

*Atlas of
Marine Invertebrate
Larvae*

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Phylum Porifera

Manuel Maldonado and Patricia R. Bergquist

INTRODUCTION

The sponges (phylum Porifera) are diploblastic organisms with an interepithelial mesenchyme called mesohyl, which is rich in intercellular collagen, amoeboid cells, and inorganic and organic skeletal elements. The body lacks true tissues and organs and is organized around a system of branched canals and choanocyte chambers that generate a water current through the sponge for feeding, respiration, excretion, and reproduction. There are neither sensory or nerve cells nor any predetermined germ cell line. The epithelia, called pinacoderms, lack basement membranes (but see Boute et al., 1996) and communicating junctions between cell membranes. This limits chemical cell-cell communication and conduction of action potentials, but does enable the totipotent cells to leave the pinacoderms temporarily and enter the mesohyl to perform different functions.

The Porifera as defined are a coherent, distinctive group but the phylum is internally diverse in many respects, including body organization. There are two subphyla: Symplasma (class Hexactinellida), characterized by the presence of syncytia, and Cellularia (classes Calcarea and Demospongiae), characterized by having discrete cells (Table 1).

OVERVIEW OF REPRODUCTIVE PROCESSES

Sponges have a number of strategies for reproduction and dispersal. Asexual reproduction utilizes the totipotent character of most cell types and includes production of gemmules and buds, and of body

fragments from which completely functional sponges regenerate (Brien, 1973; Harrison and De Vos, 1991; Fell, 1993). If sponges break during the season of sexual reproduction, body fragments are capable of carrying embryos that complete their development while the fragments are dispersed passively by currents. Thus, sexual and asexual reproduction may jointly facilitate dispersal and establishment of new, distant populations (Maldonado and Uriz, 1999).

The mechanisms for reproduction and dispersal by exclusively sexual means are diverse. Gametes are produced by choanocytes and totipotent archaeocytes; there are no gonads or reproductive ducts. Fertilization is internal in most sponges. Sperm are released in the excurrent flow and drawn into the oocyte-bearing individuals with the inhalant stream. Spermatozoa are engulfed but not digested by choanocytes, which become amoeboid and leave the choanocyte chamber to transport and transfer the spermatozoon, now in a spermiocyst, to the oocyte. Cleavage leads to formation of a solid stereoblastula or a hollow coeloblastula. In many cases, embryonic development occurs inside the sponge, leading to a larval stage that leaves the parent for dispersal. Sponges that brood their embryos are, in most cases, viviparous rather than ovoviviparous. The embryo usually develops in a 'placental membrane' of flattened cells, and is nourished by adsorption of maternal nurse cells. Nurse cells can transmit microsymbionts to oocytes and embryos. Alternatively, many sponges generically termed as oviparous forms shed their eggs. In the few cases where female spawning has been investigated in detail, the released stages were found to be mostly zygotes or early embryos. True oviparity, the

TABLE I. Larval type and development mode (viviparous vs. oviparous) in the major taxonomic categories of Porifera

<i>Taxon</i>	<i>Larval type</i>
Subphylum Symplasma	
Class Hexactinellida	
Subclass Amphidiscophora	
Order Amphidiscosida	?
Subclass Hexasterophora	
Order Hexactinosida	Trichimella (viviparous)
Order Lychniscosida	?
Order Lyssacosida	Trichimella (viviparous)
Subphylum Cellularia	
Class Calcarea	
Subclass Calcinea	
Order Clathrinida	Calciblastula (viviparous)
Order Murrayonida	Calciblastula ? (viviparous)
Subclass Calcaronea	
Order Leucosoleniida	Amphiblastula (viviparous)
Order Lithonida	Amphiblastula (viviparous)
Class Demospongiae	
Subclass Homoscleromorpha	
Order Homosclerophorida	Cinctoblastula (viviparous)
Subclass Tetractinomorpha	
Superorder Tetractinellida	
Order Astrophorida	? (oviparous)
* <i>Alectona</i> and <i>Thoosa</i>	Hoplitomella
Order Spirophorida	Direct development
Superorder Clavaxinellida	
Order Chondrosida	Clavablastula (oviparous)
Order Hadromerida	Clavablastula (oviparous)
Order Axinellida	Clavablastula (oviparous)
Order Agelasida	Clavablastula? (oviparous)
Subclass Ceractinomorpha	
Order Verticillitida	Parenchymella-like? (viviparous)
(i.e., living sphinctozoans)	
Order Halichondrida	Parenchymella (viviparous)
Order Poecilosclerida	Parenchymella (viviparous)
Family Latrunculiidae*	Parenchymella-like? (viviparous)
Family Stylocordylidae*	Parenchymella-like? (viviparous)
Order Haplosclerida	Parenchymella (viviparous)
Order Petrosiida	Parenchymella-like? (oviparous)
Order Dendroceratida	Parenchymella-like (viviparous)
Order Dictyoceratida	Parenchymella-like (viviparous)
Order Verongida	? (oviparous)
Order Halisarcida	Dispherula (viviparous)

?, taxon in which the larva remains elusive.

* Taxonomic reallocations proposed here based on developmental information.

release of unfertilized oocytes, is uncommon. Details of embryology remain unknown for most species that develop externally. It is assumed that in most cases the embryo becomes either a swimming or crawling larva that undergoes a period of active dispersal.

In the order Sphirophorida, the free-swimming larval stage has been eliminated. In some species, the morula develops externally directly into a juvenile sponge (e.g., Watanabe and Masuda, 1990). In other species, it gives an ephemeral, brooded embryo, in which some cells become ciliated for a very short period before developing into a juvenile that is expelled from the maternal body (Burton, 1931; Bergquist, 1978).

At the population level, release of propagules (gametes, zygotes, or early embryos) is highly synchronous in oviparous and ovoviviparous sponges, but asynchronous in viviparous species that release fully formed larvae. Endogenous and exogenous signals that may trigger spawning or larval release include photoperiod, cessation of water movement, lunar cycles, and pheromones. Oocytes, embryos, and larvae usually leave the parent sponge in the outgoing water flow, via excurrent canals, but the larvae of *Tedania ignis* (Poecilosclerida) and *Calyspongia diffusa* (Haplosclerida) leave the parent by creeping through the ectosome (Sivaramakrishnan, 1951; Maldonado and Young, 1996). The larva of *Scopalina lophyropoda* (Halichondrida) behaves similarly if the aquiferous canals of the parent sponges are experimentally disorganized at the time of larval release (Maldonado and Uriz, 1999), suggesting that larvae might produce an enzyme that facilitates their movement toward the aquiferous canals or the surface of the sponge (Bergquist, 1978; Fell, 1989).

BIOLOGY OF THE LARVAL STAGE

Generalizations about the larval stage in Porifera must be treated with caution, as data on larval morphology and behavior are based on only about 100 of the more than 7000 described species. Moreover, the bulk of knowledge on larval biology is derived from brooded larvae, while the externally developed larvae of most oviparous species and even of entire orders remain unknown (Table 1).

Sponge larvae are solid or hollow prolate spheroids that range in length from about 50 μm in the halisarcid *Halisarca* (Fell, 1993) to 5 mm in the dictyoceratid *Fasciospongia* (Bergquist, 1978). Hollow larvae consist of a relatively small number of cells, most of them organized in a pseudo- or monostratified epithelium around a central cavity. This cavity may be either a retained blastocoel or a secondary formation, usually filled with a nutritive fluid or maternal cells. In solid larvae, the internal space may be filled by several types of

amoeboid cells and a loose intercellular matrix; skeletal elements and microsymbionts may occur. Internal cell types may include storage cells, cells secreting the organic and inorganic skeleton (sclerocytes, collencytes), totipotent cells (archaeocytes) and, in some cases, a few choanocytes organized into non-functional choanochambers, which may be connected to incipient aquiferous canals (e.g., Okada, 1928; Saller, 1988). No vestige of mouth, anus, or digestive tract has ever been noticed, nor have sensory cells been identified convincingly.

With the exception of the recently described hoplitomella larva (Vacelet, 1999), all sponge larvae are externally ciliated to some extent. Most larvae use cilia for swimming, but larvae that creep over the substratum are also extensively ciliated. The larval cilia are produced by either monociliated or multiciliated cells and beat in metachronal waves, as in most invertebrate larvae. Larvae usually swim with a corkscrew motion, rotating around the longitudinal axis while moving forward. During the dispersal phase, larvae may alternate active swimming with periods of passive drifting. Sponge larvae have limited ability to swim directionally in the presence of current, as the maximum velocities for directional swimming range from 0.09 cm s^{-1} to 1 cm s^{-1} , depending upon species (Maldonado and Young, 1996).

As far as it is known, sponge larvae are all relatively short-lived lecithotrophs. A few field data (e.g., Lindquist et al., 1997) and many laboratory observations indicate that the dispersal phase lasts from a few hours to a few days for free-swimming larvae, and up to 3 weeks in some crawling larvae. The duration of larval life varies within species and even clutches; in one species that settles on average after 3 days, some larvae delayed settlement for up to 17 days (Ilan and Loya, 1988). Such variability may be regulated by yolk quality (Maldonado et al., 1997). Larvae that delay metamorphosis may deplete yolk reserves and compromise the survival of the early juvenile stages (Maldonado and Young, 1999). Some larvae assimilate energetically significant quantities of dissolved organic matter such as amino acids and fatty acids across the larval pinacoderm (Jaekle, 1995). It has also been reported that larvae of *Halichondria panicea* (Halichondrida) phagocytose bacteria and nanoflagellates through the cells of the body wall (Ivanova, 1999).

After a variable period of dispersal, planktonic larvae become demersal, swimming near and crawling over the substratum where they apparently test the surface before settlement. However, no tactile or chemical receptors are yet known in sponge larvae. Sponge larvae also use light for orientation during dispersal and settlement, despite the lack of identified sensory organs (e.g., Fell, 1974; Maldonado and Uriz, 1998). Behavioral observations suggest that photoreception occurs in the

region of the posterior pole and in the ciliary tuft in the larvae of some demosponges (Woollacott, 1993; Maldonado and Young, 1996; Maldonado et al., 1997), and in specialized lateral cells in the larvae of some calcareous sponges (Amano and Hori, 1992). Geotaxis has not been demonstrated in sponge larvae, but it is known that larval buoyancy decreases with age, owing to an increase in skeletal mass and consumption of buoyant yolk (Maldonado et al., 1997).

In most species, the larva attaches to the substratum at or near the anterior pole, but attachment can also take place laterally. Metamorphosis into a juvenile sponge with a functional aquiferous system usually takes from less than 1 day to a few days, but up to 1 month has been reported (Boury-Esnault, 1976).

LARVAL TYPES

Until 1994, only three larval types were recognized in sponges (Simpson, 1984; Harrison and De Vos, 1991): parenchymellae (solid larvae), amphiblastulae (hollow larvae with differentiation between macromeres and micromeres), and coeloblastulae (hollow larvae with no differentiation between macromeres and micromeres). Four additional types have been described recently: trichimella (Boury-Esnault and Vacelet, 1994), cincoblastula (Boury-Esnault and Rützler, 1997), hoplitomella (Vacelet, 1999), and dispheula (Ereskovsky and Gonobobleva, 2000). Two new types are proposed here (Figure 2.1).

The term coeloblastula has traditionally been applied to a heterogeneous assemblage of hollow larval stages in the classes Calcarea and Demospongiae, which have in common only the presence of a central cavity that is a retained blastocoel. Discrimination between potential coeloblastular types has been hindered because these larvae, which are mostly derived from embryos with external development, are difficult to collect and study. Nevertheless, the morphological heterogeneity already known in the group and the fact that the coeloblastular stage usually undergoes extensive modifications during its external development, make it difficult to formulate a general definition for a mature coeloblastula larva. Therefore, we propose use of the term coeloblastula to embrace a diverse assemblage of three unrelated, relatively hollow larval types that develop externally or internally through a retained coeloblastular stage: the calciblastula (proposed here for the larva of calcinid calcareous sponges), the dispheula (larva of halisarcid demosponges), and the clavablastula (proposed here for the larva of clavaxinellid demosponges). Further information on reproduction of some little-known groups such as hexactinellids, tetractinellids, clavaxinellids and the ceractinomorph verticillitids, petrosiids and

verongids may eventually necessitate description of additional larval types and further subdivision of the coeloblastula category.

The amphiblastula

This larva is exclusively found in Calcarea of the subclass Calcaronea (Table 1). It is ovoid, ciliated in the anterior half of the body only, and hollow. The internal cavity of the mature larva is usually small and does not correspond to an original blastocoel, despite the fact that its embryonic development goes through a coeloblastular stage produced by an unequal cleavage. Early coeloblastular stages show a large blastocoel delimited by a simple epithelium of large unciliated cells (macromeres) in one half of the body and small cells (micromeres) in the opposite half. Later, micromeres become monociliated, but their cilia appear internally and beat in the blastocoel (Duboscq and Tuzet, 1942). The formation of a swimming amphiblastula requires the cilia to become external. To achieve this, a hole appears between some cells of the non-ciliated pole producing a stomoblastula (Figure 2.2A). The stomoblastula then everts through the opening, turning inside out (Figure 2.2B) to become a hollow, externally ciliated structure, in which the new internal cavity is not a blastocoel (Figure 2.2C). However, this peculiar process may not be unique in nature as an apparently similar eversion takes place during reproduction of the colonial volvocaceous algae.

