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Stages in the ontogeny and a model of the evolution of bivalves (Mollusca)

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With 21 figures

Kurzfassung: Der Vergleich der Ontogenesen von Muscheln verschiedener Lebensräume und unterschiedlicher systematischer Position erlaubt zwei Schlüsse. Der erste ist, daß alle Muscheln sich an einen gleichartigen Entwicklungsgang halten, der sich in 6 Stufen unterteilen läßt. Die ersten drei Stufen ähneln Entwicklungsstadien, die auch bei anderen Invertebraten auftreten. Die Stufe 4 ist allen conchiferen Mollusken gemeinsam, und in der 5. Stufe wird der Organisationsgrad der Muscheln erreicht, während in der 6. Stufe die gattungstypische Organisation eingeführt wird.

Der zweite Schluß besagt, daß in diesen muscheltypischen Grundrahmen spezifische Modifikationen eingebaut werden. Der Entwicklungsverlauf bei *Teredora* ist dem vieler mariner Muscheln ähnlich, zeichnet sich darüber hinaus aber durch seine große Anpassungsfähigkeit aus. Die erwachsenen Tiere sind hingegen auf ihre Lebensweise im Holz stark spezialisiert. Bei *Anodonta* ist das Umgekehrte der Fall, und die stark spezialisierte Embryonalentwicklung enthält sogar eine Phase, während der der Embryo parasitisch lebt. Das erwachsene Tier weist eine sehr einfache und grundlegende Organisation auf. Bei *Sphaerium* sorgen Brutkammer und durchgehende Nahrungsversorgung für einen Entwicklungsablauf, der geradlinig auf die adulte Organisation hinführt.

Der stufenartige Ontogeneseverlauf zeigt einen Bauplan-Ausbau der Muschel auf, der als Modell zur Entstehung der ersten Muscheln im Kambrium genutzt werden kann. Demzufolge entwickelten sich Muscheln (Protobranchier ausgenommen) durch eine Veränderung in der Veligerphase der Embryogenese der einschaligen Vorfahren, bei der die Schalenverkalkung betroffen war und der Buccalapparat in Verlust geriet.

Abstract: Comparison of the ontogenies of bivalves of different habitats and systematic position provide two main conclusions. The first is that bivalves stick to a certain basic program of ontogeny which can be divided into six phases. The first three phases are parallel to those of some other invertebrates, the 4th phase is parallel to that of conchiferan molluscs, with, the 5th phase, bivalve characters are acquired, and in the 6th phase, genus-specific adult organization is reached.

The second is that within this basic developmental programm specific differences occur. The ontogeny of *Teredora* is similar to that of many marine bivalves and is characterized by a strong plasticity. The adult, in contrast, is highly specialized for living within wood. In *Anodonta*, the opposite is true and embryonic development even includes a parasitic stage, while the adult is of a more general organization. Due to brood-protection and embryonic nursing, the whole organogenesis of *Sphaerium* becomes directed towards adult organization.

Ontogenetic development of a general body plan of the Bivalvia provides a model for the evolution of the first bivalves (protobranchs excluded) from univalves by a one-step alteration connected with shell mineralization and loss of the buccal mass affecting the embryo near end of embryogenesis.

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Introduction

During Cambrian time the classes of Recent conchiferan molluscs arose. The phylum itself is much older and representatives entered the Cambrian with the characteristic body plan consisting of (1) the foot and head with the buccal apparatus; (2) the visceral mass with the digestive system – fluid pumps and excretion organs and (3) the mantle covering the visceral mass and extending over it laterally to form the pallial cavity. The worm-like Caudofoveata may have, up to our time, preserved much of this basic molluscan body plan (SALVINI-PLAWEN 1981). With onset of the Cambrian time, such organisms produced a shell by secretions of the mantle. As consequence, gas exchange was concentrated in the lateral cavities so that gills formed and these are connected to adaptations of the fluid pump.

Still within the Cambrian, shell and mantle formation became optimized when the conchiferan status of mollusc organization was reached (POJETA 1980, BANDEL 1982, RUNNEGAR 1983). When the mantle which arises from the shell gland rudiment after primary shell production during embryonic development, detached from tissues of the soft body, the latter remained connected to the shell only by specialized mantle cells and their organic thread secretions (NAKAHARA & BELEVANDER 1970, BANDEL & SPAETH 1983). In the ontogeny of conchiferan molluscs, the time of formation of the mantle rudiment (shell gland) during ontogeny of conchiferan molluscs became firmly fixed to the stage of development that follows right after the digestive system is laid out.

From simple bilateral univalved conchiferan ancestors, representatives of all the still existing classes developed: scaphopods by fusing the shell margins of the embryonic shell into a tube; gastropods by torsion of the soft body followed by torsion of the shell (BANDEL 1982); cephalopods by introducing chambers to the apical portion of the shell that kept in contact with the living tissue. All these groups retained the radula and buccal apparatus with the possibility to form single or divided jaws.

This otherwise omnipresent homology throughout the phylum was lost in the case of the bivalves; which, in addition, split the univalve of the ancestral conchiferan shell into two valves.

The formation, morphology and structure of the early embryonic conch of the bivalves is poorly known. The rudiments of the mantle and all shell-producing epithelia are generally supposed to undergo an invagination prior to shell formation. Transformaton of a single embryonic shell into the characteristic two valves has been observed but not well analysed. Comparison of ontogenies of systematically different representatives of the bivalves can provide information from which general trends of bivalve ontogeny can be extracted from species-specific features.

HASZPRUNAR (1985) found evidence supporting STASEK's (1961) ideas that nuculoids are not direct forerunners of the higher Bivalvia. They may represent a possible early sister group of the bivalve stock (RUNNEGAR & BENTLEY 1983). Relations between members of the different classes of conchiferan molluscs can be determined when their body plans are compared, especially in all aspects of their ontogenic development. Characters that are common to all conchiferans can be utilized in the reconstruction of the shape and organisation of their common Cambrian ancestor. Information on the early formation of the shell can only be provided by living embryos. Data obtained from the life cycle of recent animals are thus required if fossils are successfully to be interpreted. They, in turn, represent the only record available that helps to trace the actual pathway taken by evolution.

With this in mind, three different ontogenies were studied. The first is that of *Teredora malleolus,* the shipworm, living in wood that drifts in the sea. This species shows a flexible mode of embryonic development that, in its general course, is typical of and similar to the ontogenies of many species of marine bivalves. The second ontogeny is that of *Anodonta cygnea,* a

taxon belonging to an ancient family of fresh-water clams that has developed a special parasitic phase between embryonic and adult life. The third ontogeny described is that of *Sphaerium corneum*, a modern fresh-water clam that broods its young until they hatch as miniature adults.

All studied species or genera have attracted the attention of other workers who carefully observed their development from the egg to the young animal. Among these the accounts of HATSCHEK (1880) on *Teredo*, LILLIE (1885) and HERBERS (1913) on *Unio* and *Anodonta*, and ZIEGLER (1885) on *Sphaerium* provide rich information. From MEISENHEIMER's (1901) study of *Dreissensia* (= *Dreissena*) valuable data can also be extracted. Studies carried out by more recent authors provide only few data with regard to the required information, as can be concluded from the summary accounts presented by RAVEN (1958) or SASTRY (1979).

Teredora malleolus

Pieces of wood larger than a few centimeters sunken to the bottom of the shallow sea surrounding Banyuls-sur-Mer (Western Mediterranean Sea) are usually inhabited by numerous individuals of teridinid clams, commonly of the species *Teredora malleolus*. To extract sperm and eggs from the animals, the posterior portion of the body was torn open and sex products were released into the water. In June 1981 and August 1983 fertilization was carried out in vitro in this way. Sperm and eggs may also be released when the oxygen content of the water is lowered and when rapid changes of temperature occur.

1. phase: Fertilization

Mature eggs and spermatozoa were present in most individuals opened. The spherical egg measures about 25 to 35 µm in diameter and is tightly surrounded by a primary egg membrane that is covered with a gelatinous mucus layer (Fig. 1a).

During their rapid movement towards the egg spermatozoa touch the mucus cover, stop their erratic motion and position themselves vertical to the egg surface. The 3 µm long head is oriented towards the egg surface and the 10 µm long tail away from it until the head penetrates the egg cortex. Then the mucus layer detaches from the egg and removes spermatozoa still attached to it.

After fertilization the animal pole becomes flattened and here two small clear polar bodies appear (Fig. 1b). In the formerly granular egg content protoplasm flows to the animal pole, while yolk becomes concentrated at the opposite vegetative pole.

2. phase: Cleavage

At the animal pole, which later is represented by the anterior portion of the trochophore, the polar bodies lie in the furrow of the first cleavage separating a small cell rich in protoplasm (micromere) from a large yolk cell (marcromere) (Fig. 1c). The small cell lies in the position of the future dorsal side (hinge line), while the big cell is in the position of the future venter (gut). Thus radial symmetry of the embryo is lost and bilateral symmetry is reached (45 minutes; 25 °C).

The yolk macromere forms a deep cleavage furrow with a spindle in its center (90 minutes). But the lower segment rapidly shrinks in size until it is about the same size as the micromere before cells form. Several similarly small cells split from the yolk rich cell, while the micromeres divide into equal cells (Fig. 1d). When the 16 cell stage is reached (150 minutes) one side of the embryo is formed by the large yolky cell and the other side is covered by a cap of small protoplasm – rich cells. The animal pole still indicates the dividing line between both parts.

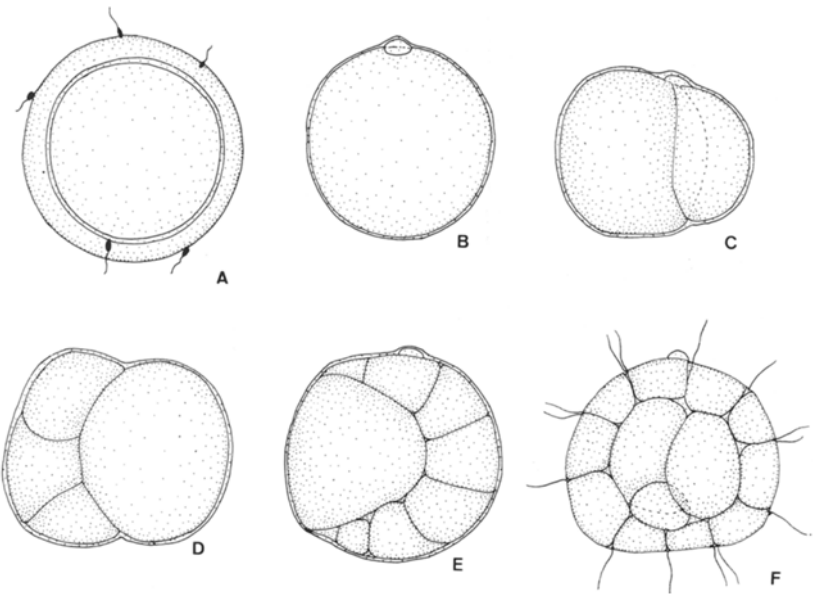


Fig. 1. Upper left to right: The unfertilized egg of *Teredora malleolus* (0.03 mm wide) is surrounded by a mucus cover to which spermatozoa attach (A). The fertilized egg loses the mucus cover and is surrounded by the primary membrane. A polar body is formed (B) before first cleavage (C). – Lower left to right: The four-cell stage shows three plasma-rich small cells and one large yolk-rich cell (D). The animal pole is marked by the polar bodies (E, F). When cells enclose the yolk-rich cell, the primary membrane dissolves and cilia form ("planula" stage) (F).

With further cell proliferation, the micromeres beginn to cover the animal pole and only the polar bodies indicate its position. The embryo becomes more rounded in shape (Fig. 1e). When the primary egg membrane dissolves (5 hours; 15–25 °C), polar bodies usually detach, but in some embryos they remain attached by small threads and still indicate the position of the animal pole.

The dissolution of the membrane coincides with the appearance of cilia and occurs shortly after the macromere has divided into two almost equal cells. A small part of the two macromeres remains integrated in the outer cell layer, with most of the cell body extending into the interior. The spherical, free swimming embryo is still of the same size as the egg (Fig. 1f).

3. phase: Gastrulation

The next phase of development may follow several paths. All are normal variations and not lethal aberrations, however, because in each case the development progresses to a normal straight-hinge veliger. In the most simple case the ciliated ball of cells (sterroblastula) changes its shape due to the formation of two indentations. It is a now irregularly oval and of somewhat flattened outline. The depressions are the rudiments of mouth and anus and the whole digestive system between them. The embryo has changed into an invagination gastrula, which afterwards increases in size and becomes more rounded in outline by the liquid pumped in and the filling of the primary body cavity between ectodermic and endodermic layers.

In the alternative case, the primary body cavity fills with liquid and expands (coeloblastula) before a digestive system has started to form. The embryo thus increases in size (up to 2 times) and may swim for up to 15 hours. At the end of this period, ciliation consists of a ring of

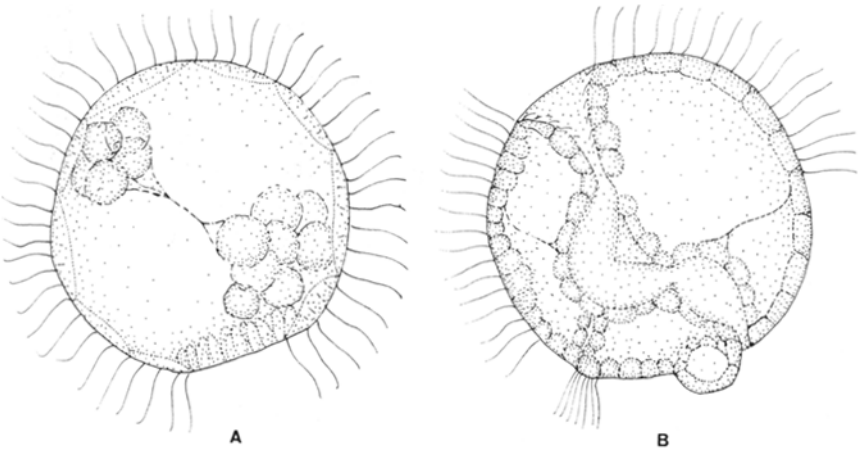


Fig. 2. The free-swimming embryo of *Teredora malleolus* forms a large primary body cavity into which cells grow from the rudiments of the mouth and the anus at the same time (A). When these cells meet, guided in their growth by mesenchymal cells, they fuse and form a functional gut of the trochophora larva (B).

long cilia (prototroch) around the animal pole, while the remainder of the body is evenly ciliated. Here cells that have split from the ectodermal cover of the embryo migrate at the same time from two opposite points into the central cavity so that the mouth forms near the prototroch and the anus near the posterior long tuft of cilia (apical flagellae) (Fig. 2a). Mesenchymal cells connect rudiments of the digestive system with each other and due to their contraction the embryo changes into long-oval shape.

