Berliner geowiss. Abh.	E **20**	25 - 33	Berlin 1997

The reasons of sponge sexual morphogenesis peculiarities

Alexander V. Ereskovsky & Galina P. Korotkova

Abstract: Sexual morphogenesis in Porifera have been analyzed on the basis of the hypothesis about the ontogenesis evolution as a multilevel and non-linear process (Korotkova, 1979, 1987). Correlative variability of different morphogenesis types in sponges (gametogenesis, embryogenesis, growth processes, blastogenesis, restoration morphogenesis etc.) is caused by a nonuniform reaction of different stages of one and the same morphogenesis as well as of the coexisting in time different morphogenesis to the stimuli of the same type. To understand the reasons of the changes in a gametogenesis pattern and relationships of gametocytes with somatic cells the whole life cycle and the somatic morphogenesis' pattern has been analyzed. Special attention has been paid to participation in the latter of somatic cells with the polypotention features, and to the capability of some somatic cells of direct transformations into other cell types. Criteria for primitivity or advancement of sexual and somatic morphogenesis within the type Porifera have been evaluated. It has been shown that the more anatomic, tissue and cellular systems appear in sponges and the more differentiated they are, the higher is probability of relatively more stable reproduction in these sponges and of the appearance of specialized blastogenesis and sexual embryogenesis in their ontogenesis. The peculiarity of sexual morphogenesis in sponges is connected not so much with their peculiar position in the system of animals, but with the preservation of low level of cell, tissue and anatomic systems' specialization and differentiation, low level of individuality and specialization of morphogenetic processes.

Keywords: Porifera, sexual morphogenesis, somatic morphogenesis, embryogenesis, evolution of ontogenesis.

Address of the authors: Dr. Alexander V. Ereskovsky & Prof. Galina P. Korotkova, Biology Faculty, Sanct-Petersburg State University, Universitetskaya nab. 7/9, Sanct-Petersburg, 199034, RUSSIA. Fax: +7 (812) 218-0852.

1. Introduction

The peculiarities of sponge embryonic development are intimately correlated with the specificity of sponge somatic body organization and functioning (underdeveloped histo- and organogenesis, filtration type of feeding and respiration), with the great adaptive abilities of their morphogenesis (life cycle structure alteration based either on the appearance of a new reproductive type or on exclusion of the old one) and with other features of their biology. Our notion of sponge sexual embryogenetic peculiarity causes are based on the hypothesis of ontogenetic phase evolution (Korotkova, 1979, 1987, 1991). The main theses of this hypothesis are following. Ontogenetic evolution is a multilevel and non-linear (non-superstructural) process. It is based on the correlative variability of sexual and somatic morphogeneses and on the conception of individuality, as of an open spatial-temporal system. Adaptive ontogenetic variability is realized by the integrative mechanisms existing at all structural levels of organization (from genome, cell and organism to population and coenosis). Correlative variability of different morphogenetic types (gametogenesis, embryogenesis, growth processes, blastogenesis, restorational morphogeneses, and others) result of non-monotypical reaction of the certain morphogenesis different stages as well as of the different morphogeneses mentioned above, coexisting in time to the monotypical stimulus arising from the integrative systems (Korotkova, 1987, 1988).

2. The main facts and discussion

Firstly, we shall discuss the examples of sexual and somatic morphogenetic interdependent variability in the same sponge species, adapted to different ecological conditions.

For instance, the various intensity of gametogenesis and larvae formation is observed in the life cycle of *Halichondria panicea* (Demospongiae, Halichondriida) depending on the environmental conditions. The various degree of the maternal sponge body degradation starting after larvae release appears to be also correlated with the environment. We shall describe the life cycle of *H. panicea* populations inhabiting the tidal zone of the Barents Sea and the shoals of the White and Baltic Seas (Ivanova, 1978, 1981; Barthel, 1986; White & Barthel, 1994; Ereskovsky, unpubl.). After intensive gametogenesis and larvae formation, the sponge mesohyl transforms to the "gonad" almost and is filled with cameras containing larvae. This period of the life cycle is characterized by the intensive expediting of somatic cells to the production of yolk inclusions in oocytes and to the formation of capsules around oocytes at first and, later, larvae These processes

take place at the end of hydrological summer and are completed with body degradation of the maternal sponges often accompanied with their fragmentation. Small fragments formed from the maternal adult look like residual bodies. Junior sponges developed from larvae as well as the adults restored from the fragments start growing during hydrological spring.

This process is finished to the new reproductive cycle. So, the life cycle of *H. panicea* populations, inhabiting high latitude sea shoals consists of 4 stages: 1) gametogenesis and embryogenesis, followed by larvae release from the maternal sponge; 2) free larvae, metamorphosis and junior sponge development; 3) postreproductive restorational morphogenesis of the maternal sponge or its fragments; 4) growth, preceding intensive gametogenesis. The second and the third life cycle stages proceed at the same time but in different adults of the population.

Different life cycle structure can be observed in *H. panicea* populations living under milder climatic conditions of the North Sea (south-western shoals of the Netherlands) and the circumlittoral zone of the White Sea (10-18 m) (Vethaak et al.,1982; Wapstra & Van Soest, 1987; Ereskovsky, unpubl.). Gametogenesis and larvae formation in these sponges is not so intensive. That is why the maternal sponge tissues undergo only local changes (closely of the source embryos). As a result, the sponges function normally during the reproductive period and avoid great destructive transformations after spawning.

The life cycles of these *H. panicea* populations consists of 3 stages (gametogenesis and embryogenesis; larvae life and metamorphosis; growth). There are no postreproductive restorational morphogenesis of the maternal sponges, which is typical of *H. panicea* inhabiting the tidal zone of the Barents Sea and the shoals of the White and Baltic Seas.

