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Observations on the ontogeny of thecosomatous pteropods (holoplanktic Gastropoda) in the southern Red Sea and from Bermuda

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Abstract The early ontogeny of *Peraclis reticulata*, *Limacina inflata*, *L. trochiformis*, *Styliola subula*, *Clio convexa*, *Cl. cuspidata*, *Hyalocylis striata*, *Creseis acicula*, *Cr. virgula*, *Cuvierina columnella*, *Diacria quadridentata*, *D. trispinosa*, *Cavolinia uncinata*, *C. longirostris*, and *C. inflexa* is described. Their larval development is characterized, and strategies of ontogeny of pteropods are viewed in the context of their biology and taxonomic position. The reconstruction of the juvenile shell into the voluminous adult shell in *Diacria* spp. and *Cavolinia* spp. is described in detail. The general features of the early ontogeny of Thecosomata does not deviate from those of other marine gastropods in essential ways as has been proposed by some authors, but postmetamorphic retainment of the sinistral coiling of the shell as well as reshaping of the juvenile shell in *Diacria* spp. and *Cavolinia* spp. are unique features of the euthecosomatous pteropods.

Introduction

In 1987 the German research vessel "Meteor" cruised twice through the Red Sea on its way to and from the Indian Ocean, passing the Gulf of Aden. On both Red Sea legs observations were made on living pteropods, a holopelagic group of gastropods. The data presented in the present study represent a continuation of previous work on planktonic gastropods carried out on living material caught off the shore of Bermuda (Bandel et al. 1984; Bandel and Hemleben 1987). We aim at an understanding of their ontogeny, and their habits in relation to their benthic relatives and their fossil predecessors.

The two basic types of Euthecosomata can be traced back to the Early Eocene. In the Paris, Aquitaine, and North Sea Basins as well as the Gulf area (Texas) characteristically left coiled Limacinidae and uncoiled Cavoliniidae are represented by several species. Intermediate forms which may phylogenetically connect both groups have not yet been observed. Limacinidae, however, seem to have a longer record ranging back into Late Paleocene time (Curry 1965; Janssen and King 1988). From the onset of pteropod history both families can be traced continuously up into the Recent. Curry and Rampal (1979) demonstrated that the cavolinids *Camptoceratops prisca*, a straight form with remnants of a coil from the Early Eocene, and *Vaginella depressa*, with a shape somewhat similar to more modern *Clio* spp. from the Miocene, basically constructed a shell which shows the helical shell structure which is characteristic to many pteropods (Bandel 1977, 1990).

In order to understand the origin of the pteropods, we have to consider their probably closest relatives among benthic gastropods, the cephalaspidean opisthobranchs. This group, as well as Allogastropoda (in the sense of Haszprunar 1985) and the Archaeopulmonata, may produce in the course of their ontogeny an embryonic shell (shell secreted by the embryo while still living within the egg capsule) and a larval shell (shell secreted by the swimming veliger) exhibiting a different direction of coiling compared with the adult shell (shell produced by the gastropod after its metamorphosis from the veliger larva). Allogastropoda, Opisthobranchia and Pulmonata incorporated in the systematic unit Heterostropha Fischer, 1885 (Bandel 1992, 1994a) were originally separated from all other gastropods by the change in the coiling direction during ontogeny,

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usually from left to right. Such a switch from sinistral to dextral coiling secreted by the pediveliger (veliger larva ready to metamorphose) can be traced back in the fossil record to the Early Carboniferous (Kollman and Yochelson 1976; Yoo 1988,1994; Herholz 1992; Bandel 1994a) and is well established in Heterostropha (Allogastropoda and Opisthobranchia) in the Triassic (Bandel 1988, 1991a, 1994a, b). Pteropods, i.e. Limacinidae, differ from the normal development of the Heterostropha by retaining the larval, sinistral shell throughout adult life (Bandel et al. 1984; Bandel 1991b). The total lack of a dextral adult shell is probably connected to the origin of the pteropods in general. It may represent a major change in the general course of ontogeny by extending the larval construction programme after metamorphosis. Furthermore, early pteropods may have become permanently pelagic by production of a mucous raft (Gilmer 1974; Gilmer and Harbison 1986).

Several rather unusual features of the euthecosomatous pteropods have been presented in literature that were considered to separate pteropods from all other gastropods. A short survey of these traits follows.

Skinny and minute forms

When Van der Spoel (1967) wrote his book about pteropods they were considered unusual gastropods which had not only developed strange shapes but some individuals of some species showed strange skinny and minute bodies in large shells. Gilmer (1986) and Lalli and Gilmer (1989) demonstrated that all these forms represent artifacts of preservation.

Vegetative reproduction

Other specimens exhibited bodies that seemed to be in the process of strobilation, a mode of vegetative reproduction known from coelenterates (Van der Spoel 1979). These ideas were not rejected by Fioroni (1982) when he discussed the different strategies of gastropod reproduction. Fioroni (1982) considered strobilation-like reproduction only to represent a very special case among molluscs, because it is not uncommon among other gastroneuralians like some polychaetes. He only criticized the use of the term "strobilation" for this kind of asexual reproduction but not the mode itself.

Shell deposition

The shell of most pteropods consists partly of the characteristic aragonitic helical structure. Bé et al. (1972) thought that pteropods had developed with the helical structure a totally new type of shell structure because their ancestors were considered to have abolished a mineral shell. However, Bandel (1977, 1990) documented that other benthic gastropods with aragonitic crossed-lamellar structure construct portions of the shell in helical structure from time to time when they change from one crossed-lamellar layer to the next with first order lamellae perpendicular to each other.

Maternal pallial brood feeding

Embryos of *Limacina inflata* were found in the mantle cavity and interpreted to feed freely in the pallial cavity of the parent attached to the tissue of the mantle (Lalli and Wells 1973; Wells 1976; Lalli and Gilmer 1989).

Movement by "flying" in the water

Unlike any other gastropods, pteropods were supposed to be very rapidly moving "butterflies of the ocean" (Richter 1973, 1977). Gilmer and Harbison (1986) demonstrated that the main survival strategy of the pteropods lies in drifting on mucous rafts. These authors found that most cavoliniids are neutrally buoyant even when they are not feeding, others sink very slowly. In all species swimming is used as an escape response and during diurnal migrations.

Filter-feeding

Subsequent to metamorphosis from the veliger stage, thecosomatous pteropods use large mucous webs to entrap food. This method involves mantle extensions and wings which had been observed and illustrated as early as Woodward (1851), but had been disregarded until the study of Gilmer and Harbison (1986). All speculations regarding filter-feeding within the pallial cavity (Oberwimmer 1898; Yonge 1929; Morton 1958; Richter 1977, 1981) have to be revised. They do not feed by ciliary collecting nor sorting fields extending from the head and the expanded natatory lobes of the foot as was assumed by Thompson (1976). Pteropods feed by swallowing mucous sheets, webs and rafts loaded with food, and the pallial cavity has no part in that. Euthecosomatous pteropods trap all kinds of planktonic organisms, as confirmed by studying stomach contents (Richter 1977). The results were supported by observations in situ by Gilmer and Harbison (1986). They suggested that the development of the mucous web, the modification of the mantle, and the morphology of the shell are the most important factors in understanding the evolution of the Thecosomata. In our present study the last two points, development of the mantle and shell growth during early ontogeny, are of main interest.

Materials and methods

Studies were carried out by observing living individuals under the microscope and keeping them alive for some time after they had been caught in the sea. This was carried out by K. Bandel on board the "Meteor" as well as in the marine station at Bermuda. The specimens were caught with plankton nets of different types and neuston sledge in the southern Red Sea, and observed on board the vessel. They could usually be kept alive for several days by holding them in glass jars. In Bermuda individuals were obtained with a small plankton net just offshore of the island, and living specimens were observed and kept alive for some time in the laboratory. Dried and cleaned shells were later photographed with the scanning electron microscope (SEM) in Tübingen (C.Hemleben) and in Hamburg (K. Bandel).

Results

Pseudothecosomata

Peraclis reticulata (d'Orbigny, 1836)

About 100 translucent spherical capsules in a single well-spaced row held within a jelly tube abandon the parent in one spawning process. Each egg capsule holds one egg (0.06 to 0.07 mm in diameter), and cell division begins when eggs are dispersed. During the course of dispersion three yolk-rich macromeres become increasingly covered by protoplasm-rich micromeres. Within 3 d of development 0.09 mm large veligers hatch, supplied with a protective shell, a short foot carrying the operculum, a simple velum, statocysts and a complete digestive system. No pallial cavity is developed.

Advanced veligers of *Peraclis reticulata* are common among the plankton of the Red Sea, exhibiting a large, four-lobed velum (Fig. 1A). The slightly larger frontal lobes may overlap onto the margin of the posterior lobes. When disturbed both frontal and posterior lobes of the velum suddenly fold towards each other along a median line and rapidly unfold again, thus causing a sudden jump foreward. The veliger withdraws into its shell and seals it with the operculum only when seriously disturbed. The operculum is large, fits the cup-like larval whorl and is held by a thin discus-like foot which has two posterior tips with sensitory cilia. The foot is not used for swimming. In the pediveliger stage two rudiments of the wings can be observed to grow from the foot below the posterior portion of the velum. The position of the head is indicated by the position of the velum, but it bears no tentacles or eyes. The veliger shell has a very wide round aperture and is almost formed like the limpet *Capulus hungaricus* (Linné, 1767), but is much smaller (Fig. 1B). The pallial cavity occupies the anterior shell while the embryonic shell is filled with the digestive gland. Just in front of the stomach lies the small heart that works jointly with the larger and more active larval heart, so that two hearts are active.

