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BIOLOGY OF ONTOGENESIS

Development of Sponges of the Order Haplosclerida

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Abstract—A comparative morphological analysis was performed for freshwater and marine sponges belonging to the order Haplosclerida (class Demospongiae, subclass Ceractinomorpha). The analysis was based on the comparison of morphogeneses alternating in the course of sexual and asexual reproduction. The most significant features of ontogenesis in the Haplosclerida compared with those in other representatives of the subclass Ceractinomorpha are (1) the alternating of sexual and asexual (of a gemmulogenesis type) reproduction in the life cycle; (2) the presence of specialized nurse cells in oogenesis and gemmulogenesis; the accumulation of yolk-type inclusions takes place at the expense of these cells; (3) the formation of yolk granules not only during oogenesis, but also in the period of cleavage; (4) sclerocytes that produce larval spicules turn the first differentiated cells of the embryo; (5) the developed larva of haploscleridans is a parenchymula showing a great degree of cytodifferentiation and the presence of both provisory (a flagellated cortical layer, a skeleton, and a spacious cavity lined with pinacocytes) and definitive (choanocyte chambers) organs; and (6) the leading role in morphogeneses during sexual and asexual reproduction is played by nucleolate amebocytes with basophilic cytoplasm (archaeocytes). These are the source of oogonia, gemmules, and nurse cells. They also play an important role in restorative morphogeneses. All these specific features allow ontogenesis in the representatives of the order Haplosclerida to be considered as a particular type of development within the subclass Ceractinomorpha, class Demospongiae.

Despite the more than hundred-year-long history of studies on the embryonal development and life cycles of sponges, their comparative evolutionary embryology is still not developed. A few surveys and monographs on poriferans also comprising chapters on comparative anatomy provide morphological descriptions of different stages in embryonal and postembryonic development within the limits of a certain taxonomic group, this, as a rule, being a class or subclass [5, 12, 25, 29, 37, 42, 59]. In some works, all known descriptions of a certain period of ontogenesis have been compared throughout the phylum Porifera: gametogenesis [17, 28, 53], larval structure and development [6, 29, 66], and asexual reproduction [30, 38]. These papers provide general ideas about the diversity of certain morphogeneses in different species of sponges. However, these approaches seem to unsufficiently provide insight into not only the specific features of the organization and biology of sponges, but their evolution as well. A search for new ideas on the evolution of ontogenesis is required, as well as comparative analyses of complete life cycles.

The first attempt to typify reproductive processes in sponges based on analysis of associated variability of morphogenetic processes that take place during sexual and asexual reproduction within the life cycle was undertaken by Korotkova [39]. The author demonstrated a correlation between the structure of the colony, the degree of complexity of the water circulation system in definitive sponges, the presence of a certain form of agamic reproduction, and the pattern of sexual reproduction. Altogether, Korotkova distinguished seven types of sexual reproduction: four in the class Calcarea (the developmental types "Clathrina," "Leucosolenia," "heterocoelic sponges," and "Petrobiona") and three in the class Demospongiae ("Oscarella," "Axinella," and "oviparous demospongians"). Moreover, in the demospongians, each type of development was characteristic of sponges belonging to a specific subclass.

Since the publication of Korotkova's paper (1981), numerous studies on the embryology of sponges have appeared, significantly contributing to our knowledge on the comparative embryology of these animals. New data on the peculiarities of sexual and asexual reproduction in the representatives of the subclass Ceractinomorpha (class Demospongiae) considered by Borojevic as characteristic of a new phylum (under the same name) [7] and described by Korotkova [39] as an "Axinella" pattern of development provide evidences that there are at least two different types of development in these sponges. These two types are characteristic of the sponges of the order Haplosclerida and all other ceractinomorphic sponges, respectively. The goal of this paper is to justify the notion of the specific developmental pattern of haplosclerid sponges, proceeding from principles of comprehensive analysis of ontogenesis in Porifera.

Morphogenetic processes accompanying the development of haplosclerida in the course of sexual reproduction and blastogenesis. The order Haplosclerida includes both marine and freshwater sponges

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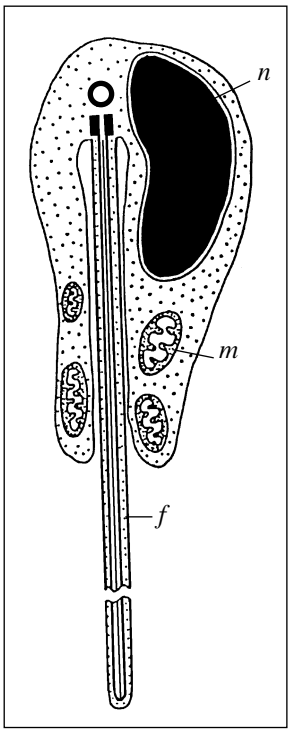

Fig. 1. Scheme of a spermatozoid characteristic of the representatives of the order Haplosclerida: *f*, flagellum; *m*, mitochondrion; *n*, nucleus.

