

## Jurassic Heteropods and their Modern Counterparts (Planktonic Gastropoda, Mollusca)

By

Klaus Bandel, Hamburg and Christoph Hemleben, Tübingen

With 34 figures in the text

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**Abstract:** Early Jurassic gastropods are described from the Posidonia Shales of Southern Germany. *Coelodiscus minutes* and *C. fluegeli* and *Pterotrachea liassica* are compared with living heteropods from the North Atlantic (Bermuda). *Coelodiscus* has no Recent counterpart but can be compared very well with the living *Cardiopoda*. The organization of the veliger larva and the adult is discussed. The soft body demonstrates that since the Early Jurassic the Heteropoda consist of at least two separate groups; but their shared features point toward a common ancestor.

**Key words:** Phylogeny, Heteropoda, Mesogastropoda, Jurassic, Plankton.

**Zusammenfassung:** Aus den Stinksteinbänken des Posidonienschiefers werden drei Arten beschrieben, die den planktonisch lebenden Heteropoda zugerechnet werden. Sie werden mit der heute lebenden *Pterotrachea* und *Cardiopoda* verglichen. Die Weichkörper-Organisation der Veliger-Larve wie des adulten Tieres wird näher beschrieben und diskutiert. Ein Vergleich mit den Atlantiden zeigt deutliche Unterschiede, die auf eine größere phylogenetische Entfernung zwischen den verschiedenen Heteropoden-Gruppen hindeuten. Die Gemeinsamkeiten allerdings weisen auf einen Ursprung hin. Dieser gemeinsame Vorfahre hat zeitlich vor dem unteren Jura gelebt.

### Introduction

Gastropods are predominantly benthic organisms; only a few remain pelagic during their entire ontogeny. However, many marine gastropods have within their life cycle a planktonic phase. This phase may occur in their early (embryonic) stage, (e.g. archaeogastropods) or it may be represented by a specialized larval phase (many marine neritaceans, meso- and neogastropods, pulmonates, and opisthobranchs). But the bulk of these snails are benthic organisms living on the sea floor in a variety of environments. Only three

groups of gastropods living in our recent seas have developed a truly planktonic mode of life. These are (1) the pteropods, which swim with the aid of two horizontal wings attached to the head, representing the anterior portion of the foot; (2) the janthinids, which float at the sea surface by means of a raft composed of mucus-covered bubbles, whose buoyancy supports the organism, (3) the heteropods, which swim with the aid of the foot that has become modified to form a vertical fin.

The paleontological history of these three planktonic gastropod groups is still rather poorly understood. Only the history of the pteropods is well documented from early Tertiary times onward. Heteropods are known from the Recent and Pleistocene only and their origin from benthic gastropods was assumed to have occurred fairly late, sometime during the Tertiary (RICHTER, 1974). Speculations about the phylogeny of living representatives of the heteropods are based on the organization of living species and genera. During a rather early historical stage of research it was assumed that evolution started from ancestors with a more or less complete spiral shell (Atlantidae), which became reduced to a rudimentary shell (Carinariidae), and finally to naked forms (Pterotrachoidae). This model was proposed by GEGENBAUER (1855), enriched with details by REUPSCH (1912), and has survived into our times (RICHTER, 1981). In RICHTER's model snails became adapted to a pelagic mode of life by reducing the weight of the shell, increasing the symmetry of the conch and by reduction of shell size. These evolutionary trends were combined in a phylogenetic line that proceeds from the less competent to the more perfect swimming organisms.

RICHTER (1981) places benthic ancestors of the heteropods close to the naticids following suggestions of THIELE (in WENZ 1938-1944). This idea, however, was subsequently challenged when MARTOJA & THIRIOT-QUIEVREUX (1975) discovered that the digestive system of heteropods resembles that of the pyramidellids. This interpretation, however, emphasizing a connection between free living planktonic gastropods (heteropods) and the large group of parasitic snails having no radula, would imply that ancestors of the heteropods occurred during Late Paleozoic (Carboniferous).

In this paper, we present key data combining observations on living heteropods with the findings of BANDEL & KNITTER (1983). These authors stated that the well-known minute gastropod shells found in high abundance in limestones of the Early Jurassic Posidonia Shales of southern Germany do not represent the last occurrence of the Paleozoic archaeogastropod Euomphalacea but are the oldest known heteropods.

In spring 1983 we were able to study heteropods off Bermuda. Among these were numerous heteropod larvae that could be studied alive, and in some cases, we observed their metamorphosis from the veliger-larva to the adult stage. The data obtained from *Cardiapoda* and *Pterotrachea* larvae combined with data extracted from the literature were used to reconstruct heteropod evolution since the Early Jurassic (Posidonia Shales). Moreover,

comparison with other heteropod larvae and adults enabled us to present a new model of heteropod phylogeny.

### Methods

The fossil specimens were prepared by breaking the shell, mounting them on stubs and plating with a gold – palladium alloy for SEM examination. The living heteropods were caught with a plankton net (mesh size 202  $\mu\text{m}$ ) three to five miles south off Bermuda. The catch was diluted and kept in 1000 ml bottles until returned to the laboratory. In the laboratory the heteropods were kept in 250 ml sea water from the collecting site and observed at regular intervals of time. For our observations (drawings and photographs) we used a Leitz inverted microscope. The different species survived under these artificial and somewhat unfavorable conditions for two to five days and during this time several individuals underwent metamorphosis.

### Historical background

Limestones of the Posidonia Shales (Toarcian) of Franconia and Swabia have been known since QUENSTEDT's time to contain large quantities of minute gastropods. Sometimes, these rocks look like an oolite wherein each oolite represents a gastropod (QUENSTEDT, 1858). Such typical limestones have received the name "Schneckenstinkstein" (gastropod containing, bituminous smelling limestone); a name that was again utilized to describe the lowermost bed found in the Posidonia Shale section of Unterstürmig near Forchheim, Franconia (BANDEL & KNITTER, 1983). Moreover, most carbonate concretions exhibit numerous minute gastropods. Other localities are at Altdorf south of Nuremberg, in Hetzles just north of Erlangen, in the cliffs of Trimeusel on the river Main north of Bamberg and in the clay pits of Mistelgau west of Bayreuth.

BANDEL & KNITTER (1983) demonstrated that these small aragonitic gastropods were usually destroyed by diagenetic alterations as they were deposited in the Posidonia Shale. The small conchs are well preserved only in those parts of the section where concretionary processes occurred prior to the desintegration and dissolution of small and delicate aragonitic shells.

QUENSTEDT (1858) and ULRICH, WILD & ZIEGLER (1979) assumed that these little gastropods fed on decaying fishes, ichthyosaurs and other vertebrates. KAUFFMAN (1981) phrased it somewhat more cautiously, but expressed the same idea, when he stated, that these snails represented members of an opportunistic species that exploited food sources within oxygen-depleted areas. However, KAUFFMAN (1981) also considered the possibility advocated by JEFFERIES & MINTON (1965) that these snails had been pelagic forms similar to the modern pteropod *Limacina*.

QUENSTEDT (1858) already noted that the minute snails are represented by two different types. One he described as *Ammonites ceratophagus* (1858,

p. 253–254, pl. 36, Fig. 7). “I want to call this small juvenile a carion feeder which occurs in very high abundances in these concretions (mummies). The ribs of these conchs are broad and cross the back of the shell and the diameter of the conch shows a rapid increase. However, I think that this conch is closely related to the spawn of the *Ammonites fimbriatus*.”

