

Parallelisms in the Evolution of Sea Cucumbers (Echinodermata: Holothuroidea)

A. V. Smirnov

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034 Russia
e-mail: sav_11@inbox.ru

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Abstract—The importance of taking into account parallelisms in the evolution of morphological characters is analyzed for the taxonomy of the class Holothuroidea. The establishment of the order Dactylochirotida and classification of the order Elasipodida serve as examples to illustrate insufficient appreciation of parallelisms in Holothuroidea. The following characters, evolving independently in different groups of sea cucumbers, are considered: a stout skeleton, reduction of the calcareous ring and the body wall sclerites; similarity of body shape; similarity in the shape of tentacles; reduction in the number of tentacles from 12 to 10 in different families and subfamilies of the order Synaptida. Based on the analysis of morphological and molecular data, the family Deimatidae is transferred from the order Elasipodida to the order Aspidochirotida. It is hypothesized that the concave cup-shaped sclerites with three to five rays occurring in the family Laetmogonidae (order Elasipodida) are of paedomorphic origin and correspond to the early growth stages of the laetmogonid wheels; the concave cross-shaped sclerites of the families Elpidiidae and Psychropotidae may have originated from laetmogonid concave cup-shaped sclerites. Emended diagnosis of the order Elasipodida is proposed. The family Vaneyellidae previously synonymized by the author with the family Cucumariidae is reestablished, and its emended diagnosis is also proposed.

Keywords: parallelism, paedomorphosis, calcareous ring, sclerites, holothurians, Elasipodida, Aspidochirotida, Dendrochirotida, Dactylochirotida, Deimatidae, Laetmogonidae, Vaneyellidae

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INTRODUCTION

Holothuroidea is a class of echinoderms of a paedomorphic origin (David and Mooi 1996, 1998; Mooi and David, 1997; Smirnov, 2014, 2015). Due to paedomorphosis, holothurians managed to escape the burden of former organization, freeing themselves of the limitations imposed by a massive skeleton embracing the entire body. In holothurians, the skeleton is represented only by a calcareous ring and microscopic sclerites in body wall, tentacles, and sometimes in the walls of other internal organs. Holothurian sclerites, certainly evolved through paedomorphosis (Cuénot, 1948; Smirnov, 2015). Apart from the loss of the skeleton, changes due to paedomorphosis led to the secondary appearance of gradual metamorphosis and to the arrangement of radial canals of the ambulacral system. The latter, in turn, caused changes in the mode of development of epineural neural cords and epineural canals (Smirnov, 2015). The appearance of the gradual metamorphosis resulted in an increase in heterochrony of the development of characters of different coordination chains, and in a greater lability in the evolution of the morpho-anatomical structures. Altogether, this allowed holothurians to colonize a large number of biotopes. At present, holothurians live at all depths of the world's oceans, from the littoral to the

hadal. In many deep water biocoenoses they are dominant forms. Holothurians include epifaunal as well as infaunal forms. Many holothurians became benthopelagic and even pelagic (*Pelagothuria natatrix*) (e.g., Rogacheva et al., 2012). The colonization of similar biotopes by different groups of holothurians at different times and adaptation to similar environments as well as acquiring a similar lifestyle should have resulted (and this did happen) in the parallel appearance of similar morphologies. This in the first hand involved external morphological characters, such as the body shape, morphology of tentacles, the development of a strong skeleton, or on the contrary, reduction of skeletal elements. The changes also involved the internal organization of holothurians leading to the parallel appearance of similar anatomical characters. Not only origin of holothurians connected with paedomorphosis, but it was also very important in their evolution and among extant holothurians there are some taxa, which have a paedomorphic origin (Smirnov, 2015). Therefore, parallel characters could also have appeared by paedomorphosis.

Despite the reduction of skeletons in holothurians, their skeletal elements are conservative in morphology, and this allows their use as “prevalent” taxonomic characters. The structure of the calcareous ring is one

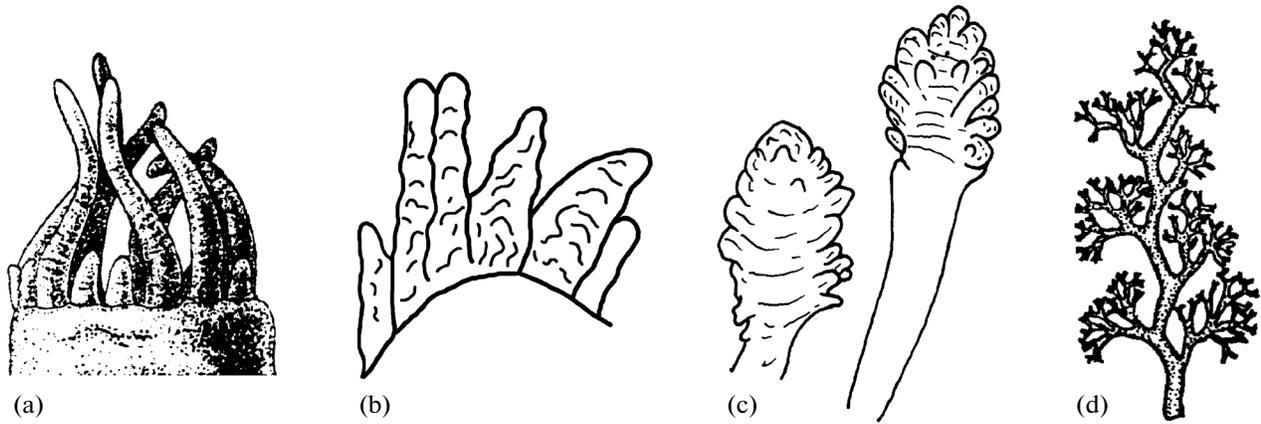


Fig. 1. Dendrochirotid holothurian tentacles: (a) *Vaneyella dactylica* (Vaneyellidae, “Dactylochirotida”); (b) *Rhopalodinia minuta* (Rhopalodiniidae, “Dactylochirotida”); (c) *Rhopalodinosia capensis* (Rhopalodiniidae, “Dactylochirotida”); (d) typical dendrochirotid tentacle; (a) from Ohshima (1918); (b) and (c) from Thandar (2001); (d) from Pawson (1966).

of the most important taxonomic characters significant extant and extinct holothurians taxonomical studying (Reich, 2015). Unfortunately, little is presently known about its 3_D morphology (Reich and O’Loughlin, 2011).

Modern molecular genetic methods have revealed that the complex morpho-anatomical structures in various taxa of holothurians could have originated parallel. So some taxa, previously considered as monophyletic, are really para- or polyphyletic. Consequently, the taxonomy and phylogeny of the class and its constituent taxa must be reinterpreted. It has become apparent that some taxonomists frequently, and undeservedly, disregarded data on the morpho-anatomical characters of some groups described by their predecessors. The recognition of simultaneously appearing parallel characters has always been an important task for taxonomists because it helped to diminish mistakes in reconstructing phylogeny of animals. The wide use of cladistics in the taxonomic practice in no way negates this fundamental principle. The present author did not intend to assemble all examples of parallel development in holothurians and only mentioned several instances of the parallel appearance of morpho-anatomical characters affecting the systematics of the class Holothuroidea.

One of the examples of underestimation of the possibility of the parallel appearance of morphological characters is the establishment of the order Dactylochirotida (Dactylochirotida) for three families previously placed within the order Dendrochirotida (Dendrochirotida) (Pawson and Fell, 1965; Pawson, 1982). The diagnostic characters of the order Dactylochirotida included: (1) simple unbranched tentacles; (2) U-shaped body; (3) test comprising imbricating calcareous plates; and (4) calcareous ring simple, lacking complex posterior processes.

1. The name of the order Dactylochirotida clearly suggests one of the major diagnostic characters of the

order. However, unbranched tentacles in modern holothurians (Figs. 1a, 1b) most certainly derived from branched ones (Fig. 1d) by reducing their branches, which is indicated by the presence in some species of branch traces (Fig. 1c). Ohshima indicated that the tentacles of *Pseudocucumis dactylicus* (currently *Vaniella dactylica*), assigned by Pawson and Fell to the family Vaneyellidae in the order Dactylochirotida (Pawson and Fell, 1965), are “seldom with a few knoblike rudiments of branches” (Ohshima, 1915, p. 272). Thandar (2001, p. 241) noted that: “Although the tentacles of some rhopalodiniids may be simple and fingerlike with short lateral branches, those of *Rhopalodinosia* at least appear to be finely dendritic.” (Fig. 1c). Simple tentacles, which certainly evolved from dendritiform tentacles are observed in the species *Psolus digitatus* Ludwig, 1894 (family Psolidae, order Dendrochirotida). Clearly secondarily simplified simple tentacles are also observed in other orders of holothurians. The paedomorphic genus *Eupyrigus* (family Eupyrigidae, order Molpadiida) could be a good example (the similarity in the morphology of the simple tentacles in this genus and the simple tentacles of *Psolus digitatus* was noted by Ludwig (1894, p. 139)). There are clearly secondary simple tentacles in the paedomorphic holothurians of the family Synaptidae (order Synaptida): *Leptosynapta minuta*, *L. brasiliensis*, *Rhabdomiologus ruber*, “*Myriotrochus*” *geminiradiatus*, etc. (Smirnov, 2015). Thus simple tentacles repeatedly evolved convergently during the evolution of different orders of holothurians, therefore the presence of simple, unbranched tentacles cannot be considered as a character of the order Dactylochirotida, distinguishing it from the order Dendrochirotida *sensu* Pawson et Fell, 1965.

