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INVERTEBRATE ZOOLOGY

Problems of Coloniality, Modularity, and Individuality in Sponges and Special Features of Their Morphogeneses During Growth and Asexual Reproduction

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Abstract—A comparative analysis of the organization of sponges has been carried out to clarify problems of their coloniality, individuality, and modularity. The morphological, physiological, morphogenetic, and immunological aspects of the problem have been analyzed. The followers of the hypothesis of colonial organization of sponges interpret the process of “new zooid” formation as an “incomplete asexual reproduction.” A comparative analysis of morphogeneses in sponges during growth processes and asexual reproduction has clearly shown them to be different. A rearrangement (remodeling) of structures accompanied by disorganization and reorganization of tissues in neighboring elements of aquiferous system is the basis of growth. Migration of polypotent and secretory cells into the core of bud development is the major mechanism of budding. The formation of new aquiferous units (aquiferous modules) does not represent an “incomplete asexual reproduction.” Thus, the terms “colony” and “zooid” cannot be applied to the sponges. A morphologically separate sponge, irrespective of its level of organization (ascon, sycon, or leucon) and the number of oscula (aquiferous modules) should be considered as an individual.

Key words: sponges, colony, modular nature, individual, morphogenesis, growth, budding.

Sponges are a group of sessile water lower multicellular organisms that have neither any pronounced intestine nor intestinal parenchyma. Moreover, they have neither nerve nor muscle tissue. In their bodies there are mobile totipotent cells, capable of differentiation into any other type of cells. In many species there are siliceous or calcareous spiculae. The aquiferous system is considered the most peculiar and genuine characteristic of sponges. The major physiological functions of this system are delivery and excretion of food particles, gas exchange, and withdrawal of gametes and larvae. The aquiferous system of sponges comprises the following components: (1) pores (ostia); (2) incurrent canals; (3) apopyle; (4) choanocyte (collar) chamber; (5) prosopyle; (6) excurrent canals; and (7) osculum (Fig. 1). The unidirectional current of water through the body of the sponge is produced by flagellated collar cells (choanocytes) united into chambers or canals.

A characteristic feature distinguishing Porifera from other Metazoa might be considered the high plasticity of their anatomical, tissue, and cellular structures throughout the life cycle. Different differentiated cells of sponges are capable of movement, transdifferentiation, and exchange of some functions for some other ones. Both morphogeneses and functional integration in sponges are possible only at the basis of mobility and reorganization of cells and cell populations. Owing to this characteristic, the sponge continually remains in the condition of rearrangement of all its structures [6, 25, 26, 48, 50, 65, 71, 81]. The direct dependence of sponges on environmental conditions and their plasticity results in the fact that they continuously change the shape of their bodies; frequently occurring processes are reduction, fragmentation, fusion, or separation of individuals in one clone [33, 49, 60, 70].

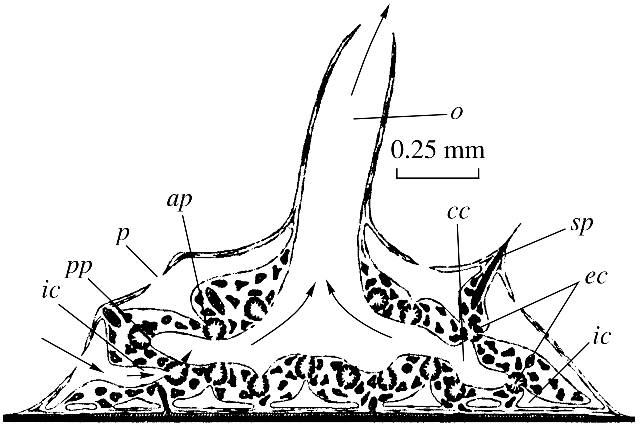

Fig. 1. Scheme of the structure of a monooscular sponge (from Weissenfels [90]); (*ap*) apopyle; (*ec*) excurrent canal; (*o*) osculum; (*p*) pore; (*ic*) incurrent canal; (*pp*) prosopyle; (*sp*) spicula; (*cc*) choanocyte chamber.

This "chronic morphogenesis" is shown to be not only a response to changes in ecological circumstances, but also a result of the active movement of the sponge along the substrate [65]. In many viviparous Demospongiae significant reorganizations have been observed during ontogenesis at the anatomical and histological levels [5, 13]. Such reorganization might result in destruction of the entire aquiferous system or a significant part of it. This phenomenon takes place when the sponge prepares itself for survival under severe environmental conditions [45, 79, 89], during processes of regeneration [14], during the development of reduction bodies [81], and in the process of gemmulogenesis and during sexual reproduction [4, 9, 42].

The problem of interpretation of the sponges from the point of view of coloniality and individuality was and still remains the most debatable in the history of spongiology. Many scientists refer sponges, irrespective of the level of their organization, to colonial organisms, considering zooids or individuals inside a solid colony as either amoeboid [37, 72] or collar cells [38, 59, 61], choanocyte chambers [54, 55], or osculum [77]. Other authors, proceeding from the generally accepted idea that the colonies in multicellular animals originate as the result of incomplete asexual reproduction [1], consider zooids in sponges as the osculum with surrounding areas of the aquiferous system [1, 12, 15, 31, 52]. According to Marfenin [67] the sponges represent colonies consisting not of zooids, but rather of modules.

