Chapter 2
Development of Sponges from the Class Hexactinellida Schmidt, 1870

Representatives of the class Hexactinellida, commonly called glass sponges, are very variable in shape. They may be tubular, cup-shaped, lumpy, branching, or lobulate (color plate III); only encrusting forms are lacking. Hexactinellid sponges have silicate triaxial spicules or their derivatives. Typically, spicules are represented by hexactins, with three axes crossing at regular angles. A loss of one or more rays results in pentactins, tetractins (stauractins), triactins (tauactins), and diactins; rarely, monactins also occur (Fig. 2.1). The axial filament of the spicule resides in a quadrangular cavity. Spicules are divided into micro- and macroscleres; the latter, often fused together, form rigid skeletal lattices (Fig. 2.2). Dense spongin or non-spicular skeletons do not occur. Living tissues of glass sponges are syncytial and consist of the dermal and the atrial membrane, the internal trabecular reticulum enclosing cellular components of the sponge, and flagellated chambers (Figs. 24, 25). Separate nucleated cells, which are situated in syncytial pockets or capsules, may be connected by specialized contacts, porous plugs. Large eurypilous flagellated chambers are organized according to leuconoid type. All glass sponges are ovoviviparous, with the trichimella larva.

The class Hexactinellida is divided into two subclasses: Amphidiscophora and Hexasterophora. About 500 species of glass sponges (approximately 7% of all known Porifera species) are distributed across 118 genera, 17 families, and 5 orders.

Glass sponges are marine, and are found at depths of 5–6,770 m. Owing to the mostly deep-water habitats of glass sponges, their development is still poorly studied.

The Hexactinellida are generally thought to be hermaphroditic (Schulze 1880a, 1887; Boury-Esnault et al. 1999; Leys et al. 2007). Pioneering information on their sexual reproduction was obtained by Schulze (1880a, 1887) from *Euplectella aspergillum*, *Farrea occa*, and *Periphragella elisae* and by Ijima (1901, 1904) from *E. marshalli* and *Vitrollula fertilis*. In particular, Schulze (1880a, 1887) demonstrated that female gametes and spermatocytes could be present both in the same individual and in different ones. Yet, a coherent picture of embryonic development in glass sponges was lacking until Okada (1928) published a paper describing gametogenesis, embryogenesis, and larval structure in *F. sollasii*. Then, there was another long gap in developmental studies of hexactinellid sponges: they were not