Once the larva is mature, it migrates from the embryonic follicle (Figure 2.3A) into an exhalant canal and leaves the maternal body in the out-going water current (Amano and Hori, 1992). The larva swims with the ciliated hemisphere directed forward (Figures 2.2D, 2.3B,D), so that the functionally defined anterior pole actually corresponds to the posterior, animal pole in the oocyte and early embryo. The free-swimming larva is relatively small, usually less than 100 µm in length. The body wall is a monostratified epithelium that lacks recognizable, special intercellular junctions and contains three cell types: (1) monociliated, small cells (micromeres) in the anterior larval half; (2) larger non-ciliated granular cells (macromeres) in the posterior half; and (3) four distinctive translucent cells, termed 'cellules en croix', located equatorially at the four quarters of the larva (Figures 2.2D,E, 2.3C).

The micromeres of the anterior hemisphere are columnar cells, with the cilium emerging from a pit formed by the cell membrane (Figures 2.4A,B). The cilia may have a basal body with an accessory centriole and two or three cross-striated rootlets. The nucleolated nucleus and the Golgi apparatus are located in the apical region of the cell, in close association with the ciliary rootlets. Abundant pigment granules concentrate in the

basal portion of the cells (Figures 2.4A,F). The granular cells (macromeres) of the posterior larval hemisphere are large and ovoid, with no clear cytoplasmic polarity (Figure 2.4D). They have a nucleus with a large nucleolus and abundant inclusions (Amano and Hori, 1992).

The four 'cellules en croix' are non-ciliated and columnar, occurring among the ciliated cells near the larval equator (Figures 2.2D,E, 2.3C). It is noteworthy that larvae with five 'cellules en croix' have occasionally been found (Tuzet, 1970). These cells derive from ciliated micromeres that lose the cilium early in blastula development (Duboscq and Tuzet, 1941; Tuzet, 1970). Their apical region contains numerous vesicles, glycogen granules, and diverse inclusions (Figure 2.4C). Between the central nucleus and the apical zone, there are aggregations of unidentified electron-dense material surrounded by numerous small vesicles, which have been termed 'anneau d'olives chromatiques' (Tuzet, 1973). This structure resembles the intracellular lens vesicles known in some ascidians (Amano and Hori, 1992). The basal region of the cell, which is enclosed by the densely pigmented basal region of the surrounding ciliated cells, contains abundant lipid droplets (Figures 2.4C,F). The function of the 'cellules en croix' remains unclear. Some reports indicate that they degenerate or are shed during early embryonic stages, before the larva is completed (Gallissian, 1983). However, other reports indicate that this occurs only after the larva becomes free-swimming (Duboscq and Tuzet, 1937; Tuzet, 1973; Amano and Hori, 1992). The latter authors have suggested a photosensitive role for the 'cellules en croix' so that a change in the sign of phototaxis is induced in the larva once these cells degenerate or are shed. A photoreceptive role can clearly not be proposed in those species where the 'cellules en croix' degenerate or are shed in early embryogeny (e.g., Vacelet, 1964; Gallissian, 1983; Harrison and De Vos, 1991).

The internal cavity of the larva is small (Figures 2.2D,E, 2.3B,C), sometimes harboring yolk-containing nurse cells, either of larval or maternal origin, and symbiotic bacteria (Figure 2.4A). Spicules have never been reported.

During the free-swimming period, the non-ciliated granular cells progressively overgrow the ciliated cells (Figures 2.3D,E), so that the larvae lose locomotory power and sink for settlement.

The calciblastula

The term calciblastula is proposed to designate the hollow larva of calcinean calcareous sponges (Table 1). Unlike the amphiblastula found in Calcaronea, the calciblastula lacks 'cellules en croix', has no differentiation between macromeres and micromeres, and does not undergo blastular eversion. Unlike the coeloblastular

larva of clavaxinellid sponges, the calciblastulae develop within the maternal body, before being released in the outgoing water flow (e.g., Johnson, 1978, 1979).

In the mature larva, the body is ovoid and entirely or almost entirely ciliated (Figure 2.5A). The body wall, made of cuboidal monociliated cells arranged in a monostratified epithelium, delimits a large blastocoel. The cavity is fluid-filled but can also contain some parental somatic cells. All cells in the larval epithelium are similar, except for one to four somewhat larger, non-ciliated cells at the posterior pole in some species (Figure 2.5A).

The cytology of the larva is poorly known, but a clear polarization of the ciliated cells has been reported in *Clathrina*, which is the best-studied genus. The apical cell region contains the cilium, which is provided with an accessory centriole, radiating microtubules and rootlets. This region may also contain numerous small vesicles, fibrillar yolk inclusions, and some pigment granules. A nucleolate nucleus is located below the ciliary root, and between these structures there is a well-developed Golgi apparatus. The basal portion of the cells bordering the blastocoel is filled with phagosomes and diverse pigment-like inclusions (Borojevic, 1969; Tuzet, 1973).

The non-ciliated cells, when present, are globose, with a central nucleus provided with a large nucleolus, and a cytoplasm packed with granular inclusions. Minchin (1900) interpreted them as being primordia of a germinal cell line. Nevertheless, because these cells are not consistently present in all individual larvae of species that typically possess them, it is more probable that they are not a distinct cell type, but are blastomeres delayed in their development (Borojevic, 1969; Fell, 1989).

Although free-swimming larvae are initially hollow, cells of the outer, ciliated epithelium shed the cilia and migrate into the blastocoel (Figure 2.5A), which is partially obliterated at the time of settlement (Borojevic, 1969; Tuzet, 1973; Fell, 1989). This massive immigration of cells may start in some species before larval release (Tuzet, 1948; Johnson, 1979).

The clavablastula

The term clavablastula is proposed to denote the larval type found in the superorder Clavaxinellida (Table 1). Unlike the calciblastula, the clavablastula is produced by a process of external embryonic development, either from externally fertilized oocytes (Lévi and Lévi, 1976; Reiswig, 1976; Fromont, 1988; Fromont and Bergquist, 1994) or internally fertilized oocytes that are shed as zygotes or early embryos (Tuzet, 1930; Borojevic, 1967; Reiswig, 1976). Cleavage and formation of a functional larva is rapid, taking from 3 h to 3 days (Nassonow, 1883; Lévi, 1956; Warburton, 1966; Borojevic, 1967).

The resulting larva is small (usually less than 250 µm), entirely ciliated, hollow, and formed by a relatively small number of monociliated cuboidal cells arranged in a monostriated epithelium that delimits a blastocoel (Figures 2.5B,D). These ciliated cells are not as specialized as those of other larval types; rather, they are little-differentiated blastomeres charged with yolk and provided with a distal cilium. Initially, planktonic larvae are subspherical, with unclear anterior–posterior differentiation, but they elongate slightly during the dispersal phase, becoming prolate spheroids. Some cuboidal epithelial cells may also become oval, slightly larger, and pigmented, marking the posterior pole in some species (Nassonov, 1883; Topsent, 1900; Lévi and Lévi, 1976).

Clavablastulae generally disperse by swimming and are typical planktonic stages, but, in a number of species, it is a demersal crawling stage during part of or the whole larval life (Borojevic, 1967; Bergquist and Sinclair, 1968; Bergquist et al., 1970; Ayling, 1980). Unlike planktonic forms, demersal larvae are flattened, with a narrow, elongated blastocoel (Figures 2.5C,D). In these crawling larvae, cilia have been reported to beat in metachronal waves, but more slowly than in planktonic larvae. Cilia, which are also shorter than in planktonic larvae, appear to have an accessory centriole, but no ciliary rootlets (Borojevic, 1967).

Internal undifferentiated cells may occur in the blastocoel of some species at different stages of the larval life (Figure 2.5B). The presence of these internal cells, which are either derived by migration of peripheral blastomeres as in the hadromerid *Tethya* (Lévi, 1956) and the agelasid *Agelas* (Reiswig, 1976), or by maternal transference as in the chondrosid *Chondrosia* (Lévi and Lévi, 1976) and some species of the hadromerid *Cliona* (Warburton, 1961), led some authors to consider these coeloblastular larvae as parenchymellae (Lévi, 1956; Warburton, 1966; Simpson, 1984). Indeed, Lévi (1956) reported that no trace of a blastocoel was evident during cleavage of *Tethya*, but he illustrated a hollow morula (Lévi, 1956, Figure 47). The issue is controversial and although further studies are required to categorize these larvae definitively, we consider, as suggested by others (Simpson, 1984; Harrison and De Vos, 1991), that they are coeloblastular larvae in which undifferentiated cells, irrespective of their origin, enter the blastocoel, where they disintegrate and provide the nutrients and energy required for dispersal and metamorphosis.

Problems in the interpretation of the larval histology overlap with taxonomic problems, as the superorder Clavaxinellida is a controversial taxon (Table 1). Some families (Latrunculiidae and Stylocordylidae) traditionally grouped in the order Hadromerida brood a parenchymella-like larva, which suggests that these

groups should be transferred from Clavaxinellida to Ceractinomorpha (Poecilosclerida), a position consistent with their reproductive mode (Kelly-Borges and Vacelet, 1995). Similarly, Chondrosida and Agelasida (Table 1), considered here as clavaxinellid orders, could be reallocated on the basis of future molecular studies, thereby rendering the name clavablastula appropriate for the larvae of Hadromerida and Axinellida only.

The cinctoblastula

This distinctive larval type, which was regarded as an 'amphiblastula' until recently, occurs only in the subclass Homoscleromorpha (Table 1). Most information on the larva relates to the genus *Oscarella* (: *Octavella*), there being only a brief report on the genus *Plakina* (Bergquist et al., 1979).

The cinctoblastula is a hollow, brooded larva (Figures 2.6A,B) that develops from a solid embryo, a stereoblastula (Tuzet and Paris, 1964). Depending on the species, the swimming larva is either entirely ciliated (Figure 2.6D) or has a small non-ciliated region consisting of a few cells at the posterior pole. The length of cilia decreases from the anterior to the posterior pole in some species (Figures 2.6E,F; Barrois, 1876; Bergquist et al., 1979). In other species, cilia are relatively short at the equator and longer at the larval poles (Meewis, 1938). Cilia typically bend toward the posterior pole. The larval epithelium surrounds a large internal cavity filled with nutritive fluid. The epithelium is mono- or pseudostratified (Figures 2.6C,E), consisting of three cell types: ciliated cells, refringent ciliated cells, and secretory cells.

Ciliated cells are columnar in the anterior hemisphere of the larva, and larger and rounder in the posterior hemisphere (Lévi and Porte, 1962). Special sealing junctions occur distally between cells, while cell contacts are loose in the basal region, where cells project short pseudopodia into the blastocoel.

A distinctive continuous, equatorial ring of refringent ciliated cells, which inspired the name cinctoblastula for this larva (Boury-Esnault and Rützler, 1997), marks the boundary between the anterior and the posterior larval hemispheres. Refringent cells are characterized by an apical nucleolated nucleus that also contains a pseudo-crystalline rod-like inclusion oriented according to the anterior–posterior larval axis. The function of these cells remains enigmatic, although a sensory role has been postulated (Meewis, 1938). Rod-like inclusions are also found in the pinacocyte nuclei of adult sponges, which are likely to derive from the refringent cells (Lévi and Porte, 1962).

A few non-ciliated flask-shaped cells packed with diverse granules and inclusions interspersed between the ciliated epithelial cells probably have a secretory role.

Secretory vacuoles also occur in the ciliated cells, more abundantly toward the anterior pole. It is thought that like the secretory cells they release material that contributes to larval attachment.

The internal face of the larval epithelium is lined by a diffuse layer of collagen and other fibrillar elements similar to those found in the mesohyl of adult sponges (Lévi and Porte, 1962). This mesohyl, which contains symbiotic bacteria, infiltrates between the basal regions of adjacent epithelial cells. On hatching, the larva is nearly spherical (Figures 2.6E), but it lengthens during the swimming period, and the anterior hemisphere enlarges in volume. When settlement approaches, the cells in the posterior hemisphere proliferate and begin to cover the anterior hemisphere, which becomes internal after settlement (Barrois, 1876; Meewis, 1938), a process also evident in the amphiblastula (Figures 2.3D,E).

The parenchymella

Parenchymellae are brooded larvae that occur in the subclass Ceractinomorpha (Table 1). There are gaps in our knowledge of the larvae of certain groups placed in this subclass. Larvae are unknown in the oviparous Verongida. The Verticillitida brood their solid larvae (Figure 2.7A) but incorporate a coeloblastular stage during development (Vacelet, 1979). Externally developing larvae of the oviparous Petrosiida need further study to confirm that they are true parenchymellae (Fromont and Bergquist, 1994). It is also quite probable that some of the above ordinal groups will be removed from the Ceractinomorpha when better information on their reproductive biology is available.

The mature parenchymella is solid and develops from a solid, non-ciliated stereoblastula (Figures 2.7B,C). At a morula stage, some internal blastomeres differentiate early into internal larval cells, mainly collencytes, sclerocytes, archaeocytes, and choanocytes. Others migrate to the periphery and divide rapidly, becoming monociliated cells that form the larval epithelium.

The free-swimming stage is relatively large (150 to 5000 μm) and is usually pigmented to match the choanosomal tissue of adults. There are three major morphological larval categories, distinguished by body form and ciliation pattern. Larvae are either: (1) entirely and uniformly ciliated, usually with a very elongated body tapering toward the posterior end (Figures 2.8A,B, 2.9A,B); (2) bullet-shaped or pyramidal and entirely ciliated, except for a protruding or flattened posterior end, which is naked (Figures 2.8C,D, 2.9C–G); or (3) bullet-shaped and entirely ciliated, except for the flattened posterior end, which is bare but surrounded by a ring of distinctively pigmented cells with long cilia (Figures 2.8E, F, 2.9H–M). Larvae in the latter two categories are initially ciliated at the

anterior pole, but a small area becomes bare during the free-swimming period (Figures 2.9E,H,N), probably to facilitate larval attachment at the anterior pole (Bergquist et al., 1979).

