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COMPARATIVE EMBRYOLOGY OF SPONGES AND ITS APPLICATION FOR PORIFERAN PHYLOGENY

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ABSTRACT

On the basis of original and literature data on embryonic development of Porifera, 7 developmental types accompanying sexual reproduction may be found within recent sponges. These types are called by the names of the resulting larvae: I - "trichimella" (Hexactinellida); II - "calciblastula" (Calcinea); III - "amphiblastula" (Calcaronea); IV - "cinctoblastula" (Homoscleromorpha); V - "disphaerula" (Halisarcida); VI - direct development (Tetilla, Spirophorida); VII - "parenchymella" which can be subdivided in to three subtypes: subtype 1 (Dendroceratida, Dictyoceratida, Halichondrida, Hadromerida); subtype 2 (Poecilosclerida); subtype 3 (Haplosclerida). The results of embryological analysis of sponges emphasize the necessity for further investigations of sponge embryology and reevaluation of phylogenetic relationships between some poriferan groups. According to morphological and embryological data the Homoscleromorpha is not subclass of the Demospongiae; this group of sponges shares several characteristics with the Eumetazoa.

KEY WORDS

Comparative embryology, Porifera, phylogeny.

INTRODUCTION

Biologists have long recognized that evolution of development is the key to morphological evolution. Comparative embryology provides many examples of conserved patterns of cell lineage, gene expression and morphogenetic movement within phyla and classes (IVANOVA-KAZAS, 1995; RICHARDSON *et al.,* 2001).

The Phylum Porifera consists of three classes: Hexactinellida, Calcarea and Demospongiae. All known Hexactinellida and Calcarea are ovoviviparous, whereas among the Demospongiae are both ovoviviparous and oviparous species. The diversity of morphogenesis accompanying reproduction in various representatives of Porifera has attracted the attention of researchers interested in classification (LÉVI, 1956; BOROJEVIC, 1970; BRIEN, 1973a; KOROTKOVA, 1981; FELL, 1989; ERESKOVSKY & KOROTKOVA, 1997, 1999). Earlier authors, however, had at their disposal only fragmentary material, in need of revision. This stimulated us to undertake original comparative-embryological investigations of a number of demosponge species.

Porifera during the development pass a series of developmental events (stages and morphogenetic movements), characteristic for Eumetazoa. The fertilized egg undergo a cleavage: successive mitotic divisions into an organized multicellular form.

There are few ways in which patterned cells cleavage can occur. A hollow (coeloblastula) or solid (stereoblastula or morula) blastula forms in a result of cleavage. Profound, but well-ordered, rearrangements of cells starts in the blastula. Cells can undergo changes either autonomously or in conjunction with their neighbors to form the embryo. The consequences of changes in cell shape and motility will be quite different if cells are joined in an epithelium than when they are unconstrained by neighbors. In this paper I define the former morphogenetic movements as "epithelial morphogenesis", for example, invagination and the later as "mesenchymal (or cellular) morphogenesis", for example, multipolar ingression. Patterns of morphogenesis vary widely but involve combinations of the some type of movements (GILBERT, 2000). Cells differentiation, larval structures development and axialisation of larva (an antero-posterior axis formation) take place during the sponge embryonic morphogenesis. Swimming larvae attach to the substrate and start a metamorphosis. In the course of metamorphosis, sponge larva undergoes a dramatic transformation into an juvenile sponge (rhagon or olynthus). During a metamorphosis occurs both epithelial and mesenchymal morphogenesis.

I propose that reproductive processes and structures in the Porifera -- such as cleavage pattern, mode of morphogenetic movements, the type of the larva and the morphogenetical processes of metamorphosis -- could be apomorphies and/or synapomorphies at high taxonomic level, as in the case with other multicellular animals.

The objective of the present research was to define the developmental types that occur in the recent sponges, to determine their specificity for sponge macrogroups and to ascertain the possibility of using comparative-embryological method for constructing phylogenetic relationships among the Porifera. By the type of development I mean an evolutionary established sequence of invariant stages characteristic of the development of animals within high taxonomic groups (above the order). Different animal groups that fall into one and the same type of development can be considered as monophyletic.

MATERIAL AND METHODS

The development of 26 species from 7 orders of the class Demospongiae from the White, the Barents, the Okhotsk and the Mediterranean Seas was personally studied (Appendix 1). Light, transmission and scanning electron microscopy were used accordingly with previous papers (ERESKOVSKY & GONOBOBLEVA, 2000; ERESKOVSKY & BOURY-ESNAULT, 2002).