In both cases of gastrulation, the resulting embryo is a trochophora with open mouth and anus connected by a tube that is widened in its centre to form a stomach (Fig. 2b). The development of a functional digestive system, from the start of gastrulation requires 5 to 40 hours. After the digestive system is completed it is utilized for plankton feeding. Particles are collected by the ciliary system of the prototroch that surrounds the head, and by cilia that cover the mouth as well as foregut (stomodaeum). Within the rather large globular stomach, food is rotated and mixed with the products of the glands of the crystal-style sac opening into it. In the development into a feeding trochophora, the blastopore as opening of the archenteron functions as the anus. Hind gut and anus form independently of the fore gut. Development proceeds directly to the use of organs in the trochophora long before the mantle appears.

4. phase: Mantle rudiment and primary shell

Mantle cells form from ectodermal cells of the dorsal side near the anus, far from the prototroch, when the embryo measures between 30 and 60 µm in diameter. At first mantle cells have a very dense appearance and form a long-oval dark zone (Fig. 3). The embryo is now marked on the ventral side by the openings of the digestive system and on the dorsal side by the dark rudiment of the mantle. When the first shell material appears, the mantle cells are arranged to form a very shallow depression. With the onset of shell growth the embryo rapidly increases in size (50–70 µm) by liquid being pumped into the body cavity. During growth, the mantle cells rapidly loose their dense aspect and become as transparent as other ectodermal cells when about one third of the primary shell is sectreted (Fig. 4). The elongate-oval organic

shell remains attached to the cells until it is large enough to fold into the shell of the straight hinge veliger. Mesenchymal cells differentiate into muscles that connect the mantle epithelium with different parts of the body. Three pairs of muscle bundles form and connect the shell to the body. One connects the shell and its mantle with the anal region; the second connects it with the velum-head area and the third connects it to the central portion of the digestive system (Fig. 4). The fibres of the last bundle increase in number and size and finally connect the two sides of the primary shell together.

5. phase: A. Transformation into the veliger

When the primary shell is completed and can cover the body, two changes rapidly appear. First the shell detaches from the cells that secreted it and the body is connected to the shell behind the shell margin with specialized cells of the mantle. Second the shell becomes convered by an aragonitic mineral deposit on the inner side of the two valves, while the dorsal side, the hinge line, remains elastic.

With the primary shell mineralized, the central muscles can contract and pull the valves towards each other and water is expelled from the primary body cavity. The dorsal fold of the primary shell is straight so that the term "straight hinge veliger" suggested in the literature is absolutely appropriate. The other two pairs of muscles at the anterior and posterior ends can also contract and pull the ciliated head (velum) as well as the tuft of cilia posterior to the anus into the cover provided by the shell. Fibres of the three pairs of muscles pull the body under the two valves and this simple process produces the mantle cavity of the veliger. With the conch now functional, the soft body can be protected against disturbance from outside.

Development of the fertilized egg into a functional veliger larva took a minimum of 68 hours in water of about 28 ° C; it took only 4 hours more in colder water, at 15 ° C (August 83). The entire development took place in sea water. Under favourable conditions these first stages of deveolpment occur within the gill (epibranchial chamber) of the mother. Usually veligers are expelled that are straight hinged or that have developed even somewhat further (Fig. 5.1 and 5.2).

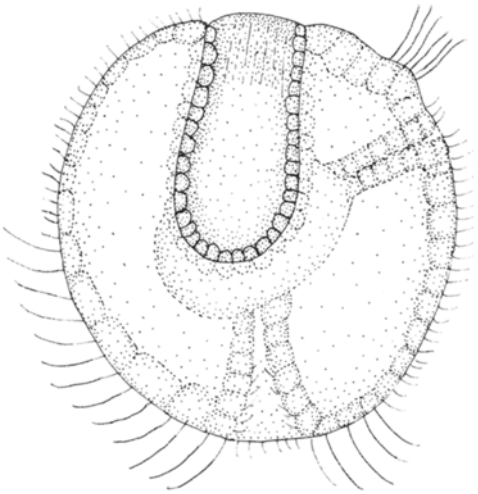


Fig. 3. Dense cells produce the primary shell (top, centre) and hold its margin form the primordium of the mantle. Ciliation differentiates and forms a food-gathering device around the mouth (bottom, centre) of the preveliger larva of *Teredora malleolus.*

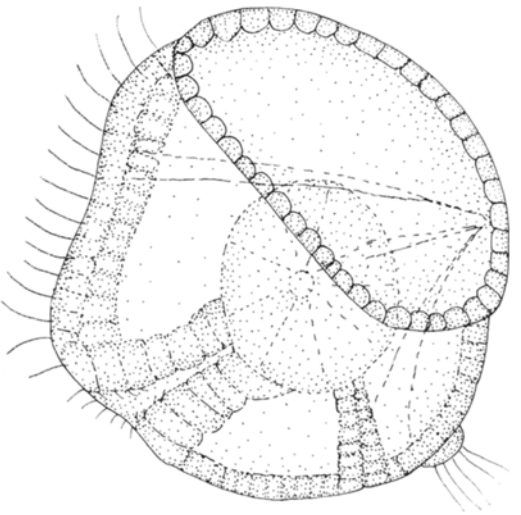


Fig. 4. Cilia of the head (left) propell the larva of *Teredora malleolus* through water and gather food that is transported into the stomach (centre). Digestive wastes leave at the anus (lower right). The forming primary conch is attached to the soft body by three pairs of rudiments of muscles.

5. phase: B. Secondary shell and veliger

The straight hinged veliger feeds on planktonic unicellular algae. Food particles are collected by cilia and transported into the mouth, which is continuous with the short ciliated oesophagus that ends in a simple globular stomach with the crystal style gland attached to it. Two digestive glands on either side of the stomach extend below the deepest concavity of the valves of the conch and discharge their secretions into the gut. The stomach is ventrally connected with the straight hind gut.

When the secondary shell is almost completed the foot differentiates as a long structure that is covered by cilia and the byssus gland in the posterior end of the foot becomes prominent. The veliconcha has thus changed into the pediveliger. The secondary shell differs in shape from the primary shell, a feature often designated in the literature by the terms prodissoconcha (1 = smooth primary shell) and prodissoconcha 2 (= growth lines on secondary shell) (Fig. 5.1). The conch is more rounded, shows growth increments and the hinge is much shorter in relation to valve width (Fig. 5.2). The hinge consists of 4 interlocking teeth, two on each valve that fit into grooves on the ohter valves (Fig. 5.2).

Veligers of *Teredora malleolus* from Banyuls-sur-Mer were not kept alive for more than a few days after formation of the straight hinge veliger. Data from the literature suggest, however, that teredinid species usually live up to 20 days in the plankton (TURNER & JOHNSON 1971). YONGE (1924) kept *Nototeredo norvagica* veligers alive for 5 weeks without obtaining metamorphosis. On the other hand teridinid veligers bred within the gill pouch of their mother may stay in the plankton for only a very short period of time (ISHAM & TIERNAY 1953). *Nototeredo norvagica* veligers for example hatched from infested wood collected near Banyuls-sur-Mer, settled within 4 days and drilled into the wood (Fig. 5.1–6).

Within the teridinids the free swimming phase can be prolonged or shortened in an opportunistic way. These animals can respond with great flexibility to favourable or unfavourable conditions. This is reflected also in the data on *Teredo navalis* presented by HATSCHEK (1880) and TURNER & JOHNSON (1971). In one case, veligers hatched and lived in the plankton for up to 20 days, in another they had a totally internal development. SCHELTEMA (1971) found phy-

toplanktotrophic veligers of teridinids (*Teredora* sp.) widely dispersed in the North Atlantic Ocean, and they are carried over great distances along the margin of continents and possibly even across oceans. This is so even though the vast majority of larvae metamorphose before the age of three weeks.

6. phase: Adult organization

Settlement and attachment to wood was by *Nototeredo norvagica* observed at Banyuls-sur-Mer, Mediterranean Sea (1976). The pediveliger produces a long thread of byssus to attach itself. If no wood is present the byssus can form a float at the water-air interface (Fig. 19) (BANDEL 1981). Suspended on it, the pediveliger metamorphoses into a juvenile and can thus survive for many days, perhaps several weeks, after the actual free swimming phase is completed and until the byssus raft comes into contact with drifting wood. Now the young can establish itself on the wood.

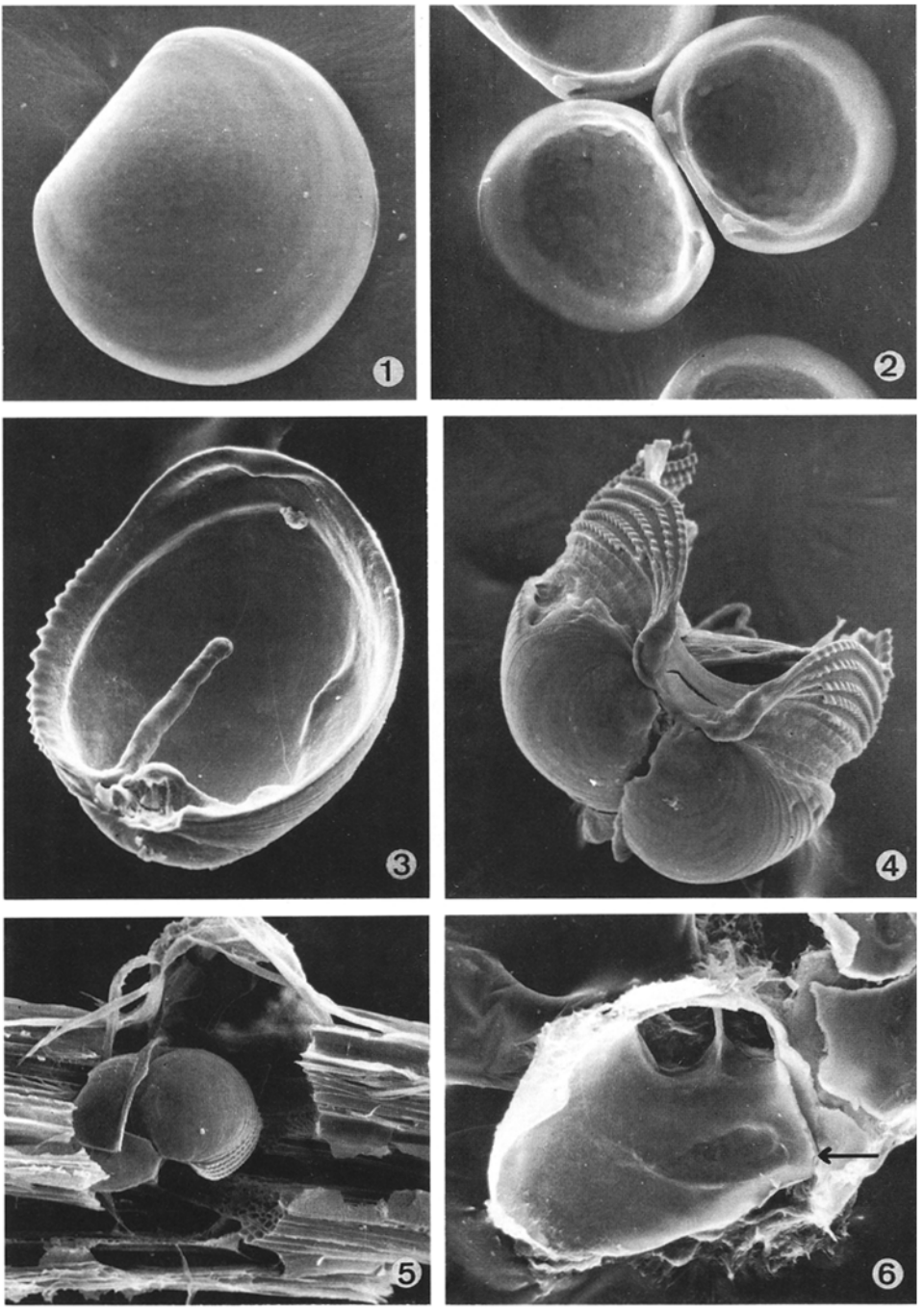
The shell formed during the floating stage is the adult shell, but it is produced at a much slower rate than that of individuals that have become attached to wood.

In pediveligers that have attached themselves to wood with the aid of byssus threads (Fig. 5.1), the organization of the body as well as the morphology and function of the conch changes, and the kidney and heart become functional around the hind gut. Food is still filtered from water by ciliary motion but of the gills rather than the velum and it is transported wrapped up in mucus rods to the former velum the wings of which have changed into mouth (labial) palps. The posterior mantle fuses to form the siphon with separated inhalent and exhalent openings.

The conch is totally transformed in shape: During a single day a long projection (apophysis) is secreted on the hinge (Fig. 5.3), a mineral attachment ridge for the internal ligament (chondrophore) forms, and a dorsal knob (condyle) fits into a depression of the other valve. Shell additions to the valves are unilateral and only the anterior margin is enlarged by calcareous increments covered with serrations on the outside (Fig. 5.4). The posterior margin does not grow, and thus a gape is formed. Where the posterior adductor muscle is attached to the valves, a deep scar forms in a roughly medial position. The anterior adductor muscle lies close to the hinge (Fig. 5.3).