The parenchymella larvae of freshwater sponges are nearly pyramidal, with a wide, rounded anterior pole and a narrow, tapering posterior pole. Although developing from a stereoblastula, the larva contains an enormous secondary cavity that occupies virtually all the anterior hemisphere. This cavity apparently functions in osmoregulation and buoyancy control (e.g., Brien, 1973; Saller, 1988).

In larvae with a ciliary tuft surrounding the bare posterior region, cells of the tuft are monociliated, with a cilium three to five times longer than those in other larval regions (Figures 2.8E,F, 2.9H,I). These longer cilia are formed immediately before larval release (Wapstra and van Soest, 1987). Cells in the tuft, which form a narrow ring (2 to 7 cells wide) around the posterior pole, are flask-shaped, with a basal globular region containing a nucleolated nucleus and a neck that expands distally into a small globular region packed with electron-dense granules. These granules are probably responsible for the distinctive pigmentation of the posterior ring in living larvae (Figures 2.8E, 2.9H).

The interior of the larva contains several cell types, intercellular and intracellular microsymbionts, collagen fibrils, and spicules. Spicules, which may represent all or only a subset of the adult spicule types, are usually packed toward the posterior pole of the larva (Bergquist and Sinclair, 1973). Internal cells usually consist of types also present in the mesohyl of adult sponges, such as totipotent archaeocytes and gray cells packed with yolk granules (Figures 2.7G,H), sclerocytes secreting spicules (Figure 2.7F), collencytes secreting collagen, bacteriocytes, and choanocytes arranged in non-functional chambers (e.g., Jaecle, 1995) and connected with incipient aquiferous canals bounded by pinacocytes (e.g., Saller, 1988).

There have been reports that parenchymella larvae can originate asexually through aggregation of archaeocytes (Wilson, 1894, 1902; Sivaramakrishnan, 1951; Bergquist et al., 1970). These interpretations were based on light microscopic observations of densely pigmented stereoblastulae where cell boundaries and nuclear detail were obscured. Bergquist et al. revised their interpretations when ultrastructural evidence demonstrated a normal sexual developmental sequence. We are unaware of any convincing evidence for asexually produced parenchymellae.

The dispherula

Dispherulae occur in the order Halisarcida (Table 1) and exhibit a distinctive embryonic development, in

which the resulting embryo may be defined as a hollow sphere within a sphere (Figure 2.10A). Such an arrangement inspired the name dispherula (Ereskovsky and Gonobobleva, 2000). Cleavage is holoblastic and leads initially to a blastula, in which a small blastocoel appears at the 16- to 24-cell stage. Later cleavage becomes slightly asynchronous and the blastomeres produced at the future posterior pole of the embryo are fewer and larger than those in the remaining blastoderm (Figures 2.10B,C). The cells of the blastoderm become polarized, developing a distal cilium and accumulating yolk granules basally. Part of this cytoplasmic yolk is extruded to the blastocoel, which becomes a fluid-filled cavity. Then an internal mass of cells is produced by either unipolar or multipolar migration or by lateral invagination of ciliated blastomeres into the blastocoel (Figures 2.10D,E). This cell behavior varies among species (Lévi, 1956; Chen, 1976; Ereskovsky and Gonobobleva, 2000). The internal cells, which divide and cytodifferentiate more slowly than those in the external layer, reorganize into a hollow, monolayered sphere that remains suspended in the fluid-filled blastocoel. Ereskovsky and Gonobobleva (2000) have reported that the epithelial cells of the internal sphere are ciliated in *Halisarca dujardini*, with the cilia beating in the innermost cavity. The presence of cilia in the internal cell sphere has never been reported in previous descriptions of *Halisarca* dispherulae (Lévi, 1956; Chen, 1976). The acquisition of the dispherula morphology occurs relatively early in embryogenesis of *H. metchnikovi*, or just before larval hatching in *H. dujardini* (Lévi, 1956; Ereskovsky and Gonobobleva, 2000).

Once the larva is mature enough (Figure 2.10F), it leaves the embryonic follicle and is expelled in the exhalant stream. At hatching, the dispherula may still be subspherical, but it rapidly elongates, so that the free-swimming stage is typically oval, measuring 50–200 μm in length, depending on the species. The larva is whitish or translucent, entirely ciliated, with a clear anterior–posterior axis defined by the fact that the ciliated epithelial cells of the posterior pole are ovoid and larger than the columnar cells of the lateral and anterior regions. Although all cells are monociliated and all cilia equally long, the posterior pole can look naked; the number of large monociliated cells is so low in this region that the cilia cannot form a typical ciliated field, as they do in the lateral and anterior regions.

The detailed cytology of the swimming larva is only known in *H. dujardini* (Lévi, 1956; Ereskovsky and Gonobobleva, 2000). The anterior and lateral regions of the epithelium consist of typical columnar, polarized cells. The distal region contains a nucleolate nucleus and a cilium emerging from a pit, which is probably provided with an accessory centriole (Lévi, 1956). The

mid and basal cell regions are filled with yolk granules. The epithelial monociliated cells of the posterior region are larger and subspherical, with numerous yolk granules, but no clear polarization.

The internal cells finally proliferate and cytodifferentiate into a mass of amebocytes, granular cells, and collencytes, which co-occur with intercellular symbiotic spiral bacteria and groups of maternal cells that were transferred to the developing embryo. The obliteration of all internal cavities may take place during either late brooded stages in some species (Lévi, 1956) or at larval attachment in other species (Ereskovsky and Gonobobleva, 2000). The solid appearance of the free-swimming larva in the former species is likely to account for it having been considered as a simplified parenchymella (Lévi, 1956). However, unlike a true parenchymella, it develops from a coeloblastula stage (Figure 2.1).

The larva swims actively for 4–36 h and, when settlement approaches, becomes almost conical with a circular, slightly concave posterior pole and a tapering anterior pole. Settlement is by either the anterior pole or an anterior-lateral zone (Lévi, 1956; Chen, 1976). Although the external, ciliated cells are apparently of two types, after metamorphosis all participate in the formation of the choanoderm of the juvenile sponge (Lévi, 1956).

The larva of halisarcid sponges has been viewed as a simplified, undifferentiated parenchymella (e.g., Lévi, 1956; Simpson, 1984; Harrison and De Vos, 1991), but arguably it is the most evolved larval type in the Porifera. The significance of the reorganization undergone by the internal cell mass to form an internal cavity has not yet been realized. This morphogenetic process is similar to the gastrulation movements that lead to the formation of the digestive tract in many metazoans (e.g., Nielsen, 1995). The dispherula stage is an ephemeral diploblastic stage, with a true coelom separating the two epithelia. The internal sphere could be a primordium of a digestive layer, the first recorded within the phylum Porifera. If this is true, halisarcid sponges, which lack both mineral and spongin skeletons, are likely to be a highly evolved group in Porifera, a suggestion also made by Bergquist (1996) based on the analysis of other histological features. Further studies on embryonic and larval stages are required to explore this possibility further.

The hoplitomella

The hoplitomella larva is unique within the Porifera in lacking cilia and in having a larval skeleton made of spicules that do not occur in the adults (Figure 2.10G). This larva was first described from plankton samples by Karawaiew (1896) and interpreted as a radiolarian. It was later thought to be an armored asexual sponge

propagule (Trégouboff, 1939, 1942). It is now known to be a sexually produced larva, for which the name hoplitomella has been proposed (Vacelet, 1999). The hoplitomella occurs in two genera of excavating demosponges, *Alectona* and *Thoosa*, which have usually been classified in the Order Hadromerida. A recent study of the larval spicules indicates that they are not hadromerids (Vacelet, 1999), but are atypical tetractinellid sponges (Table 1), as formerly suggested by Topsent (1900) and Alander (1942).

The embryonic development of the hoplitomella occurs within the maternal body and passes through a stereoblastula stage, which shows no differentiation between macromeres and micromeres. Cilia are apparently absent in all embryonic stages and in mature larvae (Vacelet, 1999). It is not known how the unciliated larva leaves the maternal body or how long it remains in the plankton. However, the presence of hoplitomellae in offshore plankton samples and the extensive skeletal and morphological changes reported during its planktonic life suggest that it has a longer dispersal period than do other sponge larvae (Trégouboff, 1942; Vacelet, 1999).

The free larval stage is nearly globular, being 120–275 μm in diameter in *Alectona* and probably somewhat larger in *Thoosa* (Topsent, 1904; Trégouboff, 1942), with no recognizable anterior–posterior axis. The most conspicuous larval trait is a hypertrophied siliceous skeleton made up of three spicule types (Figures 2.10G–I). The outer epithelium of the larva is supported by a subepithelial layer of 50–80 subcircular plates, which are discotriaenes with the rhabdome oriented inward in *Alectona* (Trégouboff, 1942; Vacelet, 1999) and discostromyles in *Thoosa* (Topsent, 1904). During the pelagic phase, only studied in *Alectona millari*, the number of discotriaenes reduces dramatically, but the size of the remaining ones (about eight) increases, and they become nearly triangular plates (Trégouboff, 1942). The larva also possesses 6–10 long, thin radial protuberances, each supported by internal, needle-like spicules 600–1000 μm long, called styles. The layer of flat disks provides support for the spherical larval body, and for the tension exerted by the long, radiating spicules. The form and arrangement of these two spicule types increases surface area without adding significant mass, a morphology that slows sinking rates in other planktonic larvae (Chia et al., 1983). A third category of minute, rod-like, spiny spicules (amphiasters) occurs scattered throughout the tissue of late embryos and mature larvae. In adult sponges, they persist and support epithelial surfaces.

The cytology of the larva has been described for *Aleutian millari* by Garrone (1974). The epithelial cells constitute a relatively flat layer, supported by an internal layer of cells with numerous vacuoles, sclerocytes and

discotriaenes. Below this skeletal layer, there is a region of fusiform cells packed with dense oval inclusions. The innermost layer contains abundant archaeocytes, and the central region of the larva is filled with choanocytes and diverse types of cells with inclusions. Intracellular and intercellular bacteria also occur. At all stages, the embryos contain collagen to an extent unknown in other sponge larvae, with collagenous fascicles even surrounding epithelial cells (Vacelet, 1999).

The skeleton of plates is completely resorbed toward the end of the pelagic period (Trégouboff, 1942), consequently the radiating protuberances also disappear progressively. The larva becomes an oval, planktonic organism (220 \times 45 μm), with only amphiaster spicules. The loss of the flotation devices and the lack of cilia must assist the larvae in sinking to the bottom for attachment.

The trichimella

This larva is found only in the class Hexactinellida (Table 1). Until recently, only the larva of *Farrea sollasii* had been described and it was considered to be a parenchymella-like type (Okada, 1928). Recent work on a reproducing, cave-dwelling population of *Oopsacas minuta* revealed that its larva, although similar in general organization to that of *Farrea*, differed from typical parenchymellae (Boury-Esnault and Vacelet, 1994; Boury-Esnault et al., 1999). Trichimella larvae were first seen in the maternal body of *Leucopsacus orthodoxus* and *Vitrollula fertile* by Ijima (1903), who described them as gemmules.

The zygote develops through coeloblastular stages that become solid by a delamination process starting at about the 80-cell stage (Boury-Esnault et al., 1999). The mature larva is solid and biconical in shape, with the anterior pole more round than the posterior one (Figure 2.11A). It is 150–180 μm long in *O. minuta* (Boury-Esnault and Vacelet, 1994) and, as inferred from the length of the larval spicules, up to approximately 200 μm long in *F. sollasii* (Okada, 1928). No cilia were noticed by Okada in his light microscope study of late-stage embryos of *F. sollasii*, but recent scanning electron microscope (SEM) studies of the larva of *O. minuta* have revealed that ciliation occurs in the trichimella in the equatorial region only, both poles being naked (Figures 2.11A,B; Boury-Esnault and Vacelet, 1994). Paradoxically, the outer larval epithelium is non-ciliated. The external cilia at the equatorial region stem from subepithelial cells (Figure 2.11C) and reach the exterior only after piercing the flat outer epithelium, which appears to be a multinucleated syncytium (Boury-Esnault et al., 1999). This arrangement is unique within the phylum Porifera. Furthermore, the subepithelial cells are multiciliated (Figure 2.11C), each having up to 50 cilia

(Boury-Esnault and Vacelet, 1994; Boury-Esnault et al., 1999). The expectation would be that sponges would have monociliated cells, as found in other diploblasts (Nielsen, 1987, 1995) and in most deuterostomes. Unlike in the monociliated cells of larvae of Demospongiae and Calcarea (Woollacott and Pinto, 1995), ciliary basal rootlets are missing in the multiciliated cells of the trichimella. The cilia have accessory centrioles (Boury-Esnault et al., 1999), which is a trait common in monociliated cells, but highly unusual in multiciliated cells (Nielsen, 1987; Woollacott and Pinto, 1995).