Data on the development of the oviparous sponges from the orders Agelasida, Astrophorida, Chondrosida, "Lithistida", Verongida and suborder Petrosina (order Haplosclerida) are either absent or fragmentary. I have not examined the orders in which the development of only one species has been investigated.

The main characters used for comparison were 1 – egg type; 2 – cleavage pattern; 3 – blastula type; 4 – features of the morphogenesis of the larva; 5 – the stage that anterior-posterior polarity is formed; 6 – larval type; 7 – ultrastructural characters of the larva; 8 – the morphogenetical processes of metamorphosis.

DESCRIPTION OF DEVELOPMENTAL TYPES

On the basis of my original research and data from the literature, 7 types of development accompany sexual reproduction in recent sponges. I propose to call these types by the names of the resulting larvae. The apomorphic characters for each developmental type are given in Tab. I.

Tab. I. Apomorphic traits of ontogenesis characteristic of developmental types of the sponges.

Developmental types	Characters
"Trichimella" type (Hexactinellida)	1. Pseudospiral cleavage.
	2. Cellular delamination accompanying larval development.
	3. Trichimella larva: a) multiflagellate cells; b) syncytial structures; c) lack of flagellar rootlet.
"Calciblastula" type (Calcinea)	1. Calciblastula larva.
"Amphiblastula" type (Calcaronea)	1. Cleavage of table palyntomy type.
	2. Stomoblastula.
	3. Excurvation.
	4. Amphiblastula larva.
"Cinctoblastula" type* (Homoscleromorpha)	1. Multipolar egression accompanying larval development.
	2. Cinctoblastula larva; basement membrane; cells with intranuclear crystalloid.
	3. Invagination during a metamorphosis.
"Disphaerula" type* (Halisarcida)	1. Polyaxial cleavage.
	2. Multipolar ingression accompanying parenchymella-like and disphaerula development.
	3. Invagination accompanying disphaerula development.
	4. Disphaerula larva.
	5. Epithelial and mesenchymal morphogenesis accompanying metamorphosis.
Direct development (*Tetilla*, Spirophorida)	1. Fertilization coat.
	2. Absence of larva in the ontogenesis.
"Parenchymella" type*	1. Telolecithal egg (in Poecilosclerida)
	2. Trophocytes in the egg (in Haplosclerida).
	3. Morular delamination (epiboly in Poecilosclerida).
	4. Parenchymella larva.

The class <u>Hexactinellida</u> is the least studied class of sponges. At present, data on the development of only two hexasterophoran species are available (OKADA, 1928; BOURY-ESNAULT & VACELET, 1994; BOURY-ESNAULT *et al.,* 1999; LEYS, 2003). Even these data, however, are sufficient to allow us to treat the type of development seen in the Hexactinellida.

I. "Trichimella" developmental type of Hexactinellida (Fig. 1)

The egg is isolecithal, oligolecithal, non-polarized (OKADA, 1928; BOURY-ESNAULT *et al.,* 1999). No specialized trophocytes have been described. Cleavage is total, equal and pseudospiral. The embryo is organized as a hollow blastula throughout the early development (OKADA, 1928; BOURY-ESNAULT *et al.,* 1999). Cleavage is followed by cellular delamination, and a two-layered stereoblastula is formed (BOURY-ESNAULT *et al.,* 1999). Antero-posterior polarity of the larva becomes expressed in the course of its differentiation. Development results in the formation of a trichimella larva (BOURY-ESNAULT & VACELET, 1994; BOURY-ESNAULT *et al.,* 1999). Perforate plugged junctions between archaeocytes-like cells are present (LEYS, 2003) and the apical-junctional complexes like a *zonula adhaerens* between multiflagellated cells might be present (BOURY-ESNAULT *et al.,* 1999). A flagellar rootlet in flagellated epithelium is absent (BOURY-ESNAULT *et al.,* 1999). Metamorphosis has not been described.

Within the class Calcarea, two developmental types, corresponding to the Calcinea and the Calcaronea can be clearly defined.