An analogous adaptive life cycle variability is observed in freshwater cosmopolitan sponge *Ephydatia fluviatilis* (Demospongiae, Haplosclerida). The most complicated structure of its life cycle consists of the following stages: 1) gemmule germination, growth and formation of junior sponges; 2) gametogenesis and embryogenesis; 3) free larvae, metamorphosis and junior sponge development; 4) gemmulation and maternal sponge degradation; 5) survival the stress conditions as gemmules or residual bodies.

Such a life cycle structure is considered typical of *E. fluviatilis* and other Spongillidae by some authors (Pronzato & Manconi, 1994). The life cycle of *E. fluviatilis* may alter depending on climatic and ecological conditions. For instance, *E. lluviatilis* populations, inhabiting some rivers in the north of Italy where cool and damp climate is stable all the year round are physiologically. active No destructive processes are observed in these sponges. However, few gemmules are constantly formed in the sponges along with inactive and inert proceeding of sexual reproduction. The intensity of gemmulation is high in winter and decreases in autumn. So, the mesohyl of these sponges contains gametes or larvae as well as gemmules all the year round (Corriero et al., 1994).

Another *E. fluviatilis* population inhabits some canals in Sicily where climates are warm and dry; short rain season and high air temperature in summer and autumn causing the canals to be dry. Active gemmulation and tissue atrophy in the sponges during the dry season are observed. That is why the interchanges of all stages stated above takes place in this *E. fluviatilis* life cycle. Gametogenesis and larvae formation go on very fast in spring and in early summer. Gemmulation starts after it (Pronzato & Manconi, 1994; Corriero et al., 1994).

A complete life cycle can also be observed in Belgian population of *E. fluviatilis*. These sponges undergo gemmule formation in autumn and in winter. But their life cycle can be changed under warm winter conditions, when the maternal sponge tissues do not degenerate and gemmules being located at the base of the functioning sponge bodies. Gametogenesis and embryogenesis take place in spring (Van de Vyver & Willenz, 1975).

Therefore, life cycle structure and reproductive tactics can be differ in different populations of the same sponge species depending on stability or instability of external conditions. Sexual and somatic morphogeneses proceeding consequently or parallel in sponge life cycle change independently but correlatively because their realization is equally subjected to internal integrative mechanisms (Simpson & Gilbert 1974; Fell et al. ,1979; Reiswig, 1983; Korotkova, 1988).

Having shown the existence of sexual and somatic morphogenetic correlative variability depending on environmental conditions we shall describe some peculiarities of sponge sexual morphogenesis and life cycle in whole which are not observed in other animals. According to our notions, the sexual morphogenesis of a sponges consists of gametogenesis, embryogenesis and larvae metamorphosis.

It should be remembered that no gonads are formed in sponges. Gametogenesis is usually diffuse. Direct transformation of nucleolar amoebocytes and choanocytes into gonia may be considered a peculiar feature of sponge gametogenesis. The principal stages of this process are similar with those of other animals (Fell, 1983; Reiswig, 1983; Simpson, 1984; Efremova, 1988).

Spermatogenesis of Demospongiae takes place inside temporal spherical formations (so called spermatocystes, separated by flattened cells). Spermatozoids of Calcaronea are solitary (Anakina, 1981; Reiswig, 1983; Simpson, 1984; Anakina & Korotkova, 1989).

Female gametes develop in choanosome diffusely or, sometimes, forming small groups. Such a distribution of oocytes is described in different Demospongiae (see Fell, 1983) as well as

in *Halisarca dujardini* from the Barents and White Seas (Korotkova & Apalkova, 1975; Korotkova & Aiseshtadt, 1976; Ereskovsky, unpubl.), in Spongillidae (Mukai, 1989; Weissenfels, 1989), in viviparous and oviparous huge sponges having low gametogenetic intensity, for instance in Myxillidae of the White Sea from the depth 20-30 m (Efremova et al.,1987), in large Xestospongiae (Fromont, 1994). Sometimes oocytes unite into so-called brood chambers. These formations are located either at the sponge base (in incrusting forms), for instance, in *Chalinula* sp. and *Niphates* sp. of the Red Sea (Ilan & Loya, 1988, 1990), in *Haliclona amboinensis* and *Niphates nitida* from the Big Barrier Reef (Fromont, 1994), or at central part of a branch (in branching forms), for instance, in *Lubomirskia baikalensis* (Efremova, 1981).

No typical vitellogenesis takes place during oogenesis in the most of sponges (Aiseshtadt, 1984). This process is replaced with the phagocytosis of the whole cells or their fragments equally with the oocyte endogenic synthesis. The phagocytized cells are unspecial, ordinary somatic ones (choanocytes, mesohyl cells) (Fell, 1983). But Haplosclerida are characterized by the appearance of the nucleolar amoebocyte peculiar population during vitellogenesis. These cells, filled up with inclusions, migrate to oocytes and are phagocytized by them. This is an evidence of the greater specialization of Haplosclerida oogenesis as compared with other Demosponges. Foregoing nucleolar amoebocytes are often called "trophocyte" or "nurse cells" which is not correct because only the cells developed from oogonium during oogenesis and feeding oocytes are generally called trophocytes in embryology. Oocytes and trophocyte are usually connected by plasmodesmas and surrounded with follicular epithelium, which is not observed in sponges (Aiseshtadt, 1984).

There are some other features of sponge oogenesis and oocyte organisation which should be considered the primitive besides unexpressive processes of typical vitellogenesis. These are the lack of ooplasm segregation (anyway, no reliable data of it), apparently the lack of cytoplasm determinants and consequently the lack of mechanisms determining larvae axes or junior sponge axis in the direct development, and the lack of egg membranes (Brien, 1973; Bergquist, 1978; Korotkova, 1981; Fell, 1983).