2. The U-shaped body is characteristic not only for Dactylochirotida (Figs. 2c, 2f), but is also found in some taxa of Dendrochirotida *sensu* Pawson et Fell, 1965, for instance for representatives of the families Psolidae,

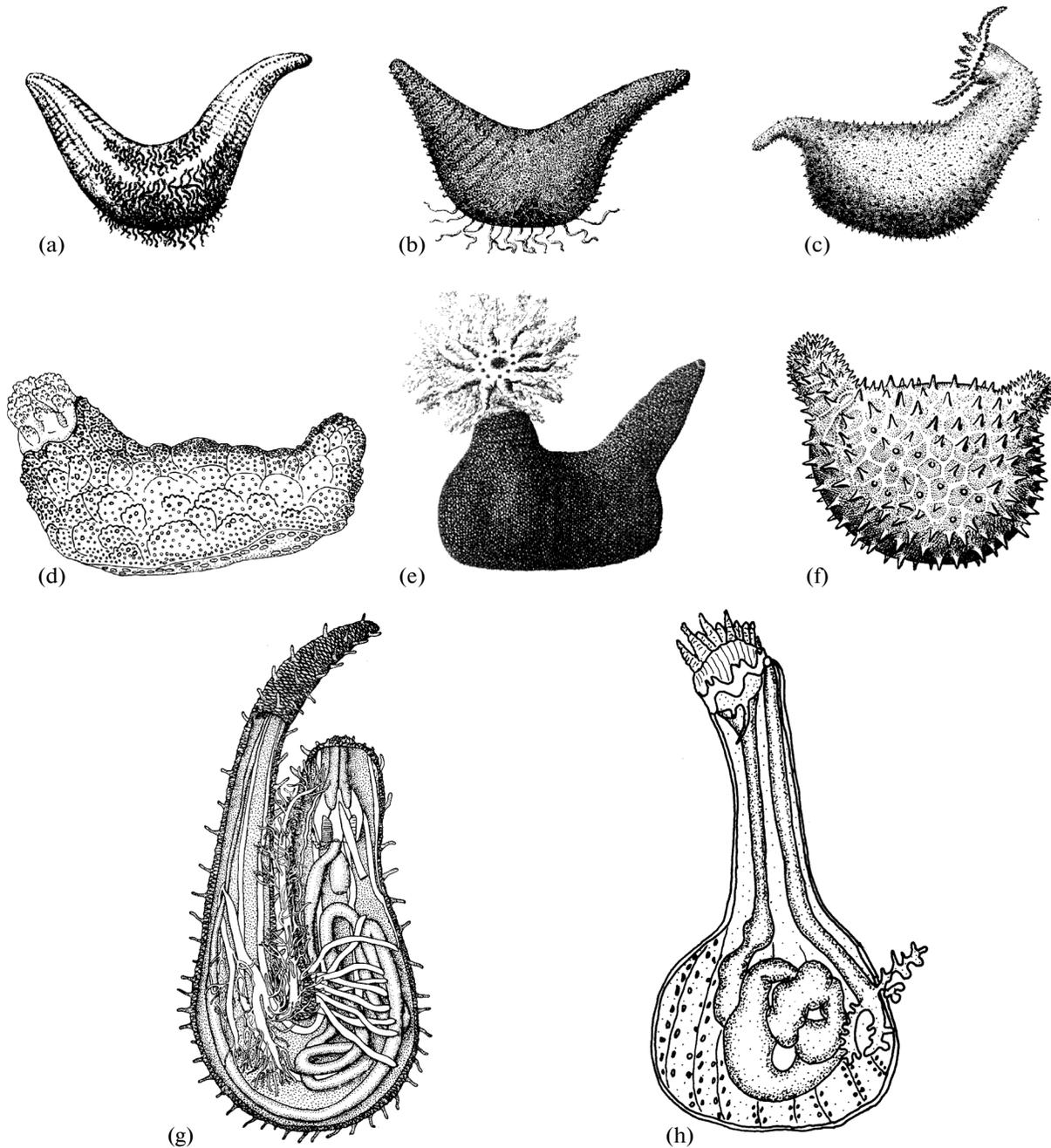


Fig. 2. U-shaped dendrochirotid holothurians: (a) *Stulus rapax* (Thyonidae, Dendrochirotida); (b) *Thorsonia investigatoris* (Thyonidae, Dendrochirotida); (c) *Echinocucumis hispida* (Cucumariidae, Dendrochirotida (family Ypsilothuriidae, “Dactylochirotida”)); (d) *Psolus solidus* (Psolidae, Dendrochirotida); (e) *Psolus phantapus* (Psolidae, Dendrochirotida); (f) *Ypsilothuria bitentaculata* (Ypsilothuriidae, “Dactylochirotida”); (g) *Heterothyone alba* (Heterothyonidae, Dendrochirotida); (h) *Rhopalodina minuta* (Rhopalodinidae, “Dactylochirotida”); (a) and (b) from Koehler and Vaney (1908); (c) from Sars (1861); (d) from Massin (1987); (e) from Madsen and Hansen (1984) after Strussenfelt; (f) from Cuénot (1948) after Ludwig (1894); (g) from Pawson (1963); (h) from Thandar (2001).

Phyllophoridae, Sclerodactylidae, Heterothyonidae, Thyonidae, and some others (Figs. 2a, 2b, 2d, 2e, 2g). Dendrochirotida *s. lato* are suspension feeders, and most likely this body shape evolved independently in different families as an adaptation to a burrowing life style. In the family Rhopalodinidae, the U-shaped

body led to a fusion of the descending and ascending halves, and development of free-living bottle-shaped forms with 10 ambulacra (Fig. 2h).

3. Reinforcement of the body wall is found in many holothurians, and is not limited to families included in the order Dactylochirotida (Figs. 2f, 3d, 3g, 3h), but

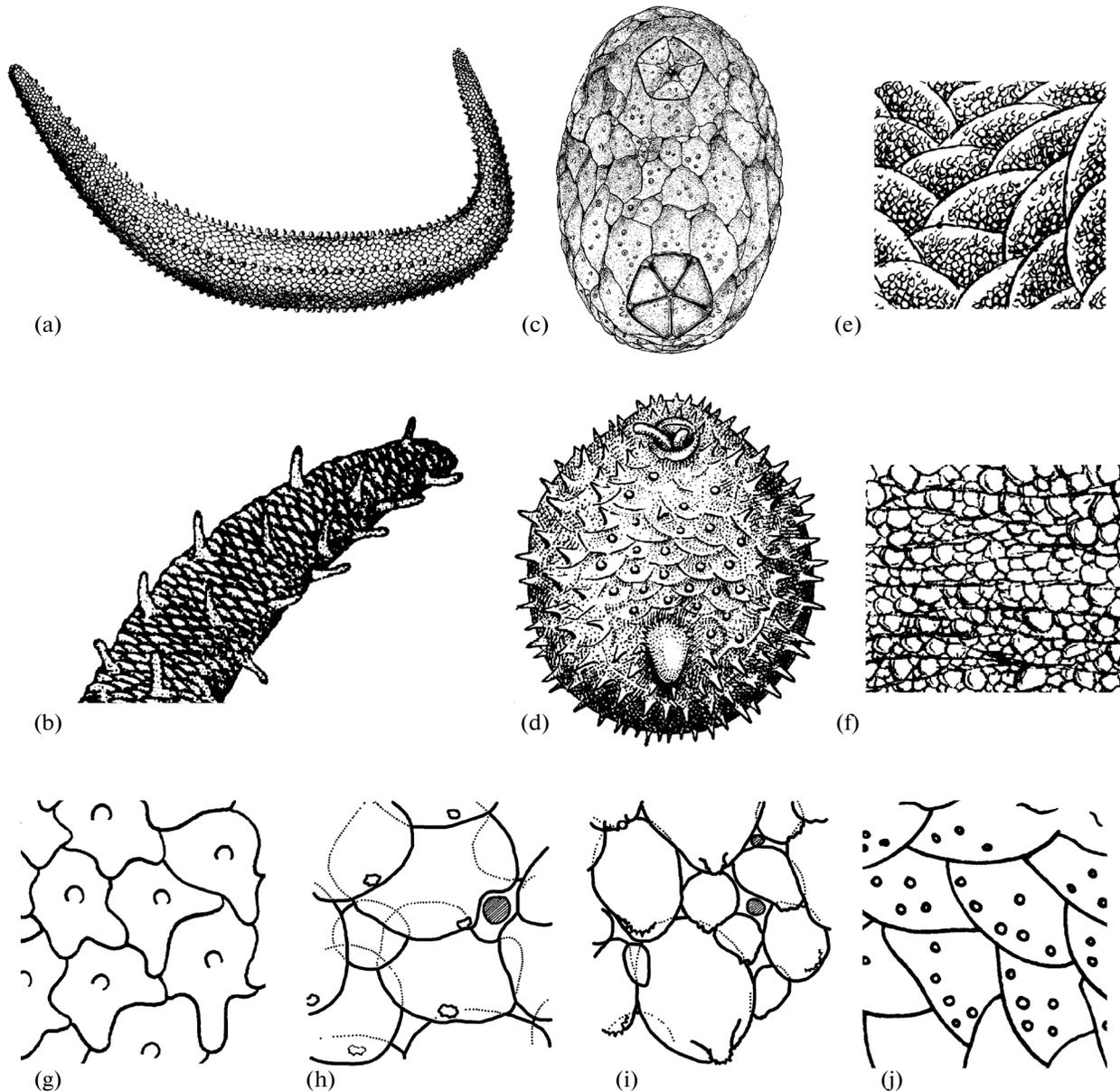


Fig. 3. Dendrochirotid holothurians the bodies of which are enclosed in a test formed by overlapping plates (scales): (a) *Pseudocnus alcocki* (Cucumariidae, Dendrochirotida); (b) *Heterothyone alba* (Heterothyonidae, Dendrochirotida), anterior part of the body; (c) *Psolus diomedeeae* (Psolidae, Dendrochirotida); (d) *Ypsilothuria bitentaculata* (Ypsilothuriidae, "Dactylochirotida"); (e) *Psolus fabricii* (Psolidae, Dendrochirotida), test fragment; (f) *Psolus phantapus* (Psolidae, Dendrochirotida), test fragment; (g) *Ypsilothuria bitentaculata* (Ypsilothuriidae, "Dactylochirotida"), test fragment; (h) *Vaneyella dactylica* (Vaneyellidae, "Dactylochirotida", test fragment; (i) *Stereoderma imbricata* (Cucumariidae, Dendrochirotida), test fragment; (j) *Psolus agulhasicus* (Psolidae, Dendrochirotida), test fragment. (a) from Koehler and Vaney (1908); (b) from Pawson (1963); (c) from Caso (1976); (d) from Cuénot (1948) after Ludwig (1894); (e) and (f) from Bell (1882); (g) and (j) from Ludwig and Heding, (1935); (h) and (i) from Ohshima (1918).