The larva is solid and contains several differentiated cell types. In *O. minuta*, the anterior pole is packed with a mass of undifferentiated macromeres filled with lipid globules (Figure 2.II.B). The posterior pole contains large cells with lipid inclusions and heterogeneous yolk granules, as well as some choanochambers in different stages of development. Choanochambers consist of anucleated collar bodies, but the syncytial pinacoderm that wraps the collar bodies in the functional choanochambers of adult sponges has never been observed in the larva (Boury-Esnault and Vacelet, 1994). Symbiotic bacteria can occur in the larval mesohyl.

The trichimella also contains stauractines, a reduced spicule type that preserves only four of the original six rays (Okada, 1928; Boury-Esnault et al., 1999). The four spicule rays are arranged in a plane paratantential to the larval surface, just under the 'ectosomal' layer, providing mechanical support to the body (Figure 2.II.D). The longest rays of the stauractines, which run from the posterior to almost the anterior larval pole, serve as longitudinal skeletal ribs, while the smaller rays make an annular reinforcement at the larval equator. Small six-rayed spicules, discohexasters, can also occur under the ectosomal layer of the posterior pole in the larva of *F. sollasii* (Okada, 1928).

The free-swimming behavior has only been observed in the trichimella of *O. minuta*, the larvae of which survived for only a few minutes in the laboratory. They swam without spiralling, moving forward while describing a trajectory in counterclockwise circles (Boury-Esnault and Vacelet, 1994).

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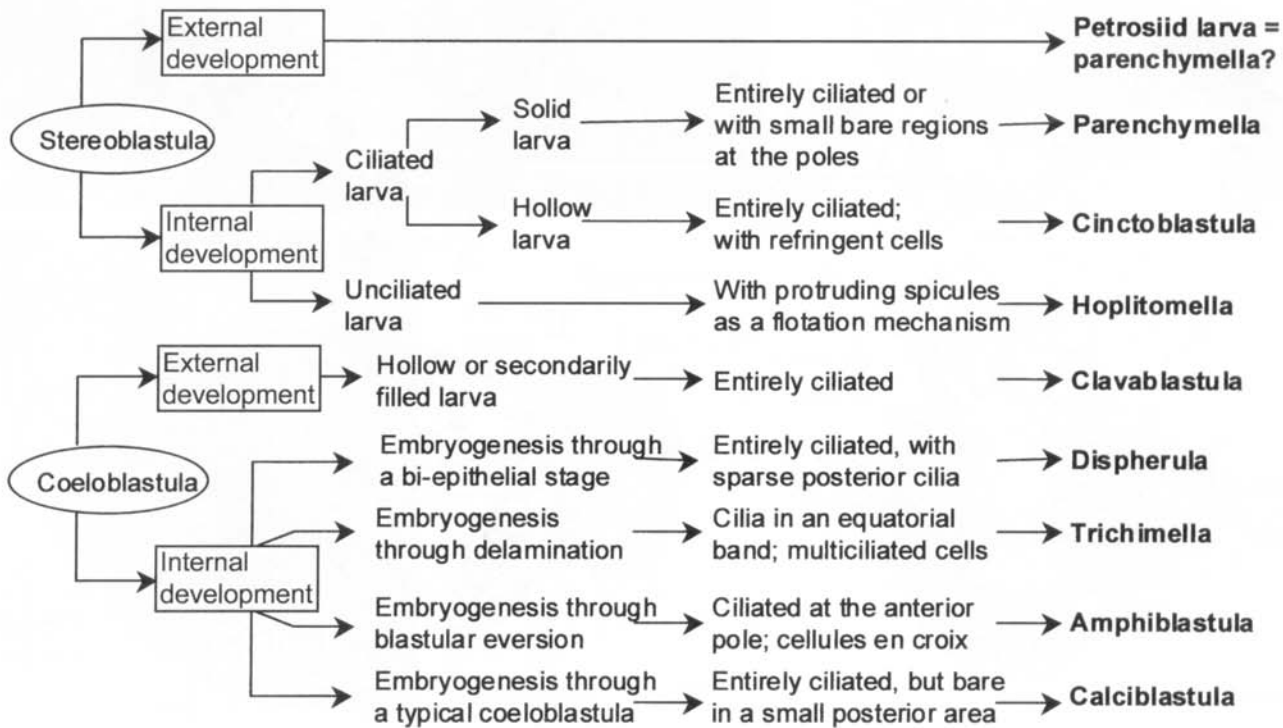


FIGURE 2.1

Schematic diagram summarizing the major developmental and anatomical features of the several larval types known in marine sponges

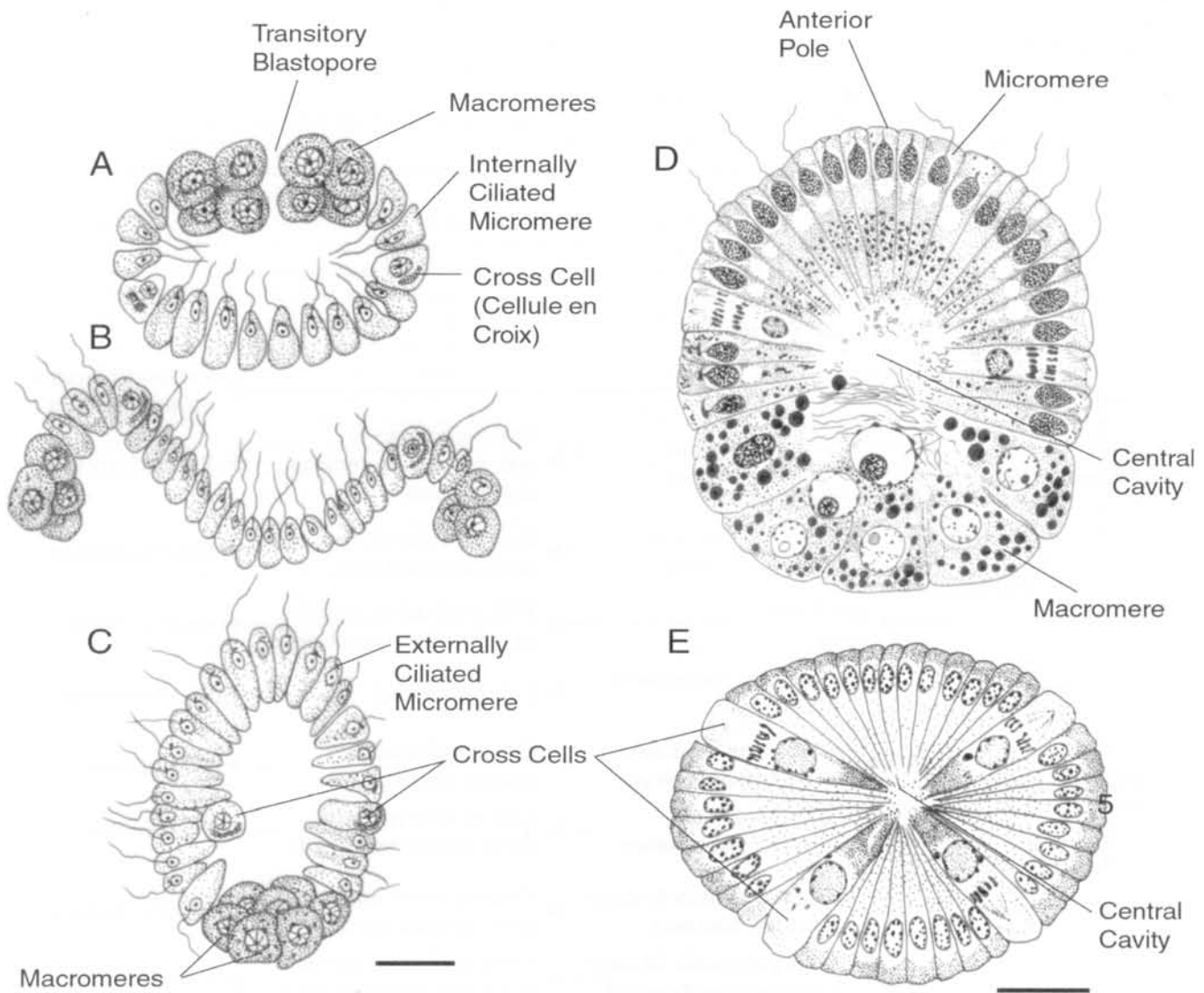


FIGURE 2.2

Amphiblastula larvae

- A. Stomoblastula of *Leucosolenia botryoidea* showing micromeres' internally ciliated ('cellules en croix') and a transitory blastopore among the macromeres. Scale bar: 10 μ m. (Reproduced with permission from Tuzet, 1948.)
- B. Blastula undergoing eversion. Scale bar: 10 μ m. (Reproduced with permission from Tuzet, 1948.)
- C. Early amphiblastula stage obtained after eversion. Scale bar: 10 μ m. (Reproduced with permission from Tuzet, 1948.)
- D. Longitudinal section of the mature amphiblastula of *Leucandra gossei* showing a central cavity, ciliated micromeres at the anterior pole, 'cellules en croix', and unciliated macromeres at the posterior pole. Scale bar: 10 μ m. (Reproduced with permission from Tuzet, 1973.)
- E. Sagittal section of the amphiblastula of *L. gossei* showing the central cavity and all four 'cellules en croix'. Scale bar: 10 μ m. (Reproduced with permission from Tuzet, 1973.)

