

A special adaptation to planktonic life in larvae of the Cassoidea (= Tonnoidea) (Gastropoda)

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Abstract. Living veligers of the Cassoidea have been observed to use a mantle appendage to form and resorb periostracum. Anatomical and histological examinations of a ranellid (*Cymatium* sp.) larva collected from the Red Sea in 1987 revealed the structure and location of the pallial appendage. The mantle edges of juvenile or adult species of the Cassoidea do not show a comparable specialization. It is demonstrated that cassoid larval conch characters are sufficient to prove the existence of a pallial appendage without anatomical confirmation. A mantle appendage is not known from teleplanic (long-living planktic) veligers of other gastropod superfamilies. In cases where the larval strategies of the latter are known they are totally different. Therefore it is suggested that the adaptation of cassoid larvae to pelagic life is unique among gastropods representing an autapomorphic character of the superfamily.

Introduction

The Cassoidea (= Tonnoidea = Doliacea) probably arose during the Lower Cretaceous and radiated to a few hundred (strictly marine) Recent species, including spectacular gastropods like helmet and trumpet shells (tritons). Many species of this superfamily prey (hunt) on echinoderms (e.g. Lyman 1937, Copland 1966, Eaton 1971, Hughes and Hughes 1971, Bandel 1976, Taylor 1980, Hughes and Hughes 1981, Bandel 1984, Bandel and Wedler 1987, Bentivegna and Toscano 1991), which is unique among gastropods (members of the Eulimidae are known to be parasites on echinoderms). The cassoids have their main distribution in the tropical zone, but there are several species which settle in cool, some (e.g. *Fusitriton* sp., Cossmann 1903) even in cold (subpolar) waters (e.g. Beu 1978, Somerton 1981). One factor which is connected to the distribution of cassoids is larval strategy. Preadult development is usually dominated by a planktotrophic veliger, but apomorphic conditions like

feeding on nurse eggs or lecithotropic development can be found in nearly all subfamilies of the Cassoidea.

In the present study emphasis was placed on the construction of the larval shell during a planktotrophic phase which is assumed to be unique among gastropods. The conchs of veligers may reach huge sizes which are otherwise found only in some Neogastropoda (Bandel 1982). The largest protoconch (embryonic and larval shell) that could be measured was that of *Tonna allium* (Dillwyn 1817), which has a height of 5.7 mm and a max. diameter of 5.45 mm (Fig. 1). The protoconch of *Cymatium* (*Ranularia*) *sinense* (Reeve 1844) consists of 6.7 whorls, which is the highest number found in the Cassoidea. However, there are several species which come close to this.

The measurements above elucidate why several malacologists described cassoid larvae as adult species (e.g. MacDonald 1855, Adams 1857, Pilsbry 1945). MacDonald (1855) even suggested a new order for pelagic gastropods which were later identified by Fischer (1887: *Dolium* sp.) as larvae of the genus *Tonna* Brünnich, 1772. In his main "plankton-work" Simroth (1895) described pelagic larvae of the genera *Dolium* (= *Tonna*) and *Triton* (used by Simroth for *Cabestana* Röding, 1798; *Charonia* Gistel, 1848 and *Cymatium* Röding, 1798). Sim-

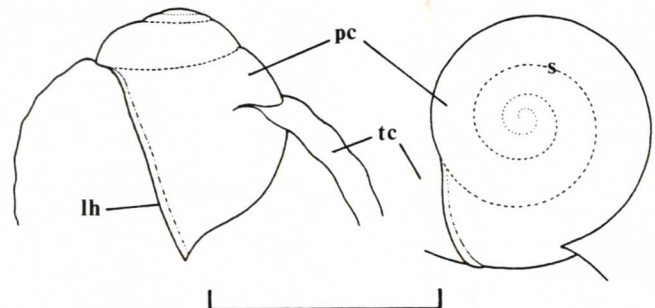


Fig. 1. *Tonna allium*. Conch of a juvenile *T. allium* with its huge larval (and embryonic) part. The periostracum covers the suture of the whorls and the sculptural patterns of the protoconch. lh: Larval hook; pc: protoconch; s: suture; tc: teleconch. Scale bar = 5 mm

roth (1895) was the first who recognized what he called "Schalenlappen" (shell flap). This larval appendage of the mantle was involved in the construction of the shells of the veligers, i.e., Simroth (1895), connected the apical chambers of the calcareous shell with it. D'Asaro (1969) discovered the larval pallial appendage in *Distorsio clathrata* (Lamarck 1816) and he also observed that this appendage is used by the veliger to build periostracal chambers. Finally, Bandel (1991, and the present paper) observed the functional morphology of the pallial appendage in species of *Tonna*, *Cymatium* and *Distorsio* Röding, 1798.

