively small embryonic shell, measuring only 0.11 mm across. The embryonic shell is ornamented with minute tubercles, which are more-or-less loosely arranged (Fig. 11F). The aperture shows a prominent varix. The transition to the larval shell is characterized by distinct growth increments, which develop to axial ridges. These sculptural elements cover densely more than half of the first larval whorl but then are confined to the upper flank of the whorls (Fig. 11E). The embryonic and the two larval whorls are 0.8 mm wide at maximum. The height amounts to 0.7 mm (Fig. 11D). Aperture and operculum are similar in the two types but show different details (compare Fig. 11A, D).

Complementary literature: Thorson 1940, 1946, Amio 1955, Giglioli 1955, Gohar & Eisawy 1967, Richter & Thorson 1975, Bandel 1975, 1976b, 1992, Scheltema & Williams 1983, Bouchet & Warén 1993.

Remarks: Larvae of Naticidae were fairly common in the plankton hauls. Generic or specific attribution is very difficult because protoconchs of the benthic juveniles or adults have not been described for naticids of the Red Sea. The embryonic shell of type 2 is unusually small for naticids, however, a comparable diameter has been described for *Polinices mammillus* (Linné, 1758) (see Gohar & Eisawy 1967), a species which is common in the Red Sea and spawns round about August (compare Methods and Materials). One egg mass of *Polinices mammillus* contains more than half a million embryos, which all hatch out as planktonic veligers (Soliman 1991). Type 2 is superficially convergent to certain neritoidean larval conchs. Differences have been discussed under Neritidae. Type 1 can be confused with certain hipponicid larval conchs, however, the

electron microscope reveals distinctive features, such as the spiral rows of tubercles on the embryonic shell of type 1 or details of aperture and operculum (compare Fig. 11C, J).

Cypraeidae

Fig. 11G-H

Generalized description: Several different larvae (at least eight species) could be observed alive. They swim with the aid of four velar lobes, each having about twice the length of the larval conch. Active swimming larvae cover their shells with mantle tissue, which like in the adults protrudes from both sides of the aperture. Pigmentation of the mantle is specific. Disturbed larvae show a well synchronized, rapid retraction of mantle and velum.

The larval shells of cypraeids have spherical to conical outlines. Coloration may be brownish as well as whitish. Overall sizes range from little more than 0.5 mm to almost 2 mm. Nevertheless, cypraeid larval conchs can be easily recognized by the sculptural pattern. The larval whorls are densely covered by rectangles formed by spiral and axial ridges. Up to four and a half larval whorls are built, and the aperture of the fully grown larva is usually of the sinusigera type. The sinusigera aperture develops fully during the early larval phase but in some species its prominent expression may decrease during the late larval phase.

The figured larval conch is comparatively large, having a height of 1.2 mm and a width of about 1.05 mm. The shell is whitish in appearance and consists of one embryonic and almost four larval whorls. The embryonic shell is "beaten" – a feature which is known from many caenogastropod taxa (see e.g. Ranelidae or Hipponicidae) – and measures about 0.15 mm across. The operculum can tightly seal the aperture of the larval conch. The nucleus of the sinistral spiral lies excentric to the left. For apertural details see figures.

Complementary literature: Ostergaard 1950, Thiriot-Quiévreux 1972, Bandel 1973, 1992, Tanaka 1980.

Remarks: Larvae of Cypraeidae were common in the plankton hauls. Subgeneric or specific attribution is very difficult, because protoconchs of juveniles (from the Red Sea) have not been described in the literature. Studies on the early ontogeny of gastropods occurring in the Red Sea (as listed by Soliman 1991) have excluded cypraeoidean species. However, it must be pointed out that the larval conchs of Cypraeidae are heterogeneous in shape, size and colour and thus have the potential to be characteristic at the species level.

Ovulidae

Fig. 12

Generalized description: The larvae are very similar to those of cypraeids. The velar lobes have about twice the length of the conch. The larval shells are brown-

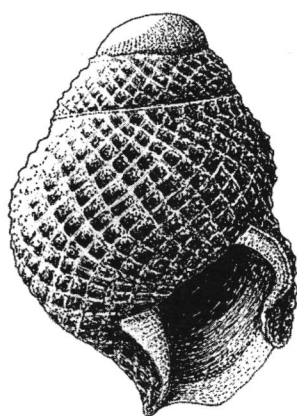


Fig. 12. The larval shell of ovulids exhibits a pattern of rhombs. Height ≈ 0.6 mm.

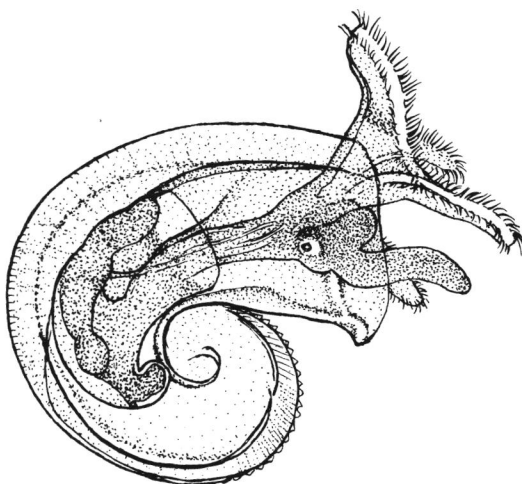


Fig. 13. The veliger of *Lamellaria* sp. secretes a gelatinous scaphoconch. Maximum diameter of the scaphoconch ≈ 1.6 mm.

ish or whitish. The mantle expands on the outer shell, but in contrast to cypraeids, covers only part of the conch. The aperture is of the sinusigera type and can be sealed with the operculum, which resembles that of cypraeids. The main character to distinguish larval ovulids from cypraeids is the ornamentation of the larval whorls. Prosocline and opisthocline ribs form a characteristic pattern of oblique rectangles. Heights of specimens range from 0.5 to about 1 mm. The embryonic shells interspecifically vary in width around 0.15 mm and show the same general pattern as in cypraeids (see remarks there).

Complementary literature: Lebour 1932, Robertson 1971, Bandel 1973, 1975, Kay 1979.

Remarks: Ovulid larvae were rare in the plankton hauls. Generic and specific attribution of larvae will be possible in comparison with protoconchs of the benthic adults. However, early ontogenies of ovulids occurring in the Red Sea have not yet been studied.