II. "Calciblastula" developmental type of Calcinea (Fig. 1)

The egg is isolecithal, oligolecithal, and non-polarized (BOROJEVIC, 1969; JOHNSON, 1979). Special trophocytes are absent. Cleavage is total, equal, and a cleavage cavity is present. The embryo is organized as a hollow blastula throughout development (MINCHIN, 1900; BOROJEVIC, 1969; JOHNSON, 1979). Antero-posterior polarity becomes expressed towards the end of larva formation. The larva is calciblastula (coeloblastula). Flagellated cells are the predominant larval cell types, bottle-shaped and vacuolar cells also present (AMANO & HORI, 2001). The flagellar rootlet is cross-striated (BOROJEVIC, 1969; AMANO & HORI, 2001). Metamorphosis is mesenchymal (see definition above) and is accompanied by the migration of some of the flagellated cells into the blastocoel and their transformation into choanocytes and amoebocytes; the cells remaining on the surface transform into pinacocytes (BOROJEVIC, 1969; AMANO & HORI, 2001). The antero-posterior axis of the larva becomes the baso-apical axis of the olynthus (juvenile sponge).

III. "Amphiblastula" developmental type of Calcaronea (Fig. 1)

The egg is isolecithal or oligolecithal, oval in shape. Its short axis is regarded as an animal-vegetative axis. A complex of specialized trophocytes is present (GALLISSIAN, 1981; FRANZEN, 1988; GALLISSIAN & VACELET, 1992). Cleavage is total, unequal, and of table palyntomy type (ANAKINA, 1997). The embryo is organized as a hollow blastula throughout the development. The blastula, however, is inverted - a stomoblastula (DUBOSCQ & TUZET, 1937; FRANZEN, 1988; GALLISSIAN & VACELET, 1992). The formation of the amphiblastula larva is accompanied by excurvation (turning inside out) of the stomoblastula (DUBOSCQ & TUZET, 1937; ANAKINA, 1981; FRANZEN, 1988; GALLISSIAN & VACELET, 1992). Antero-posterior polarity is evident from the first cleavage cycles. The anterior larval pole corresponds to the vegetative egg pole, and is formed by flagellated cells; the posterior pole is composed of non-flagellated granular cells. Four translucent cells (known as "cellules en croix") are characteristic of the larva (DUBOSCQ & TUZET, 1941; FRANZEN, 1988; GALLISSIAN & VACELET, 1992). The flagellar rootlet is cross-striated (AMANO & HORI, 1992; GALLISSIAN & VACELET, 1992). Metamorphosis is mesenchymal: flagellated cells submerge inside, forming the choanoderm, whereas granular non-flagellated cells of the posterior pole remain on the surface, forming the pinacoderm (AMANO & HORI, 1993). The antero-posterior larval axis becomes the baso-apical axis of the olynthus.