Richter (1984) gave an interpretation of shell construction in larvae of *Cymatium* sp., but mainly repeated the results of Simroth (1895), e.g. that the calcareous shell is reduced during the larval phase while additional periostracal layers are secreted and the protoconch finally consists of conchyolin only (see Simroth 1895, p. 150). Laursen (1981) provided evidence that early ontogenetic larvae have comparably larger periostracal spines than older ones of the same species. This had already been mentioned by Simroth (1895, p. 55), whose publication also contained the first hint that veligers of the Cassoidea travel much longer than previously assumed [e.g. Clench and Turner 1957: "... perhaps up to four weeks ..." (!)]. This was taken up by Scheltema (e.g. 1966, 1971, 1972, 1986), who stated that the larvae stay in the plankton for ca. 3 mo, maybe even up to 1 yr.

We provide here the first larval anatomy of *Cymatium* sp. with the intention of filling some gaps of knowledge (i.e., concerning the location and histology of the larval pallial appendage) or of correcting misinterpretations which are brought up in our introduction and are discussed below. Some larval shells are presented and additional data on the biology of cassoid veligers are given to demonstrate a special type of adaptation to pelagic life.

Materials and methods

During the 1987 (section 5/5) Red Sea cruise of the R. V. "Meteor" larvae of the Cassoidea were caught at several stations. Samples were taken with various plankton gears in water layers from 0 to 960 m depth: mooney (0.333 mm), lock nets (0.1 to 0.3 mm), and a neuston slide (0.3 mm). More information about stations, etc., can be found in the report (Weikert et al. 1988) of the "Meteor" expedition.

Larvae of different genera could be kept alive for a few days each and observed with the aid of a light microscope. It was of course not possible to observe the function of the mantle appendage continuously. Therefore the duration of processes remained unclear. However, the observation of different stages (some of which were photographed) of the functioning pallial tentacle in numerous veligers of each species (or genus) was sufficient to reconstruct most of the processes (see below).

The material was fixed in ethanol or buffered formalin. The conch of a larva of the genus *Cymatium* was removed and the soft body dehydrated using isopropanol. The specimen was then treated with benzylbenzoate, embedded in paraplast, serially sectioned (7 µm) and stained with Helioechtrubin BBL/Acidgreen 5/Acidorange 10 after Halmi (Adam and Czihak 1964). The sections were investigated and photographed with the aid of a light microscope.

Some larval specimens of every Cassoidea genus which was found in the plankton (and also of juvenile shells from other parts of the world used here for protoconch measurements only) were

cleaned, dried, mounted on stubs, coated with gold and then photographed using a SEM (scanning electron microscope) (CamScan). Two larval conchs of the genus *Cymatium* were completely decalcified (acetic acid) and examined with X-rays (Siemens).

Voucher material is deposited at the "Zoologisches Institut und Museum" of the University of Hamburg, cat. no. M 1554.

Results

The living larvae

The gross functional morphology of the pallial appendage from larvae of *Tonna* sp., *Cymatium* sp. (Fig. 2, Fig. 3: 1) and *Distorsio* sp. (Fig. 3: 2) could be observed. Secretions from the glands of the appendage emerge as spines (Fig. 3: 3), tines, etc., or as simple periostracal layers. The latter cover the calcareous shell or its regular, more or less thin, periostracum. An additional periostracum is secreted beginning during a certain larval stage. In *Tonna* sp. and *Cymatium* sp. the appendage of the mantle can be stretched to reach all parts of the larval conch and usually secretes the additional organic shell layers simultaneous with the "regular" periostracum secretions of the mantle edge surrounding the aperture of the conch (Fig. 3: 4, 5). With the exception of the primary shell (see Bandel 1982) gastropods build their conchs in more or less regular steps, as can also be seen from the growth lines. The pallial tentacle of *Tonna* sp. or *Cymatium* sp. larvae also functions during intervals of normal shell construction and can secrete and fix periostracal sculptural elements on any whorl of the conch. The spines, etc., usually have to be renewed because they are partly dissolved by the appendage itself when it pastes the whorls again with periostracal layers. In late larval stages the mantle appendage stops forming sculptural elements other than layers. A fully grown veliger can be recognized by a low varix at the aperture of the conch. In this ontogenetic phase the veligers were able to crawl