The opposite point of view is shared by authors who consider that the idea of "coloniality" cannot be applied to Porifera and, therefore, every morphologically isolated sponge is an individual [23, 29, 39, 41, 47, 57, 64, 80, 82]. According to these authors, the development of oscula occurs as a result of ordinary growth, rather than as an incomplete asexual reproduction characteristic of the arising colony. Koltun [11] considers only a monooscular sponge as an individual.

According to the other group of authors, individuality in sponges is very weakly pronounced and the major characteristics of coloniality have not developed yet; therefore, they suggest considering Porifera as "dividual" organisms [8, 19]. On the other hand, the scientists agree that in the sponges an individual could be considered as "an aggregate of cells able to perform life activities" or "ascon," in Calcarea [8].

The difficulties arising during the interpretation of organization in sponges from the point of view of coloniality or individuality are related, first of all, to the unique morphophysiological features in the organization of these organisms.

The goal of this project is to clarify the complicated problem of individuality coloniality, and modularity of adult sponges. To do this, we have supplemented for the first time the traditional morphological and physiological approaches with a comparative analysis of morphogeneses that take part in sponges in the course of growth processes and during asexual reproduction.

ANALYSIS OF ORGANIZATION IN SPONGES

Morphological Aspect

The idea of sponges as colonies of cells or a flagellated chamber has long been abandoned and no longer stands. The most controversial subject still remaining is the consideration of osculum with the surrounding system of tissues and canals as an individual, specimen, zooid, or module.

This brings up the question of how to regard the osculum. Is it right to consider the latter as an individual or zooid inside the colony or a morphological or integration center of the sponge? In sponges the osculum represents an analogue of the cloacal opening of the Eumetazoa. The role of the osculum amounts to the excretion from the body of the sponge of water with dissolved carbon dioxide, nitrogen metabolites, and fecal particles and, in the period of sexual reproduction, also gametes and larvae (Fig. 1). The water enters into the body of the sponge via numerous pore openings scattered throughout the surface of the animal (Fig. 1).

It has been shown that the size of oscula within a single sponge is prone to significant variation and their number might either increase or decrease during the life cycle of the considered specimen [20, 31, 47, 49, 50, 52, 68, 69, 70]. Moreover, the number of oscula may vary in different sponges of the same species having similar sizes [18]. Sometimes multiosculum sponges develop at the expense of neighboring juvenile specimens of the same clone fusing together. On the other hand, in two species of the family Cladorhizidae (Demospongiae, Poecilosclerida) inhabiting submarine caves (*Asbestopluma hypogea*) or the lower bathyal zone (*Cladorhiza* sp.), the aquiferous system including pores, canals, choanocytes, and oscula is entirely absent [83–85], thus providing evidence that under particular circumstances the osculum does not represent an obligatory structure determining the individuality of a sponge.

Functional Aspect

For a long time the major criterion of individuality or coloniality was the comparative anatomical "Bauplan" of the organism [1, 10]. However, since the late 1970s the problem of coloniality has expanded beyond the limits of comparative morphology, thus becoming the subject of studies from the point of view of the specific features of certain particular habitats and the physiology of organisms [2, 16].

An analysis of the distribution pattern of the elements of the aquiferous system in sponges (choanocyte chambers, incurrent and excurrent canals, and oscula), their number and size, and the weight of sponge tissues and hydrodynamic environmental conditions allowed

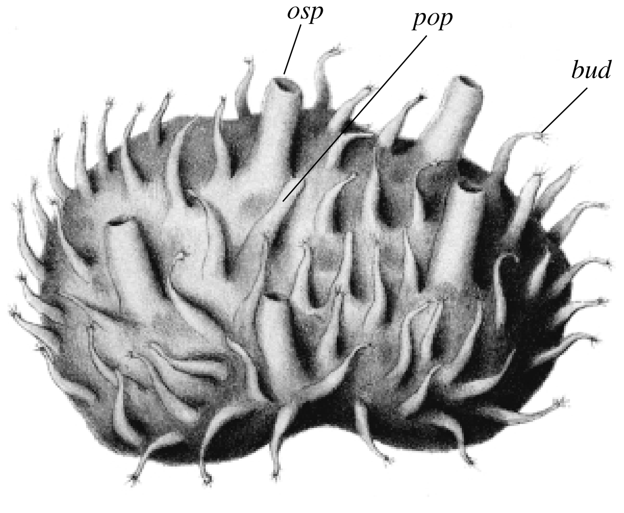

Fig. 2. Multioscular sponge *Polymastia mamillaris* (from Merezhkovskii [17]): (*osp*) ocular papilla; bud; (*pop*) pore papilla.