During metamorphosis the two rudiments of the parapodia fuse to form a single wing-like plate. It extends from the aperture and begins to flap when the velum disappears. The posterior foot with its two lobes continues to hold the transparent operculum that grows synchronously with the enlargement of the shell's aperture. The frontal foot lobes form short lips surrounding the mouth that extends upward above the wingplate. After metamorphosis the simple round margin of the aperture of the shell changes its shape to form an anterior siphonal canal. The central axis is extended into a spirally twisted anterior rostrum in contrast to the straight one of *Limacina* spp. (Lalli and Gilmer 1989). The shell margin forms a saddle accompanied by lobes. Young *Peraclis reticulata* pump fresh water into the pallial cavity by a ribbon of cilia from the neck along the left side into the apical end and from there along the roof to the right side. Thus, water enters the pallial cavity along the upper lobe of the outer lip and leaves it again through the siphonal canal and the lower lobe, taking faeces along with it.

When the shell is two whorls large, the upper right band of cilia begins to form folds and becomes transformed into a gill with a central vessel through which blood is sucked toward the heart and pumped into head and viscera. When the second whorl is completed, the gill grows to such a large size that it projects from the pallial cavity and from the shelter of the shell. The head develops a short proboscis around the mouth and two club-like tentacles but no eyes. When the pteropod is attached to its mucous raft as shown by Gilmer and Harbison (1986, Fig. 7), the wings are fully expanded, motionless, and face the mucous web. The mantle extends from the apertural lip and covers much of the shell opposite the aperture. After metamorphosis and the onset of floating, this lobe of the mantle deposits a characteristic network of calcareous ridges on the outside of the shell (Bandel et al. 1984). According to Lalli and Gilmer (1989) such a pattern of external spiral or reticulate lines is present in six of the seven species of *Peraclis* and absent only in *P. moluccensis* Tesch, 1903.

Meisenheimer (1905, 1906) and Pelseneer (1888) interpreted the gill to represent a true ctenidium, while Lalli and Gilmer (1989) explain it as a "retracted and folded mantle tissue". Up to this point the interpretation presented by Meisenheimer and Pelseneer is favoured by the authors. If this gill is not the true ctenidium, its location in the pallial cavity is the same as that of a true ctenidium.

Euthecosomata

Limacina inflata (d'Orbigny, 1836)

According to Lalli and Wells (1973), Wells (1976), and Lalli and Gilmer (1989), *Limacina inflata* broods its offspring in the parental pallial cavity. Young embryos

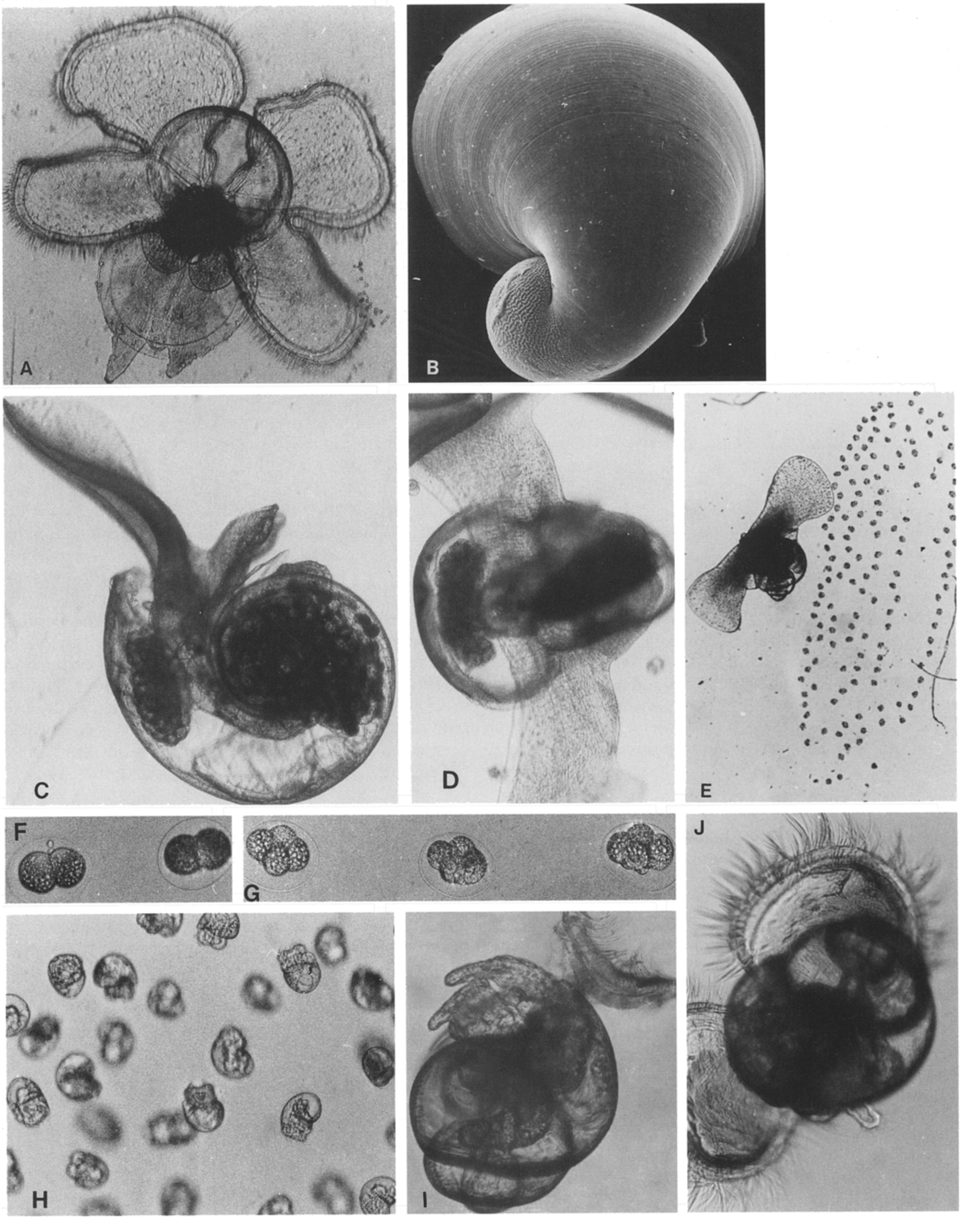
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exhibit no shell adhering to the mantle tissue in the back of the parental pallial cavity. Lalli (personal communication) believes that the late veliger may be capable of filtering small food particles which enter the mantle cavity of the parent. Brooding females are reported to contain about 45 young in various stages of development (Lalli and Gilmer 1989). This kind of embryonic development with embryos free within the mantle cavity and without the protection of an egg capsule or a brood pouch as mentioned by Lalli and Wells (1973) would be unique among gastropods.

The puzzle could be resolved by observations of mature *Limacina inflata* caught repeatedly in the Red Sea off the shore of south Sudan. Several individuals contained embryos in the shelter of the pallial cavity. These 50 to 60 embryos developed within the cavity itself, but they were kept together in a sack-like egg capsule containing the eggs (0.07 to 0.08 mm in diameter) (Fig. 1C, D, Fig. 2). Wells (1976) noticed about 45 embryos in Caribbean individuals that hatched with 0.07 mm in diameter. The egg mass is attached to the body of *L. inflata* at the back of the head just behind the attachment of the wings to the "neck". Embryos develop in a normal way into veligers until the embryonic shell and digestive tract can be utilized. At this stage, the egg capsule ruptures, and the veligers are expelled into the parents' pallial cavity to be rapidly washed into the sea by the respiratory current. Such a current is always present within the pallial cavity because the large pallial gland zone within the cavity is densely covered with cilia. Hatched veligers are able to retract into their shell and close it with the operculum, but exhibit as yet no pallial cavity. The pediveliger shows almost two whorls; a deep and ciliated pallial cavity extends into the first whorl. Furthermore a digestive system is present with a large digestive gland and hind gut that crosses from the stomach to the roof of the pallial cavity in a bridge-like connection between both tissues. At this stage the heart starts beating during metamorphosis. The blood pumping is supported by undulating movements of the mantle tissue in the roof of the pallial cavity (by a larval heart).

Fig. 1 **A** *Peraclis reticulata*, larvae with four-lobed velum and foot that carries the round operculum. Rudiments of the wings are present, but not active. **B** Protoconch of the same *Peraclis reticulata* with pitted ornament on the embryonic portion and growth lines on the conical larval shell with 0.3 mm width. **C** Adult *Limacina inflata* with brood pouch seen in lateral view attached on the head behind the tentacles and **D** the same seen in frontal view. Embryos will leave the pouch when fully developed into planktotrophic veliger larvae. **E** Adult of *Limacina trochiformis* with its spawn attached to it. **F** *Limacina trochiformis* embryo in two cell stage, **G** in four cell stage, **H** prior to hatching. **I** *Limacina trochiformis* larvae during metamorphosis and disintegration of the velum, and **J** younger larva with two lobed velum and ciliated foot visible

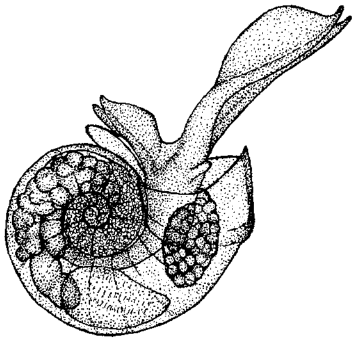


Fig. 2 Drawing of *Limacina inflata* (shell with 0.8 mm diameter) with developing embryos in a brood pouch at the back of the head

Limacina trochiformis (d'Orbigny, 1836)

Mature specimens of *Limacia trochiformis*, caught in the neuston at night, spawned in the laboratory 1 d later. According to Lalli and Gilmer (1989) the egg mass and embryonic development of this species has not been reported in literature as yet. The egg mass consists of a sheet-like jelly mass in which spherical transparent egg capsules are embedded side by side each holding one egg (Fig. 1E). One spawn contains about 80 to 100 eggs of a size of 0.06 to 0.07 mm. Cell division forms four equal yolk-rich macromeres and four plasma-rich micromeres in a perfect spiral pattern (Fig. 1F, G). The four macromeres remain undivided while plasma-rich cells continue to form until the yolk cells are surrounded and covered by the micromeres (after 6 to 8 h). As soon as the blastula stage is completed the primary body opening becomes filled with liquid which stretches the outer cell layer. Cilia develop and the embryo rotates in its egg capsule.