also occurs among members of the families remaining in the order Dendrochirotida *sensu* Pawson et Fell, 1965. In holothurians the reinforcement of the body wall can occur through the development of dense connective tissue, e.g., in the genus *Stichopus* (Stichopodidae, Aspidochirotida), and due to the presence of many small body wall sclerites, as observed in many Dendrochirotida *sensu* Pawson et Fell, 1965. Finally,

the test can be formed by large dense scales, resulting from extensive growth sclerites. Such a test is characteristic of the Ypsilothuriidae (Dactylochirotida) (Figs. 2f, 3d) and for Psolidae (Dendrochirotida *sensu* Pawson et Fell, 1965) (Figs. 2d, 3c). (In Psolidae the test of imbricated dense scales envelopes only the dorsal and lateral sides of the body, whereas the ventral side in Psolidae is transformed into the attachment

sole). The development of the test also certainly happened independently in different groups. Among Dendrochirotida *sensu* Pawson et Fell, 1965 the test is present in the families Paracucumidae and Heterothyonidae, and in some members of the family Cucumariidae and in some other families (Figs. 2a–2b, 3a, 3b, 3i). Note that the formation of the test and the size of its scales is easily changed depending on the habitat, which can be observed in the genus *Psolus*. Most species of the genus attached by the sole to the hard substrate (rocks or shells). *P. phantapus* burrows into the substrate and only its oral and anal cones rise above the seafloor. In this species, the scales are considerably smaller and far less dense (Figs. 2e, 3f), than in other species of the genus (Figs. 2d, 3c, 3e, 3j). Thus, the test appears in parallel in several groups of dendrochirotid holothurians, and this character cannot be considered as a feature distinguishing Dactylochirotida from Dendrochirotida *sensu* Pawson et Fell, 1965.

4. Morphology of the calcareous ring. The families of Dactylochirotida, Vaneyellidae (Figs. 4a, 4b) and Ypsilothuriidae (Fig. 4c) have a simple calcareous ring with no posterior processes on the radial segments subdivided into pieces, which is similar to Cucumariidae (Figs. 4e, 4f), Psolidae, Paracucumidae (Fig. 4g) and some others families of the order Dendrochirotida *sensu* Pawson et Fell, 1965. At the same time, radial segments of the calcareous ring in the family Rhopalodidae of the order Dactylochirotida have posterior processes, subdivided into pieces (Fig. 4d), which is similar to Phyllophoridae (Fig. 4h) from the order Dendrochirotida *sensu* Pawson et Fell, 1965. Therefore, the morphology of the calcareous ring, lacking subdivided posterior processes of the radial segments, cannot be considered as a character distinguishing the order Dactylochirotida from the order Dendrochirotida *sensu* Pawson et Fell, 1965. The similarity in the morphology of the calcareous ring within the order does not emerge in parallel as with the previous three characters, but, conversely, indicates the similarity of the taxa. Among both Dactylochirotida, and Dendrochirotida *sensu* Pawson et Fell, 1965 there are families with a calcareous ring lacking posterior processes on the radial segments and families with a calcareous ring with complex posterior processes on radial segments.

Thus, none of the above characters supposedly distinguishing the order Dactylochirotida from the order Dendrochirotida *sensu* Pawson et Fell, 1965 in fact discriminate between them. It could be suggested that Dactylochirotida is distinct in having an assemblage of specific characters rather than isolated characters, but the first three of the four characters, considered as specific to Dactylochirotida, commonly appear in completely different groups and are apparently connected with the lifestyle and adaptation to similar environmental constraints, whereas the “prevalent” conservative characters of the skeleton thought to be more important taxonomically clearly suggest the polyphyletic character of the order Dactylochirotida and the connection of

its families with other families of Dendrochirotida *sensu* Pawson et Fell, 1965 (Smirnov, 2012).

The analysis of “prevalent characters”, primarily skeletal elements clearly showed that the families Vaneyellidae (Figs. 4a, 4b) and Ypsilothuriidae (Fig. 4c) are similar to the families Cucumariidae (Figs. 4e, 4f), Psolidae, Paracucumidae (Fig. 4g) and several other families in the morphology of the calcareous ring lacking long posterior processes on the radial segments. Hence we proposed to establish for these taxa the suborder Cucumariina (Smirnov, 2012). In the morphology of the sclerites the family Vaneyellidae (Figs. 4i, 4j) is very similar to the family Cucumariidae (Figs. 4m, 4n). Sclerites of Ypsilothuriidae possessing an vertical dense reticular process (not homologous to the spire of the table) (Fig. 4k) are very similar to sclerites of Paracucumidae (Fig. 4o) and it is possible that the family Paracucumidae Pawson et Fell, 1965 should be synonymized with the family Ypsilothuriidae Hedding, 1942 (Smirnov, 2012, p. 823). Previously it was proposed (Smirnov, 2012) that the family Vaneyellidae Pawson et Fell, 1965 should be synonymized under Cucumariidae Ludwig, 1894, but presently author have changed his view. The history of study of the family Vaneyellidae and its diagnosis are given in the appendix.

The morphology of the calcareous ring and sclerites shows the similarity of the families Rhopalodidae (Figs. 4d, 4l) and Phyllophoridae *sensu* Smirnov, 2012. (Figs. 4h, 4p), which was previously noted by the authors studying Rhopalodidae (Hedding, 1937; Thandar, 2001). In the system of the class Holothuroidea proposed by me (Smirnov, 2012) I placed these two families near to each other in a group of families characterized by a calcareous ring with posterior processes on the radial segments.

The application of cladistic analysis does not exclude the possibility of mistakes in building a taxonomic system, and does not always produce a perfect result. Kerr and Kim (2001) used a cladistic analysis to study the taxonomy of the class Holothuroidea, for which they selected 47 characters and analyzed their distribution in 25 families of holothurians. Smirnov (2012) gave a brief analysis of that paper. In the context of the topic of parallelisms in the class Holothuroidea described in this paper it is necessary to note that while most anatomical characters selected by the authors for the cladistic analysis are selected correctly, eight characters are rigidly connected to one another morphologically and functionally and represent a single complex character. This duplication increases the number of characters used for the analysis and may skew the final result. Some of the selected characters clearly developed in parallel to one another and their use can lead to wrong results. There are primarily 11 characters related to the morphology and the structure of the calcareous ring, although parallelisms are also found among the anatomical characters. In my view, the following character states appeared independently in dif-