Embryogenesis of viviparous sponges takes place in special embryonic capsules, which are formed by the cells of choanocyte origin, for instance, in *H. dujardini*, Calcaronea, or by amoebocytes as in Haplosclerida (Fell, 1983; Simpson, 1984). The flattened cells surrounding an egg or an embryo are not the real follicular ones, as they are called by many authors, because these cells do not form any epithelial layer, have no basal membrane and do not participate in the synthesis of egg covering material but undergo no changes during embryogenesis. The embryonic capsule ultrastructure and their formation type are species-specific.

The primitivity of sponge cleavage is connected low egg specialization for the first place. The cleavage of Demospongiae is asynchronic (Korotkova & Ereskovsky, 1984) and its pattern is not stable (Levi, 1956; Brien, 1973; Korotkova & Ereskovsky, 1984; Saller & Weissenfels, 1985; Saller, 1988). However the cleavage of Calcaronea, having amphiblastula type of larvae, might be ordered and more specialized due to the early function of macromeres (feeding) and to the specific palintomic type of cleavage (Anakina, 1997). The presence of pronucleolar bodies - inactive nucleoli, described as usual nucleoli in literature, in the blastomere nuclei can be considered as an evidence of low cleavage specialization in sponge (Sizova & Ereskovsky, 1997). The penetration of endosymbiontic bacteria from mesohyl into embryos was observed during the cleavage of several species (Kaye, 1991; Sizova & Ereskovsky, 1997). Generally one can said that sponge cleavage possesses the features of Protozoa palintomy, because the blastomere formed during cleavage are polypotent and more or less equivalent.

An unusual feature of Porifera embryogenesis is the active contribution of maternal somatic cells to cleavage as well as to larvae formation, which is another evidence of the low embryogenetic specialization of these primitive animals. In the first case, an embryo gets additional nutrient substances from the embryonic capsule cells or from the feeding cells. Consequently the embryo size increases considerably (Simpson, 1894; Fell, 1089). While larva formatting the penetration of the cells containing eosinophilic inclusions through the embryonic capsule and through the larval epithelium into the developing larvae observed in viviparous demospongies, for instance, in *Microciona prolifera* (Simpson, 1968), *Halisarca nahatensis* (Chen, 1976), *H. dujardini* (Korotkova & Ermolina, 1982), *Iophon piceus* (Ereskovsky, 1986) etc. The penetration of the maternal cells released together with oocytes while spawning into the forming larvae was observed in oviparous Demospongiae, for instance, in *Cliona celata* (Warburton, 1961), *Hemectyon ferox* (Reiswig, 1976), *Chondrosia reniformis* (Levi & Levi, 1976). Finally, during the excurvation of Calcaronea amphiblastula, different somatic cells also penetrate into it - accessory cells in *Leucosolenia botrioides* and *L. complicata* (Tuzet, 1948; Anakina, 1981), amoebocytes with geterogenic inclusions and spherular cells in *Grantia compressa* (Gallissian, 1983), amoeboid microgranular cells in *Scypha ciliata* (Franzen, 1988).

Oviparous sponges of genus *Tetilla* (Tetractinomorpha) have direct development. The stage of cell differentiation and growth of the junior sponge starts just after the end of cleavage (Watanabe, 1978; Watanabe & Masuda, 1990).

Actually, there are no final stages of blastulation and no germinal layer formation (gastrulation) in sponge embryogenesis in contrast to the highly organized animal with sexual morphogenesis consisting of cleavage, blastulation, gastrulation, histogenesis and organogenesis during the development of larval or definite sponge structures. Firstly this is due to the lack of mechanisms of early cell determination in definitive sponge tissues (in the surface tissues and in the internal tissues) and especially to the lack of germ layers as ectoderm and endoderm or their homologues - cell groups determinated to the development of the gut and the coverings because there are no such tissue systems in sponges (Salvini-Plaven & Splechtna, 1979; Rasmont, 1979; Korotkova, 1981 a, b, 1988; Anakina, 1981; Seravin, 1986, 1992; Malachov, 1990). In fact, the differentiation of larval cells (flagellated cells and sclerocytes) starts at the late cleavage stages which are usually called the stage of blastula or morula. Blastomeres transform into larval cells directly, not through the stage of gastrula, which is the stage of the germ layer (ectoderm and endoderm) formation in high organized animal embryogenesis. Specialized larval cells (cover cells, skeletogenous cells etc.) have different cell fates, but these fates are not connected with germinal layers. The cleavage in sponge transforms imperceptibly into the differentiation either of larval tissue systems (development with larvae) or into definitive tissues (direct development).

The next stage of sexual morphogenesis is postembryogenesis. It consists of larvae release (in the case of viviparity), metamorphosis and formation of junior sponge with functioning canal system.

There are four main larvae types described in sponges - coeloblastula, amphiblastula and parenchymula. The structure of coeloblastula is the simplest. It has monolayer flagellated covering and spacious internal cavity, filled either with liquid unstructural substance or with solitary somatic cells of the maternal origin. The larval epithelium can contain large aflagellated cells. Coeloblastula is described in some calcisponges of subclass Calcinea and in some demosponges of subclass Homoscleromorpha (viviparous) and Tetractinomorpha (oviparous).

The structure of amphiblastula is more complicated. It has one layer of cells. Its anterior hemisphere consists of small flagellated cells and the posterior one is formed by large aflagellated cells with granular cytoplasm. Four large cells containing light-refracting body in the cytoplasm form the so-called "cross" at the equatorial region. The amphiblastula has a small internal cavity containing different maternal cells and symbiotic bacteria and having no differentiated larval cells and spicules. Amphiblastula develops inside the maternal body. This larvae type is described in some sponges of Calcaronea and Pharetronida.