After 1 d the cilia have been concentrated around the front of the embryo creating a trochophora-like shape. Yolk-rich cells have divided in its interior generating the rudiments of the digestive system. A 0.07 to 0.08 mm large embryo hatches after about 50 h of development. It bears a sinistral shell in which the body is attached at a spot near the digestive gland (Fig. 1H). Here, the retractor muscle is connected to the shell. A mantle cavity is not yet present, but the digestive system is functioning; the body can retract into its shell, and the foot seals the aperture with the operculum.

The veliger grows until ca. 2.5 whorls have been completed. Metamorphosis was observed in 1983 under laboratory conditions in Bermuda (Fig. 1I, J). While we observed this process the velum disintegrated into fragments of tissues. The pediveliger swam with the large lobated velum, and the wing rudiments moved without adding much to the mobility of the pediveliger. The adult heart began to beat and pulsated at the base of the large ciliated pallial cavity while pumping blood. The foot was slender, exhibiting sensing cilia and a functional operculum. The retractor muscle was attached to the columella of the first whorl and pulled the pteropod rapidly into its shell when it was disturbed.

Styliola subula (Quoy and Gaimard, 1827)

The embryonic shell is produced while the pteropod develops within the egg capsule showing a tipped apex, a constriction at the aperture and a length of 0.2 mm (Fig. 3A, B, Fig. 4A). The larval shell produced by the veliger is also 0.2 mm long and has a 0.17 mm wide aperture. Individuals caught off Bermuda metamorphosed in the laboratory when the shells were 0.4 mm in length. The characteristic grooves observable on the shell become visible during deposition of the juvenile shell after metamorphosis.

The shape of the early conch resembles that of *Cuvierina columnella* except for the pointed apex. The juvenile shell of *Clio convexa* is larger than that of *Styliola subula*, and is also pointed at the apex, but we did not observe any constriction that would indicate the end of the embryonic and the begin of the larval shell.

The pediveliger (Fig. 3A) exhibiting rudiments of the wings and a fully grown larval shell is equipped with a functional digestive system. Food particles can be observed to rotate within the stomach, and the tubular digestive gland participates with peristaltic motions. The anus is positioned in the margin of the mantle below the foot, and cilia whip within the hind gut. Blood is pumped by the larval heart pulsating above the oesophagus in the interior part of the mantle cavity. The construction of the final heart is in progress, directly positioned behind and lateral to the stomach. The statocysts lie dorsally at the beginning of the oesophagus. The large pallial cavity extends into the apex of the shell, and water is pumped through the pallial cavity by cilia that cover its entire interior. The velum of the pediveliger consists of two large semi-circular lobes. Its foot is represented by the two lateral growing wings and a central part, which is equipped with sensory cilia. A retractor muscle is attached to the apical end of the shell's interior. It splits into two bundles before entering the head area. The individual can withdraw deeply into its shell if necessary.

After metamorphosis (Fig. 3B) wings move by extending sideways and bending up until they hit the shell. The roof of the pallial cavity has become lacunous. From there the double-chambered heart sucks oxygen-charged blood and pumps it into the visceral mass. The surface of the roof of the pallial cavity may undulate due to contraction of fibres within the lacunous mantle roof. These undulations create a current which supports the ciliation within the pallial cavity and gas exchange. The mantle forms short ciliated tentacle-like extentions (Fig. 4B).

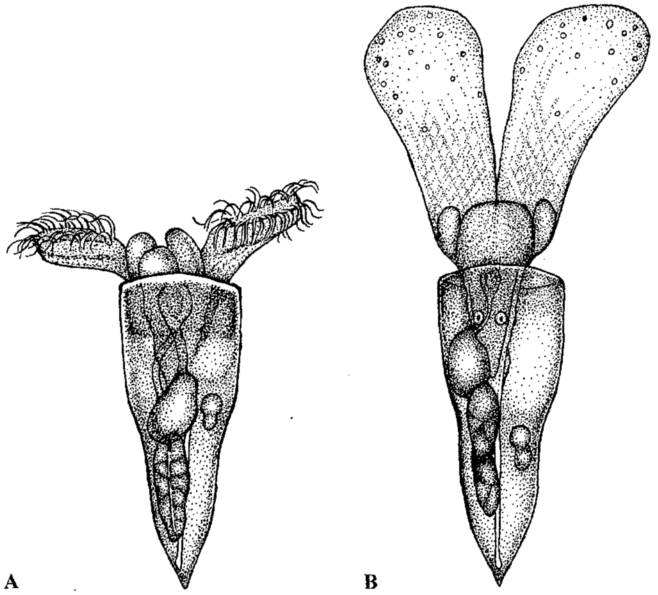


Fig. 3 A *Styliola subula* with pediveliger stage and **B** as winged juvenile right after metamorphosis with 0.4 mm long shell

Clio convexa (Boas, 1886)

Shortly after *Clio convexa* were caught they produced eggs in the ship's laboratory. The mucous jelly which was expelled contained 0.3 mm large spherical and transparent egg capsules each of which held one ovoid egg (0.2 to 0.25 mm in diameter). First division produced three macromeres which contained most of the yolk reserves and plasma-rich micromeres which became dispersed during cell division over the macromeres until they fused to form a round cell ball (sterroblastula). As soon as the ectodermal layer was complete and the macromeres were completely covered, cilia developed and the embryo began to rotate in its egg capsule.

After 35 h of development a veliger hatches from its egg capsule showing large but not yet functional rudiments of the wings (Fig. 4C, D). The young pteropod is about 0.29 mm long and equipped by a cup-like shell with a pointed apex. The intestine consists of large yolk cells covered mainly by a thin layer of mantle. A pallial cavity is not present, and the visceral mass is attached to the apical end of the interior of the shell. Muscle fibres may retract the body into the shell. The short two-lobed velum propels the larva through the water. A foot covered by sensory cilia is present but without an operculum. The mantle edge forms a ring-like thickening below the foot–velum area, and neither a heart nor a functional digestive system are present.

Three days later the shell has grown to 0.35 mm in length, and a digestive tube is visible. The stomach is not yet functional and there is still no pallial cavity nor heart. Statocysts are present, and the muscle attachment to the shell has become concentrated on one side of the shell's apex. The yolk reserves have been reduced in size, but still fill much of the visceral mass. The two wings that accompany the small foot have grown in size but are still rudimentary in their function. After 5 d the shell measures 0.4 mm, and a pallial cavity has formed. A larval heart is positioned near the base of the pallial cavity consisting of the ectodermal layer that pulsates against the visceral tube. The yolk still provides the energy needed for swimming. The wings start flapping at a shell length of 0.43 mm; the velum is reduced and finally lost. The digestive system begins to function by taking up particles of food. The yolk of the former macromeres is still visible within the cells of the digestive gland, and thus the reserves have not totally been used up. The margin of the mantle forms tentacle-like continuations which extend from the shell margin. They represent instruments for operating the mucous web, which serves from this developmental stage onward as a device for food trapping. The yolk reserves of the eggs of *Clio convexa* are large enough to neglect external food before the individual is able to construct a mucous web to trap food and to drift on it. Metamorphosis from veliger to wing-supported young individual is in phase with the utilization of the yolk reserves. The adult heart begins its function after metamorphosis has been completed and after external feeding has successfully started.

Clio cuspidata (Bosc, 1802)

The embryonic shells we caught in the southern Red Sea were of spherical appearance with a slight cyrtoconic curvature. The size was up to 0.25 mm in width and 0.46 mm in length. The caudal end possessed a reticulum of intersecting ridges arranged in alternating double rows (Almogi and Reiss 1977, Pl.1, Figs. 7–8). The anterior shell was constricted into a collar. The spherical portion of the embryonic shell was finely striated. At the apertural constriction striae changed into ridges with wrinkles between them. Beyond the collar of the embryonic shell a fine longitudinal striation was present as well as growth lines.

The size of the embryonic shell of *Clio cuspidata* gives evidence for the production of large eggs. The embryo produces a purely organic shell that remains elastic. Soon after apical and apertural regions of the shell have decreased in width, in reaction to morphological changes of the visceral mass and the decrease of yolk, the conch becomes calcified and thus stabilized in shape. Due to the size reduction of the organic shell of the embryo, a reticulate fold pattern is formed at the pointed apex and becomes fixed in shape. A groove within the apex reflects the location of the first attachment of the body to the shell which later becomes the attachment-point of the retractor muscle.

Tesch (1946) reported that the larvae of *Clio cuspidata* are held within the anterior part of the pallial cavity and adhere to the mantle opposite the position of the gizzard. However, we observed that the larvae remain in capsules which are arranged in chests and hatch after the veliger stage of ontogeny has past.

