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REVIEWS

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## In Search of the Ancestral Organization and Phylotypic Stage of Porifera

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**Abstract**—Each animal phylum has its own *bauplan*. The phylotypic stage is the ontogenetic stage during which the phylum level characteristics appear. This stage refers to different stages of development in different animals. Sponges are one of the simplest, and probably the oldest multicellular lineage of extant animals. On the basis of the analysis of sponge development during (i) sexual and asexual reproduction, (ii) regeneration from small body fragments, and (iii) cell reaggregation, we suggest a hypothetical variant of their phylotypic stage (*spongotype*): the mono-ocular juvenile—the rhagon. The major feature, which permits to consider the rhagon as the phylotypic stage of the Porifera is the final, definitive position of all the cellular and anatomical elements of the future adult sponge. It seems that at the rhagon stage the pattern of the axial complex of anlagen is already formed, and only growth processes occur at the later stages.

**Keywords:** Porifera, phylotypic stage, *Bauplan*, rhagon, metamorphosis, regeneration, budding, gemmule hatching, evolution

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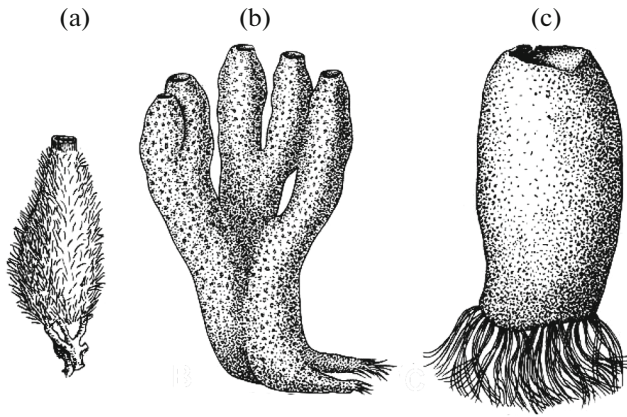
### INTRODUCTION

Bauplan (construction plan) is a key notion of developmental biology and evolutionary morphology, applied during the establishment of new taxonomic phyla and the construction of high-level classification. It is the bauplan, or morphological type, that was assumed by Cuvier (1817) to be the basis for the division of animals into four large groups (vertebrates, mollusks, articulates and radiates). Bauplan can be understood as the type of construction of a given organism, as formed within a certain group and characterized by original architectonics.

There are two main concepts involved in bauplan. The first stems from Owen's ideas concerning the archetype (Owen, 1848), and is based on the comparison of adult animal structures, with no consideration of the preceding stages of development. It is well-known, however, that similar developmental types may result in very different adult animals, while different developmental types may produce similar organisms (see for references: Ivanova-Kazas, 1995; Gilbert and Raunio, 1997). The second concept is based on the comparison of the structure of the larvae, which are rather conservative in their evolution (see: Raff, 1996), and also fails to take into account embryonic development.

Contemporary to Cuvier, the notion of the “developmental plan” was introduced by von Baer (1828), for whom each body plan was seen as being created by a particular kind of developmental organization—the Type. Therefore, the developmental plan sensu von Baer is the bauplan in the period of its ontogenetic formation, and von Baer's observations were to provide foundational evidence supporting Darwin's theory of common descent (Darwin, 1859).

Each animal phylum thus has its own bauplan and consequently, must have its own developmental plan. There are, however, groups of phyla or classes, which, while differing in development, do possess a common stage. This is the case of the coelomic Spiralia, comprising the phyla Annelida, Mollusca, and Sipunculida. The adult representatives of these phyla are essentially different, as are their morphogeneses, but most of them have a common stage—the trochophore. At this stage, the bauplan of this animals group as a whole reveals itself. Seidel (1960) was the first to focus on this stage, naming it the *Korpergrundgestalt*, while Sander (1983) later termed it the phylotypic stage. Both these authors considered such a stage to be decisive in the development of an animal group. They attached no phylogenetic significance to the intermediate pro-



**Fig. 1.** Sponges with a clear radial symmetry around the apical–basal axis. (a) The mono-ocular sponge *Sycon* sp.; (b) *Haliclona* sp. with radially symmetrical branches; (c) *Rossella* sp. with secondary osculum.

cesses and stages such as cleavage, gastrulation and morphogenesis.