[5, 43]. They differ in shape and body size. The sponges are usually multioscular; the irrigation system is of a leuconoid type. The skeleton is reticular, with 3-, 4-, or polyangular cells. There is much spongin, which can form both multispicular and aspicular cords. The megascleres are represented only by oxeas or strongyles; the microscleres, if present, are in the shape of sigmas or arcs. There is no topography-dependent differentiation of the spicules. Different forms of hermaphroditism are registered in the haploscleridans [58]. The alteration of sexual reproduction and blastogenesis (occurring according the pattern of gemmulogenesis) is characteristic of many marine and most of the freshwater representatives of this order [30]. It is important to note that, within the subclass Ceractinomorpha, gemmulogenesis is found only in Haplosclerida.

Gametogenesis is initiated in sponges after a period of growth following the germination of a gemmule or metamorphosis of larva. As in all sponges, the gonads in haploscleridans are absent.

Spermatogenesis. The processes of spermatogenesis in Haplosclerida follow the same general pattern as in Demospongiae [17, 53]. The development of male gametes takes place within spermatocysts, made up of aggregations of cell groups enclosed in a one-layer capsule of flattened pinacocyte-like cells [48, 62, 64]. The spermatocysts are scattered in choanosome, often in the basal portion of the latter. These are provisional structures that are developed only in the period of spermatogenesis. Their size and number may vary at the individual or population level. The development within a certain spermatocyst is usually synchronous, although in neighboring cysts the gametes may show different stages of spermatogenesis. The source of spermatogonia in freshwater Haplosclerida (no marine representatives have been examined), as in all demospongians, is choanocytes of flagellated chambers [20, 48, 49, 64, 67]. The mature spermatozoa are primitive. They have a great amount of cytoplasm and numerous small mitochondria, and the acrosoma is absent.

The spermatozoa of freshwater Haplosclerida (families Lubomirskiidae and Spongillidae) share a common ultrastructural pattern [62] that is different from other demospongians. Characteristic features of these animals are the location of the basal portion of the flagellum in a narrow canal-like invagination of the cell surface, the arrangement of mitochondria around this canal, and the location of the nucleus and short kinetosoma of the flagellum in the proximal portion of the sperm cell [20, 48, 49, 64, 67] (Fig. 1).

Spermatogenesis is completed by anastomosis of the spermatocysts and excurrent canals; the mature spermatozoa are released into the lumen of the latter. Together with water, they are evacuated from the sponge via osculum. The processes of fertilization in the haploscleridans have never been observed.

Oogenesis. The supposed source of female gametes in the haplosclerid sponges is either nucleolate amebocytes with basophilic cytoplasm (archaeocytes) or choanocytes. In any case, the oogonia or early oocytes pass through an amoeboid stage. The archaeocyte origin of the oogonia has been described in freshwater sponges of the family Spongillidae and Potamolepidae (*Spongilla lacustris*, *Ephydatia fluviatilis*, and *Potamolepis stendelli* [8, 9, 41, 44, 56, 57, 67]) and also in marine sponges of the family Renieridae (*Reniera elegans* and *R. simulans* [65]). In Baikal sponges of the family Lubomirskiidae (*Lubomirskia baikalensis*, *Baikalospongia bacillifera* and *Swartschewskia papyracea*), a choanocyte origin of the oocytes is assumed [3].

The appearance of specialized "nurse cells" as early as in the period of early oogenesis can be considered to be a characteristic feature of oogenesis in haploscleridans. Some mesohyl nucleolate amebocytes significantly increase in size and large phagosomes, a great number of granules, lipid inclusions, and free ribosomes appear in their cytoplasm: however, rough endoplasmic reticulum (RER) is absent. These cells increase in number and are concentrated around the developing oocytes [3, 8, 9, 14, 16, 21, 24, 34, 41, 47, 56, 57, 61, 67]. They are often called nurse cells or trophocytes [28, 59, 67], which is not correct, because, in embryology, trophocytes are generally considered to be cells developing from oogonia in the course of oogenesis. Oocytes and trophocytes are usually interconnected by bridges of cytoplasm and surrounded by follicular epithelium, which has never been mentioned for sponges [1]. Here and below, we consider nurse cells to be