QUENSTEDT (1858) also noted that the ribbed *A. ceratophagus* is accompanied by representatives of another smooth form, some of which may be ammonite spawn, while others resemble small, naticid-shaped gastropods like *Euomphalus minutus* ZIETEN, 1832, (QUENSTEDT, 1858, pl. 43, Fig. 28).

In 1884, QUENSTEDT presented under the name *Ammonites ceratophagus* an adult ammonite which subsequently has been redescribed by RIEGRAF (1985). However, this ammonite certainly does not have a ribbed ammonitella. Therefore the small juveniles of *Ammonites ceratophagus* (QUENSTEDT, 1858) are not shells of ammonites but entirely different organisms.

QUENSTEDT figures in 1884 (p. 398, pl. 200, Fig. 92,93) *Euomphalus minutus* and described the conch as a flat coil with up to 5 whorls and a narrow umbilicus. According to his observations the stratigraphic range is Lias Epsilon to Dogger Alpha (Toarcian and Aalenian).

BRÖSAMLEN (1909) revised the gastropod fauna of the Jurassic of Schwaben and redescribed the minute snail as *Coelodiscus minutus* (QUENSTEDT). He considered the highest abundances to occur in the “Stinkstein”. According to BRÖSAMLEN’s diagnosis the genus *Coelodiscus* shows a small, disk-like conch with a deep and wide umbilicus. The early whorls are lower and partly covered by the last whorl and the aperture is oval. *C. minutus* exhibits fine longitudinal lines on the surface. Interpreting BRÖSAMLEN’s figures (1909, pl. 17) it appears that he considered both, *Euomphalus minutus* and “*Ammonites ceratophagus*” (QUENSTEDT, 1858), to belong to the same species. Furthermore, he expressed the opinion that these gastropods represent members of the family Euomphalidae, and due to their minute size he regarded them as the final impoverished form of this very large and widespread Paleozoic group of gastropods.

In the Treatise of Invertebrate Paleontology (KNIGHT et al. 1960), only those forms with a raised spiral were included as *Coelodiscus* (= *Euomphalus minutus*), while WENZ (1938–1944) illustrated a planispiral smooth shell to represent the genus.

## Results and discussion

### Early Jurassic Heteropods

In the following we shall describe the group of minute gastropods occurring in the Posidonia Shales which were formerly lumped under the name *Euomphalus minutus*

Class: Gastropoda

Subclass: Prosobranchia

Order: Mesogastropoda  
 Suborder: Heteropoda  
 Family: Carinariidae  
 Genus: *Coelodiscus*

**Emended diagnosis:**

Embryonic shell of less than one whorl without sculpture; following whorls increase in width (parallel to axis of coiling) more rapidly than in height (vertical to axis of coiling), covered with spiral ribs. After 3.5 to 4.5 whorls, increments of growth become irregular (Fig. 8). Growth lines are well developed on the adult shell, but rather straight on the apical side with a low lobe on the umbilical side close to the suture. Size up to 5 mm. Type species for this genus is *P. minutus* (ZIETEN, 1832).

*Coelodiscus minutus* (ZIETEN, 1832) emended

(Figs. 1–3, 7)

1832 *Euomphalus minutus* ZIETEN 1832, P. 45, Pl. 33, Fig. 6

1858 *Euomphalus minutus* ZIETEN, 1832. – QUENSTEDT, Pl. 43, Fig. 28

1909 *Coelodiscus minutus* (ZIETEN, 1832). – BRÖSAMLEN, Pl. 17, Fig. II

**Diagnosis:** Shell resembles a helix, with a maximum of 4.5 whorls. Whorls evenly rounded and covered with growth lines and fine longitudinal striae; 33 striae on last whorl. Growth lines smooth with light concave sinus near suture. Aperture oval, higher than wide; umbilicus open.

**Remarks:** The diagnosis has to be repeated since BRÖSAMLEN (1909) utilized *Euomphalus minutus* ZIETEN, 1832, as type species for the genus *Coelodiscus*. However, *C. minutus* in BRÖSAMLEN's description and illustration comprises three distinct species. Plate 17, Fig. 9, may be an *Ammonitella* (reillustrated by WENZ 1838–1944, Abb. 38); Pl. 17, Fig. 10 could represent *Coelodiscus fluegeli* n. sp. (QUENSTEDT, 1884, description) and Pl. 17, Fig. 11, shows *Coelodiscus minutus*. KNIGHT et al. (1960) disregarded BRÖSAMLEN's original generic diagnosis of *Coelodiscus* BRÖSAMLEN 1909 but considered *Coelodiscus aratus* (TATE, 1870) as typical for the genus. QUENSTEDT's 1858 description of *E. minutus* as *Natica*-like can be excepted for *Coelodiscus*. The other two minute gastropods from the "Schneckenstinkstein" have not yet been described, even though QUENSTEDT's (1858) *Ammonites ceratophagus* probably represents our *Pterotrachea liassica* n. sp.

*Coelodiscus fluegeli* n. sp.

(Figs. 4–6, 8)

1884 *Euomphalus minutus* ZIETEN, 1832. – QUENSTEDT, p. 398, Pl. 200 Figs. 92–93

1909 *Coelodiscus minutus* (ZIETEN, 1832). – BRÖSAMLEN, Pl. 17, Fig. 10

**Diagnosis:** Apical portion of conch almost flat. Up to 5 whorls coiled with growth lines and sculptured by up to 30 longitudinal lirae, which are zigzagging to undulating. Derivatio nominis: In honor of the distinguished paleontologist ERIK FLÜGEL, University of Erlangen.