Lamellariidae

Figs. 13-14

Generalized description: The late veliger of *Lamellaria* sp. could be studied alive. It is characterized by its six-lobed velum and in particular by its gelatinous scaphoconch. Two whorls have been secreted, with the final portion detached (Fig. 13). The actual shell of the veliger is only loosely coiled and hardly calcified. Mineralization increases during metamorphosis and when having thrown off

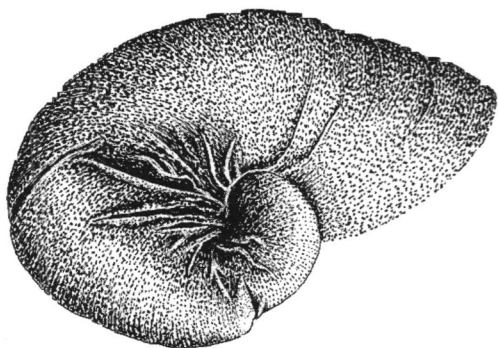


Fig. 14. The juvenile shell of *Lamellaria* sp. (off Japan) shows axial folds, which result from a secondary spiralization of the protoconch during metamorphosis. Maximum diameter ≈ 0.8 mm.

the scaphoconch, the gastropod forces the early shell into a tight spiral. The protoconch then is composed of one and a quarter whorls, which subsuturally show axial folds having resulted from the secondary deformation of the shell (Fig. 14). The scaphoconch has a maximum diameter of about 1.6 mm and is ornamented by finely denticulated keels, except for the final portion, which is smooth and bilaterally symmetric. The actual shell measures 0.8 mm in its largest dimension, and, when tightly coiled during metamorphosis, only about 0.65 mm.

Complementary literature: Lebour 1935, 1945, Thiriot-Quiévreux 1969, Pilkington 1976, Laursen 1981.

Remarks: Lamellariid veligers were rarely found in the plankton hauls of the Red Sea. The taxonomy of these gastropods is insufficient and thus specific attribution of larvae is more-or-less impossible with our current knowledge. Lebour (1937) assigned a veliger to *Lamellaria perspicua* (Linné, 1758), in which the gelatinous scaphoconch is composed of more than three whorls. It cannot be differentiated from *Lamellaria* sp. B introduced by Laursen (1981) and appears also to be identical with *Lamellaria (latens ?)* figured by Thiriot-Quiévreux (1969) from the Mediterranean. Fretter and Graham (1962), however, assigned a two-whorled scaphoconch of about one millimeter diameter to *Lamellaria perspicua*, whereas Thiriot-Quiévreux (1969: *L. perspicua ?*) figured also a two-whorled scaphoconch but measuring more than one and a half millimeter across. According to Fretter and Pilkington (1970) the scaphoconch of *L. latens* can be differentiated from that of *L. perspicua* only by its coarser denticulations. The veliger described here resembles closely the one which was questionably attributed by Thiriot-Quiévreux (1969) to *L. perspicua*. It probably represents neither *L. perspicua* nor *L. latens* (*L. berghi* (Deshayes, 1863) should be considered) but demonstrates the faunistic relations of the Mediterranean and the Red Sea (see also conclusions).

Hipponicidae

Fig. 11I-J

Generalized description: The larvae could be observed to swim with a four-lobed velum, each velar lobus having about the length of the shell. Only one type of hipponicid larval conch could be recognized and is attributed to *Hipponix conicus* (Schumacher, 1817). The fully grown larval conch is roughly spherical in outline and brown-yellowish in appearance. One embryonic and almost one and a half larval whorls amount to a height of 0.5 mm and to a width of little more than 0.5 mm. The embryonic shell measures about 0.15 mm across and is sculptured by a fine groove and ridge pattern of "beaten" appearance. The larval whorls are set with more-or-less opisthocline ribs (about thirty per whorl) and spiral ridges (about seven on the upper flank), which cross to form a pattern of rectangles. The ornamentation becomes indistinct on the latest portion of larval shell. The aperture is oblique to the apical axis, almost circular in outline and perfectly sealed with a spirally coiled operculum. The nuclear part of the operculum lies excentric to the left, but in some distance to the margin.

Complementary literature: Cernohorsky 1968, Laws 1970, Kay 1979, Bandel & Riedel 1994.

Remarks: The larvae of *Hipponix conicus* were fairly common in the plankton hauls. This species has an Indo-Pacific distribution and its veliger represents one of few in the family, which can be termed teleplanic (see Scheltema 1971).

Hipponicid larval conchs have been confused with those of Bursinae (Jung 1975: *Bursa* sp., figs. 79-81). Bursine larval shells (see under Ranellidae) bear periostracal spines, are usually composed of a higher number of larval whorls and thus are much larger, do not have an almost circular aperture, which may be oblique in hipponicids (foreshadowing limpet shape) and do not show opisthocline ribs and growth increments. The larval operculum of Bursinae grows more-or-less concentric, at least in the late veliger. Certain naticid larvae (compare Fig. 11A-C with I-J) are also somewhat convergent with regard to size, outline, sculpture of larval whorls and opercular features. The embryonic shell, however, is sculptured differently in the two family taxa.

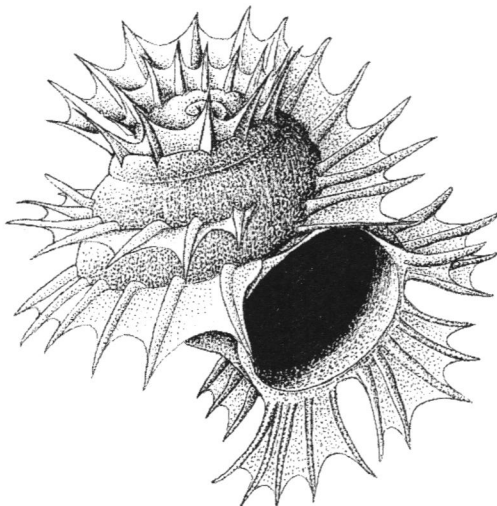
Personidae

Fig. 15

Generalized description: The single personid type of larva, which occurred in the plankton hauls, can be attributed to the genus *Distorsio* Röding, 1798 and probably represents the species *D. reticulata* (Linné, 1758). The protoconch consists of one embryonic and 2.6 to 2.8 larval whorls, is whitish in appearance and nearly transparent. Calcification is largely reduced (see remarks on Ranellidae).

The young larva has a bilobed velum, which, however, is already laterally indented, foreshadowing the quadrilobate stage in later larval ontogeny. A velar

Fig. 15. The veliger shell of *Distorsio* cf. *reticulata* is ornamented with sail-like periostracal elements. Height without periostracal processes ≈ 1.5 mm.



lobus may be stretched up to three times the length of the larval conch, which is about 1.4 to 1.5 mm high (long) and 1.3 to 1.4 mm wide, excluding periostracal sculptures. The ornamentation confines to the organic carina-like secretions of the periostracum glandular cells of a special pallial appendage (see remarks). Actually two carinae are formed. The initial one is in contact with the embryonic shell and becomes the lower carina, above which a second carina is intercalated after formation of about one larval whorl. Each carina is somewhat webbed, consisting of a row of organic spines, which are interconnected by pieces of periostracum. Aside from the carinae and faint growth lines, the embryonic as well as the larval shell is smooth. The initial embryonic whorl measures 0.35 to 0.38 mm across.

The aperture of the protoconch is holostomous and, aside from a slightly concave columellar section, is obliquely egg-shaped. The growth increments are orthocline and the outer apertural lip does not show any deviation. The operculum could not be examined in detail, but it is comparatively flexible, allowing the animal to retract it into the conch for nearly half a whorl.

Complementary literature: D'Asaro 1969, Laursen 1981, Beu 1986, Bandel et al. 1994, Riedel 1995.