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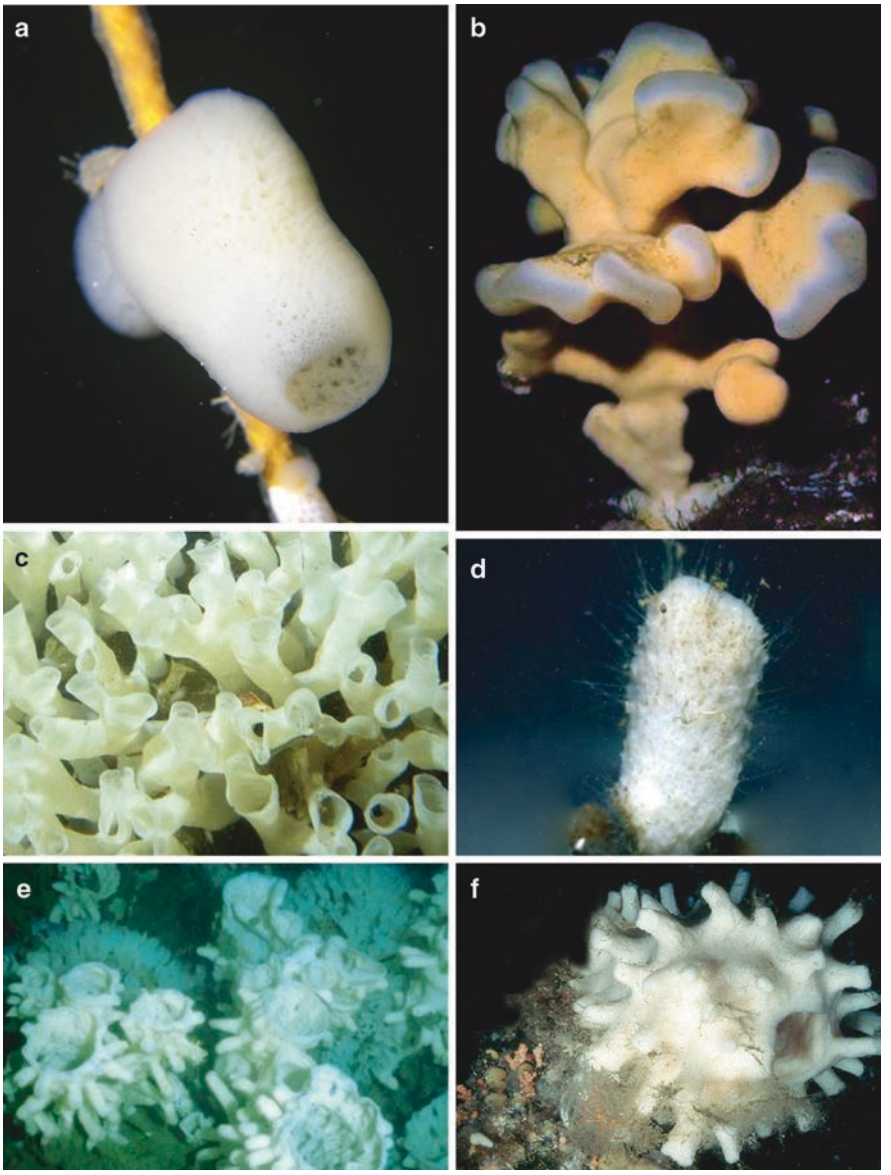

Plate III Class Hexactinellida Schmidt 1870. (**a**) *Oopsacas minuta* Topsent 1927, Mediterranean Sea (Courtesy of R. Graille). (**b**) *Aphrocallistes vastus* Schulze 1886, Okhotsk Sea. (**c**) *Farrea occa* Bowerbank 1862, Okhotsk Sea. (**d**) *Acanthascus dowlingi* Lambe 1892. (**e**) *Chonelasma calyx* Schulze 1886. Okhotsk Sea (**b–e** – Courtesy of V. Feodorov). (**f**) *Rossella nuda* (Topsent 1901) Antarctic (Courtesy of I. Gruzov)

