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System of the Class Holothuroidea

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Abstract—Various interpretations of the holothurian system and phylogeny are critically reviewed and the main characters that form the basis of the existing systematics of this group are analyzed. A system of holothurians based on thorough analysis of their morphology and anatomy is proposed. Four subclasses are recognized in the class Holothuroidea: Arthrochirotacea, Synaptacea, Elpidiacea, and Holothuriacea. The subclass Arthrochirotacea includes the extinct Paleozoic order Arthrochirotida. The subclass Synaptacea includes the order Synaptida with two suborders and three families. The subclass Elpidiacea includes the order Elasipodida with four families. The subclass Holothuriacea includes four orders: Aspidochirotida with five families; Dendrochirotida with 15 families (14 extant and one extinct); Molpadiida with three families; Gephyrothuriida with one family and two genera *Gephyrothuria* and *Hadalothuria*. The order Gephyrothuriida is re-established. The order Dactylochirotida Pawson et Fell, 1965 is synonymized under the order Dendrochirotida. A new suborder Cucumariina and new family Mesothuriidae are described. The family Vaneyellidae is synonymized under the family Cucumariidae. Four subfamilies are classified as families: Cladolabidae, Sclerothyonidae, Monilipsolidae, and Thyonidiidae.

Keywords: Holothuroidea, systematics, phylogeny

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INTRODUCTION

Smirnov's (1998; 1999) studies of the order Synaptida resulted in the refinement of the system of the order. The systematic part of this research naturally raised unresolved problems of the place of the Synaptida in the system of holothurians and of the system of the class Holothuroidea on the whole. As early as 1984, I published (Smirnov, 1984) a criticism of the system of the class Holothuroidea proposed by Pawson and Fell (1965). Analysis of publications on the system and phylogeny of this class gave me an understanding of the significance of publications of the late 19th and early 20th centuries for interpretation of the system of holothurians. Among these publications are large monographic papers by Östergren (1907) and, especially, Becher (1909).

I reported the main results of these studies at an annual session of the Zoological Institute of the Russian Academy of Sciences in 2003 (Smirnov, 2003) and at the Russian National Conference "Echinodermata. In memory of M.M. Moscwin (for the centenary of his birth)" at the Paleontological Institute in Moscow in 2006 (Smirnov, 2007).

The first part of the paper discusses the history of views and interpretations of various authors of the system and phylogeny of holothurians and analyzed the major characters used in the previous system of holothurians. The second part of the paper contains a brief explanation of the system proposed (to the family level).

THE HISTORY OF THE VIEWS ON THE SYSTEM AND PHYLOGENY OF HOLOTHURIANS AND ANALYSIS OF THE SYSTEMS AND PHYLOGENETIC RECONSTRUCTIONS PROPOSED

The First Systems of the Class and Morphological Characters Used for the System of Holothurians

Holothurians were first described by Belon (1553), who thought that they were similar to starfish and echinoids. Lamarck assigned echinoids, starfish and brittle stars, and holothurians to a separate Radiaires Échinodermés (Lamarck, 1801), within the class Radiaires. He assigned the genus *Holothuria* along with the non-echinoderm genus *Sipunculus* in the system of the order to the section Fistulides. Blainville (1834) treated holothurians as the order Holothuridea, although he did not subdivide holothurians into families and considered them within the same genus *Holothuria*. Holothurians were first considered as the class Scytodermata (Holothrioidea) by Bronn (1860). Selenka (1867) was the first to use the name Holothurioidea for a class encompassing these animals.

Ludwig (1889–1892) provided a detailed historical overview of the early system of holothurians. Therefore, I will not discuss in detail the systems of the eighteenths and nineteenth centuries, but will instead focus on the analysis of the systems of Holothuroidea and phylogenetic reconstructions, indicating the relationships within the class developed by the scientists who worked on this echinoderm group in the end of 19th–20th centuries. I will specifically focus on the taxonomic characters which have been used by the authors discussed and which remain important to the holothurian systematics.

Characters Used in the Systems in 1820–1860

Shape of tentacles. Based on tentacles Lesueur (1824) recognized three groups: (1) "with cylindrical tentaculae; summit terminated by a branched, flat, spherical or infundibuliform umbel" (p. 156); (2) "tentacula arborescent" (p. 160); (3) "tentacula pinnate; body vermiform" (p. 162), in general corresponding to extant aspidochirotid, dendrochirotid, and synaptid holothurians. Later, based on the tentacles Grube (1840), who considered all holothurians as an order, subdivided holothurians into three groups, to which he did not assign any rank, but referred to as Abtheilung (=division): (1) Aspidochiroten with shield-shaped tentacles; (2) Dendrochiroten with dendritiform tentacles; (3) Chiridoten with pinnate or digitate tentacles. Clearly these groups corresponded to groups established by Lesueur. To name these groups Grube used the names of the genera *Aspidochir* Brandt, 1835, *Dendrochir* Brandt, 1835, and *Chiridota* Eschscholtz, 1829. The morphology of tentacles is certainly a good taxonomic character but like all other characters it weights differently in different taxa. Dendritic tentacles characterize the order of dendrochirotid holothurians, whereas shield-shaped tentacles are present in aspidochurotid and elasipod holothurians. Morphology of tentacles is usually directly connected with feeding and life style. Among aspidochirotids, the subgenera *Selenkothuria* and *Semperothuria* of the genus *Holothuria* show dendritiform tentacles, which are clearly derived from shield-shaped tentacles, which was connected with these taxa becoming the suspension-feeders. The bathypelagic genus *Scotothuria* and the closely related *Dendrothuria* and *Pseudothuria* (family Synallactidae) also have dendritiform tentacles, most likely connected with their life style. In dendrochirotids, the disappearance of the branches of dendritic tentacles and their transformation into simple tentacles is also likely to be connected with a change in feeding strategy, e.g., from suspension feeding to detritus feeding.

Presence or absence of tube-feet and their arrangement. In one of the first elaborated systems of holothurians proposed by Brandt (1835), holothurians (ranked as a family) were subdivided into Pedatae possessing tube-feet and Apodes lacking tube-feet. The subdivision of holothurians into those with tube-feet and those without was accepted two years later by Burmeister (1837), who considered holothurians as the order Scytodermata, while placing all the remaining echinoderms in the order Echinodermata. Holothurians with no feet as proposed by Brandt, included representatives of the two extant orders: Synaptida (=Apodida) and Molpadida (=Molpadonia). This taxon remained as the suborder Apodia in Bronn's system (1860), the subclass Apoda Perrier's (1902) system, and the subclass Apodacea in Pawson and Fell's (1965) system.

Bronn (1860) subdivided holothurians into the order Decacrenidia, containing the genus *Rhopalodina*, with external decaradial symmetry and the order Pentacrenidia, including all the remaining holothurians. The latter order he subdivided into two suborders: (1) Apodia with the family Synaptidae (footless holothurians without respiratory trees) and Liodermatidae (footless holothurians with respiratory trees); (2) Eupodia with the families Aspidochirotae (holothurians with shield-shaped tentacles) and Dendrochirotae (holothurians with dendritic tentacles).

Presence or absence of respiratory trees (water lungs). This character was used in Jaeger's (1833) system, whereas in Brandt's system, the group Apodes was subdivided into Pneumonophorae possessing respiratory trees and Apneumonas lacking respiratory trees. The outstanding anatomist and embryologist Mueller (1850a; 1850b) considered the presence or absence of the respiratory trees as a very important character and subdivided the order of holothurians into those lacking respiratory trees (corresponding to the extant order Synaptida (=Apodida) and those with respiratory trees. Holothurians with respiratory trees were subdivided into holothurians lacking tube-feet (Molpadiiden) and those with tube-feet. The latter were subdivided based on the morphology of their tentacles into Aspidochirotae and Dendrochirotae. A similar system was accepted by Selenka (1867), in which the class Holothuroidea was subdivided into the order Pneumonophora with the families Aspidochirota, Dendrochirotae, and Liosomatidae (=Molpadidae) and the order Apneumona with the family Synaptidae. Semper (1868) published his system based on the same principles a year later. As in Bronn's system, Semper separated the genus *Rhopalodina* from the remainder of holothurians; he placed it in a separate class Diplostomidea. Other holothurians assigned to the class Holothuroidea were subdivided into: (1) lungless Apneumona (extant Synaptida) and (2) lung-possessing holothurians Pneumonophora with the families Molpadiidae (lung-possessing holothurians lacking tube-feet), Dendrochirotae and Aspidochirotae.

The holothurian systems of the 1830s–1860s, like most systems of animal groups created in the first half of the 19th century, are built as a dichotomous key, usually only using a single diagnostic character. Only one character is also used to subdivide the resulting, smaller taxa, and so on. In Brandt and Bronn's systems the main character used to subdivide holothurians into two groups is the presence or absence of tube-feet, and in Mueller, Selenka and Semper, it is the presence or absence of respiratory trees.

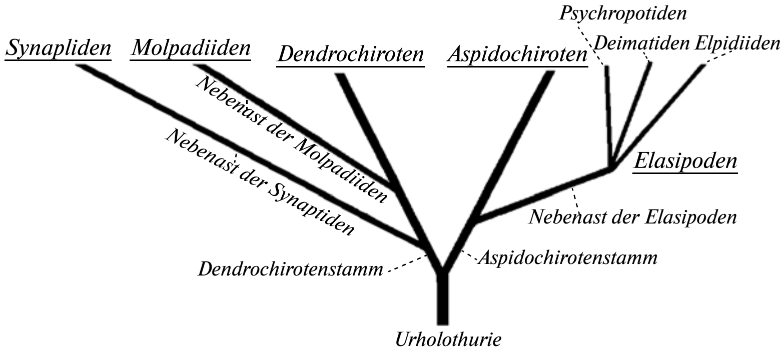

Fig. 1. Phylogenetic tree of holothurians from Ludwig (1891).

A Review of the Systems of the Class Holothuroidea Proposed 1880-early 1900s

Examination of material collected during the HMS *Challenger* expedition resulted in the description of numerous species of the then-new group of deep-sea holothurians of the order Elasipoda (Théel, 1879, 1882). Just previously, the first member of the order, *Elpidia glacialis*, classified within a separate family Elpidiidae, had been described from the Arctic (Théel, 1876; 1877). These holothurians possess modified tube-feet and lack respiratory trees. In his system of holothurians, Théel (1886), like Brandt and Bronn, considered the presence or absence of tube-feet and their morphology as the major criteria, which is reflected in the names of three orders, he recognized in holothurians: Apoda, Pedata, and Elasipoda. Apoda was subdivided into two suborders with one family in each: Apneumona (family Synaptidae) and Pneumonophora (family Molpadiidae). In the order Pedatae, he recognized three families: Dendrochirotae, Rhopalodinidae, and Aspidochirotae, and in the new order Elasipoda, he recognized three families: Elpidiidae, Deimatidae, and Psychropotidae. Lampert (1885) had a similar understanding of the system of holothurians. The systematics of the class proposed by Lampert and Théel was accepted in the third edition of "Synopsis of Zoology" (Leunis and Ludwig, 1883).

Semon (1888) suggested that echinoderms evolved from a hypothetical ancestral form Pentactea. He considered that holothurians evolved directly from Pentactea. The Pentactea theory was based on the development of the synaptid holothurian *Labidoplax digitata*, in which Semon did not observe the development of radial ambulacral canals. Cuénot (1891), who produced outstanding studies on anatomy and morphology of echinoderms, followed Semon in accepting that Synaptidae lacking radial canals are a primitive group, and placed synaptid holothurians at the base of the echinoderm branch. At that time it was not yet known that the reduction of the radial ambulacral canals in synaptids is secondary. Based on the absence of radial ambulacral canals in synaptid, Cuénot classified them as the separate class Synaptida, while the remainder of the holothurians he retained as Holothurioidea. Cuénot (1891, pp. 653–654) subdivided the latter holothurians into Elasipoda (without respiratory trees) and Pneumophora (with respiratory trees). Pneumophora were subdivided into Pedata that included Aspidochirota and Dendrochirota and Molpadidae (lacking tube-feet). Cuénot's system, although reflecting an erroneous interpretation of the ambulacral canals in synaptids, in my opinion showed the most adequate interpretation of the holothurian phylogeny (compare to the modern cladogram of the class of holothurians (Kerr and Kim, 2001), in which, as in Cuénot, synaptids are a sister group of other holothurians, and among the latter elasipodids are a sister group of holothurians with respiratory trees).