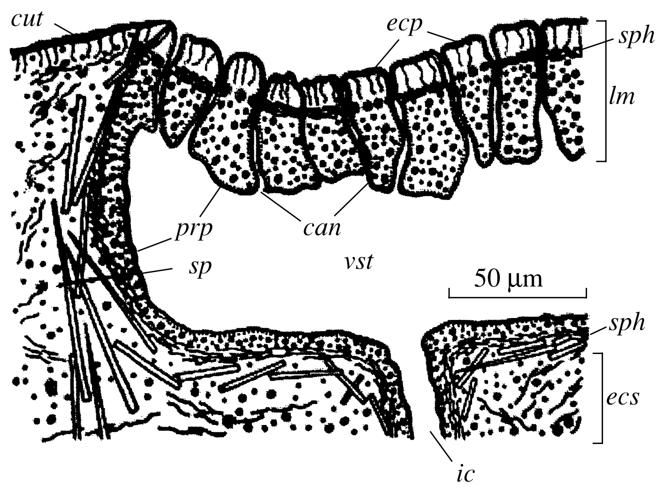

Fig. 3. Scheme of a lattice organ of *Hamigera hamigera* (from Boury-Esnault [30]): (*vst*) vestibulum; (*can*) canals; (*cut*) cuticle; (*ic*) incurrent canal; (*prp*) prosopinacoderm; (*lm*) lattice membrane; (*sp*) spicula; (*sph*) sphincter; (*ecp*) ectopinacoderm; (*ecs*) ectosoma.

Fry to formulate the idea of an “aquiferous module” [46, 47]. According to this author, the aquiferous module is a certain volume in the sponge that is supplied by a system of choanocyte chambers and aquiferous canals associated with a single osculum. Therefore, a sponge represents a modular organism, rather then a colony with zooids or a multioscular individual.

Modular organisms, unlike the unitary (solitary) organisms, consist of a set of repetitive main structural components (modules), whose number might be different in different periods of the life cycle. The development of modular organisms is not determined by any rigid program and to a significant degree depends on the relationships between these organisms and the environment [2, 16, 56].

Using the modular approach to the analysis of morphofunctional organization in sponges, different authors considered as a “module” the structures of different constructive levels, for instance, choanocyte chambers, the system of dendritically branching canals united by choanocyte chambers [22], or gemmulae [73]. However, in recent years some scientists [18, 93–95] have accepted the idea of the module advanced by Fry [46, 47]. Therefore, it would be methodologically wrong to consider sponges as modular organisms designating the modules as the fragments of aquiferous system or gemmulae, because these repetitive elements actually represent polymerized structural–functional units of the modules.

One of the most important factors correlated with the growth of sponges, their shape, and the number and distribution pattern of oscula is the hydrological regime in the area of the particular habitat [3, 18, 20, 24, 47, 69].

The ratio between the weight of tissues in the sponge and the distribution and arrangement of elements of the aquiferous system reflects a direct consequence of the optimization of some physiological factors. Some authors, for example, refer to the latter such factors as a decrease in the length of canals and a tendency toward better spatial separation between the incurrent and excurrent systems [57, 63]. In this connection, we should also bear in mind that, unlike other Metazoa, in sponges the penetration of water into the body takes place throughout the entire body surface, as they do not have any particular areas specialized for this function. Possible exceptions are representatives of the family Polymastiidae (Demospongiae, Hadromerida), whose body is usually buried into loose ground, therefore they have special porous and oscular papillae for the purpose of communication with the environment (Fig. 2) and also *Hamigera hamigera* (Demospongiae, Poecilosclerida), whose pores are arranged into particular lattice organs (“le crible”) (Fig. 3) [30].

Fry [47] has shown that the volume of water passing through a sponge for a time unit and the rate of water discharge through a single osculum are a function of the velocity of the inner laminar current, the number and size of choanocyte chambers, the inner pressure in the latter, the diameter and length of excurrent canals, and also the diameter of oscular opening. The pattern of functioning of choanocytes determines the hydrostatic pressure inside choanocyte chambers. Therefore, sponges with a small weight of tissues and a thin body wall show the optimal functioning having a single, usually widely open, osculum and a single large choanocyte chamber with low pumping pressure inside [47]. Examples of such a structural pattern might be some asconoid (*Leucosolenia* and *Clathrina*) or syconoid