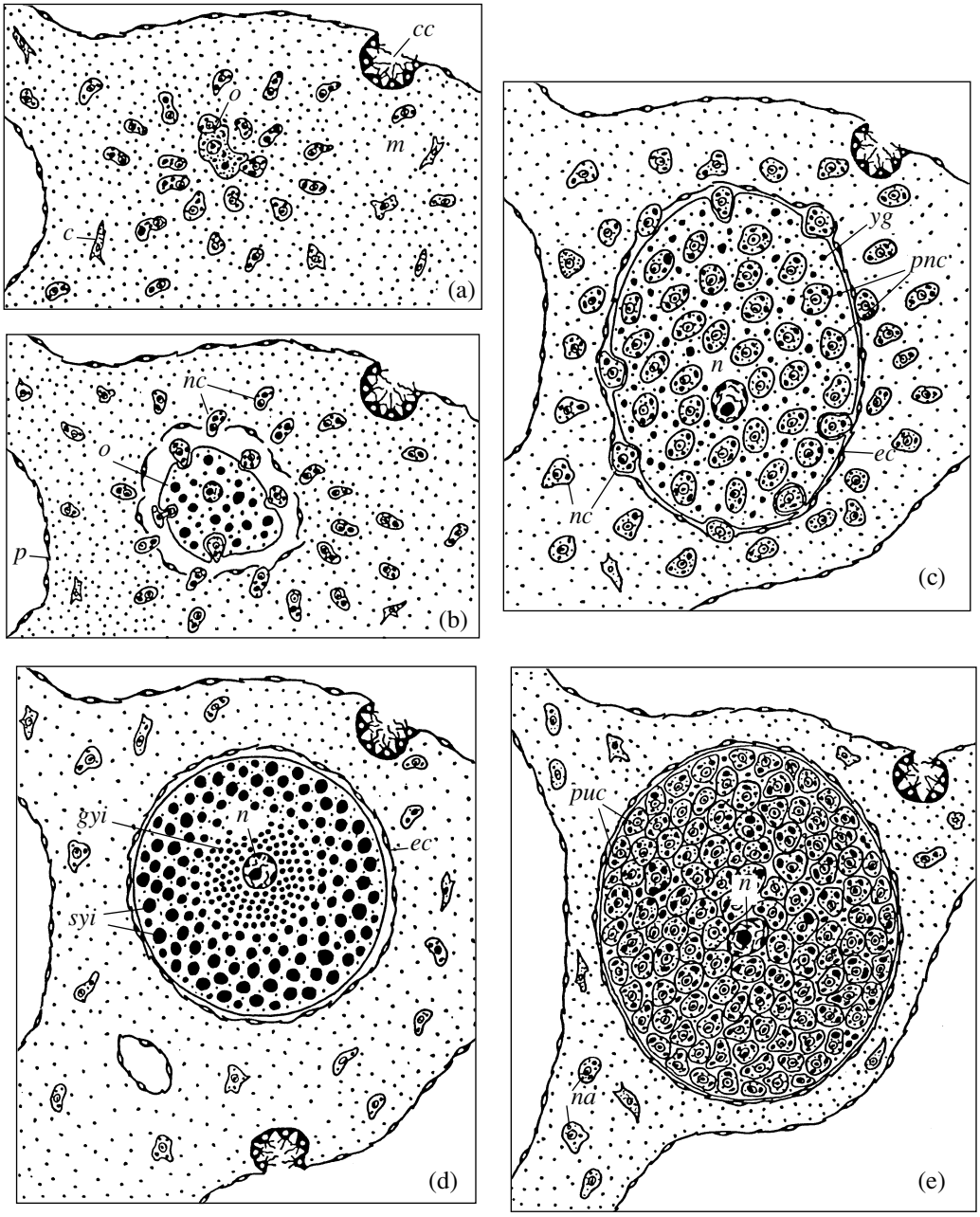

Fig. 2. Generalized scheme of oogenesis in freshwater and marine Haplosclerida. (a) Period of cytoplasmic growth; (b) beginning of vitellogenesis; (c) vitellogenesis; (d) mature egg of freshwater Haplosclerida; *gyi*, granular yolk inclusions; *yg*, yolk granules; *c*, collencyte; *m*, mesohyl; *o*, oocyte; *p*, pinacocyte; *ns*, "nurse cell"; *syi*, spherular yolk inclusions; *pnc*, phagocyted nurse cell; *cc*, choanocyte chamber; *ec*, embryonal capsule; *n*, nucleus; *na*, nucleolate amoebocyte.

somatic cells that serve as a source of yolk-type inclusions during oogenesis and gemmulogenesis. The presence of the nurse cells is evidence of the greater specialization of oogenesis in the Haplosclerida compared with that in the representatives of other demospongian orders.

A previtellogenic oocyte shows amoeboid motility, actively moving within the mesohyl, phagocyting nurse cells or their fragments by broad lobopodia and, therefore, rapidly increasing in size (Fig. 2a). In Haplosclerida, only the phagocytosis of whole nurse cells by an oocyte has been described. No other types of relations between the oocyte and nurse cells known for the representatives of other demospongian orders have been registered in haploscleridans. At this stage, besides the exogenous input of nutrients into the oocyte, there is active endogenous synthesis inside the latter, which is evidenced by the presence in the cytoplasm of oocytes

with a large amount of RER and well-developed Golgi apparatuses [3, 16, 56, 57].

Prior to the beginning of vitellogenesis, the oocyte stops close to an excurrent canal of the irrigation system, in the middle or basal portion of the choanosome. There, it is surrounded by a layer of flattened cells of a pinacocyte or collencyte nature, the so-called embryonal capsule (Fig. 2b). This process has been described in many representatives of the families Spongillidae (*S. lacustris*, *E. fluviatilis*, *E. muelleri*, *Eunapius fragilis*, and *Radiospongilla cerebellata*), Potamolepidae (*P. stendelli*, and *Malawispongia echinata*), Haliclonidae (*Haliclona ecbasis*, *H. loosanoffi*, *H. permolis*, *H. aqueductus*, *H. gracilis*, *Chalinula* sp., and *Gellius angulatus*), and Lubomirskiidae (*L. baikalensis*, *B. bacillifera*, and *S. papyracea*) [3, 8, 9, 12, 16, 21, 24, 25, 28, 34, 47, 56, 57, 67]. The number of nurse cells gradually increases; they penetrate under the embryonal capsule and into the cytoplasm of the oocyte.