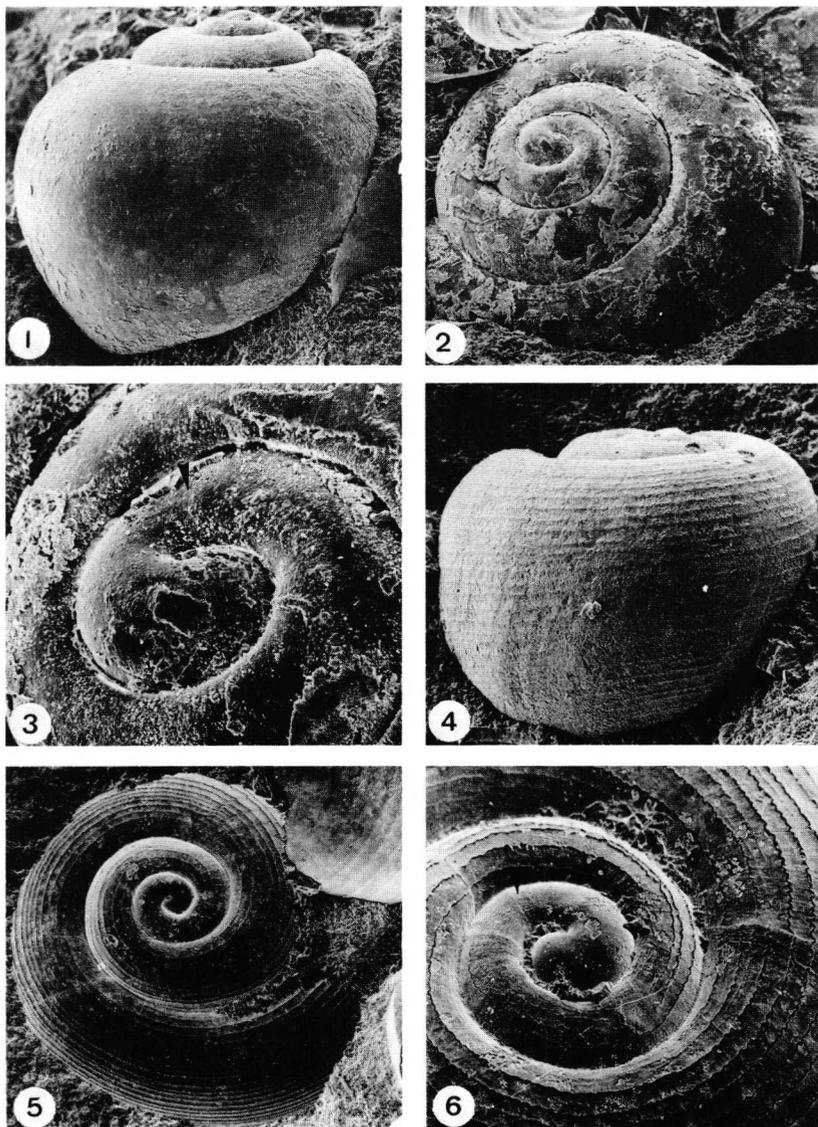


Fig. 1. Lateral view of a larval shell of *Coelodiscus minutus* showing the helicoid spiral; x40; (Holotyp).

Fig. 2. Apical view of *C. minutus*; x51.

Fig. 3. Enlarged apical view showing transition from the embryonic shell to larval shell with the onset of growth lines (arrow) in *P. minutus*; x175.

Fig. 4. Lateral view of an larval shell of *C. fluegeli* n.sp. showing the low spiral; x60; (Holotyp).

Fig. 5. Apical view of *C. fluegeli* n.sp.; x55.

Fig. 6. Enlarged apical view showing transition from embryonic shell to larval shell with the onset of growth lines (arrow) in *C. fluegeli* n.sp.; x125.

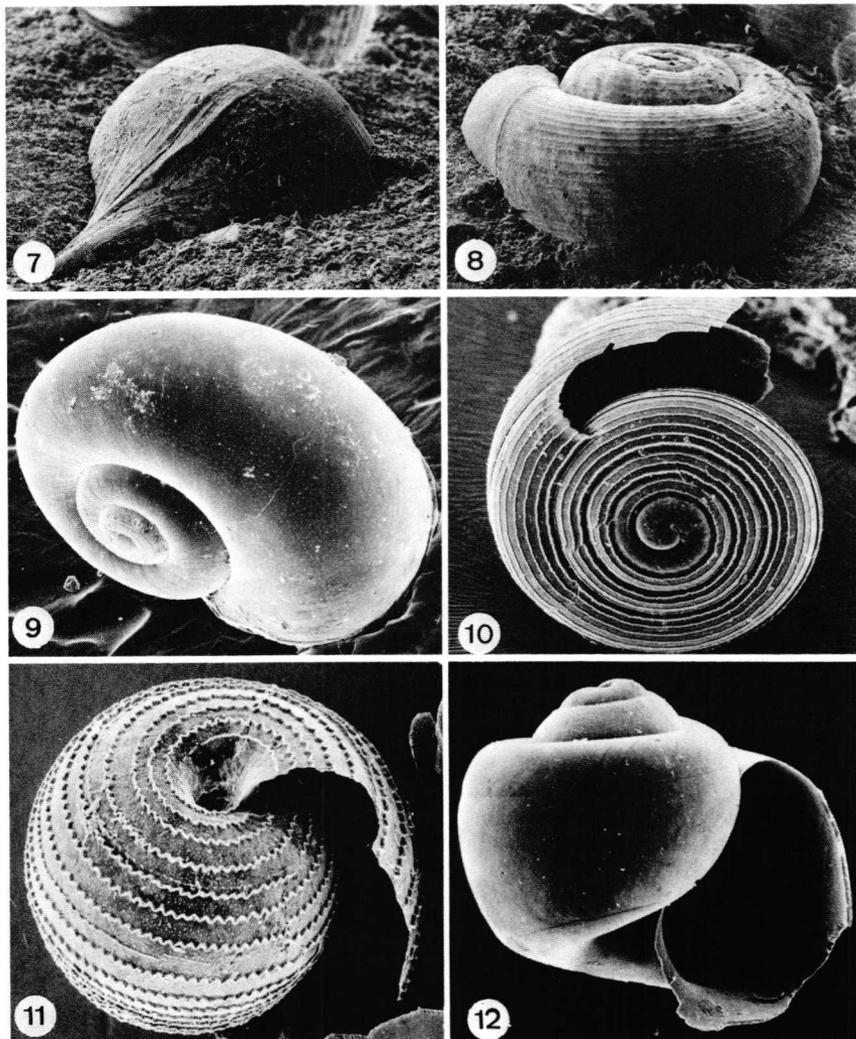


Fig. 7. Transition of larval to adult shell with irregular and dense growth lines in *C. minutus*; x57.

Fig. 8. Boundary of larval to adult shell of *C. fluegeli* showing a rather smooth surface; x35.

Fig. 9. *Cardiapoda* sp. from Bermuda resembling the conchs of *Coelodiscus* in shape; apical view, x65.

Fig. 10. Fully developed veliger conch of *Atlanta helicinoides* resembling *Coelodiscus fluegeli* with respect to the surface sculpture but showing distinct apertural sinuses; x100.

Fig. 11. Larval shell of *Oxygyrus keraudreni* showing zigzagging ribs like *C. fluegeli*, but exhibiting a different shell shape; x80.

Fig. 12. Larval shell of *Carinaria* sp. from Bermuda showing a smooth aperture similar to *Coelodiscus*; x115.

Remarks: Both species of *Coelodiscus* *C. minutus* and *C. fluegeli* are very similar to each other and can be separated by the shape of the spire. The more helix-like and spherical type matches the former *Euomphalus minutus* ZIETEN of QUENSTEDT (1858). The conch resembles in general the conchs of *Cardiapoda* (Fig. 9) while the ornamentation is more similar to species of *Atlanta* e.g. *A. helicinoides* SOULEYET, 1852 (Fig. 10). *Oxygyrus keraudreni* LESUEUR shows similar lirae with zigzag pattern as in *C. fluegeli* (Fig. 11). The shape of the aperture is like that of the modern genus *Cardiapoda*, with a shallow sinus near the suture (Fig. 12). Shell deposition decreased after the larval stage and no adult shell was secreted. The same occurs in *Cardiapoda*. In modern *Carinaria*, which also shows a similar larval shell (THIRIOT – QUIEVREUX, 1975), growth continues after metamorphosis.

Family: Pterotracheidae

Genus: *Pterotrachea*

Emended diagnosis: Embryonic conch like that of *Pterotrachea coronata* FORSKAL, 1775, (Fig. 13, 14, 15), comprising almost one whorl, smooth, no growth lines visible, almost planispirally coiled, with well rounded apex, simple straight aperture, oval in outline. Size about 0.15 mm. Larval conch exhibits pronounced growth lines; later stage with undulation of the shell following growth lines. Rounded to crested ribs are separated by depressions. Growth lines and ribs on apical side straight, on umbilical side forming a very shallow bay near suture; shell slightly trochospirally coiled.