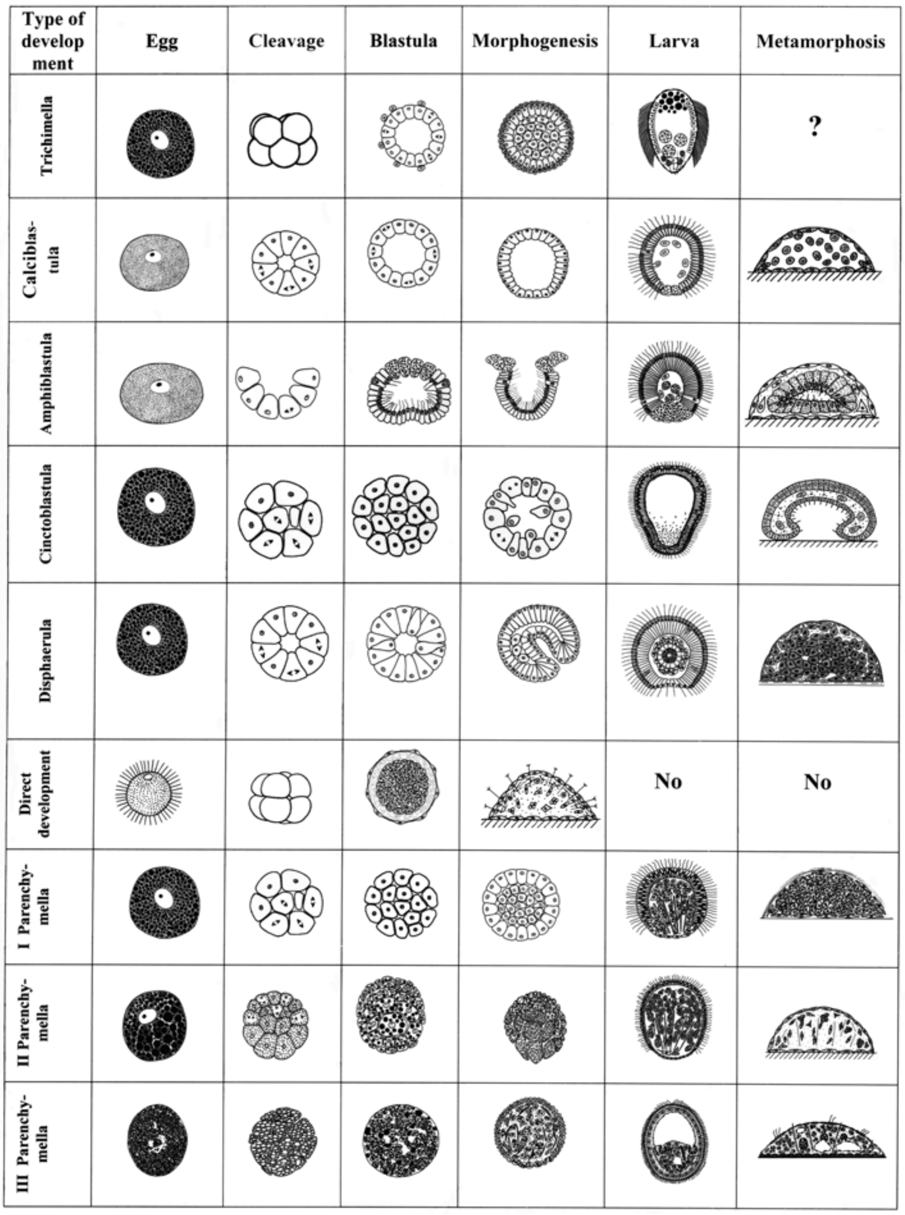

Fig. 1. Schematic diagram of the generalized developmental pathways found in the Porifera. Information for each developmental type was compiled from the authors own observation (*) and from data drawn from the literature cited in the text.

The class Demospongiae, has the greatest morphological diversity of adults among the Porifera, and also possesses the broadest range of reproductive processes.

First of all, two modes of reproduction are clearly distinct: ovoviviparity and oviparity. On the basis of these characters, LÉVI (1956) divided Demospongiae into two subclasses: Ceractinomorpha and Tetractinomorpha. However, ovoviviparity and oviparity in demosponges are also elements of their reproductive strategy. Thus, oviparity is encountered in representatives of the orders Poecilosclerida (*Hemectyon ferox*, *Neofibularia nolitangere*) and Haplosclerida (*Xestospongia*, *Petrosia*) which are usually considered as ovoviviparous (REISWIG, 1976; HOPPE & REICHERT, 1987; FROMONT & BERGQUIST, 1994). At the same time viviparity was described in some *Stylocordyla* species from the order Hadromerida the representatives of which are oviparous (BERGQUIST, 1972; SARÀ *et al.,* 2002). Many other marine invertebrates are also known to possess both viviparity, ovoviviparity and oviparity, sometimes even within the same genus, *e.g.*, in Echinodermata or Bivalvia (GILBERT & RAUNIO, 1997). In other phyla viviparity, ovoviviparity and oviparity have not been given taxonomical status.

I share the opinion of VAN SOEST (1991) that oviparity in sponges has appeared several times independently in different demosponge groups and has no phylogenetical significance at a high taxonomical level.

The development of almost all orders of Demospongiae studied has a number of specific traits. However, they are not always sufficient to justify the designation of separate developmental types. I propose to distinguish four developmental types in Demospongiae.

IV. "Cinctoblastula" developmental type of Homoscleromorpha (Fig. 1)

The egg is isolecithal, non-polarized (ERESKOVSKY & BOURY-ESNAULT, 2002). Specialized trophocytes are absent (GAINO *et al.,* 1986). Cleavage is total, equal, chaotic, resulting in the formation of an equal morula; a cleavage cavity is absent (MEEWIS, 1938; ERESKOVSKY & BOURY-ESNAULT, 2002). The development of the coeloblastula takes place by means of multipolar egression (centrifugal migration of the morula cells to the periphery) (ERESKOVSKY & BOURY-ESNAULT, 2002). Antero-posterior polarity becomes evident during cytodifferentiation (BOURY-ESNAULT *et al.,* 2003). The cinctoblastula larva is composed of one-layered flagellated epithelium. A belt of flagellated cells, each with an intranuclear crystalloid is situated at the posterior pole (BOURY-ESNAULT *et al.,* 2003). A basement membrane and belt desmosomes are present (BOURY-ESNAULT *et al.,* 2003). The flagellar rootlet is cross-striated (BOURY-ESNAULT *et al.,* 2003). Metamorphosis is of an epithelial type: the flagellated epithelium of the anterior hemisphere of the cinctoblastula invaginates to form the choanoderm and the endopinacoderm (HEIDER, 1886; MEEWIS, 1938; ERESKOVSKY & BOURY-ESNAULT, unpubl. data). The antero-posterior larval axis becomes the baso-apical axis of the rhagon (juvenile sponge).