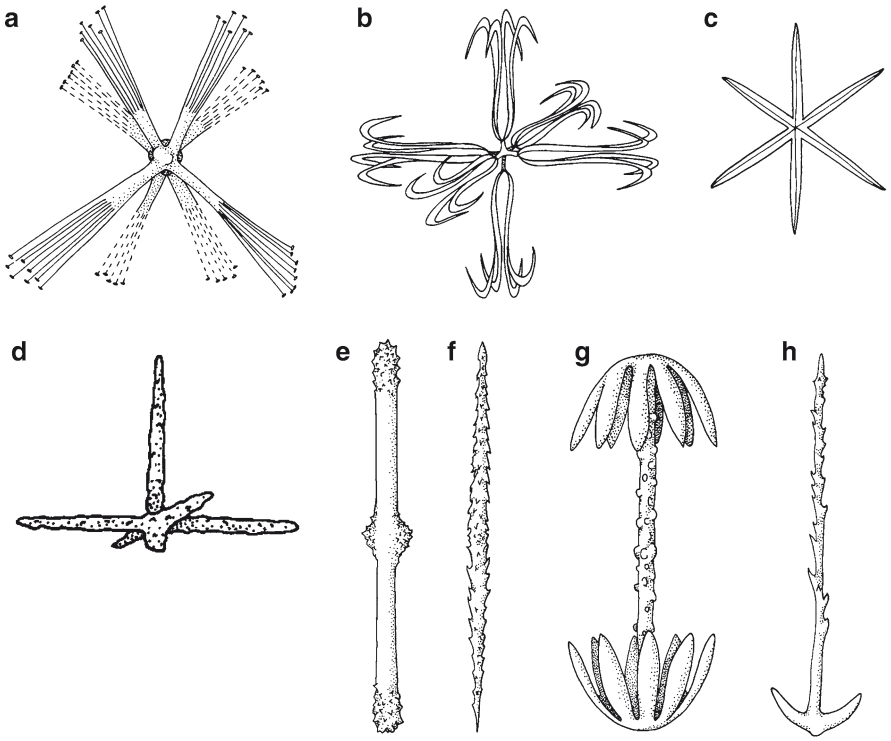

Fig. 2.1 Spicules of Hexactinellida. (**a**) Discoaster, (**b, c**) triactines, (**d**) pentactins, (**e, f**) diactins, (**g**) amphidisc, (**h**) monactin

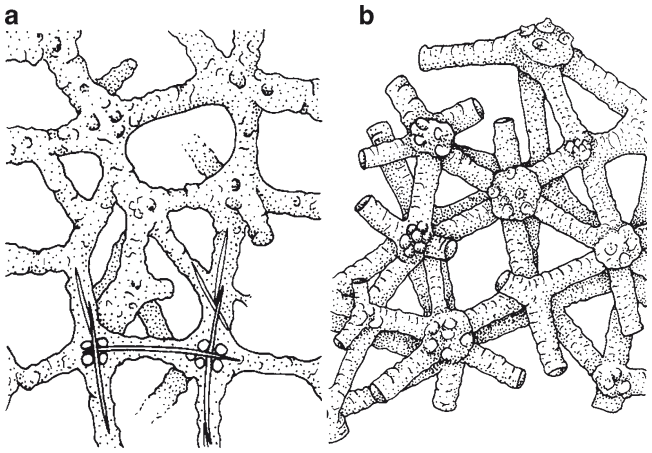

Fig. 2.2 Schematic drawings of fragments of rigid skeletons of Hexactinellida. (**a**) Dictyonal hexactin framework formed by lychnises. (**b**) Spicules fused into a rigid framework type dictyonalia (After Boury-Esnault and Rützler 1997, pp. 21, 23, Figs, 101, 113, reproduced by permission of Smithsonian Institution Scholarly Press)

mentioned in this context for 66 years. It was only in the late twentieth century that Boury-Esnault and Vacelet (1994) described, at the electron-microscopic level, the trichimella larva of a glass sponge (*Oopsacas minuta*). A detailed study of its embryogenesis followed soon (Boury-Esnault et al. 1999; Leys et al. 2006).

2.1 Gametogenesis

In Hexactinellida, both male and female gametes originate from archaeocytes, free nucleolar amoebocytes that are suspended within the trabecular reticulum between flagellated chambers (Ijima 1901; Okada 1928; Boury-Esnault et al. 1999).

Spermatogenesis. Spermatogonia arise within archaeocyte conglomerates, or *congeries* (Ijima 1901; Okada 1928; Boury-Esnault et al. 1999; Leys et al. 2006). Archaeocytes are spherical or subspherical cells with densely granular cytoplasm and numerous mitochondria; the Golgi component and endoplasmic reticulum are not prominent and phagosomes are rare. Archaeocytes in conglomerates are frequently attached to one another and to the trabecular syncytium by plugged junctions (Leys et al. 2007). Prior to differentiation, such conglomerates, as shown in *O. minuta*, are surrounded by a thin (0.5 mm) layer of the trabecular reticulum (Fig. 2.3) (Leys et al. 2007). According to light microscopic observations, spermatogenesis in the Hexactinellida follows the usual pattern. All spermatocytes are connected by plugged cytoplasmic bridges; these bridges also connect cells at the periphery of the cyst to the surrounding trabecular envelope (Leys et al. 2007). Spermatozoa are primitive; their rounded head has relatively much cytoplasm, which contains small mitochondria and dictyosomes. The acrosome has not been described.