The phylotypic stage returned to the spotlight after investigations by Slack et al. (1993), with discussions centering on the molecular-biological data. These authors characterized the phylotypic stage as the stage during which the main morphogenetic movements are complete and all the anlagen are in place, i.e. when the axial complex of anlagen has been formed. In other words, the phylotypic stage is the embryological stage during which the phylum level characteristics appear. Phylotypic stages have been revealed in many animals: the tailbud stage (pharyngula) in vertebrates, the germ band stage in arthropods, the fully segmented, ventrally closed leech embryo etc. (Slack et al., 1993; Minelli and Schram 1994; Hall, 1998; Gilbert, 2013).

Phylotypic stages are not the earliest stages in embryogenesis. Moreover, they may ‘travel’ along a relative timeline of ontogenesis in different representatives of the group. These heterochronic shifts may be associated with adaptations of early stages, with various reproductive strategies and tactics, with the nurturing needs of the embryo, etc.

At the same time, phylotypic stages themselves are the least subjected to adaptive modifications (Slack et al., 1993). Conservative phylotypic stages are sandwiched between the preceding and the subsequent, more evolutionary plastic, stages.

The morphological pattern in general has been described as the developmental hourglass model, which assumes that developmental constraints maximize during mid embryogenesis (Duboule, 1994; Raff, 1996), resulting in morphological conservation during this phase. The conserved expression of Hox cluster genes along the anteroposterior axis of various bilaterians is one of the most frequently cited examples supporting the evolutionary conservation of mid-embryonic stages (Slack et al., 1993; Duboule, 1994;

Raff, 1996). Today, based on the developmental hourglass model, conserved stages during embryogenesis and their role in constraining the animal body plan are being actively investigated (Kalinka and Tomancak, 2012; Drost et al., 2017; Yanai, 2018).

It should be noted, however, that the validity of the phylotypic stage has been questioned, both on the basis of comparative studies showing that the uniformity of the putative phylotypic stages is in fact absent, and also on the basis of considerations concerning the typological connotations of this concept (e.g. Richardson et al., 1997, 1998; Félix, 1999; Scholtz, 2004, 2005).

The phylotypic stages were described and characterized not for all animal phyla. For example, the presence or absence of the phylotypic stage in the ontogeny of representatives of such a large and diverse group as Porifera has never been discussed. This review is the first attempt to search for the phylotype stage in the development of sponges.

#### IDENTIFICATION OF THE PHYTOTYPIC STAGE IN THE ONTOGENESIS OF PORIFERA

The formation of complex body in multicellular animals during ontogenesis is controlled by sophisticated cascades of regulatory genes, whose expression is spatially and temporally ordered (Peter and Davidson, 2011). Investigations of the role of regulatory genes in the embryonic development of Porifera are few, but it has been shown that sponges have a genetic mechanism of specification of the regional morphological differentiation along the body axis of the larva and the adult sponge (Degnan et al., 2015). Indeed, all mono-ocular sponges and all radially symmetrical sponges with a secondary osculum have a clear radial symmetry around the apical-basal axis (Fig. 1). In almost all sponges, the body is regionalized into the ectosome and the endosome, with corresponding differences in the structure of the skeleton and the aquiferous system (Ereskovsky and Lavrov, 2019).

Here we will not discuss the molecular aspects of the problem of phylotypic stage in sponges due to the lack of sufficient comparative data. However, we will consider data concerning the comparative embryology of these animals from a morphological point of view.

#### *The Development of Sponges during Sexual Reproduction*

As mentioned above, the phylotypic stage refers to different stages of embryonic development in all animals studied. Morphologically speaking, it is not possible to highlight any common stage for all sponge clades due to the high polymorphism of their early development (Ereskovsky, 2010). The same cleavage pattern and the same blastula type may result in the development of different types of larvae or, conversely, larvae of the same type may result from different cleavage patterns and larval morphogenesis (Fig. 2).