Remarks: The larvae of personids were comparatively rare in the plankton of the Red Sea. The larval shells cannot be confused with those of any other gastropod family, although a peculiar veliger has been described in literature (Dawydoff 1940), bearing similar carina-like periostracal sculptures. The pallial appendage, which is used to secrete, form and fix the additional periostracum, is described in detail by Bandel, Riedel and Tiemann (1994). This anatomical feature is unique among gastropods and occurs only in genera of the three cassoid families. The pallial tentacle is regressed before the velum is lost and metamorphosis begins (see also Ranellidae and Cassidae).

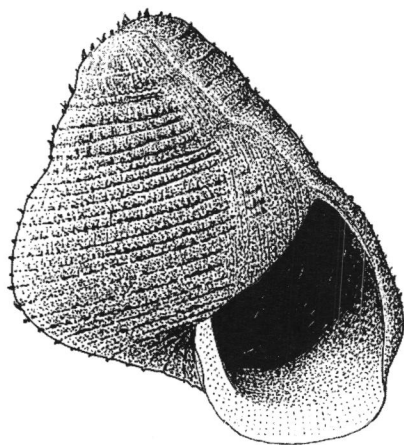


Fig. 16. The veliger shell of ?*Gyrineum* sp. is ornamented with rows of periostracal tines. Height $\approx$ 1.55 mm.

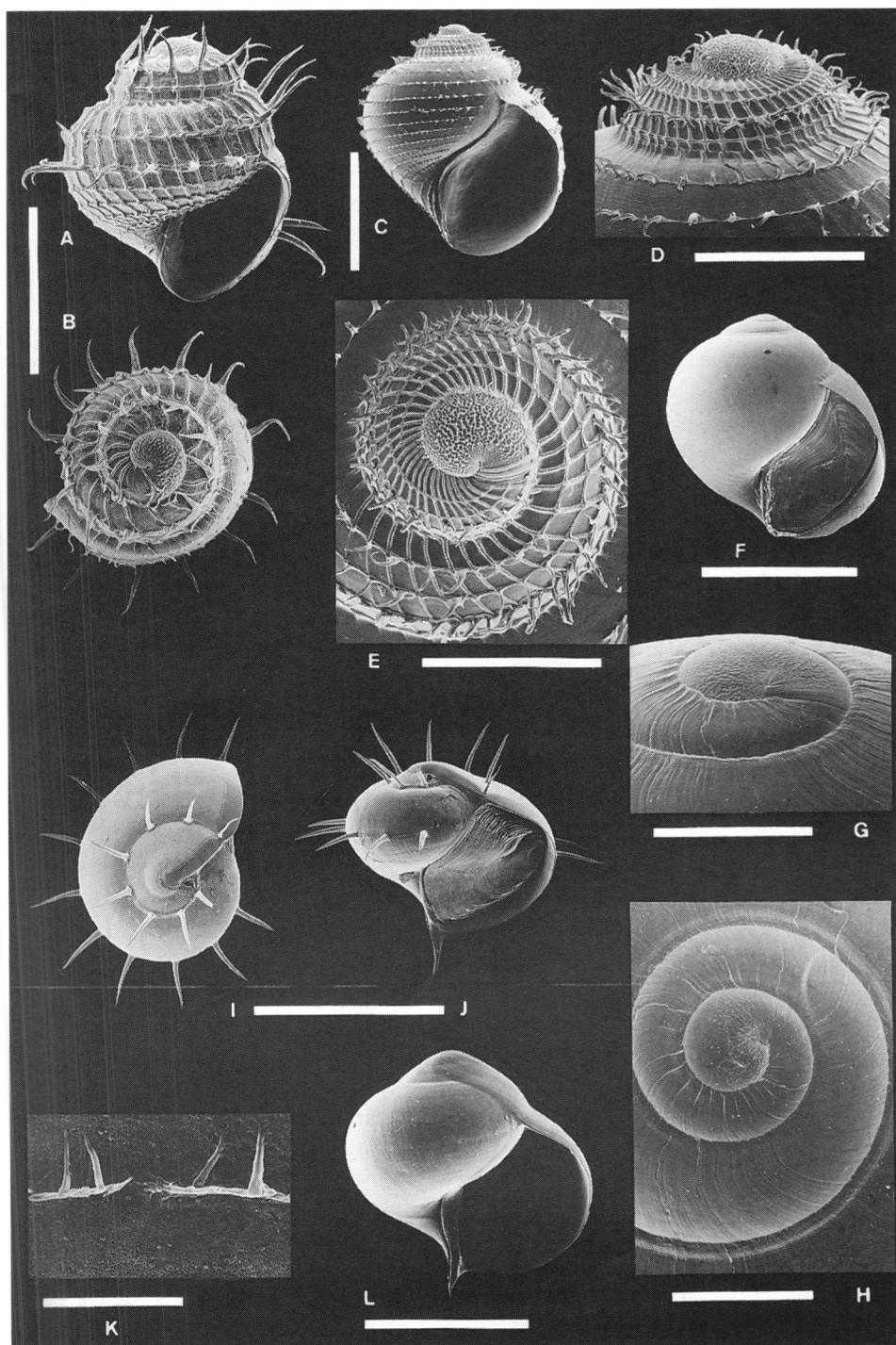
Ranellidae

Fig. 16, Fig. 17A-E

Generalized description: The ranellid larvae could be observed to swim with a quadrilobate velum. The velar lobes may be extended to more than three times the height of the conch. The stomach of a *Cymatium* larva revealed zooplankton (Foraminifera, Radiolaria, Tintinnina) as well as phytoplankton. Beside *Cymatium* Röding, 1798 (Cymatiinae, see Bandel et al. 1994) the ranellid larvae could be attributed to the genera *Bursa* Röding, 1798 or *Tutufa* Jousseaume, 1881 (both Bursinae, Fig. 17A-E) – each with several species – and to a ranelline (Fig. 16) related to *Gyrineum* Link, 1807 (see remarks).

The larvae of the Ranellidae can be distinguished quite well at the subfamily level by the mode of periostracum secretion. Bursinae form and fix periostracal spines of interspecifically varying length, the “normal” periostracum is not thickened by additional layers. The conchs are calcified during their whole post-embryonic ontogeny.

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Fig. 17. A-B: Bursine veliger shell with periostracal spines. Intermediate stage. Scale bar $\approx$ 0.5 mm. C: Fully grown veliger shell of a bursine species. Scale bar $\approx$ 1 mm. D: Ditto. Magnification of apical portion. Scale bar $\approx$ 0.5 mm. E: Ditto. The embryonic shell is clearly demarcated. The larval pattern of rectangles is confined to one and a half whorls. Scale bar $\approx$ 0.5 mm. F: Veliger shell, which probably can be attributed to *Casmaria*. Scale bar $\approx$ 1.5 mm. G: Ditto. Transition from embryonic to larval shell. Scale bar $\approx$ 0.2 mm. H: Ditto. Apical view. The first larval whorl shows rudiments of axial ribs. Scale bar $\approx$ 0.3 mm. I-J: Intermediate larval stages of *Tonna* sp. show rows of long periostracal spines and thick additional layers of periostracum, which cover the sculptural pattern of embryonic and early larval shell. Scale bar $\approx$ 2 mm. K: Ditto. Close-up of spiral lirae, which are composed of interconnected tiny spines. Scale bar $\approx$ 0.025 mm. L: In the late larval stage of *Tonna* sp. organic spines have disappeared except for the basal apertural process. Scale bar $\approx$ 2 mm.