The next system of the class was proposed by Ludwig (1889–1892) in his excellent monograph "Die Seewalzen." Ludwig subdivided the class Holothurioidea into two orders. He based his system on the ambulacral system. In this system, the order Actinopoda included forms in which extensions of the ambulacral system – tube-feet and tentacles, protube from the radial ambulacral canals. Ludwig included in this order the families Aspidochirotae, Elasipoda, Dendrochirotae, and Molpadiidae. He also placed the genus *Rhopalodina* in the Dendrochirotae. The second order Paractinopoda is distinguished by the outgrowths of the ambulacral system, i.e., the tentacles, extending from the ambulacral ring, while the tube-feet and radial ambulacral canals and respiratory trees are absent. The order includes a single family Synaptidae which corresponds to the modern order Synaptida (=Apodida). With small changes Ludwig's system was accepted by Ekman (1926), who considered the four families of Actinopoda recognized by Ludwig as suborders. Ludwig (1891) was the first to propose the phylogenetic interpretation of the class of holothurians (Fig. 1). On Ludwig's phylogenetic tree, holothurians were subdivided into two branches. Dendrochirotenstamm included synaptids, molpadiids, and dendrochirotids, and Aspidochirotenstamm included elasipodids and aspidochirotids. Interestingly, Lud-

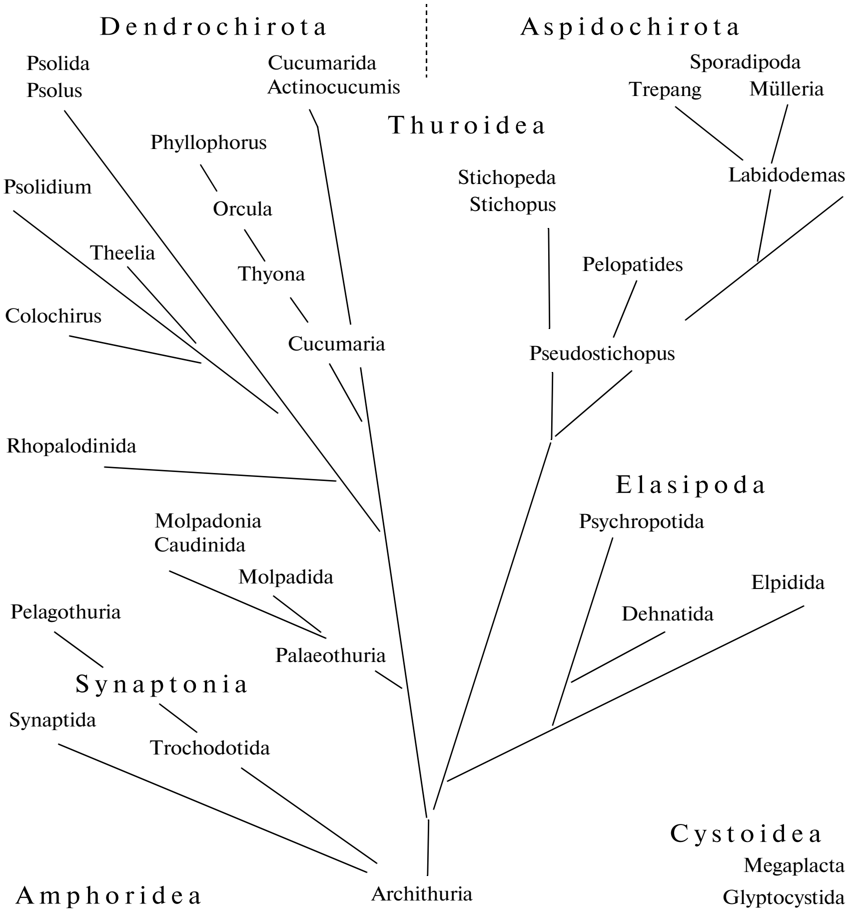

Fig. 2. Phylogenetic tree of holothurians from Haeckel (1896).

wig's system and phylogenetic scheme of the class are closely connected, but the system of the class is not a representation of the phylogenetic tree of holothurians. For instance, in his system the order Paractinopoda (=Synaptida) is considered as a separate from the rest of holothurians, whereas in the phylogenetic reconstruction, Paractinopoda are part of the Dendrochirotenstamm.

Ludwig's system was slightly modified by Haeckel (1896), and in contrast to Ludwig's system it represented the phylogenetic reconstructions of this author (Fig. 2). The class of holothurians, which Haeckel called Thuroidea, was subdivided into two branches and correspondingly two subclasses Paractinota (=Paractinopoda) and Actinopoda. In Haeckel's system, Paractinota included hypothetical ancestral holothurians (order Archituriae), order Synaptonia (=Synaptida, i.e., the order Paractinopoda Ludwig) and order Nectothuriae, which was established to accommodate Ludwig's (1894) planktonic holothurian *Pelagothuria natatrix*. Haeckel considered the primary absence of radial ambulacral canals and extension of tentacles from the ambulacral ring as the main characters distinguishing the subclass Paractinota. The subclass Actinopoda, corresponding to the order Actinopoda in Ludwig's system included four orders: Dendrochirota, Molpadonia, Elasipoda, and Aspidochirota, which corresponded to the four families recognized by Ludwig. In other words, Haeckel raised the taxonomic rank of Ludwig's families and was the first to treat the main modern holothurian orders at this rank, which they have retained until now. In Haeckel's phylogeny, as in Ludwig's scheme, dendrochirotids were placed with molpadiids, whereas elasipodids were treated as near aspidochirotids. The phylogenetic tree of holothurians illustrated by Haeckel (Fig. 2) is very similar to that of Ludwig, although with one essential difference. In Haeckel's tree, the synaptids branch off the general stem before the remaining holothurians are subdivided into the Dendrochirota-branch and Aspidochirota-branch. Thus, Haeckel's system reflects his suggested phylogeny of the class.

The next system and phylogeny (Fig. 3) of holothurians was published by Rémy Perrier (1902). He accepted Brandt's division of the holothurians into two groups (subclasses in Perrier's classification), Apoda and Pedata. Perrier considered Apoda as an ancient group, primitive but also simplified, with tubefeet absent due to reduction. Perrier considered the presence of forms with anchor-shaped sclerites in each

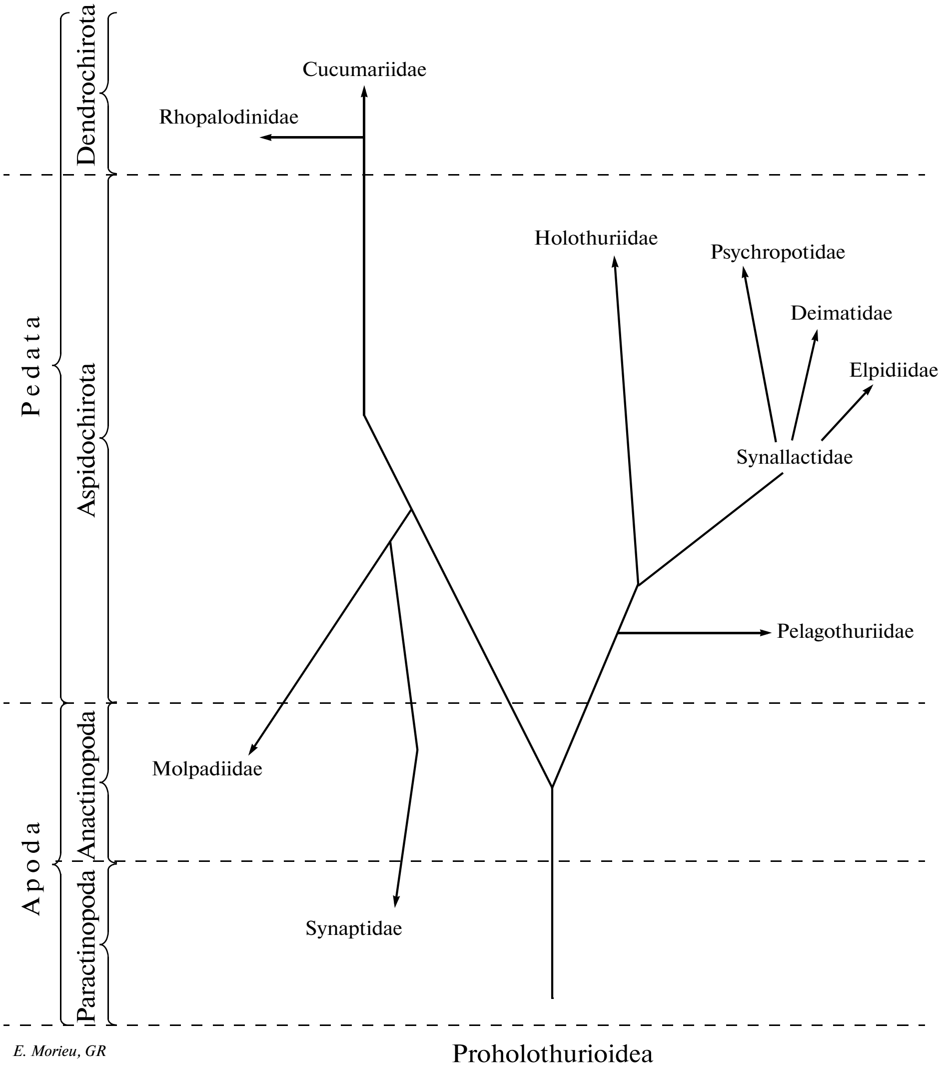

Fig. 3. Phylogenetic tree of holothurians from Rémy Perrier (1902).

order as an argument uniting the orders lacking tube feet, and justifying their placement in the same subclass. Perrier placed the orders Paractinopoda (=Synaptida) and Anactinopoda (=Molpadiida) in Apoda. The second subclass in Perrier's system was Pedatae, which as its name suggests included holothurians with tube-feet. He subdivided it into two orders: Aspidochirota and Dendrochirota. Perrier placed both aspidochirotids and elasipodids in the order Aspidochirota. In Perrier's system the order Aspidochirota included six families: Synallactidae, Deimatidae, Elpidiidae, Psychropotidae, Holothuriidae, and Pelagothuriidae. According to Perrier, characters distinguishing the order Asdpidochirota include: morphology of tentacles which terminate in discs with small processes, and the absence of retractor muscles of the pharynx. Perrier suggested that the families (Psychropotidae, Deimatidae, and Elpidiidae) evolved from Synallactidae. Therefore he rejected the order Elasipoda, and placed families previously assigned to it in the order Aspidochirota. The second order in Perrier's system, Dendrochirota, is much better characterized. These are holothurians with dendritic tentacles, with retractor muscles in the anterior portion of the body, respiratory trees, with no free ampullae of tentacles, and the stone canal not exiting outside. The order includes two families: Cucumariidae and Rhopalodinidae.

Systems and Phylogenetic Reconstructions of the Class Holothuroidea Proposed in 1906–2010

From 1906 and until the 1960s, authors publishing the system of the class Holothuroidea did not subdivide it into subclasses. The class included five or six orders, which were not united into larger taxa. MacBride (1906) recognized six orders: Aspidochirota, Elasipoda, Pelagothuriida, Dendrochirota, Mol-

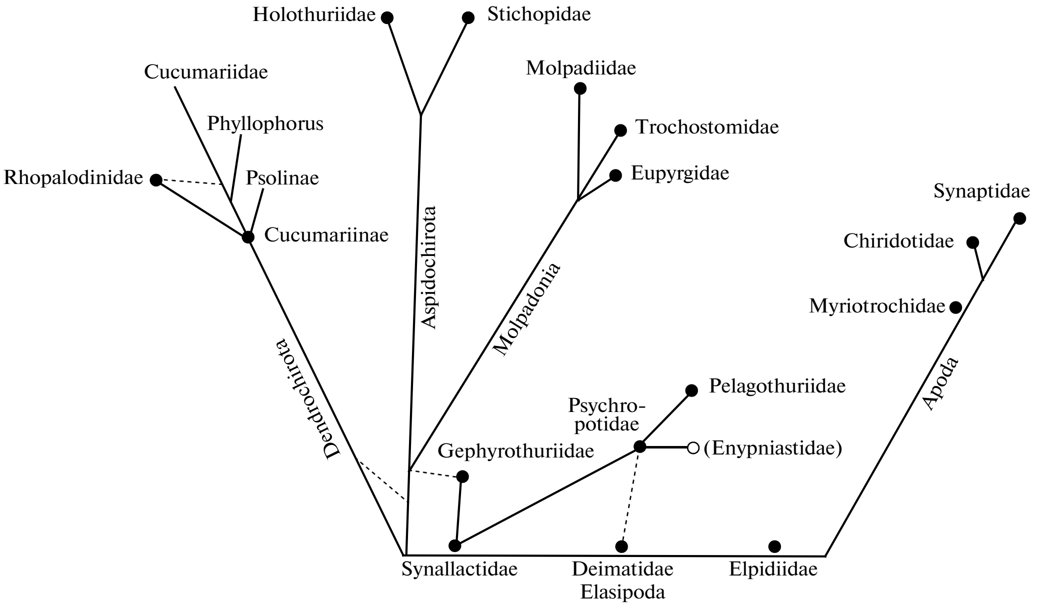

Fig. 4. Phylogenetic tree of holothurians from Östergren (1907).

padonia, and Synaptida. MacBride, like Haeckel, considered planktonic holothurians as a separate order Pelagothuriida. Subsequently, the family Pelagothuriidae was included in the order Elasipoda, however Heding (1950) again recognized planktonic holothurians as a separate order Pelagothurioidea. However, Heding's view was not supported by later workers, and at present Pelagothuriidae are classified within the order Elasipodida.

The following year, Östergren (1907) recognized five orders: Elasipoda, Aspidochirota, Molpadonia, Dendrochirota, and Apoda. The subdivision of the class into 5 orders was included in major zoological treatises (Cuénot, 1948; Hyman, 1955; Kaestner, 1963) and was used in most papers on holothurians. Although Heding (1935) classified the family Gephyrothuriidae within a separate order Gephyrothurioidea, he soon (Heding, 1940) rejected the separation of Gephyrothuriidae as a separate order and placed this family in the order Aspidochirota. The use of system in which orders were not united into higher taxa had a positive effect because it brought the end to the dichotomous system in which taxa were subdivided based on one or a minimal number of characters. In contrast, each order was now characterized by an assembly of characters. Orders were characterized by morphology of tentacles, presence or absence of ampullae of tentacles freely hanging to the body cavity, presence or absence of retractor muscles, presence or absence of radial ambulacral vessels, presence or absence of tube-feet and their morphology, presence or absence of respiratory trees. Characterization of orders also included their specific characters, e.g., presence of an introvert (introverted anterior part of the body) typical to the order Dendrochirota; presence of the button sclerites in the skin of the body in Aspidochirota; attachment of the mesentery, suspending posterior loop of intestine in the right dorsal interradius in Elasipoda; tentacular canals origin directly from the water ring, undivided longitudinal muscle that do not interrupt the layer of circular muscles at the radii, skin ossicles in the shape of sigmoids, anchors, and anchor plates in Synaptida (=Apoda) (Cuénot, 1948; Hyman, 1955; Kaestner, 1963).