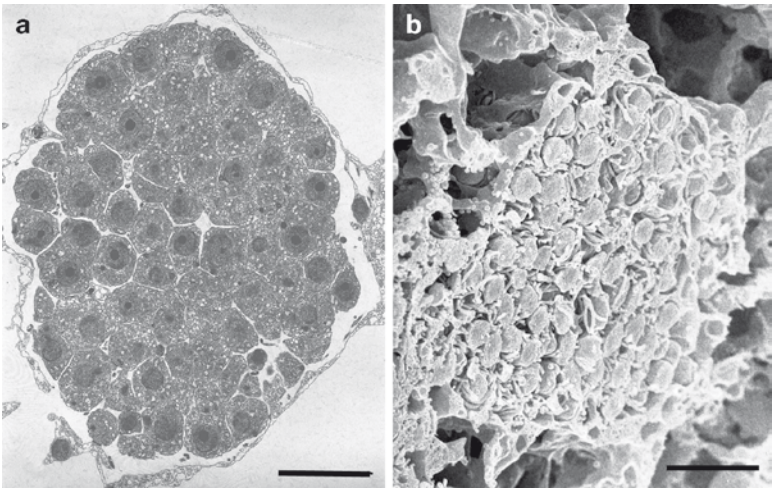

Fig. 2.3 TEM (**a**) and SEM (**b**) of a spermatocyte in *Oopsacas minuta* (Courtesy of J. Vacelet and N. Boury-Esnault). Scale bars (**a**, **b**) 10 μm

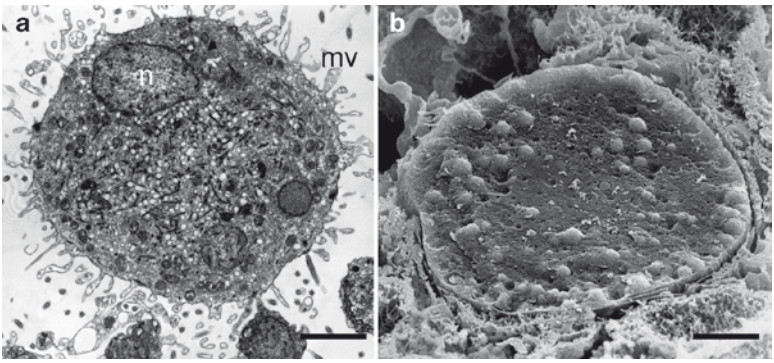

Fig. 2.4 Oogenesis in *Oopsacas minuta.* (**a**) TEM of the early oocyte during the beginning of vitellogenesis. (**b**) SEM of an egg in the sponge tissue (Courtesy of J. Vacelet and N. Boury-Esnault). *mv* microvilli, *n* nucleus. Scale bars (**a**) 5 μm, (**b**) 20 μm

Oogenesis. Oogenesis of glass sponges has not been studied in any detail. It is only known that, similar to spermatogenesis, it starts from the formation of an archaeocyte conglomerate, where the cells are connected to each other by plugged cytoplasmic bridges. Only one of the archaeocytes develops into the oocyte (Fig. 2.4a); the rest are supposed to act as nurse cells providing it with the lipid and yolk (Boury-Esnault et al. 1999). The polylecithal egg contains numerous lipid droplets and osmiophilic granules with heterogeneous content. The egg is not polarized, its nucleus is located centrally (Fig. 2.4b) (Boury-Esnault et al. 1999; Leys et al. 2006).

2.2 Embryonic Development

Embryogenesis has been described only in two hexactinellid species, *F. sollasii* and *O. minuta* (Okada 1928; Boury-Esnault et al. 1999; Leys et al. 2006).

Cleavage. In both species, cleavage is total, equal, and asynchronous up to the stage of about 32 blastomeres (Fig. 2.5a–f). The first two furrows lie in the same plane perpendicular to each other (Fig. 2.5b–d). Orientation of the first cleavage plane with respect to polar bodies varies in different embryos. The plane of the third division is perpendicular to those of the first two. In *O. minuta*, four "animal" blastomeres (situated at the pole with the polar bodies) may lie in spaces between "vegetative" ones (Boury-Esnault et al. 1999) and the authors speak about *spiral* cleavage, which is inaccurate. A displacement of interphase blastomeres is well known in the Cnidaria; this kind of cleavage should be called *pseudospiral* (Tardent 1978). Later cleavage spindles orient parallel to the embryo's surface. The result is an equal coeloblastula with a distinct blastocoel (Fig. 2.5e, f).