For example, in sponges there are four known types of cleavage: incurvational (subclass Calcarea: Calcarea), polyaxial (subclass Calcinea: Calcarea and Halisarcidae: Demospongiae), radial-like (Chondrosidae, Spirophorida, Polymastiida: Demospongiae and Hexactinellida) and chaotic (all Homoscleromorpha and most Demospongiae) (Fig. 2: 1–4). These four main cleavage patterns of sponges result in three main blastula types: stomoblastula, coeloblastula and morula (Fig. 2: 5–9). On the other hand, the latter two blastula types emerge as a result of different cleavage patterns (Fig. 2). Embryonic morphogeneses involved in larva formation in sponges are also very diverse, leading to nine larval types (Ereskovsky and Dondua, 2006; Ereskovsky, 2010).

All larvae have a strongly pronounced anterior-posterior polarity, which is expressed in the structure of the layer of external cells, in the organization of the internal cell mass (if present) and in the distribution of spicules (if present). In general, there are two principal larval constructions in sponges: first, hollow single-layered larvae (coeloblastula, calciblastula, cinctoblastula, amphiblastula), and second, two-layered larvae lacking a cavity (parenchymella, hoplitomella, trichimella) (Fig. 3) (Ereskovsky, 2010).

The main feature of the metamorphosis of sponge larvae is the acquisition of the sponge *bauplan*, which is primarily represented by the aquiferous system. The first adult structure to be formed *de novo* is the exopinacoderm, which isolates the young sponge from the aquatic environment. Later steps include the organization of the choanocyte chambers and the water current canals, the opening of the ostia and osculum, and the acquisition of the elements of the adult skeleton.

Morphogenesis during metamorphosis depends essentially on the larval type (its structure). Larval metamorphosis usually results in a mono-ocular individual, whose aquiferous system often differs from that of the adult sponge. In the Calcarea, a young individual such as this has the aquiferous system of the asconoid type and is called the *olyntus* (Minchin, 1900); in the Demospongiae and the Homoscleromorpha it has the aquiferous system of the leuconoid or syconoid type and is called the *rhagon* (Figs. 4, 5a, 5b) (Sollas, 1888). However, there are no fundamental differences between the structure of rhagon and olintus.

In sponges with direct development upon leaving the maternal organism (in cases of viviparity), or in those which develop in the aquatic environment (in cases of oviparity), development leads to formation of juveniles exhibiting rhagon structure (Watanabe, 1978; Sara et al., 2002).

#### *The Development of Sponges during Asexual Reproduction*

General characteristics of the buds formed in all sponges except *Oscarella* (Homoscleromorpha) (Ere-

skovsky and Tokina, 2007) appear during the initial stages of development, when they look like a dense conglomerate of different cell types at the parent sponge surface. Such buds have neither canals nor an osculum, and only very rare choanocyte chambers (for review see: Fell, 1993; Ereskovsky et al., 2017). After detachment from parent body, buds settle on the substrate, attach to it and begin the formation of the aquiferous system and growth. Thus, the buds of all sponges resemble first the pupae, and then the rhagon, the stage, which forms after larval settlement (Fig. 5c).