In the Cymatiinae spines or sometimes rows of triangular tines are fixed on all whorls, however, after formation of about 1 to 2 larval whorls, the whole conch is pasted with additional periostracal layers. A pallial tentacle and the normal mantle edge dissolve the spines, but behind the "pasting front" new sculptural elements are fixed on all whorls. At this larval stage decalcification of the shell begins. With every new whorl the conchiolin becomes thicker, while the aragonitic layers are very often completely dissolved. The final larval stage usually shows a smooth shell due to the functional change of the pallial tentacle, from secreting periostracal spines or similar sculptures, to secreting periostracal layers which flatten and cover the spines. In contrast, the Ranellinae very often do not smoothen their final larval shell and in most cases do not bear long spines but short tines. However, some taxa of Cymatiinae and Ranellinae can be confused in this respect. Such taxonomic confusion can be limited using shell parameters of height and width. Except for *Charonia* Gistel, 1848 (not found in our Red Sea plankton hauls), which is somewhat intermediate between Ranellinae and Cymatiinae, all known protoconchs of the latter are significantly more conical in outline (based on ratio of height and width, compare Riedel 1995).

The ranellid larval shells have a brownish colour and are commonly set with axial and spiral ridges forming a pattern of rectangles. Total covering of larval whorls with this pattern was found only in some ranelline species and total absence could be observed in certain Ranellinae as well as in Bursinae (most *Bufo-naria* Schumacher, 1817). In evolutionary lineages, reduction of the pattern of rectangles always began on the latest part formed in larval ontogeny (Riedel 1995). Thus phylogenetic remains of the sculptural pattern (as taxonomic aid) must be searched at the transition to the embryonic whorl. In the Cymatiinae maximally one and a half larval whorls are cancellated, but in most species less than one whorl. In the bursine genera *Tutufa* or *Bursa* more than two larval whorls may be set with rectangles and species with less than one cancellated whorl have not been documented (compare Riedel 1995).

In late larval stages of the Cymatiinae, the rectangles of the aragonitic shell are totally covered by additional periostracum and due to progressing decalcification the original sculpture in many species remains only as an internal moulding. In contrast, the bursine larvae can be differentiated with the aid of the pattern of rectangles also in late larval ontogeny.

The sizes of Red Sea larval cymatiines vary (interspecifically) in height from 2 mm to 3 mm (at least four species), those of the Bursinae from 1.8 to 2 mm (at least 3 species). The ranelline shell is 1.55 mm high and 1.3 mm wide across the 3 larval whorls. The Cymatiinae formed 4 to 5 larval whorls, amounting to a maximum diameter of 2 mm, while the Bursinae reach a diameter of 1.6 to 1.7 mm at 2.5 to 3 post-embryonic whorls. The embryonic shells measure 0.20 to 0.32 mm across in bursine species (Fig. 17B, E), which is almost the range of what is known from species of other regions of the world. The initial whorls of

the Cymatiinae have about the same dimensions, however, species with different geographical distribution may have embryonic shells measuring more than 0.4 mm across (Riedel 1995). The ranelline protoconch (Fig. 16) has an embryonic part of 0.39 mm width. The sculpture of the embryonic shell is the same in all Ranellidae (compare Cassidae or Hipponicidae) having a planktonic phase and consists of a network of ridges, which surround grooves ("beaten" or "malleate", see e.g. Fig. 17E). In smaller embryonic shells this pattern is usually more distinct than in larger ones.

The anterior (basal) part of the aperture in most larval conchs of the Cymatiinae is broadly channelled (see Bandel et al. 1994), while this feature is not known from larval Bursinae. Bursine protoconchs show no trace of a posterior siphonal canal, which is characteristic of their teleoconchs. The embryos hatch with a spirally grown operculum, to which in the larval phase material is added more-or-less concentrically, the nucleus usually remaining excentric to the left. The operculae of cymatiine larvae also initially grow in the spiral direction and later increase in size approximately concentric. The nuclear spiral part may be excentric to any side of the operculum and sometimes is formed convexly compared to the flat or slightly concave concentric part.

Complementary literature: Simroth 1895, Lebour 1945, Scheltema 1966, 1971, Laursen 1981, Richter 1984, Bandel et al. 1984, 1994, Beu 1986, Warén & Bouchet 1990, Bandel 1991a, Riedel 1992, 1995.

Remarks: Ranellid larvae were fairly common in the plankton hauls of the Red Sea and cannot be confused with many other taxa. The comparatively large size of larval conchs occurs elsewhere only in the Cassidae and in some neogastropod taxa (see there). Laubierinoidea Warén & Bouchet, 1990, which have also very large protoconchs have not been reported from the Red Sea. Sculptural elements of the periostracum, such as spines, appear to be confined to Cassoidae, and are secondarily reduced in some taxa (see Cassidae). The described ranelline larva may represent the genus *Gyrineum*, possibly the endemic *G. concinnum* (Dunker, 1862), of which, however, the reproductive biology is unknown. Other ranelline genera have not been described from the Red Sea (see Beu 1985, Singer 1990). Bursine larval conchs have been confused with larval Tonninae (e.g. Richter & Thorson 1975), which, however, even in early larval stages can be distinguished with the aid of the embryonic shell, which is significantly larger in most Tonninae (see under Cassidae), or by the pattern of rectangles.

Cassidae

Fig. 17F-L

Generalized description: Larval conchs of *Tonna* Brünnich, 1772 (Tonninae) and probably *Casmaria* H. & A. Adams, 1853 (Phaliinae, see remarks) could be identified. The veliger of *Tonna* was observed to swim with four velar lobes of almost four times the length of the conch. The complete larval shell (Fig. 17L) consists