Larval Morphogenesis. Unequal tangential divisions of coeloblastula cells result in the formation of a two-layered hollow blastula (Fig. 2.6a). This process resembles cell delamination characteristic of the Cnidaria (Tardent 1978). Peripheral cells

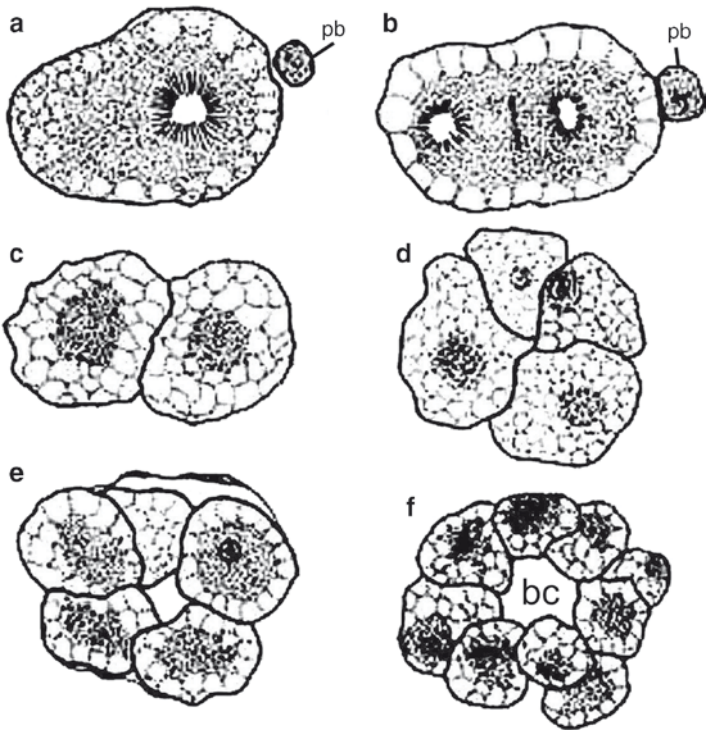

Fig. 2.5 Schematic drawing of cleavage and early stages of embryonic morphogenesis in *Oopsacas minuta*. (**a**) Egg with polar body (*pb*). (**b**) Beginning of the first cleavage division. (**c**) Two blastomeres stage. (**d**) Four blastomeres stage. (**e**) Eight blastomeres stage. (**f**) 16-cells early blastula with the blastocoel (*bc*) (From Boury-Esnault et al. 1999, p. 189, Fig 5, reproduced by permission of Balaban Publishers International Science Services and authors)

of the blastula (micromeres) are smaller than the internal cells (macromeres); during subsequent morphogenesis, they divide actively (Fig. 2.6a). As soon as they are formed, the micromeres are connected to one another by plugged cytoplasmic bridges, which may pass parallel or perpendicular to the surface of the embryo (Fig. 2.6b) (Leys et al. 2007). Internal cells, rich in yolk and lipid inclusions, also divide and fill the blastula cavity. The macromeres extend out filopodia and pseudopodia, which interact and eventually fuse with filopodia from other macromeres (Leys et al. 2007).

While the peripheral cells continue to proliferate, their derivatives differentiate and give rise to a flat syncytium, covering the whole larva, and a belt of prismatic multiciliated cells (Fig. 2.6c). Polarization of the embryo starts early in the course of differentiation. Importantly, all micromeres are interconnected by plugged cytoplasmic bridges.

The macromeres envelop the micromeres with massive filopodia (Leys et al. 2006) and then fuse to form a single multinucleated giant cell, the new trabecular syncytium (Figs. 2.6b and 2.7). This surface epithelium completely envelops the micromeres.