Although the authors of the 20th century did not unite holothurian orders into the higher taxonomic categories, their views on the relationships between holothurian taxa were reflected in the phylogenies they suggested. The phylogenetic tree proposed by Östergren (1907) (Fig. 4) contains three distinct groups. (1) The initial group of Elasipoda, which in the author's understanding includes: (a) families traditionally assigned to Elasipoda (families Elpidiidae, Deimatidae and Psychropotidae) and the planktonic holothurian family Pelagothuriidae; (b) families Synallactidae and Gephyrothuriidae, although not excluding the closeness of the latter with Molpadonia. Thus Östergren excluded the family Synallactidae from Aspidochirota and placed it in Elasipoda.. He suggested that the family Psychropotidae assigned to Elasipoda is related to the genera of *Paelopatides*, *Synallactes*, and *Bathyplotes* (family Synallactidae). In this case the respiratory trees in Psychropotidae should have been secondarily reduced. Östergren did not exclude the possibility that Psychropotidae could also evolve from the family Deimatidae. Östergren considered the genera *Mesothuria* and *Capheira* from the family Synallactidae to be close to the family Deimatidae of the order Elasipoda. (2) A group including the order Dendrochirota, order Aspidochirota *s. str.*

(without Synallactidae) and the order Molpadonia. (3) A group of footless, lungless holothurians Apoda (=Synaptida). He considered the origin of Dendrochirota (with respiratory trees) and Aspidochirota *s. str.* (including the families Stichopotidae and Holothuriidae) and Molpadonia to be connected with Synallactidae. According to Östergren Apoda (=Synaptida) branch evolved from lungless elasipodids. Östergren argued for the closeness of Aspidochirota *s. str.* and Molpadonia based on the presence in these two groups freely hanging tentacular ampullae and longitudinal muscle subdivided into two bands.

Becher's brilliant paper devoted to the phylogeny of holothurians was published in 1909. Becher consciously did not propose his own system of holothurians, and more so did not use taxonomic names above genus-level, and used German names derived from Latin taxonomic names for groups of holothurians which other workers treated as families and orders. In his paper he thoroughly analyzed the development and evolution of major morphological structures of holothurians and in his phylogenetic reconstruction (Fig. 5) not only showed his phylogenetic tree of the class, but also demonstrated the presence on the branches of five morphological characters that he considered significant, i.e., statocysts, wheel-shaped ossicles, respiratory trees, table ossicles, and freely hanging tentacular ampullae. At the base of the phylogenetic tree of holothurians Becher placed a well-distinguished branch of synaptids, with wheel-shaped sclerites and statocysts. The lower part of the tree also included two groups of elasipodid holothurians, elpidiids, which also, like synaptids, have statocysts and wheel-shaped ossicles and deimatids.[1] In the upper part of the tree he placed holothurians, which, except for two cases, have respiratory trees: (1) branch of dendrochirotids; (2) branch of molpadiids, at the base of which he placed the genera *Eupyrgus, Gephyrothuria*, and *Himasthlephora* (=*Gephyrothuria*); (3) *Synallactes woodmasoni* Koehler et Vaney, 1905 (=*Amphigymnas woodmasoni*, family Synallactidae); (4) branch *Benthothuria–Benthodytes*–psychropotides (Becher considered that psychropotides secondarily lost the respiratory trees and linked them with the synallactid genus Benthodytes (with the respiratory trees), hence their placement in this part of the tree is logical; (5) several branches that he designated as synallactids; (6) genus *Capheira* Ludwig, 1894 (in this genus the respiratory trees were not originally discovered, so it was placed in deimatids, but later it was transferred to synallactids, based on the ossicles morphology and discovery of small respiratory trees); (7) branch of holothuriids, with the synallactid genera *Gastrothuria, Mesothuria*, and *Zygothuria* at the base; (8) branch of stichopodids with the synallactid *Pseudostichopus* tentatively placed at the base. The latter two branches have the same root and correspond to the aspidochirotids of earlier authors.

In my opinion, Becher's tree adequately reflects relationships between the main holothurian groups. It also shows questions of holothurian phylogeny that were unresolved at the beginning of the 20th century. Unfortunately these questions have still not been answered 100 years later. He recognizes two major holothurian groups. The first includes synaptids, elpidiids, and deimatids (in fact laetmogonids, see Footnote 1), which have wheel-shaped ossicles, and the former two also have statocysts. The second group includes the holothurians with respiratory trees and those that (according to Becher) secondarily lost the trees. Most members of this group also have table-like sclerites. In his tree Becher indicates the presence of tables (Stühlchen) only in holothuriids, stichopodids and synalactids. At the same time he noted the presence of similar sclerites in dendrochirotids and molpadiids and even gives a morphological successive transformation of the molpadiid tables into a molpadiid anchors. For dendrochirotids, Becher noted only the presence of tables with two pillars, but did not take into account the presence of tables with four pillars in thyonids and phyllophorids. He suggested that table-like sclerites could have appeared independently, but at the same time considered that they appear on a common basis: "Die Entstehung dieser Gebilde ist eine so einfache, daßsich ihre Bildung in verschiedenen Gruppen sehr wohl trotz der großen Ähnlichkeit selbständig vollzogen haben kann. Trozdem sind sie nicht lediglich als analoge Formen zu betrachten; denn sie sind aus derselben Grundanlage, durch eine in denselben Bahnen laufende Ausbildung einer schon bei der Stammform vorhandenen Wachstumstendenz enstanden. Deshalb kann man solche Kalkkörperformen als allgemein homolog bezeichen." (Becher, 1909, p. 439–440).

Various synallactids in Becher's tree were placed at the base of a branch leading to holothuriids + stichopodids branch, and at the bases of the holothuriid and stichopodid branches. However, Becher, unlike Sluiter (1901), did not consider synallactids to be an artificial group. He suggested that this was a primitive group of "lung" holothurians, which gave rise to numerous other taxa (at present we would have referred to the principle of archaic morphological diversity) (Mamkaev, 1991). In my opinion that paper not only retained its relevance, but still remains the best study of holothurian phylogeny. Alas, it was completely forgotten, except a mention in the reference list without discussion in the text by Hyman (1955).

Cuénot (1948), in a chapter on holothurians in Treaté de Zoologie considered holothurians as one class, containing five orders. Although he did not subdivide the class of holothurians into subclasses, in his

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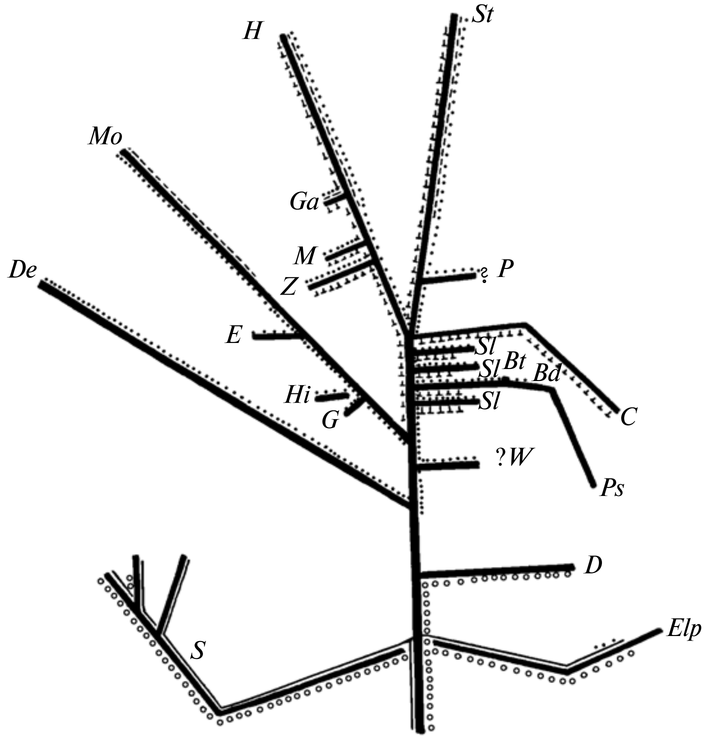
[1] At that time the family Deimatidae *s. lato* included the deimatids *s. stricto*, with plate-shaped ossicles, as well as the genera with wheel-shaped ossicles, later placed in a separate family, Laetmogonidae Ekman, 1926. Becher meant laetmogonids.



In dieser Stammbaumzeichnung ist neben den Ästen, die die einzelnen Holothuriengruppen darstellen, durch verschiedene Linien das Vorkommen oder Fehlen verschiedener phylogenetisch wichtiger Organe angedeutet.

Es bedeutet: ——— das Vorkommen von Statocysten
○ ○ ○ ○ ○ ○ ” ” ” Rädchen
.... ” ” ” Wasserlungen
⊥⊥⊥⊥⊥⊥⊥ ” ” ” Stühlchen
– – – – – ” ” ” Füuhlerampullen

ferner

Elp	Elpidiiden	*C*	*Capheira*	*Z*	*Zygothuria*
D	Deimatiden	*P*	*Pseudostichopus*	*Mo*	Molpadiiden
W	*Synallactes wood-masoni*	*St*	*Stichopus*	*E*	*Eupyrgus*
Sl	*Synallactiden*	*H*	*Holothuria* und verwandte Gattungen	*Hi*	*Himasthlephora*
Bt	*Benthothuria*			*G*	*Gephyrothuria*
Bd	*Benthodytes*	*Ga*	*Gactrothuria*	*De*	Dendrochiroten
Ps	Psychropotiden	*M*	*Mesothuria*	*S*	Synnaptiden

Fig. 5. Phylogenetic tree of holothurians from Becher (1909).

tree (Fig. 6), the group Apoda (order Synaptides) is counterbalanced by Actinopoda (Ludwig's name) (including the orders Dendrochirotés (Cucumariidés), Molpadides, Aspidochirotes, and Elasipodes). In contrast to his viewpoint on the primitive nature of Elasipodes compared to water lung holothurians (Cuénot, 1891) he now considered that the deep-sea Elasipodes evolved through neoteny from an unknown ancestor, perhaps Aspidochirotes (Cuénot, 1948, p. 110).

The latest system of holothurians was proposed by Pawson and Fell (1965). In their paper on the revision of dendrochirote holothurians they recognized three new families and a new order Dactylochirotida, and proposed a system of the class Holothuroidea. The order Dactylochirotida was established to accommodate dendrochirotid holothurians, in which the body is enclosed in a test formed by overlapping scales, and which have unbranched digitate tentacles, which sometimes bifurcate. The new order included the families Ypsilothuriidae Heding, 1942, Rhopalodinidae Théel, 1886 and a new family Vaneyellidae Pawson et Fell, 1965, which included the genera *Vaneyella* Heding et Panning, 1954 and *Mitsukuriella* Heding et Panning, 1954. A phylogenetic tree of holothurians (Fig. 7) was published as the part of the phylogenetic tree of the subphylum Echinozoa (Fell, 1965, p. 15, text-fig. 13; Fell and Pawson, 1966, p. 8, text-figs. 1–17b). Later Pawson (1982) published an expanded version of this system with diagnoses of subclasses, orders and

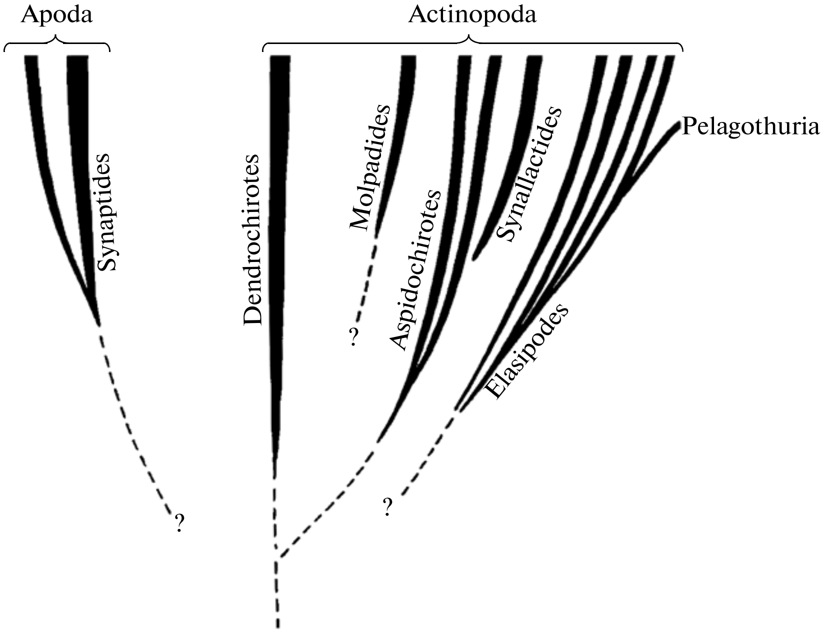


Fig. 6. Phylogenetic tree of holothurians from Cuénot (1948).

families in the reference-book "Synopsis and classification of living organisms." Pawson and Fell subdivided the class Holothuroidea into three subclasses. The diagnoses of the subclasses are given below according to Pawson (1982):

"Subclass Dendrochirotacea. The subclass is introvert (retractil oral area with tentacles), with retractor muscles always present. Tubefeet and respiratory trees are usually present. The madreporite is free in the body cavity; free tentacle ampullae are absent. The gonad is in two tufts, one to each side of the dorsal mesentery. The tube-feet are usually well developed, and the calcareous ring ranges from simple to extremely complex. The ossicles in the body vary from simple perforated plates to complex multilayered scales, baskets, and tables. The subclass contains 2 orders: Dendrochirotida and Dactylochirotida." (Pawson, 1982, p. 814).

"Subclass Aspidochirotacea. Tube-feet are present, and the tentacles are shield-shaped and 10–30 in number. No retractor muscles are present. The body has conspicuous bilateral symmetry. The 2 orders of the subclass, Elasipodida and Aspidochirotida, share several anatomical features which indicate that they may have a common ancestry." (Pawson, 1982, p. 816).

"Subclass Apodacea. The tentacles are simple, digitate, or pinnate. The tube-feet are markedly reduced, or more usually absent. The ossicles may include anchors and anchor plates. This subclass was erected to include the orders Apodida and Molpadida, for they share the characters described above. However this alignment may be artificial. The 2 orders may be quite unrelated, their similarities resulting from their adaptation of similar habitats. The anchors shared by apodids and molpadiids are clearly of different origin. Molpadiids show many similarities to dendrochirotes, whereas apodids may have been derived from other holothurian stock." (Pawson, 1982, p. 817).