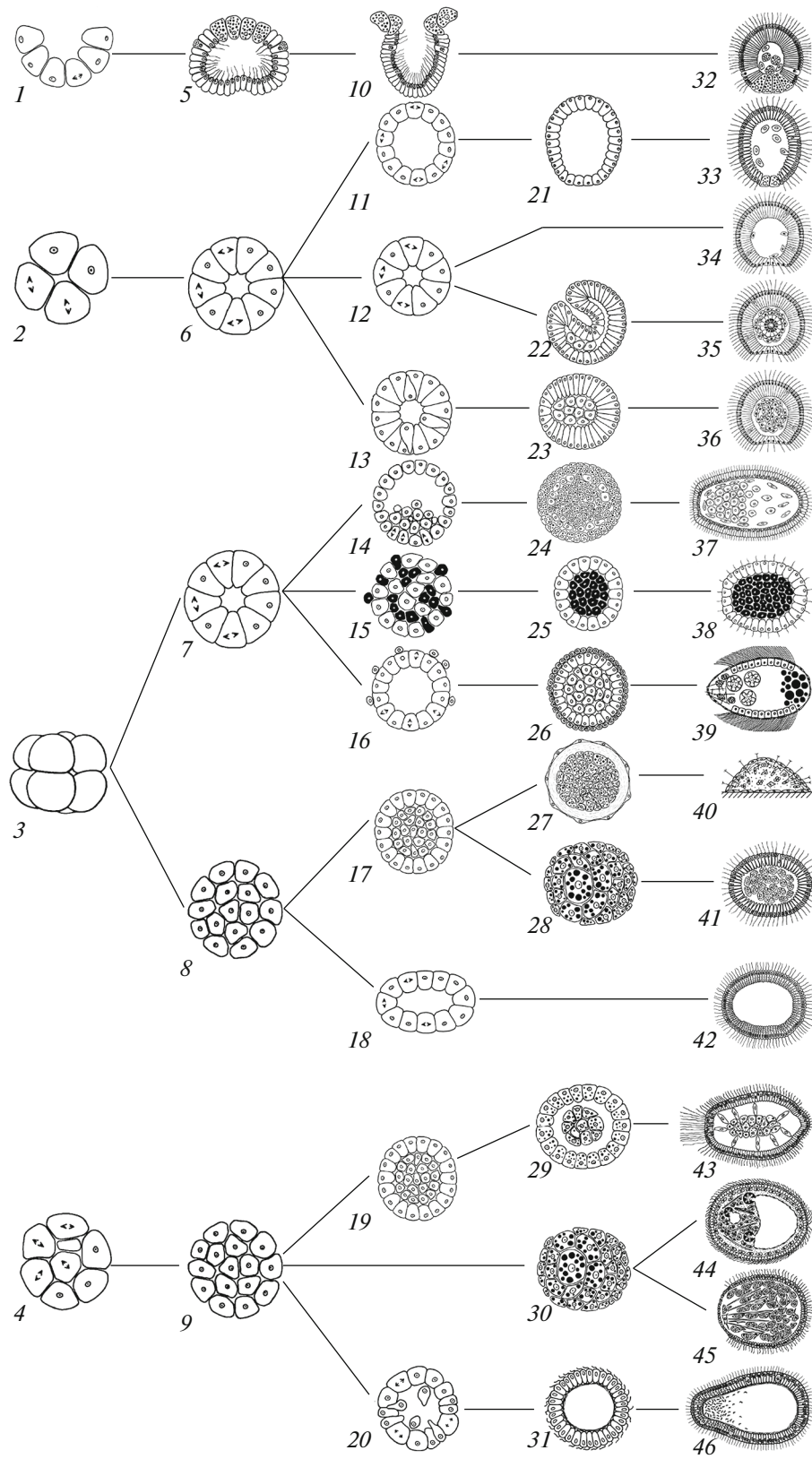
Budding in the Homoscleromorpha is essentially different from that in the other sponges, with differences concerning both morphogenesis and bud structure. The bud develops from the outgrowths of the parent body wall that is formed by the epithelial morphogenesis—evagination. The cells at budding sites do not migrate to the periphery, nor do they form condensations, nor do they proliferate. The types of cells constituting the bud is identical to that of the resulting definitive sponge (Ereskovsky and Tokina, 2007). Before attachment to the substrate, the bud has the rhagon structure with a syconoid aquiferous system.

Many freshwater and a few estuarine/marine demosponges produce dormant structures called gemmules (Simpson, 1984; Fell, 1993). Each gemmule consists of a compact mass of essentially identical cells surrounded by a collagenous capsule, which in many cases contains spicules. Gemmule hatching involves the mitotic division of the thesocytes (internal totipotent cells), active cell migration and differentiation, and results in small functional juvenile sponges with rhagon organization and leuconoid aquiferous systems (Fig. 5d) (Brien, 1932; Höhr, 1977).

In this way, sponge juveniles resulting from asexual reproduction—budding and gemmule hatching—have the same rhagon structure.