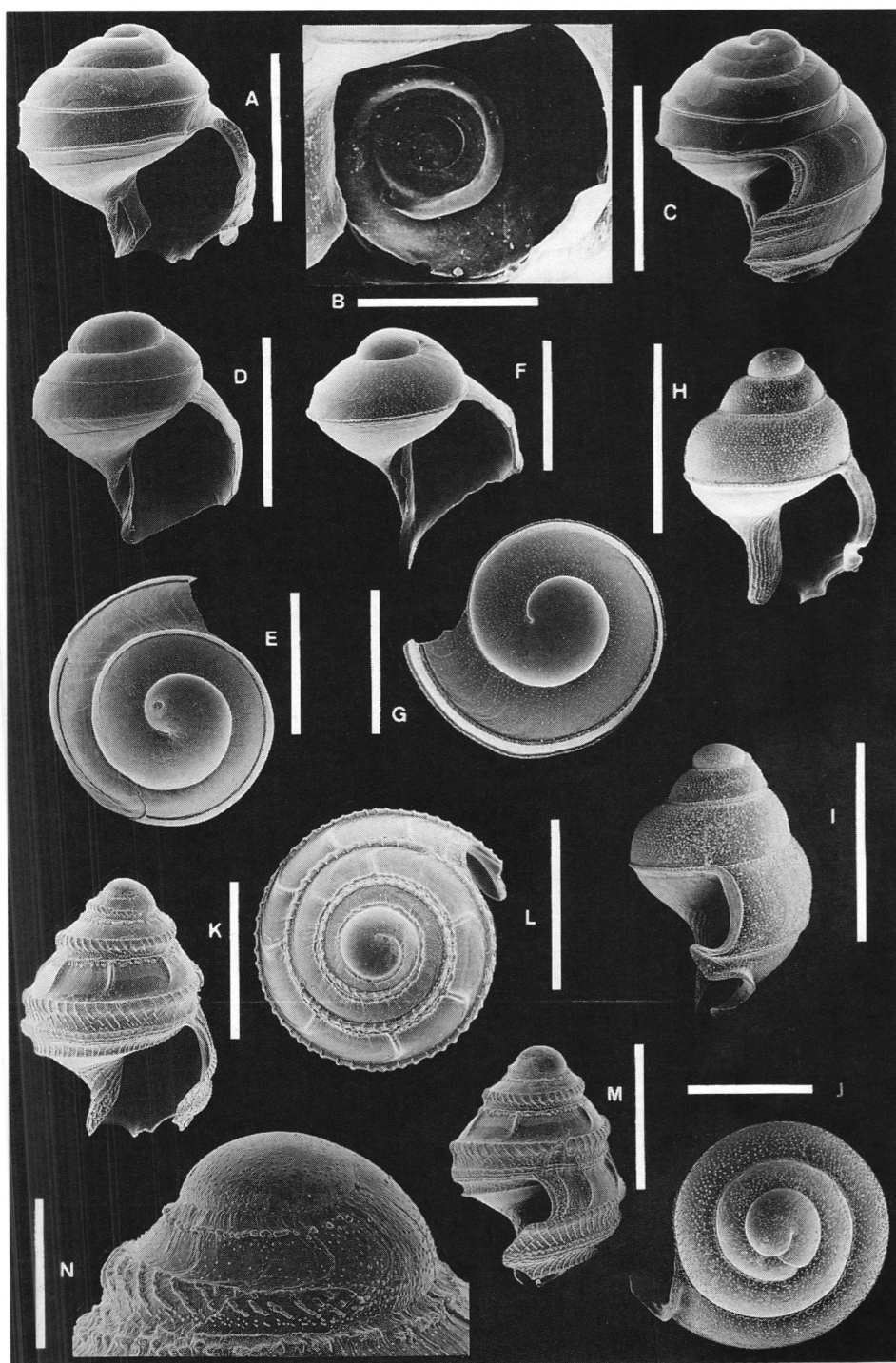
of almost four whorls of which the first one is the embryonic part. The outline of the brownish larval conch is more-or-less globular, measuring 3 mm in width and about 2.8 mm in height. The embryonic shell is "beaten" (compare Fig. 17E) and has a maximum diameter of 0.4 mm. The first 0.8 larval whorls are densely set with axial ribs, which are crossed by two spiral ridges, forming a characteristic pattern of rectangles.

Larvae of *Tonna*, which are not fully grown bear two spiral rows of long periostracal spines (Fig. 17I-J). Several spiral rows of minute (0.01 mm long) periostracal "hairs" are present (Fig. 17K), also interconnecting the spines, which may be more than 0.5 mm long. A prominent spine is formed at the base of the aperture, projecting from the columellar side. This spine is the only one which can still be recognized in late larval ontogeny (Fig. 17L) because the pallial tentacle finally dissolves the other organic spiral sculptures, smoothening the thick periostracum (compare Ranellidae). The aperture of the larval conch is about circular in newly hatched veligers, becoming subovate during larval ontogeny. The operculum (which is lost during metamorphosis) grows spirally in the young larva, however, subsequent concentric growth "shifts" the nucleus from the centre to the right margin (Fig. 17J). The interior of the operculum is characterized by a reinforcing bar.

Living larvae of (?) *Casmaria* have not been observed. The larval conchs, which are attributed to this genus have a yellow-brownish colour. The late larval shell consists of about three larval whorls, amounting to a maximum width of 2.0-2.1 mm. The height varies around 2.1-2.2 mm (Fig. 17F). The embryonic whorl is "beaten" and measures 0.24 mm across. The first larval whorl shows remains of axial ribs on its upper flank, which later transforms to a sutural ridge (Fig. 17H). There are no traces of additional periostracal layers or sculptural elements such as spines, tines, hairs, etc. The aperture of the larval conch is subovate, with a thin regularly curved outer lip and a thickened inner lip, which is concave at its upper portion and nearly straight at the umbilical region. The operculum has mainly grown concentrically (Fig. 17F), but has a small spiral nucleus, which lies excentric to the lower right.

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Fig. 18. A: Veliger shell of a nassariine species; late stage. Scale bar $\cong$ 0.5 mm. B: Ditto. Magnification of the characteristic operculum. Scale bar $\cong$ 0.1 mm. C: Ditto. Scale bar $\cong$ 0.5 mm. D: Same nassariine species but intermediate larval stage. Scale bar $\cong$ 0.5 mm. E: Ditto. Scale bar $\cong$ 0.4 mm. F: Early larval stage of another nassariine species. Scale bar $\cong$ 0.3 mm. G: Ditto. The embryonic shell exhibits most clearly interspecific differences (compare with E). Scale bar $\cong$ 0.3 mm. H-I: Muricid veliger shell related to *Rapana*. Scale bars $\cong$ 1 mm. J: Ditto. Scale bar $\cong$ 0.5 mm. K: Veliger shell of the turrid *Carinapex* sp. Scale bar $\cong$ 0.5 mm. L: Ditto. The apical view exhibits the development of axial ribs. Scale bar $\cong$ 0.4 mm. M: Ditto. The outer lip shows a beak and sinusigeral notches. Scale bar $\cong$ 0.5 mm. N: Ditto. Close-up of transition from embryonic to larval shell. Scale bar $\cong$ 0.1 mm.



Complementary literature: Simroth 1895, Thorson 1940, Lebour 1945, Turner 1948, Ostergaard 1950, Kilius 1962, Bandel 1975, 1976b, 1991a, Laursen 1981, Marshall 1992, Bandel et al. 1994, Riedel 1995.

Remarks: Larval conchs of *Tonna* were fairly common in the plankton hauls, whereas larvae of (?) *Casmaria* were comparatively rare. The species of *Tonna*, which is described and figured here does not represent *T. galea* (Linné, 1758) (compare Laursen 1981) in which the embryonic and also the larval shell are significantly larger (which also accounts for *Malea pomum* (Linné, 1758)), but may be attributed to *T. olearia* (Linné, 1758) or *T. perdix* (Linné, 1758). Gohar and Eisawy (1967) described the embryonic shell of *T. olearia*, which has a size (0.4 mm across) comparable to the figured specimen. The attribution of the second cassid larva to *Casmaria* is vague and is only based on the knowledge that protoconchs of e.g. *Semicassis* are larger in the known cases, and Barnard (1963) described *Casmaria ponderosa* (Gmelin, 1791) with a protoconch diameter equal to the larval conch, which is figured here.