Pawson and Fell's system was adopted by many general papers, but not by all holothurian researchers. Hansen (1975) opposed the assignment of Elasipodida and Aspidochirotida to the same subclass and doubted the correctness of the establishment of the order Dactylochirotida (Hansen, 1988). I considered Pawson and Fell's system in a separate paper (Smirnov, 1984), where I criticized the establishment of the subclasses. It was shown there that Pawson and Fell's system is very similar to Perrier's system of 1902, although it was apparently unnoticed by the authors. The subclass Apodacea, recognized in Pawson and Fell's system is apparently polyphyletic, and it was perceived by the authors themselves when they published their system. "The important character shared by apodids and molpadids is the almost complete absence of tubefeet. Also both groups have simple digitate or pinnate tentacles. It is possible that the apodids and molpadids bear no close relation to each other, and the characters they have in common may have arisen through parallel evolution and convergence." (Pawson and Fell, 1965, p. 6). Later Pawson (1982, p. 817, see above) pointedly discussed the artificial nature of the subclass Apodacea.

The subclass Aspidochirotacea, is, in my opinion, also polyphyletic. The hypothesis of the closeness of elasipodids and aspidochirotids begins from Théel (1886) and Ludwig (1889–1892). Ludwig, did not unite these two groups in a separate taxon, but showed their nearness in the phylogenetic tree of holothurians

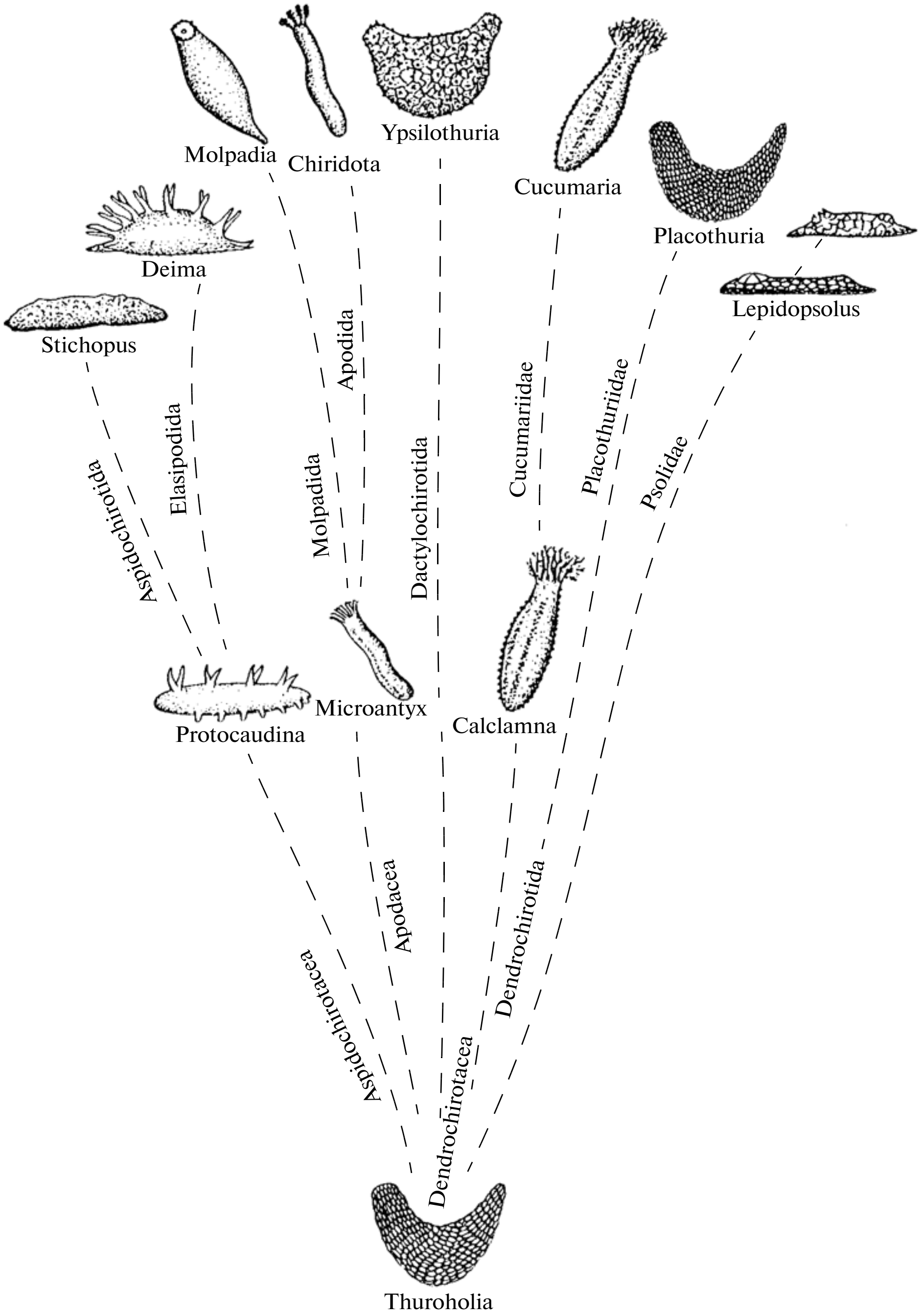


Fig. 7. Phylogenetic tree of holothurians from Fell (1965).

(where they were both at family-level). Later Haeckel (1896) also assigned these two taxa (as orders) to one phylogenetic branch. In Perrier's (1902) system the hypothesis of the closeness of aspidochirotids and elasipodids was taken to its extreme; the families of both orders were assigned to the order Aspidochirota, and Elasipoda were not considered as a separate taxon. Characters common to these groups usually include bilateral symmetry in the external morphology of the animal, shield-shaped tentacles, and the presence of dorsal tube-feet, modified into papillae. I think that these characters that only concern external morphology were most likely results of convergence. I showed previously (Smirnov, 2008) that all holothurians are bilaterally symmetrical animals and they retained the initial bilateral symmetry of ancestral echinoderms. Therefore, traces of bilateral symmetry can be easily found in virtually all holothurians. They can be more or less strongly revealed and their strengthening and weakening can easily be explained by their life style. The modification of the dorsal tube-feet into papillae and processes in aspidochirotids and elasipodids *s. str.*

could easily be independent. At the same time, differences in the anatomy (probably primary absence of the water lungs in elasipodids *s. str.*) and in the morphology of ossicles (tables in aspidochirotids, and wheels and psychropotid crosses in elasipodids *s. str.*) argue against the closeness of these two groups and their placement into the single higher taxon. The authors, suggesting a close relationship between elasipodids and aspidochirotids, based their theory mainly on the resemblance of some synallactids and psychropotids (Elasipodida) and considered synallactids as an intermediate group. Many synallactids differ from typical aspidochirotids (Stichopodidae and Holothuriidae) by the absence of free hanging tentacular ampullae and undivided muscle band. Perrier (1902) thought that all elasipodids evolved from synallactids, which secondarily lost their respiratory trees (Fig. 3). In contrast, Östergren (1907) considered synallactids as elasipodids, which acquired respiratory trees in the course of evolution and gave rise to the rest of holothurians with respiratory trees (Fig. 4). In my opinion, deimatids, which possess plate-shaped ossicles similar to table disk of synallactids and different from ossicles of other elasipodids, most likely lost their respiratory trees secondarily and acquired dorsal attachment of all three mesentries. With regard to other elasipodids, there is so far no basis for such an assumption. Hansen wrote: "A relationship between the Elasipoda and Aspidochirota has been supposed from the presence of shield-shaped tentacles in both groups, and from the similarity in external appearance between the Psychropotidae and various genera of the aspidochirote family Synallactidae. However, the fact that the calcareous deposits are entirely different suggests that the similarities in external appearance are due to convergent evolution." (Hansen, 1975, p. 209). All the above, in our opinion, suggests that the subclass Aspidochirotacea is polyphyletic.

Dendrochirotacea is a natural monophyletic group, but it does not deserve to be ranked as a subclass. The order Dactylochirotida Pawson and Fell is not a natural group and should be discarded. The main distinguishing characters of Dactylochirotida (according to Pawson) include: (1) "the tentacles number 8–30 and are not branched but digitiform or digitate, the digits some times bifurcating"; (2) "the calcareous ring is simple and lacks complex posterior processes"; (3) "the body is enclosed in a complete test composed of imbricating plates"; (4) "the body is usually U-shaped and is essentially rigid, although varying degrees of flexibility are exhibited" (Pawson, 1982, p. 815). When these characters are analyzed it becomes clear that they all appeared convergently as adaptive responses to similar environments. (1) Unbranched tentacles apparently evolved from branched ones by reduction, which is suggested by the presence of some traces of branching in them. Ohsima (1915, p. 272) indicated that in a species that he described *Pseudocucumis dactylicus* (currently *Vaneyella dactylica*), referred by Pawson and Fell to the order Dactyliochirotida, the tentacles were "seldom with a few knoblike rudiments of branches." Thandar (2001, p. 241) noted: "Although the tentacles of some rhopalodinids may be simple and finger-like with short lateral branches, those of *Rhopalodinopsis* at least appear to be finely dendritic." 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. Thus, for example, clearly secondarily simple tentacles are present in *Leptosynapta minuta* and *Rhabdomiolgus ruber* (Becher, 1906; 1907), as well as other neotenous synaptids.The genera *Eupyrgus* and *Haplodactyla* of molpadiids also could be examples of the above;similarity in the morphology of simple tentacles in these genera and simple tentacles of *Psolus digitata* were noted by Ludwig (1894, p. 139) . Thus simple tentacles repeatedly evolved convergently in the evolution of holothurians. (2) A simple calcareous ring lacking complex posterior processes is characteristic for several families of dendrochirotids, e.g., Cucumariidae and Psolidae, and it is not a character distinguishing Dactylochirotida from Dendrochirotida. (3) Strengthening of the body wall is observed in many dendrochirotids. One of the solutions of this problem is the formation of the test by overlapping calcareous scales. Evidently, this character appears independently in different branches of dendrochirotids. The test is present in the families Paracucumidae and Heterothyonidae, which those authors placed in the order Dendrochirotida *s. str.* Layers of calcareous scales are developed on the dorsal side in the family Psolidae (order Dendrochirotida), which are similar in the morphology of the calcareous ring and ossicles to the family Cucumariidae. (4) U-shaped morphology is not observed exclusively in dactylochirotids, but is also found in some dendrochirotids, e.g., in the family Phyllophoridae. Thus, none of the above characters, considered to be diagnostic for Dactylochirotida, is in fact specific for this order. It could be suggested that dactylochirotids are characterized by an assembly of characters, rather than by separate ones. However, four characters inherent to dactylochirotids easily appear in completely different groups and are apparently connected with the environment, whereas conservative and more taxonomically significant characters of the skeleton clearly indicate that the order Dactylochirotida is polyphyletic, and that the families within this order are linked to different families of dendrochirotids.

Members of the family Rhopalodinidae have a calcareous ring similar to that in the family Phyllophoridae. In these families the table ossicles are also similar. Members of these two families similarly have tentacles in multitentacular forms arranged in two rings. Finally, as show above, the genus Rhopalodinopsis possesses branched tentacles. Heding (1937) who thoroughly studied the family Rhopalodinidae considered that it is so closely related to the Phyllophoridae, that two of its genera can be placed in the family Phyllophoridae. "I prefer for the moment to maintain a separate taxonomic group for the two genera here under discussion [Rhopalodina and Rhopalodinopsis], but I suppose it must be regarded as a subfamily, the Rhopalodinae, closely related to the Phyllophorinae. In reality the only important difference between the Rhopalodinae and the Phyllophorinae is the presence of large plates in the former, as I do not think that the peculiar body shape is of any higher taxonomic value." (Heding, 1937, p. 38). Thandar (2001) also concluded that the Rhopalodinidae are closely related to Phyllophoridae and noted that "... rhopalodinids may belong to the order Dendrochirotida rather than to the Dactylochirotida. In fact the type of tentacles, their arrangement often in two rings, and their phyllophorid-like tables, demonstrate that the rhopalodinids may be closely related to the phyllophorids." (Thandar, 2001, p. 241).

The family Ypsylothuriidae Heding, 1942 that Pawson and Fell placed in the order Dactylochirotida included three genera: *Ypsilothuria*, *Ypsilocucumis*, and *Echinocucumis*. Hansen (1988) showed that the genera *Staurocucumis*, *Psolicucumis*, and *Echinocucumis* are closely related and that "A close relationship between the three genera speaks against the division of the old order Dendrochirota into two, as proposed by Pawson and Fell (1965). In this system the genera *Staurocucumis* and *Psolicucumis* belong to the order Dendrochirotida while *Echinocucumis* belongs to the order Dactylochirotida." (Hansen, 1988, p. 307). Thus, the genus *Echinocucumis* should be taken out of the family Ypsilothuriidae and placed in the family Cucumariidae.

The genera *Vaneyella* and *Mitsukuriella* that belong to the family Vaneyellidae Pawson and Fell, are similar in the morphology of their calcareous ring and ossicles to the Cucumariidae.

In my opinion, the order Dactylochirotida is polyphyletic and should be abolished, whereas the families previously assigned to it should be included in the order Dendrochirotida. The genera *Vaneyella* and *Mitsukuriella* (family Vaneyellidae) should be assigned to Cucumariidae, whereas the family Vaneyellidae should be considered as a junior synonym of the family Cucumariidae. The genus *Echinocucumis* of the family Ypsilothuriidae, based on Hansen's (1988) study should also be assigned to the family Cucumariidae. The families Ypsylothuriidae *s. str.* and Rhopalodiniidae should be assigned to the order Dendrochirotida as separate families.