V. "Disphaerula" developmental type of Halisarcida (Fig. 1)

The egg is isolecithal, non-polarized (LÉVI, 1956; CHEN, 1976; ERESKOVSKY & GONOBOBLEVA, 2000). Specialized trophocytes are absent. Cleavage is total, equal, polyaxial and a cleavage cavity is present (ERESKOVSKY, 2002). Cleavage results in the formation of either a coeloblastula or a morula (GONOBOBLEVA &

ERESKOVSKY, 2004). The latter develops by means of apolar (multi-polar) ingression of single cells (GONOBOBLEVA & ERESKOVSKY, 2004; ERESKOVSKY, 2004). Antero-posterior polarity of the embryo becomes evident during cytodifferentiation (LÉVI, 1956; ERESKOVSKY & GONOBOBLEVA, 2000). Larval polymorphism is characteristic: coeloblastula-like, parenchymella-like and disphaerula larvae can be encountered (GONOBOBLEVA & ERESKOVSKY, 2004). The internal cellular layer of the disphaerula larva is formed by invagination of the lateral surface of the prelarva (ERESKOVSKY & GONOBOBLEVA, 2000). The apical-junctional complexes like a *zonula adhaerens* is present (ERESKOVSKY, in press). The flagellar rootlet is non-striated. Morphogenesis accompanying metamorphosis is of a mixed character: exopinacoderm development is of an epithelial type, forming from the flagellated cells of the posterior larval pole, whereas development of the basopinacoderm, endopinacoderm and choanoderm is of a mesenchymal type (ERESKOVSKY, in press). The antero-posterior larval axis becomes the baso-apical axis of the rhagon.

VI. Direct development (Spirophorida, *Tetilla*) (WATANABE, 1978; WATANABE & MASUDA, 1990) (Fig. 1)

Tetilla is an oviparous dioecious sponge. Eggs are small, isolecithal, non-polarized. Collagen bundles are present on the egg's surface. Sperm penetration into the egg is followed by fertilization coat formation. Specialized trophocytes are absent. Cleavage is total, equal, and radial up to the 4th cycle. Cleavage results in the formation of equal apolar morula. Morphogenesis is by means of morula delamination. The embryo develops directly into a young sponge, without a larval stage.

VII. "Parenchymella" developmental type

This developmental type occurs both in oviparous and ovoviviparous demosponges with total chaotic cleavage, usually resulting in formation of a morula. Segregation of morular cells into the external and internal layer usually occur by morula delamination; further development leads to the formation of parenchymella larva, with diagnostic features at the order level. The flagellar rootlet is non-striated. Metamorphosis is of a mesenchymal type and might accompanied by exchange of external and internal larval cells. The larval flagellated cells sometimes are partially or completely phagocytosed in the course of metamorphosis. Three subtypes may be outlined within the type.

VII. 1. The first subtype (Dendroceratida, Dictyoceratida, Halichondrida, Hadromerida) (DELAGE, 1892; MEEWIS, 1941; LÉVI, 1956; BOROJEVIC, 1967; EVANS, 1977; FELL & JACOB, 1979; IVANOVA, 1981; KAYE, 1990; KAYE & REISWIG, 1991; MARIANI *et al.*, 2000; ERESKOVSKY & TOKINA, unpubl. data; ERESKOVSKY, in press) (Fig. 1)

The following features characterize this developmental subtype: 1) the egg is isolecithal, showing no traces of polarization; 2) the equal apolar morula (stereoblastula) is formed; 3) antero-posterior polarity of the larva becomes expressed during its cytodifferentiation.