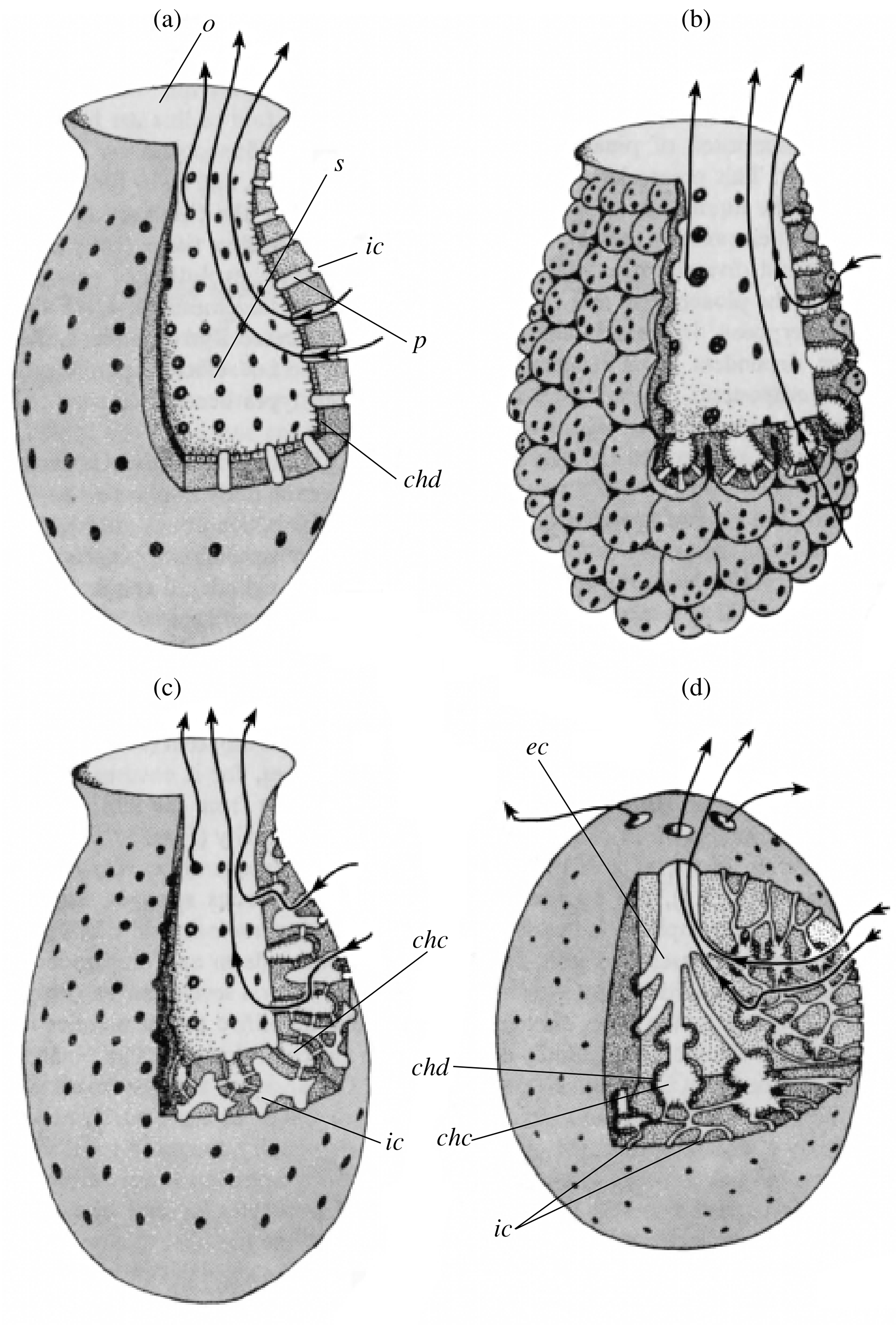

Fig. 4. Scheme of the structure of different types of aquiferous systems in sponges. (a) Asconoid; (b) syconoid; (c) transitional; (d) leuconoid (from Bergquist [23]); (*ec*) excurrent canal; (*o*) osculum; (*ic*) incurrent canal; (*p*) pore; (*s*) spongocoel; (*chd*) choanoderm; (*chc*) choanocyte chamber.

(*Sycon* and *Grantia*) sponges (Figs. 4a, 4b). The sponges with greater body weight need water currents of higher capacity (Fig. 4c). In this connection, their pumping pressure is higher and the increasing diameter of excurrent canals is equilibrated by the longer length of the latter and the greater diameter of the osculum.

In sponges with the choanocyte chamber diffusely distributed in tissues of the same thickness, more or less homogeneous distribution of incurrent and excurrent canals might be the only factor of the optimization of the canal system (Fig. 4d). The size and diameter of the canals depend on specific features of the functioning of the system in each specimen and on the thickness of the body wall in the latter. Eventually, the entire morphological diversity of sponges, as well as the number and size of aquiferous modules, is determined by their size,

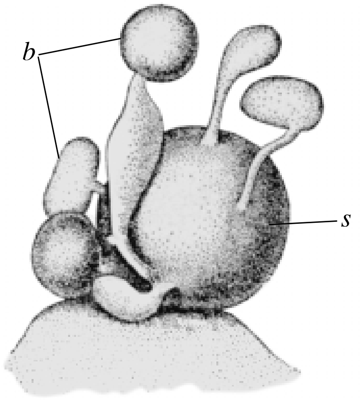

Fig. 5. A budding sponge *Tethya aurantium*: (*s*) sponge; (*b*) buds.

which, in turn, depends on external circumstances, first of all hydrodynamic conditions.

Thus, the oscula should not be considered as structural units of an individual, specimen, or zooid. Each of them rather represents either a certain marker of an isolated aquiferous system or an organization pattern, determined by forces that optimize relationships between the structure of choanocyte chambers; conditions optimal for supplying each chamber with water flow; and hydrodynamic factors that regulate the transfer of water through these chambers. All the elements of such a system are changing continuously [25, 28, 50, 57, 62, 81, 92].