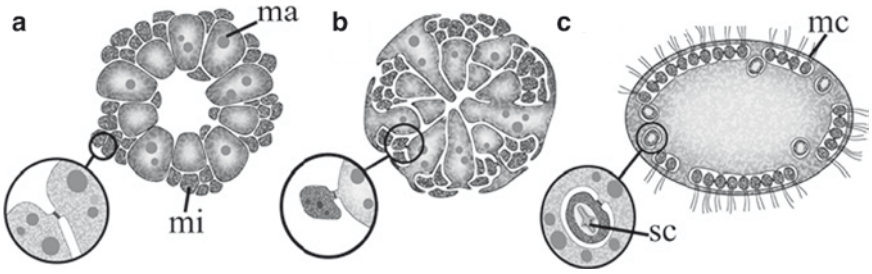

Fig. 2.6 Schematic drawing of different stages in larval morphogenesis of *Oopsacas minuta.* (**a**) Cell delamination by means of unequal cleavage to form micromeres (*mi*) and macromeres (*ma*). (**b**) Fusion of macromeres (*ma*) to form the trabecular syncytium, and envelopment of micromeres by this tissue to form the outer epithelium. (**c**) Cellular differentiation: formation of multiciliated cells (*mc*) and sclerocytes (*sc*, inset) (From Leys et al. 2007, p. 114, Fig. 54, Reproduced by permission of Elsevier Ltd.)

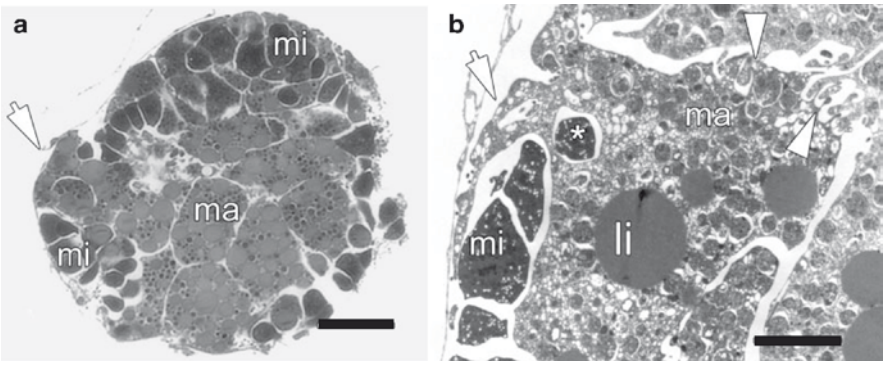

Fig. 2.7 Formation of syncytia in *Oopsacas minuta* by the fusion of macromeres. (**a**) Light microscopy of macromeres (*ma*) extended around micromeres (*mi*, *arrow*) at the surface of the embryo. (**b**) Detail of a surface region of the embryo, showing the macromere (*ma*) extending a lamellipodium (*arrow*) around micromeres (*mi*) on the *left* and forming pseudopodia that intermesh with those of another micromere at the *right* (*arrowheads*). *li* lipid droplet (From Leys et al. 2006, p. 109, Fig. 3b, c, reproduced by permission of Oxford University Press). Scale bars (**b**) 20 μm, (**c**) 2 μm

The internal cells differentiate in two ways. Large cells rich in lipid inclusions migrate toward the anterior pole, whereas cells rich in yolk inclusions and phagosomes migrate toward the posterior pole. Some of the internal cells (originating from micromeres) at the periphery of the central mass differentiate into larval sclerocytes; the latter secrete special four-rayed spicules, *strauractins*, not characteristic of adult sponges. The sclerocytes are originally uninucleate, but then become a multinucleate sclerosyncytium (Leys 2003b). After segregation of the sclerocyte line, most of the yolk-rich cells of the posterior pole merge to form a yolk syncytium, whereas amoeboid cells at the periphery of the central mass differentiate into choanoblasts (Leys et al. 2006). Choanocytes, connected to the trabecular tissue by

cytoplasmic bridges, later fuse into a choanosyncytium, consisting of several collar bodies about 30 μm in diameter in *O. minuta* (their diameter in adult sponges is 100–150 μm) (Boury-Esnault et al. 1999; Leys et al. 2006). Thus, throughout early development, this unusual embryo manages to rearrange cellular regions that are tethered to the multinucleate syncytium via cytoplasmic bridges. Membrane continuity is maintained throughout the entire embryo; there are no typical cells, or cell–cell junctions.