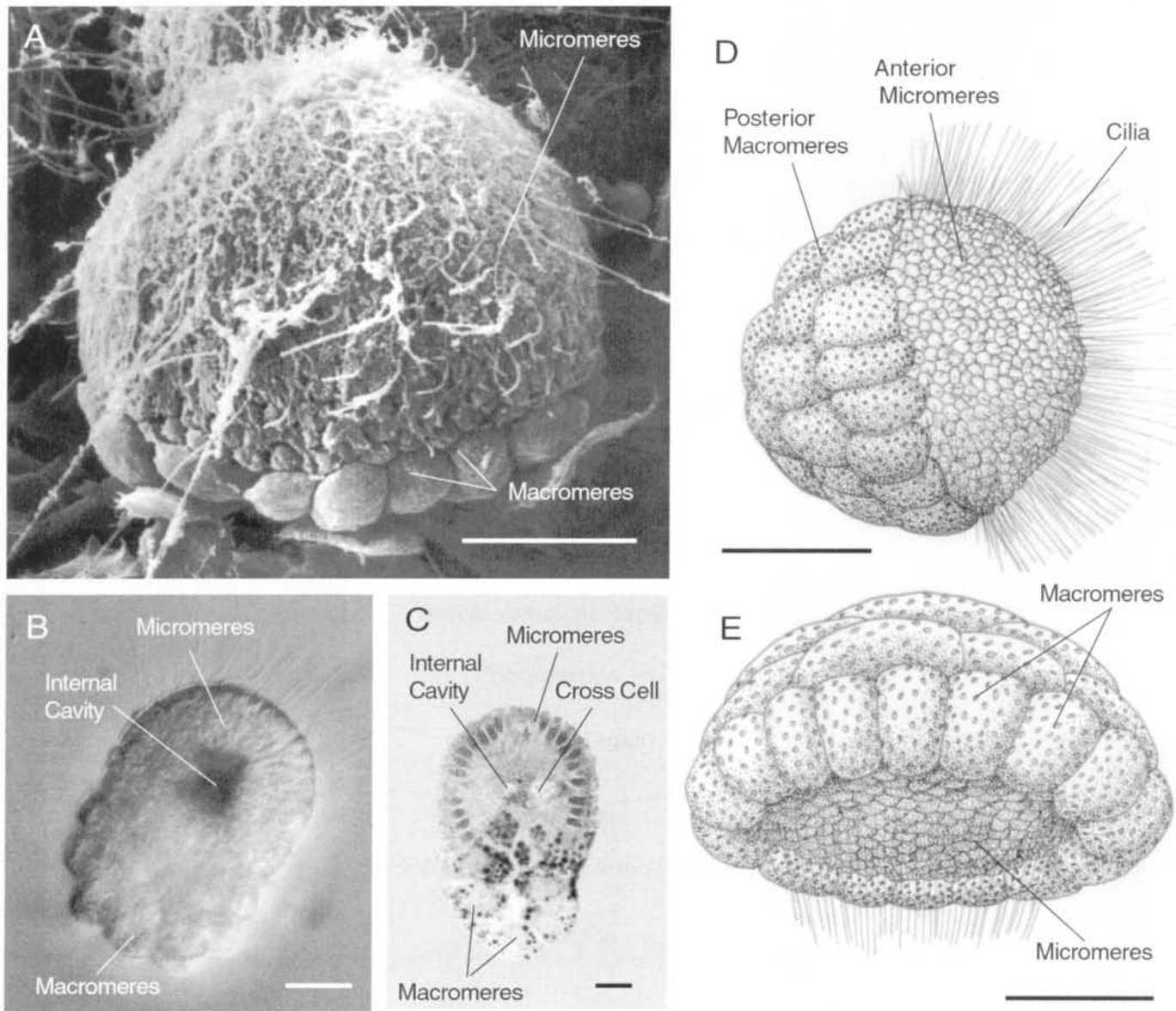


FIGURE 2.3

Amphiblastula

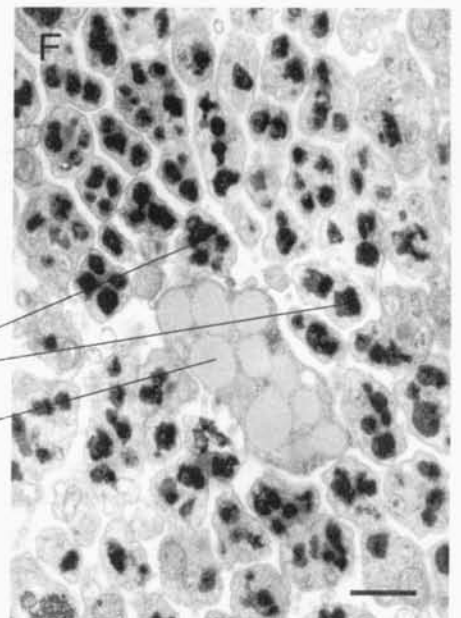
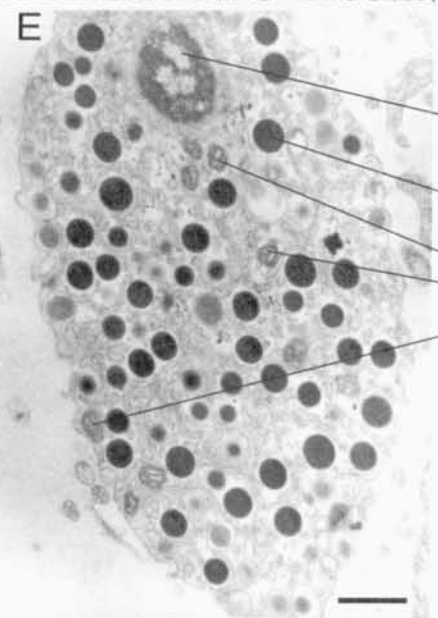
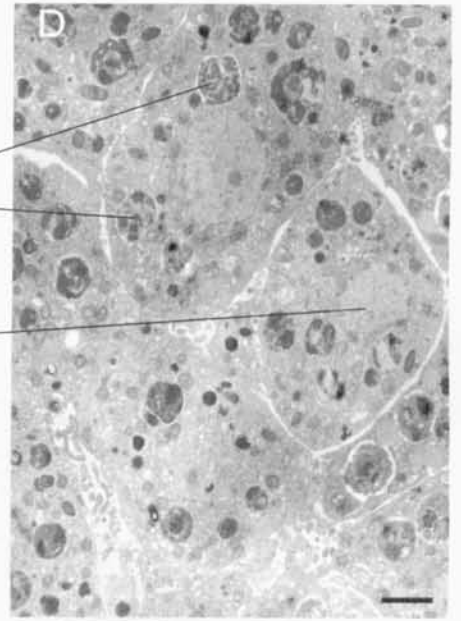
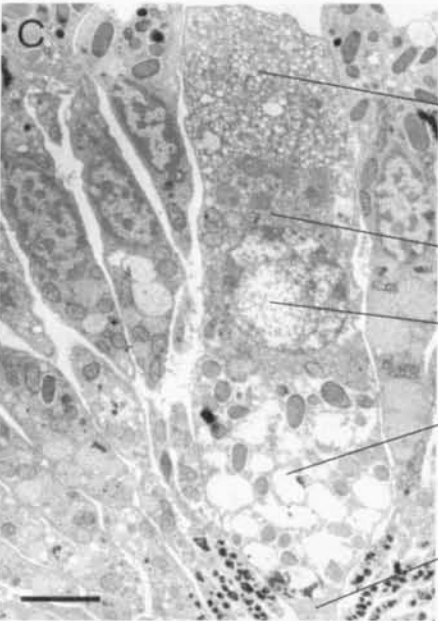
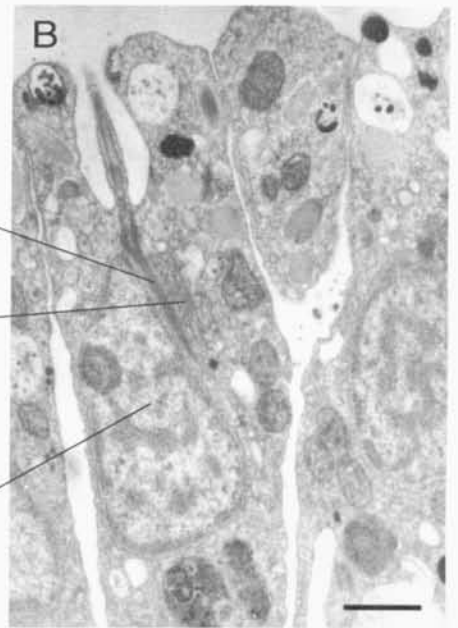
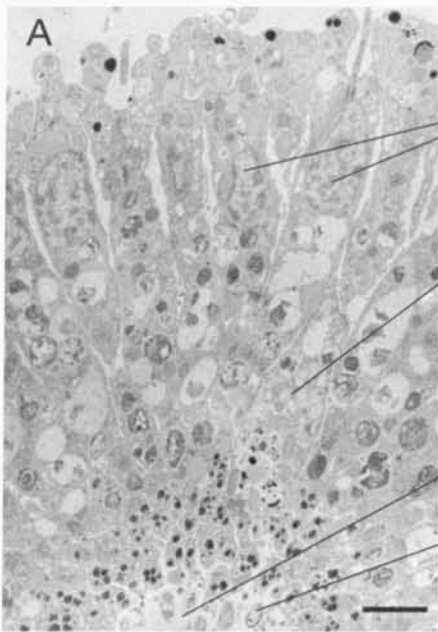
- A. Late embryonic stage of the amphiblastula of *Sycon sycandra* showing micromeres and macromeres. Scale bar: 10 μm . (Scanning electron micrograph reproduced with permission from De Vos et al., 1991.)
- B. Swimming parenchymella of *Leucandra abratsbo*, in which the anterior ciliated micromeres, the posterior macromeres, and the internal cavity are seen. Scale bar: 10 μm (Photograph kindly supplied by S. Amano).
- C. Longitudinal section of the amphiblastula of *L. abratsbo* showing anterior micromeres, posterior macromeres, the internal cavity, and a 'cellule en croix'. Scale bar: 10 μm . (Reproduced with permission from Amano and Hori, 1992.)
- D. Swimming amphiblastula of *Sycon raphanus* showing anterior micromeres and posterior macromeres. Scale bar: 15 μm . (Reproduced with permission from Schulze, 1878.)
- E. Morphology of the late-swimming amphiblastula stage in *S. raphanus* in which macromeres progress toward the anterior pole, covering the micromeres. Scale bar: 15 μm . (Reproduced with permission from Schulze, 1878.)



FIGURE 2.4

Amphiblastula

- A. Sagittal section of amphiblastula of *L. abratsbo* showing the columnar micromeres, a 'cellule en croix', and a central cavity containing four bacteria. Scale bar: 2 μm . (Transmission electron micrographs A–F reproduced with permission from Amano and Hori, 1992.)
- B. Detail of a micromere of *Sycon* sp. showing the ciliary root in close association with the Golgi apparatus and the nucleolate nucleus. Scale bar: 1 μm .
- C. Longitudinal section of a 'cellule en croix' of *L. abratsbo* showing the apical vesicular region, the sub-apical region of dense material, the nucleus, the sub-nucleolar vacuolated region, and the innermost region containing lipid droplets and surrounded by the pigmented bottom portion of adjacent micromeres. Scale bar: 2 μm .
- D. Granular cells of *L. abratsbo* showing the nucleus and numerous phagosomes. Scale bar: 2 μm .
- E. A yolk-containing cell of *Sycon* sp. showing the nucleus, yolk granules, and some small mitochondria. Scale bar: 1 μm .
- F. Transverse section of the innermost region of a 'cellule en croix' of *L. abratsbo* containing numerous lipid droplets, which are surrounded by the innermost regions of adjacent micromeres packed with pigment granules. Scale bar: 0.75 μm .



Columnar Micromeres

Ciliary Root

Cellule en Croix (Cross Cell)

Golgi Apparatus

Central Cavity

Bacteria

Nucleolate Nucleus

Apical Vesicular Region

Phagosomes

Sub-Apical Region

Nucleus

Sub-Nucleolar Vacuolated Region

Inner Region

Nucleus

Yolk Granule

Mitochondria

Pigment Granules

Lipid Droplets

FIGURE 2.5

Calciblastula and Clavablastula larvae

- A. Sagittal section of swimming calciblastula of *Clathrina blanca* showing a monostratified epithelium of ciliated cells, a blastocoel partially filled with cells, and a pair of large, unciliated epithelial cells placed at the posterior pole. Scale bar: 10 μm . (Reproduced with permission from Johnson, 1979.)
- B. Longitudinal section of a swimming clavablastula of *Chondrosia reniformis* showing a monostratified epithelium made up of both cubic cells in the anterior-lateral regions and flattened cells in the posterior pole, as well as a blastocoel virtually obliterated by cells of maternal origin, typically bacteriocytes. Scale bar: 20 μm (Reproduced with permission from Lévi and Lévi, 1976.)
- C. General appearance of the crawling clavablastula of *Polymastia robusta*. Scale bar: 50 μm . (Reproduced with permission from Borojevic, 1967.)
- D. Longitudinal section of the clavablastula of *P. robusta* showing a monostratified epithelium of ciliated cubic cells and a narrow blastocoel. Scale bar: 50 μm . (Reproduced with permission from Borojevic, 1967.)