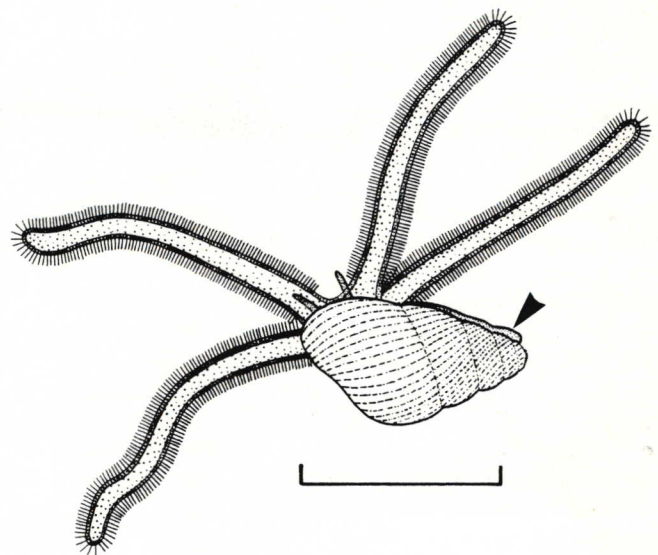


Fig. 2. *Cymatium* sp. A late larval stage of *Cymatium* sp. pasting the whole conch with periostracum layers using the pallial tentacle (arrow). Scale bar = 3 mm

