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Development of the pericalymma larva of *Solemya reidi* (Bivalvia: Cryptodonta: Solemyidae) as revealed by light and electron microscopy

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Abstract

Solemya reidi Bernard 1980 is a gutless protobranch bivalve known to possess intracellular chemoautotrophic bacterial symbionts in its gill. A light and electron microscope study on the embryology and larval development of *S. reidi* provides data for the bivalve Subclass Cryptodonta. *S. reidi* spontaneously spawned large eggs (271 μm in diameter), which developed within individual gelatinous egg capsules. The first several cleavages were equal and a distinct molluscan cross was formed at the animal pole of the embryo, features previously unreported in bivalve development. Lecithotrophic pericalymma larvae (similar to the larvae of paleotaxodont protobranch bivalves and aplacophoran molluscs) hatched at 18 to 24 h and remained in the water column for a further 5 d at 10 °C. At hatching, larvae measured from 360 to 440 μm in length and from 225 to 265 μm in cross-sectional diameter. Definitive adult structures developed within an epithelial locomotory test entirely covered with compound cilia. The test histolysed at metamorphosis and was ingested through the mouth into the perivisceral cavity. Length and height of the shell following metamorphosis was 433 μm ($\pm$ 42 μm, $n = 16$) and 282 μm ($\pm$ 29 μm, $n = 13$), respectively. Primary data and data from the literature show that the type of larval development in both paleotaxodont and cryptodont bivalves cannot be reliably estimated from egg or prodissoconch sizes.

Introduction

The protobranch bivalves consist of the two subclasses Paleotaxodonta and Cryptodonta (Newell, 1969). The embryology of the paleotaxodont protobranch bivalves *Yoldia limatula*, *Nucula proxima* and *N. delphinodonta* was described by Drew (1897, 1899a, b, 1901). However, Drew [as revealed in Morse (1913)] never found eggs in the cryptodont protobranch genus *Solemya* and as a consequence our knowledge of development within this bivalve subclass, containing the extant families Solemyidae and Nucinellidae, has been entirely lacking.

Interest in development amongst the cryptodont and paleotaxodont protobranch bivalves is due to the consideration that protobranchs may be the closest living group to the ancestral bivalve condition (Pelseneer, 1891; Drew, 1899b; Yonge, 1959; Jablonski and Lutz, 1983) and that the type of embryological and larval development in each taxon gives evidence for determining phylogenetic relationships. Recently, the discovery of the gutless condition in certain solemyid (Reid, 1980; Reid and Bernard, 1980; Kuznetsov and Shileiko, 1984) and nucinellid bivalves (Kuznetsov and Shileiko, 1984) and the description of chemoautotrophic, intracellular, bacterial symbionts in the gills of several members of the genus *Solemya* (Cavanaugh, 1980, 1983; Cavanaugh *et al.*, 1981; Felbeck *et al.*, 1981, 1983; Felbeck, 1983) has added interest both in the formation and fate of the endoderm, which normally forms the organs of digestion, and in the methods by which the endosymbionts are transmitted from one host generation to the next.

The gutless cryptodont bivalve *Solemya reidi* ranges from Southern California to southern Alaska, at depths of 40 to 600 m (Bernard, 1980), in habitats where oxygen and reduced sulfur compounds are simultaneously available, such as sewage outfalls (Felbeck, 1983; Felbeck *et al.*, 1983) and beneath log-booming grounds in the Pacific Northwest (Reid, 1980). Since *S. reidi* is increasingly being used in studies of the association between chemoautotrophic endosymbionts and host animals from sulfide-rich habitats (Felbeck, 1983; Felbeck *et al.*, 1983; Hand and Somero, 1983; Fisher and Childress, 1984; McMahon and Reid, 1984; Powell and Somero, 1985), knowledge of its development is desirable.

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This paper describes the embryology and larval development of *Solemya reidi* in order to lay a foundation for understanding the fate of the endoderm and the mechanism of symbiont transmission and to provide data crucial in answering the phylogenetic questions posed by the presumed primitiveness of the Solemyidae. Salvini-Plawen (1972, 1973, 1980) coined the term "pericalymma" to describe the larval type he considered primitive in annelids, sipunculids and molluscs. As in Jablonski and Lutz (1983), the term "pericalymma" is used in this report in its narrow sense to refer to the larval form of protobranchs and aplacophorans, much as the general term "veliger" has been applied to other bivalve and gastropod larvae. The pericalymma is a free-swimming lecithotrophic larva with a ciliated test within which all the definitive adult structures develop, including the shell, and which is cast off at metamorphosis.

Materials and methods

Adult *Solemya reidi* Bernard 1980 were collected from a depth of 40 m with a Van Veen grab in the vicinity of log-booming grounds numbers 27 and 29 in Alberni Inlet on the west coast of Vancouver Island, British Columbia, Canada (Lat. 49°12′ N; Long. 124°49′ W). Individuals 25 to 50 mm in length were either allowed to burrow in 15 to 20 cm of native sediment in 10-gallon (ca 38-l) aquaria equipped with flowing recirculated seawater or were kept without sediment in small bowls filled with filtered seawater changed at 2-d intervals and maintained at 10 °C ± 1 C°.

Numerous attempts to spawn apparently ripe *Solemya reidi* using thermal and osmotic shock, electrical and chemical stimulation, and the addition of suspensions of gametes were unsuccessful. The stripping and combining of gametes from *S. reidi* also failed to result in successful fertilization even after inducing germinal vesicle breakdown of oocytes with ammonium hydroxide (Loosanoff and Davis, 1963). Consequently, all embryos and larvae were obtained from eight spontaneous spawnings of individuals kept in either of the two adult culture conditions.

Embryos and larvae were pipetted individually (due to their extreme fragility) from bowls or aquaria and placed at a density of 2 to 3 per ml in 3-l glass beakers filled with 0.45 μm filtered seawater. Cultures were maintained at 10 °C ± 1 C° and slowly aerated until one day prior to settlement. No antibiotics were used (in consideration of the possible transmission of prokaryotic endosymbionts through eggs and embryos). Water was changed at 2-d intervals.

Developmental stages were measured with an ocular micrometer and photographed with a Zeiss Universal microscope. Fertilized eggs, embryonic stages, larvae, and juveniles were prepared for transmission electron microscopy (TEM) and scanning electron microscopy (SEM) by primary fixation in a solution of 2% glutaraldehyde, 0.2 *M* phosphate buffer, and 0.14 *M* NaCl at pH 7.3, followed by three rinses with a solution of 0.2 *M* phosphate buffer and 0.28 *M* NaCl and post-fixation in 2% OsO_4 in 1.25% $NaHCO_3$. Specimens prepared using a primary fix of 2.5% glutaraldehyde, 2% paraformaldehyde, and 0.1 *M* Na-cacodylate buffer gave inferior results. After fixation, specimens were dehydrated in alcohol. TEM specimens were infiltrated and embedded in epon, thin sectioned on glass or diamond knives, mounted on copper grids, and stained in 2% uranyl acetate and 0.2% lead citrate. Grids were examined and micrographs taken on a Philips EM 300 electron microscope. SEM specimens were critical-point dried, mounted on double-sided sticky tape, gold coated, and examined on a JEOL JSM-35 scanning electron microscope. Half to one micrometer serial sections for light microscopy were cut with glass or diamond knives on either a Sorvall MT 5000 or a Reichert UM-U2 ultramicrotome and stained in Richardson's stain (Richardson *et al.*, 1960). Late larvae and juvenile stages destined for sectioning were decalcified in 2% ascorbic acid and 0.3 M NaCl for 24 h prior to dehydration (Dietrich and Fontaine, 1975).

Results

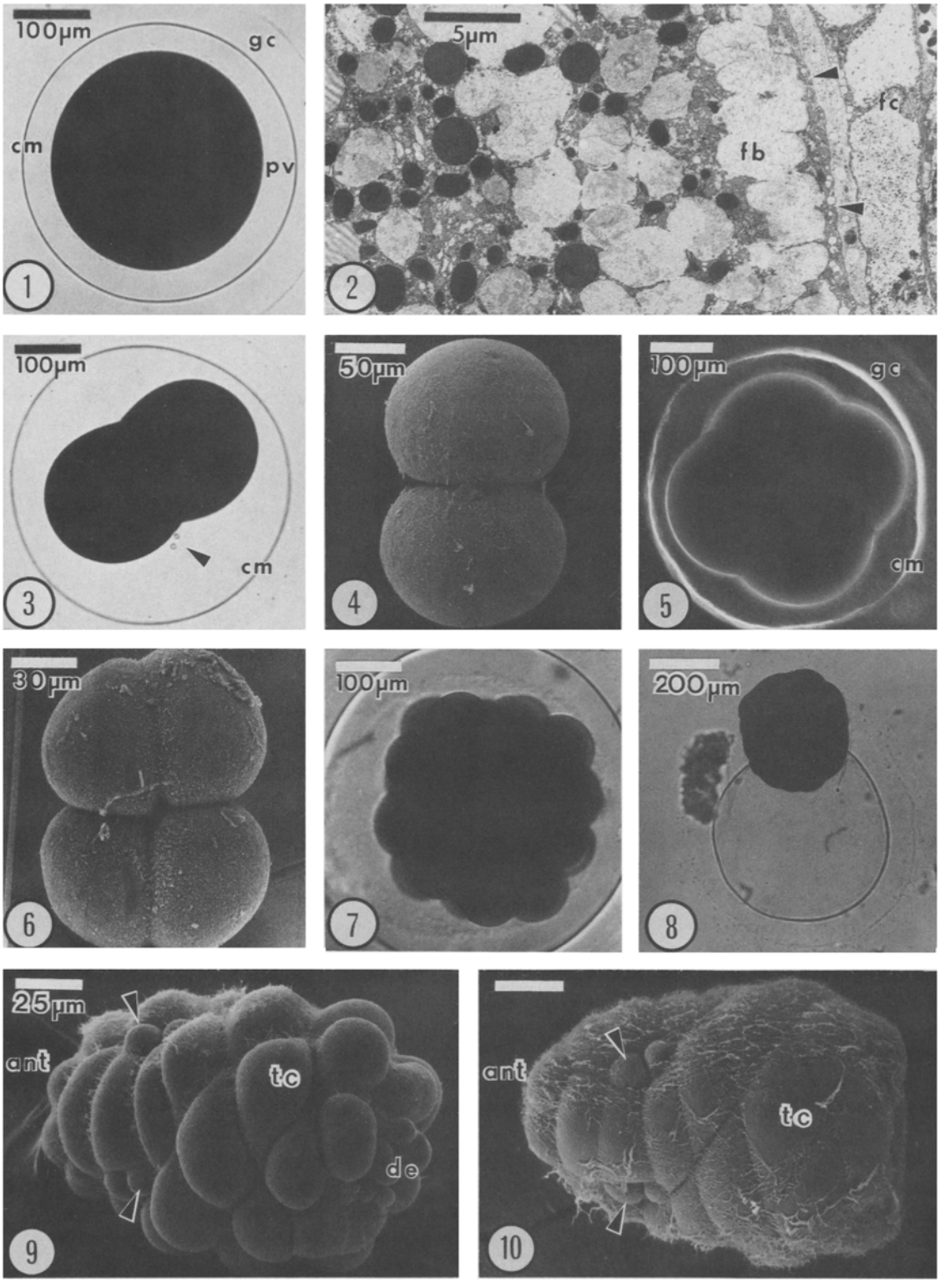
Embryonic development

Fertilized eggs are orange in color, spherical, and have an average yolk-mass diameter of 271 μm (± 11 μm, $n = 83$). The fertilization envelope is fully elevated, overlying a perivitelline space approximately 53 μm wide (Fig. 1). Naturally spawned, unfertilized eggs were not observed.

