ISSN 0031-0301, Paleontological Journal, 2015, Vol. 49, No. 14, pp. 1582–1596. © Pleiades Publishing, Ltd., 2015.

Heterochrony and Heterotopy in the Phylogeny of Sea Urchins

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Received January 16, 2015

Abstract—The role of heterochrony is evident in ontogeny and phylogeny of irregular (exocyclic) sea urchins. After metamorphosis, a juvenile passes the stage of regular (endocyclic) sea urchin, in which the periproct is surrounded by plates of the apical system. A shift of the periproct in the area of the fifth interambulacrum occurs in extant taxa at early stages of postlarval development and is accompanied by the reduction of genital plate 5. In some ancient (Jurassic) adult irregular sea urchins, the endocyclic state of the apical system is retained for a long time and the derivative of the fifth genital plate is sometimes observed even in Early Cretaceous species. Considerable transformations in the structure of the lower test surface in members of the order Spatangoida are manifested in changes in the relative positions of plastron plates and ambulacral areas I and V, separation of sternal plates from the labrum, etc. The mechanism of these changes is connected with translocation or "sliding" of sutures of particular plates as a result of nonuniform growth and partial resorption. The study of evolutionary lineages of Cretaceous and Cenozoic sea urchins has shown that the evolution was connected with the directional changes in some morphological characters at late ontogenetic stages. The process was accompanied by either extension, peramorphosis (lineages of the genera *Micraster*, *Infulaster*–*Hagenowia* in the European Province), or the loss of these stages, paedomorphosis (*Hemiaster (Bolbaster)* lineage, Late Eocene–Middle Miocene of Australia). The phenomena of heterochrony and heterotopy in the development of peripetal, marginal, and lateroanal fascioles in the Late Cretaceous and Paleocene families Hemiasteridae, Schizasteridae, and Paleopneustidae are described. The heterotopy is also illustrated by the example of the development of additional genital pores on ocular plates II and IV of the Middle Jurassic species *Pygomalus analis* (Disasteroida); its apical system has five pores instead of four. In the Late Cretaceous species *Guettaria roccardi* (Holasteroida), ocular plates II and IV have two pores each; in the apical system, there are eight genital pores instead of four. In some members of the order Holectypoida, the place of lost genital plate 5 is occupied by a new plate sometimes pierced by a pore, but judging from crystallographic data, it is not homologous to other genital plates. The order Clypeasteroida is characterized by the development of very small pores in both ambulacral and interambulacral fields; they provide passage for numerous accessory tube feet.

Keywords: sea unchins, apical system, fascioles, heterochrony, heterotopy

DOI: 10.1134/S0031030115140191

INTRODUCTION

The role of heterochrony is well pronounced in the ontogeny and phylogeny of irregular (exocyclic) sea urchins. After the metamorphosis, juveniles pass the stage of regular (endocyclic) sea urchin, in which the periproct is surrounded by plates of the apical system. A shift of the periproct in the area of the fifth interambulacrum occurs in extant taxa at early stages of postlarval development and is accompanied by reduction of genital plate 5. This process is thoroughly investigated in a number of groups of Recent sea urchins, for example, in the genus *Echinocardium* (Gordon, 1926) (Fig. 1), some Schizasteridae (Markov, 1994) (Fig. 2), and the abyssal species *Calymne relicta* (Saucede et al., 2009) (Fig. 3). In some ancient (Jurassic) adult irregular sea urchins, the endocyclic state of the apical system is retained for a long time. This is typical, for example, for genera of the order Cassiduloida, such as *Hyboclypus* (family Galeropygidae) and *Nucleolites* (family Nucleolitidae), and also for members of the superorder Spatangacea, the forms with a disjunct apical system, the so-called disasterid sea urchins (Jesionek-Szymańska, 1963; Solovjev, 1971) (genera *Pygorhytis*, *Pygomalus*) (Fig. 4). In the last genus, in the Callovian (species *P. analis*), an interesting ontogenetic change occurred in relationships of the periproct with posterior ocular plates and the fifth genital plate, which strongly decreases in size, and the apices of ambulacra I and V along with respective ocular plates are gradually shifted from the periproct towards the anterior test part (Fig. 5). This is the beginning of disconnection of ocular plates I and V, which loose links with the periproct and are displaced towards the anterior part of the apical system, with

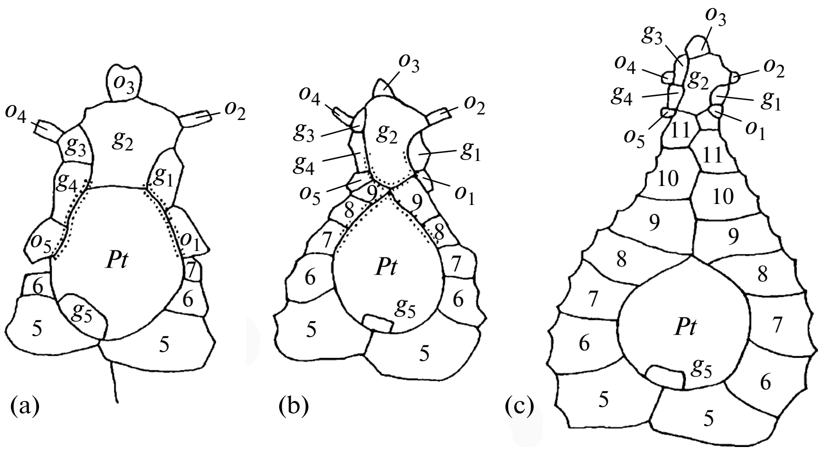

Fig. 1. Apical system of three specimens of the extant species *Echinocardium cordatum:* (a) 1.7-mm-long test; (b) 2.05-mm-long test; and (c) 3.9-mm-long test. The periproct (*Pt*) migrates early in ontogeny by translocation of certain plates. Continuous separation of interambulacral plates from ocular plates I and V results in rapid migration of the periproct during early ontogeny and in its definitive supramarginal position; Arabic figures designate numbers of interambulacral plates; (o_1–o_5) ocular plate; (g_1–g_5) genital plates (after Gordon, 1926).

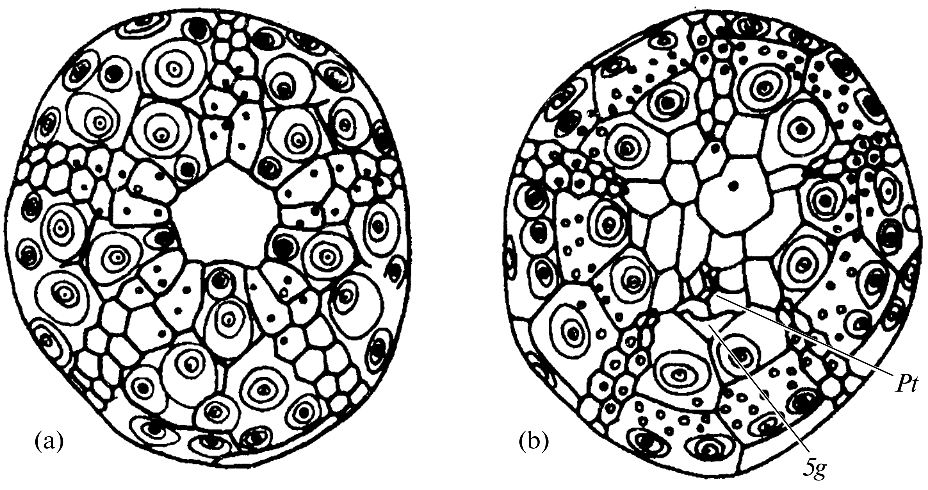

Fig. 2. Juvenile *Abatus agassizi* (Pfeffer) from the brood chamber, regular sea urchin stage: (a) oral surface view; (b) aboral surface view; endocyclic structure of the apical system is seen. Designations: (*Pt*) periproct, (*5g*) fifth genital plate (after Markov, 1994).

which they were connected at the beginning of the Cretaceous (in the Berriasian). This process developed in parallel in several groups of disasterid sea urchins. Apparently, this was finally realized in at least two evolutionary lineages of Spatangacea with closed apical system, the families Holasteridae (order Holasteroida) (Fig. 6) and Toxasteridae (order Spatangoida). Note that a derivative of the fifth genital plate sometimes occur in Early Cretaceous species of irregular sea urchins.

The shift of the periproct into the area of the fifth (posterior) interambulacrum occurred in different groups with varying asynchronism relative to the formation of its plates. Therefore, the periproct can occupy various positions on the test, ranging from upper supramarginal to inframarginal (Fig. 7). This is observed in all orders of irregular sea urchins and connected with the mode of life of particular groups.