#### *The Development of Sponges during Regeneration*

Numerous experiments on sponge cell dissociation and subsequent reaggregation have shown that in many sponges this leads to the formation of a compact spherical body, contrasting with the rather loose, irregular cellular contacts during aggregation (Lavrov and Kosevich, 2014, 2016). The formation of the pinacoderm represents the first step in the reorganization of tissue-like structures. This stage, termed “primorphs” (Custodio et al., 1998) marks the completion of the aggregation of cellular material and the separation of the internal environment from the external one by a continuous pinacoderm. After attachment and stable fixation onto the solid substrate, this stage will lead to morphogenetic processes ending in the full reorganization of the small but fully functional and well-structured sponge (Lavrov and Kosevich, 2014, 2016). This stage also has the structure of a rhagon (Fig. 5e).



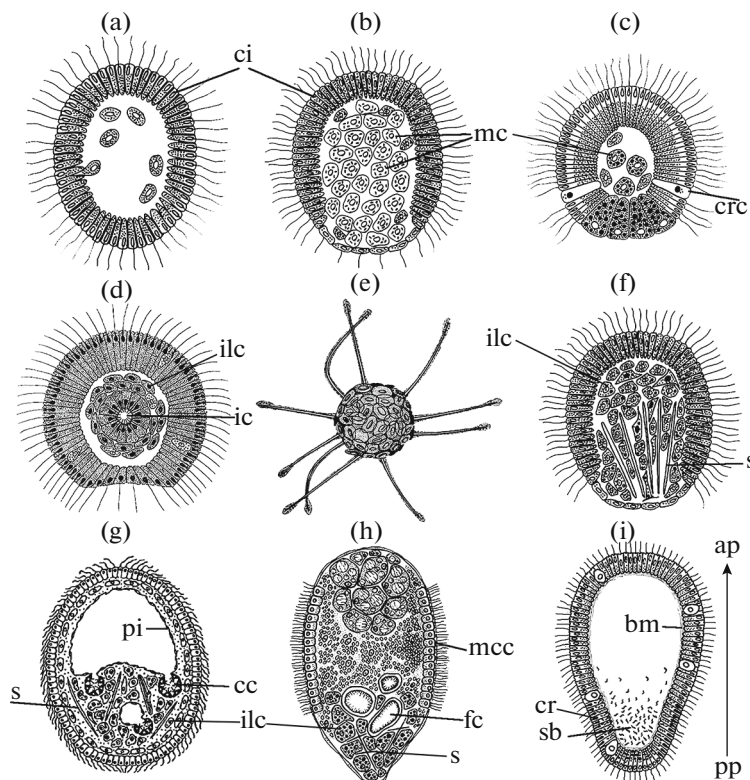
**Fig. 2.** Diagram of cleavage and morphogenesis, leading to the formation of sponge larvae. (1–4) Cleavage patterns in sponges: incurvational (1), polyaxial (2), radial (3), and chaotic (4). The three main forms of sponge blastula: stomoblastula (5), coeloblastula (6, 7), and morula (8, 9). (10–31) Morphogenesis and pre-larvae. (32–46) Larvae. (10) Incurvation; (11, 12) the coeloblastula organization is retained until the larval stage; (13) multipolar ingression; (14) unipolar proliferation; (15, 25) ingression of maternal cells (black) inside the morula; (16) cell delamination; (17) morula delamination; (18) flattening of morula; (19) morula delamination; (20) multipolar emigration; (21) coeloblastula of *Calcinea* with no basement membrane; (22) invagination; (23) pre-parenchymella; (24, 27, 28, 29, 30) morulae; (25) pre-pseudoblastula; (26) bilayered morula; (31) coeloblastula of *Homoscleromorpha* with basement membrane; (32) amphiblastula of *Calcaronea*; (33) calciblastula of *Calcinea*; (34) coeloblastula of *Halisarcidae*; (35) disphaerula of *Halisarcidae*; (36) parenchymella of *Halisarcidae*; (37) parenchymella of *Verticillitidae*; (38) pseudoblastula of *Chondrosida*; (39) trichimella of *Hexactinellida*; (40) juvenile sponge of *Tetilla* formed in the course of direct development of; (41) parenchymella of *Tethyida*; (42) coeloblastula of *Polymastia* and *Chondrilla*; (43, 44, 45) parenchymellae of *Dendroceratida* (43), *Haplosclerida* (44), *Poecilosclerida* (45); (46) cinctoblastula of *Homoscleromorpha*. (Modified from: Ereskovsky, 2010).