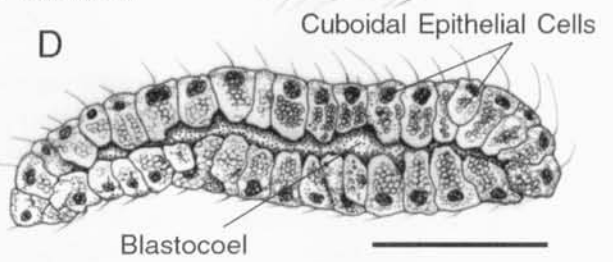
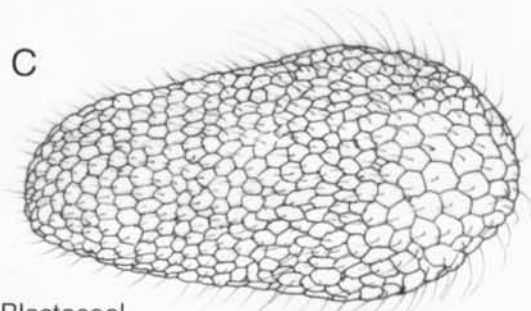
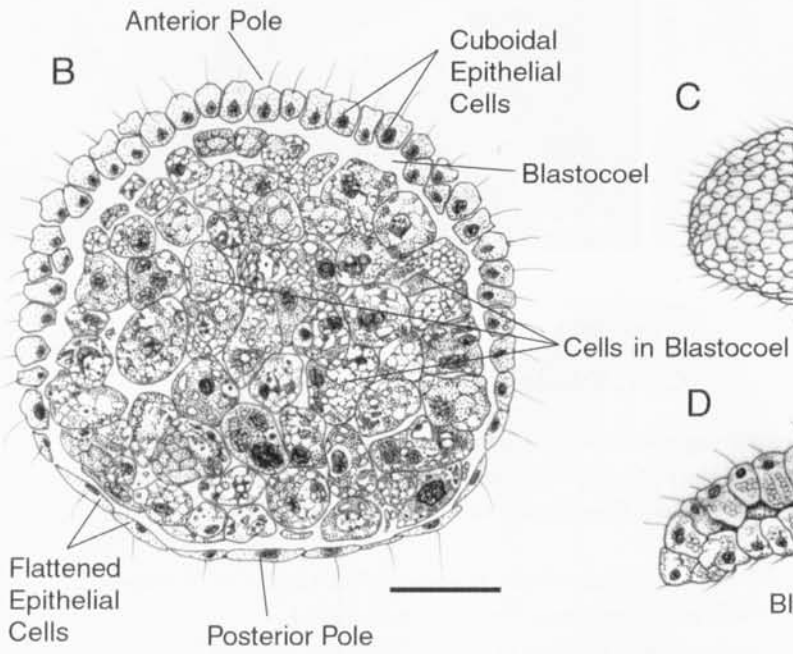
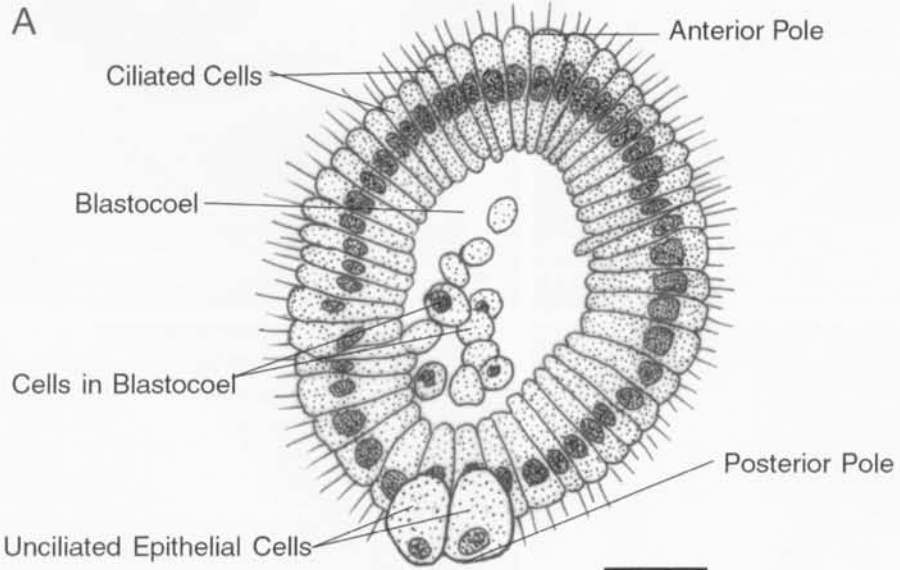
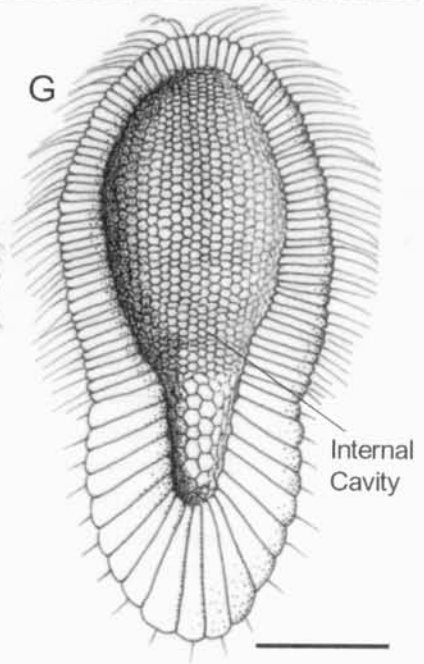
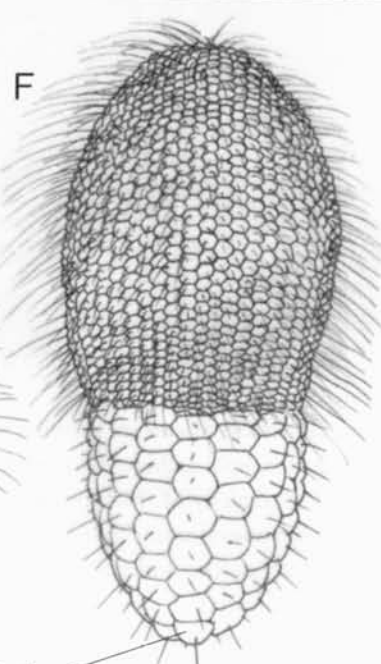
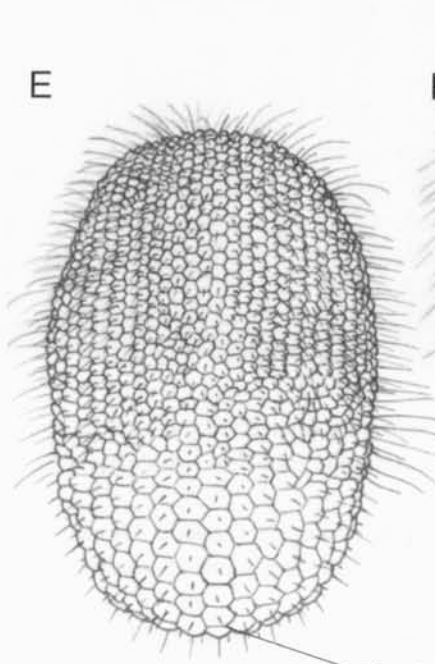
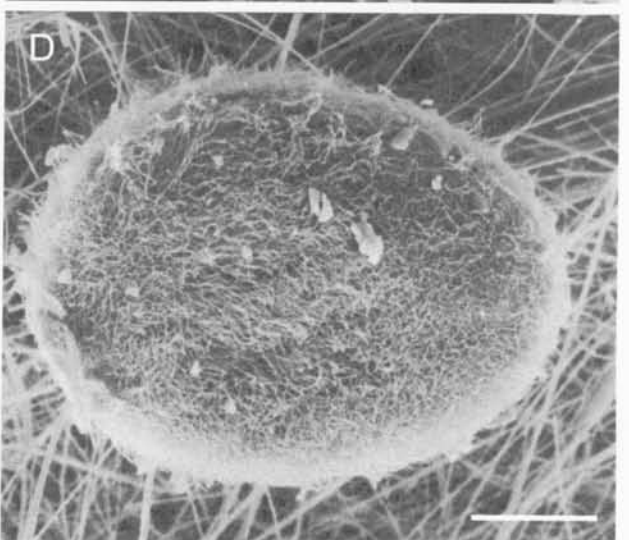
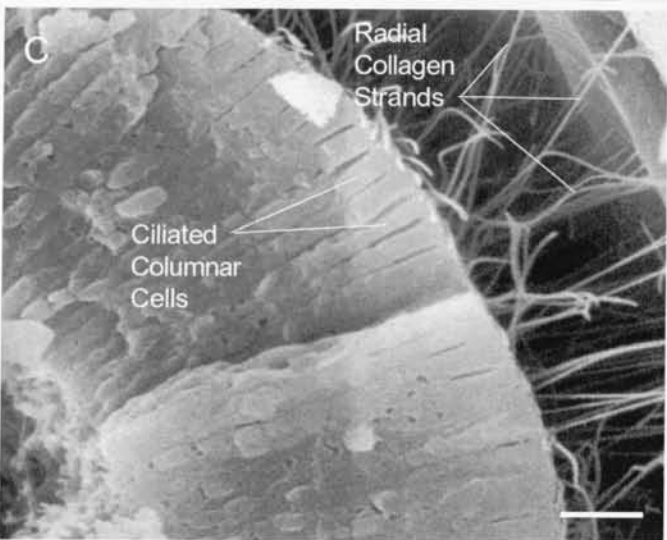
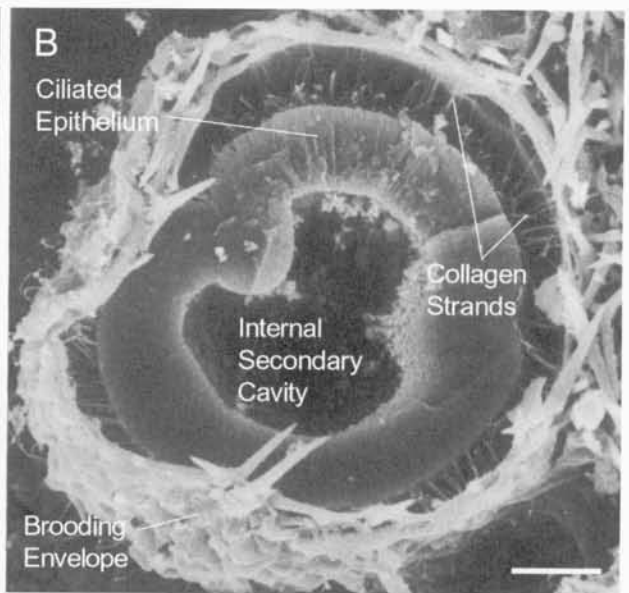
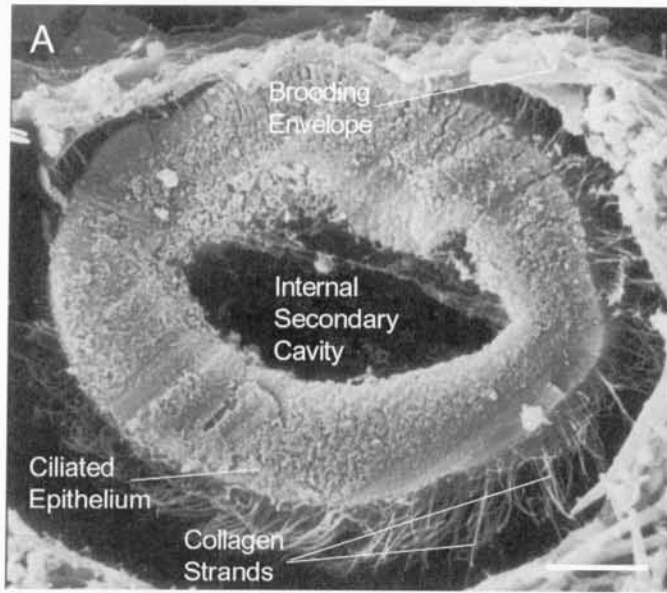




FIGURE 2.6

Cinctoblastula

- A.** and **B.** Sections of late embryonic stages of *Plakina trilopha* immediately before release showing the internal secondary cavity and the ciliated epithelium anchored to the brooding envelope by radial collagen strands. Scale bar: 25 μm . (Reproduced with permission from Bergquist et al., 1979.)
- C.** Detail of the columnar ciliated cells and radial collagen strands in a late embryo of *P. trilopha*. Scale bar: 5 μm . (Reproduced with permission from Bergquist et al., 1979.)
- D.** Mature cinctoblastula of *Oscarella lobularis*, ready to be released from the maternal body. Scale bar: 50 μm . (Scanning electron micrograph by P.R. Bergquist)
- E.** Early-swimming stage of the cinctoblastula of *O. lobularis* showing the posterior pole with larger cells provided with short cilia. Scale bar: 50 μm . (Reproduced with permission from Barrois, 1876.)
- F.** Late-swimming stage of the cinctoblastula of *O. lobularis* that has experienced body lengthening during the dispersal period. Scale bar: 50 μm . (Reproduced with permission from Barrois, 1876.)
- G.** Longitudinal section of a late-swimming stage of the cinctoblastula of *O. lobularis* showing the internal cavity. Scale bar: 50 μm . (Reproduced with permission from Barrois, 1876.)



Posterior Pole



FIGURE 2.7

Parenchymella

- A. Longitudinal section of a late embryonic stage of the verticillitid *Neocoelia crypta*. Scale bar: 50 μm . (Reproduced with permission from Vacelet, 1979.)
- B. Fracture of a late embryonic stage of the dendroceratid *Darwinella gardineri* showing the surrounding follicle of nurse cells. Scale bar: 50 μm . (Scanning electron micrograph by P.R. Bergquist.)
- C. Longitudinal section of the mature parenchymella of the haplosclerid *Haliclona* sp. showing a protruding posterior pole and some spicules. Scale bar: 50 μm . (Reproduced with permission from Amano and Hori, 1994.)
- D. Larval epithelium of the poecilosclerid *Mycale* sp. showing columnar ciliated cells, an urn-shaped secretory cell, and large ameboid archeocytes placed under the epithelium. Scale bar: 12 μm . (Scanning electron micrograph by M. Maldonado.)
- E. Longitudinal section through the posterior unciliated larval pole of the poecilosclerid *Mycale* sp. showing spicules and collagen fascicles under the epithelium. Scale bar: 30 μm . (Scanning electron micrograph by M. Maldonado.)
- F. Sclerocyte in the swimming parenchymella of *Sigmatocia caerulea*, secreting an intracellular spicule. Note also (6) mitochondria and (9) packs of intercellular collagen. Scale bar: 2.5 μm . (Transmission electron micrograph by M. Maldonado.)

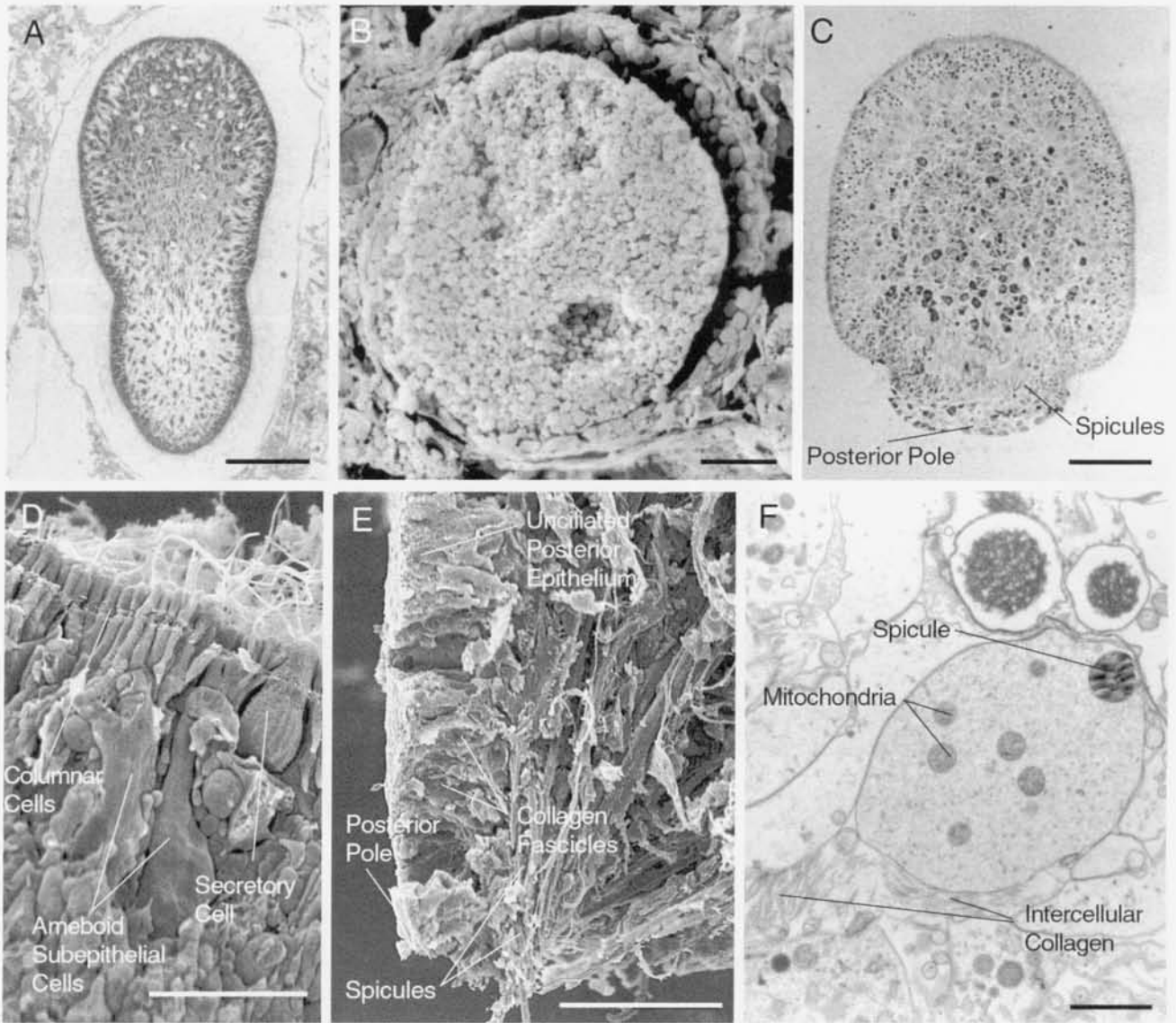




FIGURE 2.8

Parenchymella

This figure is reproduced in color between pages 606 and 607

- A.** Entirely ciliated parenchymellae of the halichondrid *Scopalina lophyropoda* during the free-swimming period (on the right) and at the beginning of the attachment process, which takes place on a lateral region (on the left). Scale bar: 200 μm . (Photographs A to F by M. Maldonado.)
- B.** Detail of the posterior ciliated end of the *S. lophyropoda* larva. Scale bar: 100 μm .
- C.** Free-swimming larva of the poecilosclerid *Crambe crambe* showing a bare posterior end. Scale bar: 200 μm .
- D.** Free-swimming larva of the poecilosclerid *Mycale* sp. showing a bare posterior end and a scarcely ciliated anterior end. Scale bar: 100 μm .
- E.** Free-swimming larva of the dictyoceratid *Ircinia oros*, showing a posterior tuft of long cilia, a pigmented ring, and a protruding anterior end. Scale bar: 200 μm .
- F.** Detail of the posterior tuft of the *Ircinia oros* larva showing the long cilia, the protruding cells of the pigmented ring, and part of the lateral ciliation. Scale bar: 50 μm .