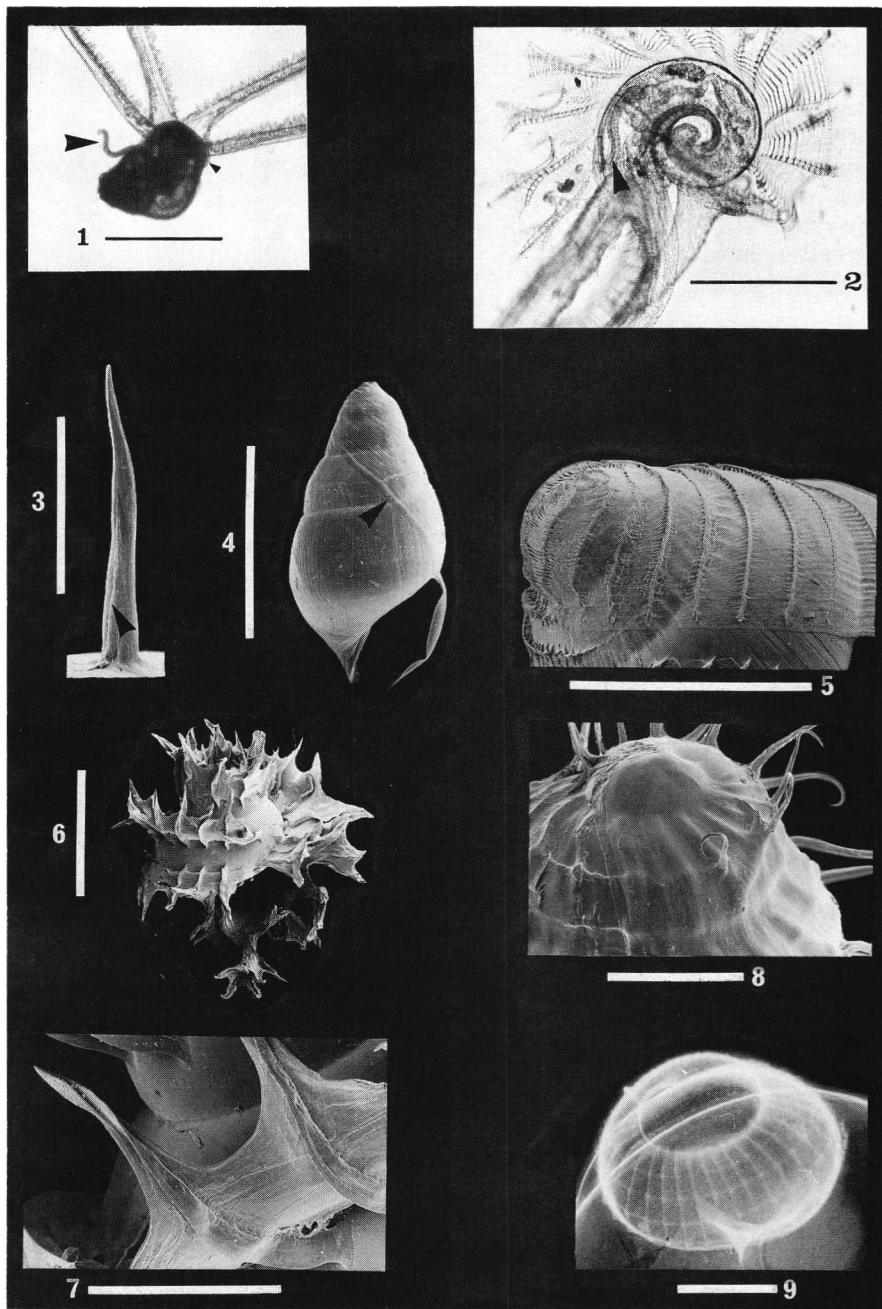


Fig. 3. *Cymatium* sp. and *Distorsio* sp.
 1: A swimming veliger of *Cymatium* sp. detaching its mantle appendage (large arrow) from the apex of the conch. Mantle edge visible as a rim (small arrow) surrounding the aperture of the larval shell. Scale bar = 2 mm. 2: Living *Distorsio* sp. larva revealing mantle appendage (arrow). Scale bar = 1 mm. 3: Periostracal spine on conch of a *Cymatium* sp. larva. The mantle appendage formed the spine by rolling a flat piece of periostracum into a hollow tube. The seam of adhesion is visible (arrow). Scale bar = 100 μ m. 4: Larval conch of the same species (not determined/determinable) of *Cymatium* sp. as was used for the section-cutting. Shell is purely (or nearly so) organic. Growth lines cross (arrow), which means they have a different origin. Diagonal lines represent growth increments of the pallial tentacle which cover the axial lines that have resulted from the secretions of the mantle edge. Scale bar = 2 mm. 5: Another ranellid protoconch demonstrating that the pallial tentacle covers the whole shell with periostracum simultaneous with the construction of a new whorl. Scale bar = 1 mm. 6: Larval conch of *Distorsio* sp. from the Red Sea. Scale bar = 1 mm. 7: Same specimen as in 6, enlargement of the periostracal sculpture. Scale bar = 0.25 mm. 8: Apical region of the larval conch of *Cymatium* sp. where the rectangular sculptural pattern of the calcareous shell is partly covered with thick periostracum secreted by the pallial tentacle. Scale bar = 0.2 mm. 9: Radiograph of the apical region of a purely organic conch of the same *Cymatium* sp. and larval stage as in 4, demonstrating that the pattern of the calcareous shell is preserved as a negative mould. Scale bar = 0.2 mm

rapidly on the bottom of the glass vessel. The mantle appendage is reabsorbed before the velum is lost and the larvae metamorphose.

In *Distorsio* sp. the pallial tentacle produces keel-like periostracal sculptures (see Fig. 3: 2, 6, 7) simultaneous with the production of new "apertural" shell by the mantle edge. The latter reabsorbs the sculptural elements when a new whorl meets the preceding one.

Further information on this complex was gained from prepreserved material only.

Anatomy and histology

The larval conch of a specimen of *Cymatium* sp. (Fig. 3: 4) which was later serially sectioned is about 3 mm high and

consists of five whorls (including the embryonic whorl). This comparably high number of whorls and the flexibility of the probably purely organic shell, together with the absence of periostracal sculptures, indicates a larval stage which was not far from metamorphosis.

The external anatomy of the (retracted) soft body does not show specializations except for the pallial appendage which projects from the right mantle edge. The distance between the rim of the aperture and the apex of the larval conch corresponds with the possible length of the pallial tentacle in the living larva. In our specimen this distance amounts to 2 mm, which is eight times longer than the retracted appendage (see below). The visceral mass fills most of the three oldest whorls of the conch. The columnellar muscle is comparably strong and attached to the

middle of the third whorl of the shell. The fourth whorl is fully occupied by the huge quadribobated velum, the organs of the pallial cavity, the anterior parts of the alimentary canal and the head. The tentacles and the eyes at their bases are well developed. The foot is large, filling the last half whorl of the conch, and bears an operculum which is functional. Fig. 4 gives a rough idea of the spatial arrangement of the soft body within the shell, i.e. of the location of the mantle appendage. The cutting edge indicates the orientation of the sections used to reconstruct the internal anatomy of the veliger.