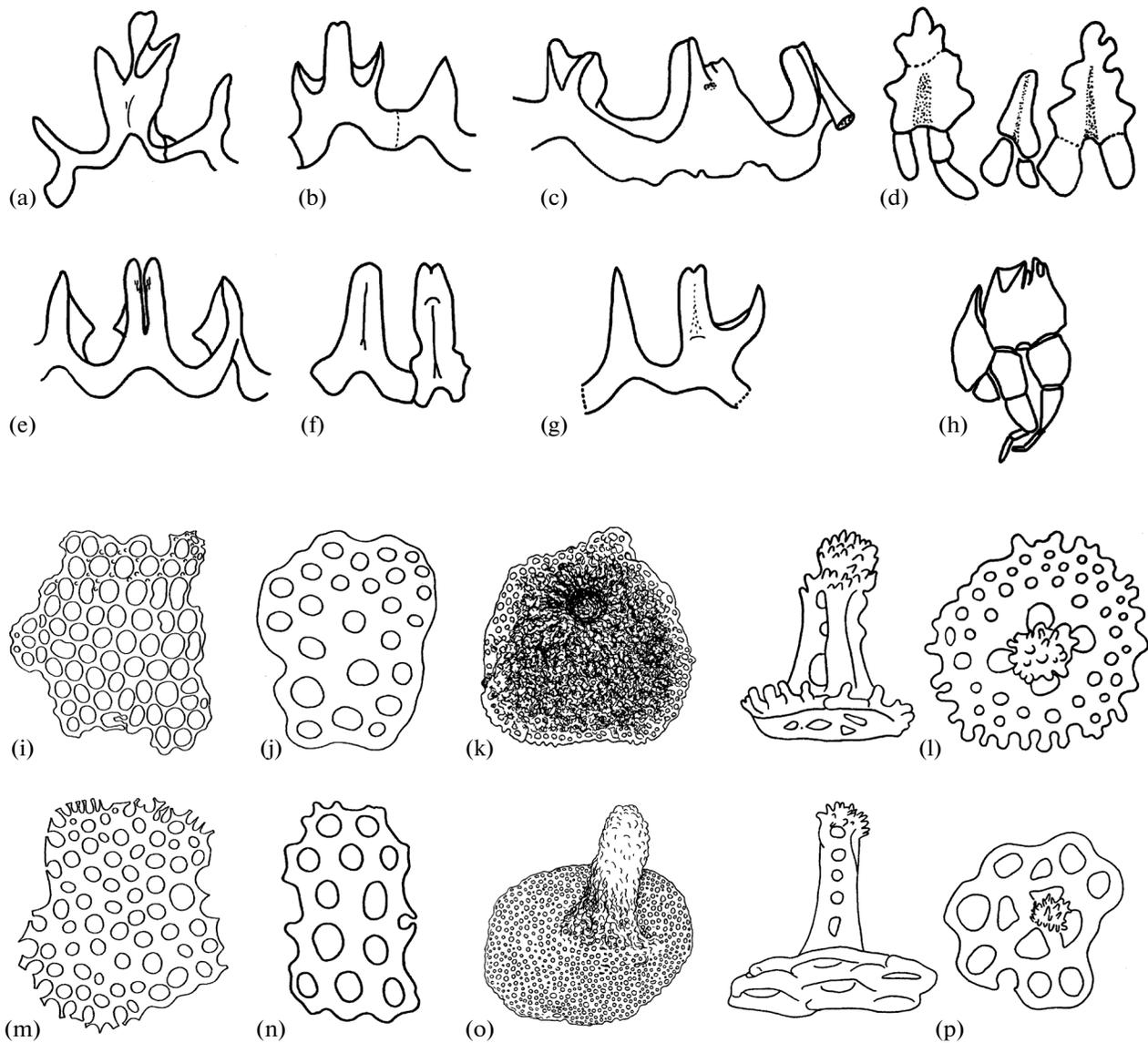


Fig. 4. Calcareous ring (a)–(h) and body wall sclerites (i)–(p) of the dendrochirotid holothurians: (a) *Vaneyella digitata* (Vaneyellidae, “Dactylochirotida”); (b) *Mitsukuriella squamulosa* (Vaneyellidae, “Dactylochirotida”); (c) *Ypsilothuria talismani elegans* (Ypsilothuriidae, “Dactylochirotida”); (d) *Rhopalodinopsis capensis* (Rhopalodinidae, “Dactylochirotida”); (e) *Trachythyone bouvetensis* (Cucumariidae, Dendrochirotida); (f) *Heterocucumis steineni* (Cucumariidae, Dendrochirotida); (g) *Paracucumis turricata* (Paracucumidae, Dendrochirotida); (h) *Phyllophorella robusta* (Phyllophoridae, Dendrochirotida); (i) *Vaneyella digitata*, (Vaneyellidae, “Dactylochirotida”); (j) *Mitsukuriella squamulosa* (Vaneyellidae, “Dactylochirotida”); (k) *Ypsilothuria bitentaculata virginensis* (Ypsilothuriidae, “Dactylochirotida”); (l) *Rhopalodina gracilis* (Rhopalodinidae, “Dactylochirotida”); (m) *Cucumaria frondosa* (Cucumariidae, Dendrochirotida); (n) *Cladodactyla senegalensis* (Cucumariidae, Dendrochirotida); (o) *Paracucumis turricata* (Paracucumidae, Dendrochirotida); (p) *Phyllophorus discrepans* (Phyllophoridae, Dendrochirotida). (a), (b), (g)–(j), (l), (o), (p) from Heding, Panning (1954); (c) and (k) from Heding (1942); (d) from Thandar (2001); (e) and (f) from Ludwig, Heding, (1935); (m) from Panning (1955); (n) from Panning (1957).

ferent orders and families of holothurians: subdivision of the longitudinal radial muscle into two longitudinal bands; presence of ampullae freely hanging in the body cavity; presence of a prominent sole; elongated and tapering posterior body end; position of the mouth (terminal-subterminal, clearly dorsal, or distinctly ventral); position of the anus (terminal-subterminal, clearly dorsal, or distinctly ventral); the length

of the dorsal interradius (considerably shorter or longer than the other interradia); imbricated body wall plates; presence of the increased dorsal papillae; presence of an opening on the radial segments of the calcareous ring; presence of long posterior processes on the radial segments of the calcareous ring; proportions of the radial segments of the calcareous ring (length and width of the segments are approximately the same

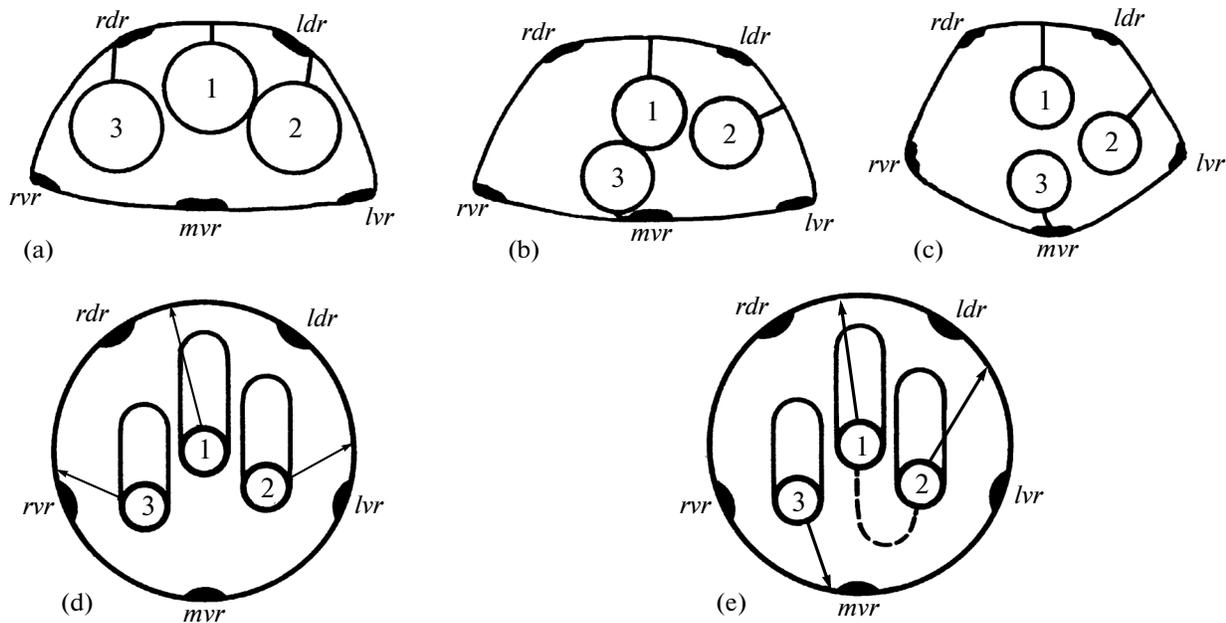


Fig. 5. Scheme of attachments of mesenteries suspending the intestine to the body wall in different orders of holothurians (a)–(c) and in different body parts of the holothurians of the order Elapsipodida (d) and (e) (oral view): (a) Elapsipodida; (b) Aspidochirotida; (c) Dendrochirotida, (d) Elapsipodida, anterior portion of the body; (e) Elapsipodida, posterior portion of the body. Designations: (*ldr*) left dorsal radius; (*lvr*) left ventral; (*mvr*) midventral radius; (*rdr*) right dorsal radius; (*rvr*) right ventral radius; (1) first descending part of the intestine; (2) ascending part of the intestine; (3) second descending part of the intestine. (a)–(c) from Ekman (1926); (d) and (e) from Gebruk (1990b), modified.

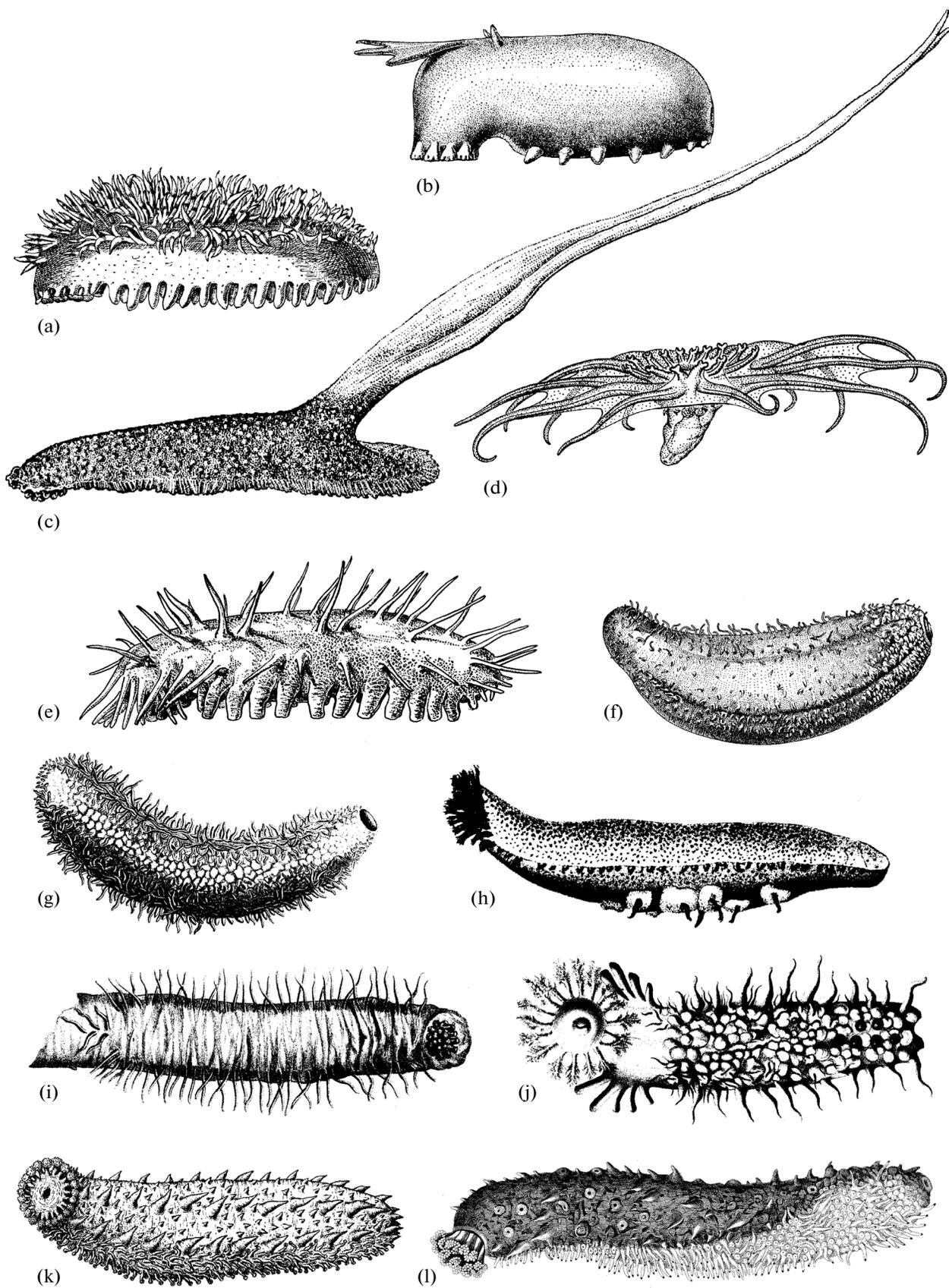
or the length of a segment is slightly greater than its width); presence a depression on the anterior margin of radial plates of the calcareous ring to accommodate tentacular ampullae; the ratio of the articular surface of the segments of the ring and the height of the inter-radial segments; presence of plate-like sclerites with a solid vertical spire; presence of dendrochirotid buttons. The above flaws resulted in Kerr and Kim (2001) supporting the recognition of the order Dactylochirotida. The above supports the evident conclusion that a cladistic analysis, the usefulness of which I in no way contest, requires a careful analysis of the selected characters to avoid their duplication, and also to consider their parallel appearance, as the output depends on what is input.

