

Polyaxial Cleavage in Sponges (Porifera): A New Pattern of Metazoan Cleavage

A. V. Ereskovsky

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Cleavage is an important stage of animal embryogenesis marked by the emergence of multicellularity of an organism and by ooplasmic segregation of morphogenetic determinants. In addition, cleavage is a highly coordinated process of diagnostic significance. Cleavage patterns are often used to investigate the phylogenetic relationships in various animal groups [1].

Analysis of early development of sponges (*Porifera*), including cleavage, is of particular interest because of their key position at the base of the phylogenetic tree for Metazoa. However, studies specially addressing the stage of egg cleavage in sponges were very few until the past two decades [2–5]. It is now well known that, in all sponge species, the whole egg divides completely (holoblastic cleavage). The process is usually uniform, but the cleavage patterns may significantly vary from species to species. In most species, cleavage division planes are randomly oriented (chaotic cleavage). A unique type of cleavage called table palintomy occurs in some species of the subclass Calcareonea [4]. In the glass sponge *Oopsacas minuta* (Hexactinellida), cleavage is pseudospiral [5]. In many oviparous species of the class Demospongiae, cleavage follows a nearly radial pattern [6].

Of particular interest is analysis of cleavage in sponges of the order Halisarcida, which are the most primitive of Demospongiae [7, 8]. The goal of this study was to reexamine the cleavage period of *Halisarca dujardini* development using light and electron (scanning and transmission) microscopy. Sponges of this species are dioecious and viviparous. Their embryos develop within temporary follicles. Each follicle consists of pinacocyte-like follicular cells and an outer collagen layer. Before maturation division, the oocyte is oval, with a round nucleus at the center. Yolk granules are uniformly distributed throughout the oocyte.

The first cleavage division in *H. dujardini* is uniform and proceeds in the meridional plane. The cleavage furrows are of the bipolar type. The subsequent cleavage proceeds asynchronously. During the second cleavage division, the orientation of mitotic spindles relative to each other varies from parallel to perpendicular (Fig. 1a). Thereafter, cleavage goes on asynchronously. From the third cleavage division onward, mitotic spindles are always formed parallel to the surface; therefore, the cleavage furrows run perpendicular to the surface (Fig. 1b). The eight-cell embryo is round or slightly oval in the cross-section and never appears as a lamina-like structure described earlier [7].

Cleavage leads to the formation of an apolar coeloblastula with a small cavity inside. The cavity is bounded with long wedge-shaped cells (Fig. 1c). At the stage of approximately 100 cells, blastomeres exhibit a distinct apicobasal polarity.

In our previous studies [2, 8], some primitive traits were described in *H. dujardini* cleavage. These were, first of all, the absence of any determinate spatial relationships among blastomeres within the embryo. Conceivably, the origin of these primitive traits should be sought in the absence of mature egg patterning (pre-patterning) [9], which is usually regarded to be a common primitive trait of egg organization in sponges [10]. Throughout the *H. dujardini* egg, its structure remains uniform. Holoblastic uniform asynchronous cleavage is typical of all the Halisarcida species studied, such as *H. dujardini*, *H. metschnikovi*, and *H. nahantensis* [2, 7, 8, 11]. A distinctive feature of the cleavage stage of *H. dujardini* development is the long retention of the blastula-like appearance by the embryo (from the eight-cell to the prelarval stage), which is due to the early formation of cleavage division planes of similar type running parallel to the embryo surface [2, 8]. The same cleavage pattern was described for *H. nahantensis* [11]. This cleavage pattern is unique among the viviparous Demospongiae but quite usual in Calcinea (class Calcarea), which form a monolayer flagellated blastula [12].

At present, eight major patterns of holoblastic cleavage are distinguished in animals [1]. Chaotic cleavage produces no patterning in blastomere distribution. Passage of all cleavage furrows along the animal–vegetal

Biological Faculty, St. Petersburg State University,
Universitetskaya nab. 7/9, St. Petersburg,
199034 Russia