Considerable transformations in the structure of the lower test surface in members of the order Spatangoida are manifested in changes in the relative positions of plastron plates and ambulacral areas I and V, separation of sternal plates from the labrum, etc. The mechanism of these changes is connected with translocation (McNamara, 1987), i.e., “sliding” of sutures of particular plates in the equatorial or meridional

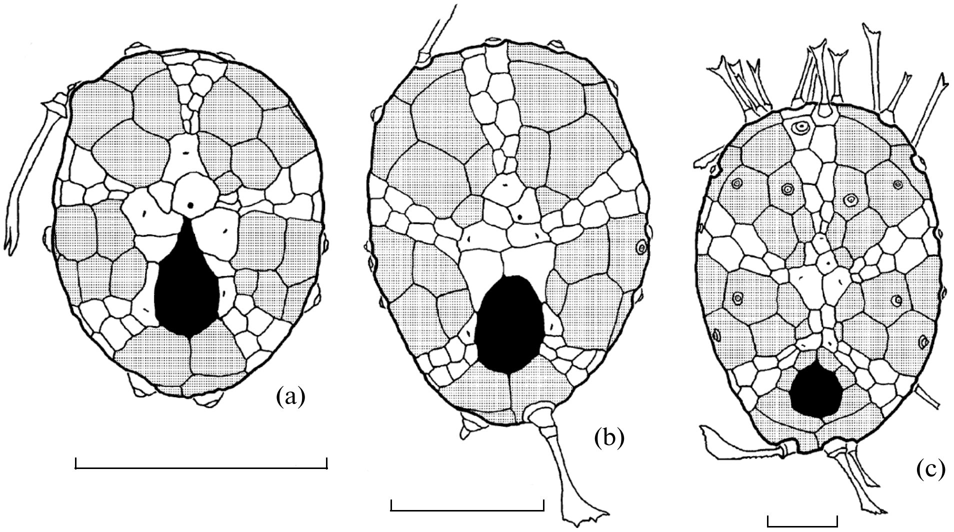

Fig. 3. Ontogeny of the living abyssal sea urchin *Calymne relicta*: (a) early postlarval imago; (b) very small juvenile specimen; (c) larger juvenile specimen with a periproct separated from the apical system. Scale bar, 1 mm (after Saucède et al., 2009).

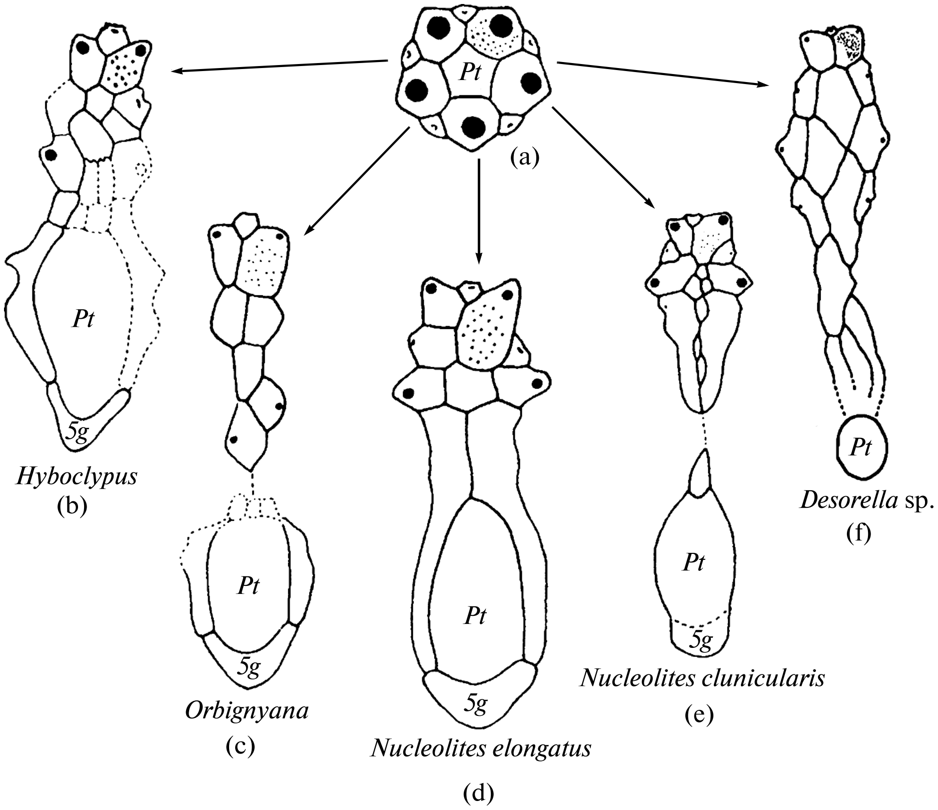

Fig. 4. Transformation of the apical system during the shift of the periproct (*Pt*) in different groups of Jurassic sea urchins: (a) typical structure of the apical system in regular sea urchins, (b) Galeropygidae, (c) Collyritidae, (d, e) Nucleolitidae, and (f) Menopygidae; (*5g*) fifth genital plate (after Solovjev and Markov, 2004b, modified).

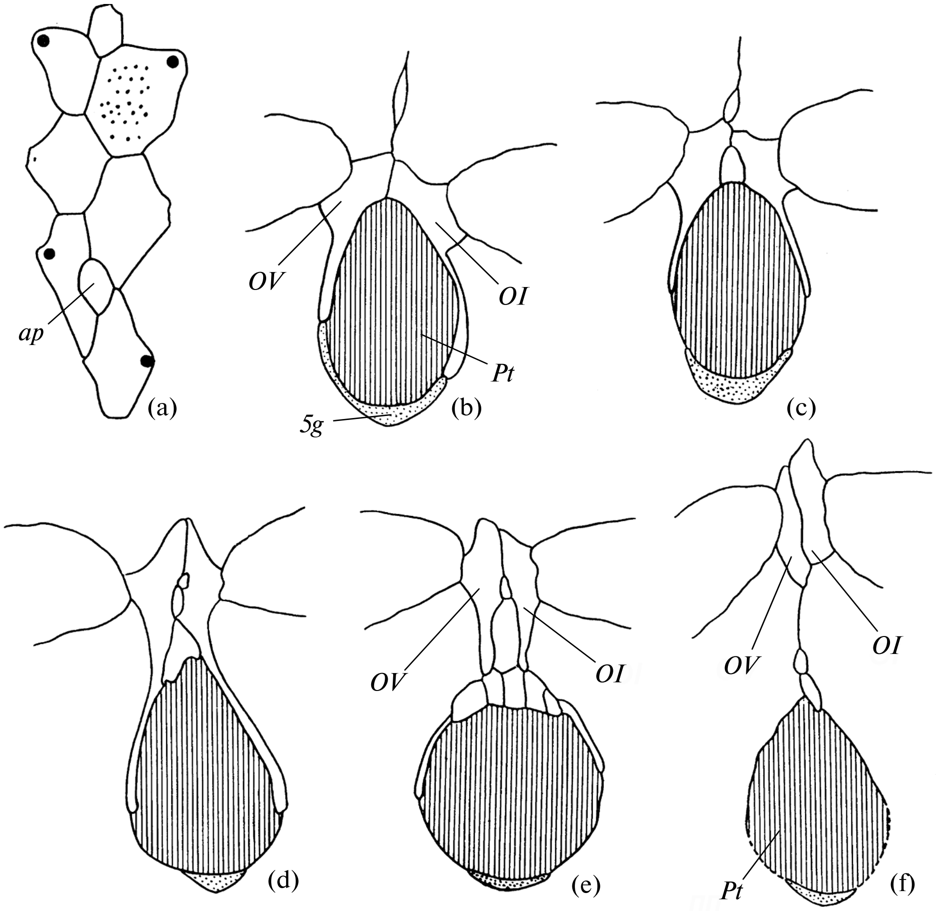

Fig. 5. Apical system of *Pygomalis analis* (Agassiz): (a) anterior part; (b–f) posterior part with the periproct: (b–d) Bathonian of Poland; (e, f) Callovian of Poland. Designations: (*OI–OV*) ocular plates, (*5g*) fifth genital plate, (*Pt*) periproct, (*ap*) additional plate (after Jesionek-Szymańska, 1963).

direction as a result of their nonuniform growth and partial resorption (Figs. 8, 9). McNamara recorded this phenomenon in the ontogeny of the Middle Miocene species *Breynia carinata* and *Lovenia woodsi* from Australia. The separation of sternal plates from the labrum occurs at late ontogenetic stages, i.e., this is anaboly (Fig. 10). During phylogeny, similar events (peramorphosis) occurred in a number of groups.

To date, several rather complete evolutionary lineages have been recognized among Cretaceous and Cenozoic sea urchins of the superorder Spatangacea. Their evolution was connected with gradual and directional changes in some morphological characters at late stages; this was accompanied by either extension (peramorphosis) or the loss of these stages (paedomorphosis). Each species represented a certain segment of such an evolutionary lineages or, in other words, a stage in its evolution. One of the most thoroughly investigated lineage is that of the Late Cretaceous (Late Turonian–Late Campanian) genus *Micraster* (Poslavskaya 1958; Nichols, 1959; Poslavskaya and Moskvin, 1959; Solovjev, 1998, 2013) (Fig. 11). In the evolution of this genus, the number of pore pairs in the petaloids of paired ambulacra increased, the peristome moved towards the anterior test margin, the labrum increase in size, the anterior sulcus became deeper, and other changes occurred. Nichols believed that these changes were caused by functional transformations connected with the improvement of adaptations for the digging mode of life under rather stable conditions (the basin depth, size of ground particles, and temperature were apparently almost constant during a long time). The evolution of the genus *Micraster* is a prominent example of peramorphosis.