Fig. 6 shows a section (surrounded by enlarged details) where the pallial tentacle is cut along its longest and thickest portion. A strong contraction of the muscle fibres indicates that the mantle appendage is completely (or nearly so) withdrawn. In the two-dimensional drawing the appendage appears to be a trunk. Actually it is a flap which, when retracted, is broader than it is long and which measures max. 250 μm in length, max. 280 μm in breadth and is max. 100 μm thick.

The mantle contains several glandular regions of which four have a very similar histology. These glands (designated A–A₃) are located in the right terminal portion and in the outer part of the base of the pallial tentacle as well as the place in this section where the left mantle edge was cut (see Fig. 6). In zones A–A₃ the epidermis consists of cylindrical cells with basal oval-shaped nuclei. The lumen is filled with a homogeneous eosinophilous secretion. The basal membrane of the cells is well developed and contacts a collagenous connective tissue which is interwoven with muscle fibres. Apically, the glandular cells show a rim of microvilli which has reacted to staining with Acidgreen 5. The surface of the glands is covered extensively by secretions which partly contain granula masses. Gland A is about two times larger (in the cut examined) than glands A₁–A₃ (see "Discussion and conclusions").

The terminal thick part of the mantle flap reveals two more different glandular zones apart from gland A (see also Fig. 5). Type B (Fig. 6) is located subepidermally and is also present in the left mantle edge where it is 1.5 times smaller (in the cut examined). The epidermis consists of a single layer of flattened cells (with flattened nuclei) which is covered by a thin acidophilous lamination. Gland B is composed of eosinophilous cells which appear homogeneous in the basal and distinctly granulated in the apical part. Eosinophilous vesicles can be found on the surface and in invaginations of the epidermis.

On top of B and A a comparably small glandular zone (D) is part of the terminal edge (epidermis) of the mantle appendage (Figs. 5, 6). The few compact glandular cells are filled with an eosinophilous secretion which forces the nuclei into the shape of a small, more or less basal, calotte.

Opposite zone A₁, an epithelium (C) which is characterized by two types of cells is pronounced (see Fig. 6). The surface of the epithelium is formed by supporting cells with small, apically lying nuclei (more or less triangular when cut). The basal part consists of large acidophilous glandular cells filled with large vesicles which have an intensive green colour. The flattened nu-

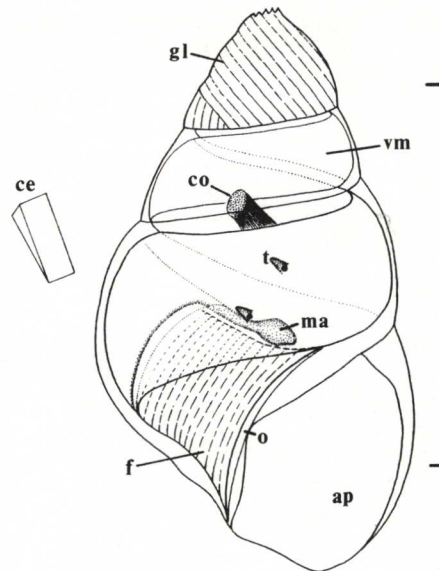


Fig. 4. *Cymatium* sp. Larval conch of the same species of *Cymatium* as used for the section-cutting. Except for the apex where the growth lines (gl) of the shell are visible, conch is drawn transparently to give a rough idea of the spatial arrangement of the soft body. The cutting edge (ce) indicates the orientation of the sections. ap: aperture; co: columnellar muscle; f: foot; ma: mantle appendage; o: operculum; t: head tentacles; vm: visceral mass. Scale bar = 2 mm