VII. 2. The second subtype (Poecilosclerida) (MAAS, 1893; SIMPSON, 1968; ERESKOVSKY, 1986; MISEVIC *et al.*, 1990) (Fig. 1)

The development of Poecilosclerida is determined by the structure of their egg, which is telolecithal and polarized. Other specific features include: 1) the cleavage is total, unequal or equal, chaotic; 2) dense, polarized, non-equal morula is formed; 3) morphogenesis has a feature of polarized delamination (ERESKOVSKY, in press); 3) animal-vegetative polarity of an egg morphologically corresponds to the larval antero-posterior polarity.

VII. 3. The third subtype (Haplosclerida) (BRIEN & MEEWIS, 1938; FELL, 1969; SALLER & WEISSENFELS, 1985; WEISSENFELS, 1989; IVANOVA, 1997a,b; ERESKOVSKY, 1999; LEYS & DEGNAN, 2001, 2002) (Fig. 1)

This developmental type is characterized by the following features: 1) the egg includes a large quantity of slightly processed phagocyted trophocytes (in marine Haplosclerida); 2) yolk granules may be formed during cleavage; 3) specialized trophocytes are present; 4) parenchymella in the freshwater species possesses almost all definitive cells types, choanocyte chambers, and has some provisional structures: external flagellated layer, skeleton, a spacious cavity lined with pinacocytes.

DISCUSSION AND CONCLUSIONS

The result of comparative-embryological analysis of sponges emphasizes the necessity of further investigation of their development, using modern methods, and of reevaluation of phylogenetic relationships between some poriferan groups.

The least investigated group of Porifera is the Hexactinellida; therefore it is impossible to discuss any phylogenetical relationships inside this class.

The profound difference between developmental types of Calcinea and Calcaronea testify to early divergence in the evolution of these two subclasses of Calcarea. The egg is only one developmental stage, uniting Calcinea and Calcaronea. The ultrastructural characteristics of eggs of all Calcarea are identical whereas they are very different from eggs of other poriferan groups.

The most complicated interrelationships between developmental types are inside the Demospongiae. "Cinctoblastula" developmental type of Homoscleromorpha has some apomorphic characters, which supports the monophyly of Homoscleromorpha (Tab. I). The traits of this developmental type with some ultrastructural features (cross-striated flagellated rootlet, type IV collagen, basement membrane in the larvae and adults, gradient of spermatogenesis inside spermatocyst) make it possible to affiliate them with Eumetazoa.

The "disphaerula" type of development of the Halisarcida also possesses some apomorphy and differ essentially from the development of other Demospongiae. Thus, developmental type of Halisarcida is very specific, which also calls for the revision of the position of this order within Demospongiae.

As for direct developmental type of *Tetilla* (Spirophorida), it is now difficult to say whether it originally consisted of one phase (without a larva) or by means of the larva loss. Anyway, what we know of this type of development until the morula, shares great similarity with "parenchymella" type.

Phylogenetic interrelationships between and within the subtypes of "parenchymella" developmental type are ambiguous. The features of Poecilosclerida development are determined by a more complex egg structure and are undoubtedly a later acquisition in the ontogenetic evolution of Demospongiae.

Haplosclerida development is sure to have undergone adaptive changes connected with adapting to life in marine coastal waters and in freshwater. This is especially the case for the families Spongillidae, Potamolepidae and Lubomirskiidae. The similarity of spermatozoids, eggs, embryological development and larvae morphology supported a close relationships between the freshwater sponges (ERESKOVSKY, 1999). The difference between the development of freshwater and marine Haplosclerida testifies to an early divergence of these two ecological haplosclerid groups.

In the order Hadromerida the development has been investigated in only three genera: *Tethya*, *Cliona* and *Polymastia* (LÉVI, 1956; BOROJEVIC, 1967; MARIANI *et al.,* 2000). Nevertheless within the Hadromerida two different kinds of morular morphogenesis are possible, resulting in the formation of larvae of two types. In the first case (*Polymastia robusta* - Polymastiidae) the morula is transformed into coeloblastula larva by means of simple flattening and re-grouping of cells (BOROJEVIC, 1967). In the second case (*Tethya aurantium* - Tethyidae and *Cliona viridis* - Clionaidae) external and internal layers differentiate in the morula as a result of morular delamination. As a result, a parenchymella larva is formed (LÉVI, 1956; MARIANI *et al.,* 2000). The paraphyly of the order or their early divergence may be the possible explanations of the profound differences between these two developmental patterns.