Another example of peramorphosis is provided by the *Infulaster–Hagenowia* lineage (Turonian–Campanian) (Fig. 12). In this case, the main changes are connected with the appearance and progressive development of the apical rostrum, which is also an extraordinary adaptation for dwelling inside the ground (Gale

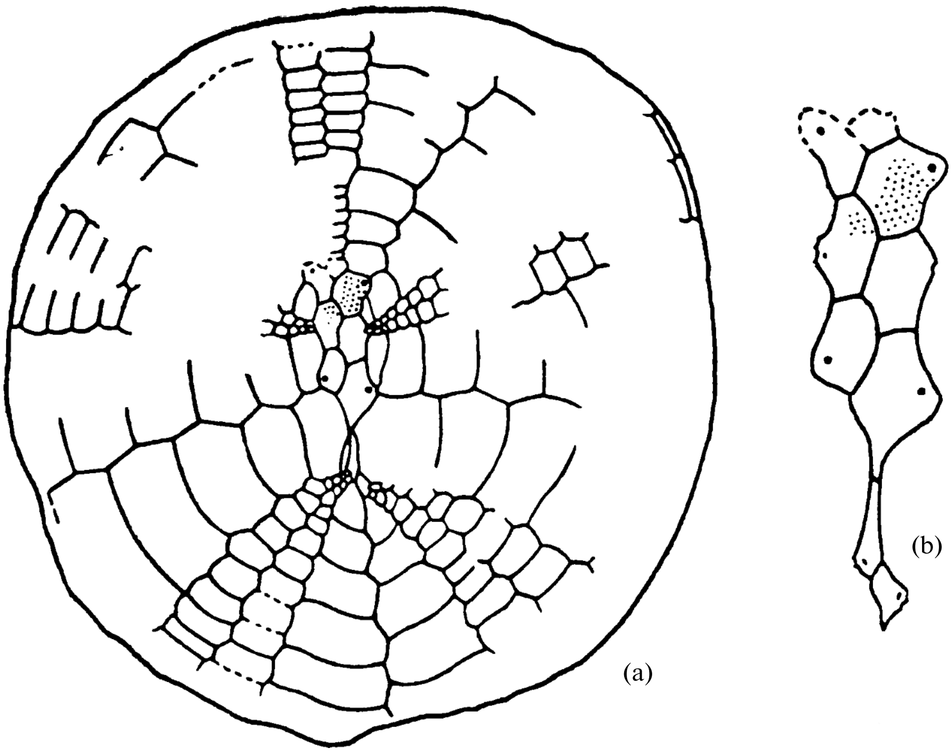

Fig. 6. *Eoholaster poslavskae* Solovjev (family Holasteridae), Berriasian of the southwestern Crimea: (a) structure of the upper test surface, (b) apical system (after Solovjev, 1971).

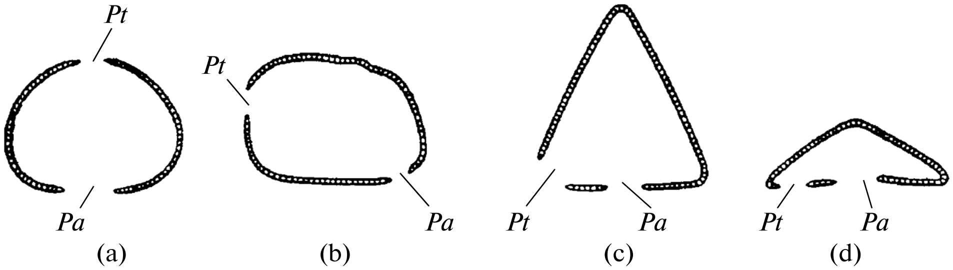

Fig. 7. Position of the periproct in regular and irregular sea urchins: (a) regular sea urchin with central periproct; (b–d) irregular sea urchins: (b) supramarginal; (c) marginal; (d) inframarginal. Designations: (*Pa*) peristome; (*Pt*) periproct.

and Smith, 1982). Examination of sea urchin lineages, primarily, the genus *Micraster* allowed a number of researchers to draw a conclusion that new species emerged slowly, by gradual transformation of whole populations (gradualism). However, a detailed analysis of the fossil record of the genus *Meoma* in the Tertiary (Chesher 1970) has shown that some characters changed rapidly to form a new morphotype which followed a long period of stasis (i.e., this was a case of punctuated equilibrium). It is noteworthy that, despite the above-mentioned completeness of these evolutionary lineages, they have some gaps, preventing reliable judgement as to which of the two evolutionary models corresponds to actual processes. In the Late Campanian species *M. grimmensis,* the plastron is broken between the labrum and sternal plates in connection with the fact that the peristome occupied the terminal position (Solovjev, 2013).

The process of paedomorphosis connected with the loss of characters of late developmental stages is observed in the evolution of the genus *Hemiaster (Bolbaster)* from the Paleocene–Miocene of Australia

(McNamara, 1987, 1989). This is manifested in an increase in the relative test height, expansion of the peripetal fasciole, and in the change in the apical system position. Note that this is probably directly connected with the change in time of the character of deposits from relatively coarse sand to fine silt (Fig. 13).

The heterochrony and heterotopy are manifested in the formation of fascioles in ontogeny and phylogeny of many groups of the order Spatangoida (Markov and Kushlina, 1990a, 1990b; Markov, 1994; Markov and Solovjev, 2001).

Fascioles are the major family-level character in the order Spatangoida. They are narrow ribbonlike bands on the test, covered with small granules; the granules provide attachment of special small club-shaped spines, clavulae, coated by ciliated epithelium and mucifying. The function of fascioles is intensification of water flows washing the test of sea urchins. The development of fascioles in members of the order Spatangoida is directly connected with the digging mode of life. Fascioles provide inflow of fresh water in the burrow and removal of products of vital functions. In the case of transition of some members of the order to the epibenthic mode of life, fascioles are usually reduced.

Let us consider the fasciole structure in three spatangoid families: the Hemiasteridae, Schizasteridae, and Paleopneustidae (Fig. 14).

Sea urchins of the family Paleopneustidae sensu Chesher, 1968 have two fascioles, peripetal (located above the ambitus, curving around the petaloid ends and passing above the periproct) and marginal (curving around the shell along the ambitus and passing under the periproct).

The family Hemiasteridae is characterized by the presence of only a peripetal fasciole.

The most complex picture is characteristic of the family Schizasteridae (this family is most similar to Paleopneustidae and probably represents its ancestor). It is usually indicated that the majority of Schizasteridae have two fascioles, peripetal and lateroanal. The last is a semiring curving along the ambitus around the posterior test part, passing under the periproct, and connected with the peripetal fasciole in posterior paired interambulacra 1 and 4 behind the ends of the anterior petaloids. The description of schizasterid fascioles by the formula «peripetal + lateroanal» is only suitable (and convenient) for adults. For example, in some adult Schizasteridae, the lateroanal fasciole is reduced, so that only one peripetal fasciole is retained (as in Hemiasteridae). To describe the cases of this kind, it is convenient to use the terminology implying that the peripetal fasciole of Schizasteridae is something whole, an integrated closed contour, and the lateroanal fasciole is something different, special, attached posteriorly to the peripetal fasciole. However, in the morphogenetic and comparative anatomical aspects, the peripetal fasciole of Schizasteridae is not a single whole (it is composed of two parts differing in origin) and the lateroanal fasciole is not a special unit. In fact, the lateroanal fasciole is a single whole with an the anterior part of the "peripetal" fasciole. The situation is as follows.

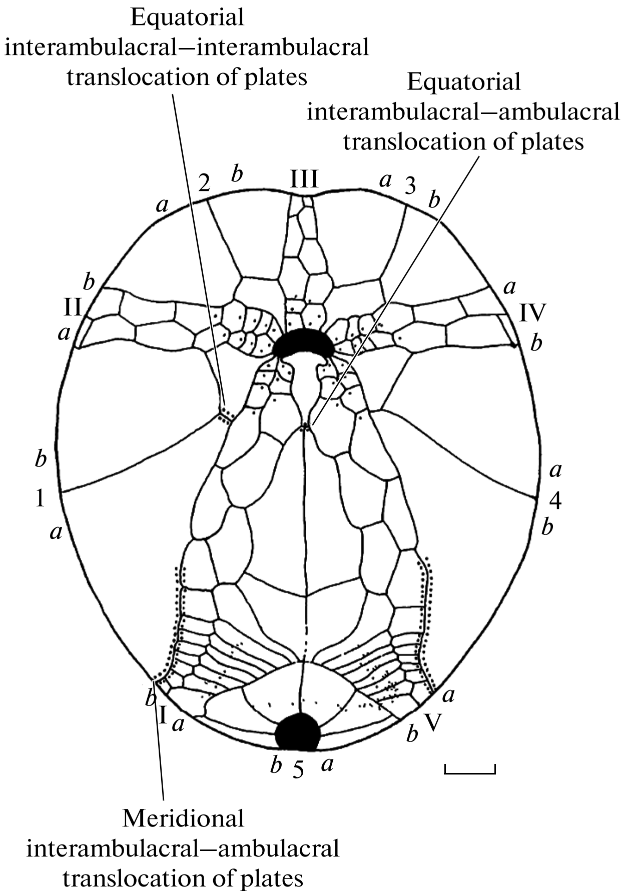

Fig. 8. *Breynia desori* (Recent), ventral view. Parallel rows of points are zones of plate translocation on the adoral surface. Scale bar, 10 mm (after McNamara 1987).