When the strong posterior adductor is contracted, the serrated anterior shell scrapes across wood, while contraction of the anterior adductor brings back the shell into its original position. When the shell moves, valves not only come closer to each other, but also are rotated against each other. The resulting rotation of the valves, different from that of other bivalves or even its own veliconcha, where valves can only close and open, is possible due to the reconstruction of the ligament. Other authors, such as HATSCHEK (1880), ROCH (1940), RANCUREL (1951), ISHAM & TIERNEY (1953), TURNER (1966), KONOPKA (1974), have reported similar function of teridinid shells.

Fig. 5. SEM photographs of *Nototeredo norvagica.*
1: The veliconcha shell of *Nototeredo norvagica,* seen from the outside, shows a straight-hinge veliger with first increments of growth laid down by the free larva; × 400.
2: Veliconcha shell opened reveals the characteristic simple hinge; × 320.
3: Conch of newly metamorphosed individual with a totally different hinge (lower side) that formed within a few hours' time after settling; × 120.
4: The shell added after metamorphosis has a totally different shape and morphology; × 100.
5: Juvenile in its hole in the wood with chimney and pallets attached near it. Soft tissue has become dried; × 100.
6: The newly calcified sipho tube of *Nototeredo* shows two holes for inhalent and exhalent current and a crescentic scar of the attachment of the sipho-tissue and pallet musculature to the tube wall (arrow); × 100.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When the pediveliger settles on wood, it cleans the site for its burrow mainly with its foot and thus produces a first low depression to which it becomes firmly attached by byssus threads. It begins to enlarge and deepen the hole by mechanical action of the shell, and the foot utilizes the scraped wood particles and faecal pellets to form a wall around the pit until a dome is formed from which only the two ends of the siphon project in separate chimneys (Fig. 5.5). The byssus is lost and the foot becomes broad and short. Within six days the bivalve has burrowed into the wood to such a depth that the conch has disappeared from the surface. Now the mucus dome surrounding the siphon becomes mineralized by a solid calcareous layer secreted onto its inner surface from slime produced by the mantle epithelia of the siphon (Fig. 5.6). At the same time the siphon walls secrete a pair of stalked lids (pallets) of paddle-like shape and the siphon attaches below these to the calcareous tube (Fig. 5.5 and 5.6). With the long siphon firmly attached to the end of the burrow, the remainder of the body becomes worm-shaped during further growth. The shell of teridinids has changed its function from a protective exoskeleton to a drilling device. Once established firmly within the drifting wood, the bivalve may grow and mature very rapidly. ROCH (1940) found, that *Teredo navalis* were sexually mature after only 6 weeks in the wood. Growth of an individual is limited to the size of burrow that it can construct. Individuals that settle on a large uninhabited piece of wood reach much greater size than those that subsequently settle on the wood but all reach maturity and reproduce. Only very young individuals of *Nototeredo norvagica, Teredo navalis* and *Teredora malleolus* may feed on wood, because larger juveniles and adults live in burrows that are totally coated by calcareous material secreted by the mantle epithelium. They feed only on particles that enter the burrow through the siphon from the outside water.

Anodonta cygnea

Numerous individuals of this fresh water clam belonging to the Unionidae were collected during summer and fall 1983 from fish ponds near Röttenbach in Franken (Southern Germany). Individuals 4 years of age and older regularly contain embryos within the brood pouch (demibranch) of the outer gill. Up to half a million embryos at the same stage of development are present in the two separate long packs within one animal.

1. phase: Fertilization

Eggs of 80 to 100 µm diameter are covered by transparent primary membranes and are suspended in liquid yolk within a transparent spherical capsule 150 to 200 µm in diameter. Spermatozoa come from other animals and enter the egg through the preformed microphyle opening of this capsule. During the process of fertilization in the brood pouch the egg usually adheres with protoplasmic threads to the micropyle.

2. phase: Cleavage

Cleavage proceeds in a way very similar to that of *Teredora* (LILLIE 1895). Two cells of unequal size are formed by the first step, but in contrast to *Teredora,* the yolk-rich cell (macromere) lies at the future dorsal side of the embryo (hinge-line), and the small cell (micromere) the position of the ventral side (foot). Yolk is enriched where future shell-mantle and median adductor muscle grow. The egg membrane dissolves very early.

3. phase: Gastrulation

The macromere divides into two cells when the micromeres have spread over its surface and have almost covered it. During the subsequent gastrulation, the dense body of cells (ster-

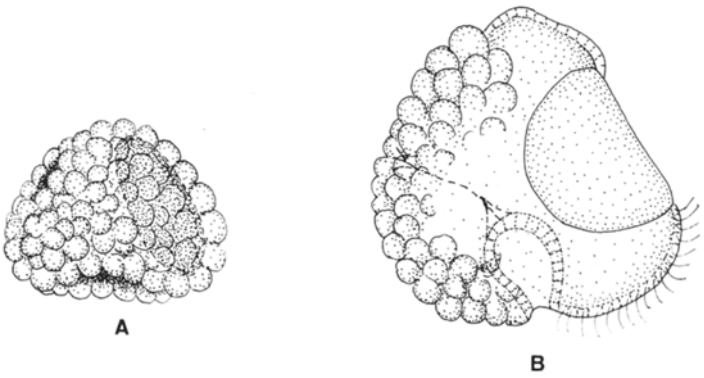


Fig. 6. Embryo of *Anodonta cygnea* during formation of the rudiment of the digestive system. The mouth (upper left) and the anus (lower centre) forms grooves (A). – After gastrulation, the body is increased in size by water pumped into the primary body cavity and yolk from the egg capsule is digested through one body opening (later the anus, bottom, centre). Rudiment of the mantle is present and produces the primary conch (B).

roblastula) forms two pits, which are the rudiments of mouth and anus. They form on either side of the polar bodies and opposite the yolk-rich area (Fig. 6a). During this stage, the embryo is motionless and not bigger than the egg. Only the rudiment of the hind gut continues to develop while the rudiment of mouth and fore gut lies dormant until the parasitic phase. The rudiment of the anus and the hind gut forms the typical invagination of the archenteron.

4. phase: Mantle rudiment and primary shell

The embryo increases in size by fluid pumped into the primary body cavity and becomes rounded to ovoid in form. The embryonic mouth is now open and a plate with dense short ciliation forms beside it, causing the embryo to slowly rotate within the egg capsule. At the same time, cells of the dark yolk-rich area of the embryo are transformed into a dense tissue that is the rudiment of the mantle and of the central muscle (Fig. 7.1). Cylindrical cells of this primordial mantle form a low depression (Fig. 6b). When this stage is reached, the embryo starts feeding on egg yolk. The beat of the cilia drives yolk into the gut where it is absorbed by storage cells into large vacuoles (Fig. 6b). The embryo as a whole increases the space of the primary body cavity and produces many storage cells so that is grows to about three times its former size, with egg capsules also expanding. The mantle forms a minute and flat organic primary shell that is attached to the cells that secrete it (Fig. 7.1). Subsequently the margin of the mantle (muscle mantle) spreads around the shell edge and fixes organic threads to the outer shell surface (Fig. 7.5) and holds the shell. Only afterwards the shell detaches from the shell mantle.

5. phase: A. Secondary shell

Due to the rapid increase in size of the embryo, mantle cells are stretched and shell is secreted rapidly. Calcification of the valves starts after detachment of the primary shell from its secreting epithelium (Fig. 8.1). From then on, shell growth and calcification are connected to each other. The mineral deposits show very regular structure of the crystallites as well as a very regular pattern of pores (Fig. 8.3 and 8.4). Mantle cells in front of the shell-secreting cells cover part of the shell and the whole shell margin from the outside (Fig. 7.5). The mouth remains open until both sides of the embryo are covered by shell (Fig. 9). Albumen cell production

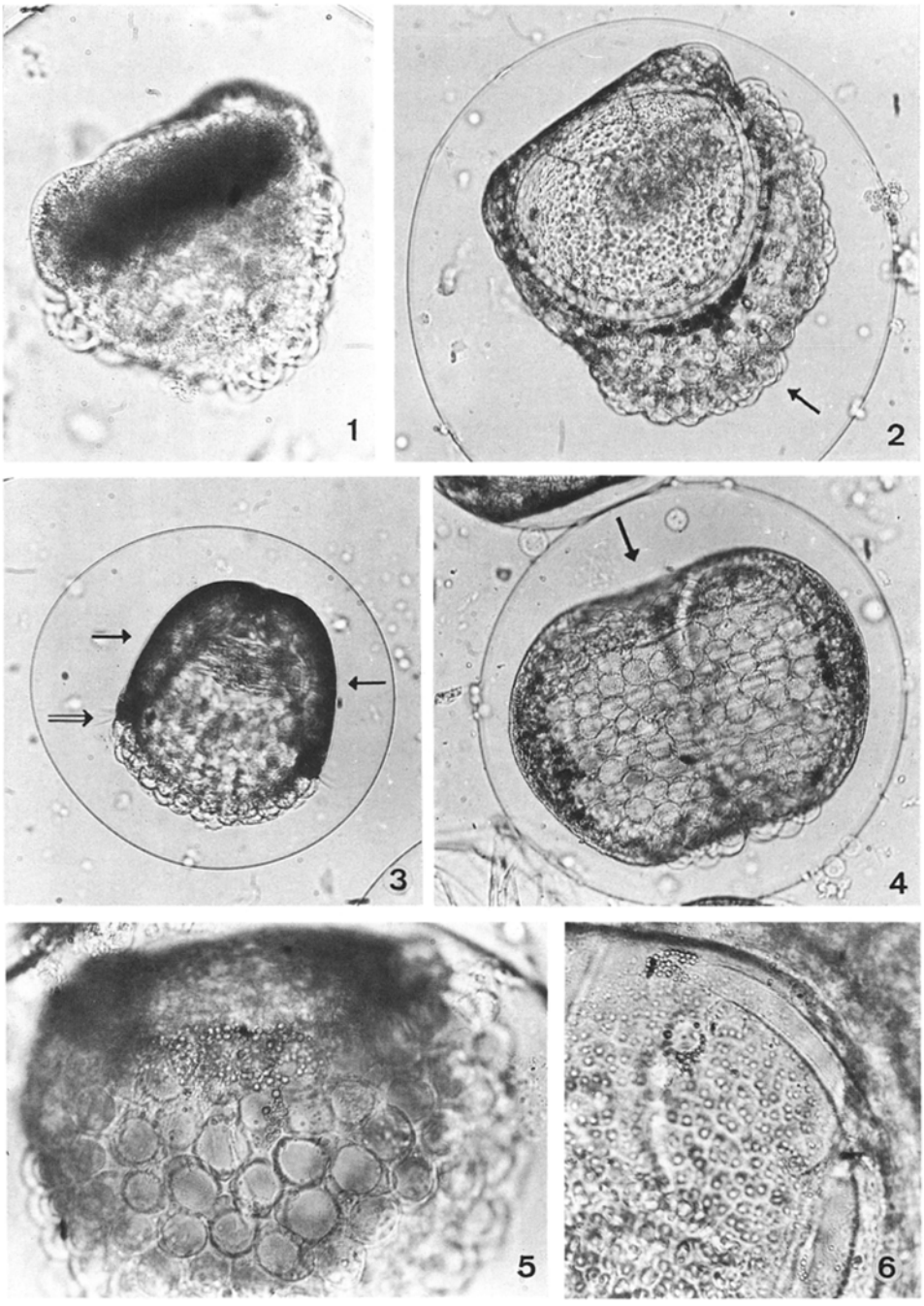
continues until most of the ventral body surface is shaped by storage cells leaving only the narrow rudiment of the foot uncovered (Fig. 7.2). During increase in embryo size, the anterior portion of the body forms liquid-filled spaces that are separated from each other by a cellular ridge that forms the rudiment of the byssus gland. Secreting cells of this gland become independent of the surrounding tissue and start to grow through the primary body cavity. Below the right valve they produce a tube that contains the raw material for byssus secretion (Fig. 7.6). Until hatching time is reached this tube coils more than two times around the large adductor muscle (Fig. 7.2 and 7.4). As soon as both sides of the embryo have been covered by shell the pressure within the body cavity is stabilized. Just before this the short gut has been pressed against the outer wall of the body and the mouth has been closed (Fig. 10).

5. phase: B. Transformation into the shell of a parasite

The secondary shell continues to grow only near the central margin of the valves. Here a thorny ridge develops that is hinged to the remainder of the solidly mineralized shell by flexible organic shell material (Fig. 8.4). The interior of the embryo is attached by three muscles to the shell, as in the case of *Teredora.* But in contrast to *Teredora* the central muscle is very large, connects the two valves with each other and fills most of the central primary cavity of the body (Fig. 11a, b). The posterior muscle is connected with the short gut and the anterior muscle lies in the rudiment of the foot. Mesenchymal cells produce other contractile fibers that connect the epithelium of the outer body with the shell and with the mantle. When these muscles become active they pull down the epithelium that crosses the gape of the valves, and during this process, produce the mantle cavity. The muscular mantle detaches from the outside of the shell and the median adductor contracts the valves periodically, probably also to aid gas exchange. The change from the bulbous larval body into a small bivalve with a mantle cavity is made possible by the expulsion of liquid from the large primary body (Fig. 11b).

When the secondary shell is completed the glochidium is ready. At this stage of development the digestive system is not open to the outside and storage yolk cells cover the mantle cavity (Fig. 11a, b). Around the small blind sac of the gut, mesodermal cells differentiate the rudiment of the pericardium, to form the kidneys and the heart. The primordia of the gills are closely associated with the rudiment of the heart and form ciliated grooves on both sides of it. Of the foot-rudiment, only the byssus gland with the long reservoir tube attached to it has grown, while the actual foot forms during the later, parasitic stage (Fig. 12).