A far more complex situation is observed in the existing system of the order Elapsipodida. The only shared character in all Elapsipodida is an unusual arrangement of mesenteries suspending the intestine. In Elapsipodida all three mesenteries suspending the intestine in the anterior and middle part of the body are

attached to the body wall dorsally (Figs. 5a, 5d) and only in the posterior part of the body, the mesentery holding the second descending part of the intestine enters the right ventral inter-radius and is attached to the body wall near the mediadorsal muscular band (Fig. 5e) (Gebruk, 1990b). In all other holothurians, the mesentery supporting the second descending part of the intestine is attached along its entire length in the right ventral interradius (Figs. 5b, 5c). The second characters common for Elapsipodida is the absence of the water lungs, also found in the order Synaptida. Other characters, usually cited for this order diagnosis are restricted by one or another families and are not characters typical for the entire order.

The analysis of the morphology of the skeletal elements, their arrangement and some other morphological characters suggests that the order Elapsipodida is polyphyletic, and the family Deimatidae traditionally assigned to it should be taken out of the order Elapsipodida and placed in the order Aspidochirotida. Externally, Deimatidae (Fig. 6e) are similar to some Laetmogonidae

Fig. 6. Holothurians of the orders Elapsipodida and Aspidochirotida: (a) *Laetmogone maculata* (Laetmogonidae, Elapsipodida); (b) *Amperima naresi* (Elpidiidae, Elapsipodida); (c) *Psychropotes mirabilis* (Psychropotidae, Elapsipodida); (d) *Pelagothuria natatrix* (Pelagothuriidae, Elapsipodida); (e) *Oneirophanta mutabilis* (Deimatidae, Aspidochirotida); (f) *Paroriza grevei* (Synallactidae, Aspidochirotida); (g) *Mesothuria squamosa* (Mesothuriidae, Aspidochirotida); (h) *Benthothuria distorta* (Synallactidae, Aspidochirotida); (i) *Bathypotes pellucidus* (Synallactidae, Aspidochirotida); (j) *Dendrothuria similis* (Synallactidae, Aspidochirotida); (k) *Apostichopus japonicus* (Stichopodidae, Aspidochirotida); (l) *Holothuria tubulosa* (Holothuriidae, Aspidochirotida). (a) from McBride (1906) after Théel (1882); (b) and (f) from Hansen (1956); (c) and (e) from Hansen (1975); (d) from Kaestner (1963) after Chun (1903); (g)–(j) from Koehler, Vaney (1908); (k) from Ivanov, Strelkov (1949); (l) from Ludwig (1889–92).



(Elasipodida) (Fig. 6a), but also resemble representatives of the order Aspidochirotida (Figs. 6i–6l). Ludwig (1894) was the first, who noted that the family Deimatidae Théel, 1882 can be subdivided into two distinct groups based on the presence or absence of lateral papillae. Ekman (1926) established new family Laetmogonidae to accommodate some members of Deimatidae, which in contrast to Deimatidae *s. str.* does not have lateral papillae, and has completely different sclerites. He also indicated that in the morphology of their sclerites, Laetmogonidae are nearer to Elpidiidae than to Deimatidae, to which they were previously assigned. The family Deimatidae *sensu* Ekman, 1926 is strikingly different from other families of the order Elasipodida, to which it was previously assigned, not only in the presence of lateral papillae, but also orientation of sclerites in the lateral and dorsal papillae. The longitudinal axis of sclerites in papillae of Deimatidae is parallel to the longitudinal axis of the papilla, and in the families of the order Elasipodida *sensu str.* is transversely to it. Perforated plate and spatulate sclerites are not found in the families of Elasipodida *s. str.* and are more similar to the plates of lung-possessing holothurians. Becher (1909, p. 445, fig. 8) commented on the resemblance of the plates of *Oneirophanta alternata* (= *O. mutabilis mutabilis*) (Fig. 7e) (Deimatidae) to those of *Synallactes woodmasoni* (= *Amphigygnas woodmasoni*) (Fig. 7a) (Synallactidae). Sclerites of Deimatidae, in the shape of plates, transformed into cruciform plates and spatulate rods (Figs. 7d, 7e) are not found in the families of Elasipodida *s. str.* These plates are very similar to, and in my opinion, homologous to the tables of Synallactidae (Figs. 7a–7c), and are the tables with reduced spire, in which only the disk has remained.

Unfortunately, little is known of the calcareous ring of Elasipodida. The families Psychropotidae and Laetmogonidae (Fig. 8f) have a ring similar to those in other orders of holothurians, differing in a very low degree of calcification (Hansen, 1975, p. 186). In the family Elpidiidae (Fig. 6b) of the order Elasipodida, the calcareous rings are reduced and composed only of radial segments. Each segment represented by a star-shaped structure formed by two radiating bunches of long narrow rod-like processes (Fig. 8g). The calcareous ring of Deimatidae (Figs. 8d, 8e) is similar to that of Laetmogonidae (Fig. 8f), but it is also similar to the

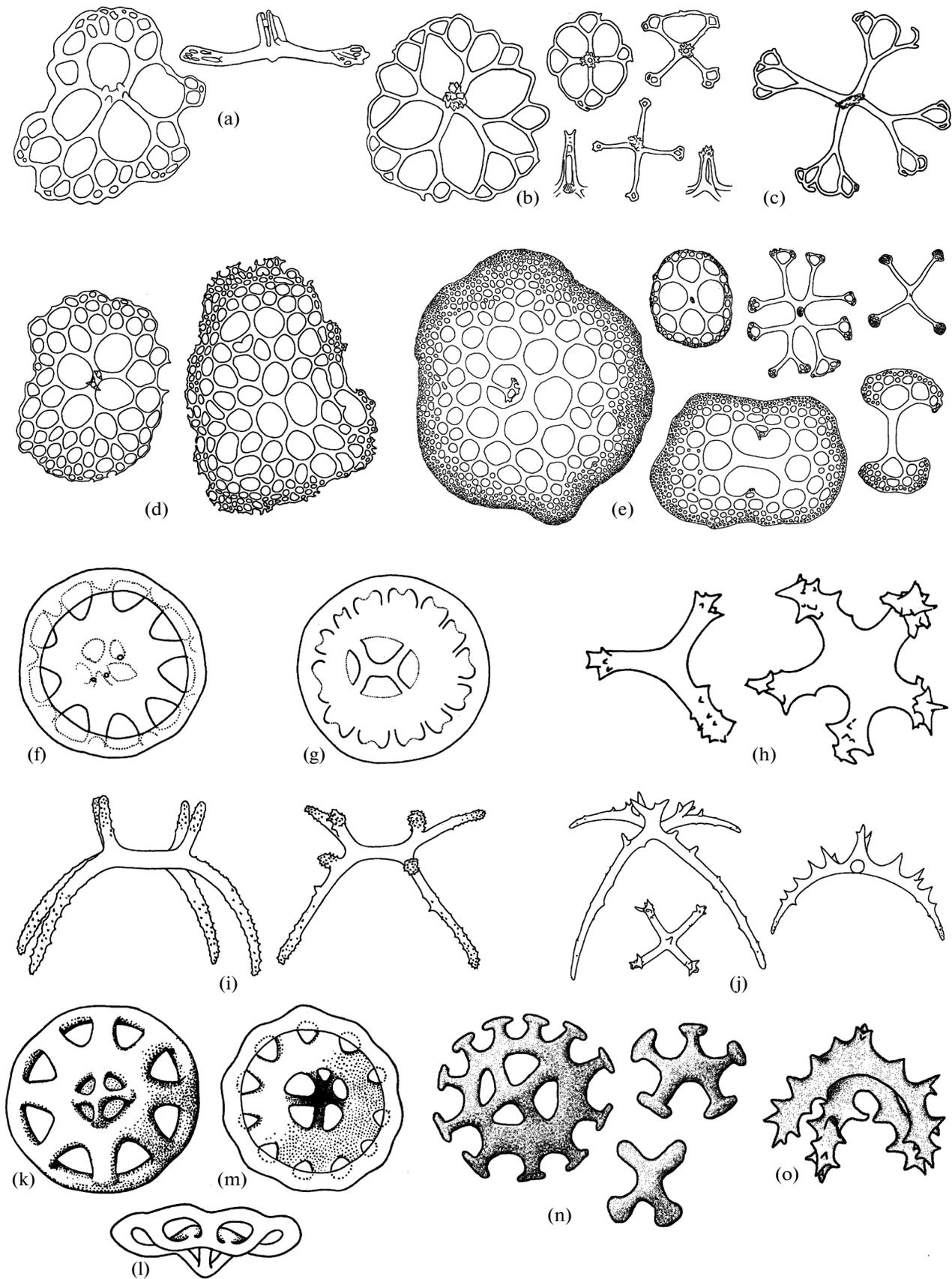
calcareous ring of Synallactidae (Figs. 8a–8c). The current state of knowledge of the calcareous ring in the order Elasipodida does not allow a positive conclusion about which ring (Elasipodida *s. str.* or Aspidochirotida) the calcareous ring of Deimatidae most resembles. The comparison of the morphology of the ring of Deimatidae and Synallactidae at least does not contradict the hypothesis of the close affinity of the families Deimatidae and Synallactidae, and the transferring of the family Deimatidae to the order Aspidochirotida.