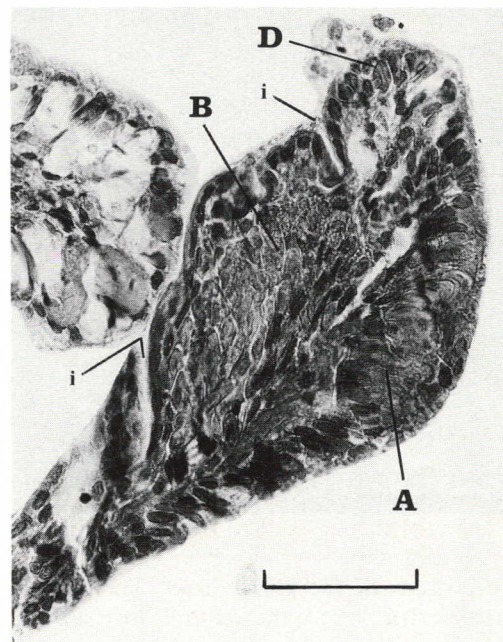


Fig. 5. *Cymatium* sp. Section of the mantle appendage photographed with the aid of a light microscope. A, B, D denote glandular zones. i: Invagination. For further information see Fig. 6. Scale bar = 50 μm

clei lie basal and project into the lumen of empty cells only.

Apart from the mantle, of course, several other organs (e.g. the foot) also contain different types of glands. Some of them appear in Fig. 6(g) together with other anatomical structures which are not explained but simply designated.