Fig. 7. Photographs of living embryos of *Anodonta cygnea* with the optical microscope.
1: Embryo during the formation of the primary conch (upper dark portion) shows yolk concentrated below the rudiment of the mantle. The primary body cavity formed below, and feeding and the production of yolk-storage cells has started; × 280.
2: Storage cells form a cap (arrow) that projects above the valves. The ciliated zone (lower part) drives the embryo in slow motion through the egg. The attachment of muscles to the shell is seen in a dark spot, and double lines following shell margins show the location of the byssus-reserve tube; × 90.
3: Embryo seen from the front show the large adductor muscle (arrow) and sensing papillae (double arrow); × 90.
4: Embryo set up like a spring trap, but not yet ready to hatch. The large retractor muscle lies more anterior (lower side) while the ciliated field and the embryonic mouth point upwards (arrow); × 90.
5: Small cells of the muscular mantle, attach the shell with the soft tissue. In a position below the mantle cells, large storage cells are seen; × 280.
6: The byssus-reserve tube (right) grows through the primary body cavity formed by a cell cap (upper left); × 280.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5. phase: C. Hatching and establishment as parasite

When the egg capsules open, the glochidia of a whole gill sac are expelled into the water by a strong exhalent jet of the mother. The valves of the glochidia gape wide and the larvae look like open traps ready to snap shut on a prey (Fig. 7.4, 8.2). The thorny valve extensions are at right angles with valve margin (Fig. 11b). The foot has developed a glandular zone surrounding the opening of the long tube that represents a large reservoir of secretion (Fig. 7.2 and 7.4). A thin byssus thread is expelled rapidly so that many glochidia become connected to each other by entangled byssus threads (Fig. 11a). At this stage the larva can survive for some time, either floating with water currents, or resting on the bottom. According to HERBERS (1914) it may survive in the water for 36 days, but usually does so for only a few days, while it is provided with food from the storage cells. No active swimming or creeping is possible and the glochidium is picked up by fish, probably during breathing and food-searching.

When a group of glochidia is sucked up and washed to the gills of the fish, their entangled byssus attaches them to the gill segments. Upon contact with the gill tissue, the sensory hairs lying close to the thorny projections of the shell (Fig. 11a, b) are activated and this cue leads to the contraction of the very strong adductor muscle. Thus the "trap" is shut tightly. The thorns of the projections are pushed into the tissue of the gill and firmly anchor the glochidium in the gill segment.

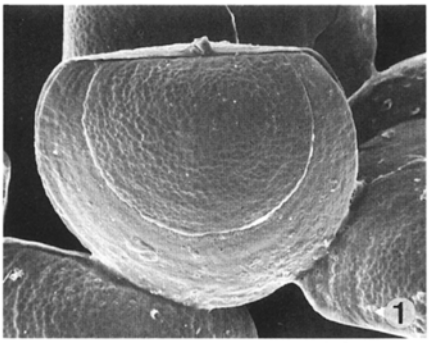
6. phase: A. Adult organization

Further history of the young *Anodonta* was examined by HERBERS (1914). The little wound made by the glochidium does not disturb the fish. Epithelium of the fish surrounds the glochidium and forms a cyst, which will remain closed until the bivalve actively breaks free from it. Under the protection of this cyst, the inner organization of the bivalve is completely changed.

At first, organs typical of the glochidium disappear. The four pairs of sensory papillae in the mantle cavity are resorbed. The actual byssus gland disappears rapidly while the long tubular sac that contained the raw material for byssus secretion disintegrates more slowly. The massive glochidium adductor muscle keeps the shell closely shut, and only after two weeks of parasitic life does it becomes detached and disintegrates.

Within the cyst, the parasite lives from the yolk reserves stored within the yolk cells, but probably also by utilizing the body fluid of the fish. Since the shell of the bivalve is tightly closed during most of its life within the cyst, food is probably absorbed through the extentions of the mantle cells that connect with the cyst liquid through the numerous small pores of the shell. These pores are closed by thin organic periostacal membranes through which the cyst liquid would have to pass through (Fig. 8.3).

Fig. 8. SEM photographs of embryonic shells of *Anodonta cygnea* (Figs. 1–5) and *Mytilus edulis* (Fig. 6.).
1: Growth lines mark the border between primary and secondary conch in some indivuduals; × 100.
2: Conch of hatched Glochidium larva in the position of a trap under tension; × 50.
3: The pores that cross the mineral shell do not pierce the periostracum (seen from the inside); × 1000.
4: The thorny ridge of the glochidium margin is connected to the solid calcareous shell with a flexible zone and along a flexible sheet. The inner shell surface shows regular pores; × 520.
5: Aberrant embryonic shell with "monoplacophoran" morphology. Here the strategy of mineralization of two independent valves below a univalve organic shell was lost resulting in the repetition of an "archaic" precursor plan; × 100.
6: Straight hinge veliger with first larval shell increments added to it by the free-swimming veliconcha. The position of the transitional muscle that folded the univalve into a bivalve has left a scar (arrow).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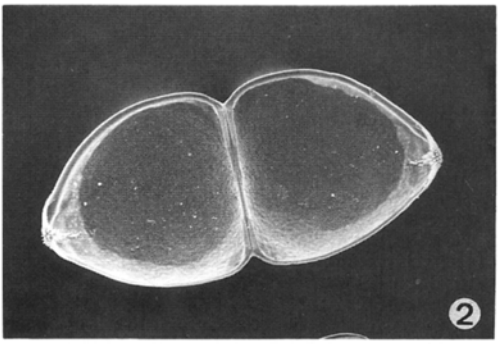
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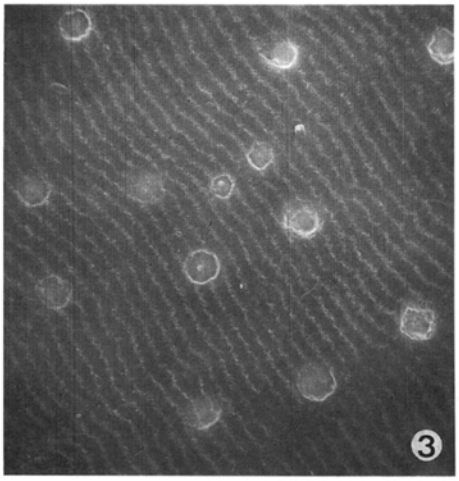
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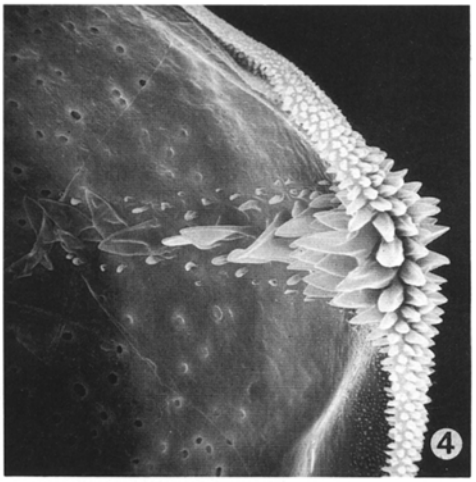
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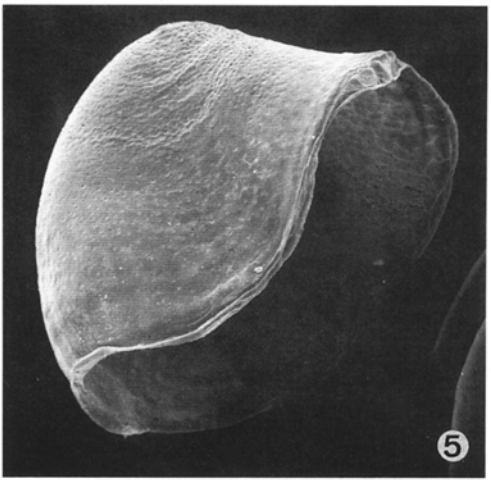
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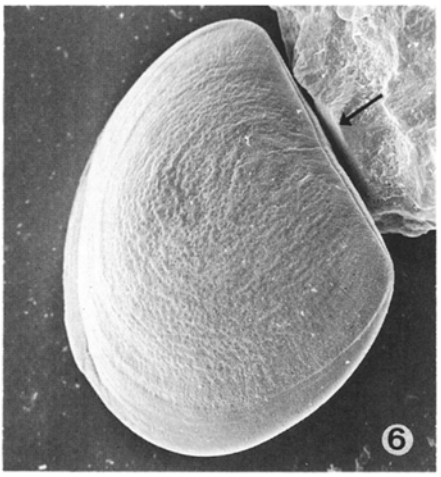
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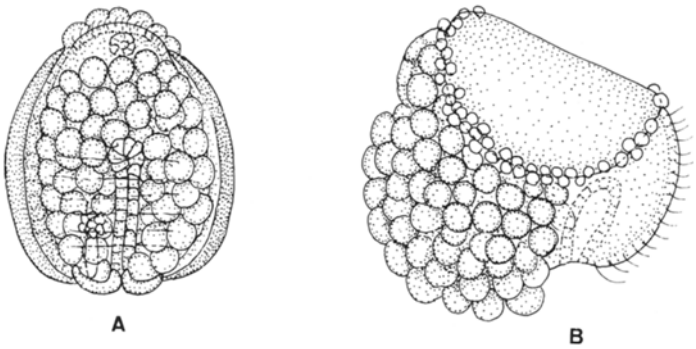


Fig. 9. The embryo of *Anodonta cygnea* during its feeding stage transports yolk into the blind gut by ciliary motion surrounding the body opening (later the anus). Yolk is stored in special cells that cover most of the body surface aside from the mantle. These large cells displace and hide the rudiment of the foot (bottom, centre). The primary conch (upper right) detaches from the cells of the mantle that secrete it, only to be reattached by cells of the muscular mantle from the outside.

By the time the bivalve is ready to break out of the cyst, the thin muscle fibers of the two adductor pairs at the anterior and posterior end have grown into functional muscles. Gills have developed two papillae. When the space that had been taken up by the large central muscle of the glochidium becomes available to the digestive system, the latter starts to grow in size, and after the third week of parasitic life it is complete. It starts to function only after hatching from the cyst, i. e. after about 1,5 to 3 months of parasitic life, according to HERBERS' experiments. At that time kidney, heart and pericardium have also differentiated and become functional. The foot has grown and can now be utilized for locomotion (Fig. 12). It has developed a new gland, probably used for mucus production during locomotion. Three ganglia have developed; the cerebral ganglion first, the visceral ganglion somewhat later in connection with the disintegration of the glochidium adductor, and the pedal ganglion last. The formation of the latter coincides with the invagination of the statocysts.

6. phase: B. Hatching from the cyst of the fish and adult organization

After 12 to 80 days as a parasite (HERBERS 1914) the bivalve tears the cyst with the aid of its foot and falls through the gill openings. While glochidia are usually produced in autumn, the

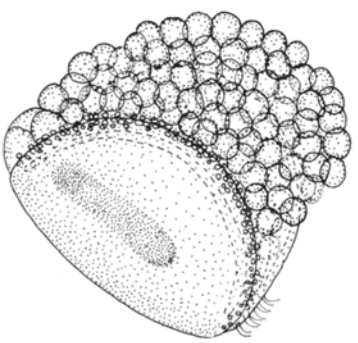


Fig. 10. The mouth of *Anodonta cygnea* embryos is closed when egg-capsule yolk has been resorbed. The body opening (lower left) opens again much later to functon as anus.

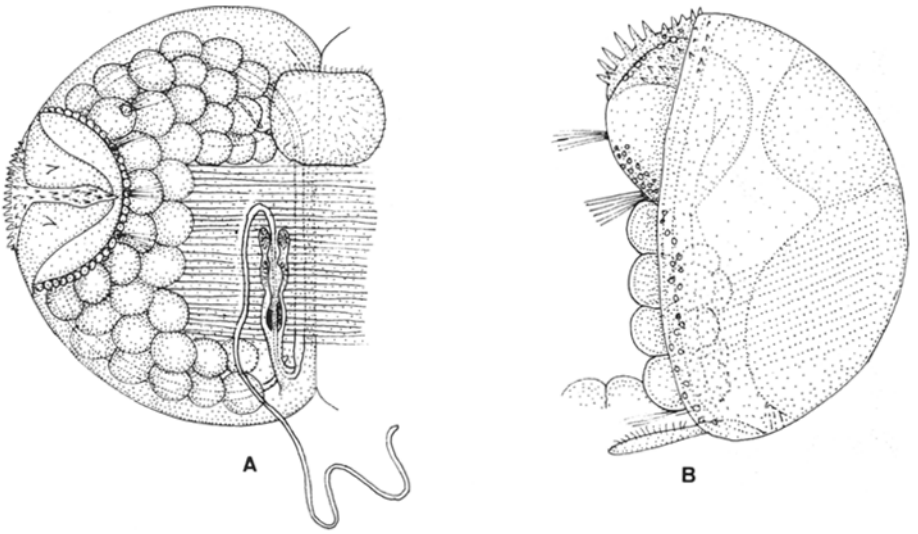


Fig. 11. Glochidium larvae of *Anodonta cygnea*, ready to hatch or freshly hatched, seen from above (A) and from the front (B) are dominated by the large adducator muscle. The ciliated plate (posterior part of animal, upper part of A) propells the larva through capsule liquid. A byssus gland (lower part of A) secretes a byssus thread. Sense papillae are arranged within the mantle cavity.