Parenchimula is characterized with the most complicated structure which varies greatly within species. Such a larvae has mono- or multilayer flagellated epithelium consisting of the greatly elongated, polarized monoflagellated cells and covering the whole larvae surface or the major part of it. The larval cavity is filled with in larval own cells differentiating to collencytes, sclerocytes and sometimes to choanoblasts (in Haplosclerida) and larval spicules. Parenchimula develops inside a maternal adult and leaves it at various stage of the provisional or (rarely) definite cell development. This larvae type is described in all sponges of subclass Ceractinomorpha (Demospongiae) and in the majority of sponges Sclerospongiae.

All sponge larvae are lecytotrophic independently on their morphology, because their main sources of energy are the vitelline granules, which have not been consumed during embryogenesis. The granules are usually located in the base of flagellated cells or inside the internal cells of larvae. However, the phagocytosis of organic particles from the environment accomplished by flagellated cells was observed in parenchymulas of *H. panicea* and some Spongillidae (Ivanova & Semionov,1997).

Sponge larvae stage lasts usually from several hours to several days. During this period it undergoes considerable morphological changes mainly connected with the preparation to settlement and metamorphosis.

The provisional organs of sponge larvae (amphiblastula and parenchymula) are the flagellated epithelium, accomplishing locomotion function (while floating), attachment (while settling) and probably feeding, and larval skeleton, used as a scaffold when metamorphosis starts. The locomotion epithelium of amphiblastula or parenchymula is phagocytized partly or totally by the internal cells during larvae metamorphosis. The main morphogenetic function in the case of the larvae types stated above is accomplished by the internal polypotent aflagellar cells and partly by flagellated cells remained at the larvae surface or immersed inward. There are usually no necrobiotic processes during the metamorphosis of coeloblastula which can be connected with the simplicity of its structure. In this case a junior sponge is formed in a result of the flagellated polypotent cell transdifferentiation.

Sponge growth and development period starts with the beginning of canal system functioning and is finished with the sexual or asexual reproduction. It is known that sexual and asexual morphogeneses more often interchange, and the sponge growth stops or slows when gametogenesis starts. Body size, its biomass and number of functioning modules (osculums with nearby canal system) increase during the growth period.

Growth phase duration and sponge body size increase may vary even among the same species adults until the beginning of sexual reproduction. For instance, newly generated junior

sponges of *H. panicea* population inhabiting the tidal zone of Barents Sea start active growing at the middle or at the end of hydrological winter (February-April). These specimens fuse with each other and spread out on the bottom occupying the area up to 1-1,5 sq m. The sponges fragmentize, undergo some reduction and start sexual reproduction at such a state at the end of hydrological spring - at the beginning hydrological summer (June) (Yereskovskij, 1995). Growth period of the Baltic Sea *H. panicea* (from the Kiel Bay) lasts for about a year (Witte & Barthel, 1994). Sponge shape and size do not change significantly during growth and before sexual reproduction, but strictly depend on the local hydrological conditions. Two generations of sponge both reproducing sexually were observed in *Halichondria* sp. estuary populations from the Mystic Estuary (Connecticut, the USA). The first generation consists of the sponges survived winter, undergone growth phase and reached normal body size. The other one includes junior postlarval specimens which have no growth phase (Fell & Jacob, 1979; Fell et al., 1979; 1984).

The stage of asexual reproduction may be considered a special period. It is known that asexual reproduction is heterogenic. Some types of blastogenesis are similar to regeneration, other are related to reducing processes and somatic embryogenesis. Obligatory blastogenesis has been observed only in demosponges of three orders - Haplosclerida (Ceractinomorpha) - gemmulation in freshwater sponges of families Spongillidae and Potamolepidae and in marine sponges of family Haliclonidae (Brien, 1973; Fell, 1975; Simpson, 1984); Hadromeridae (Tetractinomorpha) - gemmulation in sponges of Suberitidae and Clionidae (Topsent, 1888; Herlant-Meewis, 1948; Hartman, 1958; Garrone, 1974; Connes, 1977; Connes et al.,1978) and budding in sponges of Polymastiidae and Tethyidae (Merejkovsky, 1879; Connes, 1967; Battershill & Bergquist, 1990; Plotkin & Ereskovsky, 1997).

The budding type of asexual reproduction is registered nearly in all sponges independently on their taxonomic position and geographical (ecological) location (Fell, 1975; Simpson, 1984). But it is rare and random and because of this, might be considered facultative in all sponges except the two families stated above. Life cycle including obligatory asexual reproduction is typical of *r*-strategy sponges populations. The example *E. fluviatilis* of the Tagliavia Canal (Sicilia) was already stated above. *Cliona trutti* of the Chesapeake Bay also survive stress climatic period (low winter temperature of water) at the stage of gemmules, which hatch in spring (Pomponi & Meritt, 1990).

Gemmules and eggs of all sponges studied originate from the same cell sources - polypotent nucleolar amoebocytes (archaeocytes) (Simpson, 1984; Weissenfels, 1989). Gemmulation usually starts only after the end of vitellogenesis in the sponge. Such a consequence is also typical for other modes of asexual reproduction. For instance, the budding of the White Sea *Polymastia mammillaris* is the most intensive in spring and summer (the period of starting gametogenesis), but its intensity decreases during vitellogenesis (Plotkin & Ereskovsky, 1997).

An intensive asexual reproduction was usually observed after finishing of the sexual reproduction it ends the active life cycle phase in sponge populations living under instable conditions and prepares themselves to the survival the stress or to the death. In the case of populations inhabited high latitude aquatories they undergo stress conditions in autumn and in winter when temperature falls below zero and the ice covers the water surface. The similar conditions one can meet at low latitude where sponge populations survive the stress periods of aquatory drying, autumn storms or tropical rain season.