The subdivision of the class Holothuroidea into subclasses suggested by Pawson and Fell cannot be considered natural, as has been demonstrated by Hansen (1975; 1988), Smirnov (1984) and Kerr and Kim (2001).

In my paper mentioned above (Smirnov, 1984) I analyzed the system of the class Holothuroidea, proposed by Pawson and Fell. In this paper I showed the polyphyletic nature of the subclasses Apodacea and Aspidochirotacea recognized by Pawson and Fell. The main points of the paper are repeated above. I proposed to return to the system of holothurians developed by the beginning of the 20th century, i.e., to subdivide the class into several orders without recognizing subclasses in the class Holothuroidea. Along with the five traditionally recognized orders I accepted the order Dactylochirotida (which was clearly incorrect, see above) and proposed to reinstate the order Gephyrothurioidea Heding, 1935. I supported Östergren's (1907) view on a close relationship between the orders Molpadiida and Aspidochirotida *s. str.* (Stichopodidae + Holothuriidae). I now consider that the characters uniting these two groups (i.e., presence of free hanging tentacular ampullae and two muscle bands) appeared convergently.

In the early 2000s Kerr and Kim (2001) published a big paper on the phylogeny of holothurians inferred from morphology. Kerr and Kim examined the system of the class using cladistic analyses of 47 morphological characters and analyzed their distribution in 25 families of holothurians. A detailed discussion of Kerr and Kim's paper is beyond the scope of this paper, but it should be noted that not all their chosen characters are appropriate for cladistic analysis. The majority of anatomical characters were selected justifiably. These included: pharyngeal introvert (9)[2] retractor muscles (43), radial canals (27)[3], fused oral brim of papillae (34), "*rete mirabile*" (36), radial hemal vessel (37), respiratory trees (39), attachment to body wall of mesentery engaging posterior intestinal loop (40), circular muscle attachment (42), ciliated funnels (45), statocysts (46), wheels (18), tables (22), psychropotid rods (25). However, some characters were linked to each other, e.g., anal papillae (35) are observed in all holothurians with radial canals (27), and it is clear that holothurians with no radial canals cannot have anal papillae by definition; presence of the introvert (9) is definitely linked to the presence of retractor muscles (43); enlarged ventrolateral tubefeet (31) are connected to the presence of water vascular cavities (28); tentacle shape (29) is linked to feeding mode (47). At the same time the states of some characters developed in parallel and their use in this case is doubtful. This mainly concerns characters of external morphology and details of the calcareous ring, although parallelisms are also observed among the anatomical characters. The following states of characters developed independently in different orders and families: external communication of hydropore/madreporite (26), divided longitudinal muscles (41), presence of free

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[2] Figures in brackets show the number of characters used by Kerr and Kim (2001).

[3] Kerr and Kim follow Mooi and David (1997) considering that the radial canals of holothurians are nonhomologous to the radial canals of other echinoderms and call them "longitudinal vessels." I accept the homology of the radial canals of holothurians and other echinoderms. The detailed argumentation supporting my view could be found in Smirnov (2008, p. 96–97).

tentacle ampullae (30), pronounced sole (4), posterior extremely narrowed and elongated tail (5), position of mouth and anus (7 and 8), foreshortening of the dorsal interradius (10), overlapping ossicles of the body wall (17), fusion of papillae into a brim or vellum (33), presence of the enlarged dorsal papillae (32), perforated radial pieces of the calcareous ring (12), presence of the long posterior processes on radial plate of the calcareous ring (13), different proportions of radial plate of the calcareous ring (14), presence of the depressions of the anterior margin of radial plates of the calcareous ring to accommodate tentacular ampullae (15), height of articulation of the plates of the calcareous ring in proportion to interradial height (16). Completely different types of sclerites are mixed under the name "spired plates" (21). Therefore, this character can not be used in the analysis. The usefulness of the maximum body length (2) is not clear, because in large families there are species of various lengths, and in Synaptidae the length can range from 1 to 500 cm.

Despite the use of many parallel and convergent characters in the analysis, the resulting reconstruction obtained from the cladistic analysis generally confirmed the data of the beginning of the 1900s and is similar to the phylogeny proposed by Östergren (1907) and especially to that proposed by Becher (1909). I primarily talk about the tripartite scheme: Synaptida - Elasipodida – remaining holothurians (holothurians with respiratory trees). However it is not possible to agree with Kerr and Kim when they say: "As well, Dendrochirotida appears to be paraphyletic and consists of a soft-bodies grade and a testaceous clade." (Kerr and Kim, 2001, p. 76). As shown above, the order Dactylochirotida was artificial because it is recognized based solely on the superficial convergent external characters, whereas these authors did not take into consideration such characters as the morphology of the calcareous ring and ossicles. The authors themselves were uncertain about their interpretation: "There are, however, two reasons to view this interpretation with caution: support for the testaceous group that includes the dactylochirotes is strong only for successively weighted analysis (Fig. 3B) and is largely defined by a single subset of characters, those associated with a testaceous body wall." (Kerr and Kim, 2001, p. 76). In my opinion, there is no evidence supporting the paraphyly of dendrochirotides *s. lato*. Presence of two large apomorphies: pharyngeal introvert + retractor muscles and dendritic tentacles clearly supports the monophyly of Dendrochirotida *s. lato*.

The position of the families Gephyrothuriidae and Eupyrgidae was not clarified by Kerr and Kim. While the position of the former family indeed remains uncertain, Eupyrgidae, in my opinion, based on morphological characters, belong to the order Molpadiida. The external morphology, presence of 15 tentacles, respiratory trees, and table ossicles with a spire of three pillars suggest the affinity of the genus *Eupyrgus* to the Caudinidae.

Recently I (Smirnov, 2003; 2007) proposed to subdivide the extant members of the class Holothuroidea into three subclasses: Synaptacea with the order Synaptida, Elpidiacea with the order Elasipodida, and Holothuriacea with four orders (Aspidochirotida, Gephyrothuriida, Dendrochirotida, and Molpadiida. Their diagnoses, characterization, and substantiation are discussed in the section "System of the Class Holothuroidea."

The phylogenetic tree proposed by Reich (2010a, Fig. 3), reflects his interpretation of the early evolution of holothurians. The class Holothuroidea, in his opinion, appeared in the Lower Ordovician, whereas the first fossil remains are recorded from the Middle Ordovician. They belong to the extinct order Arthrochirotida, which in the author's understanding, is possibly connected with the order Synaptida (=Apodida). The first records of synaptids are dated as the Silurian (Llandlovery). These two groups are counterbalanced by two other groups – stem group representatives of Elasipoda/Aspidochirotida/Dactylochirotida/Dendrochirotida/Molpadiida, which appeared, according to Reich, in the Upper Ordovician and Elasipodida, which appeared in the Middle Devonian. In Reich's tree, Arthrochirotida + Synaptida (=Apodida) counterbalance all other holothurians. The latter contain Elasipodida, which are thereby counterbalanced (although indistinctly) by water lung holothurians. This paper is very important for the reconstruction of the general system of the class Holothuroidea, because it summarized data on the Early Paleozoic history of the class.[4]

THE SYSTEM OF THE CLASS HOLOTHUROIDEA

Holothurians are confirmed from the beginning of the Middle Ordovician (Reich, 2010a). Only skeletal elements are normally preserved as fossils. These include segments of the calcareous ring and/or far less commonly complete rings and isolated sclerites of the skin. Complete imprints of holothurians of various state of preservation are extremely rare (Giebel, 1857; Broili, 1926; Lehmann, 1958; Hess, 1973; Cherbonnier, 1978; Sroka, 1988; Smith and Galliemi, 1991;

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[4] Triradiate table-like sclerites of *Tribrachiodemas ordovicus* Reich, 2010, described from the Upper Ordovician of Gotland, Sweden (Reich, 2010b) seriously changes our understanding of the evolutionary history of the class of holothurians. This sclerite has three terminally perforated flat tips and a solid spire in the centre. The spire consists of three terminally fused pillars. Its morphology strongly resembles that of ossicles of the modern genera *Synallactes* and *Bathyplotes* (family Synallactidae) and Reich even assigned this genus to Synallactidae. It is extremely unlikely that modern synallactids existed in the Upper Ordovician. Before this discovery, the earliest known table sclerites were dated as Triassic, but they cannot be compared to ossicles of extant holothurians. Among the extant holothurians, table ossicles are only found in holothurians with respiratory trees. If it is accepted that Paleozoic holothurians with table sclerites also had respiratory trees, so the main holothurian groups diverged far earlier than it was previously thought (Reich, 2010a).

Hagdorn, 1993; Haude, 1995a; 1995b; 1997; 2002; Reich, 2004a; 2004b; Muir and Botting, 2005). In imprints, skeletal elements (calcareous ring or sclerites of the skin) are very rarely preserved, hence the taxonomic affinity of imprints can often be inferred only approximately, based on resemblance to extant holothurians. The affinity of some fossil remains to holothurians is occasionally disputed. For instance, Broili (1926) considered that *Protholothuria armata* Giebel, 1857 could not be assigned to any certain group of animals, whereas Seilacher (1961) suggested that *Protholothuria* was more likely a worm. Heding (1932) thought that *Pseudocaudina brachyura* Broili, 1926 was not a holothurian, but more likely a zoanthid, while Hess (1973), based on Ziegler's view, assigned it to Ctenophora. Other authors still consider these to be holothurians, i.e., *Protholothuria armata* was tentatively assigned to Aspidochirotida (Frizzell and Exline, 1966) or to Synaptida (Müller, 1969), and *Pseudocaudina brachyura* to Synaptida (Frizzell and Exline, 1966). Along with the traditional systems of the class Holothuroidea used in classifying extant holothurians, there is a formal system of fossil sclerites (Frizzell and Exline, 1955; 1966; Deflandre-Rigaud 1962). Systematics of sclerites is understandably formal, since it only operates with isolated skeletal elements, which are united in higher taxa based on morphological similarity. Often, sclerites that belong to individuals of the same species are assigned to different formal genera and families [paragenera and parafamilies]. Nevertheless, the formal systematics of sclerites allows us to classify the morphologically diverse holothurian sclerites. No formal systematics have so far been proposed for segments of the calcareous ring. The parallel existence of two systems of holothurians (extant holothurians and sclerites) is not only justified, it is necessary. However, attempts are made to correlate these two systems, as this allows to analyze the data on the appearance, evolution, and distribution of some extant holothurian taxa. Both paleontologists and zoologists have tried to correlate formal taxa of fossil sclerites with the modern system of the class. Deflandre-Rigaud (1962) and Pawson (1966) assigned some genera of fossil holothurian sclerites to extant orders, whereas Pawson (1980) attempted to correlate some of the formal sclerite genera with extant holothurian genera. Smirnov (1989) correlated all then-known fossil anchor and anchor plate sclerites, with the taxa of the extant family Synaptidae. Gilliland (1993) thoroughly correlated the formal sclerite taxa of extinct holothurians with the extant taxa of Holothuroidea. Although formal systematics is applied in descriptions using paragenera and parafamilies, specimens described are put in correspondence with the extant holothurian families (Gilliland, 1992; Reich, 2002; 2003a; 2003b; 2003c; 2003d).

If the Mesozoic and Cenozoic taxa, whether imprints of entire holothurians or skeletal elements (segments of calcareous ring and sclerites) in most cases can be correlated at least with extant orders of holothurians, the analysis of the Upper Paleozoic taxa allows only an assumption of their correspondence with the extant orders. With regard to the Early Paleozoic taxa, although their skeletal elements suggest an affinity to the extant orders Synaptida, Elasipodida, and Aspidochirotida (Reich, 2010a; b), it is still preferable to talk about the ancestral forms for the extant orders or about Synaptacea, Elpidiacea, and Holothuriacea clades. Table sclerites characteristic for respiratory trees (water lung) holothurians (subclass Holothuriacea) are found from the Upper Ordovician (Reich, 2010b) and therefore it can be assumed that ancestors of all three modern branches of holothurians appeared in the Paleozoic, and possibly in the Early Paleozoic.

The system proposed is based on the analysis of morphological, primarily anatomical characters and interpretation of their significance for the systematics that has been achieved after 180 years of holothurians study. The morphology of the calcareous ring is very important, although it is very difficult to describe its morphology and even more difficult to characterize features distinguishing the orders. It is only possible to support a recent concept postulating the significance of the SEM and CT studies of calcareous rings for understanding of holothurians evolution and phylogeny (Reich, 2010a). Apart from the calcareous ring, very important characters include: presence or absence of radial canals of the ambulacral system and origin of tentacles from the radial ambulacral canals or from the ambulacral ring; presence or absence (primary or secondary) of respiratory trees; attachment of mesentries supporting the posterior loop of intestine in the right ventral or in the right dorsal interradius; whether or not the ring muscles are interrupted by longitudinal muscle bands or form a continuous layer; presence or absence of statocyst; morphology of tentacles; presence or absence of the introvert and retractor muscles. Presence or absence of the principal ossicle types, wheels or tables is also very important.

Very important for the systematics of the orders is the use of the character states, which in different orders evolved independently and in parallel, including the degree of development of "rete mirabile," presence and morphology of the processes of the calcareous ring, fused oral brim of papillae, etc. In addition, the systematics of the orders or families takes into account presence and state of features specific for this taxon, e.g., presence or absence of specialized types of ossicles, such as psychopotid crosses in Elasipodida, presence or absence of ciliate funnels in Synaptida, morphology of anchors and anchor plates in the family Synaptidae, etc.

The system proposed is largely based on the views of Becher (1909) on the phylogeny of holothurians, naturally taking into account data obtained in the 100 years after its publication. It also takes into account cladistics analysis data of the class of holothurians, by Kerr and Kim (2001). The conclusions of the latter authors about the phylogeny of holothurians are similar to those of Becher, although it is apparent that the conclusions were achieved independently. The main differences between the system proposed here and the cladogram published by Kerr and Kim, are the interpretations of the system of dendrochirotides *sensu lato* (see discussion above). This paper also takes into consideration molecular-phylogenetic data (Smith, 1997; Lacey et al., 2005) and data of the most recent paleontological studies, particularly Haude (2002), Reich (2010a, 2010b) and others.