Buccinidae

Fig. 18A-G

Generalized description: Larvae of nassariine species were observed shortly before and during metamorphosis. The velum is quadrilobate, each lobus having about the length of the shell. The foot of the pediveliger is comparatively small (but large in the adult). The larval heart had ceased to work prior to metamorphosis. Gill and osphradium are well developed and inhalant water is channelled by a short siphon. During final metamorphosis the velum is desintegrated and calcification of the shell increases rapidly.

The shell of the most frequent larva is composed of one embryonic and two larval whorls, which have a height of 0.72 mm and a maximum diameter of about 0.77 mm (Fig. 18A). The embryonic shell measures 0.25 mm across, has no ornamentation and its aperture shows already a prominent beak. The larval whorls are set with numerous minute tubercles and are sculptured by three spiral ridges. The ridges have a brown colour while the remaining shell is whitish to transparent. One ridge precedes the suture, begins to form right after hatching, and divides off upper and lower flank of the whorls. A second spiral ridge conditions a slight angulation of the upper flank and begins in short distance to the transition between embryonic and first larval whorl (Fig. 18E). The third ridge is formed just below the sutural ridge and is introduced on the second half of the first larval whorl. The larval conch is (pseud-) umbilicate. The aperture is of the sinusigera-type, the beak showing additional spiral ornamentation (Fig. 18C). The operculum is characterized by its projecting spiral ridge. The nucleus lies excentric to the left (Fig. 18B).

Complementary literature: Lebour 1930, 1937, Thiriôt-Quévèreux 1969, 1980a, Bandel 1975, Richter & Thorson 1975.

Remarks: The described larva was common in the plankton hauls and can probably be assigned to *Nassarius* Duméril, 1806. A very similar protoconch was found e.g. in *Nassarius coronatus* (Bruguière, 1789) (off Queensland, Australia). Features of the larval shell appear to be insufficient to differentiate at the species level. The shell of a young veliger of *Nassarius* is figured here (Fig. 18F, G), which can be distinguished from the described protoconch only with the aid of the embryonic shell (see conclusions).

Muricidae

Fig. 18H-J, Fig. 19

Generalized description: The muricid larval shells are probably best placed with the Rapaninae Gray, 1853 sensu Kool (1993).

One larval species, which is related to *Rapana* Schumacher, 1817 had secreted one embryonic and two and a quarter larval whorls (Fig. 18J). The embryonic shell measures about 0.32 mm across, is ornamented with minute tubercles and its aperture is clearly demarcated. The larval whorls are well rounded, show a sutural ridge and are also sculptured by tubercles, larger than those of the embryonic whorl. The larval aperture is of the sinusigera-type (Fig. 18I). The protoconch has a total height of about 1.35 mm and a maximum diameter around 1 mm.

A second larval type is related to *Drupa* Röding, 1798 (see remarks, Fig. 19). The protoconch is composed of one embryonic whorl measuring 0.18 mm across and four larval whorls, altogether having a height of 1.6 mm and a maximum diameter of 1.1 mm. The embryonic shell is densely covered with arago-

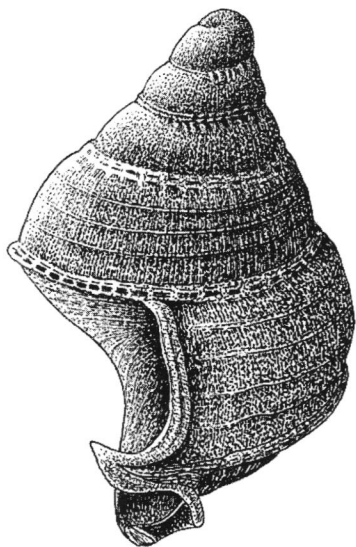


Fig. 19. Rapanine sinusigera shell, which may be assigned to *Drupa*. Height $\approx$ 1.6 mm.

nitic tubercles. Tubercles of smaller size are spread over the larval whorls. Three suprasutural lirae interconnect short axial plicae, composing a characteristic spiral chord. Additional periostracal lirae (1-4) are formed on the upper flank of the final two whorls (Fig. 19). The larval aperture is of the sinusigera-type. A second species in this relation shows a very similar larval shell. Shape, size and ornamentation are almost identical, except for the periostracal lirae, which are missing, and there are only three and a quarter larval whorls (see remarks).

Complementary literature: Thorson 1940, Radwin & d'Attilio 1976, Kay 1979, Scheltema 1979, Kool 1993.

Remarks: The protoconch type, which is seen here in the relation of *Rapana*, has been figured by Scheltema (1979) and was assigned to *Drupa* Röding, 1798. We follow here Kool (1993), whose investigations coincide with personal observations. The second type of larval shell, which is placed here with *Drupa* may also be connected to *Morula* Schumacher, 1817; *Nassa* Röding, 1798 or *Pinaxia* H. & A. Adams, 1853 (not described from the Red Sea), which according to Kool (1993) all include species with very similar protoconchs (compare Kay 1979). The minute interspecific or intergeneric differences are also evidenced by our material. The characteristic common ornamentation, the spiral chord, is described by Kool (1993) to be subsutural. It is, however, formed above the suture as can be seen from the veliger shell but not from the protoconch of a juvenile.