Morphogenetic Aspect

The authors regarding multioscular sponges as colonies of zooids consider the process of development of new oscular units as an incomplete asexual reproduction [1, 10, 12, 53].

Let us discuss this problem from the morphogenetic point of view. Asexual reproduction in sponges takes place in the form of fragmentation, gemmulogenesis, or external budding [43, 45, 81]. Let us dwell in some more detail on the characteristics of external budding. In sponges only one form of budding has been described so far, namely, parietal budding (Figs. 2, 5). The latter occurs in the representatives of all groups of Porifera: Hexactinellida, Calcarea, Demospongiae, and Homoscleromorpha. A common characteristic of almost all buds developing in sponges might be considered the fact that at the initial stages of their development they represent dense conglomerates of cells, mostly polypotent archaeocytes. A bud has neither choanocyte chambers, nor canals, nor osculum [32, 43, 44, 81]. The budding takes place as epimorphosis. In the beginning of budding there is a migration of polypotent cells with their following differentiation into the definitive cells. The exception is Homoscleromorpha, where budding follows the pattern of morphallaxis. The developing buds involve all tissue structures of the parental sponge (Fig. 6). Detaching buds settle on a substrate and attach to it. These blastogeneses in sponges do not differ significantly from the processes observed in other animals, but show fundamental differences from growth morphogeneses in sponges.

The splitting of the body in a multioscular sponge is a facultative process that might be a result of either locomotion or the effects of damaging factors [51]. Different areas of the modular organism can move along the substrate with different speeds or in different directions, which causes fragmentation of the initial sponge [26, 33, 65, 70]. Let us emphasize here that such processes are possible due to the modular organization of these animals. Such a mechanism of splitting of an

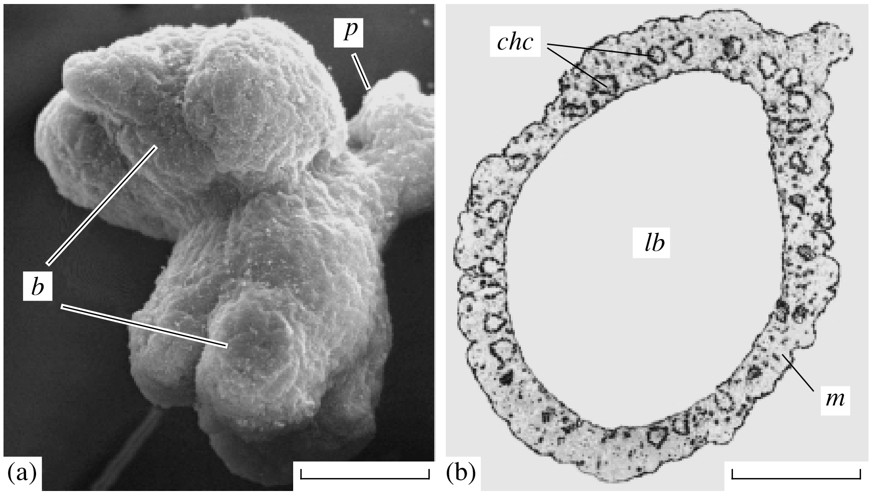

Fig. 6. Buds in *Oscarella tuberculata*: (a) gross view of a developing bud (SEM); (b) semi-thin section of a bud: (*m*) mesohyl; (*p*) peduncle of the bud; (*b*) buds; (*lb*) lumen of the bud; (*chc*) choanocyte chamber. Scale bar: (a) 200 µm; (b) 100 µm.

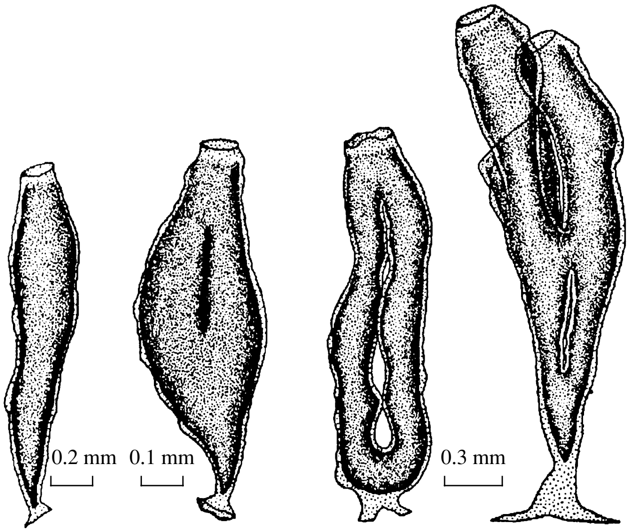

Fig. 7. Different stages of the complication of the aquiferous system in the asconoid sponge *Clathrina blanca* (from Hadži [53]).