A young sponge, which develops from a small body fragment, has the same rhagon structure in spite of the differences in the adult sponges (donors) body structure (Fig. 5f). In the case of asconoid sponges, this development does not involve any breakdown of the three-layer organization of sponges: pinacocyte epithelium, mesohyl and choanocyte epithelium. These layers bend inwards, thus closing off the inner cavity (Jones, 1957). Small fragments of the syconoid sponge body undergo complicated, destructive changes in the parts of the canal system adjoining the wound surface (Korotkova et al., 1965). Development of leuconoid

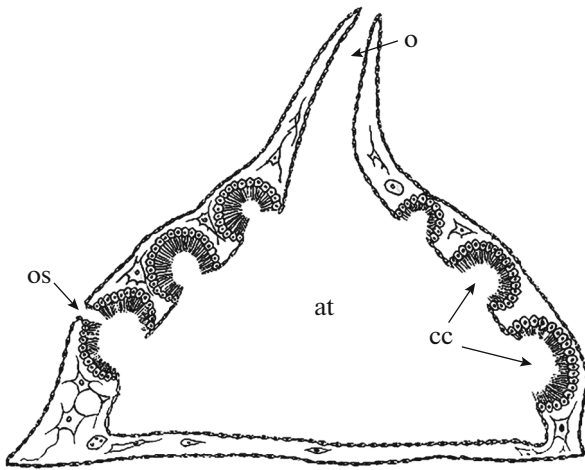
sponges from small fragments of the body also involves dramatic reconstruction of the initial structure (Connes, 1966; Korotkova and Nikitin, 1968).

*Rhagon—The Phylotypic Stage of Porifera*

On the basis of the analysis of sponge development during (i) sexual and asexual reproduction, (ii) regeneration from small body fragments, and (iii) cell reaggregation, a hypothetical variant of their phylotypic stage (*spongotype*) can be suggested. This is the monocular juvenile—the rhagon: the organization type of



**Fig. 3.** The types of sponge larvae. (a) Calciblastula; (b) Pseudoblastula; (c) Amphiblastula; (d) Disphaerula; (e) Hoplitomella; (f) Parenchymella (example of *Poecilosclerida*); (g) Parenchymella of *Haplosclerida*; (h) *Trichimella*; (i) *Cinctoblastula*. ap— anterior pole, bm—basement membrane, cc—larval choanocyte chamber, ci—ciliated cells, cr—cells with intranuclear crystalloids, crc—cross cells, fc—flagellated chamber, mc—maternal cells, ic—internal chamber, ilc—internal larval cells, mcc—multiciliated cells, pi—larval pinacoderm, pp—posterior pole, s—larval spicules, sb—symbiotic bacteria. (Modified from: Ereskovsky, 2010.)