2.3 Larva

The name *trichimella* (from the Greek "bearing long threads") was coined for the *O. minuta* larva (Boury-Esnault and Vacelet 1994) and then extrapolated for the larvae of all hexactinellids. Several unique characters distinguish trichimellae from all other sponge larvae. They are distinctly polarized along the anterior–posterior axis and divided into three zones: the rounded anterior pole, the ciliated middle zone, and the conical posterior pole (Fig. 2.8). The major larval tissue is the syncytial trabecular reticulum, which is continuous throughout the whole larva and forms the bulk of the inner mass of both anterior and posterior poles, as well as the surface epithelium.

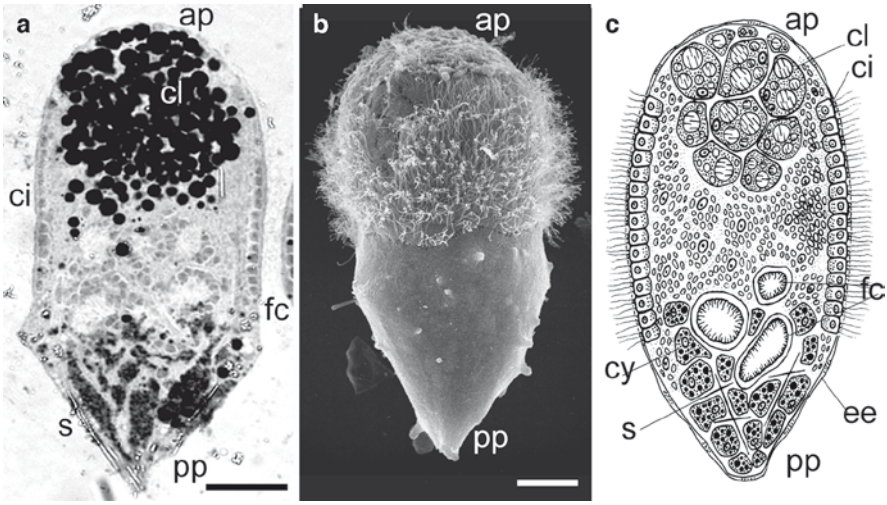

Fig. 2.8 Trichimella larva of Hexactinellida. (**a**) Semi-thin section of *Oopsacas minuta* larva. (**b**) SEM micrograph of *O. minuta* larva. (**c**) Scheme drawing. *ap* anterior pole, *ci* ciliated cells, *cl* cells of anterior pole with lipid droplets, *cy* cells of anterior pole with yolk granules; *fc* flagellated chambers, *ee* external syncytium, *pp* posterior pole; *s* stauractin spicules (**b** – Courtesy of J. Vacelet and N. Boury-Esnault). Scale bars (**a**, **b**) 25 μm