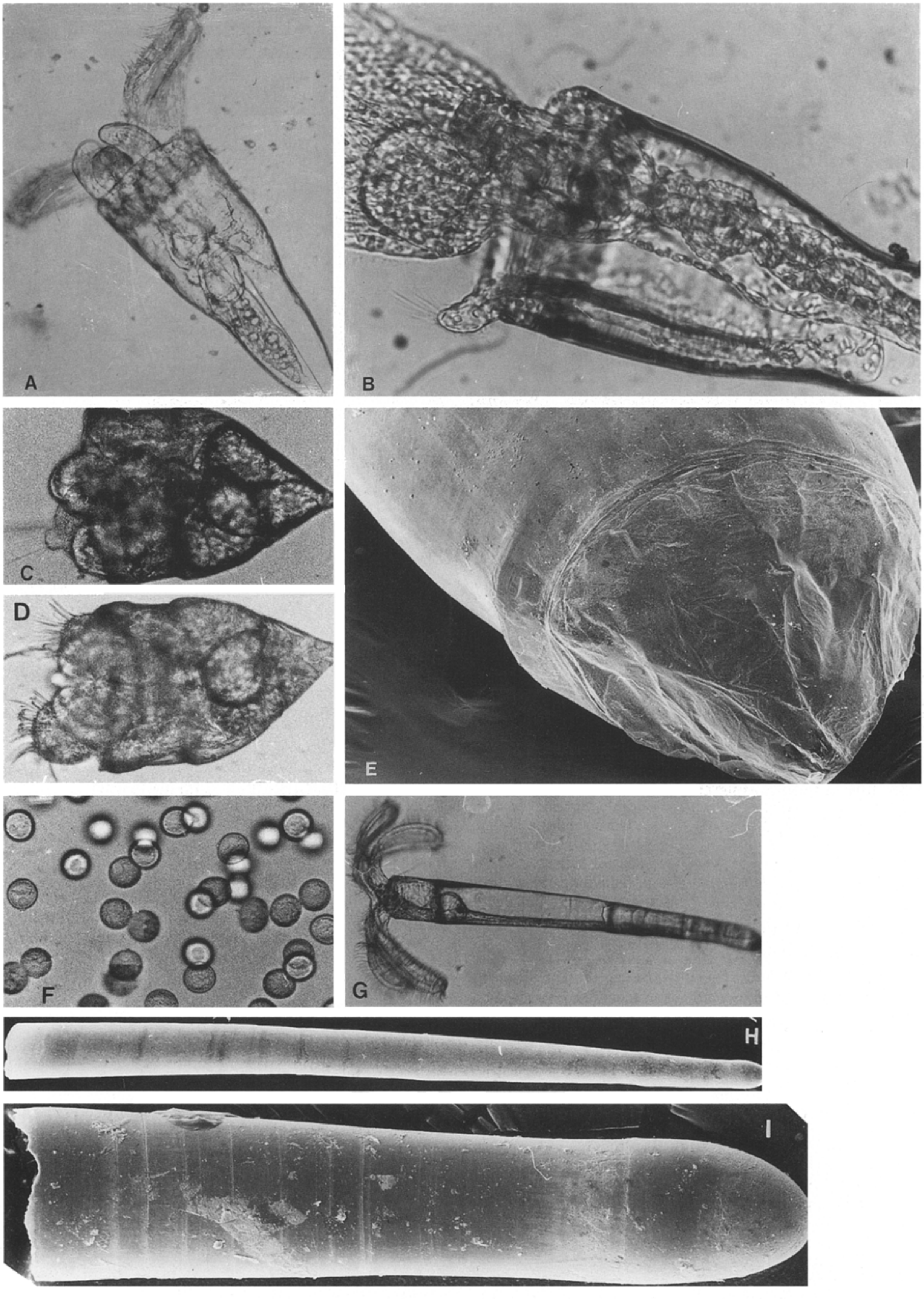
Hyalocylis striata (Rang, 1828)

Fol (1875) noted a metamorphosis 6 d after hatching. This observation, however, is difficult to place within the developmental stages of the early shell portion of *Hyalocylis striata* from the Red Sea. We observed shrunken and wrinkled remains of a purely organic embryonic shell (Fig. 4E) that had a width of at least 0.7 mm. This shell was thin and elastic, and encompassed a considerable amount of yolk stored within the developing embryo. The embryo was protected within some kind of egg capsule or parental shelter where a 1.4 mm high and calcified shell tube exhibiting a large aperture (1 mm in width) may have been formed. Before these shell-protected juveniles hatched, the early organic portions of the shell decreased in volume and became wrinkled. This pattern was preserved due to mineral layers added from the inside. After hatching the characteristic transversal undulation of the shell was formed during further shell growth. The apex is usually discarded after some shell growth, and a solid rounded septum in the apical portion of the shell tube is formed.

The retractor muscle of the juvenile is attached to the wall on the inner side, approximately two-thirds of shell length from the aperture into the tube but not at the apex. A big stomach and a large gizzard including a digestive gland in front are positioned within the posterior half of the shell. The anterior half of the shell encompasses mainly a large pallial cavity that has a glandular roof. Regular waves of contractions of the mantle tissue transport blood from the front to the back where the heart pumps the blood from the lacunous mantle tissue into the visceral region and the head.

Creseis acicula (Rang, 1828)

Mature individuals caught in the Gulf of Aden produced eggs in the laboratory 12 h later. The 0.06 to 0.07 mm large eggs were kept in spherical capsules arranged in thin sheets of mucus. During spawning the whole storage area of reproductive material behind the digestive gland was emptied and 110 to 130 fertilized eggs were produced. Polar bodies appeared, and differentiation of a yolk-rich zone at the vegetative pole and a plasma-rich zone at the animal pole was quite evident (Fig. 4F). Cell division proceeded similarly to that observed in *Creseis virgula.* When the blastula stage was reached the embryo resembled a trochophora rotating in its egg capsule propelled by two rings of cilia.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After about 60 h of development, veligers hatch, provided with an approximately 0.1 mm long tubular shell into which they can withdraw entirely. Some specimens may hatch before the primary shell is detached from the mantle. A pallial cavity has not yet developed. The retractor muscle is anchored at the apical end of the shell in an excentric position. The stomach contains a small digestive gland consisting of a few cells only and is attached to the inner side of the shell with its own constricted bundle of muscle. The hind gut terminates at the mantle margin above the head. The embryonic shell is about 0.07 mm in width and 0.09 to 0.11 mm in length. Its transition into the shell of the larva is indistinct and in most cases not connected with a decrease in apertural diameter; only few individuals show a constricted aperture that is connected with hatching from the egg capsule (Fig. 4I). The larval shell is 0.9 to 1.1 mm long and usually does not differ in its morphology from the adult shell. The transition in some cases proceeds along with a decrease of shell diameter. Metamorphosis from veliger to adult organization was described by Thiriot-Quievreux (1969) on examples from the Mediterranean Sea. Her report can be confirmed by our observations on metamophosing individuals from Bermuda (Fig. 4G, H, I). The pediveliger swims with a four-lobed velum, and the long shell floats vertically downward. An adult heart pumps in addition to a larval heart, the first sucking blood from the mantle, the second from the velum. With metamorphosis the larval heart ceases to contract, and the adult heart remains to pump the blood. The space of the pallial cavity extends all the way into the apex of the shell (Fig. 5).

Creseis virgula (Rang, 1828)

Mature representatives caught at night in the neuston at several locations in the southern Red Sea spawned when held in a jar for a few hours. About 70 to 80 eggs were expelled in one egg spawning process. The eggs (0.05 to 0.07 mm in diameter) were kept in spherical transparent capsules (Fig. 6B). They attached to each other forming gelatinous strings that drifted off or remained suspended from the spawning individual (Fig. 6A). The eggs left the mother uncleaved. Prior to cell division separation of a yolk-rich and a plasma-rich zone occurred in a uniform pattern.

After 3 to 4 d of development veligers hatch from the egg capsules with a 0.05 mm wide and 0.08 mm long uncoiled shell. At hatching the primary shell may still be connected to the mantle margin, or it may have already become detached from it. A pallial cavity is not yet present, and the individual will not retract into its shell when disturbed. A retractor muscle is clearly visible, attached at the apical end of the shell, splitting into two bundles before entering the two velum wings, but they do not yet appear to function. Not long after hatching (some hours), muscles begin to function. The digestive system is provided with a large stomach connected to a posterior digestive gland. It also starts to function right after hatching. The transition from the primary shell of the embryo to the shell of the veliger larva is evident, with first appearance of growth lines and disappearance of the sculpture pattern of the embryonic shell. This early shell pattern consists of minute and shallow grooves forming a surface with hammered appearance. This transition is in phase with hatching.

The end of the veliger phase has been observed in individuals caught in the Arabian Sea just outside the Gulf of Aden. When the shell is about 0.4 mm long (Fig. 6C) the veliger is equipped with a four-lobed velum of which each wing is half the length of the shell. The long retractor muscle is attached to the shell in an

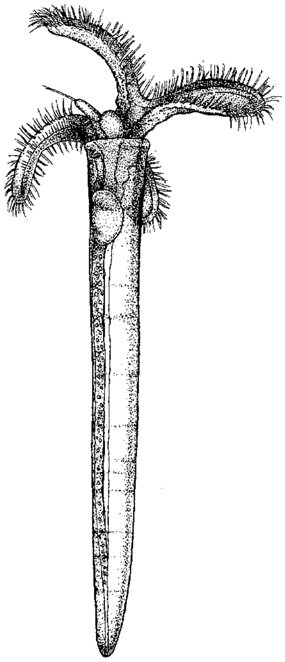

Fig. 5 Pediveliger of *Creseis acicula* (about 1 mm long). Exhibits the long retractor muscle accompanied by a long digestive gland and the large velum and small developing foot with rudiments of the wings. The stomach lies close to the shell aperture and the intestine ends near its margin. Mantle cavity takes up much of the interior of the shell that is covered by the thin sheet of mantle tissue