Asexual reproductive elements (gemmules, statoblasts, buds) undergo phases analogous to metamorphosis and growth. But cleavage and larvae formation are never observed during blastogenesis because the starting stage of it is always a multicellular primordium containing somatic cells of different origin.

Finishing the brief review of the main sponge sexual and asexual reproductive peculiarities, it seems possible to formulate their causes. If the level of animal organization, tissue and cell differentiation and specialization as well as the presence of special integrative system were considered the main criteria of organizational complication of an animal, then analogous criteria should be used for estimation of morphogenetic specialization degree and consequently the specialization degree of the cells contributed to these processes, reproductive process type stability degree and its determination.

Since fragmentation, residual body gemmule and bud formation exist in sponge life cycle alongside with sexual reproduction, then somatic and sexual morphogeneses interchange or sometimes proceed in parallel. As a result, monotypical (usually more polypotent) cells contribute to the alternative morphogeneses. The level of specialization of reproductive cell does not appear to be high and no conditions are produced for strict specialization either for sexual or for somatic morphogenesises in life cycle in this case. The lack of high-differentiated anatomical organization and the low level of differentiation in sponges, their low determination equally with the morphogenetic plasticity as was stated above do not lead to the formation of specialized gametogenetic forms, and embryogenetic stages of sponges are thus not completely homologous to those of the higher-organized Metazoa. The embryogenesis in the case of direct development (genus *Tetilla*) represents the formation of the morulae-like primordium, comparable to a blastozooid or to a residual body. Its cells start to form sponge definitive tissue without blastulation, gastrulation and other embryogenetic stages which are typical of all higher organized animals. Such

stages might be complicated and high-specialized due to the prolonged evolution of sexual embryogenesis and gametogenesis as compared with other reproductive type evolution. Sponges have not achieved such a sexual embryogenetic specialization.

The low embryogenetic stage specialization is also observed in the case of viviparity and larvae development inside maternal sponge tissues. As was stated above, the cleavage is continuous with the larval cell differentiation imperceptibly. The major part of these cells accomplish provisional functions. The cells transpositions during larvae formation and metamorphosis are not homologous to the gastrulational ones as they do not promote the formation of germinal layer-like embryonic structures from which the homologous tissues develop in the majority of animals. There are no basis for germinal layer formation structures in sponges that are endodermal gut lining and ectodermal epithelium. External tissues (pinacoderm and choanoderm) and mesohyl tissues develop in sponges instead of the foregoing structures but they are not homologous to the gastral and covering epithelium and to mesoderm.

It may be supposed that the peculiarity of sponge sexual morphogenesis is due to the conservation of the initial filtrate type of feeding and of the low cell, tissue and anatomic systems specialization and differentiation, to the low level of individuality and differentiation and morphogenetic specialization in the recent sponges rather to their special location at the phylogenetic system of animals (so to say, to their location at the side of the main evolutionary way of multicellularity) and somatic morphogenetic primitivity or progressiveness within the phylum Porifera they are evident. The more anatomic, tissue and cell systems have developed inside sponge body and the higher they are differentiated, the higher the probability of the existence of comparatively more stable reproductive forms and of the appearance of specialized blastogenetic and sexual morphogenetic forms in these sponges. In order to study the causes of gametogenetic type variations and of gametocyte - somatic relationship changes, the whole life cycle and the origin of somatic morphogeneses (growth processes, blastogenesis, reducing blastogenesis and restorational morphogeneses) should be analyzed. The contribution of some more or less polypotent cell groups (groups of blastogenetic line cells) to all foregoing morphogenesises, the degree of somatic cell phagocytizing capability and the accumulative degree of the reserve inclusions to be used later during somatic morphogenesis in the cells, and also the capability to the direct transformations of some somatic cells - all these factors are correlated with the somatic cell behavior during gametogenesis with the formation of the auxiliary structures such as embryonic capsules, with the trophic processes, with the phenomenon of excurvation, and with other processes.

The modern sponges have passed a long way of the parallel adaptive evolution and this is why no monotypical initial prototype can be determined among them. Progressive species as well as primitive ones are observed within every sponge taxon. Furthermore the features of high specialization together with those of low specialization are observed in morphogenesis of each sponge taxon. For instance, spermatozoa with acrosome unique in sponges were recently described at *Oscarella lobularis,* a species considered primitive (Baccettti et al., 1986). Besides, the prevalent features of this sponge vitellogenesis are similar to those of Eumetazoa (Gaino et al., 1986).

Finishing the analysis of sponge sexual morphogenetic peculiarity it should be emphasized that such an analysis needs the comparision of the alternative morphogeneses (asexual and sexual) coexisting of interchanging in the sponge life cycle and the elucidation of different cell group determination degree using modern experimental embryological, cytological and genetic methods.

References

Aiseshtadt, T. B. 1984. Cytology of oogenesis.- Moskow. "Nauka". 1-247. In russ.

Anakina, R. P. 1981. The embryological development of Barents Sea sponges *Leucosolenia complicata* Mont. (Calcarea).- In: Korotkova G. P. (Ed.) Morfogenesi u gubok. Leningrad, Izdat. Leningr. univer. 52-58. In russ.

Anakina, R. P. 1997. The cleavage of Barents Sea Sponge *Leucosolenia complicata*.- Berliner geowiss. Abh. 20: this volume.

Anakina, R. P., Korotkova, G. P. 1989. Spermatogenesis in *Leucosolenia complicata* Mont., Barents Sea Sponge.- Ontogenez. 20: 77-86. In russ.