*Pterotrachea liassica* n. sp.

(Figs. 16–18)

1858 *Ammonites ceratophagus* QUENSTEDT. – QUENSTEDT, p. 253–254 Pl. 36, Fig. 7

Diagnosis: Larval conch with ribs which are slightly angular at their crest, up to 2.5 whorls and maximum diameter of 3.5 mm. Increase of shell diameter is rapid, doubling height and width with each whorl; aperture wider than high.

Comparison with *Pterotrachea coronata* FORSKAL, 1775: The aperture of *P. coronata* is as wide as it is high and the outgrown larval shell measures only 0.8 mm in maximum diameter. Larval and embryonic shell consist of 1.5 whorls when the shell is discarded and the snail becomes naked (Fig. 25).

Remarks: The absence of an adult shell formed after metamorphosis of the veliger is characteristic for *Pterotrachea* conchs. *P. liassica* had a more extended larval period than *P. coronata*, because one additional whorl is present.

### Observations on living heteropods

#### A) Veliger organization of *Pterotrachea* (Figs. 19–24)

The egg mass of *Pterotrachea* described by OWRE (1964) consists of an egg string carried in the nidamentary filament that extends from the tail of the female. The larvae are released as free swimming veligers provided with shell and operculum (GEGENBAUER 1855). The veligers have the usual organization

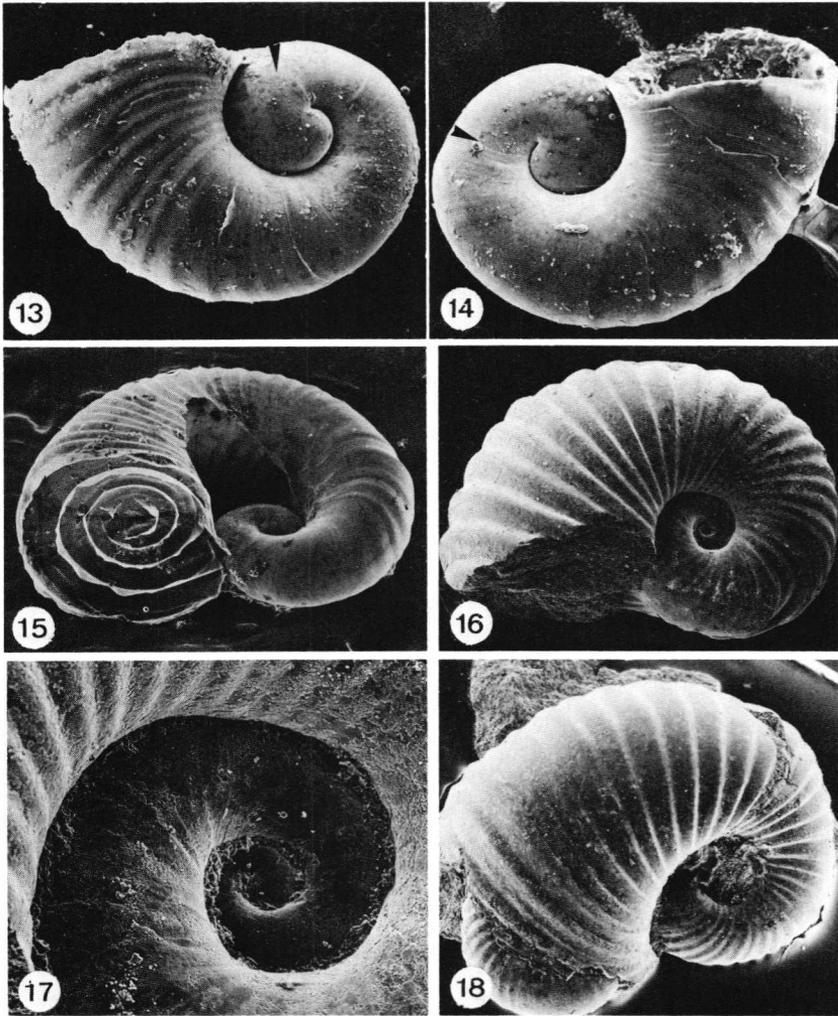


Fig. 13. Apical view of an embryonic shell and the begin (arrow) of the larval shell of *Pterotrachea coronata* from Bermuda; x125.

Fig. 14. Umbilical view of an embryonic shell and the begin (arrow) of a larval shell of *Pterotrachea coronata* from Bermuda; x135.

Fig. 15. Umbilical view of the completed larval shell of *Pterotrachea coronata* with an operculum closed aperture; x85.

Fig. 16. Umbilical view of the completed larval shell of *Pterotrachea liassica* n.sp. from Unterstürmig (Franconia); x25.

Fig. 17. Larval shell of *P. liassica* n.sp. showing a transition from smooth to ribbed surface; note the shell repair in the centre of the shell; x120.

Fig. 18. Lateral view showing the low trochospiral of the conch of *P. liassica*; x23.

of prosobranch larvae with conch and operculum. The two-lobed velum serves to collect food (small planktonic organisms) and propels the larva during swimming (Figs. 19.1-6, 20.1-9, 21-24).

The digestive system is simple and originates where the ciliary grooves of the velum margin (Fig. 19.1) fuse with the mouth opening (Fig. 19.2). From there the ciliated oesophagus (Fig. 19.5) transports the collected food particles into the large stomach (Figs. 19.4, 21). Muscular pulses of the stomach and the walls of the digestive gland mix food with digestive enzymes. Fecal matter leaves the body through a short hind gut that twists from the end of the stomach to the umbilical side of the body opening near the edge of the mantle into the pallial cavity.

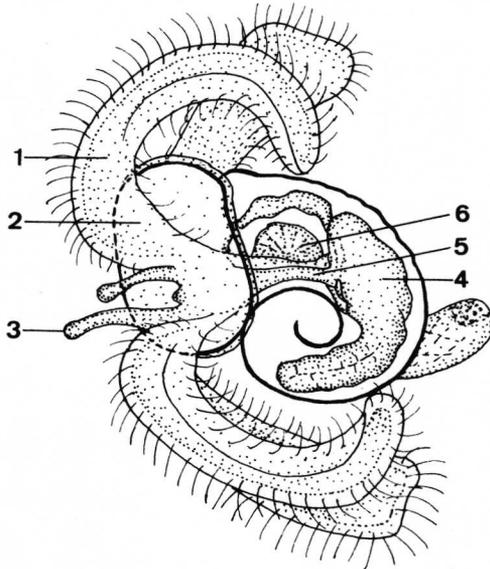


Fig. 19. Umbilical view of a recent *Pterotrachea coronata*, veliger. 1 = velum; 2 = mouth; 3 = tentacles; 4 = stomach; 5 = oesophagus; 6 = larval heart.