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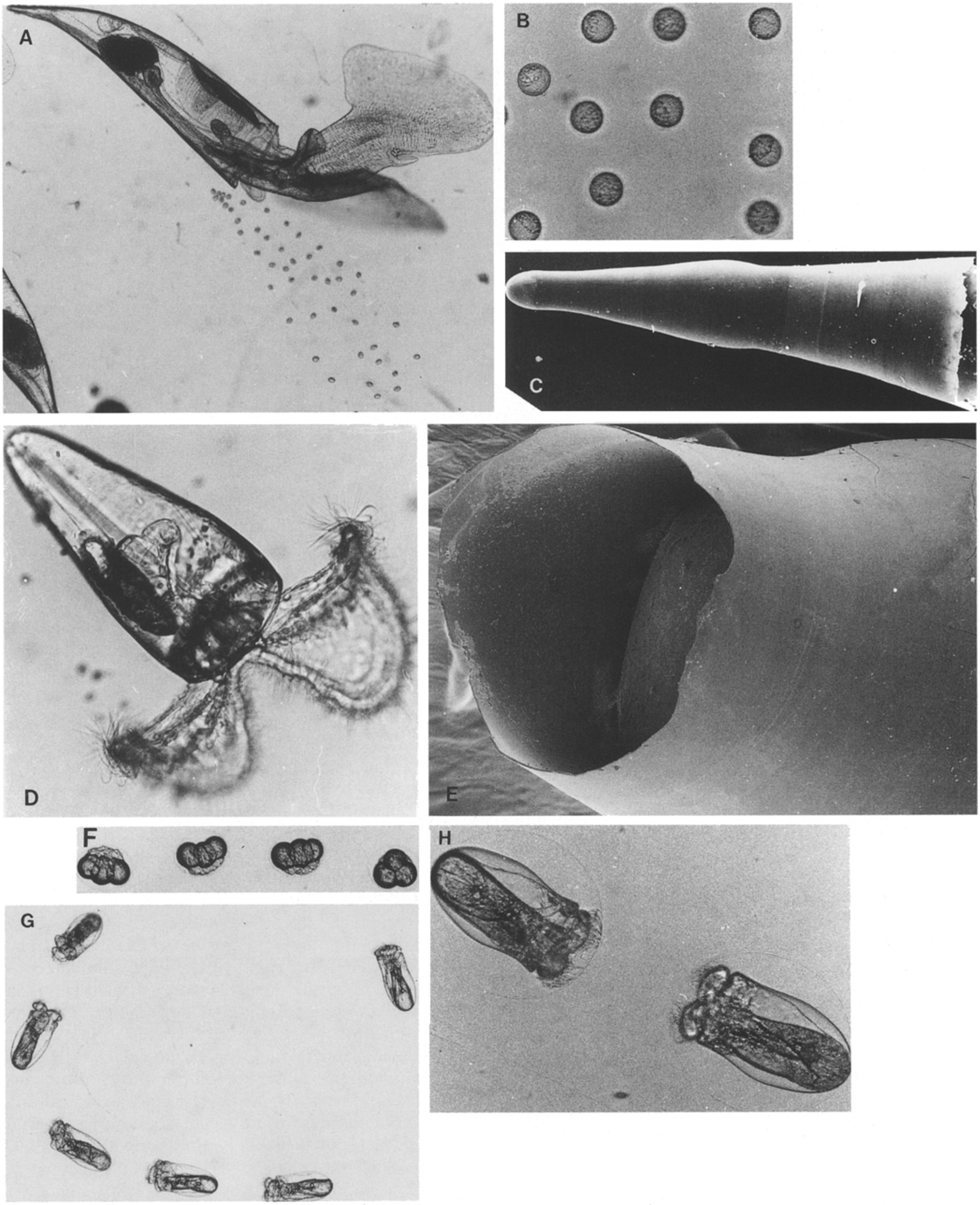
Fig. 4 A *Styliola subula* pediveliger with organs of the digestive system visible and wings present, but still swimming with the velum. **B** *Styliola subula* adult with mantle appendage and mantle cavity. **C** *Clio convexa* with ciliated foot and **D** velum visible. The visceral sac holds large yolk reserves represented by the remnants of the macromeres. **E** *Hyalocylis striata*, caudal end of the shell (about 0.3 mm wide) with shrunken originally fully organic embryonic shell attached to the teleoconch. **F** *Creseis acicula* eggs, **G** fully grown veliger with four lobed velum, **H** caudal shell part with embryonic and larval shell almost indistinguishable from begin of teleoconch in the almost 3 mm long juvenile shell, **I** *Creseis acicula* with most caudal shell part with embryonic shell and begin of larval shell (0.4 mm long)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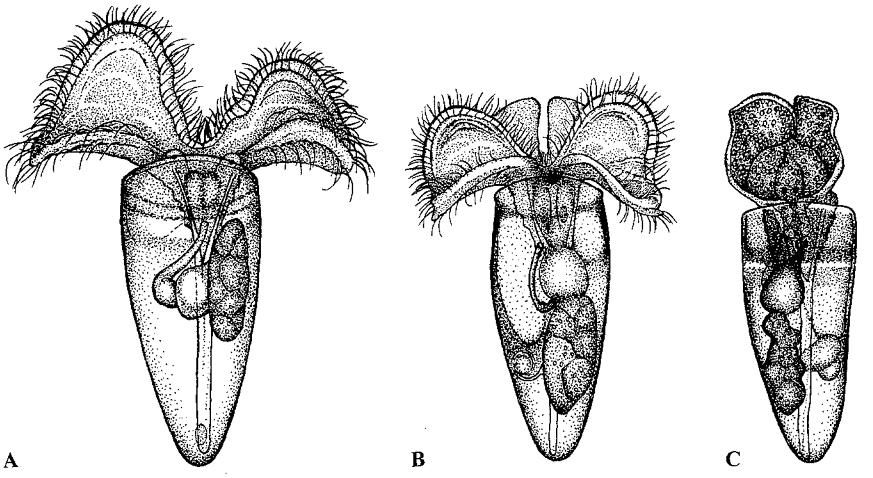


Fig. 7 *Cuvierina columnella.* Stages of metamorphosis. **A** Veliger with retractor muscle and digestive system well visible through the shell, **B** pediveliger with enlargened head and foot with wings forming, and **C** postmetamorphic juvenile that moves with wings and has lost the velum. Shell about 0.4 mm long

apical position, splits into two bundles near the stomach and ends within the velar lobes. Blood is pumped by a larval heart from the velum into the visceral mass. The pallial cavity is rather wide above the head and narrow below the visceral mass. Mantle covering the shell interior and the visceral mass are fused with each other only in the very apical portion of the shell. This allows rapid withdrawal of the soft body deep into the tubular shell. When the shell measures about 0.45 mm in length metamorphosis occurs. During its course the velum is lost, and the larval heart is substituted by the double chambered adult heart positioned behind the stomach. The adult heart sucks blood from the mantle of the roof of the pallial cavity and pumps it to the intestines and head. The instant of metamorphosis may or may not be marked on the shell. There may be a slight break in the uniform increase of the shell width (Fig. 6C). A change in shell sculpture or shell structure is not present.

Cuvierina columnella (Rang, 1827)

Large eggs measuring at least 0.15 mm, probably more than 0.2 mm, develop into a veliger that hatches just prior to metamorphosis. The embryonic shell is 0.4 to 0.43 mm long, has a max. width of 0.15 to 0.17 mm, a circular diameter and is constricted at its aperture. The regularly rounded and smooth apical cup is 0.13 mm long and followed by an anterior portion exhibiting growth lines. A larva representing this stage of development was caught off Bermuda (Fig. 6D). *Cuvierina columnella* swims with the aid of a simple velum with two round lobes. The mantle is free from shell margin. The larval heart is the main blood pump of the veliger, and the two-chambered adult heart is developing but not yet functional. The retractor muscle is anchored to the apical end of the shell and can pull the body into the shell by contracting (Fig. 7A). During metamorphosis the shell becomes only slightly larger compared to the early veliger stage (approx. 0.4 mm long); the velum is lost, and the rudiments of the wings have grown into functional organs (Fig. 7B, C). The larval heart is still pumping but now aided by the adult heart. It sucks blood from the mantle and transports it forewards to the stomach and head. The pallial cavity is ciliated. A first flap as expansion of the mantle has been formed, aiding in handling the mucous float that serves the young *C. columnella* to float within the water and to trap food.

Individuals of *Cuvierina columnella* with an early ontogenetic, unbroken shell and without a septum have been described under the species name *Styliola sinecosta* (Wells 1974). These individuals were caught near Barbados, measured between 0.7 to 4 mm length, and had an apertural width of ca. 1 mm. A shell collected by us from the Red Sea with its early ontogenetic portion discarded is shown in Fig. 6E.

Fig. 6 **A** Adult of *Creseis virgula* spawning, **B** eggs during differentiation of their yolk content, **C** larval shell with begin of the teleoconch marked by decrease in diameter (length 0.8 mm). **D** *Cuvierina columnella* larva with large bilobed velum and organs visible through the shell. The retractor muscle is attached in the apex, while the digestive system lies far in front. **E** The apex of the adult shell of *Cuvierina columella* just after septum formation and after the juvenile shell has been discarded. **F** *Diacria quadridentata* embryos with three macromeres, **G** with embryos prior to hatching still in the egg capsules, **H** the same in detail with the stretched out remnants of the macromeres as yolk reserves

Diacria quadridentata (Blainville, 1821)

Mature individuals collected with the neuston sledge in the Gulf of Aden off Djibouti transferred spermatophores along the footlobe from one individual to the other. The following day spawn was released that consisted of transparent tubes (0.6 to 0.7 mm in width) holding ovoid egg capsules (0.16 to 0.19 mm in width) which were arranged in a row. The eggs measured about 0.1 mm in diameter, and after spawning they completed the first cell division. Three yolk-rich macromeres became successively covered by plasma-rich micromeres (Fig. 6F). Later macromeres split into four parts, and after approx. 24 h, they were totally covered by ectodermal cells. The trochophora-like embryo was 0.18 mm long and 0.12 mm in width having grown in size compared to the egg due to the uptake of yolk that was contained within the egg capsule. Its ciliated front does not represent the pole of the individual since preserved polar bodies were positioned at the side.