Baccetti, B., Gaino, E. & Sara, M. 1986. A sponge with acrosome: *Oscarella lobularis*.- J. Ultrastr. Molec. Struct. Res. 94: 195-198.

Barthel, D. 1986. On the ecophysiology of the sponge *Halichondria panicea* in Kiel Bight. I. Substrate specificity, growth and reproduction.- Mar. Biol., 32, 291-298.

Battershill, C. N. & Bergquist, P. R. 1990. The influence of storms on asexual production, recruitment, and survivorship of Sponges.- In: New Perspectives in Sponge Biology (K. Rutzler, ed.). Washington: 397-403.

Bergquist, P. R. 1978. Sponges.- Univ. Calif. Press, Los Angeles. 1-268.

Brien, P. 1973. Les Demosponges.- In: P.-P. Grasse (ed.) Traité de Zoologie. Maison Cie. Paris. 1 (III): 133-461.

Chen, W. T. 1976. Reproduction and speciation in *Halisarca*.- In: Harrison, F. M. & Cowden, R. R. (Eds.) Aspects of sponge biology. Acad. Press. New York. pp. 113-139.

Connes, R. 1967. Structure et developpement des bourgeons chez l'Eponge siliceuse *Tethya lincurium* Lamarck.- Arch. Zool. Exp. Gen. 108: 157-195.

Connes, R. 1977. Contribution a l'etude de la gemmulogenese chez la Demosponge marine *Suberites domuncula* (Olivi) Nardo.- Arch. Zool. Exp. Gen. 118: 391-407.

Connes, R., Carriere, D. & Paris, J. (1978) L'etude du developpement des gemmules chez la demosponge marine *Suberites domuncula* (Olivi) Nardo.- Ann. Sci. Natur. Zool. Paris. 20: 357-387.

Corriero, G., Manconi, R., Vacarro, P. & Pronzato, R. 1994. Life strategies of *Epfydatia fluviatilis* (L.,1758) in two different environments. In: Van Soest, R., Van Kempen, T. & Braekman, J.- C. (Eds.) Sponges in Time and Space. A. A. Balkema, Rotterdam: 321-326.

Efremova, S. M. 1981. The structure and ebryogenesis of the Baikal sponge *Lubomirskia baikalensis* (Pallas) and relations of the Lubomirskiidae with another sponges.- In: G. P. Korotkova (Ed.) Morfogenesi u gubok. Leningrad, Izdat. Leningr. univer.: 93-107. In russ.

Efremova, S. M. 1988. The origin of the germ cells and the problem of germinal way in Sponges. In: V. M. Koltun, S. D. Stepaniants (eds.) Porifera and Knidaria. Leningrad: 17-22. In russ.

Efremova, S. M., Ereskovsky, A. V. & Tokina, D. B. 1987. Gametogenesis in sponges of the family Myxillidae from the White Sea. 1. Oogenesis in *Myxilla incrustans* and *Iophon piceus* (Demospongiae, Poecilosclerida).- Onthogenesis, 18, 257-262. In russ.

Ereskovsky, A. V. 1986. Larval formation in *Iophon piceus* (Demospongi ae, Poecilosclerida).- Zool. journ. 65: 1614-1621. In russ.

Fell, P. E. 1974a. Porifera.- In: A. C. Giese & J. S. Pearse (eds.) Reproduction of marine invertebrates. Acad. Press. New York. 1: 51-132.

Fell, P. E. 1983. Porifera.- In: K. G. Adiyodi & R. G. Adiyodi (eds.). Reproductive biology of invertebrates. Vol. 1. Oogenesis, oviposition and oosorption. John Wiley and Sons, Ltd., Chichester: 1-29.

Fell, P. E. 1989. Porifera.- In: K. G. Adiyodi & R. G. Adiyodi (eds.). Reproductive biology of Invertebrates. Vol. 4. Fertilization and larval development. John Wiley and Sons, Ltd., Chichester: 1-27.

Fell, P. E. & Jacob, W. F. 1979. Reproduction and development of *Halichondria* sp. in the Mystic Estuary, Connecticut.- Biol. Bull. 156: 62-75.

Fell, P. E., Lewandrowski, K. B & Lovice, M. 1979. Postlarval reproduction and reproductive strategy in *Haliclona loosanoffi* and *Halichondria* sp.- In: Levi, C., Boury-Esnault, N. [Eds.] Biologie des Spongiaires. CNRS. 291, Paris. 113-122.

Franzen, W. 1988. Oogenesis and larval development of *Scypha ciliata* (Porifera, Calcarea).- Zoomorphology (Berlin). 107 (6): 349-357.

Fromont, J. 1994. The reproductive biology of tropical species of Haplosclerida and Petrosiida on the Great Barrier Reef.- In: Van Soest, R., Van Kempen, T. & Braekman, J. - C. (Eds.) Sponges in Time and Space. A. A. Balkema, Rotterdam: 307-311.

Gaino, E., Burlando, B. & Buffa, P. 1986. Contribution to the study of egg development abd derivation in *Oscarella lobularis* (Porifera, Demospongiae).- Inv. Repr. Dev. 10: 297-305.

Gallissian, M. F. 1983. Etude ultrastructurale du developpement embryonaire chez *Grantia compressa* F. (Porifera, Calcarea).- Arch. Anat. microsc. morphol. exp. 1: 59-75.

Garronne, R. 1974. Ultrastructure d'une "gemmule arme" planctonique d'eponge clionidae.- Arch. Anat. Micros. Morph. Exper. 63: 163-182.

Hartman, W. D. 1958. Natural history of the marine sponges of southern New England.- Bull. Peabody Mus. Natur. Hist. 12: 1-155.

Herlandt-Meewis, H. 1948. La gemmulation chez *Suberites domuncula*.- Arch. Anat. Micros. 37: 289-322.