Individuals studied in Bermuda (Fig. 19-33) show that the body fluid is at first distributed only by the larval heart (Fig. 19.6). This muscular contractile organ is placed at the base of the velum in front of the visceral mass (Fig. 20, 22). Each pulse expands the fluid into the pallial cavity and with each contraction blood enters the velum (Fig. 20.1). Later the two-chambered adult heart is organized near the stomach (Fig. 20.7), opposite the hind gut (Fig. 20.8) that ends at the apical side of the visceral mass. Both heart organs operate together for some time, before the larval heart ceases shortly before metamorphosis.

The pallial cavity enlarges during growth of the veliger in size. At the head, two long tentacles (Figs. 19.3, 23) are equipped both with a basal light organ

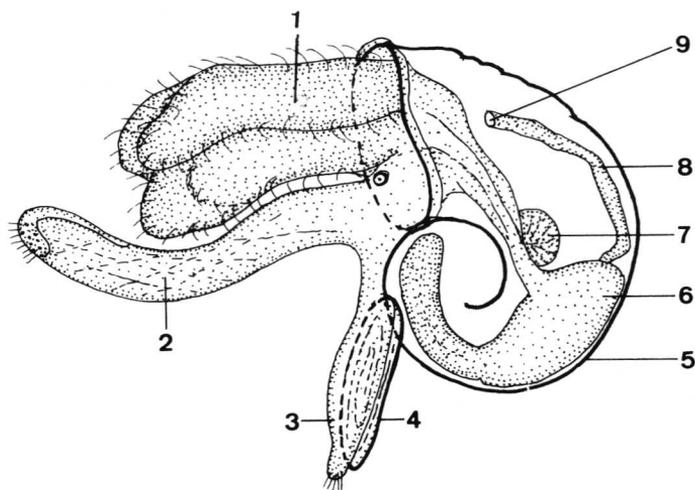


Fig. 20. *Pterotrachea coronata*, veliger. 1 = unfolded velum; 2 = trunk of anterior foot; 3 = posterior foot; 4 = operculum; 5 = shell; 6 = stomach; 7 = larval heart; 8 = hind gut; 9 = anus.

within a dark pigmented cup. Head and pallial cavity are densely ciliated. When the animal withdraws into the shell the mantle retracts and the velum is coiled and head and foot are withdrawn by contraction of the adductor muscle until the operculum (Figs. 20.4, 24) seals the aperture.

The foot consists of two parts: the typical veliger disc-like flat end (Fig. 20.3), carrying the unmineralized operculum (Fig. 20.4) and the long anterior trunk (Figs. 20.2, 24), which is very mobile and as long as the lobes of the velum (Fig. 20). The velum lobes increase in size considerably until the veliger is stabilized enough to swim with four large velum-lobes. The trunk is continuously active cleaning the shell and the velum, supported by secretions of gland cells at its tip. Furthermore, it serves perhaps as a defensive organ.

When the larva has evolved as far as metamorphosis, only the double chambered heart is active. This seems to be the only drastic change which occurs rather rapidly. Within one night the shell is discarded, the operculum lost and the velum resorbed or devoured. OWRE (1964) observed this drastic change in *Firoloida desmaresti* LESUEUR, 1817, where the shell and operculum were shed (OWRE, 1964, Fig. 7) and the naked, miniature adult swam off (OWRE, 1964, Fig. 8).

The larva of a second *Pterotrachea* species (Figs. 19, 20) observed in Bermuda shows the same kind of organization of the soft body, but with an evolute coiled shell. In both larvae of *Pterotrachea*, the shell is held in a posterior position while swimming but it does not hang down like in atlantid larvae.

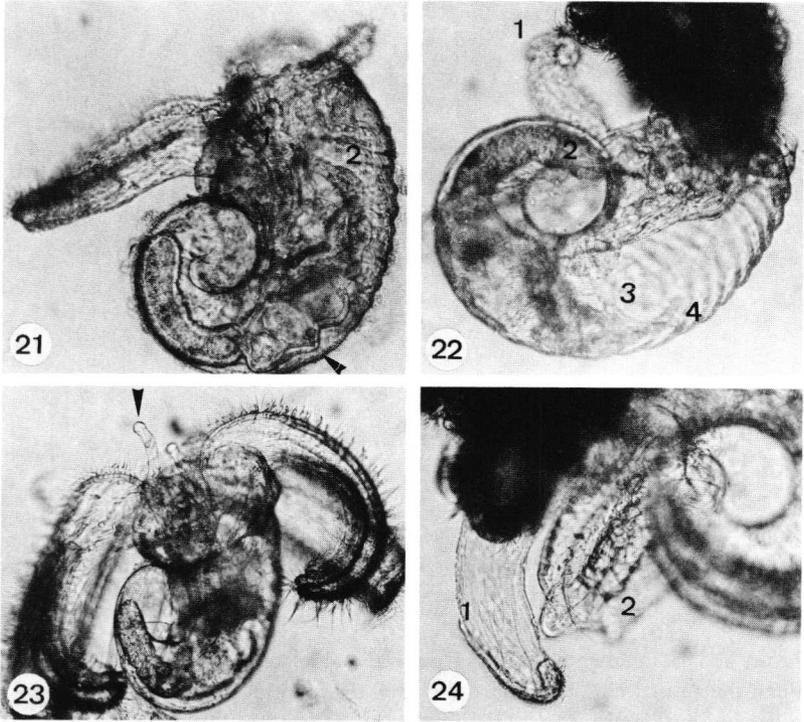


Fig. 21–24. *Pterotrachea coronata* (veliger) in swimming position.

Fig. 21: stomach (arrow) including fore (1) and hind gut (2); x80.

Fig. 22: showing 1 = tip of the foot trunk; 2 = digestive gland; 3 = larval heart; 4 = hind gut with anus; x70.

Fig. 23: unfolded, ciliated velum and the head tentacles (arrow); x90.

Fig. 24: 1 = anterior trunk; 2 = operculum on the posterior foot; x102.

### B) Adult organization of *Pterotrachea* (Fig. 25)

The organization of the adult *Pterotrachea* was described in detail by REUPSCH (1912). The general organization is similar to that of the cardiopods as described here from Bermuda, except that the shell is lost prior to metamorphosis.

The visceral mass in the genus *Pterotrachea* forms an epithelium covered pear-shaped body (1), the so called nucleus. This nucleus is rather small compared to the visceral mass of the unshelled *Cardiapoda*. An adult *Pterotrachea* (length approximately 8 cm) exhibits a 5 mm long nucleus. From the nucleus the hindgut opens to the dorsal surface of the body. The nucleus itself contains the digestive gland and the heart. Two groups of gills are positioned opposite the anal opening. They show similar organisation as the

gills of the diotocardians (archaeogastropods). The blood collected from the body cavity is pumped by the larger posterior heart chamber. On its way it passes through the gills and becomes oxygenated. Then, the blood is pumped forward into the body by the anterior heart chamber. The main aorta sends also a branch to the tail (Fig. 25.8) (in contrast to the cardiopods), thus providing the brains, fin (Fig. 25.5), head (Fig. 25.2) and buccal apparatus (Fig. 25.1) with oxygenated blood. As in the cardiopods oxygen depleted blood returns to the nucleus (visceral mass, Fig. 25.7) through the liquid-filled body spaces below the outer skin (Fig. 25.3).