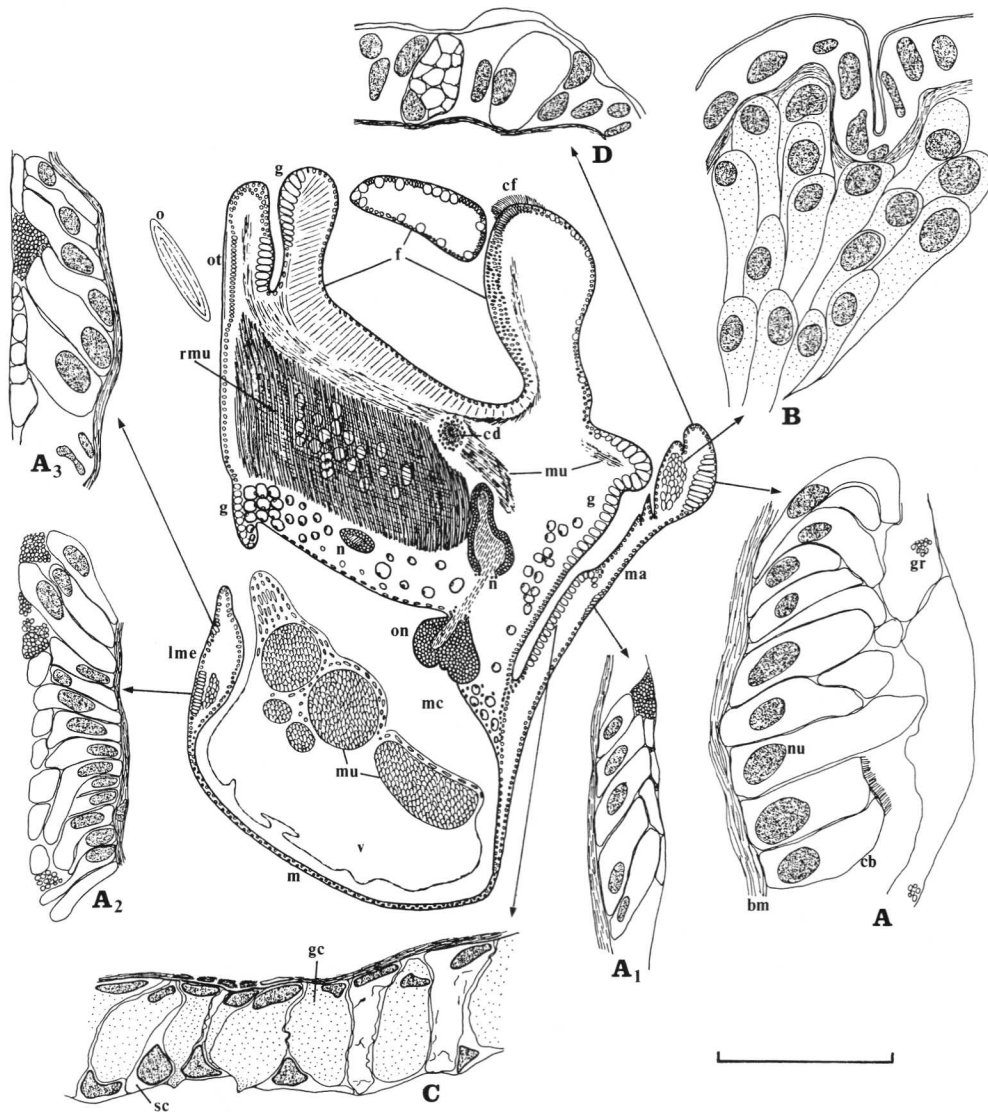


Fig. 6. *Cymatium* sp. Section of *Cymatium* sp. larva with the pallial tentacle (ma) is depicted at its longest and thickest part, surrounded by enlargements (12 times) of the glandular zones A–A₃, B, C, D, which are briefly described in “Results – Anatomy and histology”. bm: Basal membrane; cb: cell boundary; cd: ciliated ductus of the pedal gland; cf: ciliation of the foot; f: foot; g: glandular regions other than described; gc: glandular cell; gr: granulae; lme: left mantle edge; m: mantle; mc: mantle cavity; mu: muscle; n: nerve; nu: nucleus; o: operculum; on: osphradial nerve; ot: operculum connecting tissue; rmu: retractor muscle; sc: supporting cell; v: velum (not drawn). Scale bar for the whole section = 0.3 mm, for A to D = 25 μ m

The sections of the visceral mass revealed that the stomach of the larva contains Foraminifera, Radiolaria and phytoplankton.

The pallial appendage is not present in adults, as was determined by the examination of some representatives of the three families of the Cassoidea. From the Ranellidae (to which the sectioned larva also belongs) *Argobuccinum pustulosum tumidum* (Dunker 1862), *Cabestana spengleri* (Perry 1811), *Charonia lampas rubicunda* (Perry 1811), *Tutufa rubeta* (Linné 1758), from the Cassidae *Cassia cornuta* (Linné 1758), *Phalium labiatum* (Perry 1811) and from the Personidae *Distorsio* sp. were examined.

The conchs

The mode of formation of the periostracal sculptures found on cassoid protoconchs depends on ontogenetic as well as on phylogenetic differences (as was mentioned in the “Introduction”). We refrain from listing specific characters, referring instead to the corresponding literature (e.g. Simroth 1895, Lebour 1945, Pilkington 1976,

Laursen 1981, Warén and Bouchet 1990), but point out the different strategies. Among the Cassoidea only the larvae of the Personidae link periostracal elements to sail-like sculptures (Fig. 3: 2, 6, 7); however, the layers covering the calcareous shell stay comparably thin. The latter can also be found in the Bursinae (Ranellidae = Cymatiidae) where even in late larval stages the sculptural pattern of the aragonitic shell (or its original periostracal matrix as the case may be) is clearly visible. This pattern usually more or less vanishes (Fig. 3: 8) during the larval ontogeny of most other Ranellidae or Cassidae covered by periostracal layers. In several cases the thickness of the organic shell can be directly correlated to the number of whorls of the larval conch because every newly constructed whorl means an additional pasting with periostracum of all the older whorls (see “Introduction”). A thick periostracum “allows” a larva to resorb parts (layers) or sometimes all of the calcareous shell (compare Simroth 1895, Richter 1984). A radiograph (Fig. 3: 9) of a purely organic larval conch demonstrates that the internal shell bears a negative of the former calcareous rectangular sculpture (compare Richter 1984; see “Discussion

and conclusions"). During or shortly after metamorphosis the internal mould is again filled with a calcareous secretion (compare Richter 1984).

In all larval conchs examined for this study the characters of the periostracal sculptures – e.g. vanishing of apical sculptures during late larval stages, additional growth lines on all parts of the external shell or remodelling of spines, etc. – are sufficient to claim the existence of a pallial tentacle independently from anatomical confirmation (see "Discussion and conclusions").

The teleoconchs of the Cassoidea gave no hint of special periostracal sculptures for which a pallial tentacle might be needed.

Discussion and conclusions

The Cassoidea are the only (known) superfamily in which larvae use a mantle appendage to construct a special conch, although other gastropod groups also contain veligers which are said to be teleplanic (e.g. Laursen 1981). This term was coined and defined by Scheltema (1971) and is used here for larvae travelling (potentially) several months before ocean currents cause them to drift from their reproduction to the settlement area (see Thorson 1961, Robertson 1964, Scheltema 1971). The designation teleplanic (long-living planktic) subliminally implicates special adaptations to planktonic life. Such adaptations are not known from several groups containing teleplanic larvae (e.g. Strombimorpha, Cypraeoidea or certain Neogastropoda) but where they are known the functional morphology of the larvae (e.g. the echinospira type; see Bandel et al. 1993) is totally different from cassoid veligers.