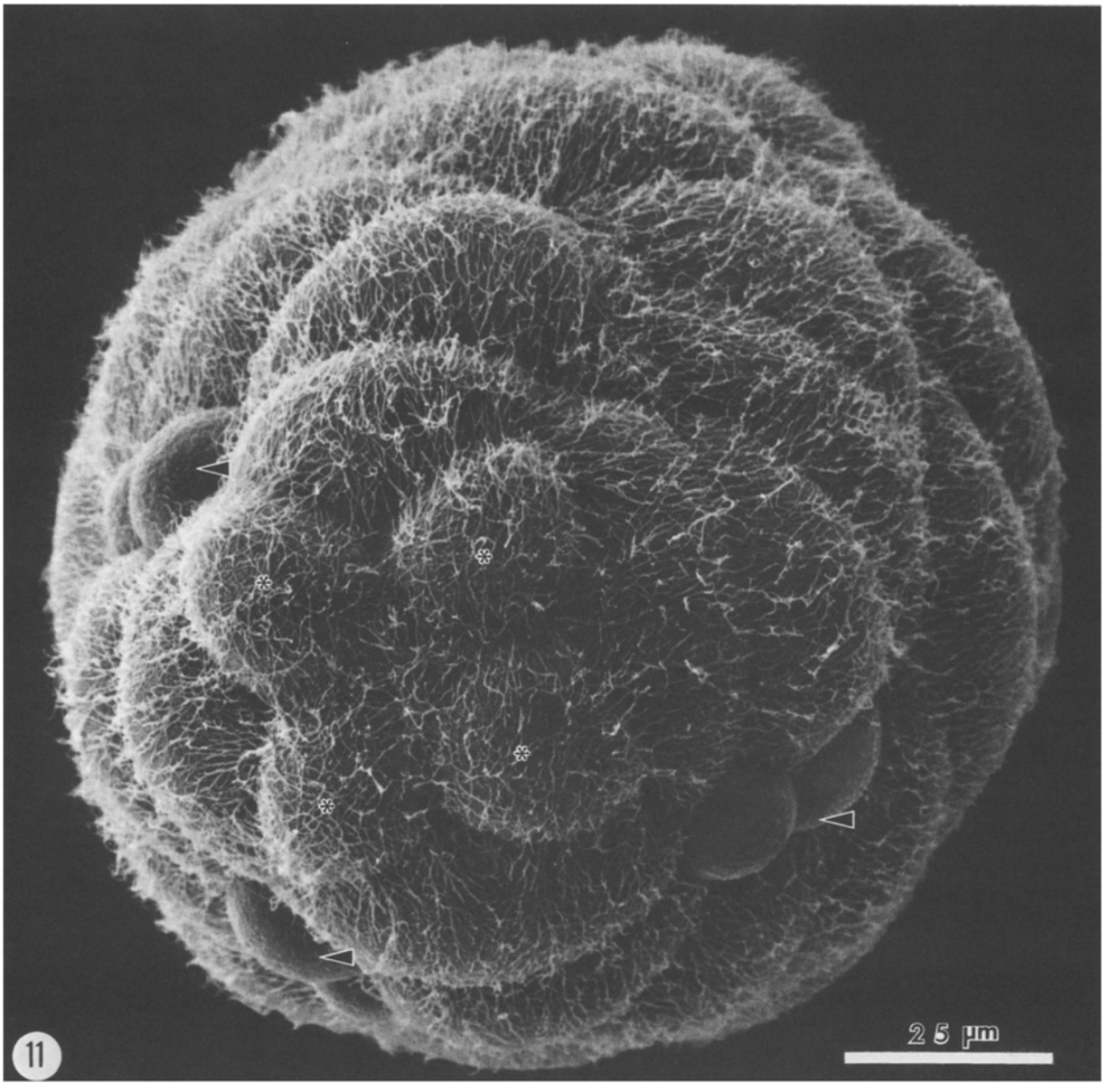
The fertilization envelope is surrounded by a clear, gelatinous egg capsule approximately 48 μm thick (Fig. 1), which persists around all developmental stages until hatching. The gelatinous layer increases the overall egg capsule diameter to about 465 μm, which enlarges to a mean of 566 μm (± 25 μm, $n = 11$) by the 2nd division, owing to expansion of the perivitelline space. This gelatinous coat is not present in stripped, unfertilized ova. Egg capsules are sticky and negatively buoyant, becoming covered with detritus when spawning occurs over natural sediment. The periphery of the egg cytoplasm is lined with numerous granules containing a fibrillar mucus substance (Fig. 2).

Unfertilized eggs are primary oocytes between germinal vesicle breakdown and first polar body emission, which occurs within 40 min of fertilization. A meridonal, equal cleavage begins about 1.5 h after fertilization and results in two equalized blastomeres (Figs. 3 and 4). Second cleavage is also equal, at right angles to the first, and is completed from 2.5 to 3 h after fertilization (Figs. 5 and 6). The second cleavage is not strictly meridonal, but rather somewhat spiral, and results in the formation of a polar furrow with the first and second cleavage furrows having a short stretch in common (Fig. 6). At no time was the formation of a polar lobe observed.

The third cleavage is equatorial and spiral, occurs 4 to 4.5 h after fertilization, and results in eight approximately



Figs. 1–10. *Solemya reidi.* **Fig. 1.** Light micrograph of living fertilized egg, enclosed by the egg capsule. pv, perivitelline space; cm, inner capsule membrane; gc, gelatinous coat. **Fig. 2.** Transmission electron micrograph of cytoplasmic portion of ripe ovarian oocyte. The periphery of the oocyte can be seen at the far right of the micrograph (arrowheads). fb, cortical mucous granule; fc, follicle cell. **Fig. 3.** Light micrograph of living 2-cell stage embryo showing location of the two polar bodies (arrowhead) within the egg capsule. Blastomeres are essentially equal in size and average 227 μm in diameter. cm, inner capsule membrane. **Fig. 4.** Scanning electron micrograph of 2-cell stage embryo removed from the egg capsule. Blastomeres are of equal diameter. **Fig. 5.** Light micrograph of living 4-cell stage embryo showing equality of division of all blastomeres. gc, gelatinous coat; cm, inner capsule membrane. **Fig. 6.** Scanning electron micrograph of 4-cell stage embryo removed from the egg capsule. **Fig. 7.** Light micrograph of living stereoblastula. **Fig. 8.** Light micrograph of living gastrula in the process of hatching out of the egg capsule. **Fig. 9.** Scanning electron micrograph showing external morphology of embryo-larva removed from the egg capsule prior to hatching. Arrowheads indicate two of the three pairs of cells which reside between the 2nd and 3rd row of test cells. tc, test cell; de, proliferating definitive ectoderm cells; ant, anterior. **Fig. 10.** Scanning electron micrograph of 1-d-old pericalymma larva showing two of the three pairs of small unciliated surface cells between the 2nd and 3rd row of test cells (arrowheads). ant, anterior, tc, diamond-shaped test cell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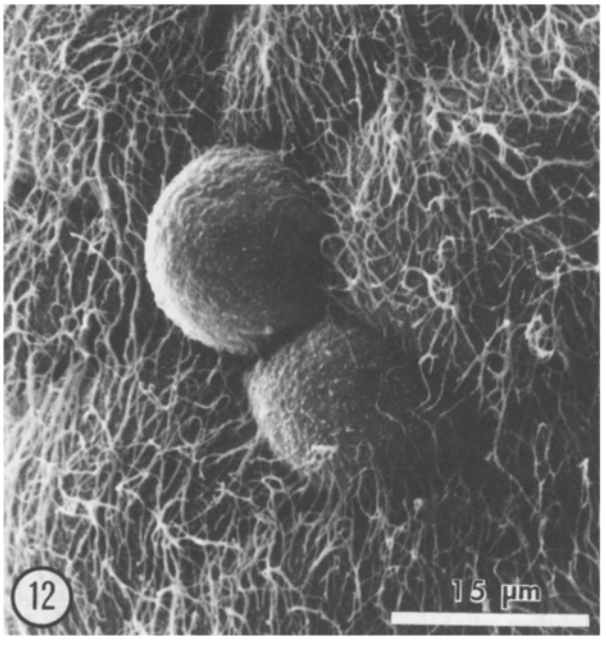
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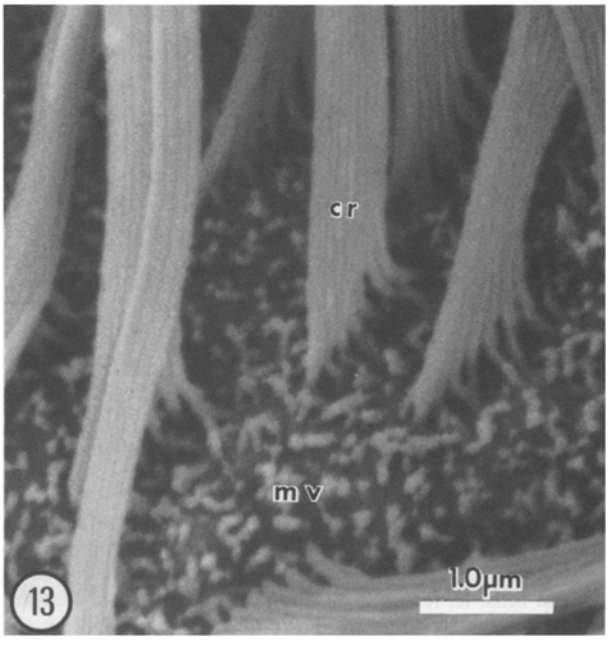
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equal blastomeres. Successive cleavages result in a ciliated stereoblastula which begins rotating within the egg capsule by 15 h after fertilization (Fig. 7). Elongated gastrulae begin hatching from the egg capsules 18 h after fertilization; the last hatching occurs 28 h after fertilization (Fig. 8). Embryos removed from the egg capsule before hatching are elongated and undergoing gastrulation and ciliogenesis (Fig. 9).