This paper contains a description of extant and Mesozoic holothurian taxa from subclasses to subfamilies. For each taxon there is a description, records of occurrences of fossilized complete body impressions, time of appearance, and the taxa of sclerites which could certainly be correlated with extant holothurian taxa[5], major references for the group and author's remarks. This work also containes the diagnosis of the extinct Paleozoic subclass Arthrochirotida, however the description of the taxa included, and the description of the parataxa of holothurian sclerites, is beyond the scope of the present paper.

CLASS HOLOTHUROIDEA
SELENKA, 1867[6]

The Echinodermata combining the bilateral and pentameral symmetries. The bilateral symmetry of holothurians evolved as a return to the initial bilateral symmetry of the ancestral echinoderms. The plane of bilateral symmetry of the larva becomes the bilateral plane of an adult holothurian.

In holothurians the anterior and posterior ends, the dorsal and ventral sides are distinct. Five longitudinal ambulacra run along the entire body from the mouth to the anus. The ambulacral system, nervous system, epineural and hyponeural canals and haemal system are pentameral. The radial parts of these systems occur along the entire body, along the radii (ambulacra). The ventral side, trivium, contains three radii and two interradii, the dorsal, bivium, contains two radii and three interradii. The mouth is surrounded by tentacles. The body shape of holothurians is usually cylindrical, but can vary from elongated worm-like to spherical. Sometimes holothurians have a U-shaped body, while in the family Rhopoladinidae, the dorsal side is strongly reduced, so that the mouth and the anus are closely approximated and the body becomes pseudodecameral.

The ambulacral system consists of the ambulacral (water) ring, from which five radial ambulacral canals (reduced in the order Synaptida)[7] extend. The tube-feet extend from the radial canals (reduced in the order Molpadiida). The end of the radial canals terminated in the anal papillae. One or several Polian vesicles and the stone canal terminating in the secondary madreporites extend from the ambulacral ring. The stone canal can exit outside by a pore canal through the ampullae, but in many holothurians the connection between the stone canal and the outside environment is interrupted and it blindly terminates in the body wall or opens in the body cavity. Sometimes several stone canals are present. The secondary madreporite of holothurians is not homologous to the madrepore plate of other echinoderms. Tentacles of holothurians are different in origin. The five primary processes of the left mesocoel (hydrocoel) in holothurians give rise to 5 primary tentacles, rather than radial canals as in other echinoderms. These tentacles then become connected with the radial canals, whereas in the holothurian order Synaptida, lacking radial ambulacral canals, they remain connected with the ambulacral ring. Radial canals develop later between the five primary tentacles. The remaining tentacles are modified tube-feet and extend from radial canals, whereas in Synaptida secondary tentacles develop on the ambulacral ring.

Holothurians are lack of a single axial organ that is present in starfish, brittlestars, and sea urchins. It is subdivided into the ampullae of the protocoel and stone canal on one side and the axial sinus and axial gland on another side.

The body wall is formed by the external epithelium, a layer of connective tissue containing ossicles, ring muscles, and, along the radii, by longitudinal muscle bands. Because of the well developed muscles, most holothurians are able to contract their body strongly and can considerably change their shape.

The skeleton of holothurians is composed of calcareous ring, consisted of five radial and usually five interradial segments, and isolated microscopic skeletal elements (called ossicless or spicules in the publications dealing with extant holothurians and sclerites in paleontological publications) located in the body skin, tentacles, and sometimes in the wall of the stone canal, Polian vesicles, and gonads. In some species, the scler-

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[5] The correlation of the fossil sclerites with the extant holothurian taxa was mainly based on Gilliland (1993). The correspondence of the fossil anchor and anchor plates sclerites with the taxa of the extant family Synaptidae was previously published by Smirnov (1989).

[6] Research on authorship and synonymy of class by H.B. Fell and J.W. Durham see in Frizzell, Exline, and Pawson (1966).

[7] Radial canals of holothurians in my opinion are homologous to the radial canals of the rest of echinoderms and are not a newly developed structures, referred to as the longitudinal vessel, as suggested by David and Mooi (David and Mooi, 1996; 1998; Mooi and David, 1997). See the evidence supporting the homology of the radial canals of holothurians and other echinoderms and the explanation of the features of the ambulacral system of holothurians differentiated into five primary tentacles and the radial canals themselves in Smirnov (2008, pp. 96–97, 101–102). The arguments against the interpretation of the radial ambulacral canals of holothurians as newly developed structures are also brought by Haude (2002).

ites are completely lost. Some families of the order Dendrochirotida have a test composed of overlapping scales (massive plates), which completely or partially covers the holothurian body.

The digestive system comprises the mouth, pharynx, slightly differentiated stomach, and the intestine. The intestine is looped within the coelom. The intestine first descend along the middorsal region, then bends and ascends anteriorly along the left side and turns again to descend directly backward to the anus (in some species the ascendant part of the intestine is not developed). The last part of the intestine called large intestine or rectum. In the subclass Holothuriacea respiratory trees open into the terminal part of large intestine forming cloaca. Cloaca is attached to the body wall by cloacal suspensors, composed of the connective tissue and muscle fibers. The digestive tube is suspended in the body cavity on mesenteries.

The main part of the haemal system consists of two large vessels (sinuses) (dorsal or mesenterial and ventral or antimesenterial) on the either side of the intestine, which are connected by anastomoses and the network of lacunae, surrounding the intestine. In some orders, intestine vessels form a meshwork of small vessels, referred to as *rete mirabile*. Apart from that, there is a haemal ring aroud the pharynx, from which five radial canals (sinuses) extend. In Synaptida radial haemal canals are not found.[8]

In most cases vessels do not have their own lining and are not strictly speaking vessels. However in large-dimension species (*Isostichopus badionotus*) large vessels have an endothelial epithelium. The circulation is provided by contractions of walls of some vessels, and large forms have "systems of hearts".[9] The axial gland is connected with the haemal system.

Holothurians have only ectoneural and entoneural systems. The endoneural (aboral) system is absent. The ectoneural system consists of the ectoneural ring and five radial ectoneural nerves extending from the ring. The ectoneural ring gives nerves to tentacles. Five hyponeural radial neural strands are closely adjacent from inside to five ectoneural radial neural strands. The hyponeural ring is not developed. The ectoneural and hyponeural radial nerves are connected by neural bridges.[10] The ectoneural system is located in the epineural ring and epineural radial canals. The epineural canals of the radial ambulacra, unlike those in sea urchins and brittle stars, don't develop through the closure of the epineural folds, but by development of a cavity in the tissue outside the radial nerves, unconnected to the external epithelium. The hyponeural radial nerves are located in the hyponeural canals. Members of the orders Synaptida and Elasipodida have statocysts (organs of balance).

The reproductive system, unlike other echinoderms, is represented by a single gonad. The gonad is subdivided into two parts to either side of the mediodorsal mesentery and is formed by unbranched or branched tubules. In some taxa right bunches can be lost. The gonoduct opens externally in the mediodorsal interradius near the tentacles. Most holothurians have two sexes, although there are also hermaphrodite species. Fertilization is external in most species. Eggs are dispersed in water and are not laid in a clutch.

The families Synaptidae, Stichopodidae, and Holothuriidae have indirect development with two larval stages, planktotrophic auricularia larvae and non-feeding doliolaria larvae. Most holothurians have direct development, when the auricularia stage is absent. Some holothurians look after their offspring, including carrying eggs on the ventral surface and between the tentacles, in specialized brood pouches and dorsal pockets. Some forms brooded embryos internally in the perivisceral coelom or in the ovary.[11] Some forms are viviparous. Holothurians have evolutive metamorphosis, when most larval tissues are included in the body of the adult animal.

In ontogeny only left and right somatocoels and undivided left axohydrocoel are formed. The right axocoel and hydrocoel do not develop.

Chemically, holothurians can be characterized by presence of triterpene glycosides which are specific for this class. Triterpene glycosides are found in almost all holothurians and apart from them, among animals, only occasionally in sponges.

The class Holothuroidea is subdivided into four subclasses: Arthrochirotacea, Synaptacea, Elpidiacea, and Holothuriacea. This subdivision, in my opinion, reflects an accepted interpretation of the system of the class Holothuroidea. Based on studies of morphology and anatomy many authors consider synaptids to be totally separate from the remainder of holothurians. Semon (1888), Cuénot (1891), and Haeckel (1896) considered synaptids as primitive forms close to the base of the holothurian lineage, whereas Cuénot (1891) considered them as a separate class from the rest of the holothurians. These authors suggested that the absence of the radial ambulacral canals in synaptids and the organization of their ambulacral system is an original trait. However, even after it was established that the radial ambulacral canals in holothurians were secondarily lost, many authors continued considering them as a primitive, but strongly modified group of holothurians (Ludwig, 1889–92; Clark, 1910; Cuénot, 1948; Kerr and Kim, 2001). At present this view is sup-

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[8] Cuénot (1948) in the section devoted to the hemal system of the "ordre des synaptides" wrote: "Il n'y a pas du tout de lacunes radiales ni de réseaux admirables." (p. 105).

[9] Herreid II, LaRussa, and DeFesi (1976).

[10] Until recently it was believed that ectoneural and hyponeural nerve cords of holothurians were not connected. Mashanov et al. (2006) showed that ectoneural and hyponeural nerve cords interconnected with one another via a short neural bridge.

[11] Smiley et al. (1991, p. 727).

ported by molecular-phylogenetic methods (Smith, 1997; Lacey et al., 2005).

The subdivision of other holothurians into lungless Elasipodes and holothurians with water lungs was proposed by Cuénot (1891). Smirnov (2003, 2007) proposed a similar tripartite scheme for subdivision of the class Holothuroidea into the subclasses Synaptacea–Elpidiacea–Holothuriacae. He recognized elasipodids as a separate subclass Elpidiacea, and considered them separate from the earlier lineage of synaptids, and the lineage of advanced “lung” holothurians. Based on cladistics analysis (Kerr and Kim, 2001), elasipodids are the sister group of lung holothurians. This placement of elasipodids is also supported by the molecular-phylogenetic data (Smith, 1997; Lacey et al., 2005). Thus, the phylogenetic reconstructions of modern authors are similar to those of Cuénot (1891).

The study of the Early Paleozoic fossil holothurians and remains of their calcareous rings led a number of authors to the hypothesis that the Early Paleozoic holothurians, of the order Arthrochirotida are similar to Paleozoic holothurians of the order Synaptida or ancestors of the Synaptida. Seilacher (1961) placed the orders Apodida (=Synaptida) and Arthrochirotida in the superorder Apoda. Kutcher and Sieverts-Doreck (1977) placed the order Arthrochirotia in the subclass Apodacea Pawson et Fell, together with the recent orders Apodida and Molpadiida. The similarity of Arthrochirotida and Synaptida (=Apodida) and their separation from the ancestors of other groups of extant holothurians was accepted for the phylogenetic reconstruction proposed by Reich (2010a). It is possible that the subclasses Arthrochirotacea and Synaptacea recognized in this paper can be assigned to Archiholothuroidea, whereas two other subclasses Elpidiacea and Holothuriacea can be assigned to Euholothuroidea.

SUBCLASS ARTHROCHIROTACEA SUBCLAS NOV.

Holothuroidea with plated tentacles and remains of radial ambulacral system; exoskeleton of sieve plates (Reich, 2010a). Calcareous ring well developed, stout; interradial segments are similar to radial segments in shape and size.

The subclass includes one extinct order Arthrochirotida.

Order Arthrochirotida Seilacher, 1961

Diagnosis: As for the subclass.

Middle Ordovician–Lower Devonian (Reich, 2010a)

The order includes an imprint of the holothurian *Palaeocucumaria hunsrueckiana* Lehmann, 1958. This species is distinguished from all extant holothurians by the presence of plated tentacles. The x-ray study of *P. hunsrueckiana* (Bartels et al., 1997) showed at least one short adoral row of ossicles possibly signifying vestigial ambulacrals (Haude, 2002, fig. 2). It is possible that traces of uniserial skeletal ossicles of possible ambulacrals were also found on an as yet undescribed holothurian from the Early Llandeilian, Ordovician of Wales (Muir and Botting, 2005). Reich (2010a) assigned to this order occurrences of calcareous ring and skin sclerites from the Early Devon (Lehmann, 1958; Seilacher, 1961; Kutscher and Sieverts-Doreck, 1977; Haude, 1995a) and occurrences of isolated segments of calcareous ring from the Silurian (Reich, 1999; Reich and Kutscher, 2001; Reich, 2010a).

SUBCLASS SYNAPTACEA CUÉNOT, 1891

[nom. transl. pro subclassis Al. Smirnov, 2007 (ex Synaptida Cuénot, 1891, pro classis)]

Usually worm-like Holothuroidea. Tentacles peltato-digitate, digitate, pinnate, or, can be secondarily simplified, simple or forked. Radial canals absent; tube-feet and anal papillae absent; canals of tentacles extending from the ambulacral ring; ampullae of tentacles are not free hanging into the body cavity. No radial hemal canals. Ring muscles not interrupted by radial muscle bands. The suborder Synaptina has organs of balance (5 pairs of statocysts) in places where radial nerves extend from the neural ring. Topographically, the primary tentacles are arranged in the way that they were initially connected with the following now missing radial canals: two with medioventral, two—with the left dorsal, and one—with the right dorsal (Fig. 8). The stone canal is attached to the body wall and opens externally or terminates in the body wall or opens into the body cavity. Respiratory trees absent. The mesentery supporting the posterior loop of the intestine is attached to the body wall in the right ventral interradius. Longitudinal muscle bands are undivided. The calcareous ring is stout. The radial and interradial segments are usually similar in shape and size. Radial segments of the ring in their upper (anterior) part have a perforation for a nerve, or sometimes it is secondarily not closed on the top and is in a shape of notch (in paedomorphic species, the segments are simple, without an anterior projection, while the radial segments do not have a perforation, or a noch for passage of the nerve). Ossicles: myritrochid or chyridotid wheels, sigmoids, anchors and anchor plates. There are no tables.