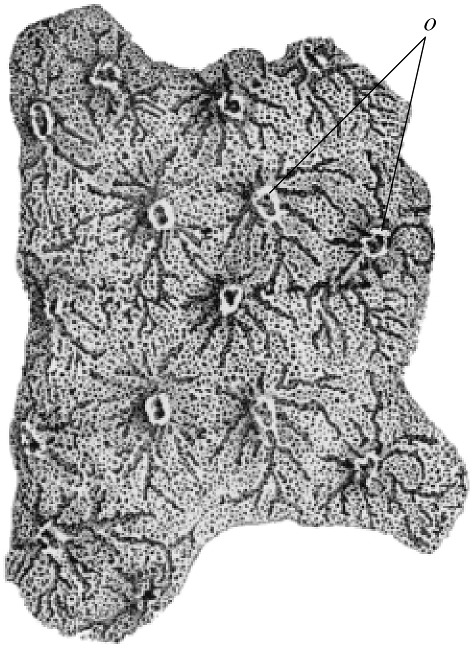

Fig. 8. An encrusting sponge *Potamolepis leubnitzae* (from Brien [32]): (*o*) oscula.

individual cannot be regarded as incomplete asexual reproduction. Such a fragmentation is also characteristic of other modular organisms, like bryozoans [66] and ascidians [75, 76].

The newly arising oscula are not connected to the neighboring ones and the initial aquiferous system never shows any kind of separation following the pattern of longitudinal division or budding, as is the case during the budding of hydroids. The case of asconoid sponges of the genus *Clathrina* discussed in the paper of Hadži [53], which is usually cited by the followers of the hypothesis of the colonial nature of sponges, is an example of the process of the development of external surface outgrowths to optimize hydrodynamics in this simply organized growing organism (Fig. 7).

Finally, the process of the development of new morphofunctional units cannot itself be regarded as incomplete asexual reproduction, which also casts doubt on the idea of considering multioscular sponges as colonies.

The thickness of tissues in a sponge is determined by the volume of space supplied by incurrent and excurrent canals. The increase in the size of sponges (encrusting, tubular, or clumpy sponges) is a result of increasing volume of the tissue layer against its constant thickness (Fig. 8). The divisions of cells occur in the entire volume of tissues of the sponge. Marginal growth is accompanied by migration and redistribution of cells. The thickness of tissues in the “parental” portion of the sponge remains constant; therefore, the new system of canals develops *de novo* in its proper marginal zone and never appears at the expense of division in the older central portion of the sponge. In sponges of different shapes (vasiform, cupped, and some encrusting sponges) the thickness of the body wall increases without significant increase in the area or density of canals and oscula (Fig. 9). The diameter of incurrent and excurrent canals increases instead; therefore, the volume of liquid passing through becomes greater.

The morphogenetic basis of the development of new structural–functional units (aquiferous modules) and permanent structural reorganizations in sponges is the processes of disorganization and reorganization in tissues and elements of the aquiferous system, which results in reorganization (remodeling) of the latter [25, 40, 48, 81]. During these processes the oscula may close and turn overgrown. First, choanocyte chambers break apart, then the adjoining canals disintegrate. The cell elements of the disorganized structure either dedifferentiate or fit into newly developing modules. In intact sponges, when a certain aquiferous system stops functioning, the structural elements of the latter often do not dissipate into cells, but rather fit in large fragments into the newly arising system [25]. The result of such a remodeling is intensification of aquiferous system functioning of the entire sponge and growth of the latter into the desired direction [25, 81]. The localization of proliferation in the course of growth depends on the shape of the sponge. In branched forms the proliferation takes part in apical areas of branches [7], and in encrusting forms it occurs in the marginal zone [78]. The disappearance of oscula and remodeling of the aquiferous system throughout the life cycle have been described repeatedly in several species of sponges, for example *Ephydatia fluviatilis* [92].

It has been shown that the size of pores on the surface of sponges and their distribution in exopinacoderm are prone to continuous fluctuations [57]. The

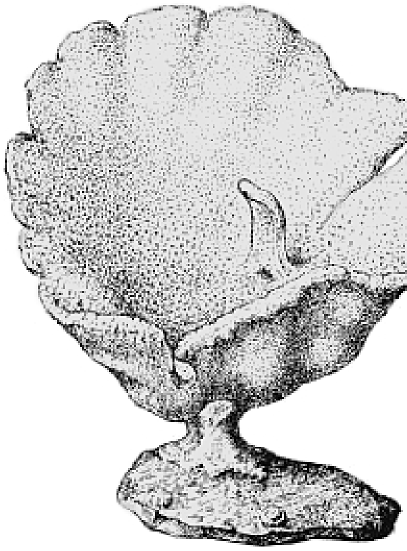

Fig. 9. A cupped sponge *Phakellia arctica* (from Koltun [11]).

terminal areas of incurrent canals or subdermal cavities should also undergo respective changes. By using the technique of time-lapse photography on intact sponges, it has been shown that remodeling of the aquiferous system in *E. fluviatilis* also comprises the movement of certain choanocyte chambers in the column of mesohyl [25]. During this process the chamber may detach from some canals, but become associated with some other canals. The excurrent canals also change permanently their general outline, size, and position. A clear tendency is observed of movement of small canals toward larger ones. The movement of canals and choanocyte chambers is passive and takes place due to mesohyl cells associated with these canals. It is significant that all the processes of rearrangement and remodeling are not reflected in the normal functioning of the sponge [25].