The first molecular-genetic data received from the study of the species *Deima validum* showed that this species is similar to the species *Benthothuria funebris* and *Paroriza prouhoi* (Solís-Marín, 2003), which are currently assigned to the family Synallactidae and have developed water lungs. It is not important in this context that the family Synallactidae is polyphyletic in molecular-genetic data; at least three groups can be recognized within it (Solís-Marín, 2003). It is significant though, that *Benthothuria funebris* and *Paroriza prouhoi* both similar to *Deima validum* but have developed water lungs, and that suggests a connection between the Deimatidae and lung possessing holothurians of the order Aspidochirotida.

It is possible, that in Deimatidae, the water lungs reduced due to their life in a deep-water environment, since in many deep-water echinoderms, the respiratory organs have become reduced (A.N. Mironov, pers. comm.). As for the position of the mesentery supporting the second descending part of the intestine in the anterior and middle parts of the body (Figs. 5a, 5d), it could happen in parallel in Deimatidae and Elasipodida *s. str.*

The transfer of the family Deimatidae from the order Elasipodida to the order Aspidochirotida allows Elasipodida *sensu* Smirnov, 2012 to be considered as a monophyletic taxon. Supposedly, the cup-like concave sclerites occurring in Laetmogonidae with three–five rays (Figs. 7h, 7o) are of pedomorphic origin and represent the extensively growing initial stages of a wheel of the letmogonid type (Fig. 7n). The concave cup-like sclerites with processes found in Laetmogonidae could give rise to the curved cruciform sclerites of Elpidiidae (Fig. 7i) and Psychropotidae (Fig. 7j). As mentioned previously, families in the order Elasipodida (Figs. 6a–6d) are connected to one another by a series of intermediate characters. Laetmogonid wheel sclerites characteristic for the family Laetmogonidae

Fig. 7. Holothurian sclerites of the orders Elasipodida and Aspidochirotida: (a) *Amphigygnas woodmasoni* (Synallactidae, Aspidochirotida); (b) *Bathyploetes punctatus* (Synallactidae, Aspidochirotida); (c) *Synallactes heteroculus* (Synallactidae, Aspidochirotida); (d) *Deima validum validum* (Deimatidae, Aspidochirotidae); (e) *Oneirophanta mutabilis mutabilis* (Deimatidae, Aspidochirotidae); (f) wheel *Laetmogone violacea* (Laetmogonidae, Elasipodida), upper side; (g) wheel *Amperima rosea* (Elpidiidae, Elasipodida), basal side; (h) cup-like, curved sclerites with 3–5 rays *Laetmogone violacea* (Laetmogonidae, Elasipodida), upper side; (i) curved cruciform sclerites *Peniagone azorica* (Elpidiidae, Elasipodida); (j) curved cruciform sclerites *Psychropotes longicauda* (Psychropotidae, Elasipodida); (k) wheel *Laetmogone violacea* (Laetmogonidae, Elasipodida), basal side; (l) wheel *Laetmogone violacea* (Laetmogonidae, Elasipodida), lateral view; (m) wheel *Benthogone rosea* (Laetmogonidae, Elasipodida), upper side; (n) development of wheels *Benthogone rosea* (Laetmogonidae, Elasipodida), basal view; (o) cup-like, curved sclerites with four rays *Laetmogone violacea* (Laetmogonidae, Elasipodida), lateral view; (a) from Koehler, Vaney (1905); (b) and (c) from Hedding (1940); (d)–(j) from Hansen (1975); (k)–(m) from Ekman (1926); (n), (o) from Perrier (1902)



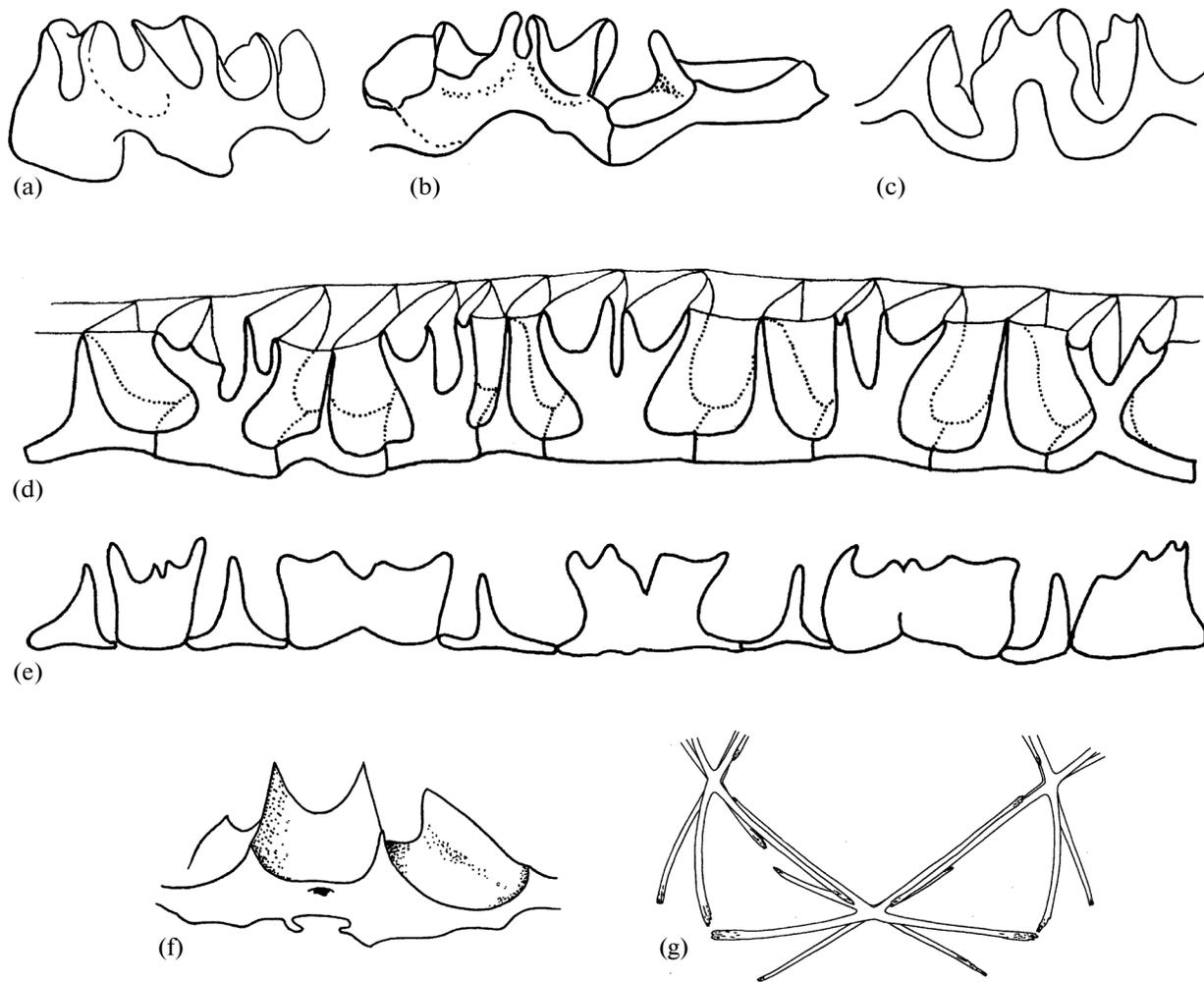


Fig. 8. Calcareous ring of holothurians of the orders Elaspodida and Aspidochirotida: (a) *Bathyploetes punctatus* (Synallactidae, Aspidochirotida); (b) *Pseudostichopus mollis* (Synallactidae, Aspidochirotida); (c) *Zygothuria marginata* (Mesothuriidae, Aspidochirotida); (d) *Oneirophanta setigera* (Deimatidae, Aspidochirotidae); (e) *Oneirophanta mutabilis* (Laetmogonidae, Elaspodida); (f) *Laetmogone maculata* (Laetmogonidae, Elaspodida); (g) *Elpidia glacialis* (Elpidiidae, Elaspodida). (a)–(c), (f) from Heding (1940), (d), (e), (g) from Hansen (1975).

(Figs. 7f, 7k–7m) are also sporadically present in some species of the family Elpidiidae (Fig. 7g), which may indicate the similarity of these two families (Ekman, 1926). Concave sclerites of Laetmogonidae (Fig. 7h) are probably homologous to concave cruciform sclerites of Elpidiidae (Fig. 7i) and Psychropotidae (Fig. 7j). The family Psychropotidae (Fig. 6c) is also connected to the planktonic family Pelagothuriidae (Fig. 6d) (Gebruk, 1989; 1990a).

The above information allows the diagnosis of the order Elaspodida to be emended.