The complete specimen species *Achistrim* sp., with hook-shaped sclerites is provisionally described from the Middle Pennsylvanian of Illinois, USA (Sroka, 1988). This species probably belonged to the order Synaptida. Hook-shaped sclerites, that can be compared with sigmoids of the extant Synaptacea (ordo Synaptida, family Chiridotidae), are confirmed from the early Middle Devonian (Reich, 1999; 2010a). Wheel-shaped sclerites, resembling wheels of the

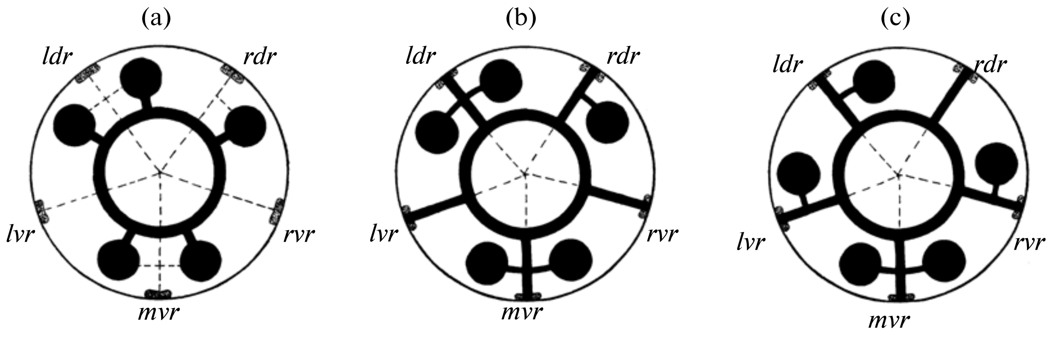

Fig. 8. Connections between the primary tentacles of holothurians and radiall ambulacral canals. Designations: (*ldr*) left dorsal radius; (*lvr*) left ventral radius; (*mvr*) midventral radius; (*rdr*) right dorsal radius; (*rvr*) right ventral radius. (a) Synaptida; (b) Denrochirotia and Molpadiida; (c) Aspidochirotida.

extant myriotrochids are known from the Middle Devonian (Boczarowski, 2001).[12] It can be suggested with a high degree of certainty that the synaptid branch of holothurians appeared at least in the Middle Devonian. The perforated radial segments of the calcareous ring, similar to the segments of the ring of Myriotrochina, are known from the Early/Middle Silurian of Gotland, Sweden (Reich, 2010a, fig. 2).

The subclass includes one order Synaptida.

Order Synaptida Cuénot, 1891

(=Chiridoten, Grube, 1840; Apneumona Selenka, 1867; Paractinopoda Ludwig, 1889–92; Synaptonia Haeckel, 1896; Apoda Östergren, 1907; Apodida auct.)

Diagnosis. As for the subclass.

References: Östergren (1898), Clark (1908), Heding (1931b; 1935), Smirnov (1998; 1999), Kerr (2001), O'Loughlin and VandenSpieegl (2007; 2010).

Remarks. This group was first recognized at the taxonomic rank of order by Selenka (1867). The name Apneumona, proposed for the order by Selenka, was short-lived, as well as the name Paractinopoda proposed by Ludwig (1889–92). In 1907 Östergren proposed the name Apoda for the order, which in my opinion is not a good choice. As shown above, this name was used for groups comprising the extant orders Synaptida and Molpadiida: Apodes for a subfamily (?) (Brandt, 1835); Apodia for a suborder (Bronn, 1860); Apoda for an order (Lampert, 1885; Théel, 1886) and for a subclass (Perrier, 1902); Apodacea for a subclass (Pawson and Fell, 1965; Pawson, 1982). The name *Apoda* is used for a genus in Lepidoptera (Zagorodniuk, 2004). In addition, the name Apoda and derived from it are used for large taxa in Crustacea, Pisces, Amphibia, and Aves (Lakshminarayana and Rama Rao, 1977; Zagorodniuk, 2004). Therefore I propose to follow Cuénot (1891, 1948) and MacBride (1906) and to use the name Synaptida for the order, which is based on the generic name *Synapta* and the family-group name Synaptidae. The order includes two suborders: Myriotrochina and Synaptina.

Suborder Myriotrochina Al. Smirnov, 1998

Synaptida with 10 or 12 digitate or peltato-digitate tentacles. Segments of the calcareous ring with large anterior projections; excavations for tentacular ampullae on anterior side of the ring. Madreporite is located close to the ambulacral ring. Ciliated funnels absent. One Polian vesicle. Ossicles: mytriotrochid, acanthotrochid, and lepidotrochid wheels with wide flat hub sometimes with four perforations in the centre and a large number of spokes (8–25).

Typical acanthotrochid wheels (paragenus *Acanthotheelia*, parafamily Theelidae), comparable with the wheels of the genus *Acanthotrochus* of the family Myriotrochidae appear in the Middle Triassic, while the mytriotrochid wheels (paragenera *Hemisphaeranthos* and *Stueria*, in the parafamily Theelidae) are known beginning from the Lower Jurassic (Gilliland, 1993; Smirnov, 1999). The sclerite *Trematrochus smirnovi* (parafamily Theelidae) from the Late Cretaceous (Maastrichtian) of Greifswald, Germany (Reich, 2002) belongs to the subgenus *Oligotrochus* of the genus *Myriotrochus*.

The suborder contains one family Myriotrochidae Théel, 1877.

Family Myriotrochidae Théel, 1877

Diagnosis: As for the suborder.

References: Belyaev (1970); Belyaev, Mironov (1980, 1981a, 1981b, 1982); Gage and Billett (1986); Reich (2002).

Suborder Synaptina Al. Smirnov, 1998

Segments of calcareous ring lacking large anterior processes. Excavations for tentacular ampullae occur-

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[12] The wheels of the extinct *Gagesiniotrochus astralis* (Boszarowski, 2001, p. 161, Fig. 75), which can be considered as ancestral to the extant myriotrochids, also somewhat resemble laetmogonid wheels of extant elasipodids.

ring on the external side of the ring. Madreporite is situated at the end of the long stone canal far from the ambulacral ring. Ciliated funnels present. From one to many Polian vesicles. Five pairs of statocysts located at the place where radial nerves extend from the neural ring. Ossicles: chiridotid wheels and/or sygmoids or anchors and anchor plates. Wheels of larvae and juveniles with flat hub, large number of spokes and small denticles on the inner side of the rim.

Wheels similar to the larval wheels of extant Synaptidae are recorded from the Middle Triassic (Gilliland, 1992; 1993).

References: Heding (1928, 1929).

Suborder contains two families: Chiridotidae and Synaptidae.

Family Chiridotidae Östergren, 1898

Synaptina with 10, 12 or 18 peltato-digitate, pinnate, or secondarily simple tentacles with forked terminations. Ossicles: chiridotid wheels and/or sigmoids. Chiridotid wheels with six spokes, numerous small denticles on the inner rim and complex hub. The lower side of each spoke branches toward lower side of the egg-shaped hub to form a star-shaped structure in the centre. The tentacles and the body wall also contain rod-like ossicles with branching ends.

Typical chiridotid wheels (paragenera *Theelia, Jumaraina*, and *Palaeotrochodota*, parafamily Theeliidae) comparable with the wheels of the extant chiridotids are known beginning from the Middle Triassic (Smirnov, 1999).

References: Reich (2003b).

Family contains two subfamilies: Taeniogyrinae and Chiridotinae.

Subfamily Taeniogyrinae Al. Smirnov, 1898

Chiridotidae with 10 or 12 tentacles. Ossicles: chiridotid wheels and/or only sigmoids. Radial segments of calcareous ring lacking perforations for the nerve but sometimes with small notch on anterior (upper) surface.

Subfamily Chiridotinae Östergren, 1898, sensu Al. Smirnov, 1998

Chiridotidae with 12 or 18 tentacles. Ossicles: chiridotid wheels, assembled in papillae and/or rods. Radial segments of calcareous ring with perforation or deep notch on upper side. 4–30 Polian vesicles.

Family Synaptidae (Burmeister, 1837), sensu Östergren, 1898

Synaptina with 10–27 pinnate, digitate or secondarily simple tentacles. Juveniles with simple tentacles. Inner side of tentacles with sensory cups. Ossicles: anchors and anchor plates. Two larval stages in the life cycle: planktotrophic larvae (auricularia) and non-feeding larvae (doliolaria).

The anchor *Calcancora sieboldi* (parafamily Calcancoridae), which cannot be correlated with any extant subfamily of Synaptidae is described from the Late Jurassic.

References: Frizzell and Exline (1957); Smirnov (1989), Reich (2003c).

Family includes four subfamilies: Rynkatorpinae, Leptosynaptinae, Synaptinae, and Rhabdomolginae.

Subfamily Rynkatorpinae Al. Smirnov, 1989

Synaptidae with 12 digitate tentacles with one or two pairs of terminal digits. Anchor plates develops from a rod which lies parallel to shank of developing anchor. Anchor plates with great number of holes or with small number of holes but with two large holes on both sides of the longitudinal axis of the plate. Articular part of plate with a bridge for articulating with keel of anchor spindle formed by fusion of several bars and raised over plate. Anchors with serrated arms, without minute knobs on vertex and without constriction of shank anterior to the stock.

The subfamily includes anchor-plates of the paragenus *Rigaudites* (parafamily Synaptitidae). The first anchor-plate unequivocally belonging to subfamily Rynkatorpinae appears in the Upper Jurassic. Almost all sclerites of the genus *Rigaudites* can be assigned to the extant genus *Protankyra*. The anchors *Calcancora mississippiensis, Calcancora* sp. Bertels, 1965, and *C. ahmadi* (parafamily Calcancoridae) can be assigned to the same genus. *Rigaudites punctatus* and *Calcancora michaeli* from the Early Cretaceous (Albian) of northern Germany can be assigned to the extant genus *Rynkatorpa* (Smirnov, 1989).

Subfamily Leptosynaptinae Al. Smirnov, 1989

Synaptidae with 10, 11 or 12 pinnate tentacles, with 4–9 digits on either side. Digits increase in size from the base to the top of tentacles. Anchor plates develop from a rod that lies at a right angle to longitudinal axis of developing anchor shank. Anchor plates with a few holes; usually with 7 (6+1) holes in main part of plate: six holes encircle the central one. Articular end of plate usually with a ledge for articulation with the keel of anchor. Anchor arms serrated, rarely naked, and without minute knobs on vertex. Shank with noticeable constriction anterior to the stock.

The subfamily includes anchor-plates of the paragenus *Synaptites* (parafamily Synaptitidae) and anchors *Calcancora gallica* and *C. arduohamata* (parafamily Calcancoridae), and recently described sclerites (anchor-plates *Rigaudites nudus* + anchor *Calcancora pomerania*) from Upper Cretaceous (Maastrichtian) of the Isle of Rügen, NE Germany (Reich, 2003c). The first anchor-plate unequivocally belonging to the subfamily Leptosynaptinae appears in the Upper Cretaceous (Smirnov, 1989, 1999; Reich, 2003c).

Subfamily Synaptinae Burmeister, 1837, sensu Al. Smirnov, 1989

Synaptidae with 10–25 pinnate tentacles with 5–40 (usually 10–40) digits on either side. Digits near middle of tentacle are longest. Anchor plates develops from rod which lies at a right angle to shank of developing anchor. Anchor plates (except in the genus Synapta) with 7 (6 + 1) holes in the main part of the plate: six holes encircling the central one. Articular end of plate usually has a bridge, formed by single crossbeam, for articulation with the keel of the anchor shank. In the genus *Synapta,* anchor plates large with many (up to 100 and more) smooth holes. Anchors with naked arms but with minute knobs on vertex.

The subfamily contains the anchor-plates of the paragenus *Croneisites* (parafamily Synaptitidae) and the anchors *Calcancoroidea spandeli* (parafamily Calcancoridae). The first anchor-plate unequivocally belonging to subfamily Synaptinae appears in the Eocene (Smirnov, 1989, 1999).

The subfamily includes two tribes: Synaptini and Euaptini.

Tribe Synaptini Burmeister, 1837 sensu Al. Smirnov, 1989

Synaptinae with anchor plates with numerous (about 100 and more) smooth perforations (genus *Synapta*), or with seven (6 + 1) holes in the main part of the anchor plate with denticles along the circumference of the hole. Denticles on the upper and lower side of the plate are situated only along half the hole circumference, but on the opposite sides of the hole. As a result, the denticles completely surround the hole. Articular part of the anchor plate not separated from the main part of the plate by constriction. Anchors with unbranched stock. Cartilaginous ring well developed and perforated in the lower part.

Type genus *Synapta* Eschscholtz, 1829.

The tribe includes four genera: *Synapta, Synaptula, Pendekaplectana*, and *Polyplectana*.

Remarks. The genus *Synapta* is distinguished from the rest of the genera of the tribe by large anchor plates with numerous smooth perforations. However, Heding (1929) described in *S. oceanica* anchor plates with 7 holes in the main part of the plate typical for other genera of Sinaptini.

Tribe Euaptini Al. Smirnov, 1989

Synaptinae with denticles of upper side of the plate situated along entire the hole circumference whereas denticles on the lower side of the plate are situated only along half the hole circumference. Articular end of anchor plate separated from the main part of the plate by constriction or shaped as short quadrangular handle. Anchors with branched stock. Cartilaginous ring either absent, or perforated in the upper part.

Type genus *Euapta* Östergren, 1898 sensu Fischer, 1907.

The tribe includes 2 genera: *Euapta* and *Opheodesoma.*

Subfamily Rhabdomolginae Al. Smirnov, 1989

Synaptidae with 10 simple tentacles with sensory cups. Segments of calcareous ring simple, slightly narrowed in the middle part, without anterior projections; radial segments not perforated or notched for passage of nerves. No ossicles in the skin and tentacles. Tentacular nerves envelope the tentacular ambulacral canal. The ring canal is connected to the Polian vessel. Gonad unpaired.