In the ontogeny of Schizasteridae, the ring fasciole is the first to develop and curve around the apical system, passing under the periproct. This occurs very early, at the stage of 1–2-mm-long test, in which the periproct is still located inside the apical system. This fasciole is named "juvenile marginal" (Markov, 1994). Subsequently, the periproct comes out of the apical system and moves towards the posterior test end. As new ambulacral and interambulacral plates are formed, the marginal fasciole is displaced from the aboral shell surface onto the lateral surface. As the space between the periproct and apical system becomes sufficiently large, the second fasciole place

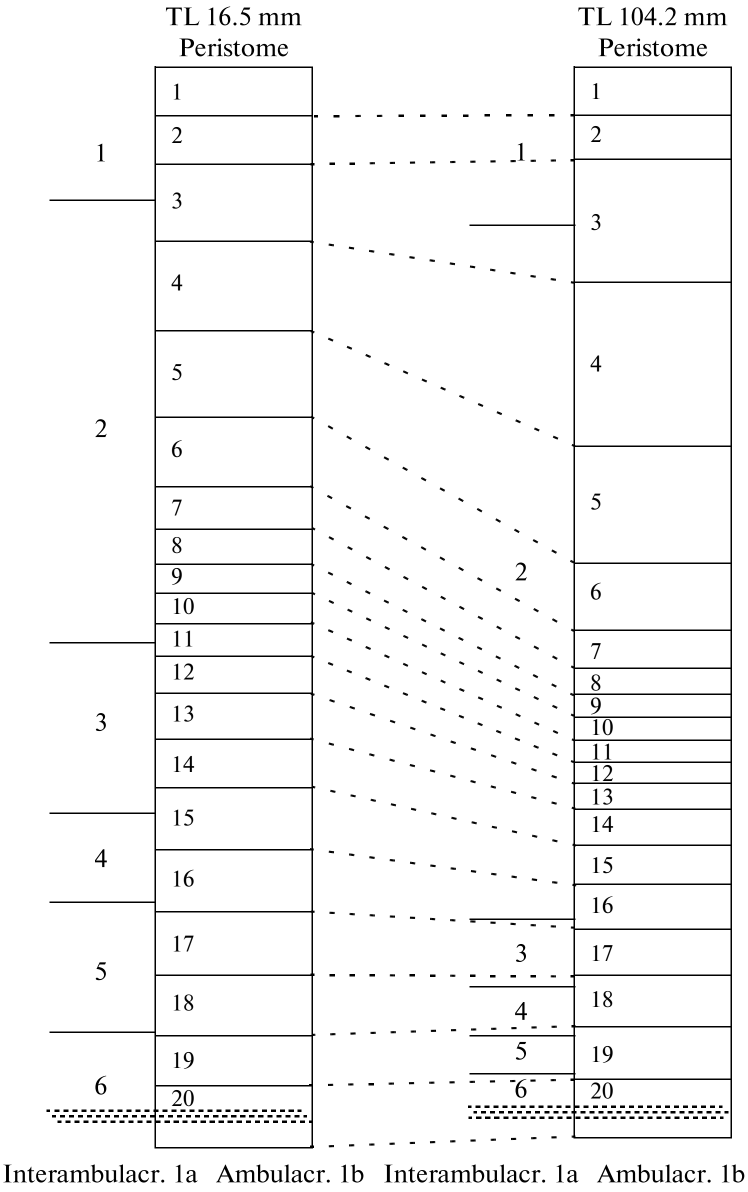

Fig. 9. Scheme of relative positions of plates in shells of *Breynia desori* (Recent) differing in age, showing positive allometric growth of plate 2 and respective meridional translocation of plates along the boundary between interambulacral 1a and ambulacral Ib rows. Designations: (*TL*) total test length (after McNamara 1987).

looking like a straight band with free ends is formed there and crosses transversely the aboral test surface. This fasciole is named semiperipetal. Then, its ends are connected to the marginal fasciole (Mortensen, 1951; Markov, 1994). In the majority of Schizasteridae, the link is confined to the fifth plates of interambulacral series lb and 4a or, considerably less frequently, to the fourth plates of the same series (other variants have not been recorded). The semiperipetal fasciole along with the anterior part of the marginal fasciole (with its part located anterior to the junction) are just what is usually named the peripetal fasciole of Schizasteridae. The posterior part of the marginal fasciole posterior to the junction is the lateroanal fasciole.

Thus, the peripetal fasciole of Schizasteridae is not homologous to the peripetal fasciole of Hemiasteridae and Paleopneustidae. However, the marginal fasciole of Schizasteridae (=lateroanal + anterior part of peripetal) is apparently homologous to the marginal fasciole of Paleopneustidae (Markov, 1994). This is evidenced by the fact that, in both groups, the marginal fascioles pass on approximately the same plates of the test.

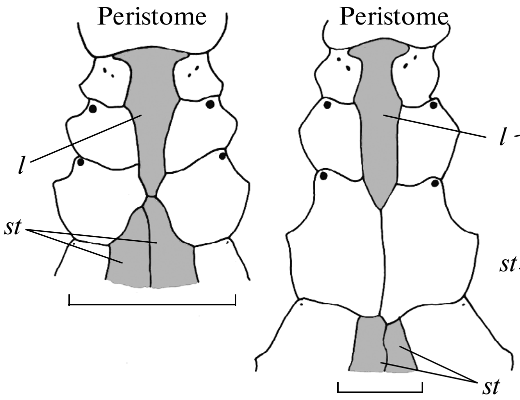

Fig. 10. Separation of sternal plates from the labrum during the ontogeny of *Breynia* aff. *carinata* (Middle Miocene). Designations: (*l*) labrum, (*st*) sternal plate. Scale bar, 5 mm (after McNamara 1987).

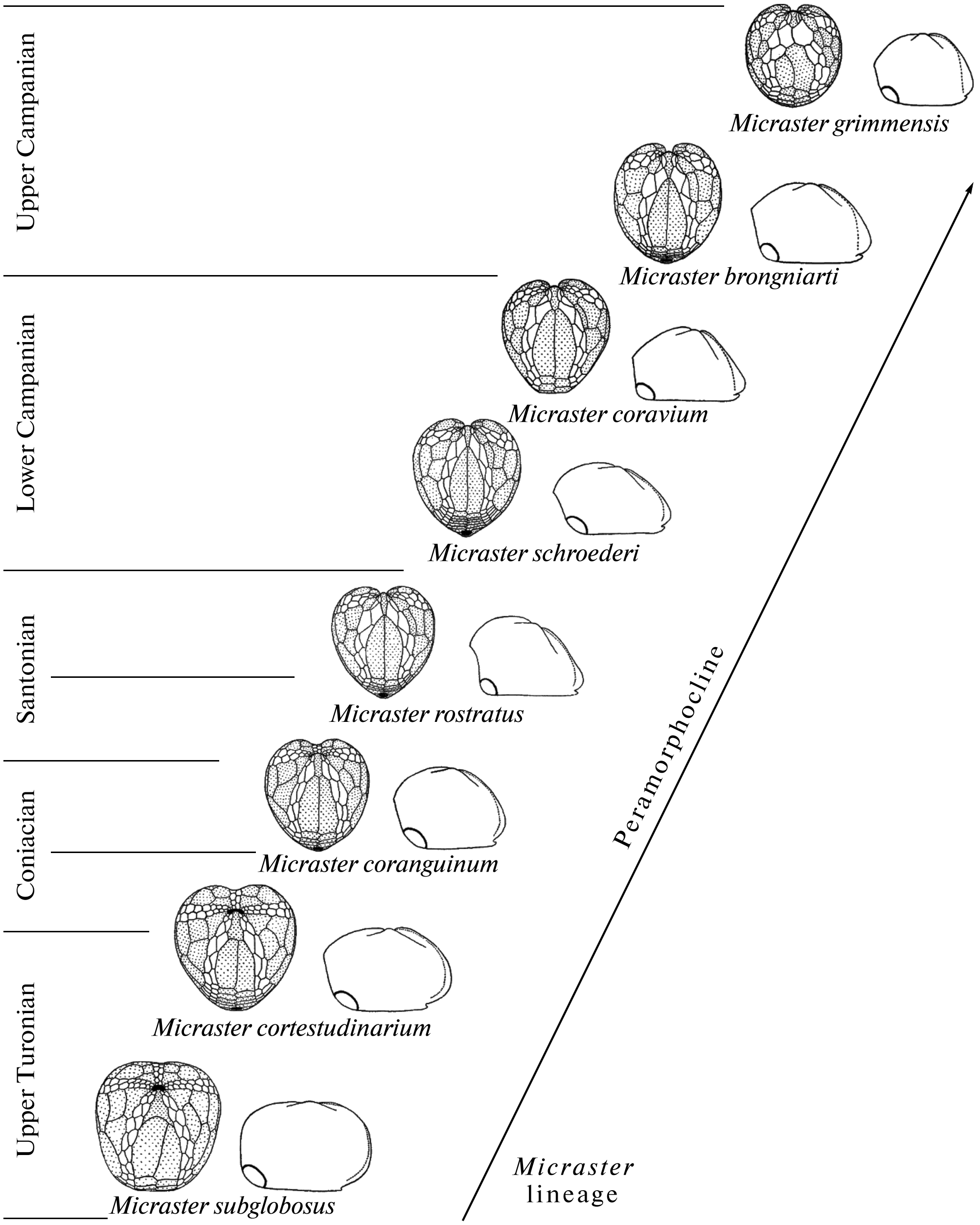

Fig. 11. Evolutionary lineage of *Micraster* (after Solovjev 1998, 2013, modified).