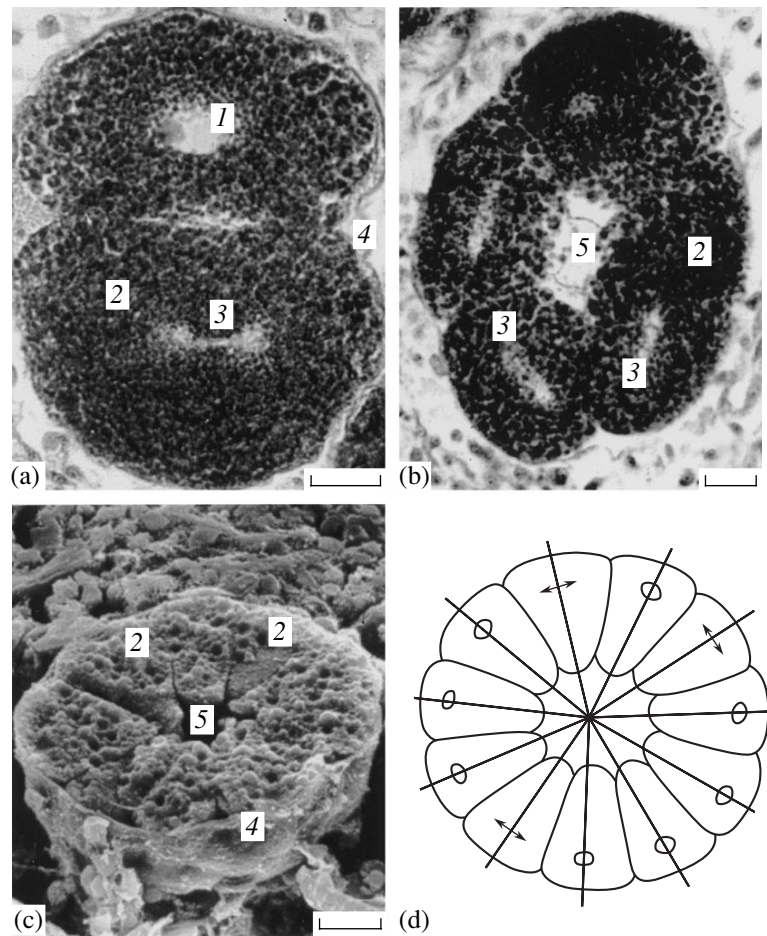


Fig. 1. Sections of *H. dujardini* embryos at various stages of polyaxial cleavage: (a) two-blastomere stage just before the second cleavage division; (b) four-blastomere stage just before the third cleavage division; (c) early blastula; and (d) scheme of polyaxial cleavage, with straight lines depicting the symmetry axes of the embryo. Scale bar, 20 μm . Designations: 1, nucleus; 2, blastomere; 3, mitotic spindle; 4, follicle; and 5, blastocoel.

axis is typical of table palyntomy (Calcarenea). Tetrahedral cleavage (Cnidaria) affords a large degree of autonomy to blastomeres and results in the tetrahedral shape of the four-cell embryo. If an embryo undergoes bilateral cleavage (Nematoda and Ascidiacea), it retains bilateral symmetry. Embryos that undergo biradial cleavage (Ctenophora) exhibit twofold radial symmetry in combination with eightfold radial symmetry. Spiral cleavage (Mollusca and Annelida) is specific in that, from the third cleavage division onward, mitotic spindles are oriented at an angle of 45° to the embryo's axis of polarity. In embryos that undergo radial cleavage (Echinodermata), longitudinal divisions alternate with latitudinal divisions. Such embryos exhibit absolute radial symmetry, with the symmetry axis coinciding with the primary axis of the egg. Orthogonal cleavage (Brachiopoda) differs from radial cleavage in that the fourth and the fifth cleavage furrows run in the meridional plane.

The cleavage pattern of *Halisarca* differs from any of these eight types. I propose to classify it as a separate—polyaxial—type of metazoan cleavage. The

observations that form the basis for this proposal are as follows: (1) cleavage of *Halisarca* eggs is complete, uniform, and asynchronous; (2) the positions of the second- and third-cell-cycle spindles vary; (3) from the eight-cell stage until the end of cytodifferentiation, cleavage division planes are perpendicular to the embryo surface; (4) during the third cell cycle, the blastocoel is formed, which persists until the end of embryogenesis; (5) at every stage of the cleavage period, the number of symmetry axes of the embryo equals the number of blastomeres; the axes radiate at certain angles to one another from the same point, which is the geometric center of the embryo; and (6) embryos lack the anteroposterior polarity.

Polyaxial cleavage is intermediate between chaotic and radial. Regular spatial relationships between cleavage division planes distinguish it from the former. Compared with the latter, polyaxial cleavage lacks a discernible animal–vegetal axis, which determines the radial type of symmetry of an embryo. It is likely that polyaxial cleavage also occurs in *Calcinea* (class Calcarea). The polyaxial type of cleavage is typical of eggs

that form no prepatterns. Establishment of the antero-posterior axis late in embryogenesis also correlates with polyaxial cleavage.

The evolutionary relationships among cleavage patterns are a matter of discussion in many studies. Unfortunately, Cnidaria, rather than sponges, which are the most primitive Metazoa, are the starting point in this analysis. Many researchers suppose that the ancestral form of cleavage is radial [1, 13, 14]. Ivanova-Kazas [1] argues that table palyntomy of Calcaronea (class Calcarea) is ancestral to other cleavage patterns. In my opinion, table palyntomy is a unique and largely aberrant type of cleavage (like the entire development of Calcaronea). It is not a good idea to treat table palyntomy as an evolutionary source of other patterns. A more likely scenario for evolution of early embryogenesis in Metazoa is the evolution in which the most primitive types of cleavage are chaotic and polyaxial. The radial pattern may have arisen from any of them.

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