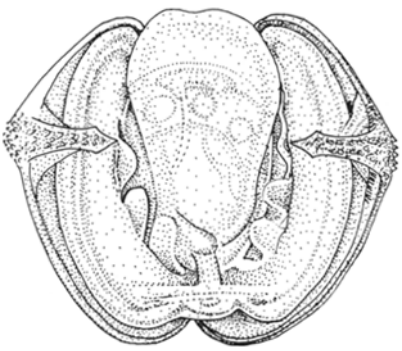


Fig. 12. Parasitic larva of *Anodonta cygnea* ready to leave the cyst of a fish. Redrawn from HERBERS (1914, Fig. 32).

young hatch from the cyst in spring, that the parasitic phase bridges the time when life is difficult in streams and ponds. It is only now that the glochidium conch with its characteristic shape, function and structure is abandoned and covered by new shell layers on its inner surface. Also the outer morphology of the conch totally changes during further growth until it looks like a miniature adult. Shell increments consist of periostracum as an organic layer on the outside, underlain by large columnar aragonitic prisms that become covered by nacre further away from the shell margin. The gills filter food particles from the water and transport them to the mouth, wrapping them into slime on their way. The four fleshy palps (lips) surrounding the mouth (two on each side) take hold of the food rods and transport them into the mouth. Here they are swallowed by ciliary action and transported in the same way into the stomach where food particles are mixed with the secretions of the liver and the crystalline style. The mid gut develops long loops before it continues in the straight hind gut. The anus is

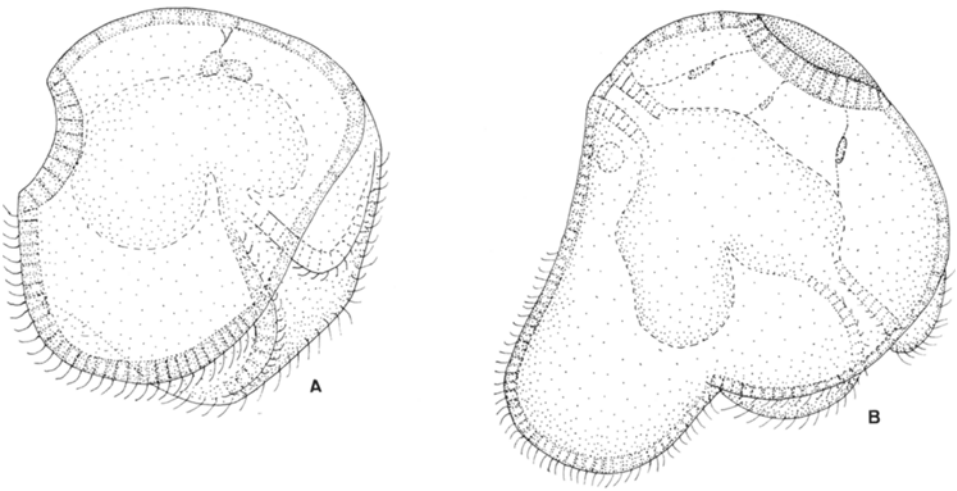


Fig. 13
A: Embryo of *Sphaerium corneum* with almost complete digestive system but no rudiment of mantle. Its future location is marked by some mesenchymal cells (upper centre). The mouth (right) is accompanied by the ciliated primordia of the palps and the foot (lower centre). The cells of the primordium of the hind gut (left) have often been mistaken for the shell gland.
B: In the embryo of *Sphaerium corneum* with mantle cells and primary shell formed the primordium of the hind gut has been pulled inward by increase of the primary body cavity. The foot has grown and mesenchymal cells have formed muscle fibres (upper centre) that connect the gut with the mantle and shell (see Fig. 14.1).

a long vertical slit opening into the space between the lobes of the mantle, above the posterior end of the gills. Faecal rods are compacted and represent large particles that sink rapidly.

The straight rectum (hind gut) lies behind the visceral mass and is surrounded by the pericardial sac with the pulsating heart. The heart receives its blood through spongy auricles that suck blood past the gill attachments from the interstices between mantle tissue and mantle cavity lining. Each beat of the heart drives blood through transparent arteries foreward through the visceral mass into the head. This organization of adult *Anodonta* is a very general, unspecific one, found commonly within bivalves.

Sphaerium corneum

Animals were collected in the vicinity of Röttenbach in shallow creeks with almost stagnant water. Full-grown individuals carry brood chambers in each gill. The number of brood chambers depends on the size of the individual (maximum 14). The smallest chambers hold the least developed embryos and lie deeply embedded in the fold of the gill, whereas the biggest are suspended from the gill end and hold miniature, adult-like embryos. Two to six embryos of similar but not the same age are present in each brood chamber, which is a closed, multicellular sac. The body liquid (blood) of the mother enters through a blindly ending tube which secretes the nursing liquid from which the embryos feed until they hatch. The observations carried out on material collected during summer and fall 1981 and 1983 agree with the precise account of ZIEGLER (1885) and the review of HAAS (1937).

Phase 1 and 2: Fertilization and cleavage

According to ZIEGLER the egg is covered by a primary membrane that dissolves after fertilization, at the onset of cleavage (6 cell stage). Cleavage pattern is similar to that of *Teredora.* First cleavage produces a large yolk-rich cell and a small plasm-rich cell. ZIEGLER observed a blastula with a primary cavity of the body already developed at the 13-cell stage.

3. phase: Gastrulation

According to ZIEGLER (1885) the gastrula shows a very prominent blastopore that is supposed to become closed after its first appearance, while the embryo increases in size. These observations are not in agreement with ZIEGLER's figures 14, 15, 16 on plate 27, which show a complete digestive system and the rudiment of the mantle.

Embryos from Röttenbach clearly show a trochophora stage, in which the rudiment of the mantle is not present but the digestive system is functional (Fig. 13 A). The embryo increases in size partly due to tissue growth, but also due to an increase of liquid pumped into the primary body cavity. With the latter process, most ectodermal cells are stretched, but at the same time the denser cells of the proctodaeum – hind-gut are pulled inward and the tube of the hind-gut forms. The mouth is wide and shows a ciliation that extends from lateral lobes into the mid-gut. The stomach is connected with two rudiments of the midgut gland (liver). Food particles rotate in the stomach and thus demonstrate its activity at this early stage of development. Between anus and mouth the foot rudiment is clearly visible and covered by short cilia. The opposite portion of the body is not ciliated. Several mesodermal cells (rudiments of muscles) are present close to the location where a little later ectodermal cells will be transformed into mantle cells (Fig. 13 B).

If the trochophora stage of *Sphaerium* is compared with that of *Teredora,* two major differences can be seen. One is the presence of a foot primordium that functions in the locomotion of the embryo within its brood chamber. The other is the presence of rudiments of the palps in the place where *Teredora* developed the prototroch. Transitional ciliation and organs as present in the *Teredora* embryo in *Sphaerium* embryos are replaced by ciliated surfaces of rudiments of adult organs.

4. phase: Mantle rudiment and primary shell

The mantle rudiment appears as an elongate-oval spot of cells opposite the foot (Fig. 14.1). The mesodermal cells have grown into muscle cells connecting the new mantle epithelium with the mid-gut (Fig. 15). Cells of the mantle, from their first appearance onward, are similar to those near the newly formed shell in *Anodonta* and *Teredora.* They produce a slightly concave and purely organic shell which detaches from the cells producing it when it is still minute, and is held to the tissue by muscular mantle attached just behind the shell edge.

5. phase: Secondary shell

A mineral layer below the organic primary shell appears after reorganization of the mantle edge. From the somewhat irregular first crystallites, a regular calcareous deposition develops (Fig. 14.2) consisting of a regular hinge and two equal valves.

During further growth the embryo becomes mushroom shaped (Fig. 14.2 and 14.3). The umbrella is formed by continuous growth of the mantle and the shell; the stalk by the foot. In the foot, mesodermal cells produce a network of muscles, which a little later, when the cavity of the foot is filled with liquid, have a regular pattern of transversal and radial fibres (Fig. 15). These give the foot its great mobility. Almost its whole surface is ciliated and only its posterior

portion is devoid of cilia. Here the byssus gland is differentiated, a twisted reservoir for byssus secretion which is much smaller than that of *Anodonta.*

Below the umbrella of the mushroom-like embryo, within the mantle cavity, the gill primordium forms as simple lobes which then rapidly expand and form folds. These are densely ciliated and produce a current in the liquid that fills the brood chamber. Such currents continuosly produced by gill, mouth lobe and foot ciliation wash the surface of the embryo and enable a steady gas exchange across the surface of the whole body.

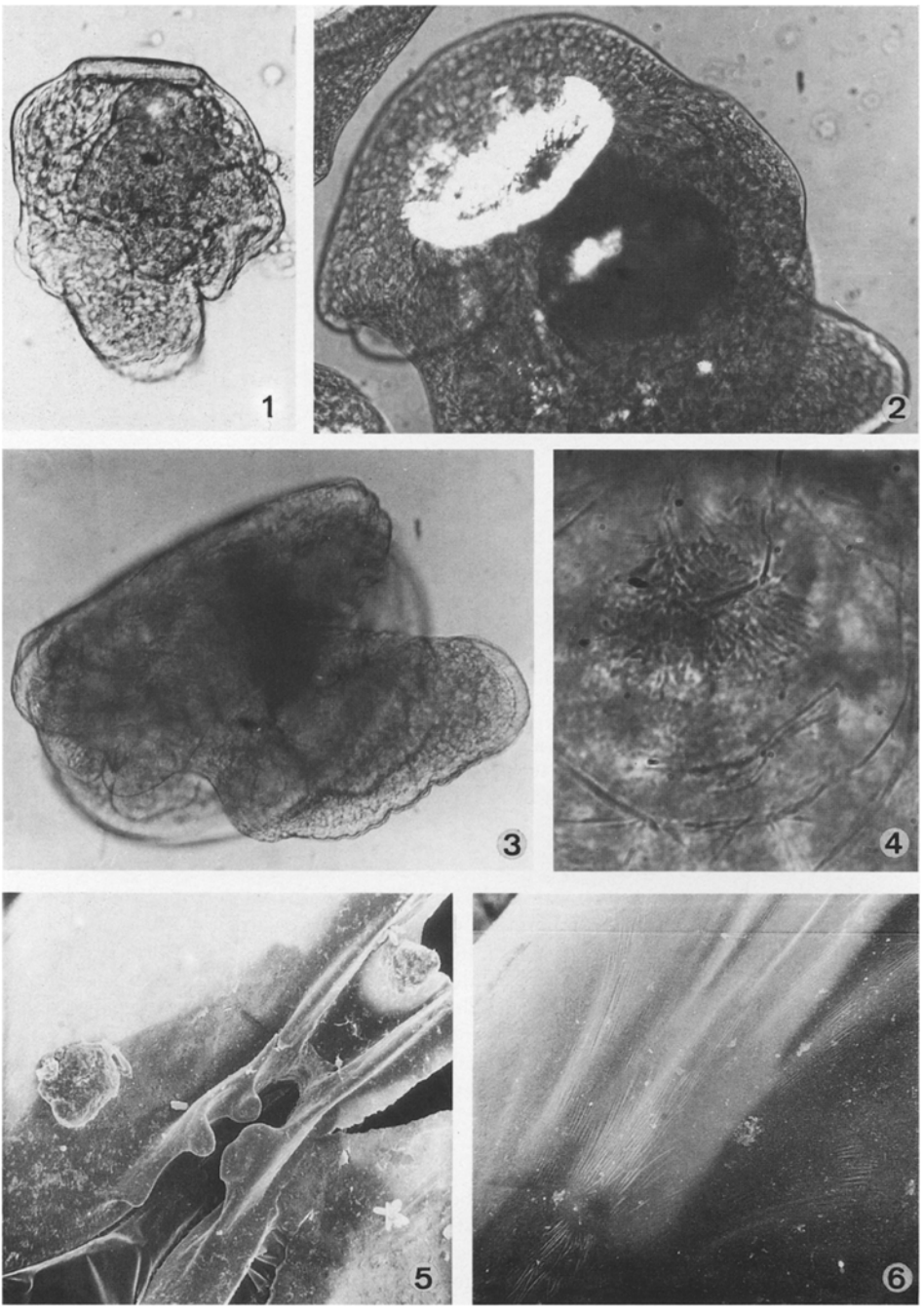
On both sides of the hind gut cells grow into the rudiment of the kidney/heart/pericardium system. MEISENHEIMER (1901) has shown that these cells are derived from ectodermal cells from the neighbourhood of the anus. Clusters of cells are expanded by liquid pumped into their center and form sacs which in turn connect to the outside by narrow tubes with a ciliated internal funnel-like end. The kidneys link up with the body liquid held in the pericardial sac through a filter system. ZIEGLER (1885) analysed in detail how these sacs grow until they are connected with each other around the hind gut. MEISENHEIMER (1901) corrected some minor details of this description and showed that the way in which the heart rudiment forms is like that in *Dreissenia* and other bivalves that have a free larval stage. When all sacs are connected, muscle fibers form and tie these tissues to each other; the heart is filled with liquid and starts pulsating. Body liquid is pumped from the space between the mantle and its inner cover through the pericardium fore-chambers into the main heart sac and from there foreward towards the midgut with its glands and into the head/mouth region.

6. phase: A. Bivalve phase

After the circulatory system that pumps the body liquid, has been completed and the gills have grown to a considerable size, the valves of the shell are pulled towards each other. This process is preceded by the formation of an internal ligament attached to the mineral shell in a ligament groove on both valves (Fig. 14.5). Muscle mantle grows around the shell margins and attaches the mantle to the outside. The transformation from a shallow concave univalve conch with preformed mineralized valves into the functional clam is slow (Fig. 14.3). It is carried out by the muscular system of the mantle alone until valves can close around the soft body and protect it. At that time there is no transitional special adductor as in *Teredora* and, in modified form, *Anodonta.*

During the phase of shell folding the byssus gland extrudes a byssus thread that attaches the embryo to the wall of the brood chamber. Only when the two valves have reached a slightly gaping position do the adult adductors become visible and their fibers attach through mantle cells to the anterior and the posterior region of each valve (Fig. 14.4). The attachment