The reorganization of the aquiferous system is a way of intensification of the functions of the latter. Therefore, the interpretation of the increase in size and complexity of sponges as a process of asexual reproduction and oscular or aquiferous units as zooids also seems dubious.

Proceeding from the above discussion, I would agree with the authors who proposed to consider any morphologically isolated sponge as an individual, irrespective of its constructive level (ascon, sycon, or leucon) and the number of oscula.

Obviously, there are different levels of organism integration in sponges depending on the number and distribution pattern of aquiferous modules in their bodies. This fact is most clearly pronounced in the experiments on restorative morphogeneses in sponges [14]. However, there is no direct correlation between the level of organism integration and the complexity of aquiferous system in sponges. The monooscular sponges (*Sycon* and *Disyringia*) showing among Porifera the highest level of organism integration, which agree with the integration of the aquiferous module (Fig. 10), might be regarded as an extreme case in this series [12, 14]. On the other end of this series one could place multioscular sponges, for example *Reniera* or *Haliclona,* whose aquiferous modules are more or

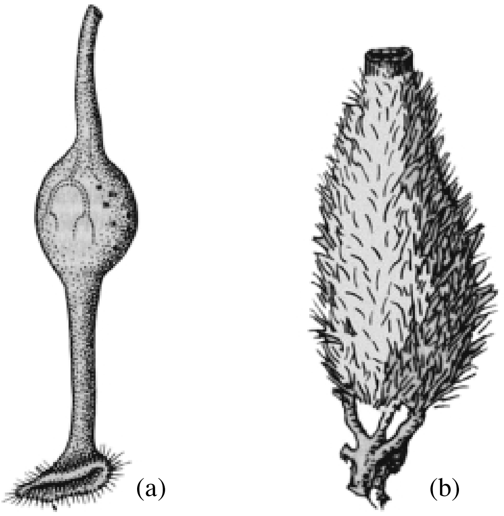

Fig. 10. Monooscular sponges: (a) *Disyringia*; (b) *Sycon.*

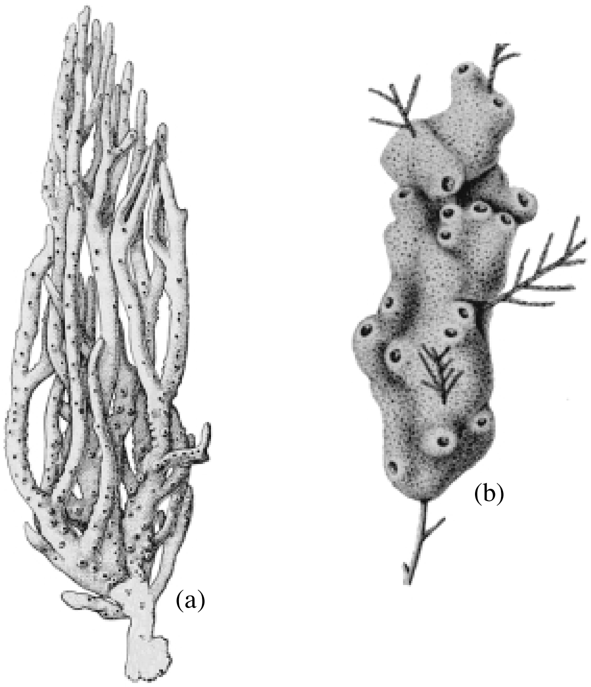

Fig. 11. Multioscular sponges: (a) *Chalina oculata* (from Brien [32]); (b) *Reniera cinerea* (from Merezhkovskii [17]).

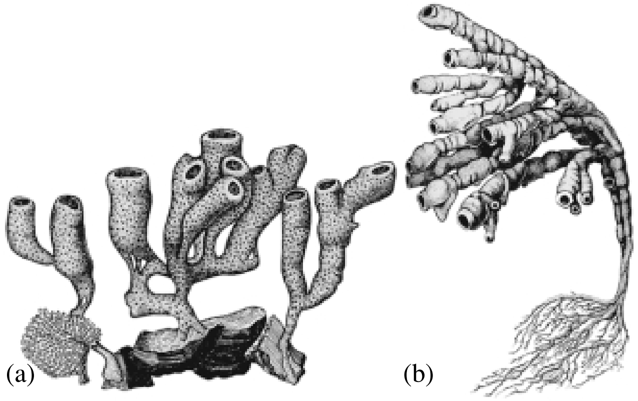

Fig. 12. Sponges with well-pronounced oscular tubules: (a) *Reniera implexa*; (b) *Siphochalina annulata* (from Ridley and Dendy [74]).