Ilan, M. & Loya. Y. 1988. Reproduction and settlement of the coral reef sponge *Niphates* sp. (Red Sea). In: Proc. 6th Intern. Coral Reef Symp. Australia, 1988. Vol. 2: 745-749.

Ilan, M. & Loya. Y. 1990. Sexual reproduction and settlement of the coral reef sponge *Chalinula* sp. from the Red Sea. Mar. Biol. 105: 25-31.

Ivanova, L. V. 1978. Morphogenetic processes and seasonal changes of the anatomical and tissue organisation of the Barents Sea sponges *Halichondria panicea* (Pallas). Archiv Anatom., hysotlog., embryol. 10: 62-71. In russ.

Ivanova, L. V. 1981. The life cycle of the Barents Sea sponge *Halichondria panicea* (Pallas). In: G.P. Korotkova (ed.). Morfogenezy u gubok. Leningrad. 59-73.

Ivanova, L. V. & Semenov, V. V. 1997. Feeding habits of the larvae of sponges.- Berliner geowiss. Abh. E 20: this volume.

Ivanova-Kazas, O. M. 1976. Blastogenesis and embryogenesis.- Zool. Journ. 55: 172-182. In russ.

Ivanova-Kazas, O. M. 1977. Asexual development of animals.- Leningrad. Publ. Leningrad University. 1-240. In russ.

Kaye, H. R. 1991. Sexual reproduction in four Caribbean commercial sponges. II.

Oogenesis and transfer of bacterial symbionts.- Inv. Reprod. Dev. 19: 13-24.

Korotkova, G. P. 1979. The origin and evolution Ontogenesis.- Leningrad. Publ. Leningrad University. 1-370. In russ.

Korotkova, G. P. 1981a. General characteristic of Sponge organisation.- In: G. P. Korotkova (ed.). Morphogenesis in Sponges. Leningrad. Publ. Leningrad University. 3-51. In russ.

Korotkova, G. P. 1981b. Sexual embryogenesis of Sponges and objective laws of its evolution.- In: G. P. Korotkova (ed.). Morphogenesis in Sponges. Leningrad. Publ. Leningrad University. 108-136. In russ.

Korotkova, G. P. 1987. The integrative systems and the evolution of ontogenesis.- In: J. Mlikovsky, V. J. A. Novak, (eds.) Towards a new synthesis in evolutonary biology. Proc. Intern. Symp. Praha: 155-156.

Korotkova, G. P. 1988. Peculiarities of organisation and types of the development in Sponges.- In: V. M. Koltun, S. D. Stepanianz (eds.) Porifera and Cnidaria. Leningrad: 34-40. In russ.

Korotkova, G. P. 1991. The principles of wholeness and evolution of ontogenesis.- In: Vorobjova, E. I., Vronsky, A. A. (eds.). The modern evolutional morphology. Kiev: 118-129. In russ.

Korotkova, G. P. & Aiseshtadt,T. B., 1976. A study of oogenesis in the marine sponge *Halisarca dujardini*. I. The origin of the oogonia and early stages of oocyte development.- Tsitologia. 18: 549-555. In russ.

Korotkova, G. P. & Apalkova, L. V. 1975. Oogenesis of the Barents Sea sponge *Halisarca dujardini*. In: Comparative and experimental morphology of the sea organisms.- Kolske filial Acad. Sci. USSR. 9-26. In russ.

Korotkova, G. P. & Ereskovsky, A. V. 1984. Peculiarities of the egg cleavage of White Sea Sponge *Halisarca dujadrini* Johnston.- Vestnik Leningrad University. 21: 36-42. In russ.

Korotkova, G. P. & Ermolina, N. O. 1982. Period of development of the larvae *Halisarca dujardini* (Demospongia).- Zoolog. Journ. 61 (10): 1472-1479. In russ.

Levi, C. 1956. Etude des *Halisarca* de Roscoff. Embryologie et systematique des Demosponges. Travaux de la Station Bibliog. de Roscoff N.S. 7 (34): 3-181.

Levi, C. & Levi, P. 1976. Embryogenese de *Chondrosia reniformis* (Nardo), demosponge ovipare, et transmission des bacteries symbiotiques.- Ann. Sc. Nat. Zool. Biol. Anim., Serie 12, 18: 367-380.

Malachov, V. V. 1990. Enigmatic groups of marine Invertebrates. Trichoplax, Ortonectida, Dyciemida, Porifera.- Moskow: 1-144. In russ.

Merejkowsky, C. S. 1878. Les Eponges de la mer Blanche.- Mem. l'Acad. Imper. Sci. St-Petersbourg. 26 (7): 1-51.

Mukai, H. 1989. Growth and reproduction in four species of freshwater sponges cultured in their natural surrounding.- Sci. Rep. Fac. Educ. Gunma Univ. 38: 25-47.

Plotkin, A. S., Ereskovsky, A. V. (1997) Ecological features of asexual reproduction of the White Sea Sponge *Polymastia mammillaris* (Demospongiae, Tetractinomorpha) in Kandalaksha Bay.- Berliner geowiss. Abh. E 20: this volume.

Pomponi, S. A., Merritt, D. W. (1990) Distribution and life history of the boring sponge *Cliona truitti* in the Upper Chesapeake Bay.- In: K. Ruetzler (ed.): New Perspectives in Sponge Biology Washington: 383-390.

Pronzato, R., Manconi, R. (1994) Life history of *Ephydatia fluviatilis* as model for adaptive strategies in discontinuous habitats.- In: R. Van Soest, T. Van Kempen & J.- C. Braekman (eds.): Sponges in Time and Space. A. A. Balkema, Rotterdam: 327-331.