After 3 d of growth embryos are ready to hatch. They carry a tubular 0.12 mm wide and 0.18 mm long shell of oval shape. The mantle margin is still attached to the shell margin. Inside the shell the mantle of the most apical part of the body adheres to the shell where later the retractor muscle is anchored. When hatching the muscle is not developed. The intestine is filled with the four yolk cells. These become elongated, pointed at their apical ends and are twisted due to the torsion of the visceral mass (Fig. 6G,H). They are used as an energy source to keep the veliger alive for several days before being totally digested. At this time no food is collected. The velum is short and two-lobed. A pair of statocysts exist at the velum base. A short foot with cilia-like bristles acts as a sensitive organ. Hatching and detachment of the mantle edge from the shell edge are not quite in phase with each other. First growth lines appear some time after hatching (Fig. 8A).

Metamorphosis from veliger to adult-like organization probably occurs soon after hatching, and during this period the veliger larva produces no shell. The mantle and intestine withdraw from more apical portions of the shell, and the retractor muscle is anchored anterior to the apical end of the shell interior when the shell is approximately 4 mm long. When the individual is 4.2 mm long, the mantle folds begin to project from the wide anterior slit. The transition from the long juvenile shell with a rather narrow flattened apertural portion to the voluminous, short and spacious, wide shell of the adult is connected with the abandonment of the early shell. During the course of this transition the visceral mass moves foreward, a septum forms and apertural shell portions are thinned by dissolution of the mineral layers at its inner side. Later the juvenile shell breaks off and the adult shell is reshaped in the same way as described in the cases of *Cavolinia uncinata* and *C. longirostris* (see below).

Diacria trispinosa (Blainville, 1821)

The embryonic shell (0.19 mm in width and 0.28 mm height) of *Diacria trispinosa* is sculptured by rounded minute tubercules on a smooth surface, its cross section is of elliptical shape, and it has an oval outline. Its aperture is constricted (0.12 mm in width) and marks the beginning of growth lines. We could not determine whether the hatching specimen was a veliger or had already metamorphosed. It probably does not feed on plankton with its velum and will only do so when utilizing its mucous web and raft after metamorphosis is completed.

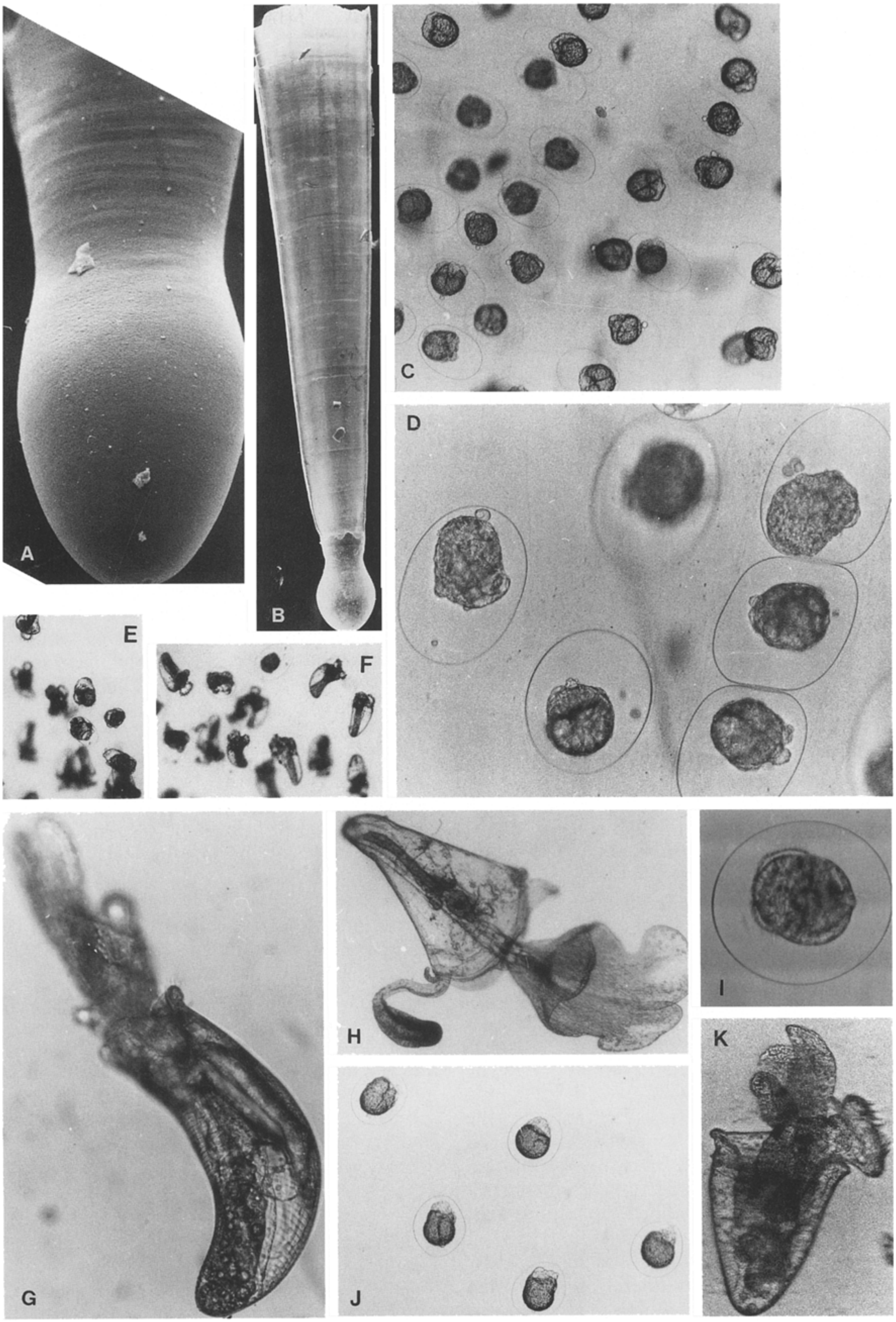
In *Diacria trispinosa* the juvenile portion of the shell is not cast off as in *D. quadridentata*. The embryonic shell has a more oval to spherical outline compared with *D. quadridentata* and is wider (0.19 mm) and higher (0.28 mm) (Fig. 8B). The apertural region is more strongly constricted, and the first growth lines become visible. It is quite possible that *D. trispinosa* hatches with a more or less adult organization being sustained by yolk reserves, since their eggs must be larger than those of *D. quadridentata*. Early ontogenetic shells of *D. trispinosa* are illustrated by Van der Spoel (1974) and Almogi and Reiss (1977, Pl. 6, Fig. 2).

Cavolinia uncinata (Rang, 1829)

Shortly after mature individuals of *Cavolinia uncinata* had been caught they produced egg strings consisting of mucous tubes that held ovoid transparent egg capsules of 0.4 mm width each containing one egg (0.08 mm width) (Fig. 8C). This agrees in general with the data presented by Lalli and Gilmer (1989), who reported an egg diameter of this species of about 0.1 mm. After first cell divisions micromeres grow around a few yolk-rich macromeres. After 24 h the first embryonic shell cap appears. The presence of polar bodies on the embryo demonstrates that neither the rudiment of the velum is positioned at the animal pole nor the rudiment of the shell at the vegetative pole; only the yolk-rich cells are concentrated at the vegetative pole (Fig. 8D).

After 3 d of development a 0.3 mm long cyrtocone shell forms (Fig. 8E, F), sculptured by very regular transversal lines. These lines represent sculptural elements of the primary shell and not growth lines, since the margin of the mantle is firmly connected to the shell edge. A velum rotates the embryo within the egg capsule. While the digestive system is being completed, well-formed statocysts guide swimming orientation;

Fig. 8 **A** *Diacria quadridentata.* Protoconch clearly distinguished from the embryonic shell that has no growth lines and is about 0.12 mm wide. **B** *Diacria trispinosa.* Protoconch attached to the juvenile shell of about 2 mm length. **C** *Cavolinia uncinata.* Embryos after first cleavage into micro- and macromeres, **D** with micromeres covering the macromeres, **E** embryos with cyrtocone shell in lateral view, **F** in frontal view. **G** *Cavolinia inflexa.* Juvenile specimen just after metamorphosis, **H** a little older specimen with pronounced mantle appendage. **I** *Cavolinia longirostris.* Embryo as early veliger in its egg, **J** during cleavage and macromere differentiation. **K** *Cavolinia uncinata* just hatched from its egg with foot and velum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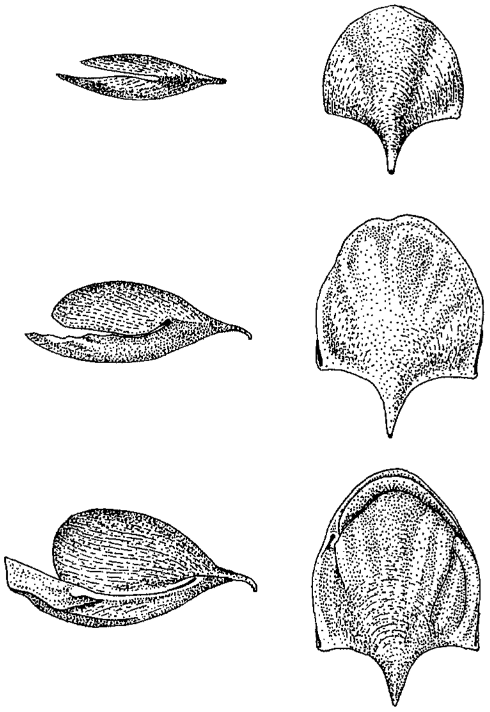

Fig. 9 *Cavolinia uncinata*. Sketch showing transition from flat and mineralized juvenile shell with intermediate reshaping and shell enlargement phase, to the more globular final adult teleoconch that is again well mineralized. A similar transition had been observed and sketched by Schiemenz (1906)

a functional blood pump is not present, and no pallial cavity was observed. On Day 4 of development the pallial cavity has been formed and wings appear next to the velum (Fig. 8K). On Day 5 all offspring hatch from their egg mass and start to swim with their velum. The wings have almost been completed and the digestive system functions, even though undifferentiated remains of the macromeres are still present as yolk reserves. Blood is pumped by the heart from the tissue of the mantle into the visceral mass and head.