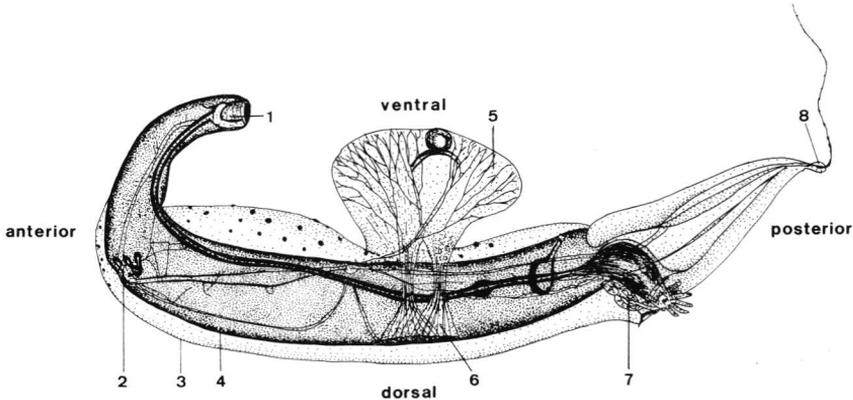


Fig. 25. Adult *Pterotrachea* (modified after REUPSCH, 1912).

1 = buccal mass and mouth; 2 = head with eyes; 3 = outer skin, 4 = inner muscular layer; 5 = fin; 6 = fin muscles; 7 = visceral mass (nucleus); 8 = tail.

The bulk of the pterotrachean body consists of an inner and outer liquid filled mass of connective tissue, the inner one of which is surrounded by a muscular tissue (Fig. 25.4), the outer by the skin (Fig. 25.3). The inner mass contains the gut, the larger nerves and ganglia, and the large veins. The muscular layer serves as attachment for the fin muscles (Fig. 25.5). Their contraction and dilatation produce the typical undulating motion of the fin. In the female, the inner body cavity extends into a tube at the end of the tail serving as a brood chamber when the eggs have become fertilized and encapsuled. They are protected until larvae are ready to hatch. This can be observed in *Pterotrachea* as well as in *Firoloida* (OWRE, 1964).

### C) Veliger organization of *Cardiopoda*

The shell of the *Cardiopoda* veliger (Figs. 26–27) is trochospirally coiled and exhibits a very similar morphology comparable to the *Carinaria* veliger (THIRIOT-QUIEVREUX, 1975). The velum of the evolved larva is very large and develops 6 lobes. It needs much space when it is folded into the conch

occupying more than half of it. It withdraws rather rapidly into the shell but it takes a while emerging again; first the disc-like portion of the foot holding the operculum (Fig. 26); next, the long trunk appears (Fig. 27). This trunk is a hollow muscular tube connected with the foot exhibiting gland cells at its tip; it is held upwards while swimming. Last, the velum opens and uncoils.

The larva reacts to light, as a simple light organ is developed and positioned in a pigmented cup. The head is equipped by a pair of long, retractile tentacles (rhinophores). The fully developed digestive system and the head are comparable with those of the *Pterotrachea* veliger.

The operculum and posterior foot are kept on the side when the larva swims; the trunk and velum point toward the direction of movement and the conch is kept posterior, not hanging down. During metamorphosis the foot

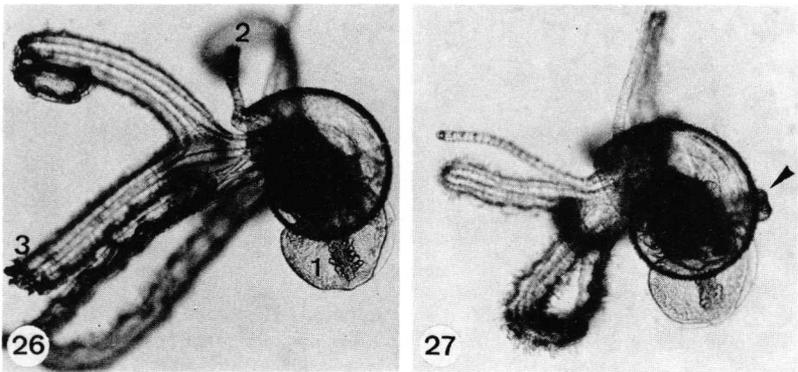


Fig. 26. Veliger of *Cardiapoda*; 1 = posterior foot with operculum; 2 = head tentacles; 3 = lobed, ciliated velum; x32.

Fig. 27. Veliger of *Cardiapoda* exhibiting tentacles, velum and foot; trunk-like anterior foot (arrow); x32.

discards the operculum and is modified into the tail. Dense cells form on its surface the sucker (clasper), which is obviously not homologous to the sucker or clasper of the atlantids that evolve from the anterior part of the foot. The change from the late larval to the early juvenile stage is rather drastic (Figs. 26, 27 and Figs. 28, 29–30).

#### *Cardiapoda* organization after metamorphosis (Figs. 28–30)

Our observation confirms that metamorphosis in *C. placenta* (LESSON, 1830) takes place overnight. It is a rather distinct change in organization of the whole body. The early juvenile cardiapods have a tubular shape and the shell covers only a small portion of the total animal. Locomotion is now performed by a fin (Fig. 28.14). Cardiapods swim in an inverted position with

the foot in the same orientation as the veliger, but the morphology has changed totally. The head-foot-tail has become large and elongated and laterally somewhat compressed. The former larval shell now protects the viscera (Fig. 28.12) and the organs of the pallial complex (mantle cavity). Neither head and foot, nor the tail can be withdrawn into the shell.

The apical end of the body shows a large sucker (Fig. 28.13) with a black pigment. During normal activity the sucker is folded; when opened, it forms two wing-like structures with crenulated margin and a deep purple coloration. The body in contrast, is colourless and transparent.

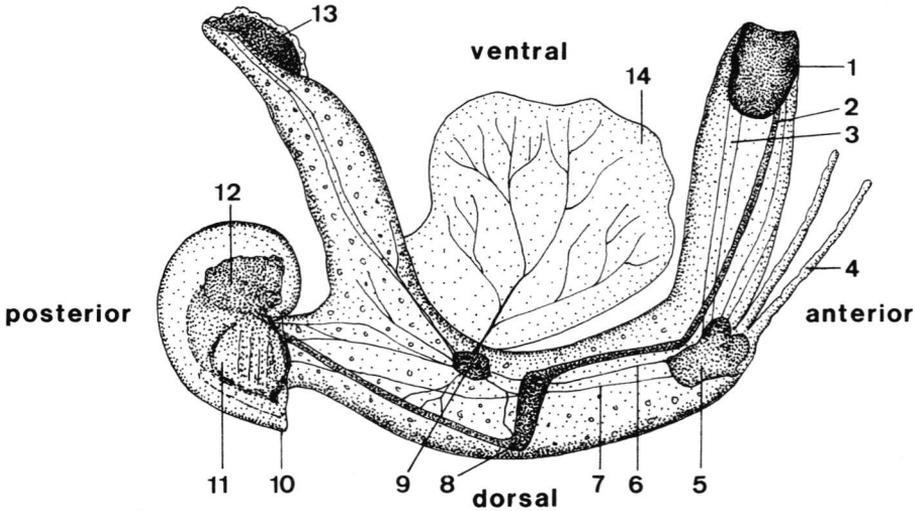


Fig. 28. *Cardiapoda placenta*, shortly after metamorphosis. 1 = buccal mass; 2 = oesophagus; 3 = connectives of head and buccal mass ganglia; 4 = tentacles; 5 = eyes and cerebral ganglia (head brain); 6 = connectives of head and pedal ganglia; 7 = connectives of head and visceral ganglia; 8 = crop; 9 = pedal ganglia (fin brain); 10 = shell; 11 = gills and pallial cavity; 12 = visceral mass; 13 = sucker; 14 = fin.