In some haploscleridans, nurse cells entering the cytoplasm of the oocyte undergo almost no cytolysis (Fig. 2b). For example, in *H. ecbasis* and *H. loosanoffi*, only the nuclei of the nurse cells ingested by the oocyte degenerate: their cytoplasm shows almost no changes [24, 25, 27]. In *G. angulatus*, the plasma membranes of the ingested cells are disintegrated and their cytoplasm is transformed into large (up to 62 μm in diameter) granules, whereas the nuclei of these cells, with nucleoli inside, remain almost unchanged in the granules for a long time [21]. We observed similar processes in *H. aqueductus* and *H. gracilis*. In *E. fragilis*, the undigested nurse cells might be retraced up to the beginning of cleavage [47].

By the end of vitellogenesis, the egg is filled with either partially digested nurse cells or yolk-type inclusions differing in size and composition. The latter are divided into granular inclusions that occupy the central space around the nucleus and larger, spherical inclusions located on the periphery of the egg [47, 56, 57] (Fig. 2d). By this period of development, only the embryonal capsule remains around the egg [28]. In cases when the nurse cells undergo only weak resorption, the eggs resemble a spherical morula-like mass of cells. Fell [25, 28] proposes that the nurse cells retain active metabolism even within the egg.

As only yolk development is a specific feature of oogenesis in Haplosclerida, the absence or small fraction of typical yolk inclusions in the cytoplasm of the haploscleridan oocyte might be considered a primitive feature.

Cleavage. Cleavage in haplosclerid sponges, as in all demospongians, is considered to be complete, unequal, and asynchronous [12, 25, 29, 39, 59]. In some African freshwater sponges (*P. stendelli* and *M. echinata*) and in Baikal sponges, the cleavage is equal [9, 13, 54]. However, until now, nobody has been able to definitely describe early cleavage. This process in the haploscleridans is difficult to examine due to the dense aggregation of large, yolk-type inclusions or nurse cells at different stages of utilization in the cytoplasm of the eggs and blastomeres. These inclusions conceal dividing nuclei and the margins of the blastomeres (Fig. 3). For example, the embryo of *H. ecbasis* shows no morphological differences from the mature egg at early stages of cleavage [24]. The nuclei of the cleavage stage become visible in this species only when their number reaches 15–20. The cell margins are clearly noticeable in the morula, consisting of about 1000 cells [24]. In *G. angulatus*, the nuclei of the cleavage stage become visible after three or four divisions and are located between large yolk granules. They differ from the undigested nuclei of nurse cells by their larger diameter [21]. According to our data, in *H. aqueductus*, the nuclei of cleavage and the margins between the blastomeres become visible only at the morula stage.

The period of early egg cleavage in *E. fluviatilis* is also not accompanied by any visible cytotomy. The nucleus of the egg undergoes one or two divisions in the central portion of the cell, giving rise to several nuclei of the same size surrounded by small granular inclusions (Fig. 3a) [14, 56]. This is followed by cytotomy. The blastomeres developed are of different sizes [56, 67]. Two- and four-nucleus stages of cleavage preceding cytotomy have also been registered in *S. lacustris* [57]. At the same time, in *S. papyracea*, cleavage is complete from the very beginning and the blastomeres show clearly pronounced margins [54].

Cleavage is completed by development of the morula (Fig. 3c). The active utilization of the fragments of the nurse cells and the formation of yolk granules both begin to occur in this period. At the same stage, the first signs of cytodifferentiation are revealed (Fig. 3d).

The morula stage in the sponges seems to be the last one that might have been homologous to a certain stage in the embryogenesis of other multicellular animals. Instead of arising from primordial layers, there is a process of differentiation of provisory larval structures. The first differentiated cells in the embryos of many haploscleridans are sclerocytes, the cells that synthesize larval spicules. This process is initiated immediately after the beginning of the process of utilization of the fragments of nurse cells or yolk granules by the cells of the morula [8, 9, 10, 12, 14, 24, 46, 56]. The first spicules are located in either the peripheral parts of the embryo (*Adocia cinerea* and *H. ecbasis*) or in its central part (*E. fluviatilis* and *S. lacustris*), or they are scattered throughout the embryo (*P. stendelli* and *Corvospongilla thysi*). The surface cells of the embryo are progressively reduced in size and lose yolk inclusions; the nucleolus in the nucleus disappears. After a series of divisions, these cells differentiate into the provisory layer of flagellated cells of the larva (Fig. 3e).