Lalli and Gilmer (1989) reported on the hatching of veligers 92 h after spawning. One day later the velum starts to degenerate as wings begin to be used for swimming. The juveniles grow until the shell becomes much wider and a wide slit-like aperture appears. The mantle forms outgrowths which extend into long tentacle-like appendages and form sheets that cover the shell continuously along the margins. A flat shell forms, shaped like a shovel with margins open, representing the slit-like aperture (Fig. 9). The outer shell surface is often totally surrounded by a muscular mantle that extends from the marginal slit. The shell then becomes largely demineralized and subsequently is reconstructed to a larger and different shape within a short time. As soon as full shell size is attained, the shell reshapes from its flat shape to the typically bulging shape characterizing the late adult stage. During the transformation process that is described in more detail for *Cavolinia longirostris*, the shell is extremely thin but remineralizes immediately afterwards.

Cavolinia longirostris (Blainville, 1821)

Mature individuals caught in the Gulf of Aden off Djibouti produced gelatinous egg ribbons in which 0.3 mm large spherical egg capsules were forming two alternating rows. The egg in Fig. 8I, J measured 0.2 mm in diameter, and during the first steps of development three equal sized macromeres with a cap of micromeres became differentiated. Micromeres multiplied and slowly covered the macromeres. After 24 h of development the embryo was rotating in its capsule and measured 0.21 mm in diameter. After 2 d, a cup-like shell, two velar lobes, a foot with ciliated median portion, and a lateral pair of wing rudiments were present. On Day 4 offspring hatched and swam with the velum for some time. On Day 5 of development all juveniles moved around with their wings and the velum had been reduced. At that stage of growth the individuals began to feed.

Lalli and Gilmer (1989) found that *Cavolinia longirostris* from the Gulf Stream spawn two or three egg masses over a 12 h period. The egg masses contain 130 to 200 eggs each, but eggs are only 0.1 mm in diameter, which is half the size of those found in the Gulf of Aden. At 3 mm shell length, the visceral mass begins to withdraw from the horn-like apical portion of the shell. Shell surface can now be almost totally surrounded by muscular mantle that originates in the marginal slit. Thus, the mantle covers the upper and the lower surface of the shell (Figs. 10B, 11A).

When the shell has grown to about 4.8 mm length, a septum closes off the horn-like early ontogenetic shell and it breaks off (Fig. 10A, B). Cracks form behind the thin septum formed by the withdrawn visceral mass. A little later the early shell is lost. The rather flat shell is scarcely mineralized and flexible.

The shell is now largely demineralized and will subsequently be reconstructed to a larger and different shape within a short time (Fig. 10C, D). During this stage of ontogeny the activity of the heart is reduced, and the individual is not at all able to withdraw itself into the shell. The sheets of muscular mantle that cover the shell on the outside are firmly attached to the shell. The shell is demineralized to a degree that it is deformed when pulled out of the water. As most of the

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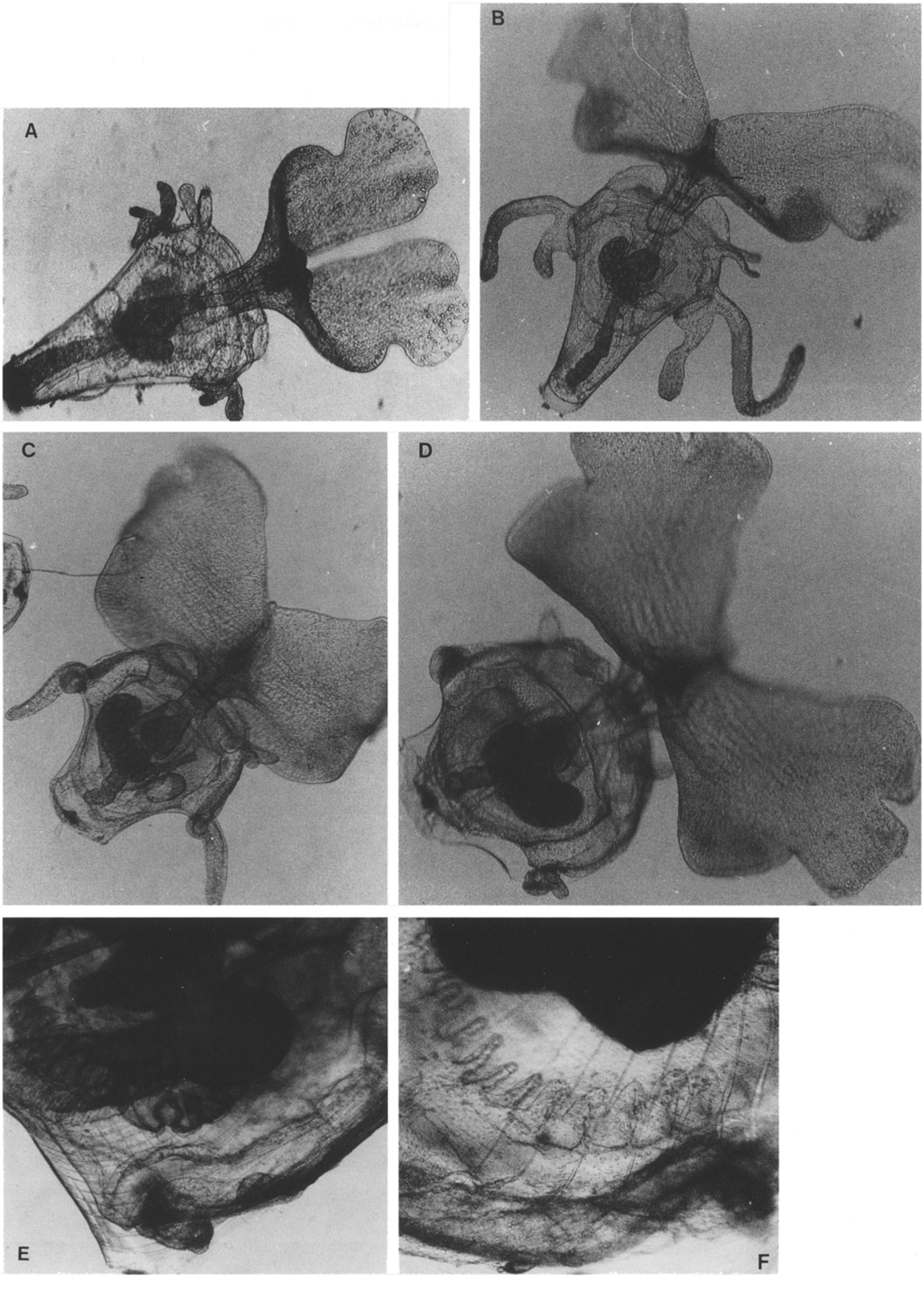
Fig. 10 *Cavolinia longirostris*. **A** Young individual during the formation of a septum at its caudal end, **B** a little later when the septum is present, **C** further developed having grown a broader shell, **D** and even later with shell ready to be demineralized and reshaped from flat to more globular. **E** The crenulated margin of the gill in an older individual, **F** forms as simple folds in a younger individual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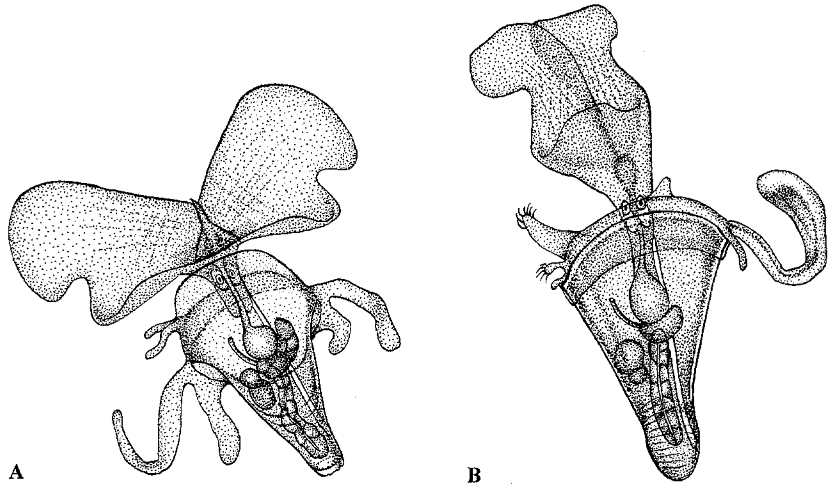

Fig. 11 *Cavolinia longirostris* and *C. inflexa*. **A** Juvenile stages of *C. longirostris* from the Red Sea with much of the about 3 mm long shell covered by mantle and **B** *C. inflexa* from Bermuda with the anterior portion of the about 2 mm long shell covered by mantle. They represent the time of ontogeny before transformation of the shell into more globular shape. The mantle margin not only surrounds parts of the shell but is also enlarged and forms tentacle-like flaps, while the mantle cavity remains simple

aragonite is dissolved, the shell grows rapidly in size until almost its final length. At this stage the interior is still quite narrow, and the space for the soft body is rather limited.

As soon as full shell size is attained, the shell is reformed from its flat shape to the typical bulging shape characterizing the late adult stage. The deforming forces are the muscular mantle on the outside and the mantle covering the interior of the shell, as well as the muscles attached to it. The outer mantle is provided with strong muscle fibres crossing over from left to right and pulling the flexible shell into the bulge by contraction. During this process the shell is extremely thin and will shatter and deform when touched by feather forceps. Right after reshaping due to the activity of the mantle, the shell is rapidly mineralized and thus fixed in its new shape. The mantle detaches from the outside, and the mantle flaps are free from then on. In case of emergency the pteropod can now fully retract itself into the shelter of its shell. The heart starts beating regularly again.