The anterior end of the body consists of the head and snout (Fig. 29), which makes up one quarter of the total length of the body. The foot lies ventral to the visceral mass (Fig. 28.12) and expands into a large muscular fin at the central portion of the body. The body is stretched while the animal swims and the fin undulates sideways. When fin movement stops, the animal curls up by bending the tail and the head-snout towards the fin.

At the base of the rhinophores, the eyes (Fig. 28.5, 29) have become more prominent and highly differentiated and are encompassed by a capsule. This does not imply a rather narrow view downward when swimming, as assumed by VAN DER SPOEL (1976); the eyes are very mobile and can be turned in all directions as desired, even upwards.

The buccal mass (Fig. 28.1) of the cardiopods is an independent apparatus having its own musculature, which is not connected with the head. It is attached to the epithelium of the mouth at the snout's end. The jaw apparatus is connected with a powerful radula apparatus that has been described in detail by REUPSCH (1912) in the case of *Pterotrachea*. The animal prey is caught and pulled into the gut by the long lateral and marginal teeth of the radula and is conveyed into the mouth by the central teeth.

The gut is clearly visible through the transparent body until the shell hides it. The round opening of the mouth is connected with the buccal apparatus (Fig. 28.1). The left and right salivary glands secrete into the foregut (Fig. 28.3). The long oesophagus (Fig. 28.2) is visible throughout the tubular body with the exception of the tail. It consists of a simple tube with a central dilated region, the crop (Fig. 28.8), just below the fin. Food, e.g. embryonic fishes, or crabs, which are swallowed entirely, can be stored in the crop.

The gut twists when it enters the shell-covered visceral mass in front of the digestive gland. The hind gut is very short and ends at the margin of the shell on its umbilical side. The gill (Fig. 28.11) is positioned opposite to the pallial complex, on the dorsal and apical side of the aperture of the shell. In the young animal, the gill consists of 5 folds of the roof of the pallial cavity. The posterior portion of the shell is filled with the digestive gland (Fig. 28.12), which enlarges during growth until it covers nearly the whole shell (THIRIOT-QUIEVREUX 1975). The shell remains enclosed in the mantle and gills protrude from the mantle cavity (VAN DER SPOEL 1976).

The nervous system of *Cardiapoda* resembles that of *Pterotrachea* (described by REUPSCH, 1912), although two main differences can be observed:

1. *Cardiapoda* has a direct connective nerve between the cerebral ganglia and the heart-visceral mass (Fig. 28.7; 30), while in *Pterotrachea* the fin ganglia are innervated first and then the heart-visceral mass (Fig. 25).
2. The mouth ganglia are connected by a pair of nerves with the head ganglia in the cardiopods, not so in *Pterotrachea*.

Moreover, in the cardiopods, the sucker (Fig. 28.13) is positioned on the tail and not on the fin; fin veins (Fig. 28.14) form no network. The crop lies in the center of the body (Fig. 28.8), and the shell is not discarded when the larval organization is changed into the adult system. Furthermore, the Atlantidae lack the nerve pair of the pedo-visceral connectives. Comparison of the organization of the nervous system of *Cardiapoda* with other heteropods, clearly show similarities between *Carinaria*, *Pterotrachea* and *Firoloida* (TESCH 1913). TESCH showed that *Carinaria*, *Pterotrachea* and *Firoloida* have additional, straight nerve connectives between pedal ganglia (fin brain) and visceral ganglia (heart, digestive gland). Summarizing, the nervous system within the genera *Cardiapoda*, *Carinaria*, *Pterotrachea* and *Firoloida* show some variations, but they exhibit more similarities than the atlantid nervous system, which is rather differently organized.

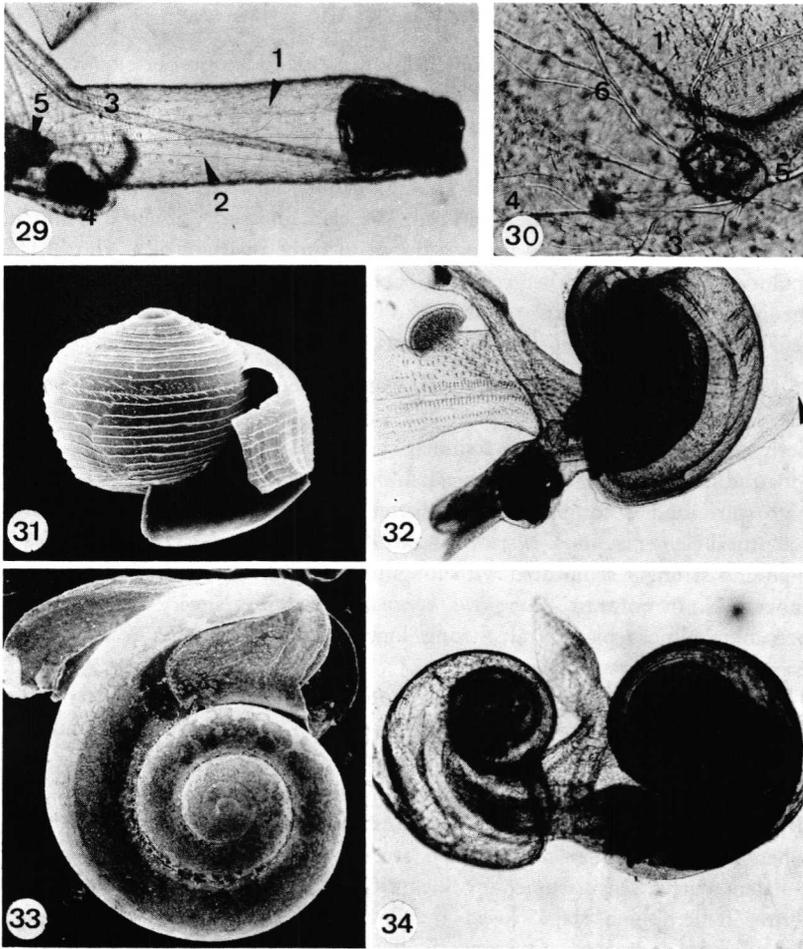


Fig. 29. Head and snout of a metamorphosed *Cardiapoda*. 1 = main arterie; 2 = nerves; 3 = oesophagus; 4 = eyes; 5 = head brain; x30.

Fig. 30. Fin brain of a *Cardiapoda*. 1 = fin; 2 = ganglia; 3 = connective of cerebral and visceral ganglia; 4 = arteria; 5 = connective of cerebral and pedal ganglia; 6 = connectives of pedal and visceral ganglia; x110

Fig. 31. Larval shell of *Atlanta helicinoides* showing the sutural and central lobes supporting the velum stalks; x70.

Fig. 32. Juvenile atlantid exhibiting the attachment of the mantle edge to the carina (arrow); x25.

Fig. 33. Conch of *Atlanta peroni* after metamorphosis. The umbilical larval lobe has been closed and a carina is developed; x55.