The difficulties of phylogenetical interpretation of comparative embryology of Porifera are connected with the high degree of polymorphism of their development. The same cleavage pattern and blastula type may be characteristic for several different larval types. For example, radial-like cleavage and formation of an equal morula are characteristic of *Polymastia* (Hadromerida) that has a coeloblastula-like larva and for *Tetilla* (Spirophorida) that lacks a larva (BOROJEVIC, 1967; WATANABE, 1978). On the other hand, the same larval types may be developed from different cleavage patterns and methods of morphogenesis. For example, the parenchymella of *Reniera* (Haplosclerida) develops as a results of chaotic cleavage and morular delamination, and the parenchymella-like larva of *Halisarca* (Halisarcida) - as a results of polyaxial cleavage and multipolar ingression (LEYS & DEGNAN, 2002; GONOBOBLEVA & ERESKOVSKY, 2004). Nevertheless the results of the present research demonstrate that comparative-embryological method can be successfully used in modern spongiology, together with morphological and molecular biological methods.

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Appendix 1. List of species, analized on the basis of literature and original (bold) data.

Type of development	Order	Species	Reference
«Trichimella» (Exactinellida)	Hexactinosida	*Farrea sollasi, Oopsacas minuta*	OKADA, 1928; BOURY-ESNAULT & VACELET, 1994; BOURY-ESNAULT *et al.*, 1999; LEYS, 2003.
«Calciblastula» (Calcinea)	Clathrinida	*Ascetta primordialis, A. clathrus, Clathrina blanca, C. coriacea, C. contorta, C. cerebrum, C. reticulum, C. laxa, Ascandra minchini, A. falcata, Leucettusa lancifer*	SCHMIDT, 1877; MINCHIN, 1896, 1900; TUZET, 1948; BOROJEVIC, 1969; JOHNSON, 1979; AMANO & HORI, 2001.
«Amphiblastula» (Calcaronea)	Leucosoleniida	*Grantia compressa, Sycon (Schypa) ciliatum, S. raphanus, S. sycandra, S. elegans, S. calcaravis, Leucosolenia botrioides, L. complicata,* ***Amphoriscus kuekenthalli,*** *Leucandra abratsbo*	SCHULZE, 1875; MINCHIN, 1900; DUBOSCQ & TUZET, 1937, 1942; TUZET, 1947; SARÀ & RELINI ORSI, 1975; GALLISSIAN, 1981, 1983; ANAKINA, 1981, 1997; GAINO *et al.*, 1987; FRANZEN, 1988; AMANO & HORI, 1992, 1993.
	Lithonida	*Petrobiona massiliana*	VACELET, 1964; GALLISSIAN & VACELET, 1990, 1992.
«Cinctoblastula» (Homoscleromorpha)	Homosclerophorida	***Oscarella microlobata O. imperialis, O. lobularis, O. viridis, Oscarella* sp., *O. tuberculata, Corticium candelabrum, Plakina trilopha, P. iani, Pseudocorticium jarrei***	SCHULZE, 1877, 1880, 1881; HEIDER, 1886; MEEWIS, 1938; GAINO *et al.*, 1986; ERESKOVSKY & BOURY-ESNAULT, 2002, BOURY-ESNAULT *et al.*, 2003.
«Disphaerula» (Halisarcida)	Halisarcida	***Halisarca dujardini,*** *H. metschnikovi, H. nahantensis,* ***Halisarca* sp.**	LÉVI, 1956; CHEN, 1976; ERESKOVSKY & GONOBOBLEVA, 2000; ERESKOVSKY, 2002; GONOBOBLEVA & ERESKOVSKY, this volume.
Direct development	Spirophorida	*Tetilla japonica, T. serica*	WATANABE, 1978; WATANABE & MASUDA, 1990.
" Parenchymella"	Dendroceratida	*Aplysilla* sp., ***Aplysilla sulfurea,*** *Dictyodendrilla dendyi, Dendrilla cactus, Darwinella gardineri*	SCHULZE, 1878; DELAGE, 1892; BERGQUIST *et al.*, 1979; WOOLLACOTT & HADFIELD, 1989; PINTO & WOOLLACOTT, 1992; ERESKOVSKY, in press.
	Dictyoceratida	*Spongia barbara, S. graminea, S. cheisis, S. officinalis, Spongia* sp, *Hippospongia lachne, H. communis, Dysidea pallescens, Ircinia fasciculata, I. variabilis,* ***I. oros,*** *Ircinia* sp., *Phyllospongia foliascens,* ***Pleraplysilla spinifera***	SCHULZE, 1879a,b; MAAS, 1893; HAMMER, 1906; LÉVI, 1956; TUZET & PAVANS DE CECCATTY, 1958; SCALERA LIACI *et al.*, 1971; BERGQUIST *et al.*, 1979; GAINO *et al.*, 1984; KAYE, 1990, 1991; KAYE & REISWIG, 1991; ERESKOVSKY, in press; ERESKOVSKY & TOKINA, unpubl. data.