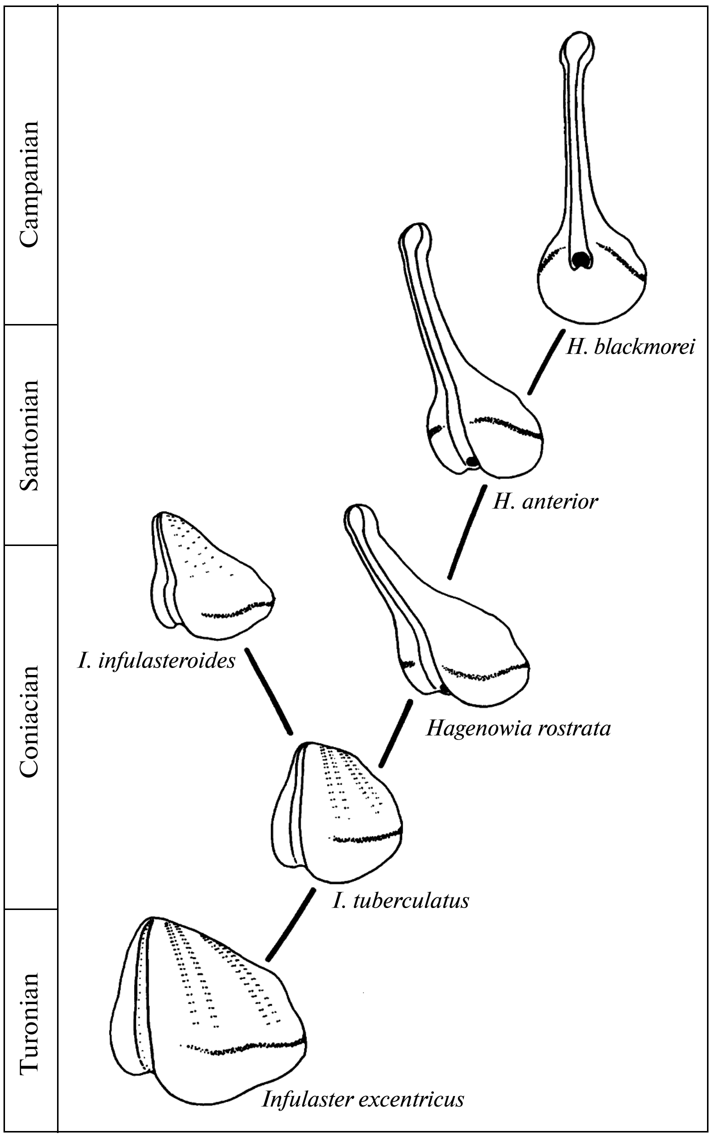

Fig. 12. Evolutionary transformations to the series of the Late Cretaceous genera *Infulaster–Hagenowia* (peramorphocline) (after Gale and Smith, 1985).

The following general patterns of ontogenetic development of fascioles have been revealed.

Since the main and sometimes the only character which distinguishes the families in question from each other is the fasciole structure, we briefly reviewed the knowledge of fascioles, primarily of the modes and patterns of their formation in the ontogeny of Hemiasteridae, Schizasteridae, and Paleopneustidae (Markov and Solovjev, 2001).

Summarizing all known facts, it becomes evident that the fasciole in the three families usually conform to the following rules:

Rule 1. Fasciole apparently cannot be shifted from some plates of the test to others during the growth of a sea urchin. Throughout the animal's life, they are retained on the plates on which they initially appear (but reduced on some plates). This is supported among other things by the morphology of juveniles at the stage of regular sea urchins. These animals, with the test ranging from 1.5 to 3 mm in diameter, have been described in the schizasterid genera *Brisaster, Abatus,* and *Schizocosmus* (Mortensen, 1951; Markov, 1994). All of them already have an anlage of the marginal fasciole, which curves as a ring around the apical system and in located on the fourth–fifth plates in all interambulacral series. At the stage of regular sea urchin,

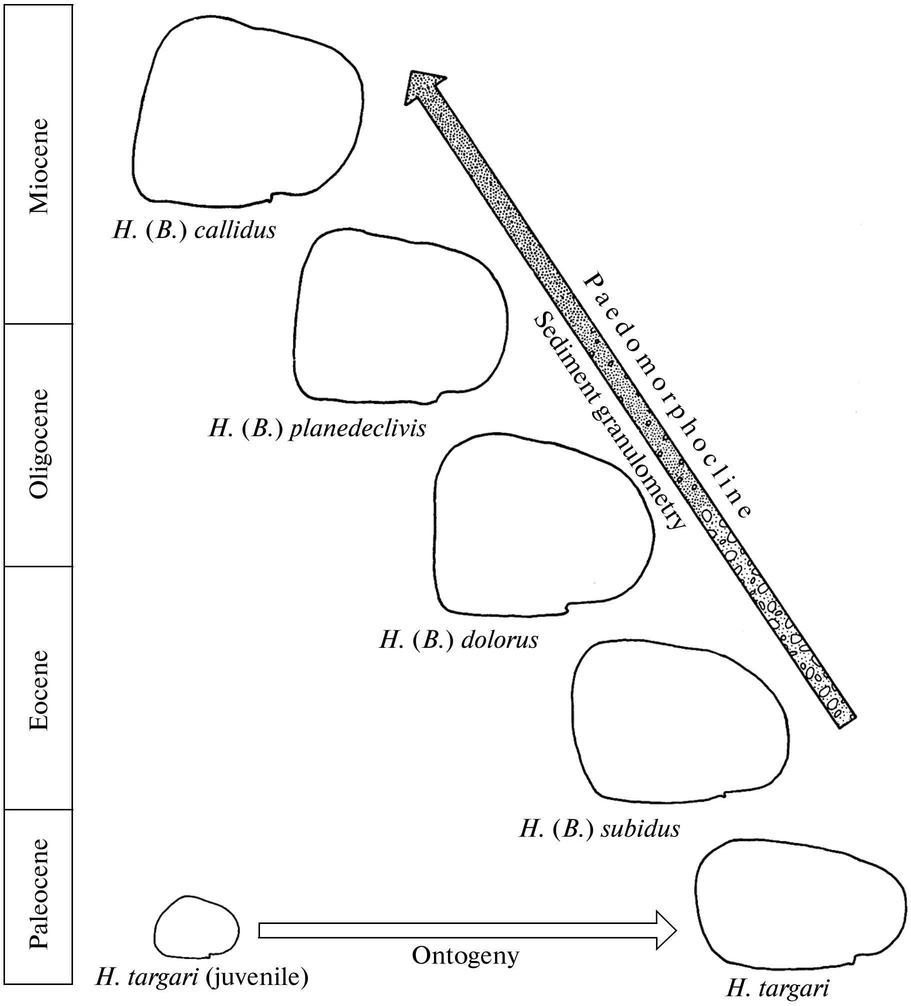

Fig. 13. Paedomorphic change in the lateral test outline in the evolutionary lineage *Hemiaster (Bolbaster)* (Paleocene–Miocene of Australia) (after McNamara, 1987).

these plates are adapical. In the course of further development, 5–7 new plates are formed in each interambulacral series. The marginal fasciole remains on the fourth–fifth plates of interambulacra during the entire life of sea urchins. It gradually moves from the apical system to the definitive position in the area of the ambitus.

Rule 2. Fasciole are usually formed in the shape of an integrated anlage rather than separate parts. This is true of the peripetal fasciole of Hemiasteridae and the marginal and semiperipetal fascioles of Schizasteridae. In the Paleopneustidae, early stages are not known; however, there is no reason to believe that this family differs from the other two in this respect.

Rule 3. Fascioles cannot appear in ontogeny earlier than plates that bear these fascioles in adults are formed. This rule is a direct consequence of rules 1 and 2.