Due to reconstruction of the shell, the mantle cavity becomes much more spacious. Gas exchange is increased by the formation of a gill (Fig. 10E, F). Up to this stage, the heart has sucked blood from the roof of the pallial cavity, now it sucks blood from the gills. They appear first as a row of folds in the roof of the pallial cavity (Fig. 10F) and are covered by a ribbon of cilia transporting water continuously across its surface. These folds grow into lamellae (Fig. 10E), and the lamellae continue to grow until a circular gill fills much of the large pallial cavity and encircles the visceral mass.

Cavolinia inflexa (Lesueur, 1813)

According to Van der Spoel (1967), eggs of *Cavolinia inflexa* float near the surface in rounded mucus masses containing about 16 eggs each. We did not observe any incidences of spawning. Offspring hatch from the egg mass as veligers. Thiriot-Quievreux (1969) observed *C. inflexa* in the Mediterranean to metamorphose with a shell length of 0.3 mm. The veliger moves with a two-lobed velum.

Our observations from Bermuda indicate that the larval lifespan is rather short, and no food is needed during its course. The time of hatching is documented on the shell as a change in ornamentation. While the embryonic shell has very regular rings (Van der Spoel 1967, Pl. 5, Figs. 1,2, Pl. 10, Figs. 8, 10), the shell formed after hatching has obvious growth lines and less regular ribs. Just metamorphosed juveniles from Bermuda show a strong retractor muscle which is attached close to the apical tip of the inner side of the shell and which splits into two bundles before reaching the wings (Fig. 8G).

The pallial cavity occupies almost the whole inner space of the shell, while the visceral mass rests on the concave shell wall. The large heart pumps blood from the tissue of the roof of the mantle cavity into the visceral mass and head. Large statocysts lie directly next to the headring of nerve centres, between the branches of the retractor muscle and below the entrance into the pallial cavity. The open cyrtoconic shell is curved in bilateral symmetry twisting to a dorsal position.

Within 2 d of keeping the individuals in the laboratory, a large appendix to the mantle margin grew, which may function in operating the mucous web (Fig. 8H). The wings move like the wings of butterflies against each other and not backwards as is the case in *Limacina* spp. Only very strong disturbance will cause the pteropods to withdraw into their shells. The tissue of the mantle can be extended over the shell (Fig. 11B).

Discussion and conclusions

Skinny stages were observed in the case of *Clio pyramidata*, minute stages in *Cavolinia globulosa* and *Diacria quadridentata* (Van der Spoel 1967). These occur in samples, where other individuals are not skinny and minute, so that Gilmer's (1986) reply cannot explain this difference in shrinkage among individuals of the same species. But Gilmer found most contracted bodies within the thinnest shells, while older individuals in thicker shells did not contract as much. Gilmer (1986) and Lalli and Gilmer (1989) rejected Van der Spoel's (1967, 1973) idea of skinny and minute forms and found that these were produced by contraction during preservation. Although juveniles are found in shells with length and width dimensions similar to those of adults, the juvenile shells are thinner, and the ratio of body weight to shell weight is the same in both juveniles and adults. There seems to be no reason to believe that shell deposition of pteropods differs from that of other molluscs (Lalli and Gilmer 1989). In addition, the observations of Schiemenz (1906) had not been taken into consideration by Lalli and Gilmer (1989) or any other author during the last decades concerning the Cavolinidae. Schiemenz noted in preserved material that young individuals of *Cavolinia* spp. possess shells as long as those of adults. But he also noted that further growth was promoted by demineralization and reshaping of the shell. Schiemenz (1906, Pl. 1) illustrated this reconstruction of the shell and the transformation of *Cavolinia tridentata* from juvenile to adult stage. He noted that the curvature of the older ontogenetic stages was greater compared to the younger stages. Therefore he suggested that the individuals dissolve part of their shell, deform it and remineralize. In this process the outer lappets of the mantle played an important role according to Schiemenz (1906). This type of ontogenetic development, that is rather characteristic for these advanced pteropods, is confirmed by our observations of living material.

Janssen (1984) noted lateral wrinkles at the base of the early teleoconch in fossil *Vaginella austriaca* Kittl, 1886 and *V. depressa* Daudin, 1800 from the Miocene and related them to a mechanical transformation from juvenile shells with elliptical cross section to adult shells with almost circular cross section. These features present strong evidence for shell reconstruction and transformation in fossil *Vaginella* spp., which would resemble modern *Cavolinia* spp. and *Diacria* spp. in this respect. Reshaping was promoted by mechanical force that was applied to the shell by the tissue of the pteropod, as had been suggested by Janssen (1984). In addition dissolution of the mineral shell prior to the deformation process and renewed mineralization after its completion must be considered in the interpretation of the wrinkled shell of *Vaginella* spp.

Strategies of early ontogeny in the pteropods

Embryonic phase

Pteropods construct their shells in the same way as other conchiferan molluscs (Bandel 1982), which contradicts Van der Spoel (1967, 1973) according to whom the shell of pteropods may form in a mucus layer in contact with the tissue of the mantle. After the appearance of a rudimentary mantle on the embryo, a primary shell is secreted. It is attached to the epithelium that is producing it. Attachment between body and shell remains continuous until the primary shell is completed and the shell can function as an exterior skeleton. After the shell secreting, epithelium of the mantle edge and primary shell detach from each other, this shell may become mineralized. Attachment between soft body and shell is relocated from the mantle edge to the mantle below the attached muscle in a position on the posterior visceral mass. It may retain its shape or it may shrink and thus change its original shape. The change in shape is connected to the amount of yolk present within the egg. Those species that produce small eggs usually retain the original shape of the primary shell and stabilize it with the first mineralization. Other species having large amounts of yolk change more or less the shape of their primary shell before it calcifies.

Observations on early shell development in pteropods have been published by Van der Spoel (1967), Troost and Van der Spoel (1972), Haagensen (1976), Bé and Gilmer (1977), Van der Spoel and Boltovskoy (1981), and Bandel et al. (1984). The species of *Peraclis*, *Limacina*, *Creseis*, and *Styliola* which we discussed in the present study exhibit very little yolk, thus their primary shells do not change their morphology. All species hatch as planktotrophic veligers. *Clio pyramidata*, *Cuvierina columnella*, *Diacria* and *Cavolinia* species hatch as pediveligers and carry out metamorphosis before catching their first food. *Cl. cuspidata* and *Hyalocylis striata* most probably hatch after metamorphosis has been completed; in these two species the primary shell alters its original shape. It shrinks in *Cl. cuspidata* and forms a reticulate apical point. In the case of *H. striata*, it is almost totally abandoned by the body when the individual starts to mineralize it.

Veliger phase

Shell size and morphology reflect the mode of early ontogenetic development in pteropods as in other marine gastropods (Bandel 1975, 1981, 1990). In the case of the planktotrophic veliger, which has a small embryonic shell that is more or less identical to the primary shell, the young hatch as soon as the shell is functional. Here further energy for development is extracted from marine phytoplankton with the aid of the ciliary collecting system of the velum. In the pteropods such shells measure less than 0.1 mm in diameter, which is small when compared with other marine gastropods with a similar mode of development (Bandel 1975).

In other cases, species hatch as non-feeding veligers that have yolk reserves which are sufficient to sustain them for a few hours or days until metamorphosis from veliger to adult-like organization occurs. The embryonic shell may be identical to the primary shell, or it may be different. The size of the embryonic shell measures between 0.1 and 0.4 mm. In the case of *Diacria quadridentata* the shell is not yet detached from the mantle when the young hatch. A larval shell may be added before the teleoconch is secreted, e.g. *Cuverina columnella*, or the embryonic shell is succeeded by the teleoconch, e.g. *Cavolinia* spp.

A third case may be seen in *Clio cuspidata* and *Hyalocylis striata* where the young pteropods hatch in the completed postmetamorphic stage, and the embryonic shell is larger than 0.45 mm and shows signs of shrinkage and subsequent mineralization.

All these features agree well with what is known from other gastropods (Bandel 1982). The morphology of the early ontogenetic shell simply reflects the strategy of embryonic development either with little yolk and planktotrophic veliger, with more yolk and pediveliger hatching, and with much yolk and miniature adult hatching. Fioroni (1982) argued that the early ontogeny of pteropods reflects the transformation of final stages into their early ontogeny. This statement can only be verified in regard to the adult shell of the pteropods, while pteropods show similar modes of early development with other marine gastropods in all essential aspects.

An apparent difference to many other gastropods is documented in the shape of embryonic and larval shells, which are in many pteropods not coiled. However, this is not only a feature that can be observed in pteropods. Some benthic dorid opisthobranchs produce a veliger shell very much like that of a pteropod with uncoiled shell (observation by KB), and the embryonic and larval shells of the gymnosomate pteropods are uncoiled. Uncoiled shells occur as pathologic cases in many marine gastropods which are usually coiled (Bandel 1975, 1982) and uncoiling of the larval shell is also observed among some caenogastropods, like the caecids (Bandel 1991b). Usually an aberrantly uncoiled embryonic or larval shell of a coiled adult leads to a non-functional teleoconch and is thus exterminated when the larva settles to the ground. This restriction does not apply to the pteropods, where an uncoiled shell is no disadvantage. This may be due to selection by phylogenetically biased processes at the beginning of pteropod evolution during the late Paleocene and early Eocene, where straight early ontogenetic shells can be observed (Curry 1965). Thus, we have to consider a mode of development that favoured the pathological case of benthic gastropods, as seen in the calvoliniid line of pteropod evolution (Bandel 1991b). The presence of non-coiled early ontogenetic shells in thecosomatous pteropods provides us with evidence for the holopelagic existence of this lineage of the heterostrophic branch of the gastropods. It is conceivable that the late Paleocene coiled members of this lineage still had a more or less extended stay in the benthos shortly after their metamorphosis, producing a mucous raft only later in life. With non-coiled larval shells they could no longer adapt themselves to benthic life. These early pteropods thus stayed in the plankton throughout their life and probably produced mucous rafts right after metamorphosis, like their modern relatives.

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