Rasmont, R. 1979. Les Eponges: des metazoaires et des societes de cellules.- In: C. Levi, N. Boury-Esnault (eds.): Biologie des Spongiaires. Colloq. Internat. C.N.R.S. Paris. 291: 21-30.

Reiswig, H. M. 1976. Natural gamete release and oviparity in Caribbean demospongiae.- In: F. M. Harrison, R. R. Cowden (eds.): Aspects of sponge biology. Acad. Press. New York. pp. 99-112.

Reiswig, H. M. 1983. Porifera.- In: K. G. Adiyodi & R. G. Adiyodi (eds.): Reproductive biology of Invertebrates. Vol. 2. Spermatogenesis. John Wiley and Sons, Ltd., Chichester: 1-23.

Saller, U. 1988. Oogenesis and larval development of *Ephydatia fluviatilis* (Porifera, Spongillidae).- Zoomorphology (Berlin). 108 (1): 23-28.

Saller, U. & Weissenfels, N. 1985. The development of *Spongilla lacustris* from the oocyte to the free larvae (Porifera, Spongillidae).- Zoomorphology. 105: 367-374.

Salvini-Plaven, L. & Splechtna, H. 1979. Zur Homologie der Keimblätter.- Ztschr. zool. Syst. Evolut. 17 (2): 77-81.

Seravin, L.N. 1986. The nature and origin of the Spongia.- Proc. Zool. Inst. USSR. Leningrad, 144: 94-112. In russ.

Seravin, L. N. 1992. Originality of the organisation and embrional development of the Sponges.- Vestnik S-Petersburg Gos. Univ. Ser. 3. 2 (10): 13-28. In russ.

Simpson, T. L. 1968. The biology of the marine sponge *Microciona prolifera* (Ellis and Sollander). II. Temperature-related annual

chamges in functional and reproductive elements with a discription of larval metamorphosis.- J. Exp. Mar. Biol. Ecol. 2: 252-277.

Simpson, T. L. 1984. The cell biology of Sponges.- Springer-Verlag. New York, Berlin. -662p.

Simpson, T. L. & Gilbert, J. J. 1974. Gemmulation, gemmule hatching and sexual reproduction in fresh-water sponges. II. Life cycles events in young, larvae-produced sponges of *Spongilla lacustris* and unidentified species.- Trans. Amer. Micros. Soc. 93: 39-45.

Sizova, N. A. & Ereskovsky, A. V. 1997. Some features of early embryogenesis of the White Sea Sponge *Halisarca dujardini* (Demospongiae, Dendroceratida).- Berliner geowiss. Abh. E 20: this volume

Topsent, E. 1888. Sur les gemmules de quelques silicisponges marines.- C. R. Acad. Sci. Paris. 106: 1298-1300.

Tuzet, O. 1948. Les premieres stades du developpement de *Leucosolenia botrioides* Ellis et Sollander et de *Clathrina (Leucosolenia) coriacea* Mont.- Ann. Sci. Natur. 10: 103-114.

Van de Vyver, G. & Willenz, P. 1975. An experimental study of the life cycle of the fresh-water sponge *Ephydatia fluviatilis* in its natural surroundings.- Wilhelm Roux's Arch. 177: 41-52.

Vethaak, A. D., Cronie, R. J A. & Van Soest, R. W. M. 1982. Ecology and distribution of two sympatric, clousely related sponge species, *Halichondria panicea* (Pallas, 1766) and *H. bowerbanki* Burton, 1930 (Porifera, Demospongiae), with remarks on their speciation.- Bijdrag. Dierkunde. 52 (2): 82-102.

Wapstra, M. & Van Soest, R. W. M. 1987. Sexual reproduction, larval morphology and behavior in Demosponges from the southwest of the Netherlands.- In: N. Boury-Esnault & J. Vacelet (eds.): Taxonomy of Porifera. NATO ASI Ser. G.13: 281-307.

Warburton, F. E. 1961. Inclusion of parental somatic cells in sponge larvae.- Nature (London). 191: 1317.

Watanabe, Y. 1978. The development of two species of *Tetilla* (Demosponge).- Natur. Sci. Rep. Ochanomizu Univ. 29: 71-106.

Watanabe, Y. & Masuda, Y. 1990. Structure of fiber bundles in the egg of *Tetilla japonica* and their possible function in development.- In: K. Ruetzler (ed.): New Perspectives in Sponge Biology. Washington: 193-199.

White, U. & Barthel, D. 1994. Reproductive cycle and oogenesis of *Halichondria panicea* (Pallas) in Kiel Bight.- In: R. Van Soest, T. Van Kempen & J.- C. Braekman, (eds.): Sponges in Time and Space. A. A. Balkema, Rotterdam: 297-305.

Weissenfels, N. 1989. Biologie und microscopishe Anayomie der Süsswasserschwämme (Spongillidae). Fischer, Stuttgardt, New York. 1-110.

Yereskovskiy (Ereskovsky), A. V. 1995. On the population structure and distribution of sponges in the intertidal zone of Easter Murman.- Hydrob. J. 31 (3): 15-29.

BERLINER
GEOWISSENSCHAFTLICHE
ABHANDLUNGEN

Reihe E Band 20

Alexander V. Ereskovsky, Helmut Keupp & Rolf Kohring (Eds.)

„Modern Problems of Poriferan Biology“

Proceedings of the first All-Russia meeting of spongiologists
St. Petersburg, February 1996

FU • TU • TFH
Berlin
1997

Berliner geowiss. Abh.	E **20** (Paläobiologie)	1-157, 26 plates	Berlin 1997

"Modern Problems of Poriferan Biology"

Proceedings of the first All-Russia meeting of spongiologists
St. Petersburg, February 1996

Alexander V. Ereskovsky, Helmut Keupp & Rolf Kohring (Eds.)