Rule 4. Fascioles tend to appear in ontogeny as early as possible. This is true not only of the suborder Hemiasterina, but also the suborder Micrasterina (the subanal fasciole is formed very early in ontogeny). In all known cases, fascioles are formed almost immediately after the formation of respective plates. This rule is apparently of dual nature, adaptive and constructive. On the one hand, fascioles are apparently particularly important for juveniles (Gordon, 1927; Markov, 1994). In many Schizasteridae and Paleopneustidae, fascioles are developed in young sea urchins to a much greater extent than in adults, although an opposite situation has not been recorded. On the other hand, for fascioles it is probably "easier" to be formed in young, just appearing plates of the test, which lack well-developed tuberculation, spine cover, and pedicellariae.

Rule 5. Fascioles initially tend to form closed contours, which either become ringlike or fuse with

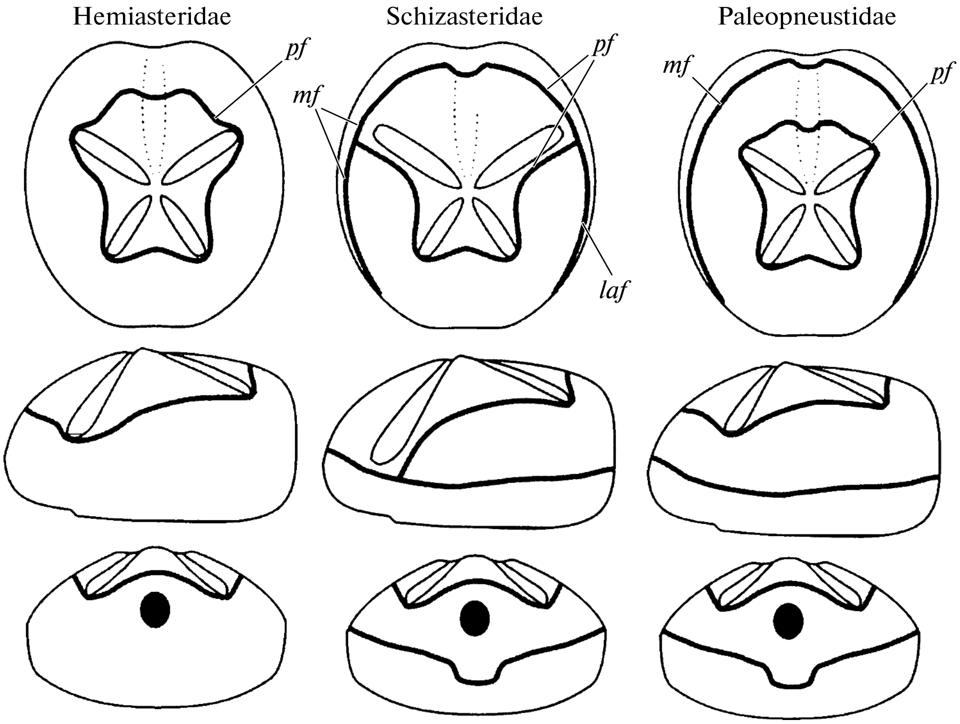

Fig. 14. Fascioles of Paleopneustidae, Schizasteridae, and Hemiasteridae (scheme). Designations of fascioles: (*pf*) peripetal, (*mf*) marginal, and (*laf*) lateroanal (after Markov and Solovjev, 2001).

other fascioles; they "do not like" blind ends. The marginal fasciole of Schizasteridae and peripetal fasciole of Hemiasteridae are initially formed as a closed ring; the semiperipetal fasciole is fused by its free ends with the marginal fasciole soon after formation. This rule is likely of constructive nature and meaningless from the adaptation point of view. In particular, in many Schizasteridae, after reduction of the anterior part of the lateroanal fasciole, its subanal part looking like a curved band with blind ends is retained. This does not prevent efficient functioning (push water back along the sanitary canal, removing products of vital activity).

Rule 6. With rare exception, fascioles tend to curve around the petaloid areas of ambulacra, coming as close as possible to their ends, rather than cross these areas. This rule is of adaptive nature; the fasciole intensifies the water flow washing the tube feet of petaloids, functioning as gills; if the fasciole cuts the petaloid, the gills located external to it would be washed insufficiently intensively; if the fasciole passes too far from the petaloid end, the entire petaloid would function less efficiently. Possibly, this rule also has a constructive aspect; the same plate of the test cannot be simultaneously and a petaloid and fasciolar plate.

The analysis of available data on the morphology, ontogeny, and stratigraphical range of Hemiasteridae, Schizasteridae, and Paleopneustidae allowed Markov and Solovjev (2001) to draw the conclusions listed below.

The Schizasteridae evolved from Hemiasteridae with long anterior petaloids, so that the ontogenetic mechanism of initiation of fasciolar rings worked two times; first, it was manifested at the stage of regular sea urchin (marginal fasciole) and, second, when the periproct came out of the apical system (the semiperipetal fasciole was formed), as in ancestral Hemiasteridae. The fact that the second fasciole was fused with the first and did not form a separate ring resulted from the same factor as prerequisites to all of these transformations, i.e., the long anterior petaloids (Figs. 14, 15).

The Paleopneustidae evolved from Schizasteridae with the secondary shortened anterior petaloids as a result of shift of the point of connection of fascioles from lateral to anterior interambulacra.

Let us consider heterotopies in different sea urchin groups. It has been shown that, in the evolution of irregular sea urchins, the fifth gonad and, gradually, genital plate 5 were reduced. Genital plates 1, 2, 3, and 4 with pores are retained. However, the Middle Jurassic (Bathonian) species *Pygomalus analis* (order Disasteroida) has anomalies with five incipient gonads, as follows from the presence of an

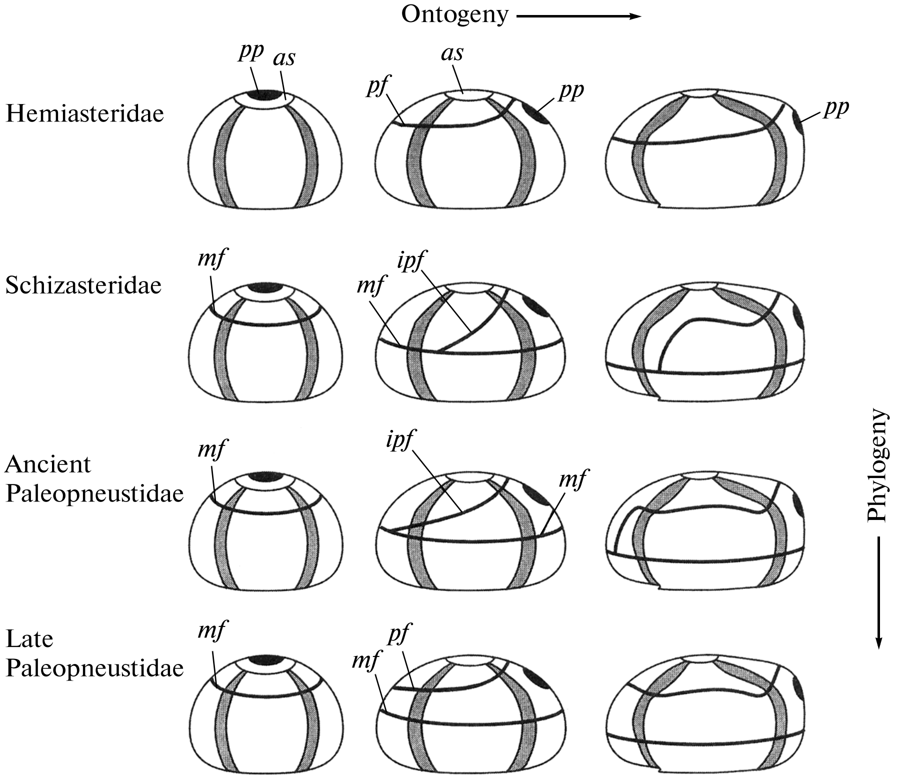

Fig. 15. Evolution and morphogenesis of fascioles in the suborder Hemiasterina (scheme). Designations: (*as*) apical system, (*pp*) periproct, (*mf*) marginal fasciole, (*pf*) peripetal fasciole, (*ipf*) incomplete peripetal fasciole (after Markov and Solovjev, 2001).