Fig. 14. *Sphaerium corneum.* 1–4: photomicrographs of living embryos, 5–6: SEM photographs.
1: Embryo with mantle and primary shell (upper part), foot (lower part) and gut with stomach (centre), mouth (right) and anus (left); × 140.
2: The mineralized valves secreted under the univalve organic conch appear well when light is polarized. The conch is not yet folded to form the bivalve; × 36.
3: When the folding of the conch begins, practically all organs of the bivalve are present. The foot (lower right) shows the large byssal gland (on the left side). Gill folds mark the posterior (left) and the large brain is seen above the mouth (right); × 36.
4: Muscle cells are attached to the primary shell in the same way as found in bivalves with a free larval life (wrinkled starlike spot) but this transitional muscle only supports formation of the mantle cavity but does not fold the shell; × 110.
5: Hinge of embryo prior to hatching shows mineralized teeth like those of the adult and an internal ligament; × 50.
6: The outer surface of the shell of a hatched individual shows a wrinkled periostracum, produced when the shell was folded by the action of the muscular mantle; × 260.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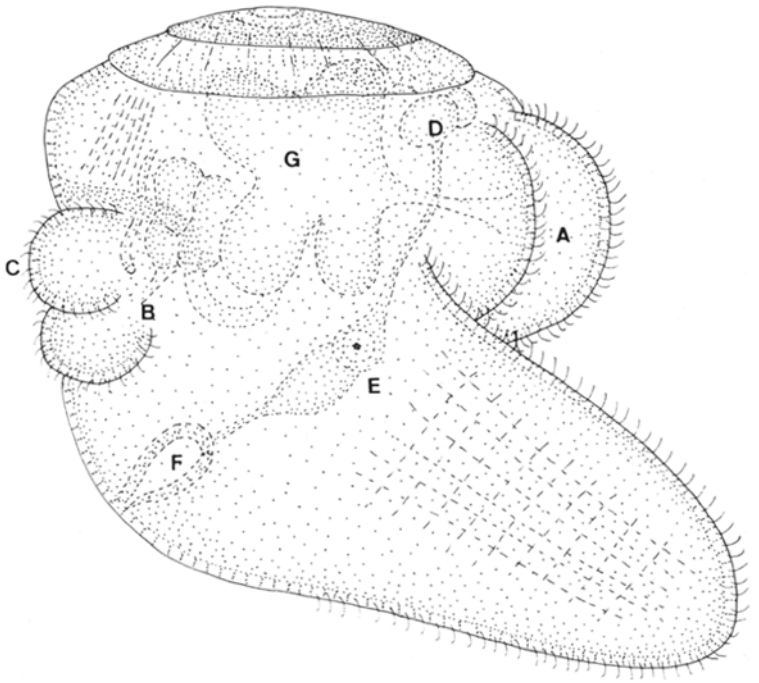

Fig. 15. The embryo of *Sphaerium corneum* has secreted a primary conch to which muscle fibres attach that meet in one spot (see Fig. 14.1). The digestive system is functional with mouth and palps (A) and anus (B). Around the hind gut (G), pericardium, heart and kidney have developed nearby the ciliated gill primordia (C). The foot is large and well supplied by a network of muscle fibres. Through it, nerves are seen that connect the cerebral ganglion (D) with the statocyst-pedal ganglion (E) and the byssus gland (F).

point of the muscle/mantle, which was on the outside of the shell, slowly migrates below the shell, starting at the posterior shell margin and continuing forewards.

At this stage, a functional miniature adult lies in the brood chamber of its mother, feeding on the nursing liquid with the aid of two ciliated grooves of the foot and ciliary action of the gills. The nervous system is completed with the pedal ganglion attached to the paired statocysts. Nerves connect to the large cerebral ganglion above the mouth, which is connected to the visceral ganglia in the neighbourhood of the heart-kidney hind-gut area. The whole organization of the body is bilaterally symmetrical.

6. phase: B. Hatching

The young bivalve leaves the brood chamber of its mother as a miniature adult. The only important modifications during further growth are the differentiation of the sexual organs and the penetration of the shell by small holes that are etched by extensions of mantle cells. The byssus gland of the foot is lost and, as in the case of *Anodonta*, replaced by a slime-producing gland.

The function of the secondary shell penetrations, which are also secondarily etched through the embryonic shell, remains unknown. SIMROTH (1908) thought that the pores in

Sphaerium were connected to sensory organs similar to those of polyplacophoran shell plates. However, the dimension and mode of formation of *Sphaerium* pores are different from those of polyplacophores, but instead are similar to those found in some marine bivalves (WALLER 1980), some fissurellid gastropods (BANDEL 1982), in the glochidium shell of *Anodonta* (GIUSTI 1973). Perhaps they are utilized by *Sphaerium* and *Pisidium* in the absorption of organic substances dissolved in the fresh water in which they live.

General features of bivalve ontogenesis

When the ontogenies of *Teredora*, *Anodonta* and *Sphaerium* are compared with each other and when additional data from the literature are considered, a general pathway of the bivalve ontogenesis can be reconstructed. In it six phases can be differentiated and characterized on the basis of distinct features of the organogenesis.

1. phase: Fertilization

A. Size and membranes

Eggs of bivalves usually are spherical, comparatively small and covered by two layers. The egg with its yolk is usually enclosed within a thight primary egg membrane. According to KNUDSEN (1970), the amount of yolk held within the egg determines the type of development seen in the embryo. In species with eggs up to 85 µm, a planktotrophic veliger forms that feeds on phytoplankton for an extended period of time. Where eggs measure between 90 and 140 µm, a free-swimming phase lasts only several hours or a few days and no food has to be collected before benthic life is taken up. In the third group with eggs measuring 150–200 µm, no swimming phase is present.

This general scheme does not cover all cases. Where brood protection connected with nursing is developed, as in the case of *Sphaerium* and related bivalves like *Pisidium*, eggs may belong to the medium-size group but the young hatch at very advanced and adult-like stages. *Teredora* eggs and those of several other species of teredinids may develop into young with an extended larval phase starting very early when threadened by starvation or with a short one starting late during embryogenesis when in favourable conditions. In the case of the long-term larva of *Planktyoma*, a rather large (270 µm) straight hinged veliger shell may indicate that a veliger with an extremely extended planktonic life developed from a yolk rich egg (ALLEN & SCHELTEMA 1972).

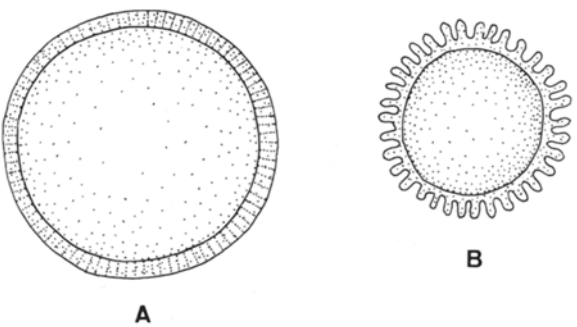

Fig. 16. Freshly shed eggs of *Lima* (0.1 mm wide; A) and *Venerupis* (0.04 mm wide; B) before fertilization are covered with a gelatinous layer.

B. Gelatiationous cover and fertilizan

The second layer surrounding the egg and its primary membrane consists of gelatinous material in *Teredora* (Fig. 1a) and in *Lima loscombi* and in *Venerupis pullastra* (Fig. 16a, b). The latter two species shed their eggs in captivity (Laboratoire Arago in Banyuls-sur-Mer). The cover in *Lima* has a vertically striated appearance, whereas that of *Venerupis* is crenulated. MEISENHEIMER (1901) noted a gelatinous cover in the fresh-water species *Dreissensia* (= *Dreissena*) *polymorpha* and a similar feature was again observed by LUTZ et al. (1982) in *Arctica islandica.* The former author also noted its transitional existence on the egg, which may explain why it had not been noted by other authors (SASTRY 1979).

The mucus cover on the egg surface accumulates spermatozoa, that become arranged with their heads pointing towards the primary membrane within the mucus cover. Spermatozoa must work their way through the mucus layer before coming into contact with the membrane and before penetrating it. After fertilization the mucus cover loses its contact with the egg and takes all surplus spermatozoa with it. Its function could be threefold. It could attract spermatozoa chemically, select the most active spermatozoa, and finally rid the fertilized egg from surplus spermatozoa.

In some cases, as in *Sphaerium* (ZIEGLER 1985) a mucus layer may be lacking. It is also absent around the 40 µm large eggs of *Anomia ephippium* from Banyuls-sur-Mer. The egg and its primary membrane may also be held within an egg capsule, as is the case in *Anodonta* and other unionids. Between capsule wall and egg, a layer of nutrious liquid is stored to be used by the embryo during later development.

2. phase: Cleavage

A. Immobile stage

The egg membrane can disappear rapidly or it may be retained through several steps of cleavage. In the case of *Dreissensia polymorpha* it is no longer present when the first cleavage begins (MEISENHEIMER 1901). This leads to the formation of typical intermediate bumps when micromeres separate from the macromeres (Fig. 17). In *Anodonta* the primary membrane dissolves early (LILLIE 1885), in *Teredora,* in contrast, it disappears only when the ciliated phase is reached.

Cleavage in different bivalves follows similar pathways and bilateral symmetry appears with first cleavage [oysters, HORST (1880); BROOKS (1880); *Dreissensia,* MEISENHEIMER (1901); *Teredo,* HATSCHEK (1880); *Unio,* LILLIE (1885) and others]. Only in the case of *Pinctada maxima* does cleavage seem to produce 4 equal cells at first before micromeres and macromeres are differentiated (SASTRY 1979).

MEISENHEIMER (1901) expressed the opinion that cleavage is governed in its course by the later organization of the body. This is certainly true regarding bilateral organization of bivalves, but it can be further supported by the way in which yolk reserves are organized. As the two-cell stage a large yolk-rich cell usually has been separated from a small less yolky cell. Polar bodies mark the animal pole of the embryo and also the region that will develop into the anterior velum and head. In the case of *Anodonta,* the yolk cell lies in the position of the later dorsal side where the mantle and the massive adductor muscle will form the largest organs of the following stage of development. In the case of *Teredora* and *Sphaerium,* the yolk-rich cell lies on the later venter and supports the rapid growth of the digestive system.

The time involved in cleavage clearly depends on temperature as well as yolk content of the egg. *Teredora* and also members of the genera *Martesia, Nototeredo* and *Bankia,* with eggs measuring 30 to 60 µm reach a stage of organization and develop rapidly and within 3–5 hours that allows free swimming (TURNER & JOHNSON 1971).

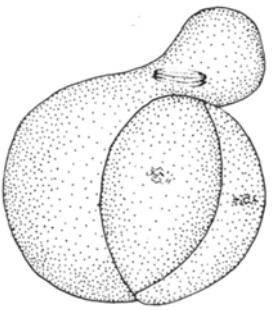

Fig. 17. Early cleavage stage of the embryo of *Dreissenia polymorpha* with bulging micromere separating from the macromere due to the absence of a primary membrane. Redrawn from MEISENHEIMER (1901: pl. 1, Fig. 7).

B. "Planula"

The first stage in which active locomotion is possible occurs when the morula (sterroblastula) or blastula (coeloblastula) blastaea of (NIELSEN 1985, 1987) becomes ciliated, as in *Teredora* (Fig. 1f) and related teredinids. The embryo at this stage is basically composed like a planula and can actively swim.

3. phase: Gastrulation

A. Formation of the gut rudiment

The onset of gastrulation is similar in the three cases of bivalves and also at the same stage in gastropods (BANDEL 1982). The sterroblastula or coeloblastula forms two concavities. One represents the tissue of the mouth and foregut, the other that of the anus and hindgut. Large differences can be observed in further development of these rudiments. In the case of some *Teredora* and all *Sphaerium*, development is direct and the two concavities grow into pits that then extend to become tubes in the interior of the embryo. Here they meet, connect and differentiate to form the globular stomach. These invaginations are produced not only by cell growths of the newly formed endoderm but epithelia are also pulled inwards by the interaction of mesenchymal cells that differentiate into muscle fibers. A complete digestive system is formed when foregut and hindgut meet and connect.

In the case of individuals of *Teredora* bred under optimal conditions and of *Anomia*, rudiments of the digestive system, formed during gastrulation, stop further differentiation for some time. The shallow pits of the gut primordium disappear when embryo size increased due to fluid that is pumped into the primary body-cavity. When cells from the rudiments continue to grow, they are connected and pulled towards each other by mesenchymal cells. Muscle fibers connect with the growing tissues and with the ectodermal outer wall. The close connection of mesodermal cells with the formation of the gut is well known (see GOETTE 1891).

In the case of *Anodonta* only the rudiment of the hind gut grows and forms a blind-ending digestive sac which serves as embryonic mouth and ciliary motion transports the liquid yolk of the egg cover into the embryo. The cells of the gut partly transform into yolk reserve cells. This primary mouth will later close, and much later it is formed again but then functions as opening of the hind gut (anus). Mouth-anus reversal within an ontogeny is also present in gastropods, for example *Viviparus* (discussion: see BANDEL 1982), where it also connected

with feeding of liquid egg yolk. The presence of the archenteron with the earliest functional digestive opening (mouth) of the blastoporus that later in ontogeny functions as anus in some molluscs does not fit well into the "trochea" theory (NIELSON 1985, 1987) and needs clarification. Can this feature be taken as evidence for a closer affinity to the "tornea group" (Notoneuralia), or does it represent a simplification of the Gastroneuralia branch of the invertebrates?

B. Confusion of shell gland with rudiment of gut

The processes of formation of the rudiment of the digestive system has possibly been misinterpreted in the literature. SASTRY (1979), reviewing older literature, stated that the blastopore (primary body opening) generally develops by the invagination of the archenteron (rudiment of the gut). It is supposed to be wide at its beginning, but later becomes narrow and reduced into a longitudinal slit that finally closes. Both ends of this slit are later to be reopened and to form the mouth and the anus.

The present author has not observed such a feature, neither in the three ontogenies described here nor in other ontogenies of conchiferan molluscs (BANDEL 1982), and considers it as an artifact that may have originated when sections of dead and fixed material were studied and the observations were not sufficiently supplemented by observations on the living embryo.

The one half of the digestive system may have been confused with the shell gland. SHASTRY (1979), for example, explains the formation of the shell gland in the following way: First a spot of the ectoderm is thickened; it then invaginates deeply into the embryo and later evaginates; only then does it begins to secrete the larvel shell. Why this is so and for what reason, is not stated. Similar observations have a long history and are based on studies carried out by quite a number of authors like HATSCHEK (1880) on *Teredo*, BROOKS (1880) on *Crassostrea*, HORST (1884) on *Ostrea*, HERBERS (1914) on *Anodonta*, MEISENHEIMER (1901) on *Dreissensia*, FLEMMING (1975), RABL (1876), LILLIE (1885) on *Unio*, D'ASARO (1967) on *Chione* and others up to our time (see SASTRY 1979). Perhaps cells of the developing hind gut, which closely resemble those of the rudiment of the mantle in general shape and often form close to it (BANDEL 1982), have been confused with a "dorsal invagination".