Order Elaspodida Théel, 1882
(=Elasmopoda Théel, 1879)

Diagnosis. Holothuroidea with distinct bilateral symmetry and well-developed ventral sole usually bound by marginal ventrolateral feet (excluding the

planktonic family Pelagothuriidae). Tentacles peltate. Radial canals developed. Tube-feet and papillae (modified tube-feet) present. Papilla usually dorsal. In some taxa dorsal papillae fused to form specialized locomotory organs: anterior brim and a caudal swimming lobe in the posterior part. Ventral tube-feet often enlarged and modified into ambulatory feet. In Psychropotidae, ventrolateral feet can be fused to form lateral folds. The modified posterior feet can be fused to form in some Elpidiidae a posterior swimming lobe. Ambulacral appendages of some elaspodids of the families Elpidiidae and Laetmogonidae have strongly expanded ampullae (typical of Elpidiidae and Laetmogonidae). Canals of tentacles extend from radial canals. Radial hemal canals present. Stone canal with madreporite usually attached to body wall and can open externally. Ring muscles interrupted by radial muscles. Radial muscle bands undivided. Mesentery,

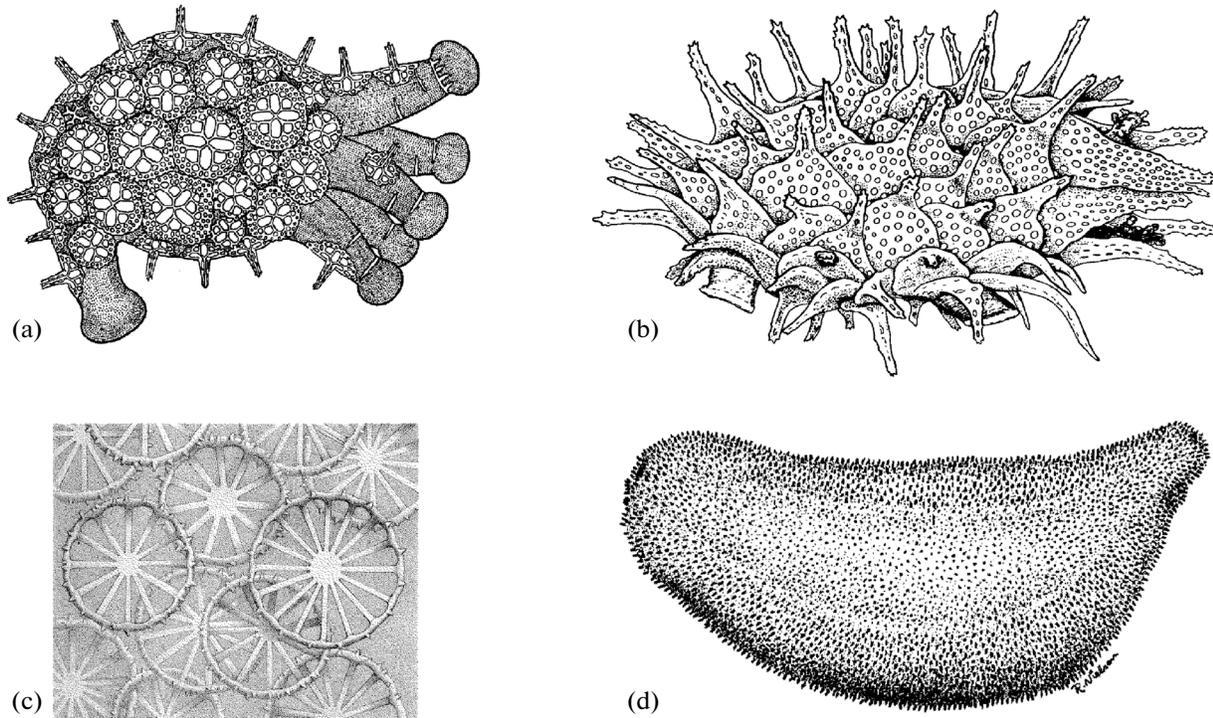


Fig. 9. Holothurians with a test of sclerites: (a) and (b) juvenile and (c) and (d) mature paedomorphic holothurians: (a) *Apostichopus japonicus* juv. (Stichopodidae, Aspidochirotida); (b) *Heterocucumis steineni* juv. (Cucumariidae, Dendrochirotida); (c) *Trochoderma elegans* (Myriotrochidae, Synaptida), body wall fragment; (d) *Eupyrigus scaber* (Eupyrigidae, Molpadiida); (a) from Malakhov and Cherkasova (1992); (b) from Ekman (1927); (c) from Théel (1877); (d) from Madsen and Hansen (1994).

suspending second descending part of intestine, attached to body wall anteriorly and medially in right dorsal interradius. Family Elpidiidae has two pairs of statocysts arranged near the base of the lateroventral radial nerves. Respiratory trees absent. Calcareous ring poorly calcified, sometimes consisting of strong connective tissue; in some taxa decreasing with age or absent. Ossicles: laetmogonid wheels (Laetmogonidae and some Elpidiidae), three–five rays cup-like concave sclerites (Laetmogonidae), cruciform psychropotid crosses (Elpidiidae and Psychropotidae) and rods and ossicles derived from them. In some forms skeletal elements are absent. Laetmogonid wheels concave-convex, with smooth rim (in the genus *Pannychia*, rim with large inward-facing denticles), hub usually with four perforations; on the side opposite to rim branches extend from edge of hub merging above center of wheel to form flat or more or less convex cup. Curved cruciform psychropotid sclerites with one (in the center of the cross), four (on each ray), or five (in the center of the cross and rays) orthogonal processes.

The order includes four families: Laetmogonidae Ekman, 1926, Elpidiidae Théel, 1882, Psychropotidae Théel, 1882, and Pelagothuriidae Ludwig, 1893.

As in many animal groups, the parallel evolution of many characters, and first of all characters of external morphology is related to adaptation to similar habitats. Parallel characters can also appear due to paedo-

morphosis. In the small paedomorphic species *Trochoderma elegans* (Myriotrochidae, Synaptida) (Figs. 9c; 10a, 10c) and *Eupyrigus scaber* (Eupyrigidae, Molpadiida) (Figs. 9d; 10b, 10d) the body is covered by a dense layer of tightly packed and even overlapping sclerites forming a rigid test, while in most species of these orders have a thin body wall with a few sclerites. It is possible that in these small-sized taxa of 10–25 mm, the test appeared by paedomorphosis. This is indirectly supported by the presence of the test in juvenile holothurians of other orders: Aspidochirotida (Fig. 9a) and Dendrochirotida (Fig. 9b), which disappear in adults (Smirnov, 2015).

Along with the process of strengthening of the body wall and development of increasingly dense and strong calcareous skeleton in all orders of holothurians there is also an opposite trend toward the complete disappearance of body wall sclerites and even the calcareous ring. In deep-water and swimming taxa, the body wall sclerites are scarce and can be completely absent. For instance, sclerites are absent in the genera *Benthoturia*, *Paroriza*, species *Paelopatides appendiculata*, *P. atlantica*, *P. dissidens*, *P. mammilatus*, *P. mollis*, *P. rotifer*, *Pseudostichopus peripatus*, *P. mollis*, and *Molpadiodemas depressus* (Synallactidae, Aspidochirotida). Sclerites can be absent in some specimens of the species *Benthodytes typica* and *B. sanguinolenta* (Psychropotidae, Elasipodida), and are completely absent in

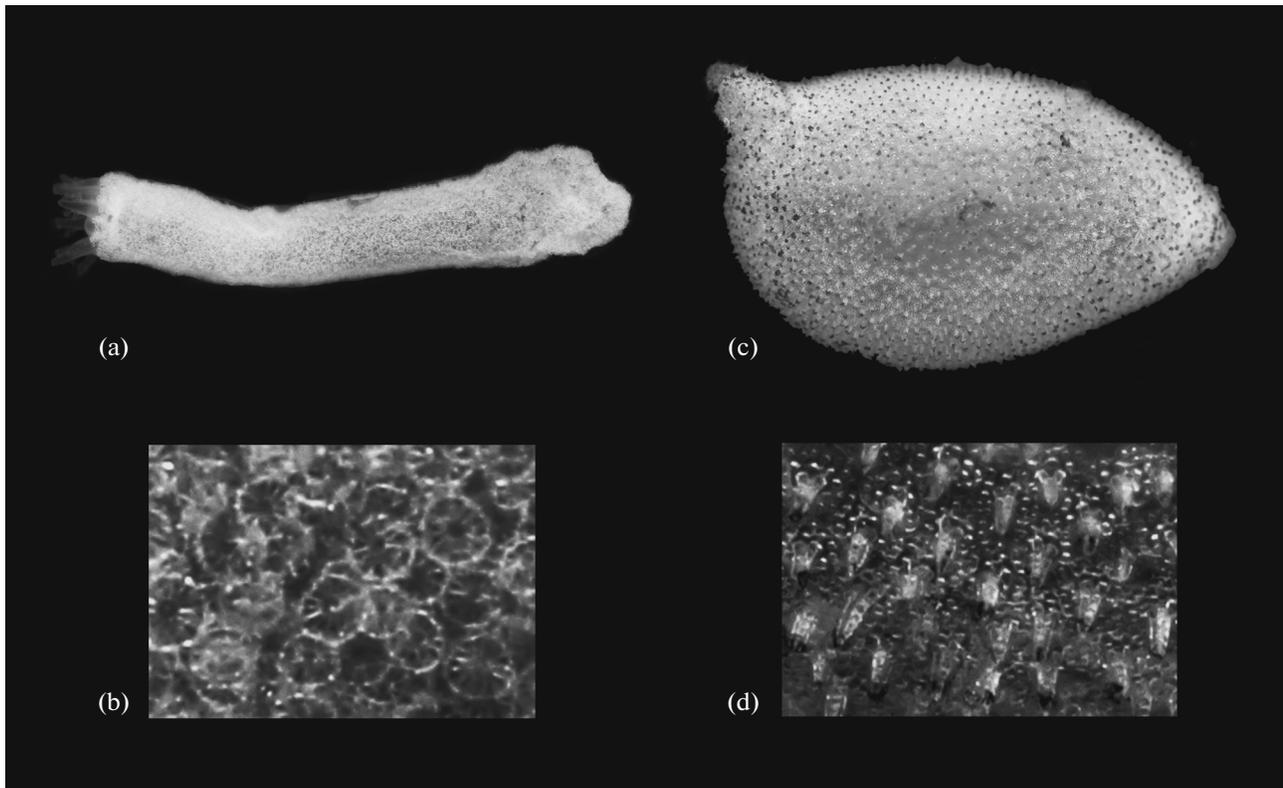


Fig. 10. Paedomorphic holothurians with a test composed of sclerites: (a, b) *Trochoderma elegans* (Myriotrochidae, Synaptida), (a) general view; (b) body wall fragment; (c, d) *Eupyrgus scaber* (Eupyrgidae, Molpadiida), (c) general view; (d) body wall fragment. Photograph by O. Zimina.