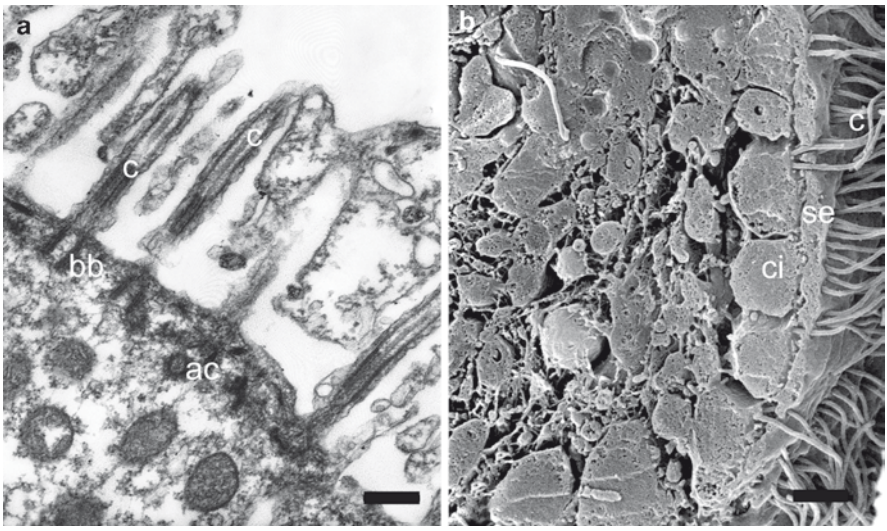

Fig. 2.9 Multiciliated cells of *Oopsacas minuta* trichimellae in the middle part of the larva. (**a**) TEM and (**b**) SEM micrographs. *ac* accessory centriole, *bb* basal body, *c* cilia, *ci* ciliated cells, *se* syncytial epithelium (**a, b** – Courtesy of J. Vacelet and N. Boury-Esnault). Scale bars (**a**) 0.5 μm, (**b**) 3 μm

Inside the larva, there are chambers formed by anucleate collar bodies. Contrary to the situation in the adult sponge, these chambers are not arranged into a reticulum. In the posterior pole, there is a unique stauractin skeleton (Fig. 2.8a, c). Larval spicules of the modern hexactinellids resemble the spicules of their ancestors, representatives of the genus *Protospongia* and *Diagoniella* from the early Palaeozoic family Protospongiidae (Mehl 1996).

Another peculiar feature of trichimellae is multiciliated cells, which form a broad belt in the middle of the larva (Fig. 2.9). Each such cell bears about 50 cilia, which have basal bodies and an accessory centriole but lack the rootlet. Each cilium passes in a special opening in the syncytial epithelium. The cell bodies are connected to one another and to the trabecular tissue above and below by plugged cytoplasmic bridges (Boury-Esnault et al. 1999; Leys et al. 2006). Similar junctions are present between the posterior pole cells, containing yolk granules.

2.4 Metamorphosis

The few available observations on metamorphosis were made on *O. minuta* (Leys et al. 2007). Most larvae settle and metamorphose into the juvenile sponge within 12–24 h after release from the parent. Larvae attach to the surface by the rounded anterior pole and flatten. After 24 h, the lipid inclusions remain at the base of the postlarva, whereas the center and former posterior pole undergo a massive change.

During morphogenesis, the reticular tissue undergoes a radical reorganization. Most of the yolk-filled inclusions disappear. The multiciliated cells resorb their cilia; their fate in the postlarva is unknown. Flagellated chambers enlarge and become enveloped by the reticular tissue, as in the adult.

Embryonic developmental studies of *F. sollasii* and *O. minuta* (Okada 1928; Boury-Esnault et al. 1999) show that syncytial organization arises during embryogenesis – more precisely, during larval histogenesis, when the sclerosyncytium, the choanocyncytium, and the cover syncytium develop. These data are an additional argument in favor of the idea that syncytial organization in the Hexactinellida is secondary (Leys 2003a). At the same time, they contradict the hypothesis that syncytial organization in the Hexactinellida arose early in the course of multicellularity formation, as a result of uncompleted cytotomy, uncompleted cleavage, or fusion of blastomeres (Rieger and Weyrer 1998).

2.5 Asexual Reproduction

Asexual reproduction in the form of external budding has often been described in Hexactinellida representatives (see Tuzet 1973b). However, we failed to find any papers especially concerned with this morphogenesis. According to some of the pictures published (Schulze 1887a; Tuzet 1973b), budding in Hexactinellida seems to be epimorphic. In *Rhabdocalyptus dawsoni*, the bud's cavity is separated from the atrial cavity of the parent sponge, but the cytoplasm of the trabecular syncytium connecting the parent with the bud is continuous (Mackie et al. 1983).

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