C. Trochophora

The typical free-swimming larva of the embryo after gastrulation is the trochophora. Its difference from the "planula" stage is due to a rearrangement of the cilia into rings and tufts connected with the formation of the digestive system. A trochophora stage is present in *Teredora* and *Anomia* as well as in *Sphaerium*. It can thus be a true free larval stage during which food is collected from the seawater or it can be an embryo that feeds on nurse-liquid within a brood chamber. Cilia around the head are used for collecting and transporting food particles into the mouth, where they are carried into the midgut through the ciliated tube of the oesophagus. The hind-gut is short and simple. Development of the digestive system and food-collecting ciliation is direct and not connected with a partially closed blastopore as is suggested by the theoretical formation of gastroneuralian larvae (NIELSEN 1985, 1987).

The trochophora stage may be omitted in development of yolk-rich eggs, as well as in eggs maintained in capsules or brood chambers. *Crassostrea virginica*, for example, has small eggs and a free-swimming trochophora (BROOKS 1880), whereas *Ostrea edulis*, with larger eggs, develops a free-swimming larva at a later stage of development (HORST 1884). The molluscan trochophora can be compared with the annelid trochophora only up to this stage of development. With further organogenesis embryos of both groups of invertebrates differ in characteristic ways from each other.

4. phase: Mantle rudiment and primary shell

A. Shell gland

The rudiment of the digestive system in all bivalves as well as in other conchiferan molluscs forms prior to the rudiment of the mantle (shell gland) (BANDEL 1982). Because of the confusion of a part of the digestive system with the shell gland, the formation of the first shell remained mysterious in many studies which otherwise are detailed and exact. WALLER (1981) expressed this situation when he stated that the structure of the shell gland and the earliest formed shell are among the most poorly known aspects in larval morphology. Some authors, like COX (1969), decribed the shell gland as a patch of cells that forms a thickened part of the ectoderm and secretes a cuticle (primary shell). Often this patch of cells was illustrated in a correct way as in the case of GOETTE (1891) for *Anodonta* and of ZIEGLER (1885) for *Sphaerium.* But both authors did not draw the right conclusion from their own observations. The rudiment of the mantle consits of very similar looking cells as the rudiments of the gut. But while the latter sooner or later invaginate, the former remains on the surface of the embryo.

B. Pre-veliger

With shell gland formation and secretion of a first shell the organization of ciliation on the free-swimming embryo is rearranged. The shell successively covers more and more of the body so that its ciliated portions become narrow and are concentrated and enlarged into wing-like processes of the velum. This stage is easily distinguished from the trochophora by the presence of mantle epithelium and a developing shell. The embryo has no functional shell which differentiates it from the true veliger. FIORONI (1966), therefore, called it a pre-veliger.

In the literature the term trochophora is often carried beyond comparable embryonic stages of the annelids and includes pre-veliger and veliger as well. MEISENHEIMER (1901), for example, considered the molluscan trochophora to carry a conch. A similar opinion is still held by WALLER (1981) who describes the trochophora of an oyster as carrying a crown of mobile cilia (protoconch) as well as the shell gland that disrupts the symmetrical outline of the embryo.

In the case of *Nucula, Yoldia, Selemya* and related species, the preveliger phase shows a morphology which probably is characteristic to all protobranch bivalves. Here the shell forms under the cover of tissue. The whole outer surface of the larva remains ciliated and no velum is differentiated (DREW 1899, 1901; GUSTAFSON & REID 1986). This outer body tissue covers the rudiment of the mantle (shell gland) before onset of shell formation, as we know it from squids (BANDEL & BOLETZKY 1979) or from some pulmonate gastropods (BANDEL 1982). Nuculoids thus retain the general morphology of the trochophora even though their internal organization changes and the appearance of a shell places them into the pre-veliger type.

C. Primary shell

The first-formed shell (primary shell, BANDEL 1982) remains in contact with the cells secreting it, which often form the only attachment between tissue of the mantle and shell. The primary shell of bivalves consists of a single conch of oval outline and organic composition. The transition of the univalve to the bivalve phase is not well described in the literature and is poorly known in general. This is based on the misconception that the rudiment of the mantle (shell gland) first invaginates and later evaginates. WERNER (1939) assumed that initial shell secretions form when the shell gland is still invaginated, but the conch of the straight-hinged veliger shows very regular patterns of surface sculpture that indicate uninterrupted shell secretion from the very beginning of shell formation onward, supporting the observations on living embryos.

5. phase: Secondary shell and veliger

A. Secondary shell

The free-swimming preveliger stage usually ends when the shell has grown large enough to cover the body when folded. The transition from the univalve to the bivalve stage here is clearly expressed in the resulting change of shell morphology.

In the cases where the stage of development occurs in a brood pouch or nurse chamber, the situation may be more complicated. However, in all cases, this phase of organogenesis is connected to the transition from primary to secondary shell when the gland zone of the mantle detaches from the shell and the shell edge is free. The periostracum cells of the mantle lose their direct contact with the shell margin so that continuous shell secretion ends and periodical shell desposition begins. This change-over is reflected on the shell surface as borders between the uniform, primary shell and the secondary shell with growth lines (Fig. 8.1 and 8.6). The morphology of shell increments that are added periodically to the shell margin is controlled by the muscular mantle that lies in front of the gland zone.

B. Shell mineralization

The primary shell is purely organic. Only after its completion does it become mineralized. The formation of a continuous calcareous layer on the inner shell surface is connected with the detachment of the shell margin in the bivalves as well as in other conchiferan molluscs (BANDEL 1982). Only after the two calcareous valves have been deposited on the inside of the organic primary shell, can the conch be transformed into regular valves by becoming folded along the unmineralized central zone. WERNER's (1939) observation that all bivalve veligers studied by him had a mineralized shell, thus, is not surprising.

When mineralization covers the whole primary shell, as was observed in some pathologic cases of *Anodonta* embryos (Fig. 8.5), the bivalve shell organization cannot be formed later (Fig. 18). Totally unmineralized conchs are not known. Where the larval conch is secreted with purely organic, shell material as is the case of the planktotrophic *Planktomya,* the portion of the former primary shell is mineralized (ALLEN & SCHELTEMA 1972). Onset of mineralization on the inner surface of the thin organic primary conch has sometimes been mistaken for the first shell deposition, for example by BROOKS (1880) and is responsible for reports of paired shell rudiments in some bivalves (Fig. 14.2).

C. Shell deformation

Special median adductor muscles usually bend two mineralized valves along the median line of the organic hinge into bivalve shape (BANDEL 1982). They have except for those of *Anodonta* and other unionids, escaped the attention of former authors. As soon as the transitional muscle has successfully completed its task, it is usually replaced by new and shorter adductor muscles. Often the primary adductor muscle leaves a typical attachment scar, as observed in the case of *Mytilus* from the Oosterschelde (Fig. 8.6) and *Anomia* from Banyuls. The development of first muscles in *Anodonta* deviates considerably from that of other bivalves because the muscle outgrows the other organs considerably and occupies much of the primary body cavity that usually provides space for the gut. This large muscle remains active much longer than usual, for weeks, well into the parasitic phase (HERBERS 1914). This muscle, in *Anodonta* and also in *Lasimona* (TOMPA 1979), not only transforms the shell into a straight hinge glochidium, but also serves as powerful adductor of the shell trap into which the larval shell grows before hatching occurs (Fig. 7.4).

Another exception to the usual case of univalve to bivalve shell transformation in which the adductor muscles bend the shell is present in *Sphaerium* (Fig. 14.4), where the muscular

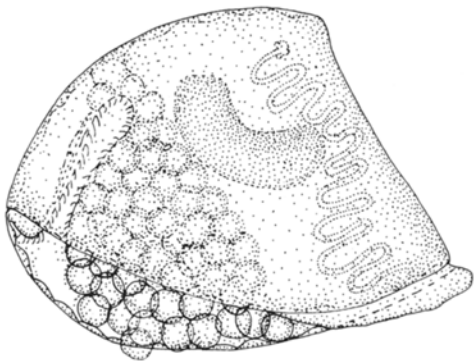

Fig. 18. Aberrant larva of *Anodonta cygnea* with a univalve shell, while other organs are normal, short hind gut serving as mouth (left), reserve cells with stored yolk, large, but here non-functional adductor muscle (centre) and reserve tube of byssus secretion.

mantle and the muscles that connect it to the muscular foot bend the shell. The two final adductors attach to the shell only after the bivalve stage is present. The transitional central muscle connects the embryonic head and foot to the shell, but does not deform the latter. If the embryo of the free-swimming preveliger-veliger transition is taken for comparison, the primary – secondary shell transition and shell transformation in *Sphaerium* have shifted more towards adult phase than in *Anodonta.*

D. Straight-hinged veliger

When the preveliger is transformed into the veliger, a characteristic shell results which has received the name prodissoconcha I, veliger shell, or straight-hinged veliger. The last term is the most descriptive and is based on the characteristic feature produced by the folding of the univalve into the bivalve along a straight median line (Fig. 8.2 and 8.6). In most marine bivalves and in the fresh-water *Dreissensia* (= *Dreissena*) this stage occurs within about the same stage of embryonic development. It is brought about by the same process of activity of a transitional muscle.

Quite often bivalves hold their developing young within the shelter of the shell and the mantle cavity until a straight – hinged veliger has developed. Hatching young are then provided with an external shell that can tightly close around the soft body. Usually a functional digestive system and a foodcatching device is also present. In the life cycle of the basically sessile bivalve the phase of planktotophic drifting most commonly begins with straight-hinged veliger organization, but it has to be considered that the presence of a straight hinge veliger shell on the conch of a bivalve species provides us with no conclusive information with regard to the location where it has formed. It may have developed within the protection of the shell of the mother or in the free water. In this regard, bivalves are similar to archaeogastropods but differ from higher gastropods (BANDEL 1982).

When WALLER (1981) stated that the prodissoconcha I to II boundary represents nothing more than the onset of valve closure, this expresses only one part of the process and cannot encompass all of the cases. Closely connected and responsible for the change of sculpture is the separation of mantle tissue from the shell margin. When development occurs within eggs or brood chambers, as is the case in *Sphaerium* (Fig. 14.2 and 14.6) and *Anodonta* (Fig. 8.1), the change between the shell without growth lines (prodissoconcha I) and with growth lines (prodissoconcha II) is not in phase with the folding of the shell over the body.

A special case is developed among protobranch bivalves. According to DREW (1899, 1901), confirmed by GUSTAFSON & REID (1986) the straight hinge conch here develops below a cover of ciliated cells. It is likely that this cell cover represents mantle epithelium that opens when the conch has become functional. Benthic life starts right after straight-hinge conch formation and no further embryonic stage is present. Protobranchs, thus, develop no veliger stage.

E. Veliconcha

The veliger swimming in the sea and feeding on planktonic organisms was termed veliconcha (WERNER 1939). The conch of the straight hinge veliger is enlarged and changed in its morphology in a characteristic way. The veliconcha shell in its morphology differs from the straight hinge conch as well as from the adult conch and can be utilized for systematic purposes (LOOSANOFF et al. 1966, CHANLEY & ANDREWS 1971, LUTZ & HIDU 1979). Also a denticulated hinge forms which, in structure, is typical for this phase of life and changes when pelagic life ends. It is of great systematic value because it is characteristic of certain bivalve groups (LEPENNEC 1980).

F. Larval feeding

The digestive system of the veliconcha begins with the velum from which ciliary motion transports planktonic microorganisms via food groove on the margins into the ciliated foregut (stomodaeum, oesophagus), and then into the stomach. The midgut consists of the simple globular stomach into which the glands (liver) and the crystal style gland discharge their products that aid digestion and transport of particles through the digestive system. The hind gut changes from straight to a simple loop. Wastes are expelled through the anus as faecal pellets, washed away with the aid of cilia.

Where there is no phase of planktotrophic feedings, as in the case of *Anodonta,* a complete digestive system can be absent until the adult organization for filter- or suspension-feeding is constructed. In the glochidium and in the parastic phase rudiments of the gut are not open to the outside and food additional to that stored in albumen cells is probably absorbed through ectodermal cells of the mantle. The mantle cells are in contact with the body liquid of the fish through pores with organic filters at their ends, while the valves of the conch are more or less closely shut. In the case of nurse liquid feeding of *Sphaerium,* a normal digestive system is developed, like that of free-living larva. But, in contrast to the latter, it is not the velum which collects food particles but the primordium of the papillae of the mouth.

G. Formation of the mantle cavity

The mantle cavity forms by the simple process of folding of the two sides of the univalve primary conch. The epithelia below the shell are folded towards the central part of the body that holds the digestive tract as well as most muscles. The space needed for this process is provided by the expulsion of liquid from the primary body cavity. There is usually no inward growth, invagination or growth-folding of the mantle cavity as assumed by some authors.

In *Sphaerium,* in contrast, the mantle cavity is already present when the shell is folded at a rather late stage of ontogeny (Fig. 14.3). Here it forms through differential growth of the mantle margins with the shell connected to them on one side and the head-foot area on the other side.

H. Foot rudiments

The veliconcha usually shows very little of the foot rudiment until rapid growth at metamorphosis. The same can be stated for *Anodonta,* whereas *Sphaerium* again deviates consider-

ably from the usual situation by forming the primordium of the foot together with the rudiment of the mantle (Fig. 14.1).

The byssus gland of the foot rudiment appears quite early during veliconcha stage. Its formation is a factor that can be observed in all bivalves that have been studied in this respect, regardless of their mode of development. The onset of spinning of the first byssus threads can indicate the end of the veliconcha period.

Byssus-gland formation and morphology was documented by WALLER (1981) in the case of *Ostrea edulis*, where a gland is present in newly hatched veligers. In the case of *Dreissensia polymorpha*, the byssus gland of the veliconcha produces a large reserve tube filled with secretions (MEISENHEIMER 1901). In *Anodonta*, this "Larvenfaden" (HERBERS 1914) is even bigger.

Two invaginations of the foot form during veliconcha life. These close and form the statocysts, fluid-filled sacs containing a dense body (statolith). It provides the larva with a balancing sense organ (CRAGG & NOTT 1977). The statocysts are situated on the base of the foot on either side of the bilobed pedal ganglion. They contain ciliated cells that keep the statoliths in constant motion and hair cells connected to nerve cells provide contact with the ganglion.