Gastrulation is difficult to observe, but appears to occur in two stages, similar to gastrulation in the paleotaxodont protobranchs (Drew, 1899a, b, 1901) and aplacophorans (Thompson, 1960): initially by invagination of large, pre-existing cells into the interior of the embryo in combination with epibolic overgrowth by the test, forming an abapical depression that resembles a blastopore; and secondarily, by proliferation of smaller cells at this "pseudo-blastopore", with the subsequent ingression of these cells into the inner regions of the embryo (Fig. 9). The first of these phenomena results in the differentiation of endoderm, while the second results in the formation of all future adult ectoderm. The endoderm thus comes to lie deep within the embryo, eventually cut off from the exterior by a layer of definitive adult ectoderm. The pseudo-blastopore forms neither the adult mouth nor anus in these forms (Thompson, 1960) and is merely the site from which proliferation and ingression of definitive ectoderm occurs. Mesoderm was not differentiated at this stage.

Most of the remaining cells on the surface of the embryo will form the larval locomotory test. However, there are three groups of two cells each which do not form part of the locomotory test; they are located on the anterior lateral aspect of the embryo between the 2nd and 3rd cell rows of the test (Figs. 9, 10) and are destined to invaginate. Their fate is uncertain as their cell lineage could not be traced with confidence.

Larval development

Newly hatched larvae of *Solemya reidi* range in length from 360 to 440 μm with a maximum cross-sectional diameter of 225 to 360 μm (Fig. 10). An apical quartet of ciliated cells lies at the extreme anterior end of the larvae (Fig. 11). The cells directly posterior to and between these apical cells comprise the molluscan cross.

The larvae are uniformly ciliated with the exception in young larvae of three pairs of small cells lying between the 2nd and 3rd row of the test (Figs. 11 and 12). Many cirri composed of from 6 to 9 cilia each arise from each test cell (Figs. 12 and 13), while microvilli are spread over the intervening cell surface (Fig. 13). Each cirrus is up to 40 μm in length and beats in a dexioplectic manner, giving rise to metachronal waves which cause the larva to move forward in a clockwise helical spiral. The larval test consists of a series of nine rows of ciliated cells encircling the embryo (Fig. 14), each row containing four diamond-shaped cells (Fig. 10), giving a total of 36 test cells.

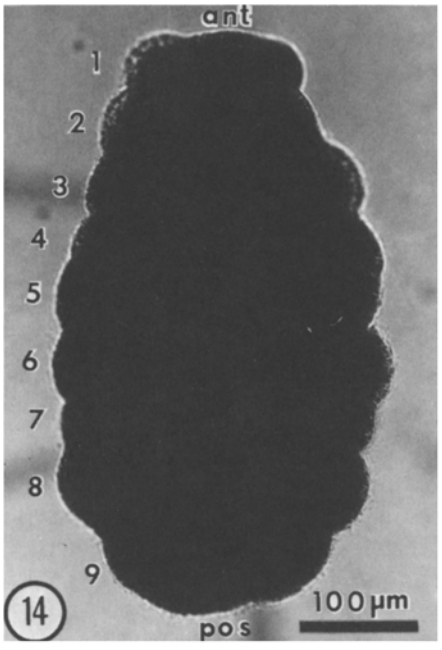
By the 2nd to 3rd day after fertilization several changes in external appearance of the larvae have occurred. The cells making up the test have further flattened and extended, making it difficult to observe their number and shape (Figs. 15, 16). The three pairs of unciliated cells, which were located between the 2nd and 3rd rows of test cells, have invaginated, leaving behind three depressions marking their former location (Figs. 15, 16). In addition, the four apical cells have either invaginated or become incorporated into the first row of test cells, leaving a cross-shaped depression at the apical end of the embryo (Fig. 15). The area immediately around the pseudo-blastopore and in the pseudo-blastopore cavity is unciliated and proliferation and ingression of definitive ectoderm at this site has ceased (Fig. 17). A tuft of cilia is never formed on the apical plate of *Solemya reidi.*

Healthy larvae never rest on the bottom of the culture containers, passing the entire 5-d pericalymma stage in the water column. They are very active and swim, apical end first, in a vertical sinusoidal path while rotating counterclockwise about the long axis of the body when viewed from the anterior. When swimming, the apical end of the larvae is uppermost, owing to an anterior accumulation of lipid (Fig. 18). The young larvae concentrate near the water surface in the culture containers under both light and dark conditions, suggestive of negative geotaxis.

The internal morphology of a 5-d old pericalymma larva is shown in Figs. 19 and 20. A large lumen representing the perivisceral cavity is bounded ventrally by the visceral mass and dorsally and laterally by the mantle. Within the perivisceral cavity lies the stomach rudiment. The single-layered larval test separates the rest of the larva from the environment. The test and definitive tissues are closely applied early in development, but by the 3rd day after fertilization an internal space develops and these tissues remain attached only in the region surrounding the apical plate.

The formation of mantle and shell is accompanied by lateral compression and dorsoventral widening of the larva as the test is forced to conform to the outlines of the developing shell (Fig. 21). Mineralization of the larval shell was not detected by polarized light birefringence in swimming larvae, even though the shell outline was easily seen through the test.

Figs. 11–13. *Solemya reidi.* **Fig. 11.** Scanning electron micrograph of the apical region of a 1-d-old pericalymma larva. Surrounding the animal pole are the four apical cells (asterisks). The cells making up the four arms of the molluscan cross are situated slightly posterior to and between the apical cells. The three pairs of small unciliated cells (arrowheads) can be seen between the 2nd and 3rd row of test cells. **Fig. 12.** Scanning electron micrograph showing detail of one of the three pairs of unciliated surface cells which are located between the 2nd and 3rd row of test cells in a 1-d-old pericalymma larva. **Fig. 13.** Scanning electron micrograph of surface of the test showing the cirri and microvilli (mv) which cover the test cell surface. Each cirrus (cr) is composed of from 6 to 9 cilia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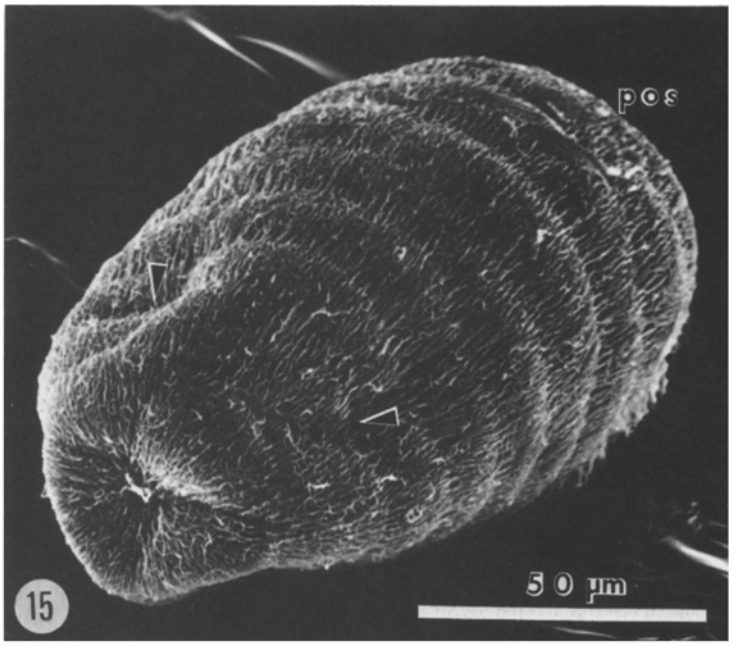
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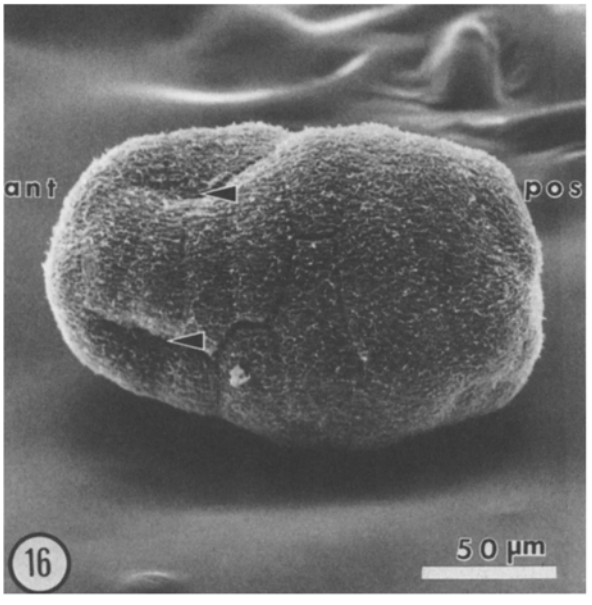
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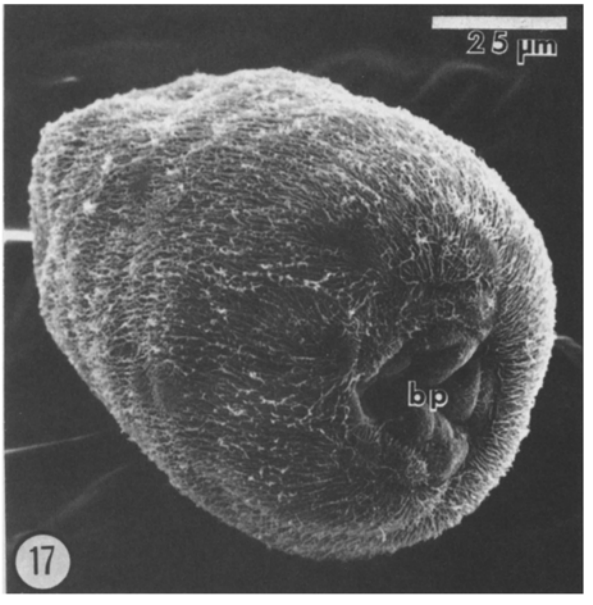
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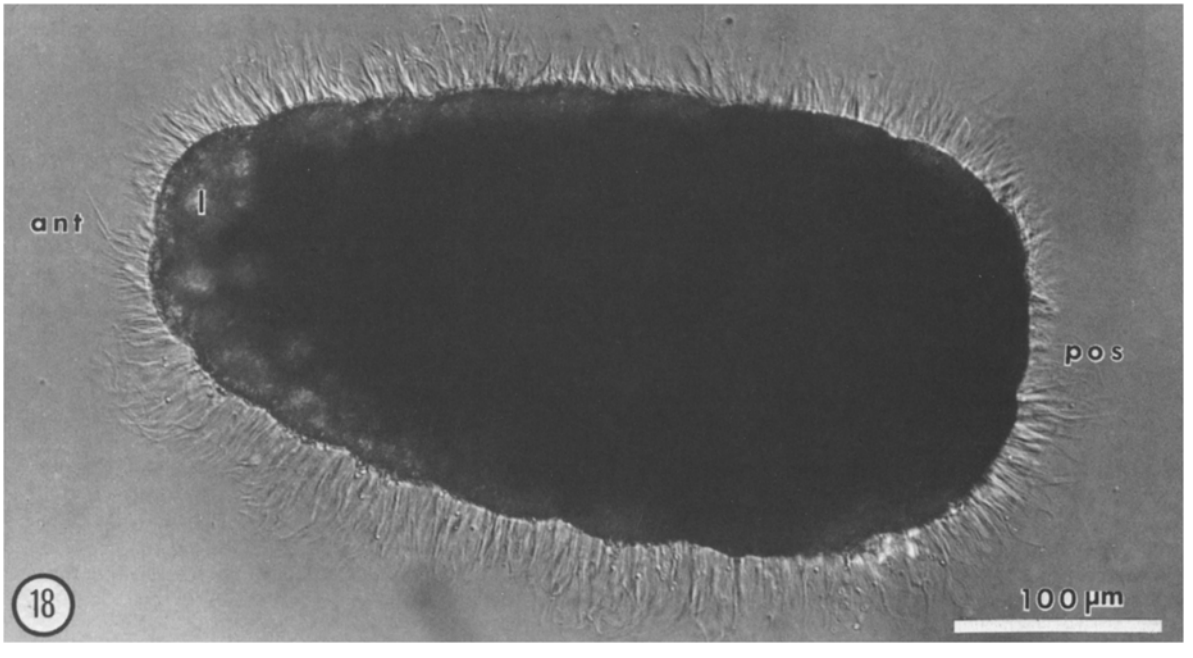
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Metamorphosis