Parenchymella

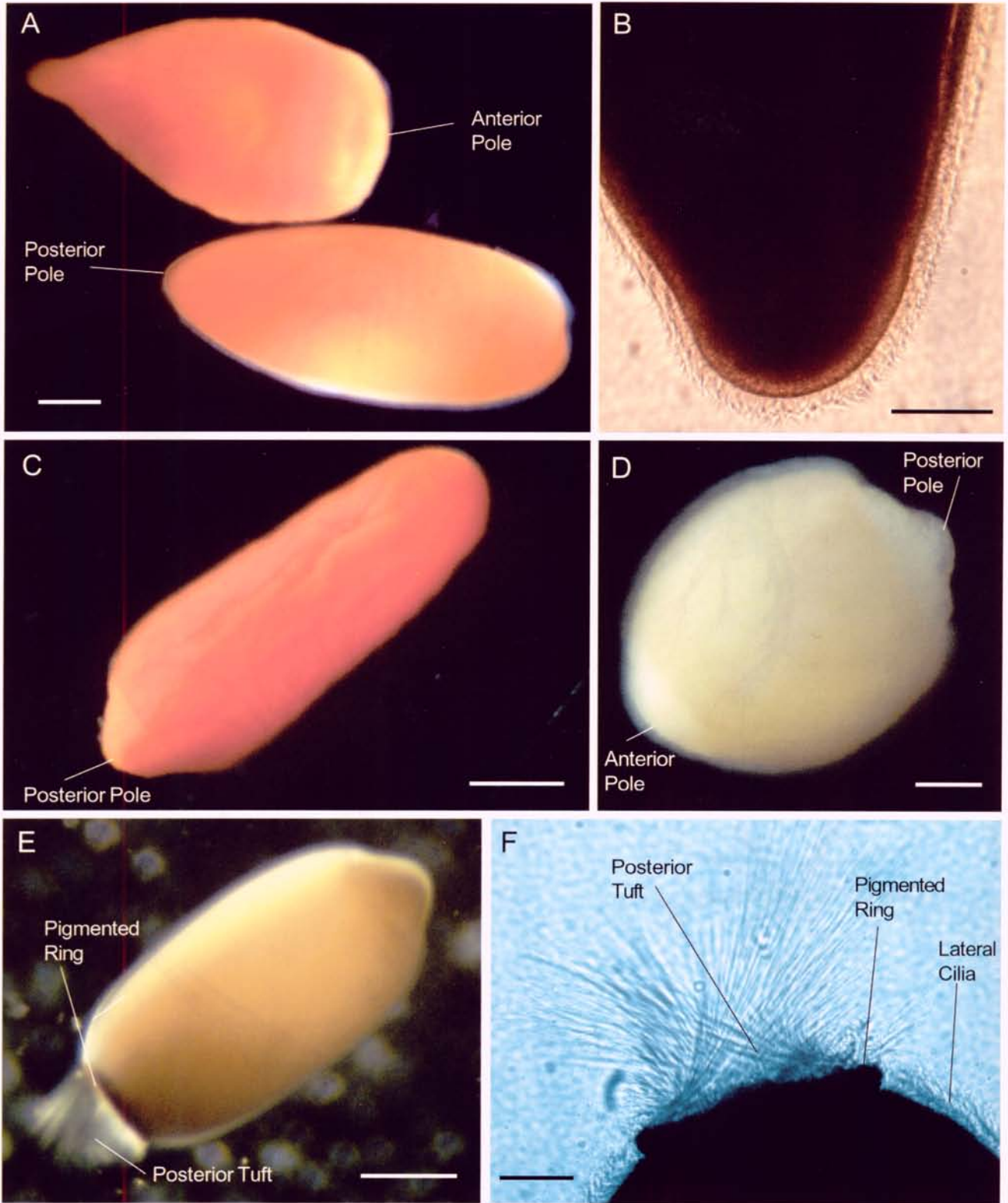


FIGURE 2.9

Parenchymella

- A. Mature parenchymella of the halichondrid *S. lophyropoda*. Scale bar: 450 μm . (Scanning electron micrograph by M. Maldonado).
- B. Parenchymella of the haplosclerid *Haliclona petrosioides*. Scale bar: 200 μm . (Scanning electron micrograph reproduced with permission from Bergquist et al., 1979.)
- C. Parenchymella of the poecilosclerid *Lissodendoryx isodictyalis* showing a protruding, naked posterior pole. Scale bar: 50 μm . (Scanning electron micrograph reproduced with permission from Lévi 1998.)
- D. Parenchymella of the poecilosclerid *Coelosphaera transiens*. Scale bar: 50 μm . (Scanning electron micrograph by P.R. Bergquist.)
- E. Detail of the anterior pole of the *C. transiens* larva, which becomes bare when settlement approaches. Scale bar: 25 μm . (Scanning electron micrograph by P.R. Bergquist.)
- F. General view of the posterior pole of the *C. transiens* larva showing a central bare region. Scale bar: 50 μm . (Scanning electron micrograph by P.R. Bergquist.)
- G. Detail of the posterior pole of *C. transiens* showing a bare region of vesicular appearance. Scale bar: 25 μm . (Scanning electron micrograph by M. Maldonado.)
- H. Swimming parenchymella of the haplosclerid *Sigmatocia caerulea* showing a posterior tuft of cilia, a pigmented ring, and a small bare region at the anterior pole. Scale bar: 100 μm . (Photograph by M. Maldonado.)
- I. Parenchymella of the haplosclerid *Haliclona oculata* showing a posterior tuft. Scale bar: 50 μm . (Scanning electron micrograph kindly supplied by R.W. van Soest.)
- J. Detail of the posterior tuft of *H. oculata* and the central bare area. Scale bar: 25 μm . (Scanning electron micrograph kindly supplied by R.W. van Soest.)
- K. Parenchymella of the halichondrid *Halichondria panicea* showing a posterior tuft of tangled cilia. Scale bar: 100 μm . (Scanning electron micrograph reproduced with permission from Wapstra and van Soest, 1987.)
- L. Parenchymella of the dictyoceratid *Spongia reticulata* showing the posterior tuft. Scale bar: 150 μm . (Scanning electron micrograph reproduced with permission from Bergquist et al., 1979.)
- M. Parenchymella of the dendroceratid *Darwinella gardineri* showing the posterior tuft. Scale bar: 50 μm . (Scanning electron micrograph reproduced with permission from Bergquist, 1996.)
- N. Detail of the anterior pole of the swimming parenchymella of *D. gardineri*, which becomes bare and vesicular when settlement approaches. Scale bar: 25 μm . (Scanning electron micrograph reproduced with permission from Bergquist et al., 1979.)