I. Nerve system

The development of the pedal ganglion takes place at the same time as that of the statocyst and may occur together with the formation of the two other nerve centers of the visceral ganglion and the cerebral ganglion situated at the ends of the digestive system. The cerebral ganglion may be connected to light sensing organs as in the oyster (WALLER 1981).

J. Muscles

The muscular system consists of adductors (usually one pair) and retractors that provide the velum and the remaining body with the ability to be pulled into the shelter of the shell when valves are closed. Attachment to the mantle and shell in a free-living larva often differs from that in later adult stages. In the development of *Sphaerium*, which is strongly oriented towards adult organization from the beginning, the adductors form without interruption.

6. phase: Adult organization

A. Byssus production

The onset of production of byssus marks the end of the embryonic stage and is characteristic of the transition into adult organization. In protobranch bivalves, a byssus stage is probably not developed. Byssus production in its most obvious functon results in an attachment of the swimming larva to a hard substrate. This function has also been preserved in such specialized ontogenies as that of *Anodonta* and *Sphaerium*. In the former it is most important for the attachment of the glochidium to its fish host and much of the embryonic energy reserves are employed in the production of a large reservoir of preformed secretions.

In most marine bivalves and in the fresh-water *Dreissena* as well, the byssus gland develops along with the crawling foot and both start to function at about the same time. The growth of the foot, however, may not be correlated with the production of byssus. In *Sphaerium*, for example, the foot becomes active long before byssus is produced. In the teleplanktic *Planktomya* a large foot has formed a long time prior to metamorphosis and is utilized by the larva to clean the shell from adhering particles (ALLEN & SCHELTEMA 1972). *Anodonta*, in contrast, produces byssus at a time when no foot has yet formed.

Byssus may also be utilized in extending the free-swimming mode of life beyond metamorphosis. Teredinid larvae can attach byssus threads to the water-air interface (Fig. 19) and individuals may be suspended on it and survive for some time after metamophosis into a min-

Fig. 19. An individual of *Nototeredo norvagica* that has metamorphosed prior to finding a wooden substrate for settlement survives on a byssus raft that is attached to the water-air interface.

iature adult (BANDEL 1981). Bysuss threads as a mode of transport of *Mytilus* juveniles was observed by LANE et al. (1982). Here even 1.5 to 2 mm sized juveniles can reenter the plankton and drift suspended by a single large byssus thread which is acted upon by water currents. These authors named this phase in the life cycle the plantigrade stage. Such cases were also observed in oysters and scallops. The ability of post-larval individuals to embark on secondary drifting in a bysso-pelagic phase extends the potential duration of planktonic life.

B. Pediveliger

The term pediveliger is descriptive and refers to the development during which a crawling foot coexists with the velum still functioning as a swimming device. This type of larva is only developed in species with a free-swimming larval stage. It is not found where metamorphosis occurs within a brood chamber (*Sphaerium*) or as a parasite within a cyst (*Anodonta*).

During the phase of the transformation of the "planula" larva into the trochophore, the digestive system begins to form; the preveliger differentiates the mantle complex; during veliconcha stage the foot complex is developed; during the pediveliger stage the kidney-, heart-, pericardium-complex begins to function. Its fully activity usually starts just before or shortly after onset of benthic life (Fig. 20).

Another feature to be noted in the transition from the larval to adult organization is the appearance of ligament pits and the resilium (internal fibrous ligament) (LUTZ et al. 1982; WALLER 1981).

Evolution of bivalves

Six steps of ontogeny represent general features common to all bivalves with the exception of the protobranchiate bivalves. In the latter, the fifth phase with all its characteristics is missing.

1. phase: Fertilization

The egg measures between 0.03 and 0.2 mm in diameter and is covered by a primary membrane. Size differences, due to differences in the content of yolk, influence the length and mode of the free-swimming phase. Additional envelopes may surround the egg and can serve in fertilization and provide a capsule for nutrients.

2. phase: Cleavage

The cleavage is governed by future organization of the embryo. Yolk-rich and plasma-rich cells are usually present from the two-cell stages onward. Their place on the ventral or dorsal side is connected to the following course of organogenesis. The primary membrane may disappear sooner or later. The animal pole is marked by the polar bodies only. A primary body cavity may or may not occur. A first possible free-swimming stage is present with a "planula-like larva, blastaea" in blastula or morula cell organization.

3. phase: Gastrulation

The first complex of organs that forms is that of the gut with two independent openings. Development into a functional digestive system may be continuous and direct. Retardations

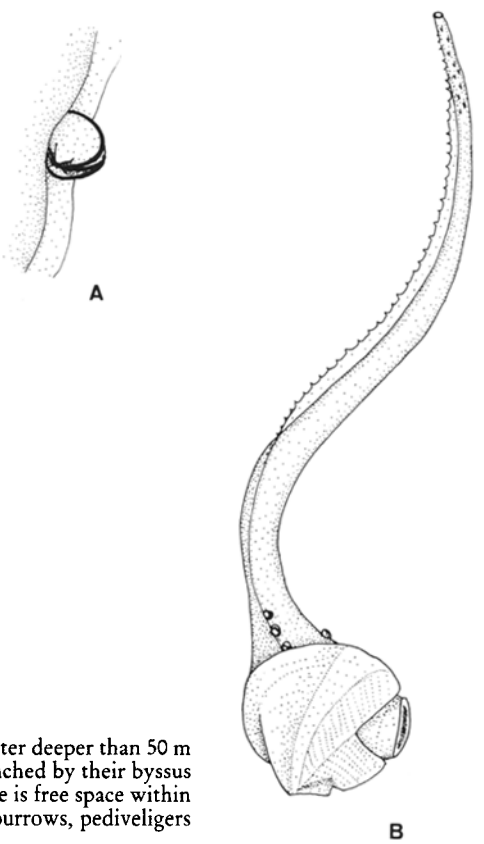

Fig. 20. To the syphons of *Xylophaga dorsalis* from water deeper than 50 m (Mediterranean Sea, Banyuls-Sur-Mer) young are attached by their byssus threads. Metamorphosed young hatch as long as there is free space within the wood, when the wood is riddled by shipworm burrows, pediveligers hatch and swim off in search of new wood.

may occur in all parts of the primordium. What functions as the mouth in the embryo may be the anus in the adult. Cell growths of the entoderm into the primary cavity of the body is accompanied and channeled by mesodermal cells. The free-swimming larva of this phase is the trochophore.

4. phase: Mantle rudiment and primary shell (organogenesis)

The mantle rudiment represents a differentiation of external cells of the embryo into mantle cells without in- or evagination. The mantle complex always forms after the rudiment of the digestive system has been differentiated. The primary shell is fully organic, elastic and remains fully attached to the epithelium secreting it. The free-swimming stage is the preveliger larva.

The protobranch bivalves form the primary shell as endocochlear conch covered by a ciliated epithelium. The fourth phase is characteristic of all conchiferan molluscs.

5. phase: Secondary shell (larval development)

The onset of this phase is characterized by the detachment of the mantle from the shell margin. The mineralization of the univalve primary shell with two separate valves differentiates the class Bivalvia from other conchiferan molluscs. In free-swimming embryos the univalve shell is deformed into the straight hinge veliger by means of a transitional muscle. The typical planktotrophic larva is the veliconcha. In cases with brood protection, deformation may be lost. In the foot rudiment a byssal gland, statocysts and a pedal ganglion form. The cerebral ganglion above the mouth and the visceral ganglion near the hind gut appear. The end of the phase is indicated by the beginning of byssus production. Its absence differentiates protobranchiate bivalves from others.

6. phase: Adult organization

Locomotion changes from ciliary swimming to crawling with the aid of the foot. Free-swimming phases can be prolonged by special features of byssus production. Transformation can be carried out in places like the cyst of a fish as parasite in the case of the unionids. The kidney-heart-pericardium-genital complex takes up its function as the last group of organs. Usually gills are utilized as food-gathering apparatus together with the lips. A tertiary shell is produced. Under nurse pouch conditions, the secondary and the teritary shell may be very similar to one another.

Organization of the ancestral prebivalve

Derivation of bivalves from monoplacophoran ancestors with serially arranged muscles was explained by VOGEL & GUTMANN (1980) as a step by step change connected to adaptational improvements leading from grazing to filter feeding habits in response to the migration from firm substrate into soft sediment. In their model lateral compression of an uncalcified or spicule-covered shell preceded the appearance of lateral centers of calcification.

The theoretical arguments presented by VOGEL & GUTMANN (1980) for the derivation of the Bivalvia from a soft-shelled ancestor according to RUNNEGAR & BENTLEY (1983): "are both unconvincing and unnecessary". The latter authors follow the model that bivalves evolved from rostroconchs in the Early Cambrian by decalcification of the posteriodorsal margin of the shell. An elastic dorsal margin would allow first bivalves thus derived from rostroconchs to close without a gap and to burrow efficiently (POJETA 1980). RUNNEGAR (1983) expressed the opinion that the step that gave rise to the Bivalvia was the development of a divided larval

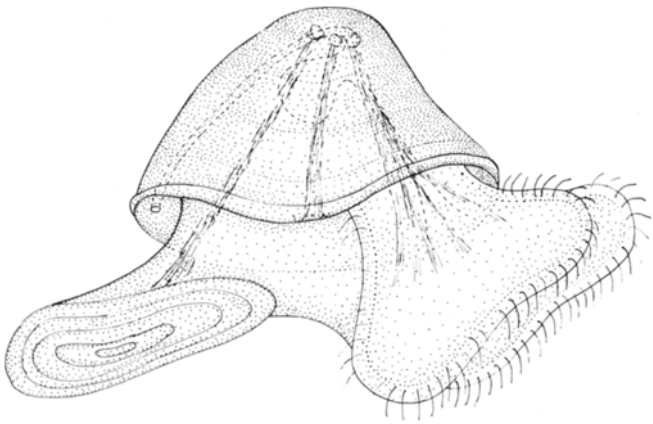

Fig. 21. Hypothetical prebivalve in the stage of a free-swimming veliger. Such an embryonic univalve veliger by accident of localized mineralization could have become a bivalve. Foot, operculum and anus (left); 3 muscle pairs and digestive system (centre); velum and mouth (right).

shell. The ancestors of the bivalves, in his opinion, were preadapted for bivalve conditions in having a hatchet-shaped foot, well diversified pallial and adductor muscles and suitable structure for collecting particulate food. RUNNEGAR & BENTLEY (1983) discuss in detail two Lower Cambrian bivalves, *Pojetaia* as the first representative of the nuculoid stock and *Fordilla* as an ancestor to the mytiloid stock.

The shell shape of the Cambrian univalve probivalve is reflected in pathogenic embryos of recent *Anodonta* where, during the fifth phase of embryogenesis, mineralization is not carried out in the bivalve plan but, by mistake and atavistically, in the univalve plan. The result is a cyrtoconic shell of the shape of real existing fossil forms as they have been found from earliest Cambrian strata (YÜ WEN 1979). According to RAUP (1966) geometry and coiling of bivalve shells suggests a non-coiled cyrtoconic univalve as ancestor. But such a morphology of the shell does not have to be present during the whole life of the prebivalve but only for the conchs of the juveniles or embryos, since the change from univalve to bivalve organization in recent bivalves occurs when the organizational level is that of a veliger, perhaps of an ancestor with the shape of *Scenella* which was in existence at Late Proterozoic (RUNNEGAR 1983).

A reconstruction of the body plan of a prebivalve in the veliger stage of ontogeny corresponds to the 5th phase of bivalve embryo-genesis and is reconstructed in Fig. 21. The conch is bilaterally symmetrical and has a cyrtoconic twist to the apex towards the anterior. The mantle is free of the shell margin and soft body and conch are connected to each other where muscles attach to the mantle. Two bundles of muscles in symmetrical arrangement are fixed to the apical portion of the conch by specialized mantle cells. From here, muscles split into three bundles going to the head region, the second connects with the musculature of the foot and the third runs into the visceral mass and the free mantle. When muscles contract, head, foot and mantle edge are withdrawn below shell cover and an operculum may have sealed the aperture.

The head consists of a two-lobed ciliated velum that enables the animal to swim and to collect food particles which are transported into the ciliated esophagus and from here into the midgut. Digestion is aided by secretions of glands that connect with the stomach. The hind gut ends near the posterior mantle edge.

At this level of embryogenesis, the nervous system of the adult type as well as kidney, heart and gills are in the process of becoming differentiated and are not yet working. The buccal mass with radula apparatus is not yet in construction, as it is in most gastropods at this stage of embryonic development. Change-over to the bivalve organization from such univalve of a very simple prebivalve/pregastropod can be imagined in a single alteration at the end of the free-swimming phase in the pediveliger stage. During this stage recent archaeogastropods mineralize their shell while the shell of the swimming veliger is not mineralized (BANDEL 1982). When mineral deposits are only concentrated on the sides and do not cover the median line of the primary shell, the muscular strings connecting with the mantle pull the shell sides towards each other. Such a "pathological case" during ontogenesis of a conchiferan univalve can have produced the first bivalve (not protobranchs). Folding and pulling in of the mantle produced a cavity (pallial cavity) and brings mantle margins close to each other. The result is a shell-covered mollusc that can close the shell tightly. When valves are gaping mantle edges can be held close to each other so that particles of the sediment can be kept from entering the mantle cavity.

This one alteration thus changes a conch constructed for swimming and later for clinging to hard substrates and with wide-open aperture into a two-valved conch with which it is possible to enter soft substrates and here keep the pallial cavity clean. The buccal mass could have become lost during this "pathological" process while velum lobes remained functioning and developed into the lips of the adult (palps, labial lobes). The operculum became obsolete and may have been shed after shell folding, but the production of the organic shell on the apical posterior side of the foot was not lost but rearranged in order not to secrete the increments of growth of a spiral lid, but of a continuous thread (byssus). To discard an operculum is no problem, as can be observed in many marine opisthobranch and pulmonate gastropods when the phase of the larval life ends.

Characteristic features of bivalves, like hinge structure and ligament, elaboration of mantle edge, mantle shell attachment and filter-feeding by gills, are later developments but have evolved quite rapidly in bivalve evolution (POJETA 1978).

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