Metamorphosis in *Solemya reidi* processes slowly over a period of several hours, involving the transformation from a swimming pericalymma larva to a benthonic bivalve via histolysis of the test. On the 6th day after fertilization, larvae begin to swim near the bottom of the culture containers. The most posterior test cells begin to round up and break their connections with each other, thus allowing the shell to poke through the ruptured larval test (Fig. 22). These cells are gradually drawn ventrally and anteriorly, revealing the two valves of the larval shell beneath (Fig. 23). The cilia on the test cells continue to beat, causing the larva to swim in circles on the bottom of the culture containers. Some of the test cells lose their connections to adjacent cells and swim off on their own, but the majority are ingested through the larval mouth.

The cells making up the dorsal wall of the stomach dissociate at metamorphosis so that the esophagus opens directly into the perivisceral cavity. Thus the test material ingested at metamorphosis comes to lie within the lumen of the perivisceral cavity (Figs. 24, 25).

Post-larval morphology

Recently metamorphosed *Solemya reidi* are distended by the ingested test material and the major organs in the mantle cavity are poorly developed (Fig. 26). The overall length and height of the shell is 433 μm ($\pm$ 42 μm, $n = 16$) and 282 μm ($\pm$ 29 μm, $n = 13$), respectively. Cellular remnants of the test are still visible within the anterior, pre-oral portion of the mantle cavity of settled juveniles (Figs. 26, 27).

Several presumptive adult structures can be recognized within the mantle cavity. A tuft of cilia protrudes from the anus, which is located in the extreme posterior part of the mantle cavity. A small cluster of post-anal cilia is also present in this region (Fig. 28). A group of ciliated cells occupies a portion of the visceral mass immediately posterior to the proximal part of the foot (Figs. 26 and 29). This band of ciliated cells and accompanying mantle mucous glands are possible rudiments of the adult hypobranchial gland, which is ciliated in the adult (Morton, 1977). Two gill buds located on opposite sides of the visceral mass posterior to the ciliated band (Fig. 29) will eventually form the adult ctenidia. The prominent mouth lies in the anterior mantle cavity; the region immediately surrounding it is densely ciliated (Figs. 26, 30). The foot is visible in the mid-section of the mantle cavity attached dorsally to the visceral mass; however, it is poorly developed (Fig. 26) and the juvenile is incapable of crawling or burrowing for at least a week after metamorphosis. The anterior margin of each lobe of the juvenile foot is ciliated and the opening to the pedal gland can be seen on the posterior mid-line of the foot (Fig. 26). At no time during metamorphosis or subsequent juvenile development are byssal threads produced by the pedal gland.

There are no obvious concentric growth lines on the larval shell (prodissoconch) nor is there a distinction between a prodissoconch I and II shell (Figs. 31, 32, 33). There is also no coarse or irregular punctate surface texture on the shell, which is normally indicative of the prodissoconch I (Jablonski and Lutz, 1980). However, there are irregular folds or wrinkles on the shell surface, which is usually indicative of brooded larvae (Jablonski and Lutz, 1980). Although several attempts were made to dissolve the hinge ligament of larval and juvenile shells by immersion in 5% sodium hypochlorite (following the method of Lutz *et al.*, 1982), the valves failed to disarticulate and a view of the hinge morphology was not obtained.