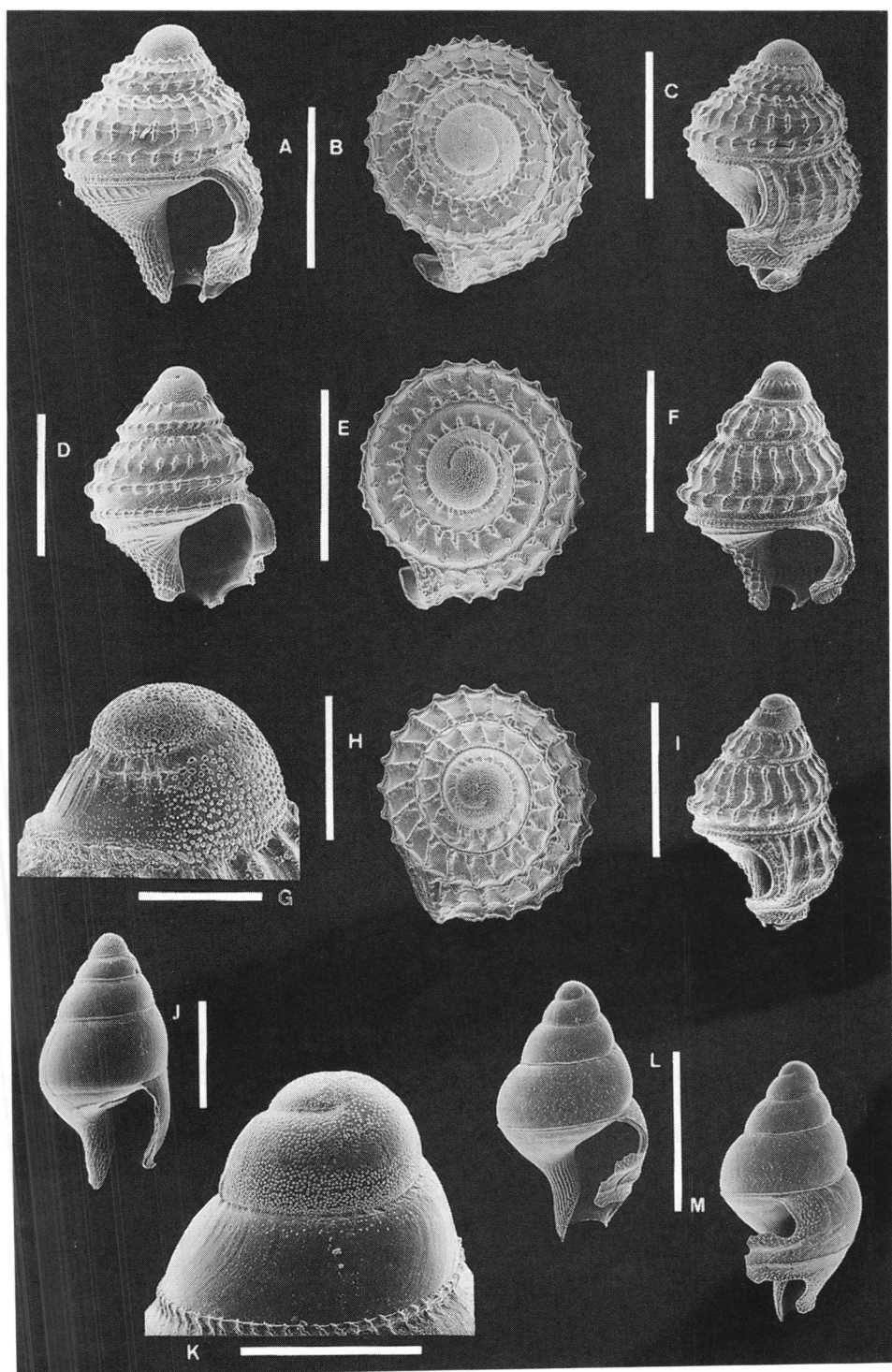
Coralliophilidae

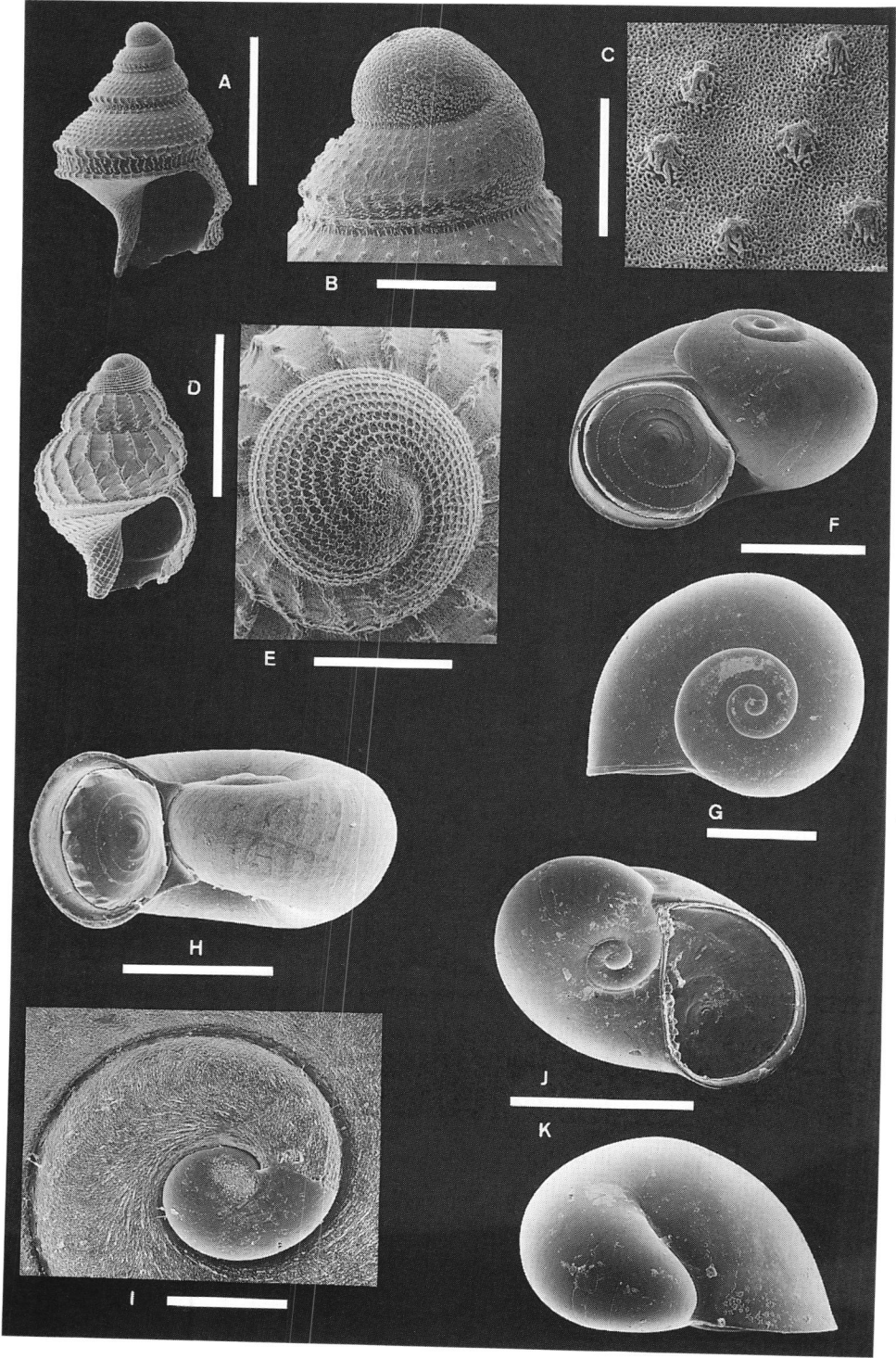
Fig. 20A-I

Generalized description: Larval shells of at least three species could be recognized. The protoconch of species 1 (Fig. 20A-C) is composed of one embryonic shell measuring 0.25 mm across and two and a quarter larval whorls amounting to a height of 0.85 mm. The maximum diameter is 0.75 mm. The protoconch of species 2 (Fig. 20D-E) has the same total dimensions. The embryonic shell with a diameter of 0.23 mm is a little bit smaller, however, two and a half larval whorls had been formed, allowing a more significant distinction. The proto-