Parenchymula. A larva, the parenchymula, which differs from the parenchymulas of all other ceractinomorphs, develops in all haploscleridans. First of all, it is important to mention the presence of a voluminous

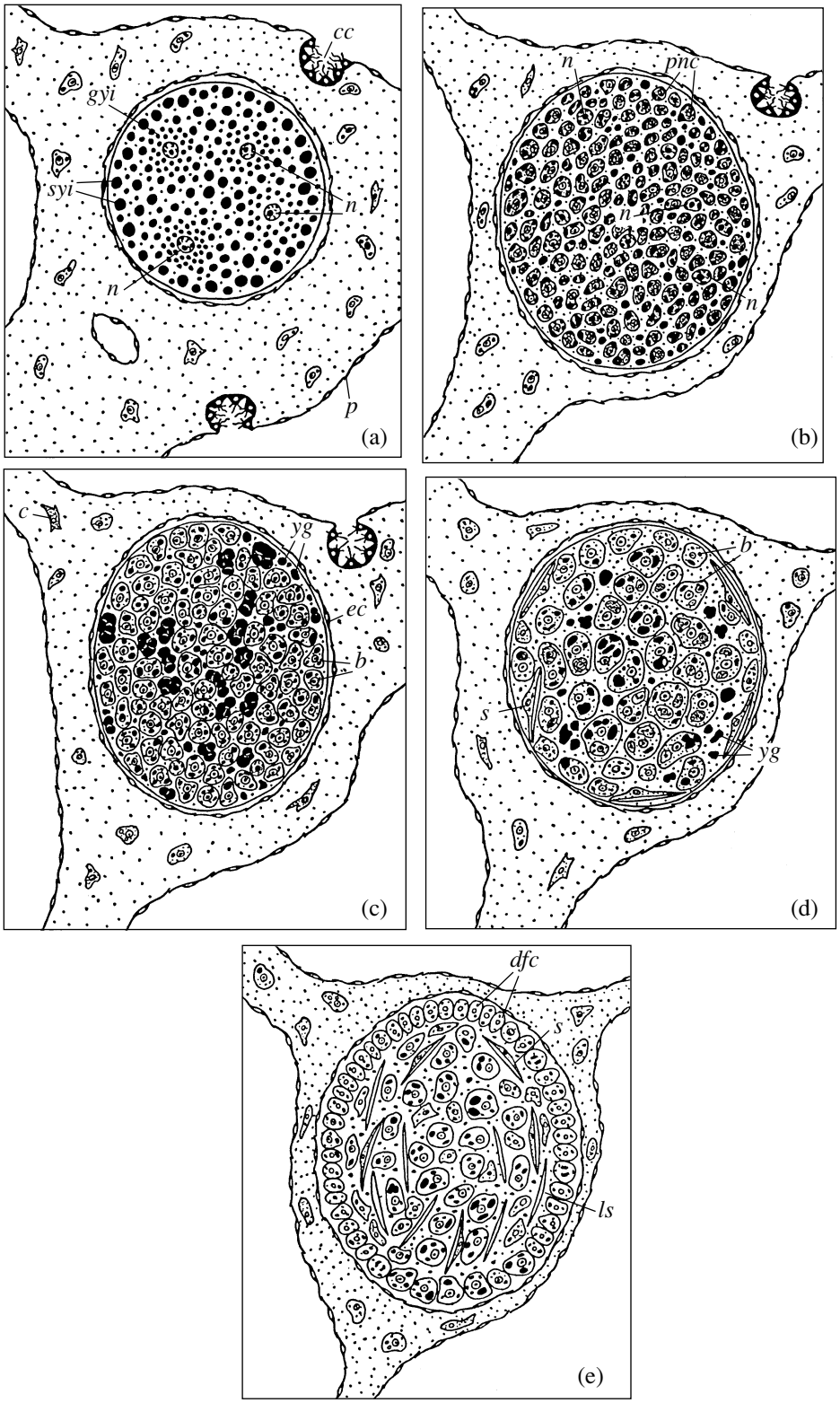

Fig. 3. Scheme of embryonal development in freshwater and marine Haplosclerida. (a) Early cleavage of freshwater Haplosclerida of the family Spongillidae; (b) cleavage of marine Haplosclerida; (c) morula stage; (d) beginning of cytodifferentiation of the embryo: development of larval sclerocytes; (e) beginning of differentiation of flagellated cells. *b*, Blastomeres; *gyi*, granular yolk inclusions; *dfc*, differentiating flagellated cells; *yg*, yolk granules; *c*, collencyte; *ls*, larval spicules; *p*, pinacocyte; *syi*, spherular yolk inclusions; *s*, scleroblast; *pnc*, phagocyted nurse cell; *cc*, choanocyte chamber; *ec*, embryonal capsule; *n*, nucleus.