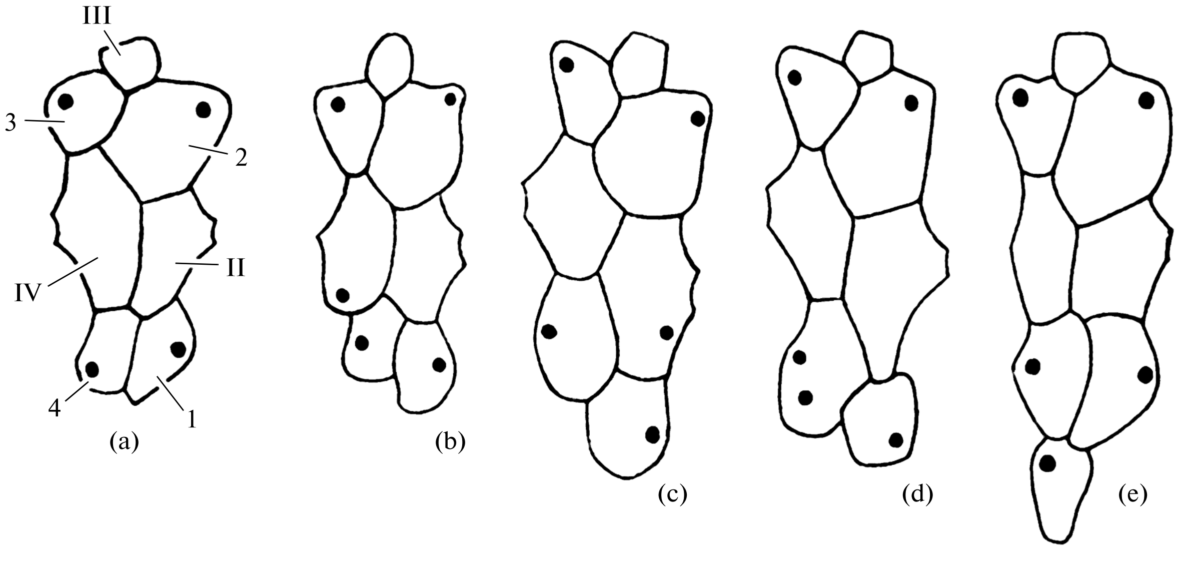

Fig. 16. Anterior part of the apical system of *Pygomalus analis* (Agassiz), Upper Bathonian of Poland: (a) typical structure (four genital pores are located on genital plates 1, 2, 3, and 4); (b–e) apical system with five genital pores: (b) additional pore located on ocular plate IV, (c) additional pore located on ocular plate II, (d) additional pore located on genital plate 4, (e) additional pore located on additional plate, which is nonhomologous to other plates of the apical system (after Jesionek, 1956, modified).

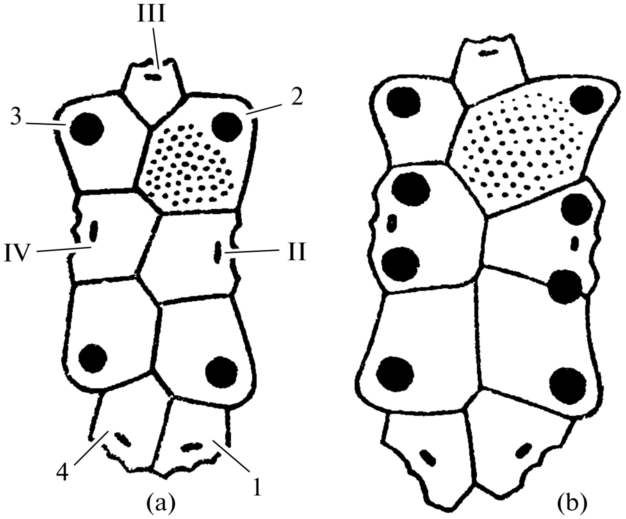

Fig. 17. Apical system in members of the order Holasteroida: (a) *Holaster subglobosus* (Leske), Cenomanian of the northern Caucasus; typical structure, with four genital pores located on genital plates 1, 2, 3, and 4; (b) *Guettaria rocardi* Cotteau, Maestrichtian of the Kopet Dagh, apical system with eight genital pores, additional pores are on ocular plates II and IV (after Poslavskaya and Solovjev, 1964).

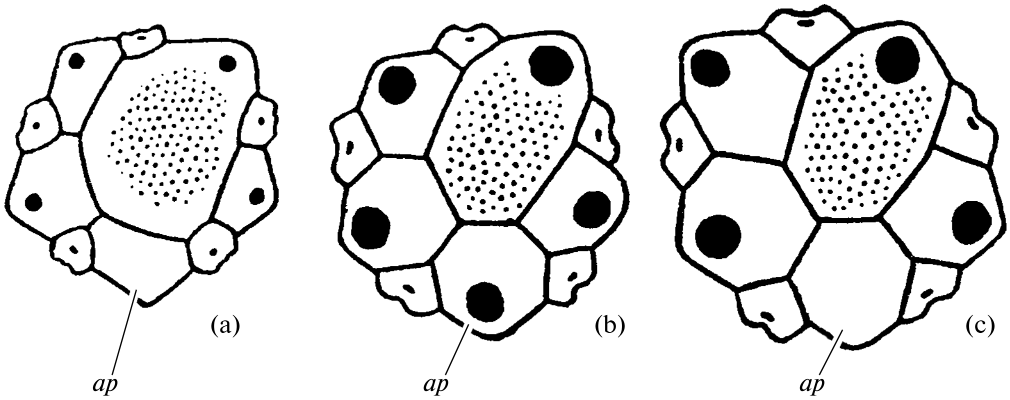

Fig. 18. Apical system in members of the order Holectypoida: (a) *Holectypus hemisphaericus* (Agassiz), Jurassic of Western Europe; (b) *Discoides minimus* (Agassiz), Cenomanian of Western Europe; (c) *Camerogalerus cylindricus* (Lamarck), Cenomanian of the northern Caucasus. All species have an additional plate (*ap*) in the fifth interradius, which is nonhomologous to other plates of the apical system; in the second species, it has a genital pore (after Schmidt and Solovjev, 1964).

additional genital pore in different plates of the anterior part of the apical system, including ocular plates (Fig. 16).

The increase in the number of gonads to eight is observed as a constant character in the Late Cretaceous (Maastrichtian) species *Guettaria rocardi* (order Holasteroida); at the same time, additional genital pores are formed on ocular plates II and IV (two in each) (Fig. 17).

In Jurassic and Cretaceous species of the order Holectypoida, the fifth interradius of the apical system frequently has an additional plate which is not homologous to genital or ocular plates, as is evidenced by crystallographic data (Jesionek-Szymańska, 1959). In some cases, this plate has a genital pore, suggesting the initiation of the fifth gonad. The apical system of such species acquires ideal pentactinal symmetry, making it similar to that of regular sea urchins (Fig. 18).

The order Clypeasteroida is characterized by the development on the aboral and oral sides of the test of numerous microscopic ambulacral pores, which occur

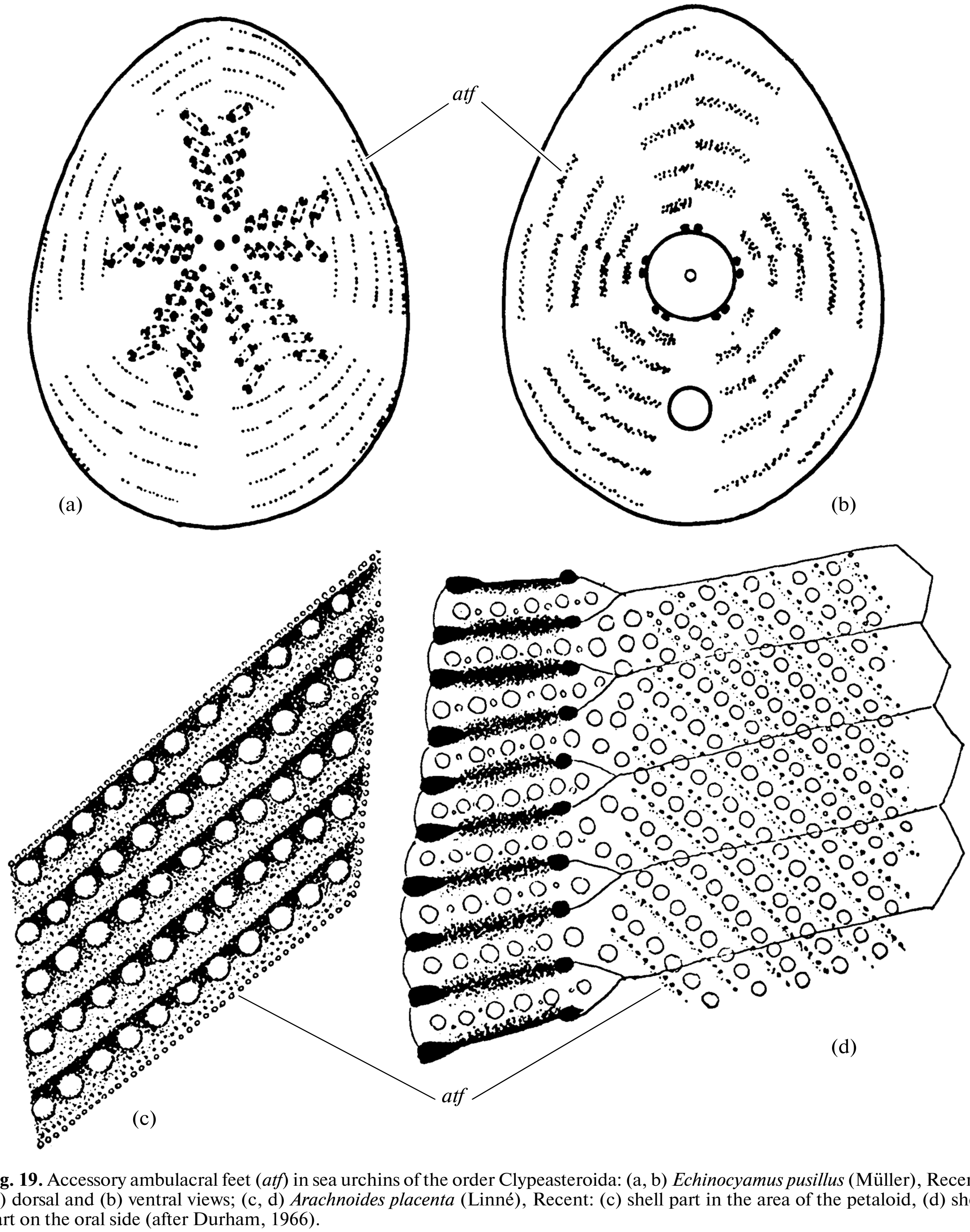

Fig. 19. Accessory ambulacral feet (*atf*) in sea urchins of the order Clypeasteroida: (a, b) *Echinocyamus pusillus* (Müller), Recent: (a) dorsal and (b) ventral views; (c, d) *Arachnoides placenta* (Linné), Recent: (c) shell part in the area of the petaloid, (d) shell part on the oral side (after Durham, 1966).

not only in the ambulacral fields, but also on the interambulacra. These pores provide passage for accessory ambulacral feet, which, along with the ciliate epithelium on the test surface, provide a specific feeding mode, extraction of food particles from the surface ground layer by sieving (Fig. 19).