Fig. 34. Cannibalism in juvenile atlantids; the right one feeds on the left one holding it with its sucker; x40.

### Short characterization of the Atlantidae

According to our current knowledge the Atlantidae produce both single and strings of egg capsules which are released into the water. The embryo develops within the capsule and hatches as a fully equipped planktotrophic veliger, which shows no differences compared to veligers of other highly developed marine prosobranchs. The embryonic shell has no increments of growth, except close to the aperture. The shell measures about 0.1 mm in largest diameter and makes up two thirds to three quarters of a whorl. The sculptured surface is rather coarse in *Oxygyrus keraudreni* (LESUEUR, 1817) medium coarse in *Atlanta turriculata* d'ORBIGNY, 1836, and very delicately sculptured in *Atlanta helicinoides* SOULEYET, 1852.

The larval shell of the Atlantidae shows a variety of shapes. *Atlanta peroni* (LESUEUR, 1817) has a low spiral and smooth conch, with a well rounded periphery. *A. helicinoides* has a similar shape, but the sculpture shows strong longitudinal lirae. The almost conical *A. inclinata* (GRAY, 1850) shows a rather high spire, and is equipped with a flattened single keel; tubercles occur as sculptural elements. In *A. turriculata* and *A. fusca* SOULEYET, 1852, the spire is high and strongly sculptured with longitudinal lirae, zigzag lirae and lines of tubercles. In contrast, *Oxygyrus keraudreni* exhibits a very involute spire becoming almost planispiral; strong longitudinal lirae and zigzag-lirae are present.

In the early larval stages of the atlantid ontogeny the larva begins to modify the outer lip of the aperture at the base of the two lobes of the velum and thus the position of the head is stabilized by forming sinuses in the shell (Fig. 31). One of these indentations is located near the suture, the other one develops on the outer lip itself. These slits stabilize the shell below the velum, when the veliger is swimming, and are not designed to direct inhalent or exhalent currents as assumed by BATTEN & DUMONT (1976). Therefore the term "Bellerophina stage" used by BATTEN & DUMONT (1976) for this developmental stage in *Oxygyrus* is misleading, and even morphologically incorrect, since *Bellerophon* has only one slit. This slit was not used for a velum but probably functioned in pallial sanitation.

Metamorphosis in the atlantids occurs after an extended period of larval life, during which a conch of 4–5 whorls is formed. This change appears to be rather rapid and drastic regarding both the shape of the shell and the body, but it does not involve a rapid increase of the volume of the shell. The idea, expressed by VAN DER SPOEL (1976) or BATTEN & DUMONT (1976), according to which the atlantids can retract completely into the shell and be sealed off by the operculum, is not correct. As soon as metamorphosis is completed, the edge of the mantle becomes attached to the keel (Fig. 32) where cells of the muscular mantle secrete the keel parts. The atlantidae are able to withdraw large parts of their body (head and foot) into the space of the pallial cavity, while the edge of the mantle remains firmly attached to the

keel (Fig. 32, 33) on the outside of the shell aperture. Only extreme irritation causes a detachment of the muscular mantle from the keel resulting in the withdrawal of the mantle edge from the shell edge. The question of the function of the keel discussed earlier by BATTEN & DUMONT (1976) can be answered by looking at the digestive system. The hind gut ends in the anus within the pallial cavity of the fully developed veliger on the umbilical side of the conch. Faeces are washed out of the cavity by ciliation of its epithelia. After metamorphosis, the pallial sanitation is improved and the pallial cavity takes over the function of breathing, the slit becomes closed (Fig. 32). To avoid defaecation, which might cause problems for gas exchange within the pallial cavity a ciliated groove connected with the anal opening ends in the slit the aperture's outer lip of the adult shell, where faeces are released. The mantle is continuously held in place by the attached mantle, thus breathing and defaecation are well separated. The slit in the aperture of the adult conch is positioned below the keel, and comparable to the slit of fissurellids or perhaps that of bellerophonitids. It serves to orient the exhalent faeces-loaded current. It no longer stabilizes the velum which is only present in the larva. The keel is also functional in streamlining the shell, as suggested by RICHTER (1981).

The feeding behaviour in the atlantids as observed on Bermuda specimens probably reflects the general mode of feeding in these planktonic gastropods. The prey is held by the clasper-sucker and slowly eaten by bites of the radula with aid of the snout.

### Fossil Carinariids and Pterotracheids and the evolution of the heteropods

When FORSKAL (1775) described *Pterotrachea* as the first heteropod genus, the family was of unclear taxonomic position. GEGENBAUER (1855) lumped the pelagic gastropods Pteropoda and Heteropoda and considered them as a separate class of the Mollusca, the Cephalophora, because they swim with wing-like or fin-like modifications of the foot. THIELE in WENZ (1938–1944) placed heteropods into the Mesogastropoda based on the morphology of the radula, as later emended by RICHTER (1961).

THIRIOT-QUIEVREUX (1973) reviewed the heteropod systematics and organization including 25 species of heteropods of which 13 belong to the Atlantidae, 7 to the Carinariidae and 5 to the Pterotracheidae.

While it was assumed that the Carinariidae and Pterotracheidae represent the most recent families of the heteropods (GEGENBAUER 1855, RICHTER 1981), fossil representatives (*Coelodiscus* and *Pterotrachea*) demonstrate that these families are much older. Since the last 170 million years these pelagic gastropods have changed very little.

### Conclusions

Our investigation reveals several differences between the Atlantidae and the Carinariidae/Pterotracheidae.

1. Presence of a brood chamber in *Pterotrachea* and *Firoloida*, while *Atlanta* sheds its egg capsules into the water directly.

2. Veligers produce a trunk in *Cardiapoda*, *Pterotrachea* and *Firoloida*. Veligers of the Atlantidae have no such feature.

3. The larval conchs of Carinariidae and Pterotracheidae have no larval hook, while such a feature is always found in the Atlantidae.

4. The nervous system of the Carinariidae and Pterotracheidae shows additional connectives between fin brain and visceral mass, while the nervous system of the atlantids is organized like a normal prosobranchiate gastropod.

5. Metamorphosis in Pterotracheidae and Carinariidae is very drastic while in the Atlantidae it follows more usual pathways.

6. Pterotracheidae and Carinariidae catch food and swallow it as whole into the crop. Such a feature is not found in the Atlantidae, where food has to fit into the space of the conch.

These differences indicate a greater phylogenetical distance between these groups of heteropods than previously assumed. However, the fact that atlantids and carinariids/pterotracheids have so much in common, (swimming mode, feeding and shape of radula; features of the embryonic and larval shell and overall organization of the body) clearly demonstrates a close ancestral affinity. These heteropod ancestors should be present in rocks older than Jurassic. This group again gives us good reason to see the necessity of using great caution in constructing models of phylogeny of molluscan families and superfamilies extracted purely from the living fauna without the aid of fossil evidence.

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Anschrift der Verfasser:

- Prof. Dr. KLAUS BANDEL, Geol.-Paläont. Institut und Museum, Universität Hamburg, Geomatikum, Bundesstraße 55, 2000 Hamburg 13.
- Prof. Dr. CHRISTOPH HEMLEBEN, Geol. Institut Universität Tübingen, Sigwartstr. 10, 7400 Tübingen 1.