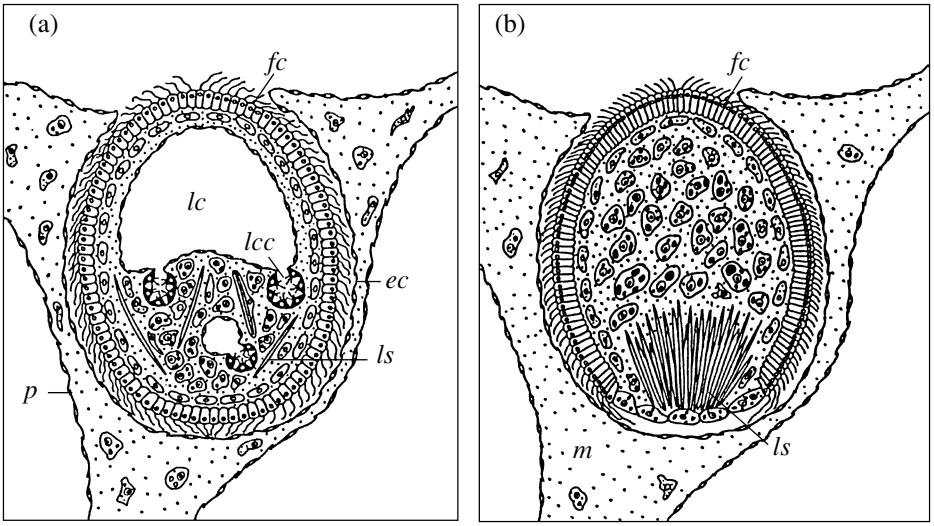

Fig. 4. Larvae of Haplosclerida prior to hatching from the parental organism. (a) Larva of freshwater Haplosclerida; (b) larva of marine Haplosclerida; *fc*, flagellated cells; *lc*, larval cavity; *ls*, larval spicules; *lcc*, larval choanocyte chamber; *m*, mesohyl; *p*, pinacocyte; *ec*, embryonal capsule.

cavity lined with larval pinacoderm in the anterior part of the larva and also the presence of larval choanocyte chambers. These larval structures are primarily characteristic of the freshwater sponges of the families Spongillidae (*E. fragilis, C. thysi*, *Ochridaspongia rotunda, S. lacustris, E. fluviatilis, E. muelleri, R. cerebellata, S. moorei, P. stendelli*, and *M. echinata* [11–14, 32, 33, 35, 47, 56, 57, 63]) and Lubomirskiidae (*L. baikalensis, B. bacillifera*, and *S. papyracea* [2, 16, 18]) (Fig. 4a). Larval choanocyte chambers have been found only in two species of marine haploscleridans: *Haliclona limbata* and *Chalinura* sp. [34, 45]. In the larva of African freshwater sponges of the family Potamolepidae, no cavities or choanocyte chamber arise [8, 9, 11].

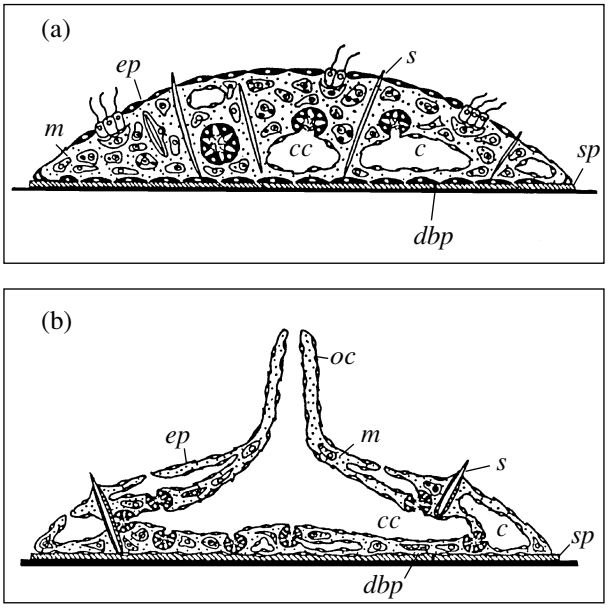

Fig. 5. Metamorphosis of Haplosclerida. (a) Metamorphosing larva, an early stage; (b) rhagon stage; *dbp*, developing basopinacoderm; *c*, canals of water circulation system; *m*, mesohyl; *os*, osculum; *s*, spicules; *sp*, basal spongin layer; *cc*, choanocyte chamber; *ep*, exopinacoderm.

The following features are characteristic of the larvae of marine haploscleridans: the absence of flagellated cells in the posterior pole, which is fringed by a circle of cells with longer flagella; the presence of a skeleton representing a dense bundle of oxeas located in the posterior portion of the larva (freshwater larvae have a fan-shaped skeleton); and the concentration of pigment in the cells of the posterior pole devoid of flagellum (Fig. 4). These characters have diagnostic value in the systematics of sponges [6, 31, 59, 66, 68].

Metamorphosis. The metamorphosis of the larvae is rather fast and is often accompanied by partial or total elimination of provisory flagellated cells via phagocytosis of the latter by underlying collencytes or amebocytes (Fig. 5a). Later on, the latter cells give rise to exopinacocytes. The larval choanocyte chambers continue to function, and the definitive choanocytes arise by means of division of the larval archaeocytes that make up aggregations of choanoblasts, which then become choanocytes. New populations of sclerocytes synthesize definitive spicules. The remaining definitive cells are differentiated from the larval archaeocytes [14, 16, 18, 19, 33, 67]. However, in *H. permolis* and in some Spongillidae, partial formation of choanocytes at the expense of transformation of larval flagellated cells in the course of metamorphosis has been recorded [4, 36]. Metamorphosis is completed by formation of a united irrigation system; after this, the sponge just