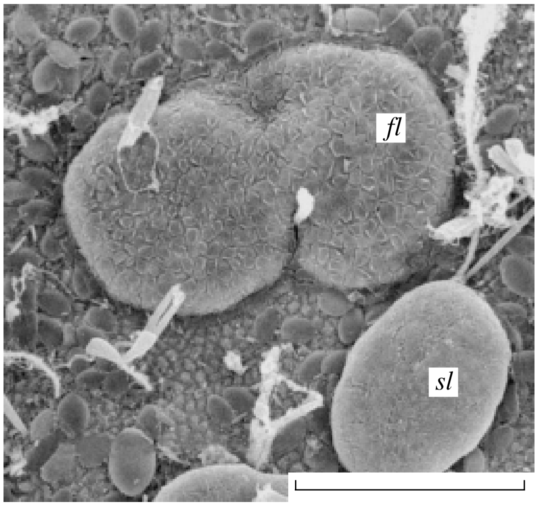

Fig. 13. Fused larvae and a solitary larva of *Halisarca dujardini* in the first stages of metamorphosis (SEM): (*sl*) solitary larva; (*fl*) fused larvae; (Scale bar) 75 μm.

less homogeneously scattered throughout the body (Fig. 11). In such sponges the general integration at the organism level suppresses the integration of certain modules [12, 14]. The intermediate position between these two groups is occupied by sponges with a small number of well-pronounced oscular tubules, like, for example, *Leucosolenia*, *Siphochalina annulata*, and *Reniera implexa* (Fig. 12). In this group of sponges the integration at organism level does not suppress strongly the integration of modules. Vasiform, tubular, cylindrical sponges with well-developed secondary osculum that are characterized by even greater organism integration on the basis of oligomerization of oscula seem to be closer to the first group (Fig. 9).

Immunological Aspect

There is a widespread opinion that sponges in different stages of ontogenesis are able to fuse to each other to form a solid organism [10, 11, 33]. In some recent papers it has been shown that metamorphosing larvae, in different numbers, could actually fuse together to form a solid sponge (Fig. 13) [9, 27, 44, 58, 86]. Moreover, the process of fusion of tissues has been described many times in the germinating gemmulae of freshwater sponges [90, 91]. However, it has been shown both in natural circumstances and under experimental conditions that complete fusion is possible only in the case of a mass germination of gemmulae or the growth of young sponges belonging to the same clone, i.e., genetically identical [86, 91]. This also refers to the fusing larvae; such a process is possible only between the offspring of one parental sponge (Fig. 13).

In order to get evidence of the immunological uniqueness of a spatially isolated sponge (an individual), numerous experiments have been carried out on syngenic, allogenic, and xenogenic transfers of tissues (see Simpson [81]). It has been shown in different species of sponges that allogenic and xenogenic transplants are never accepted and the mechanisms of graft rejection and immune reactions might show significant variations even in closely related species [34–36, 39, 87, 88]. For instance, in the contact zone between specimens of *Ephydatia fluviatilis* belonging to different clones, a collagen barrier develops produced by collencytes and spongiocytes migrating from deeper layers of the sponge [36]. The allogenic and xenogenic rejection represent an expression of mechanisms that under normal conditions allow the retention of the morphological, physiological, and genetic integration of an individual [87].

The fundamental characteristics of a biological individual are its genetic uniqueness and guaranteed preservation in cases of interactions with environmental factors. Accordingly, every organism, irrespective of its level of organization, could distinguish its own components from alien ones; i.e., it is capable of quasi-immune recognition. As we have ascertained, Porifera represent no exclusion from this rule, therefore the immunological evidence might realistically be regarded in favor of the point of view that considers any morphologically isolated sponge as an individual.

CONCLUSIONS

The above analysis allows us to conclude that sponges cannot be regarded as colonial animals, as they have no zooids. Growth and budding in sponges are based on different mechanisms. During growth, as well as in the course of movement, the major mechanism is rearrangement of structures accompanied by disorganization and reorganization of tissues and elements of the aquiferous system and also the migrations of different cells in proportions characteristic of a normal mesohyl. During budding in Demospongiae this is the migration of polypotent and secretory cells into the nucleus of the developing bud. In Homoscleromorpha budding takes place as protrusions of the body wall by means of evagination. The buds of sponges, unlike modules, always detach from the body. Blastogenesis by means of division has never been described in sponges. Therefore, we cannot consider sponges as colonies of zooids arising as a result of an incomplete asexual reproduction. The multioscular body of sponges consists of modules rather than of zooids. The pattern and causes of morphogenesis of a module and blastogenesis during budding are different.

A biological module is considered as "any of multiple parts of an organism having a constructive importance" [16]. All structures in organisms of sponges are polymerized, and they have no "solitary" organs except the osculum in monooscular specimens. It is pertinent to note that major structural–functional units of the aquiferous system (choanocyte chambers and incurrent and excurrent canals) are characterized by a stable size in every particular species [21, 22]. It should be emphasized, however, that the aquiferous module, at least in some demospongians, does not have any stable size and shape. For example, a monooscular aquiferous system (module) of *Polymastia mamillaris* provides life activities of sponges of any size and the development of new aquiferous systems does not affect the growth of the sponge [18]. Sponges of the same species having the same size might comprise different numbers of aquiferous modules depending on particular environmental conditions.

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