ACKNOWLEDGMENTS

I am grateful to A.V. Guzhov and G.V. Mirantsev for help in the preparation of the paper.

This study was supported by the Program of the Presidium of the Russian Academy of Sciences “Problems of the Origin of Life and Formation of the Biosphere" and the Russian Foundation for Basic Research, project no. 13-05-00459.

REFERENCES

Chesher, R.H., Evolution of the genus *Meoma* (Echinoida, Sphatangoida) and a description of a new species from Panama, *Bull. Mar. Sci.,* 1970, vol. 20, pp. 731–761.

David, B., Significance of architectural patterns in the deep-sea echinoids Pourtalesiidae, *Proceedings of the Fifth International Echinoderm Conference,* Galway, 1984, pp. 237–243.

David, B., How to study evolution in echinoderms?, in *Echinoderm Studies,* Jangoux, M. and Lawrence, J.M., Eds., (Rotterdam) Brookfield: Balkema, 1993, pp. 1–80.

Durham, J.W., Clypeasteroids, in *Treatise on Invertebrate Paleontology: Part U, Echinodermata 3,* 1966, vol. 2, pp. 450–491.

Gale, A.S. and Smith, A.B., The palaeobiology of the Cretaceous irregular echinoids *Infulaster–Hagenowia, Palaentology,* 1985, vol. 25, pp. 11–42.

Gordon, I., The development of the calcareous test of *Echinocardium cordatum, Phil. Trans. Roy. Soc. London. B,* 1926, vol. 215, pp. 253–313.

Jesionek, W., Obserwacje nad morphologia *Pygomalus analis* (Agassiz) (Echinida, Disasteridae), *Acta Palaeontol. Polon.,* 1956, vol. 1, no. 1, pp. 49–68.

Jesionek-Szymańska, W., Remarks on the structure of the apical system of irregular echinoids, *Acta Palaeontol. Polon.,* 1959, vol. 4, no. 3, pp. 339–352.

Jesionek-Szymańska, W., Échinides irréguliers du Dogger de Pologne, *Acta Palaeontol. Polon.,* 1963, vol. 8, no. 3, pp. 293–414.

Jesionek-Szymańska, W., Irregular echinoids—an insufficiently known group, *Lethaia,* 1968, vol. 1, pp. 50–65.

Markov, A.V., Fascioles of sea urchins of the family Shizasteridae, *Byull. Mosk. Obshch-va Ispyt. Prir. Otd. Geol.,* 1989, vol. 64, no. 5, p. 124.

Markov, A.V., Morphology, systematics, and phylogeny of sea urchins of the family Schizasteridae, *Tr. Paleontol. Inst. Ross. Akad. Nauk,* 1994, vol. 258, pp. 1–93.

Markov, A.V. and Kushlina, V.B., Postlarval development of some spatangoid sea urchins, *Paleontol. Zh.,* 1990a, no. 2, pp. 60–68.

Markov, A.V. and Kushlina, V.B., Quantitative aspects of age changes in some spatangoid sea urchins, *Paleontol. Zh.,* 1990b, no. 4, pp. 49–56.

Markov, A.V. and Solovjev, A.N., Sea urchins of the family Paleopneustidae (Echinoidea, Spatangoida): Morphology, system, phylogeny, *Tr. Paleontol. Inst. Ross. Akad. Nauk,* 2001, vol. 280, pp. 1–108.

McNamara, K.J., Taxonomy, evolution, and functional morphology of southern Australian Tertiary hemiasterid echinoids, *Palaentology,* 1987. vol. 30, part 2, pp. 319–352.

McNamara, K.J., The role of heterochrony in the evolution of spatangoid echinoids, *Geobios, Mèm.,* spec., 1989, no. 12, pp. 283–295; *Paleontology,* vol. 30, part 2, pp. 319–352.

Mortensen, Th., *A Monograph of the Echinoidea,* Copenhagen: Reitzel Publ., 1951, vol. 5, part 2.

Nichols, D., Changes in the chalk heart-urchin *Micraster* interpreted in relative to living forms, *Philos. Trans. Roy Soc. London, B,* 1959, vol. 242, pp. 347–437.

Poslavskaya, N.A., On species and generic criteria in some Spatangoida, *Byull. Mosk. Obshch-va Ispyt. Prir. Otd. Geol.,* 1958, vol. 33, no. pp. 159–160.

Poslavskaya, N.A. and Moskvin, M.M., Echinodermata, in *Atlas verkhnemelovoi fauny Severnogo Kavkaza i Kryma* (Atlas of the Upper Cretaceous Fauna of the Northern Caucasus and Crimea), Moscow: Gostoptekhizdat, 1959, pp. 237–304.

Poslavskaya, N.A. and Solovjev, A.N., Sea urchins: Order Spatangoida, *Osnovy paleontologii. Iglokozhie, gemikhordovye, pogonofory i shchetinkochelyustnye* (Fundamentals of Paleontology: Echinoderms, Hemichordates, Pogonophores, and Chaetognathans), Gekker, R.F., Ed., Moscow: Nauka, 1964, pp. 174–189.

Saucède, T., Mironov, A.N., Mooi, R., and David, B., The morphology, ontogeny, and inferred behavior of the deep-sea echinoid *Calymne relicta* (Holasteroida), *Zool. J. Linn. Soc.,* 2009, vol. 155, no. 144 (2), pp. 630–648.

Shmidt, O.M. and Solovjev, A.N., Sea urchins: Order Holectypoida, *Osnovy palentologii. Iglokozhie, gemikhordovye, pogonofory i shchetinkochelyustnye* (Fundamentals of Paleontology: Echinoderms, Hemichordates, Pogonophores, and Chaetognathans), Gekker, R.F., Ed., Moscow: Nauka, 1964, pp. 167–169.

Solovjev, A.N., Late Jurassic and Early Cretaceous disasterid sea urchins of the USSR, *Tr. Paleontol. Inst. Akad. Nauk SSSR,* 1971, vol. 131, pp. 1–124.

Solovjev, A.N., Evolutionary lineages of some Cretaceous and Cenozoic genera of sea urchins and their interpretation, in *Tezisy Dokladov XLIV sessii Paleontologicheskogo obshchestva* (Reports of the XLIV Sessions of the Paleontological Society), St. Petersburg, 1998, pp. 94–95.

Solovjev, A.N., Apical system of Jurassic irregular sea urchins, in *Yurskaya sistema Rossii: problemy stratigrafii i paleogeografii. IV Vserossiiskoe soveshchanie. Nauchnye materialy* (IV All-Russia Meeting on the Jurassic System of Russia: Problems of Stratigraphy and Paleogeography), St. Petersburg, 2011, pp. 205–207.

Solovjev, A.N., Symmetry, asymmetry, and dissymmetry in sea urchins, in *Morfogenez v individual'nom i istoricheskom razvitii: simmetriya i asimmetriya. Seriya "Geo-biologicheskie sistemy v proshlom* (Geobiological Systems in the Past: Morphogenesis in Individual and Historical Development: Symmetry and Asymmetry), Moscow: Paleontol. Inst. Ross. Akad. Nauk, 2013, pp. 232–240.

Solovjev, A.N. and Markov, A.V., Early stages of the evolution of irregular sea urchins, in *Ekosistemnye perestroiki i evolyutsiya biosfery* (Ecosystem Rearrangements and Evolution of the Biosphere), Barskov, I.S., Leonova, T.B., and Ponomarenko. A.G., Eds., Moscow, Paleontol. Inst. Ross. Akad. Nauk, 2004, vol. 6, pp. 77–86.

Solovjev, A.N. and Markov, A.V., Trophic features of sea urchins at different stages of historical development of the class, in *Evolyutsiya biosfery i bioraznoobrazie* (Evolution of the Biosphere and Biodiversity), Moscow: KMK, 2006, pp. 316–333.

Translated by G. Rautian