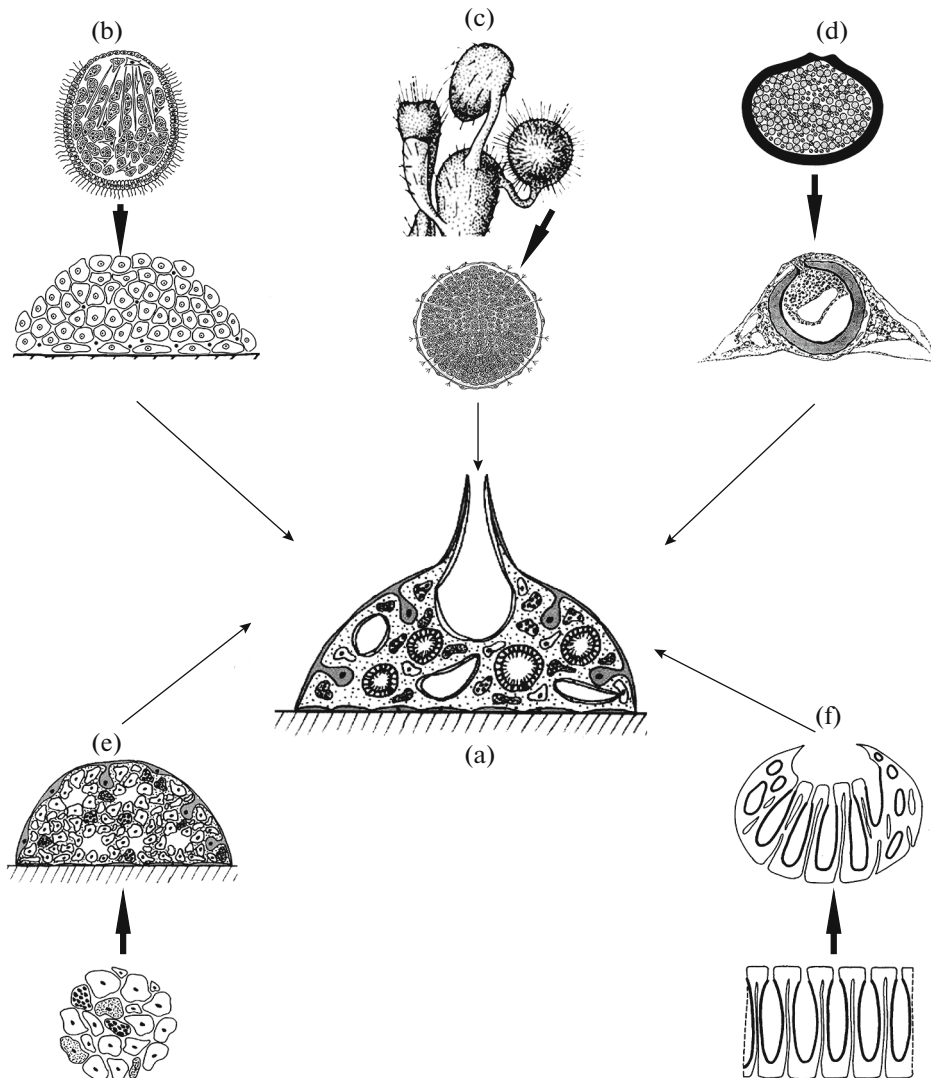
**Fig. 4.** The stage of rhagon. at—Atrium; cc—choanocyte chambers; o—osculum; os—ostium. (Modified from: Sollas, 1888).

the Demospongiae, and the olinthus corresponding to it in the Calcarea (Figs. 4, 5a). The rhagon is a small sponge (up to 1–2 mm) with a surface formed by flattened epithelial cells (pinacocytes) that excrete the extracellular matrix. It is characterized by radial or radial-like symmetry and well-defined apical-basal axis.

The major feature which allows to consider the rhagon as the phylotypic stage of Porifera is the final, definitive position of all the cellular and anatomical elements of the future adult sponge. It seems that at the rhagon stage the pattern of the axial complex of anlagen is already formed, and only growth processes occur at the later stages.

**CONCLUSIONS**

To conclude, this review has shown that development of almost all representatives of sponges occur-



**Fig. 5.** Different ontogenetic processes leading to the formation of a spongotype. (a) Spongotype; (b) larval metamorphosis; (c) sponge development from a bud; (d) sponge development from a gemmule; (e) cell reaggregation; (f) regeneration of sponge from small body fragment.

ring in different situations (sexual/asexual reproduction, regeneration) and by different set of morphogenesis lead to the stage common for all Porifera: that of the rhagon, which can be characterized by its structural similarity across this phylum. We propose that this stage can be considered not only as a phylotypic stage, but also as a model of putative ancestral sponge—a *spongotype*. The stage of rhagon is typical for Demospongiae, and it corresponds to olintus, characteristic of Calcarea (Figs. 4, 5a). In order to confirm or disprove these conclusions, it is necessary to conduct a detailed study of the molecular mechanisms that regulate the formation of rhagon in representatives of different phylogenetic groups of sponges. Such a study will improve our understanding of the mechanisms involved in the evolution of the body plans of sponges and other multicellular animals.

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#### COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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