Type of development	Order	Species	Reference
	Halichondrida	***Halichondria panicea,*** *H. coliata, H. okadai, H. moorei, H. melanadocia, H. bowerbanki, H. magnicolulosa, Halichondria* sp., *Hymeniacidon caruncula, H. sanguinea, H. perlevis, H. heliophila, Ulosa* sp., *Scopalina lophiropoda, S. ruetzleri, Svenzea zeai*	TOPSENT, 1911; MEEWIS, 1941; LÉVI, 1956; DIAZ, 1973; BERGQUIST & GREEN, 1977; FELL & JACOB, 1979; IVANOVA, 1981; BERGQUIST& GLASGOW, 1986; WAPSTRA & VAN SOEST, 1987; WOOLLACOTT, 1990; WHITTE & BARTHEL,1994; RÜTZLER*et al.,* 2003; ERESKOVSKY in press.
	Hadromerida	*Tethya aurantium, Raspailia pumilla, Polymastia robusta, Cliona celata, C. viridis*	LÉVI, 1956; WARBURTON, 1961; BOROJEVIC, 1967; DIAZ *et al.*, 1973; POMPONI & MELONE, 1990; MARIANI *et al.*, 2000.
	Poecilosclerida	*Myxilla rosacea,* ***M. incrustans,*** *Axinella cristagalli, Clathria coralloides, Tedania charcoti, Microciona prolifera, M. rubens, Iophon radiatus,* ***I. piceus,*** *Hamigera hamigera, Crambe crambe,* ***Phorbas paupertas,*** *Mycale lovenzi, M. contarenii,* ***M. lobata,*** *M. fistulifera,* ***Crellomima imparidens, Abyssocladia*** **sp.**	DELAGE, 1892; MAAS, 1893; BURTON, 1931, 1932; LÉVI, 1956, 1964; BOROJEVIC & LÉVI, 1965; BOROJEVIC, 1966; BERGQUIST & SINCLAIR, 1968; SIMPSON, 1968; BOURY-ESNAULT, 1976; BERGQUIST& GREEN, 1977; BERGQUIST *et al.*, 1979; ERESKOVSKY, 1986; EFREMOVA *et al.*, 1987; MISEVIC *et al.*, 1990; ILAN, 1995; JAECKLE, 1995; MEROZ & ILAN, 1995; URIZ *et al.,* 2001; ERESKOVSKY, in press.
	Haplosclerida	*Chalinula fertilis, Chalinula* sp., *Adocia cinerea, Reniera elegans, R. simulans, Reniera* sp., *Haliclona ecbasis,* ***H. aqueductus,*** *H. loosanoffi, H. permolis, H. gracilis, H. limbata,* ***H. mediterranea,*** *Spongilla lacustris, S. moorei,* ***Ephydatia fluviatilis,*** *E. muelleri, Eunapius fragilis, Radiospongilla cerebellata, Potamolepis stendalli, Malawispongia echinata, Corvospongilla thysi, Lubomirskia baikalensis, Baikalospongia bacillifera, Swartschewskia papyracea, Ochridaspongia rotunda*	KELLER, 1880; MAAS, 1893; TUZET, 1932; MEEWIS, 1941; BRIEN & MEEWIS, 1938; BRIEN, 1967, 1969, 1973a,b; FELL, 1969, 1976; HARRISON & COWDEN, 1975; GILBERT & HADZISCI, 1977; BERGQUIST *et al.*, 1979; EFREMOVA & EFREMOV, 1979; ALEKSEEVA, 1980; EFREMOVA, 1981; SALLER & WEISSENFELS, 1985; WAPSTRA & VAN SOEST, 1987; SALLER, 1988; MUKAI, 1989; WEISSENFELS, 1989; ILAN & LOYA, 1990; WOOLLACOTT, 1993; ROPSTORP & REITNER, 1994; AMANO & HORI, 1996; IVANOVA, 1997a,b; ERESKOVSKY, 1999; LEYS & DEGNAN, 2001, 2002; ERESKOVSKY, in press.