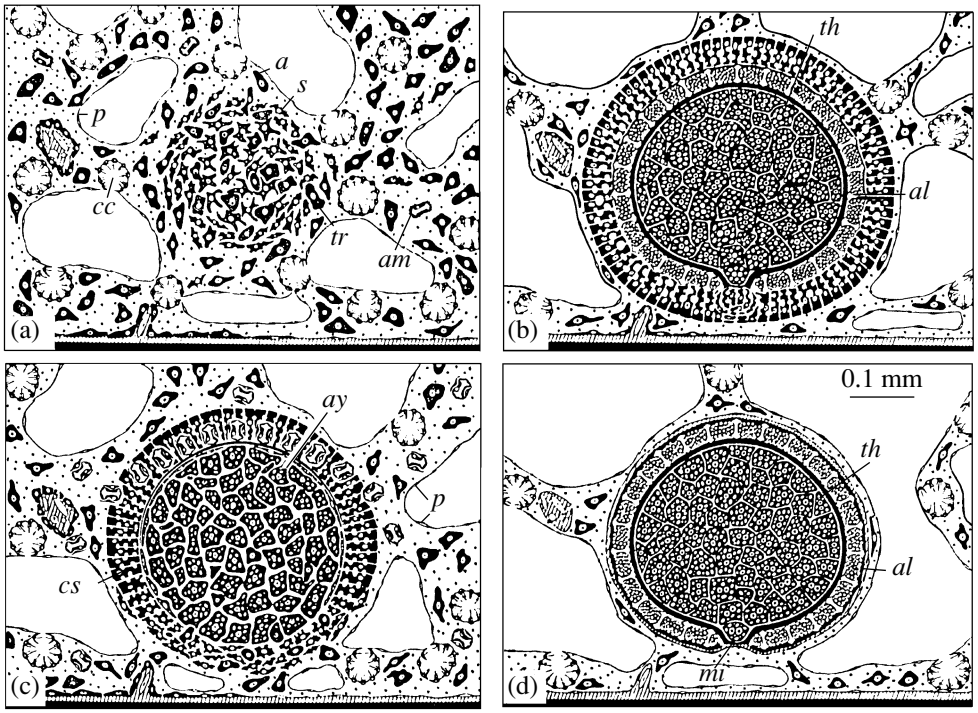

Fig. 6. Scheme of gemmulogenesis of freshwater Haplosclerida (according to Langenbruch [40]). (a) Beginning of gemmulogenesis; (b) beginning of gemmule-envelope formation; (c) formation of alveolar layer, micropyle, and differentiation of thesocytes; (d) fully developed gemmule; *a*, archaeocytes; *ay,* archaeocytes with yolk plates; *am*, amphidiscoblast with a young amphidisc; *al*, alveolar layer; *mi*, micropyle; *p*, pinacocytes; *s*, spongocytes; *cs*, columnar layer of spongocytes; *th*, thesocytes; *tr*, trophocytes; *cc*, choanocyte chamber.

grows and new modules of the irrigation system arise within the body of the animal (Fig. 5b).

Gemmulogenesis. Gemmulogenesis usually begins after the completion of sexual reproduction or during the period of embryogenesis. The development of gemmules was best studied in freshwater Spongillidae, where it comprises a series of stages (Fig. 6). Gemmulogenesis begins with movements of gemmular nurse cells, archaeocytes, and spongocytes, particularly towards certain areas within the mesohyl (Fig. 6a). Here, the cells make up dense aggregations 250–500 μm in diameter. These three types of cells might be considered to have the following common features: a large (about 6 μm) nucleus with a nucleolus; numerous Golgi complexes; and ribosomes, mitochondria, and cytoplasmic inclusions of different sizes [15, 59]. Within the aggregations, the archaeocytes actively phagocyte the nurse cells accumulating in their cytoplasm, which is characteristic of the yolk plates of these cells [15, 60]. In the course of yolk-plate development, two layers arise around the cell aggregations: an inner one consisting of flattened archaeocytes and an outer one composed of flattened spongocytes, which make up a columnar layer. During the formation of the latter, the microsclerocytes of the mesohyl bearing developed microsclerae (amphidiscs or rhabds) migrate toward the developing gemmule to be incorporated into its columnar layer (Fig. 6b).

The process of gemmule-envelope formation begins at one pole and gradually extends toward the opposite pole, where, later on, a micropile arises, an area of the envelope devoid of spicules [40] (Fig. 6c). A developed gemmule consists of a dense three-layered envelope and an inner homogeneous mass of cells, the thesocytes (Fig. 6d) [15, 40, 59, 67]. These cells are characterized by the presence of a large number of yolk plates (in freshwater sponges) or yolk granules (in marine species). The thesocytes of spongillids each have two nuclei, whereas, in marine haplosclerids, these cells are mononuclear [12, 25, 59]. In general, it is important to note that the processes of gemmulogenesis are very similar in marine and freshwater haplosclerids. In both cases, blastogenesis is accompanied by either significant or total disorganization of the water circulation system and the mesohyl of the parental sponge.

Similarities between certain stages of gemmulogenesis and oogenesis have been repeatedly mentioned by various scientists. For example, both the gemmules and female gametes (in species that have both types of reproduction in the life cycle) develop from nucleolate amebocytes (archaeocytes) [14, 41, 44, 56, 57, 59], whereas, in Lubomirskiidae, which do not have asexual reproduction, a choanocyte origin of the oogonia is assumed [3]. The pattern of development of the yolk-type inclusions is also similar during the vitellogenesis of oocytes and during gemmulogenesis in both marine

and freshwater sponges. In both cases, there is phagocytosis of whole nurse cells or their parts [15, 59]. In *S lacustris, E. fluviatilis, E. muelleri*, and other species, gemmulogenesis may begin even prior to the completion of sexual reproduction, which is also evidence that the same nurse cells are involved in both these processes [47, 56, 57]. It is assumed that the movement of nurse cells toward the center of gemmulogenesis is performed by means of chemotaxis [52, 55, 59]. In the course of oogenesis, the nurse cells also show chemotaxis to chemical substances bound to the oocyte membrane [28]. In several species of spongillids, both multinuclear blastomeres and multinuclear thesocytes have been described, which, in the opinion of the authors, cannot be mere coincidence [40, 56, 57].