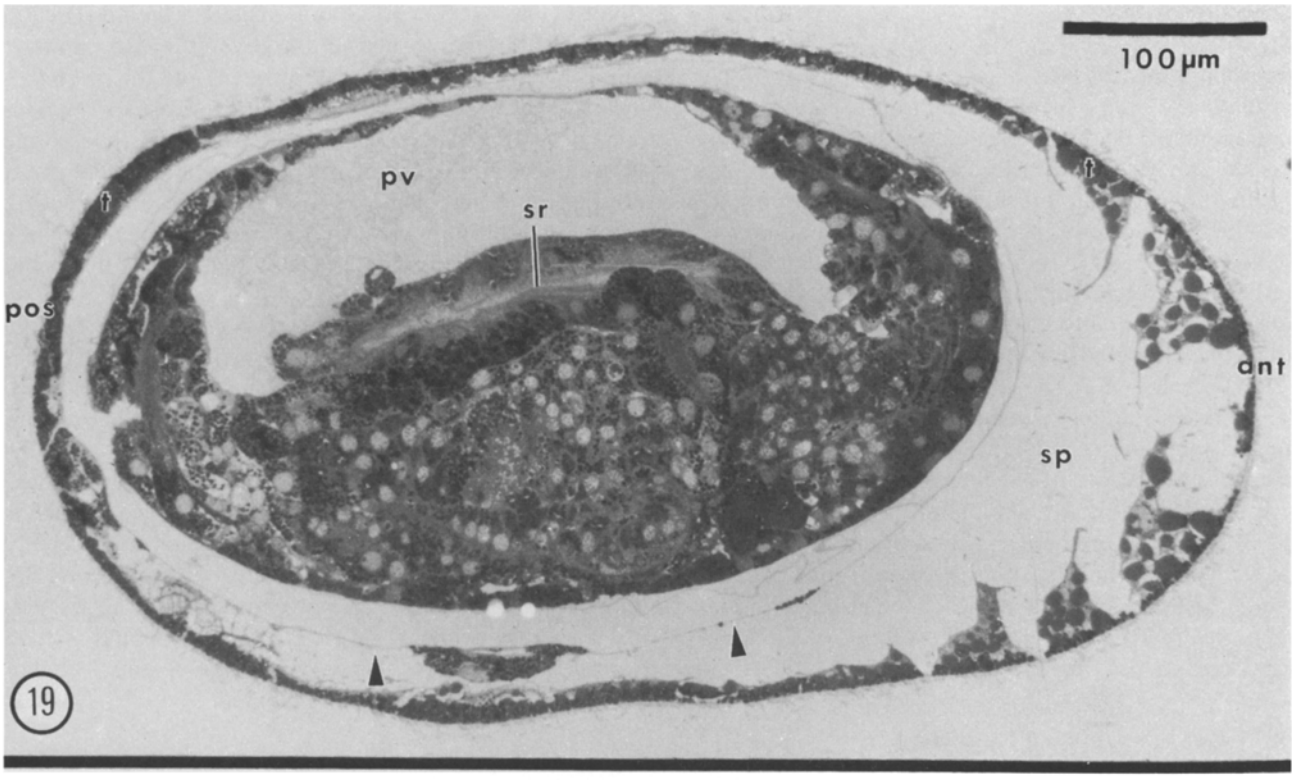
Discussion

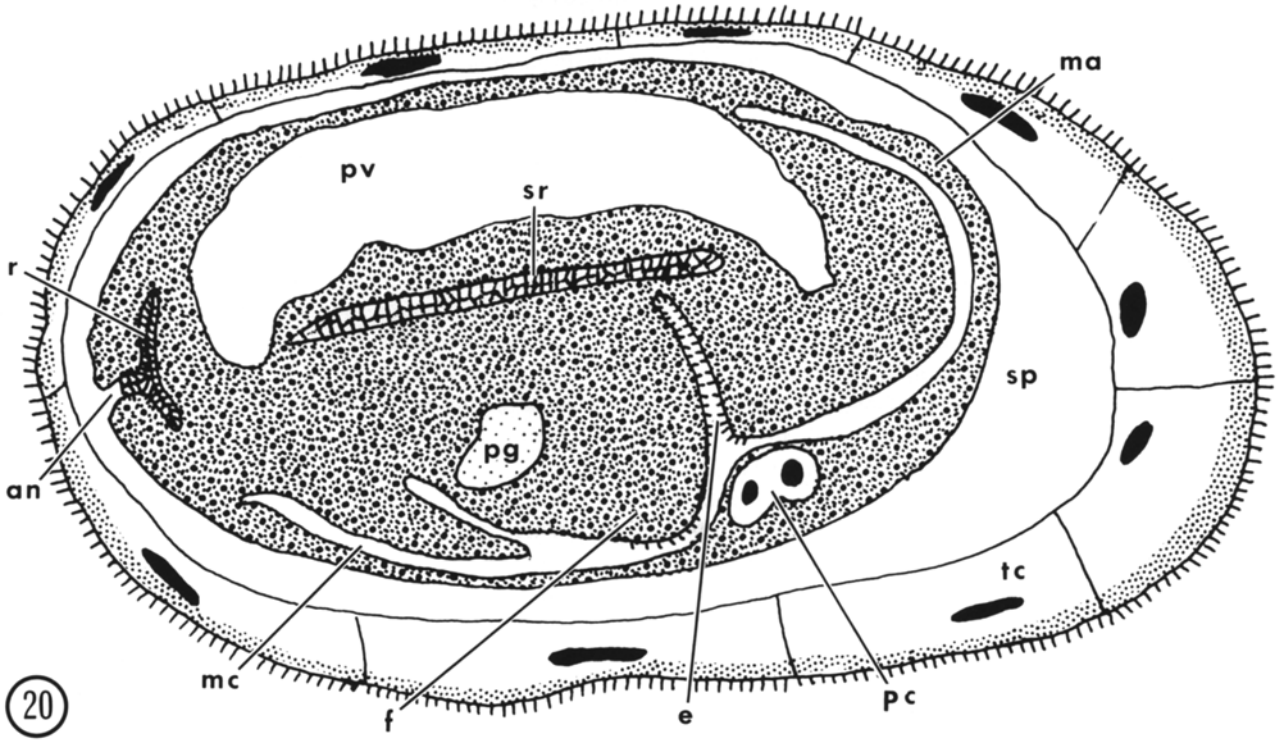
A lecithotrophic pericalymma larva with its ciliated epithelial test, within which the definitive adult structures develop, has been described for the paleotaxodont protobranch bivalves *Yoldia limatula* (Drew, 1897, 1899a, b), *Nucula proxima* (Drew, 1899b), *N. nucleus* (Lebour, 1938), *N. turgida* (Lebour, 1938; Trevallion, 1965), *Nuculana pernula* (Trevallion, 1965), and *Acila castrensis* (personal observation), and for the aplacophoran molluscs *Nematomenia* (=*Dondersia*) *banyulensis* (Pruvot, 1890), *Rhopalomenia* (=*Proneomenia*) *aglaopheniae* (Pruvot, 1892), and *Neomenia carinata* (Thompson, 1959, 1960). To this list can now be added the cryptodont protobranch bivalve *Solemya reidi*.

Egg capsule

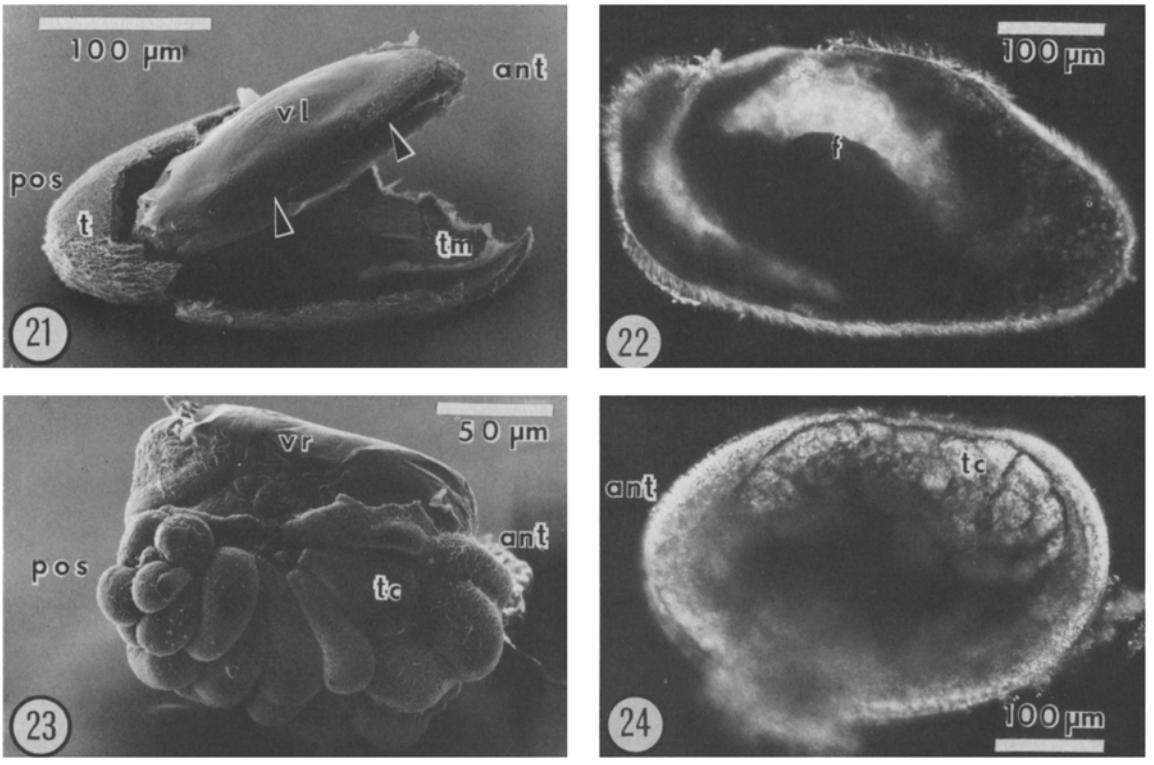
The gelatinous coat surrounding the egg of *Solemya reidi* appears to be secreted by the egg itself, subsequent to spawning and fertilization. It was never seen surrounding stripped, unfertilized ova, but was present around all natu-

Figs. 14–18. *Solemya reidi.* **Fig. 14.** Light micrograph of 1-d-old pericalymma larva showing arrangement of the nine rows of test cells (1–9) making up the ciliated test. ant, anterior; pos, posterior. **Fig. 15.** Scanning electron micrograph of 2 to 3-d-old pericalymma larva. The three pairs of unciliated surface cells (cf. Fig. 11) have invaginated, leaving behind three depressions on the anterior surface of the test (arrowheads). The apical cells (cf. Fig. 11) have either invaginated or lost their distinctiveness in becoming incorporated into the test. pos, posterior. **Fig. 16.** Scanning electron micrograph of a 3-d-old pericalymma larva showing sites of invagination (arrowheads) of two of the three pairs of unciliated surface cells (cf. Fig. 11). ant, anterior; pos, posterior. **Fig. 17.** Scanning electron micrograph of posterior aspect of 3-d-old pericalymma larva. The cells lining the cavity of the pseudo-blastopore (bp) are unciliated. **Fig. 18.** Light micrograph of 3 to 4-d-old pericalymma larva showing the extent of test ciliation and accumulation of lipid (l) in the anterior of the larva. ant, anterior; pos, posterior





Figs. 19–20. *Solemya reidi.* **Fig. 19.** Light micrograph of one micrometer longitudinal section through a 5-d-old pericalymma larva. Arrowheads indicate the position of the test membrane. t, test; pv, perivisceral cavity; sr, stomach rudiment; sp, space separating test and definitive tissues; ant, anterior; pos, posterior. **Fig. 20.** Diagrammatic depiction of the section shown in Fig. 19. ma, mantle; an, anus; pv, perivisceral cavity; r, rectum; sr, stomach rudiment; e, esophagus; pg, pedal gland primordium; mc, mantle cavity; tc, test cell; pc, problematic cells; f, foot; sp, space separating test and definitive tissues. Scale as in Fig. 19



Figs. 21–24. *Solemya reidi.* **Fig. 21.** Scanning electron micrograph of a 4-d-old pericalymma larva that has had a portion of the surrounding test removed, revealing a dorsal view of the enclosed definitive shell and tissues. The dorsal hinge line is indicated by arrowheads. tm, test membrane; vl, left valve; t, test; ant, anterior; pos, posterior. **Fig. 22.** Light micrograph of a living pericalymma larva at the beginning of metamorphosis. The test cells have begun to separate in the posterior region and the outline of the shell is visible through the test. Anterior is to right. f, foot primordium. **Fig. 23.** Scanning electron micrograph of 6-d-old pericalymma larva undergoing metamorphosis. The test cells (tc) have become detached from the internal structures at the posterior (pos) and dorsal margins and have moved anteriorly and ventrally. vr, right valve; ant, anterior. **Fig. 24.** Light micrograph of a living 15-d-old juvenile showing the perivisceral cavity packed with ingested test material (tc) visible through the transparent shell. Dorsal is towards the top of the micrograph. ant, anterior