It has been shown that the mantle edge (including the appendage) of the *Cymatium* sp. larva contains different types of glands. A–A₃, and B (see Figs. 5, 6) are typical glandular zones which are known from other gastropods to be involved in the production and secretion of periostracum (see e.g. Bernard 1890, Neumann 1928, Gostan 1966, Bevelander and Nakahara 1970). The cells of type C form the hypobranchial gland.

The configurational differences between the left mantle edge and the pallial tentacle are obvious (see Fig. 6). Gland B is found opposite the more basal-lying A₂ (compared to A₃) in the former and opposite the more terminal-lying gland A (compared to A₁) in the latter. This indicates that the mantle appendage did not evolve from a simple elongation of a mantle edge bulge but that the part containing gland B grew allometrically. Glands A and B are much more voluminous compared to their counterparts along the "normal" mantle edge, which perfectly coincides with the observation that the pallial tentacle is solely responsible for the extra periostracum. Invaginations of the appendage epidermis are evidently connected with the formation of sculptural elements.

There is no possibility for the pallial tentacle to form calcareous chambers (as was discussed by Simroth 1895), for the simple reason that they are built after metamorphosis. The chambers are created when the juvenile or adult gastropod inserts apical septa to strengthen the

fragile first whorls of the conch (Bandel and Hemleben 1975). The fragility, of course, has to be seen relative to that of the teleoconch, or to the different ecology of the benthic gastropod.

The mode of periostracum construction of the Cassoidea specimens examined here allows us to claim the existence of a larval pallial tentacle without anatomical confirmation, although the histology of the appendage (i.e., size of the glands) probably is correlated with the periostracal sculptures typical for a certain taxa. A *Cymatium* sp. larva certainly produces much more periostracum than does a *Bursa* sp. veliger, which means the cassoid taxa must have different strategies for surviving in the plankton. Bandel (1981) and Richter (1984) agree that additional periostracum layers protect the larvae from boring organisms and epibionts. However, there is still no explanation why larval conchs with a thin periostracum [i.e., those Bursinae which are also known to be teleplanic (e.g. Scheltema 1972)] seem to be unaffected by such organisms as well.

Richter (1973) compared the speed of sinking of smooth larval conchs and more or less sculptured ones; however, he did not consider the data on the size and shape of larval conchs, which of course may also have an important "braking" effect (see e.g. Tiemann and Betz 1979).

The same author (1973) denies that the periostracal spines have any effect other than that of reducing the speed of sinking. He suggests that the whole larval shell is useless as protection from predators because the veliger has to expose its soft body in order to swim. However, the veliger would not sink more than 2 m min⁻¹ (under poor conditions) when the velum is retracted. Mileikovsky (1973) claims a swimming speed for a gastropod veliger (not specified) of 78 cm min⁻¹. The speed of a newly hatched veliger of *Cabestana spengleri* (Perry, 1811) (Ranellidae = Cymatiidae) is 30 cm min⁻¹ (Riedel 1992). It is generally known that many gastropod veligers perform diurnal vertical migrations which may amount to several hundred meters. Based on these arguments it is evident that a veliger is able to sink when contacted by an enemy without being lost in the abyss of the ocean. Therefore, the shell can indeed be a source of protection from certain predators. Moreover, the periostracal spines increase the size of the veliger, which probably is an additional source of protection from small predators (e.g. copepods). In this context it is interesting that young larvae have relatively larger spines.

There is evidence that the larval mantle appendage has an apomorphic character which defines the Cassoidea as a monophyletic group. This implies that in the Lower Cretaceous the first cassoid veligers already used a pallial tentacle. It can be speculated about the original functional morphology of the larval mantle appendage; however, one strategy of Recent species can be observed in fossil conchs as well. In those cases in which the larval conch bears a thick periostracum (as in *Cymatium* sp.) which has been secreted and pasted as described (see "Results"), the calcareous whorls are separated from each other by the organic material. The disintegration of the periostracum leaves an "open" suture of the calcareous shell,

which indirectly demonstrates the thickness of the organic layers. Thus it can be stated that the oldest known cassoid protoconchs (Campanian of Mississippi, USA) did not have a thick periostracum. The fossil record indicates Eocene times for the evolution of this character.

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