Achlyonica tui (Elpidiidae, Elasipodida), and also in the genus *Gephyrothuria* (Gephyrothuriidae, Gephyrothuriida).

However, not only body wall sclerites, but also the massive, large structure of the calcareous ring can become reduced. The reduction of the calcareous ring is characteristic of many holothurians of the family Synallactidae (order Aspidochirotida). A reduced calcareous ring is present in the benthopelagic species *Bathyploetes natans*, whereas in large specimens of this species, it can be completely reduced. In the genera *Benthothuria* and *Paelopatides* no calcareous ring is present. The reduction of the calcareous ring is present in the order Elasipodida. In the family Laetmogonidae the calcareous ring is poorly developed, and in the family Psychropotidae the ring is not calcified but is composed of connective tissue. As noted above, in the family Elpidiidae the calcareous ring includes only radial segments, and each segment represented only by a star-shaped structure formed by two radiating bunches of long narrow rod-like processes. Naturally, in the pelagic *Pelagothuria natatrix* (Pelagothuriidae, Elasipodida) neither the calcareous ring nor the body wall sclerites are present.

The reduction of skeletal elements in swimming and deep-water taxa (most swimming holothurians are

deep-water dwellers) is understandable and explained by adaptation to their lifestyle. Apparently, a similar lifestyle, i.e., living within the substrate, explains the thin body wall and the presence of only a few sclerites in burrowing taxa, which include many members of the orders Synaptida and Molpadiida. In almost all representatives of the order Synaptida, sclerites in their thin body wall are weakly developed, and in some species are represented only by small rods. In some, usually monotypic, genera, the body wall sclerites are completely absent, e.g. *Kolostoneura* (Taeniogyrinae, Chiridotidae), *Paradota* (Chiridotinae, Chiridotida), *Dactylapta* (Rynkatorpinae, Synaptidae), *Anapta* (Lep-tosynaptinae, Synaptidae), *Rhabdomolgus* (Rhabdomolginae, Synaptidae), and *Achiridota* (Myriotrochidae). In some species of holothurians of the genus *Molpadiia* (Molpadiidae, Molpadiida), the sclerites disappear with age. It is interesting that the disappearance of sclerites with age is observed in some holothurians of the order Dendrochirotida, which have a thick and dense body wall. For instance, in the species *Cucumaria frondosa* and *Staurocucumis turqueti* (Cucumariidae) sclerites in the most of the body wall disappear and are only retained near the anus.

Considering the parallel appearance of morphological characters, it is necessary to take into account

that many species of holothurians have a paedomorphic origin and therefore in some groups it is possible to encounter “simplified” structures, which appeared due to paedomorphosis. One of the examples is the parallel appearance of the following paedomorphic for order Molpadiida characters in the species *Molpadia blakei* (family Molpadiidae) and *Eupyrgus scaber* (family Eupyrgidae) such as the absence free hanging tentacles ampullae and undivided longitudinal muscular bands (Heding, 1935).

The decrease in the number of tentacles in different families and subfamilies of the same order can also occur in parallel. The order Synaptida originally had 12 tentacles. However, many taxa in this order are small, which could be products of paedomorphism. In different families the reduction of the number of tentacles from 12 to 10 was also parallel. Ten tentacles are present in the genera *Sigmodota*, *Rowedota*, *Scoliorhapis*, *Kolostoneura*, *Psammothuria* (even eight!) (Taeniogyrinae, Chiridotidae); a number of species *Leptosynapta* (Synaptidae); *Prototrochus*, *Siniotrochus phoxus*, *Parvotrochus*, *Trochoderma* (Myriotrochidae). It is possible that this process could occur in parallel in related groups, therefore genera established based solely on the number of tentacles can be polyphyletic. In different families of Synaptida, the intestinal loop disappears in parallel. In *Scoliorhapis* spp., *Taeniogyrus havelockensis*, *Kolostoneura novaezealandiae*, *Psammothuria ganapatii* (Taeniogyrinae, Chiridotidae), *Leptosynapta minuta*, *Rhabdomolgus ruber* (Synaptidae) the intestine is suspended only by mediodorsal mesentery along almost its entire length (Smirnov, 2014; 2015).

The above discussion of Dendrochirotida includes consideration of the parallel development of simple tentacles in different families. The structure of the tentacles is certainly determined by feeding strategy. The aspidochirotid holothurians, the majority of which are deposit feeders, have peltate tentacles used for gathering food from the substrate (Figs. 6i, 6k, 6l). The genera *Pseudothuria*, *Dendrothuria* and *Scothothuria* (family Synallactidae) have tentacles (Fig. 6g) slightly resembling tentacles of holothurians of the order Dendrochirotida, which are suspension feeders and use their dendritic branched tentacles gather plankton and suspended particles. The manifestation of the convergent characters in the above genera is clearly connected with the transition to suspension feeding and possibly, as suggested by Hansen (1978), with an adaptation to swimming.

A careful study of the development of parallel structures not only allows the refinement of the taxonomy and phylogeny of the group, but also shows that that using modern taxonomic techniques should be associated with a careful analysis of existing morpho-anatomical data. A careful study of the development of parallel structures not only allows the refinement of the taxonomy and phylogeny of the group, but also shows that using modern taxonomic techniques

should be associated with a careful analysis of existing morpho-anatomical data. This allows focus the study not only on “uncertain” taxa, but also on groups which have traditionally been accepted without hesitation. The latter is well illustrated by the example of the family Deimatidae, the morphological characters of which (primarily its skeletal elements) have been studied and summarized by Ekman as long ago as 1926. The analysis of parallelisms in evolution certainly facilitates a deeper understanding of the external and internal causes and factors of the evolution of organisms, and helps to finding interesting model objects to study patterns of evolutionary biology.

APPENDIX

Family Vaneyellidae Pawson et Fell, 1965

The genera *Vaneyella* and *Mitsukuriella* were described by Heding and Panning (1954) and together with the genus *Paracucumis* Mortensen, 1925 assigned to “group B” of the multi-tentacle subfamily Thyonidiinae they recognized in the family Phyllophoridae, because they had 12–20 tentacles. Pawson and Fell (1965) proposed the family Vaneyellidae to accommodate the genera *Vaneyella* and *Mitsukuriella* which have 15–20 tentacles, and assigned the genus *Paracucumis* to their new family Paracucumidae. Later, the 8-tentacle genus *Psolidothuria* Thandar, 1998 with test composed by simple imbricated plates was also assigned to the family Vaneyellidae. Smirnov (2012) proposed to consider the family Vaneyellidae Pawson et Fell, 1965 a synonym of the family Cucumariidae Ludwig, 1894, based on the similarity of the morphology of the calcareous ring and body wall sclerites. Currently, I consider that proposal to be somewhat premature. The family Vaneyellidae should be retained for the multi-tentacle genera *Vaneyella* and *Mitsukuriella*, while the question of the separation of the family Vaneyellidae should await further revision of the suborder Cucumariina. The 8-tentacled genus *Psolidothuria* Thandar, 1998 with the species *P. octodactyla* Thandar, 1998, and *P. yasmeena* Thandar, 2006 assigned to Vaneyellidae are clearly of paedomorphic origin. These species are small-sized—28 and 8 mm, respectively. It is possible that their poorly developed test was inherited from a juvenile stage because in many dendrochirotids, juveniles have a test composed of ossicles (Smirnov, 2015) (Fig. 9b). This hypothesis is in my opinion also supported by the morphology of sclerites in *Psolidothuria* which represent simple perforated plates, the development of which was arrested at an early stage of development. This hypothesis is also supported by the morphology of the underdeveloped simple tentacles of *Psolidothuria octodactyla*, which are not very simple, and have short lateral branches (Thandar, 1998, p. 80), whereas in *P. yasmeena*, the tentacles are finger-shaped but finely branched (Thandar, 2006, p. 44, fig. 15H). Some holothurians of the family Cucumariidae, for example

C. frondosa and *C. vegae* have two underdeveloped ventral tentacles and considering the trend to reduce the ventral tentacles in some Cucumariidae it is possible to suggest that in the genus *Psolidothuria* this reduction was complete. Considering the above, I propose to assign the genus *Psolidothuria* to the family Cucumariidae, and to retain in the family Vaneyellidae the two multi-tentacle genera *Vaneyella* Heding et Panning, 1954 and *Mitsukuriella* Heding et Panning, 1954, which were placed in this family when it was established (Pawson and Fell, 1965).

D i a g n o s i s: Cucumariina with 15–20 tentacles. Body U-shaped, covered by test of plates. Tube feet arranged along radii. Segments of calcareous ring with a high central part and low lateral parts. The lower edge of segments with small depression in center and lacking processes. Ring segments not subdivided into pieces. Segments connected by lateral regions corresponding to lower lateral regions of ring of other holothurians. Ring sinusoidal. Sclerites simple monolayered, plated with numerous relatively large perforations.

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