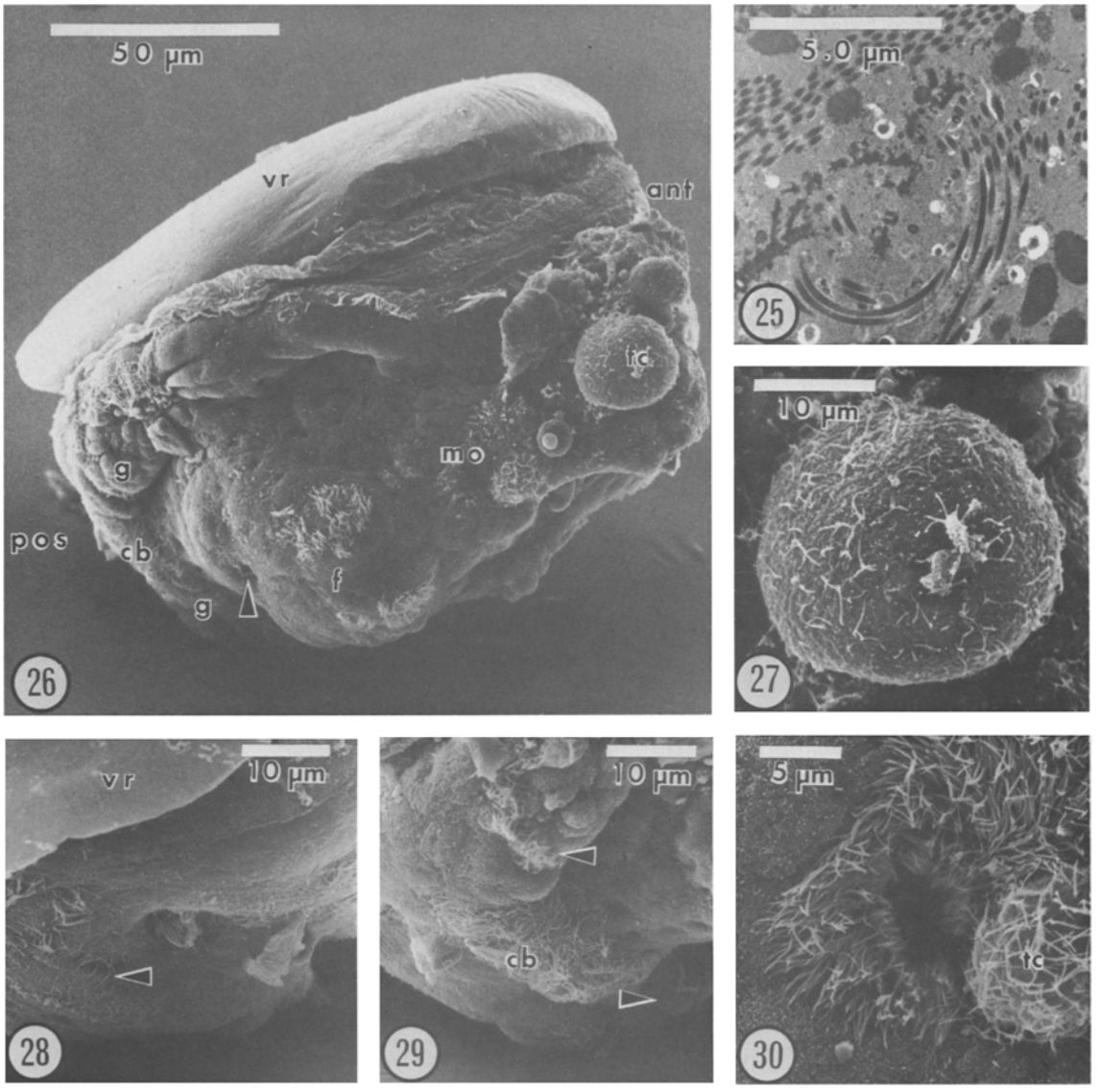
rally spawned and fertilized ova, and a layer of cortical mucous granules was present in ovarian oocytes but absent in encapsulated ova. A similar secretion of an egg capsule by bivalve oocytes has been reported for *Pandora inaequivalvis* (Allen, 1961) and *Astarte* spp. (Saleuddin, 1964), although only ovarian eggs of *Astarte* spp. were examined. In contrast, the hypobranchial gland secretes the external incubatory egg sacs of *Nucula delphinodonta* (Drew, 1901), while seasonally developed cells of the mantle edge of *Turtonia minuta* secrete its egg capsules, which are attached to byssal threads (Oldfield, 1955, 1964). The origin of gelatinous egg capsules in other species of bivalves is unknown.

Cleavage

Solemya reidi is the first bivalve reported to possess equal cleavage, i.e. the first two cleavages result in four practically equal blastomeres. Although cleavage is equal in many gastropods (Raven, 1966; Wada, 1968) and chitons (Wada, 1968; Pearse, 1979), as well as in one known aplacophoran (Hadfield, 1979), unequal cleavage has been considered the rule in the Bivalvia (Korschelt and Heider, 1900; Raven, 1966; Wada, 1968; Sastry, 1979). ÓFoighil (personal communication) has seen equal cleavage in the galeommatacean bivalve *Lasaea subviridis*; conversely, a large D-quadrant blastomere was seen in early blastulae of *Lasaea rubra* by Oldfield (1964), suggestive of unequal cleavage.

The absence of polar lobe formation in *Solemya reidi* has no bearing on the presence of equal cleavage, since many bivalves are known to cleave unequally without the formation of a lobe (Verdonk and van den Biggelaar, 1983). Two other protobranchs, *Nucula delphinodonta* (Drew, 1901) and *Acila castrensis* (personal observation) are known to form polar lobes.

Perhaps as a result of equal cleavage, *Solemya reidi* is also the only known bivalve to exhibit both a distinct molluscan cross and apical rosette cells during development. Their fate in this study has not been determined. In typical bivalve embryos, a large size difference exists between blastomeres, and cleavage does not occur simultaneously in all quadrants, resulting in an irregular arrangement of the cells and an obscuring of the molluscan cross and apical rosette (Raven, 1966; Verdonk and van den Biggelaar, 1983).

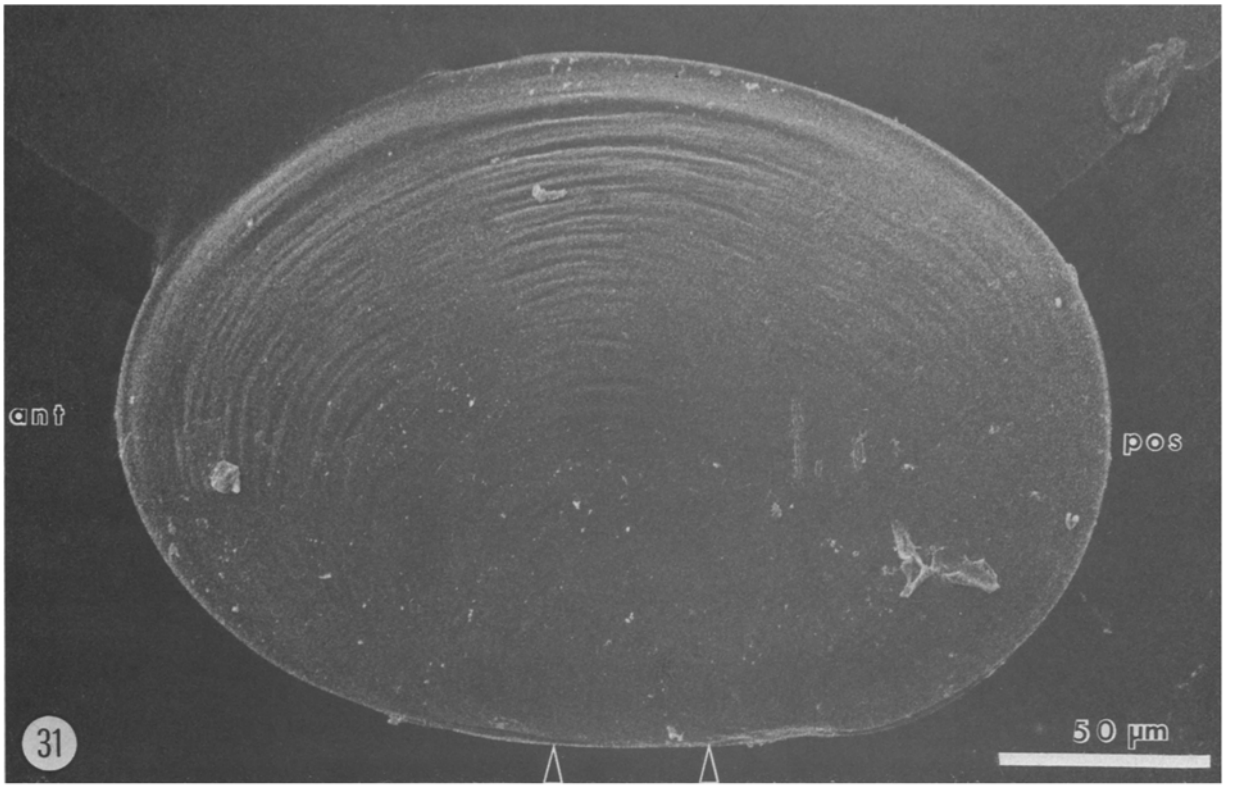


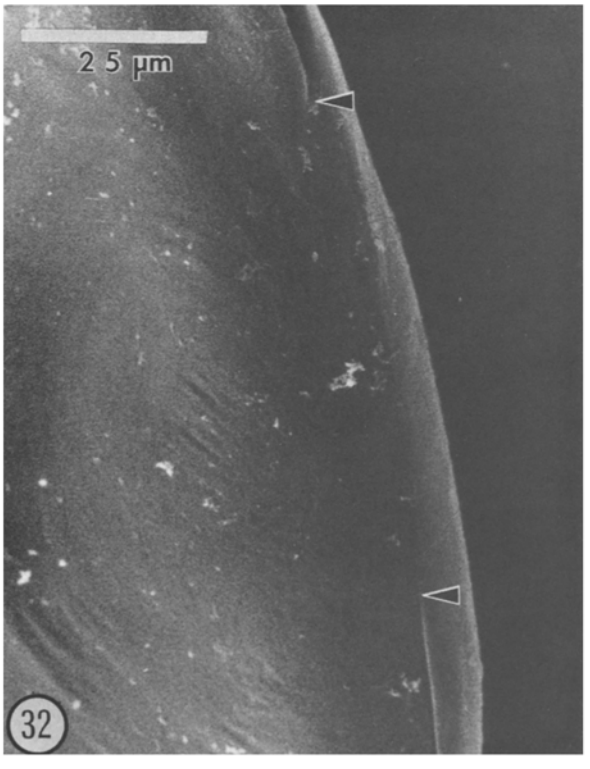
Figs. 25–30. *Solemya reidi.* **Fig. 25.** Transmission electron micrograph showing ingested test material and associated cilia within the perivisceral cavity of a juvenile. **Fig. 26.** Scanning electron micrograph of a 6-d-old, recently metamorphosed juvenile. The body is greatly distended due to the ingestion of large quantities of the test, a few cells of which (tc) remain in the anterior mantle cavity. The opening of the pedal gland is indicated by an arrowhead. vr, right valve; g, presumptive gill; cb, band of cilia; f, foot; mo, mouth; ant, anterior; pos, posterior. **Fig. 27.** Scanning electron micrograph showing close-up of the test cell remnant visible in Fig. 26. **Fig. 28.** Scanning electron micrograph showing ciliated opening of the anus and a tuft of post-anal cilia (arrowhead) in the same specimen as depicted in Fig. 26. vr, right valve. **Fig. 29.** Scanning electron micrograph of the presumptive gill rudiment and part of presumptive hypobranchial gland in the posterior portion of the mantle cavity of the same individual as depicted in Fig. 26. The presumptive gill consists of two gill buds (arrowheads) on either side of the mantle, while the band of cilia (cb) running across the floor of the posterior mantle cavity will give rise to part of the hypobranchial gland. **Fig. 30.** Scanning electron micrograph showing detail of the ciliated region around the mouth of a recently metamorphosed juvenile. The remnants of a test cell (tc) can be seen to the right