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Fig. 20. A-C: Veliger shell of a coralliophilid (sp. 1) in frontal, apical and lateral view. Scale bars $\cong$ 0.5 mm. D-E: The veliger shell of a coralliophilid species (sp. 2) differs only in detail from species in A-C and G-I. Scale bars $\cong$ 0.5 mm. F: Larval conch of another coralliophilid species (sp. 3). Scale bar $\cong$ 0.5 mm. G: Close-up of F – transition from embryonic to larval shell. Scale bar $\cong$ 0.1 mm. H: Apical view of F. Scale bar $\cong$ 0.4 mm. I: Lateral view of F. Scale bar $\cong$ 0.5 mm. J: Veliger shell of columbellid relation. The apertural beak is broken. Scale bar $\cong$ 0.5 mm. K: Ditto. Magnification of early whorls to show differences in ornamentation between embryonic and larval shell. Scale bar $\cong$ 0.2 mm. L-M: The veliger shell of a second columbellid species exhibits a prominent apertural beak. Scale bar $\cong$ 0.5 mm.





ture (Robertson 1970 but see Robertson 1974). The protoconch of *P. radiata* (Röding, 1798) appears to be identical with the larval conch, which is described here. The second species, *P. oxytropis* A. Adams, 1855, has a larger protoconch.

Veligers of *Pseudomalaxis* were extremely rare in the plankton samples. Specific attribution is not yet possible. The larval conch with its almost planispiral coiling and circular aperture resembles that of Caecidae (not found by us in the Red Sea plankton). These, however, can be distinguished by their smaller size (less than 0.5 mm) and by the malleate sculpture of the embryonic shell. Moreover, hyperstrophy has not been described for caecid species.

?Pyramidellidae

Fig. 24J-K

Generalized description: No observations were made on the living larva, which had secreted the larval shell that is introduced here. The protoconch is composed of one embryonic and two larval whorls with a maximum diameter of 0.9 mm and a height of 0.6 mm. The embryonic shell measures 0.11 mm across and shows a more-or-less malleate sculpture at least on its initial portion. The two larval whorls are smooth except for growth lines. The coiling is sinistral in the first two and a half whorls and, with a change of the growth direction for about ninety degrees, becomes dextral in the terminal half whorl. Thus heterostrophy is conducted already prior to metamorphosis. The larval aperture is comparatively large and crescent- to teardrop-shaped. The operculum is multispiral with the nucleus left and below the centre, coils sinistrally, and seals the aperture perfectly (Fig. 24J).

Complementary literature: Lebour 1937, Babio & Thiriot-Quiévreux 1975, LaFollette 1979, Graham 1988.

Remarks: Actually it is not even clear if the larval conch can be attributed to the pyramidelloids or is better placed with cephalaspideans. The knowledge of larval development in these groups is extremely sparse. Pyramidelloidean or ceph-

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Fig. 24. A: The larval conch of the drilline gastropod *Ceritoturris* sp. is characteristically bicarinate. Scale bar $\approx$ 0.5 mm. B: Ditto. Close-up of transition from embryonic to larval shell. Scale bar $\approx$ 0.1 mm. C: Ditto. Magnification of the sculptural pattern formed on the upper flank of larval whorls. Scale bar $\approx$ 0.025 mm. D: Daphnelline veliger conch related to *Raphitoma*. Scale bar $\approx$ 0.5 mm. E: Ditto. Close-up of the embryonic shell showing the characteristic sculptural elements. Scale bar $\approx$ 0.1 mm. F-G: Architectonicids secrete hyperstrophic larval shells. The veliger shell of *Philippia* ?*radiata* lacks significant ornamentation but its shape is characteristic. Scale bars $\approx$ 0.5 mm. H: The veliger shell of the architectonicid *Pseudomalaxis* sp. is almost planispiral. Scale bar $\approx$ 0.5 mm. I: Ditto. The magnification of the initial whorls exhibits that the umbilical side of the embryonic shell represents the apex and thus clearly demonstrates hyperstrophy of larval whorls. Scale bar $\approx$ 0.1 mm. J-K: In this ?pyramidellid the change from sinistral to dextral coiling was conducted during larval life and not during metamorphosis. Scale bar $\approx$ 0.5 mm.

alaspidean protoconchs are usually composed of a one-whorled embryonic shell and one to two larval whorls, which in analogy to caenogastropods presumably reflect a planktonic larval phase. It is thus somewhat strange that plenty of protoconchs have been described in the literature from the apices of the benthic juveniles (e.g. Babio & Thiriot-Quiévreux 1975), but corresponding veligers usually do not occur in studies on pelagic gastropod larvae (see conclusions).

CONCLUSIONS

Taxonomic problems with larvae have been briefly discussed under Remarks. Identifications at the specific level are the exception. Although the correct specific or generic assignment would be plausible in several cases, we have been reticent in doing so. Intraspecific variety of protoconch features is usually very low. Thus it appears to be important to describe minutest details to get an idea of the number of different species producing planktonic larvae. Some veligers, e.g. Nassariinae could be differentiated only with the aid of the embryonic shell and not using larval shell characters. Especially in early veliger stages, size and ornamentation of the nuclear whorl may represent the only characters to trace systematics. It must, however, be emphasized that mainly fully grown larvae were found in the plankton hauls, which may indicate that most larvae reach their maximum size comparatively soon, independent of the maximum duration of their stay in the plankton. In *Litiopa* the protoconchs of two species correspond in detail. It must be presumed that this may be the case also in other taxa and thus veligers of some more gastropod species occur in the plankton as was possible to recognize. Among the Heterostropha only larvae of *Philippia* sp. (Architectonicidae) were frequently found and those of the very diversified pyramidelloideans or cephalaspideans were strikingly rare. It can be presumed that the larvae which have been described here stay in the plankton for at least several weeks. In contrast, the veligers of most pyramidelloideans and cephalaspideans probably metamorphose already after few to several days and thus remain in coastal waters.

We are well aware that plankton samples, which were taken during a few weeks cruise cannot be representative of the diversity of gastropods with planktonic development that live in the Red Sea. This is e.g. evidenced by the absence of the veliger of *Charonia tritonis* (Linné, 1758), which is known to occur in the Red Sea (several more examples could be given). The number of at least 75 different species, which could be recognized to produce planktonic veligers, however, hints at a well diversified fauna. Richter and Thorson (1975) evaluated 915 plankton hauls, taken over four years (all seasons) in the Gulf of Naples and recognized "only" 68 planktonic gastropod larvae.

The faunal exchange between the Red Sea and the Mediterranean Sea via migration through the Suez Canal (see e.g. Steinitz 1968, Thorson 1971) appears to be very low among planktonic larvae. The veliger shells described here

do not correspond at the species level with any of the protoconchs figured by Richter and Thorson (1975), except maybe for a species of *Lamellaria* (see remarks on Lamellariidae). Active migration via the Suez Canal by gastropod larvae is unlikely, but veligers may be introduced via ships (ballast water). An increase of faunal exchange can be expected in time, however, there exist only a few species which could tolerate the very different environments of both seas. Probably only the eastern Mediterranean Sea is ecologically suitable for potential gastropod immigrants from the northern Red Sea and vice versa (compare Barash & Danin 1972, 1977).

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