A correlation between the spatial location of embryogenesis and gemmulogenesis might be revealed in the development of different haplosclerid sponges. For example, in gemmulogeneous species, the processes of embryogenesis and gemmulogenesis are concentrated in the basal portion of the choanosome, and, during sexual reproduction, only a local disintegration of parental organism tissues takes place. This is characteristic of both marine (*H. permolis, H. ecbasis, H. loosanoffi*, and *H. occulta*) [22, 24, 26] and freshwater sponges of the families Spongillidae and Potamolepidae [11, 12, 14, 59, 67]. In life cycles in which the gemmulogenesis is either absent or reduced, the spatial distribution of reproductive elements in organisms of marine and freshwater (perennial) sponges is prone to variation and is dependent on the ecological circumstances and reproductive strategy of the population [23, 31].

CONCLUSION

The major goal of comparative embryology is to investigate the rules of the evolution of ontogenesis in different groups of animals. As the reproductive cycle is an essential component of the life cycle of every organism, the evolution of organisms is impossible without mutually dependent transformations of different morphogeneses that either replace each other or take place simultaneously in the course of ontogenesis. Thus, to understand changes in one or another stage of sexual or asexual reproduction, it is necessary to analyze the whole life cycle of the sponge.

Our comparative analysis of the morphogenetic processes accompanying sexual and asexual reproduction in the life cycles of one order of sponges revealed correlations between their transformations in the course of evolution. On the other hand, comparison of ontogeneses in different groups of sponges within the subclass Ceractinomorpha (class Demospongiae) resulted in the discovery of a series of significant peculiarities that differentiate the latter from the other representatives of this subclass in the ontogenesis of the representatives of the order Haplosclerida.

The normal alteration of sexual and asexual reproduction (according the type of gemmulogenesis) in the life cycle of many marine and freshwater sponges may be considered to be the most significant peculiarity of ontogenesis in the Haplosclerida. Other developmental peculiarities of the haplosclerids are as follows: (1) The leading role in morphogeneses during sexual and asexual reproduction is played by nucleolate amebocytes with basophilic cytoplasm (archaeocytes). These are a source of oogonia, gemmules, and nurse cells and also play an important role in restorative morphogeneses. (2) The accumulation of yolk-type inclusions takes place primarily as a result of the phagocytosis of specialized nurse cells by the oocyte during oogenesis or by archaeocytes during gemmulogenesis. At the stage of late vitellogenesis, the egg resembles the gemmule in the period of envelope development, which is due to insignificant utilization of the phagocyted nurse cells. (3) The process of formation of yolk granules can take place not only in oogenesis, but also during the period of cleavage. (4) Early cleavage may be incomplete in marine representatives of the order and in freshwater sponges of the family Spongillidae. (5) Within the homogeneous morula, differentiation of sclerocytes, which synthesize larval spicules, begins early. Later on, after a series of divisions in the covering cells, the differentiation of a provisory flagellated layer takes place. (6) The developed haploscleridan larva is a parenchymula with a high degree of cytodifferentiation and the presence of provisory (a flagellated cortical layer, a skeleton, and a voluminous cavity lined with pinacocytes) and definitive (choanocyte chambers) organs. All of the above-listed peculiarities of ontogenesis allow us to define the ontogenesis of sponges in the order Haplosclerida as a particular type within the class Demospongiae.

Representatives of the order Haplosclerida are distributed worldwide; they inhabit not only all waters of the World Ocean, but also freshwater basins of all continents. Moreover, the haplosclerid sponges most often inhabit the most unstable habitats, such as brackish-water lagoons, estuaries, and freshwater bodies that dry up in tropical and subtropical regions or freeze in the winter at low temperatures and high latitudes. To penetrate such habitats, sponges had to develop mechanisms to protect their populations against extinction during unfavorable periods. One such adaptation is gemmulogenesis, because the gemmules of haploscleridans are capable of surviving drying, freezing, and the effects of other physicochemical factors for long periods of time [59, 67]. One of the adaptations of freshwater Haplosclerida (family Spongillidae) is the possibility of excluding gametogenesis from the life cycles of populations inhabiting ecologically unstable conditions [51], while at the same time retaining the potential capability to restore sexual reproduction if necessary.

It is assumed that it was the inclusion of gemmulogenesis into the life cycle of marine shallow-water ancestors of the haplosclerid sponges that favored the

penetration of these animals into intertidal, estuarine, and freshwater environments [51]. Therefore, the life cycle involving alternating sexual and asexual reproduction might be considered typical of sponges of the order Haplosclerida and might also be considered the initial life cycle for the family Spongillidae.

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