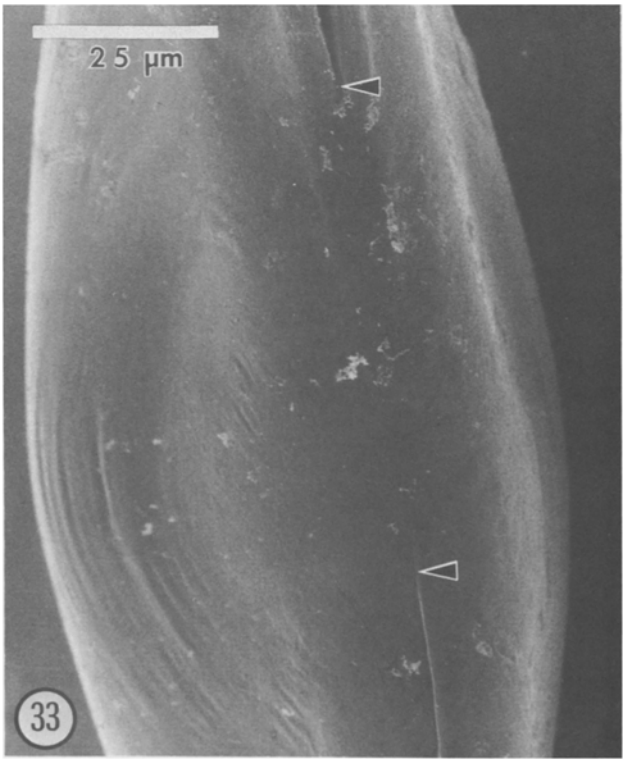
Ciliation and locomotion

The pattern of ciliation and the arrangement of the test cells differ markedly between the paleotaxodont protobranchs, the aplacophorans, and the cryptodont protobranch *Solemya reidi,* in which the test is evenly covered by locomotory compound cilia, no apical tuft is present and 36 cells are arranged in nine tiers of four cells each. Like *S. reidi,* the direct developing *S. velum,* from the east coast of the USA, elaborates a test entirely covered with cilia (J. Pechenik, personal communication).

A series of five rows of encircling cells comprise the test of the free swimming paleotaxodonts; the middle three rows, and sometimes a fourth, possess a band of cilia, which provides the locomotory force for swimming. The test is composed of 42 cells in *Yoldia limatula* with at least eight cells in each row (Drew, 1897). An apical tuft of cilia issues from the center of the apical plate and can be lashed







Figs. 31–33. *Solemya reidi.* **Fig. 31.** Scanning electron micrograph showing the right valve of a post-metamorphic juvenile. Distinctive boundaries between prodissoconch I and II and the dissoconch are not apparent. Arrowheads delineate the dorsal hinge line. ant, anterior; pos, posterior. **Fig. 32.** Scanning electron micrograph showing the dorsal hinge line (between arrowheads) of a post-metamorphic juvenile. The periostracum of the hinge ligament and shell valves appears to form a continuous structure. **Fig. 33.** Scanning electron micrograph showing the dorsal hinge line (between arrowheads) of a post-metamorphic juvenile

vigorously from side to side in *Nucula proxima, Y. limatula* (Drew, 1899b, 1901), and *Acila castrensis* (personal observation).

In the direct-developing *Nucula delphinodonta,* the test also consists of five rows of cells, encloses all of the definitive tissues, and is discarded at metamorphosis. However, the cilia on the test cells of *N. delphinodonta* are not collected into bands but rather are evenly scattered over the surface of the test and an apical ciliary tuft is absent (Drew, 1901).

Pruvot described a pericalymma larva consisting of three regions in *Nematomenia banyulensis* (1890) and *Rhopalomenia aglaopheniae* (1892); an apical region bearing an apical tuft and consisting of two rows of ciliated cells, a middle row of unciliated cells, and a posterior region consisting of two more rows of ciliated cells. A prominent prototroch projects out from between the middle row and the posterior region of the test. The direct-developing aplacophoran *Halomenia gravida* also elaborates a test that is presumably discarded at metamorphosis (Heath, 1918). The most complete account of development in an aplacophoran pericalymma larva has been provided by Thompson (1959, 1960) for *Neomenia carinata,* wherein the test consists of five rows of cells, with up to 16 cells per row, and a number of loosely arranged apical cells. A motile apical tuft is present and the cilia on the middle cell row are collected into a prototroch.

Chia *et al.* (1984) classified ciliary locomotion into three categories, based on the pattern of ciliation: uniform ciliation; ciliated bands or rings; and ciliated lobes or arms. With the addition of the uniformly ciliated pericalymma larva of *Solemya reidi,* all three types of ciliary locomotion are now known to occur in bivalve larvae.

Nervous system

The nervous system of the aplacophoran *Neomenia carinata* arises from six separate shallow depressions in the larval test ectoderm: two in the apical test cells, which will form the cerebral ganglia; two in the second pre-trochal row of test cells, which will form the pedal ganglia; and two in the first pre-trochal row of test cells, which will form the ventral nerve cords (Thompson, 1960). These three pairs of invaginations resemble the invagination of the three pairs of unciliated surface cells in the anterior portion of the test of larval *Solemya reidi* (Figs. 11, 12, 16). Although the fate of the invaginating cells in *S. reidi* was not determined, it is possible they will form some part of the adult nervous system.

Metamorphosis

In *Solemya reidi* the stomadeum has been resorbed and the mouth is functional by the time metamorphosis commences on Day 6, and all that is cast off is the test itself and the apical plate. In *Yoldia limatula,* casting of the test occurs 90 to 120 h after fertilization and includes the stalk connecting the test to the cerebral ganglia, the apical plate, and the stomadeum between the blastopore and the definitive mouth (Drew, 1899a, b). Metamorphosis in *Nucula*

Table 1. Egg size, prodissoconch length and adult size in extant and extinct protobranch bivalves. Species are arranged according to current classification within the two protobranch subclasses and families. Asterisks indicate data were obtained from measurements of spawned eggs; all other oocyte data based on measurements of ovarian oocytes

Species	Egg size (μm)	Prod. length (μm)	Adult size (mm)
Paleotaxodonta			
Nuculidae			
Nucula delphinodonta (a)	* 210	320	4.0
Nucula proxima (a)	* 90	–	–
(b)	100	–	6.6
(c)	–	142	4.5–6.0
Nucula tenuis (d)	120–140	–	–
(e)	130–140	–	16–17.3
Nucula nitidosa (f)	> 150	–	10.3
(g)	–	162	–
Nucula nucleus (h)	* 100	–	–
(i)	180	–	–
Nucula turgida (h)	* 90	–	–
(j)	* 160–180	–	?
(k)	125	–	8–10
Nucula sulcata (j)	* 125	–	?
(l)	160	–	–
Nucula bengalensis (m)	200	300	22.4
Nucula donaciformis (m)	–	220	19.1
Nucula annulata (b)	120	–	3.3
Nucula subovata (b)	270	–	–
Nucula granulosa (b)	120	–	2.2

Table 1 (continued)

Species	Egg size (μm)	Prod. length (μm)	Adult size (mm)
Nucula cancellata (b)	135	–	3.3
Nucula verrilli (b)	125	–	4.3
Nucula darella (n)	~ 130	160–200	2.0–3.5
Nucula calcicola (o)	–	220	1.5–1.9
Condylonucula cynthiae (o)	–	210	0.6
Condylonucula maya (o)	–	220	0.5
Acila divaricata (m)	150–160	230	16–35
Acila castrensis (p)	* 128	150	10–20
Nuculanidae			
Yoldia limatula (a)	* 150	200	60.0
(q)	–	340	–
Yoldia hyperborea (e)	150 × 140	–	34–44.7
Yoldia thraciaeformis (e)	~ 150	–	35.5
Nuculana pernula (d)	120–140	–	?
(e)	~ 135	–	32.0
Nuculana minuta (e)	150 × 110	–	15.7
Nuculana fumosa (m)	–	580–660	7.1
Nuculana pontonia (n)	> 150	245–350	10–18
Nuculana trochila (c)	–	160 (380)	8.5
Portlandia arctica (e)	~ 140	–	28.5
Portlandia lenticula (e)	~ 120	–	8.3
Ledella messanensis (r)	109	< 600	1.8–4.1
Yoldiella jeffreysi (r)	96	< 600	?
Spinula filatovae (s)	–	385	6.1
Spinula scheltemai (s)	–	375	11.5
Spinula subexcisa (s)	–	450	4.4
Malletia conspicua (m)	–	400	24–28
Tindariidae			
Tindaria cervola (n)	120–140	320	10–15
Tindaria murrayi (m)	–	185	8.0
Tindaria callistiformis (t)	≧ 150	–	4.5–8.4
Tindaria hessleri (t)	~ 110	–	2.5
Siliculidae			
Silicula filatovae (u)	70	290–310	3.4–5.2
Silicula fragilis (u)	70	200	2.0–5.0
Silicula mcalesteri (u)	90	580	6.5–10.0
Lametilidae			
Lametila abyssorum (u)	70	370	2.0–3.5
Prelametila clarkei (u)	–	190	< 2.5
Pristiglomidae			
Pristigloma nitens (v)	190	260	3.5
Pristigloma alba (v)	115	190–200	1.2
Microgloma yongei (v)	120	290	1.1
Microgloma turnerae (v)	120	260	1.0
Praenuculidae (Extinct)			
Pojetaia runnegari (w)	–	150 (300)	1.0–1.5
Family Incertae Sedis			
Pseudotindaria erebus (t)	~ 142	–	3.0–6.0
Cryptodonta			
Solemyidae			
Solemya reidi (x)	* 271	433	25–60
Solemya velum (y)	* 200	–	25

(a) Drew (1899b); (b) Scheltema (1972); (c) LaBarbera (1974) (Miocene fossil); (d) Thorson (1936); (e) Ockelmann (1958); (f) Rachor (1976); (g) Mortimer (1962), [quoted in Rachor (1976)]; (h) Lebour (1938); (i) Thorson [quoted in Jørgensen (1946)]; (j) Trevallion (1965); (k) Davis and Wilson (1983); (l) Franzen (1983); (m) Knudsen (1967); (n) Rokop (1979); (o) Moore (1977); (p) R. Gustafson, (unpublished observation); (q) Sullivan (1948); (r) Lightfoot *et al.* (1979); (s) Allen and Sanders (1982); (t) Sanders and Allen (1977); (u) Allen and Sanders (1973); (v) Sanders and Allen (1973); (w) Runnegar and Bentley (1983) (Early Cambrian fossil); (x) this study; (y) J. Pechenik, personal communication

proxima (at 60 h) and *N. delphinodonta* (at 2 weeks) involves casting the test, the stomadeum and part of the apical plate (Drew, 1899b, 1901). In *Y. limatula* and *N. proxima*, metamorphosis is quite rapid, taking anywhere from a few minutes to half an hour (Drew, 1899a, b); several hours are required in *N. delphinodonta* (Drew, 1901). In *S. reidi*, metamorphosis is completed over a period of several hours.