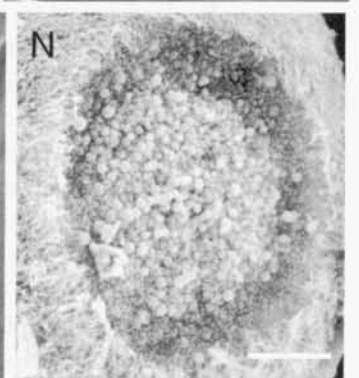
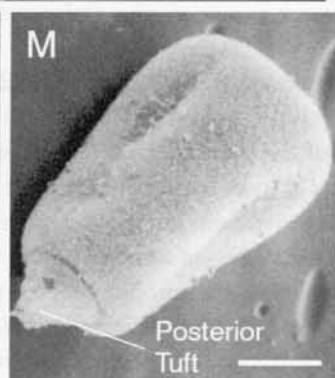
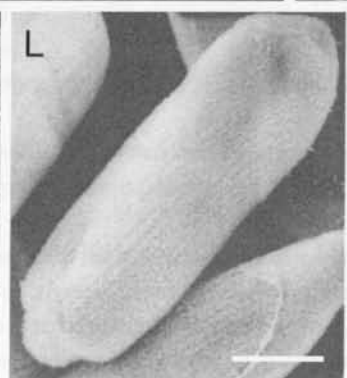
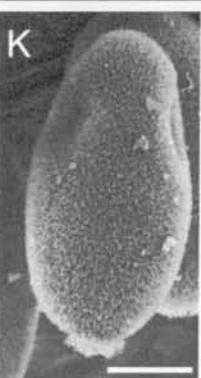
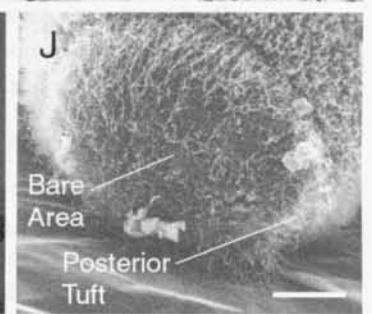
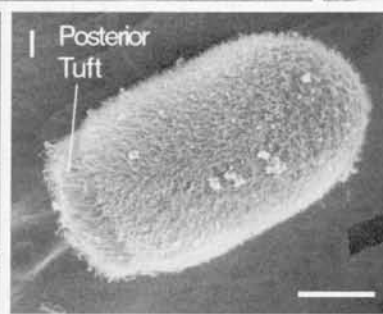
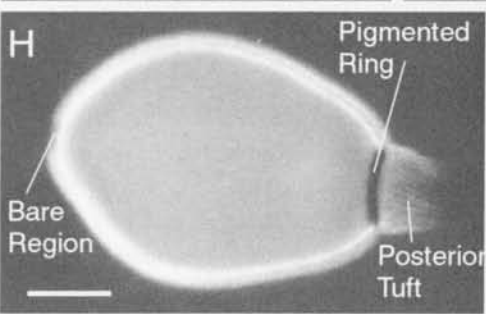
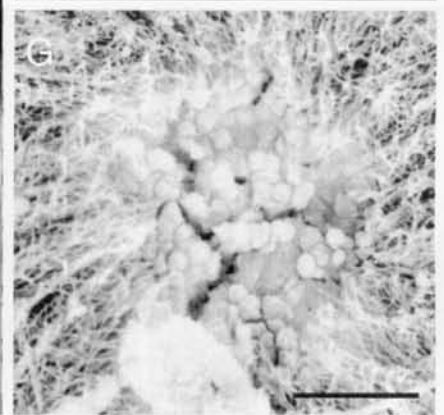
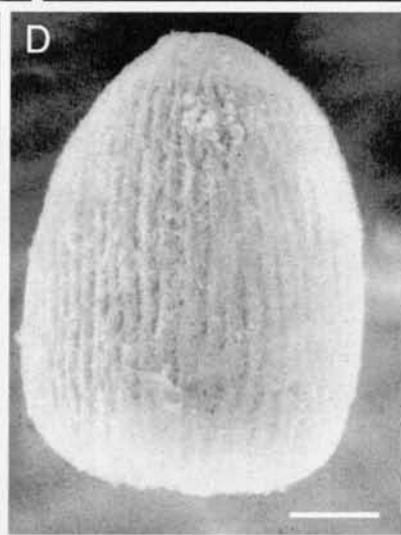
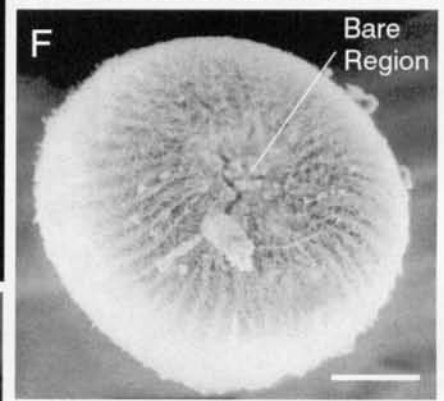
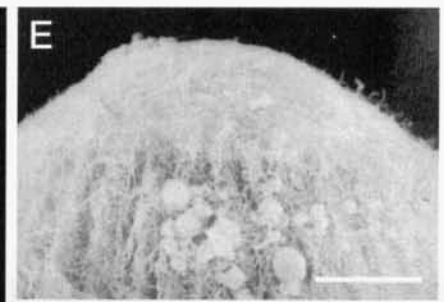
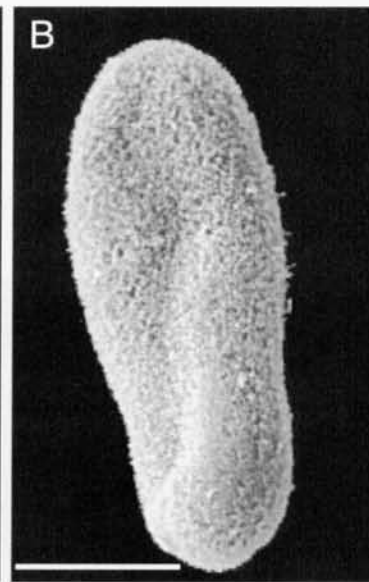
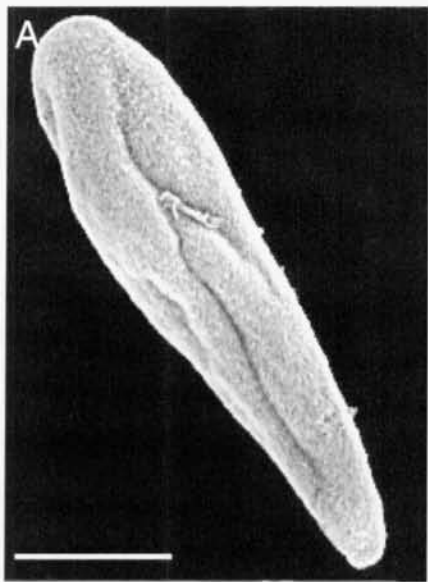
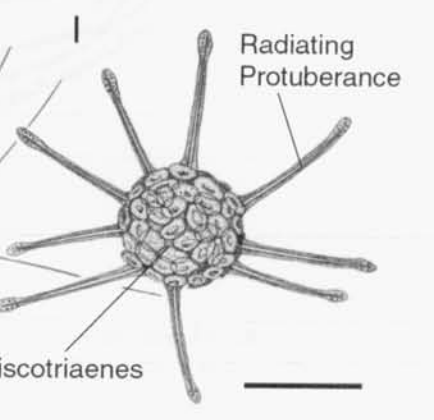
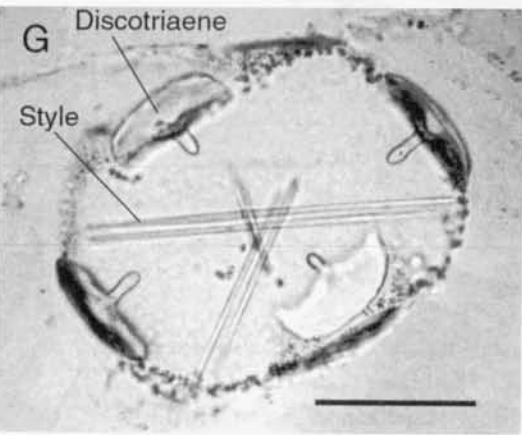
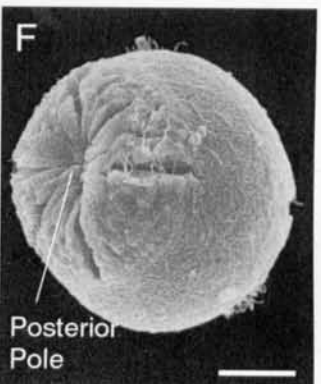
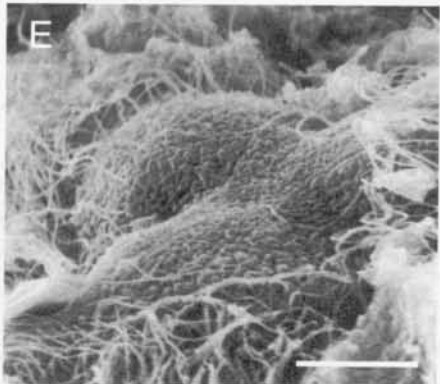
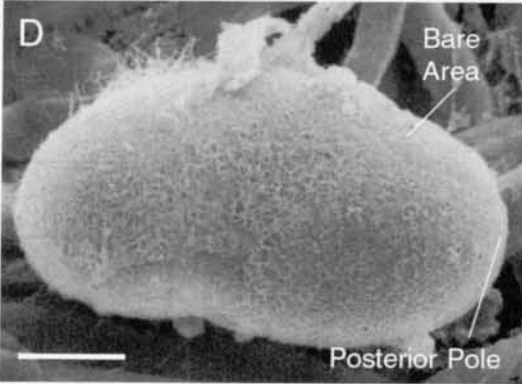
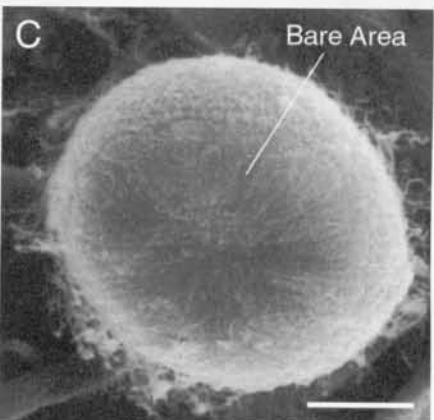
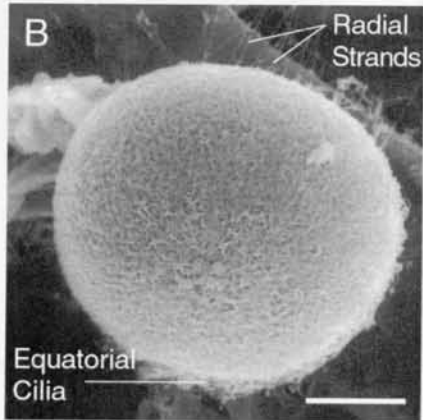
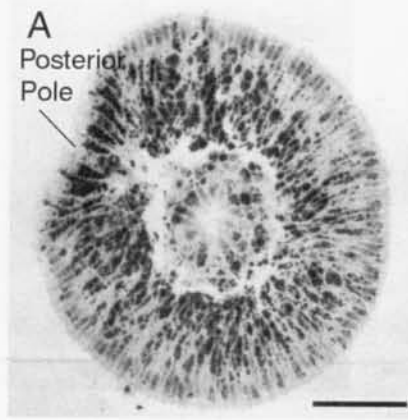




FIGURE 2.10

Dispherula and hoplitomella larvae

- A. Longitudinal section of the mature dispherula larva of the halisarcid *Halisarca dujardini* showing two cell layers organized into two hollow spheres. Note the slightly concave posterior pole. Scale bar: 25 μm . (Photograph kindly supplied by A.V. Ereskovsky.)
- B. Detail of the anterior, densely ciliated pole of a late embryo of *H. dujardini*. Note radial strands between the embryo and the maternal tissue. Scale bar: 10 μm . (Scanning electron micrograph by P.R. Bergquist.)
- C. Posterior pole of an embryo of *H. dujardini* showing a bare area, which will later become sparsely ciliated. Scale bar: 10 μm . (Scanning electron micrograph reproduced with permission from Bergquist, 1980.)
- D. Lateral view of a developing embryo of *H. dujardini* showing two bare areas, which are likely spots where epithelial ciliated cells migrated toward the larval cavity to form the innermost spherula. Scale bar: 19 μm . (Scanning electron micrograph by P.R. Bergquist.)
- E. Detail of a bare region in a developing embryo of *H. dujardini*. Scale bar: 10 μm . (Scanning electron micrograph by P.R. Bergquist.)
- F. Larva of *H. dujardini* seen from the posterior pole. Scale bar: 25 μm . (Scanning electron micrograph kindly supplied by A.V. Ereskovsky.)
- G. Embryonic stage of *Alectona wallichii* showing the peripheral skeleton of discotriaenes and three internal pairs of styles during development of the hoplitomella. Scale bar: 135 μm . (Reproduced with permission from Vacelet, 1999.)
- H. Late embryonic stage of *Thoosa armata* showing a skeleton of subepithelial discostrongyles and radiating styles. Scale bar: 350 μm . (Reproduced with permission from Topsent, 1904.)
- I. Swimming hoplitomella larva of *Alectona millari* showing a subepithelial skeleton of discotriaenes and radiating protuberances, each internally supported by a style. Scale bar: 250 μm . (Reproduced with permission from Trégouboff, 1942.)



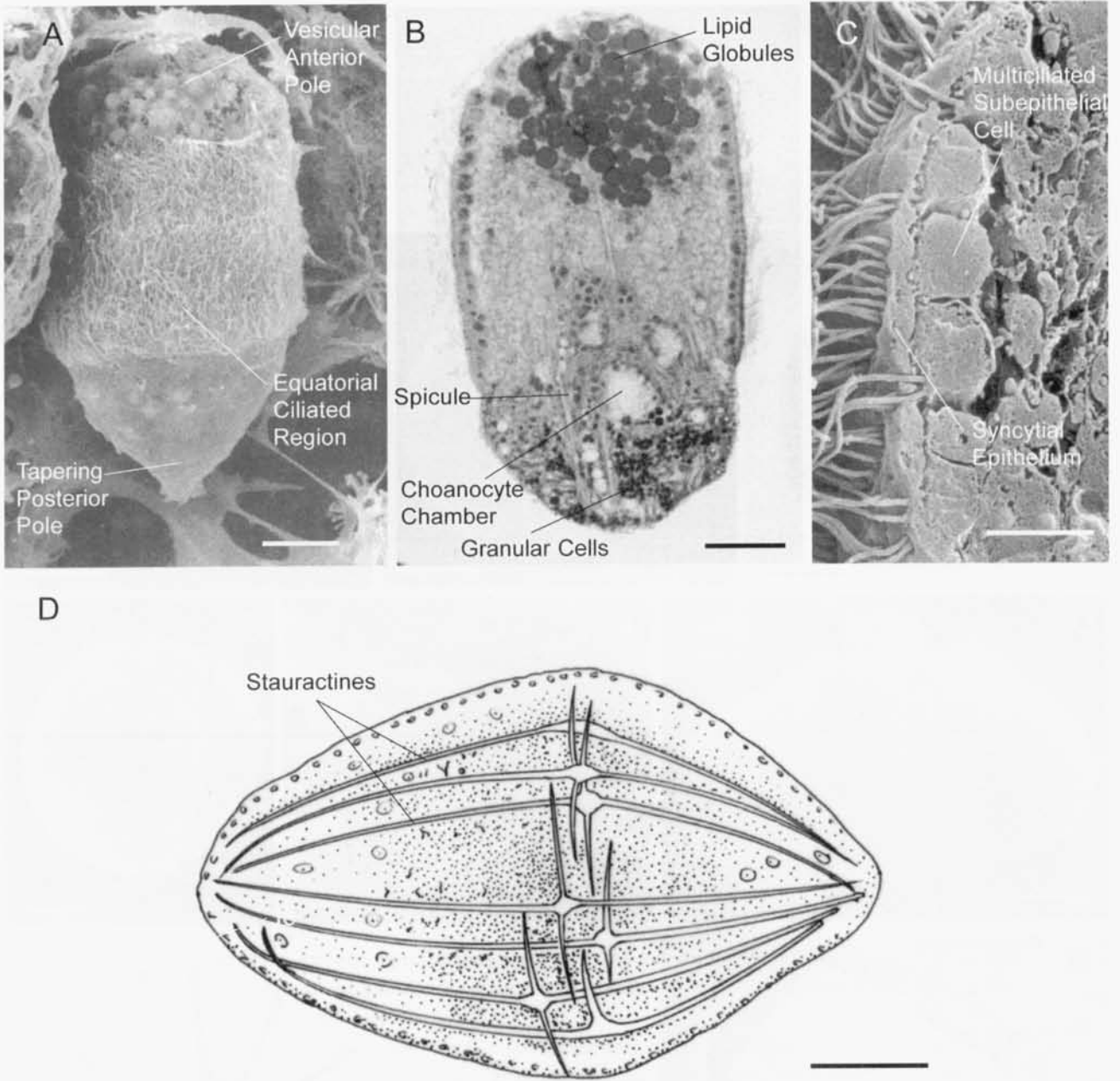


FIGURE 2.II

Trichimella larvae

- A.** Mature trichimella of the lyssacinoid *Oopsacas minuta* showing the equatorial ciliated region, the vesicular anterior pole, and the tapering posterior pole. Scale bar: 25 μm . (Scanning electron micrograph reproduced with permission from Boury-Esnault and Vacelet, 1994.)
- B.** Longitudinal section of a mature larva showing numerous lipid globules in the anterior pole. There are also spicules, choanocyte chambers, and granular cells in the posterior pole, and multiciliated cells in the equatorial region. Scale bar: 25 μm . (Reproduced with permission from Boury-Esnault and Vacelet, 1994.)
- C.** Detail of the ciliated region showing the cilia of the subepithelial multiciliated cells piercing the flat syncytial epithelium. Scale bar: 5 μm . (Scanning electron micrograph reproduced with permission from Boury-Esnault and Vacelet, 1994.)
- D.** Diagram of a trichimella of the hexactinoid *Farrea sollasi* showing the internal skeleton of stauractines. Scale bar: 25 μm . (Reproduced with permission from Okada, 1928.)