In all three paleotaxodonts studied by Drew the digestive diverticula ("liver pouches") were reported to "go to pieces" immediately after metamorphosis, leaving the stomach without either dorsal or lateral walls. Drew attributed this phenomenon to pressure within the perivisceral cavity as the two valves are first closed following loss of the test. A similar dissociation of the stomach rudiment occurred in *Solemya reidi*, but it did not appear to result from pressure caused by shell closure. Drew (1901) reported that the dorsal and lateral walls of the stomach in *Nucula delphinodonta* begin to re-form by 2 to 3 days after metamorphosis, and eventually, the scattered cells of the larval digestive diverticula collect into two masses, which will form the definitive adult digestive diverticula. Some of the digestive diverticula cells that Drew saw in the perivisceral cavity may have been ingested test cells. Drew (1901) stated that a portion of the diverticula cells in *N. delphinodonta* were digested within the newly formed digestive gland.

The ingestion of portions of the larval locomotory organs at metamorphosis is not unusual amongst invertebrate larvae. Sigerfoos (1907) and Cole (1938) suggested that portions of the velum are swallowed during metamorphosis in bivalve shipworms and European oysters *Ostrea edulis*, respectively. More commonly, the velum of lamellibranchs is said to be "lost" or resorbed. Ingestion of portions of the velum of gastropod larvae is quite common (Fretter, 1972; Bonar and Hadfield, 1974; Switzer-Dunlap and Hadfield, 1977; Bickell and Kempf, 1983). In addition, the prototrochal cells of some sipunculid larva are passed into the coelom at trochophoral metamorphosis (Rice, 1978). The larval test cells of the aplacophoran mollusc *Neomenia carinata* are also passed into the persistent blastocoel at metamorphosis (Thompson, 1960).

The poorly developed foot in newly metamorphosed *Solemya reidi* is similar to that in juveniles of *Nucula proxima* and *N. delphinidonta* immediately after metamorphosis (Drew, 1899b, 1901). Drew (1899b, 1901) reported that feeble movements of the foot are apparent in *Y. limatula* even before the test is cast and burrowing begins within a few hours of metamorphosis. At hatching, juvenile *S. velum* have a well developed foot and are able to crawl (J. Pechenik, personal communication).

Egg and prodissoconch size as indicators of development type

Ockelmann (1965) established criteria whereby the development type of most marine bivalves could be determined if either the ripe eggs of the prodissoconch were available for study. A bivalve species with a ripe egg diameter of be-

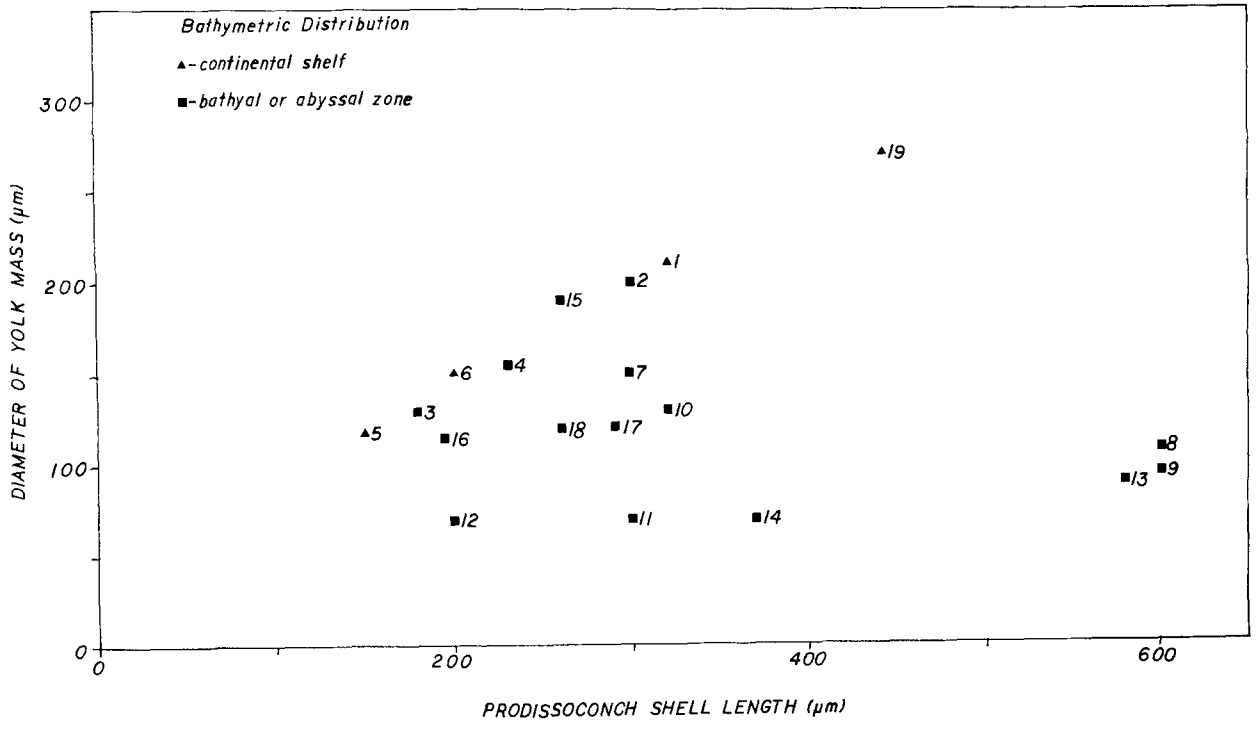


Fig. 34. Relationship between the diameter of yolk mass of the ripe egg and length of the first larval shell (prodissoconch I) in nineteen species of protobranch bivalves (see Table 1 for references). (1) *Nucula delphinodonta;* (2) *Nucula bengalensis;* (3) *Nucula darella;* (4) *Acila divaricata;* (5) *Acila castrensis;* (6) *Yoldia limatula;* (7) *Nuculana pontonia;* (8) *Ledella messanensis;* (9) *Yoldiella jeffreysi;* (10) *Tindaria cervola;* (11) *Silicula filatovae;* (12) *Silicula fragilis;* (13) *Silicula mcalesteri;* (14) *Lametila abyssorum;* (15) *Pristigloma nitens;* (16) *Pristigloma alba;* (17) *Microgloma yongei;* (18) *Microgloma turnerae;* (19) *Solemya reidi*

tween 40 and 85 μm, a prodissoconch I of 70 to 150 μm in length, and a prodissoconch II size of 200 to 600 μm will have planktotrophic development. A bivalve with a ripe egg diameter of between 90 and 140 μm and a prodissoconch I of 135 to 230 μm in length will develop lecithotrophically. Species with direct development will have a ripe egg diameter of 150 μm and higher, and a prodissoconch I size of between 230 and 500 μm or larger (Ockelmann, 1965; Jablonski and Lutz, 1980). Based on the above criteria, the large egg (271 μm) and the prodissoconch length (370–440 μm) of *Solemya reidi* would suggest direct development. However, this study has shown *S. reidi* to develop lecithotrophically.

Table 1 is a compilation of egg size, prodissoconch size, and adult size of paleotaxodont protobranch bivalves, extracted from the literature. A prodissoconch II stage is not evident in protobranchs, therefore the entire prodissoconch has been taken to represent the prodissoconch I. Where both egg and prodissoconch size are known for a single species, these data have been plotted in Fig. 34 (see Ockelmann, 1965; Bayne, 1976, p 83), for mytilid bivalves).

In some species – e.g. *Ledella messanensis, Yoldiella jeffreysi, Silicula mcalesteri, S. fragilis, S. filatovae, Lametilla abyssorum* – egg size indicates planktotrophic or lecithotrophic development while prodissoconch size indicates lecithotrophic or direct development. This paradox was first noted by Allen and Sanders (1973). Although egg size (200 μm) in *Solemya velum* is smaller than in *S. reidi* (271 μm), it is a direct developer (J. Pechenik, personal communication), while *S. reidi* has a free-swimming lecithotrophic larva. Thus data on protobranch bivalves are at variance with Ockelmann's rule and egg and prodissoconch size in this taxonomic grouping are not good indicators of development type.

Conclusions

Jablonski and Lutz (1983) showed that, based on our current knowledge of the distribution of larval types in the Bivalvia, the direction of evolutionary change of development type within this class is open to multiple interpretation. Extension of the lecithotrophic pericalymma larval type to the cryptodont bivalves will hopefully assist in interpreting this question involving the phylogenetic relationship of perocalymma and veliger larvae.

Dissociation at metamorphosis of cells comprising the dorsal and lateral walls of the stomach, common to both protobranch bivalve subclasses, has likely been a factor in the establishment of the adult gutless condition in *Solemya reidi* and other gutless cryptodont protobranchs. Subjects for future study include the ultimate fate of the endoderm and loss of the digestive tract, the mechanism of endosymbiont transmission between host generations, and the derivation of the nervous system in *S. reidi.*

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