Type genus *Rhabdomolgus* Keferstein, 1862.

References: Keferstein (1862), Becher (1907), Menker (1970), Smirnov (1989).

SUBCLASS ELPIDIACEA SUBCLASS NOV.

Holothuroidea with distinct bilateral symmetry and well-developed ventral sole (excluding planktonic family Pelagothuriidae). Tentacles shield-shaped. Radial canals developed. Tube-feet and papillae (modified tube-feet) present. In some taxa ventro-lateral tube-feet and dorsal papillae can fused to form a brim and specialized swimming lobes. Ventral tube-feet often enlarged and modified into the walking feet. Ambulacral appendages of some elasipodids of the families Elpidiidae and Laetmogonidae with strongly expanded ampullae. Canals of tentacles extending from radial canals. Radial hemal canals present. Stone canals with madreporite usually attached to body wall and often opens externally. Ring muscles interrupted by radial muscles. Radial muscle bands undivided. Mesentery, suspending posterior loop of intestine, attached to body wall anteriorly and medially in right dorsal interradius. Respiratory trees absent. Calcareous ring poorly calcified, sometimes consists of strong connective tissue; in some taxa decreases with age or absent. Ossicles: laetmogonid wheels (Laetmogonidae and some Elpidiidae), cross-like psychropotid crosses (Elpidiidae and Psychropotidae) and rods and ossicles derived from them. Laetmogonid wheels concave-convex, smooth rim (in the genus *Pannychia*, rim with large facing inward 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. Cross-like psychropotid sclerites with one (in the center of the cross), four (on each ray), or five (in the center of the cross and rays) vertical processes. In the family Pelagothuriidae ossicles and calcareous ring are absent.

Sclerites, resembling extant psychropotid ossicles, assigned to the parafamilies Stichopotidae (paragenera *Tetravirga* and *Praeeuphronides*) and Palelpidiidae (paragenus *Parelpidia*) are known from the Triassic and Jurassic (Gilliland, 1993). Sclerites resembling laetmogonid wheels (parafamily Palaeocaudinidae Boczarowski, 1997), are knowing beginning from the Middle Devonian (Boczarowski, 1997; 2001). If Boczarowski is correct in his hypothesis that sclerites of the genus *Paleocaudina* were ancestral to the extant Laetmogonidae and Elpidiidae, it can be suggested that the elaposidid clade could have appeared in the Middle Devonian.

The subclass includes one order Elasipodida.

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

Diagnosis: As for the subclass.

Order includes four families:[13] Laetmogonidae, Elpidiidae, Psychropotidae and Pelagothuriidae.

References: Théel (1882), Ekman (1926), Hansen (1975), Gebruk (1988; 1989a; 1995), Gebruk, Tyler, and Billett (1997).

Remarks. The order Elasipodaida is heterogeneous and difficult to characterize. However, its families are united by a number of characters. Laetmogonid wheels typical of the family Laetmogonidae also sporadically occur in Elpidiidae, which suggested that these families are related (Ekman, 1926). Elpidiidae and Psychropotidae are similar in having psychropotid cross-like ossicles. Gebruk (1990b) showed that the planktonic family Pelagothuriidae was related to the family Psychropotidae.

The attachment of the mesentery of the second descending loop of intestine in the right dorsal interradius was the single apomorphy distinguishing the order Elasipoda. Now, when the family Deimatidae has been excluded from Elasipodida and included into Aspidochirotida, it is clear that this character could have arisen independently in different families. It is possible to talk about some general trends in different families of Elasipodida, related to a similar life style. For instance, the decreased number of ventral tube-feet and their larger size could be related to the transition to walking motion on the substrate, which could lead to the development of expanded ampullae and intradermal ambulacral cavities. The transition to a bathypelagic life style was accompanied by the merging of the tube-feet and papillae and the development of different swimming lobes. However, these trends, as well as the reduction of the calcareous rings in various families, cannot be sufficient evidence that the order is a monophyletic taxon.

Authors of the early 1900s suggested that some families of elasipodids are connected with different members of the polyphyletic family Synallactidae (order Aspidochirotida). Perrier (1902, p. 433) considered that psychropotids, deimatids and elpidiids could have evolved independently from synallactids. Östergren (1907) thought that the family Psychropotidae was related to synallactids (to be exact, with the genera *Paelopatides, Synallactes*, and *Bathyplotes*). He considered synallactids as elasipodids, which developed the respiratory trees and placed Synallactidae in the order Elasipoda.

The families now assigned to the order Elasipodida were located in different parts of Becher's tree. Elpiidiidae and Deimatidae (=Laetmogonidae) are branched off from the base of the holothurian tree, whereas Psychropotidae are placed among lunged holothurians. Becher treated psychropotid cross-shaped sclerites as related to synallactids tables. He considered the respiratory trees to be secondarily lost in the family Psychropotidae and thought psychropotids to be related to the genus *Benthothuria* from the family Synallactidae. In my opinion, and contrary to Becher's, it is incorrect to relate the typical psychropotid cross-shaped sclerites (with monolith vertical processes) to the table sclerites of synallactids (with the spire formed by several vertical pillars connected by transverse bars). The external similarity of the genera *Benthodytes* (family Psychropotidae, order Elasipodida) and *Benthothuria* (family Synallactidae, order Aspidochirotida) is convergent.

Hansen (1975) subdivided the order Elasipodida into two suborders: (1) Deimatina with the families Laetmogonidae and Deimatidae and (2) Psychropotina with the families Elpidiidae, Psychropotidae, and Pelagothuriidae. Hansen considered that the suborder Psychropotina comprised the families Elpidiidae, Psychropotidae, and Pelagoturiidae, which are related to each other (see above). The suborder Deimatina, in my view, is polyphyletic, because there are no characters shared by the families Deimatidae and Laetmogonidae.

The family Deimatidae is very different from other families of the order Elasipodida and in a number of characters is similar to the family Synallactidae and assigned to the order Aspidochirotida. In the present paper I consider Elasipodida as a monophyletic taxon.

Family Laetmogonidae Ekman, 1926

Bilaterally symmetrical Elasipodida with 15–20 tentacles. Medioventral feet may be present or absent. Ossicles: laetmogonid wheels and variously shaped rods. Gonad formed by slender and branched tubules, arranged in several clusters.

Remarks: Ludwig (1894) noted that the family Deimatidae Théel, 1882 can be readily subdivided into two distinct groups based on the presence or absence of lateral papillae. Ekman (1926) separated a new family Laetmogonidae from Deimatidae sensu Théel, 1882.

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[13] I excluded the family Deimatidae Théel, 1882, sensu Ekman, 1926 from the Elasipodida and included it into Aspidochirotida (see below).

Laetmogonidae is characterized not only by the absence of lateral papillae, but also by wheels ossicles. He also noted that, based on wheels ossicles, Laetmogonidae are closer to Elpidiidae than to Deimatidae.

Family Elpidiidae Théel, 1882

Bilaterally symmetrical Elasipodida with 10–12 tentacles. Ventrolateral tube-feet large, widely spaced and usually non numerous. Midventral feet absent. Dorsal processes represented by papillae. In some taxa anterior and posterior dorsal papillae are fused to form a velum (anterior dorsal lobe) or posterior swimming lobe. There are two pairs of statocysts at the bases of lateroventral radial nerves. Calcareous ring of only five radial segments, arranged in a regular pentagon. Each segment represented by a star-shaped structure formed by two radiating bunches of long narrow rod-like processes. Ossicles: laetmogonid wheels; cross-shaped psychropotid ossicles, dichothomically branched rods possessing a small tubercle on each ray, rod-like ossicles, three-ray ossicles, "Elpidia"-rod-like ossicles with two pairs of horizontal and one pair of vertical processes, C-like ossicles. The lower region of the large expandable rectum of many elpidiids with a blind process (caecum). Gonad mostly unpaired, with the left part apparently present.

Family includes two subfamilies: Peniagoninae and Elpidiinae.

References: Théel (1877; 1879; 1882), Gebruk (1990a; 1994), Rogacheva (2007).

Subfamily Peniagoninae Ekman, 1926

Elpidiidae with a number of processes in the bunches of segments of calcareous ring, usually more than six on each side. Ossicles: cross-like psychropotid ossicles, dichotomously branched rods, three-ray ossicles. Rectum without caecum.

Subfamily Elpidiinae Théel, 1882, sensu Ekman, 1926

Elpidiidae with 4, less commonly 5–6 processes in the bunches of calcareous ring segments on either side. Ossicles: rods, three-ray ossicles, "Elpidia"-type ossicles, C-shaped ossicles. Rectum usually with ventral caecum.

Family Psychropotidae Théel, 1882

Bilaterally symmetrical Elasipodida with 10–18 tentacles. Sole surrounded by brim formed by fused tube-feet. Medioventral tube-feet present. In specialized forms the fused dorsal papillae transformed to sail. Calcareous ring represented by diffuse network of dense connective tissue or absent. Ossicles: psychropotid crosses and rod-like ossicles. Gonad paired.

Family Pelagothuriidae Ludwig, 1894
(=ordo Nectothuria Haeckel, 1886; ordo Pelagothuriida MacBride, 1960; ordo Pelagothurioidea Heding, 1950)

Elasipodida with 13–16 or 19–20 tentacles. Swimming holothurians. Body wall thin or gelatinous. Processes of ambulacral system represented by rudimentary anterior papillae on dorsal radii and feet on ventrolateral radii (the latter can be absent); medioventral ambulacral processes absent. Anterior swimming lobe embracing body dorsally (genus *Enypniastes*), or surrounding it entirely and fused ventrally (genus *Pelagothuria*). Posteriorly, two swimming lobes (merged tube-feet), along lateroventral interradii (genus *Enypniastes*) may be present. Tentacle ampullae extends from ambulacral ring rather than from radial canals. Mouth and anus terminal (genus *Pelagothuria*), or mouth slightly shifted ventrally, and anus shifted dorsally (genus *Enypniastes*). Polian vesicles absent. Gonad paired, cluster-like in females and consists of small tubules in males.

The family contains two genera: *Pelagothuria* Ludwig, 1894 and *Enypneastes* Théel, 1882.

Remarks. The family was established by Ludwig (1894) for new genus and species *Pelagothuria natatrix*. Haeckel (1896) recognized this family as a separate order Nectothuriae. The second genus in the family – *Enypniastes* was described somewhat earlier by Théel (1882) in the family Elpidiidae, but Théel (1882, p. 11) suggested that *Enypneastes* has a "a closer alliance with the family Psychropotidae." Östergren (1907) suggested that this genus could be recognized as a separate family Enypniastidae and noted that the anterior swimming lobe of *Enypneastes* could be homologous to circumoral papillae of psychropotids. Heding (1950) recognized planktonic and pelagic holothurians as a separate order Pelagothuroidea, to which he assigned the family Pelagothuriidae with the genus *Pelagothuria* and the family Planktothuriidae, which he established to accommodate the genus *Enypniastes* Théel, 1882. However, later authors suggested that Pelagothuriidae should be considered as a family in the order Elasipodida. Billett, Hansen, and Huggett (1985) noted the relationship between Pelagothuriidae and the families Psychropotidae and Elpidiidae, whereas Gebruk (1990b) substantiated the relationship of Pelagothuriidae with Psychropotidae and the origin of the swimming lobe of Pelagothuriidae from the anterior portion of the lateral brim of psychropotids.

References: Théel (1882); Ludwig (1894); Heding (1950), Billett, Hansen, and Huggett (1985); Gebruk (1989b; 1990b).

SUBCLASS HOLOTHURIACEA SUBCLASS NOV.

Variously shaped Holothuroidea. Tentacles shield-shape, dendritic, digitate, secondarily simple. Radial canals present; ambulacral processes represented by tube-feet, papillae (modified tube-feet), and anal papillae. Tentacles canals extending from radial canals. Radial hemal canals present. Statocysts absent. Ring muscles interrupted by radial muscle bands. Radial muscle bands undivided or subdivided into two. Mesentery suspending posterior loop of intestine, anteriorly and medially attached to body wall in right ventral interradius or medioventrally, and in the family Deimatidae in right dorsal interradius. Respiratory trees present or secondarily absent (family Deimatidae, order Aspidochirotida). Calcareous ring usually calcified and well-developed. The main type of ossicles in the subclass is tables and ossicles derived from them. At the table base there is a perforated plate, its central part with four (rarely three or two) processes (pillars). The pillars are located around one or more central openings, or next to each other without holes in between. The pillars can be parallel or oblique each other and in the latter case their upper apices may merge. Sometimes the pillars can be fused almost along their entire length. In some tables the pillars can be connected by transverse beams. The plate located at the base of a table is called a disk, while the group of pillars and cross beams above the disk is called a spire.[14] The disc of tables sometimes have a form of three or four rayed plate, with expanded and perforated ray terminations. Other types of ossicles are: plates, baskets, rods and many other kinds. Wheels absent. In the order Gephyrothuriida ossicles absent.

Sclerites similar to the tables of the extant Holothuriacea, and those not found in the extant holothurians belong to the parafamily Priscopedatidae. Table-like sclerites *Tetravirga* n. sp. from the Upper Permian (Mostler and Rahimi-Yazd, 1976) are somewhat similar to tables of the extant family Synallactidae. Tables, similar to those of the extant form, but not assigned to any of the extant orders, first appear in the Middle Triassic (Gilliland, 1993).[15]

Sclerites *Tribrachiodemas ordovicus* Reich, 2010 from the Upper Ordovician of Gotland, Sweden are very similar to tables of the extant holothurian genera Synallactes and Bathyplotes from the family Synallactidae (Reich, 2010b) (see Footnote 4).

The subclass includes four orders: Aspidochirotida, Dendrochirotida, Molpadiida, and Gephyrothuriida.

Remarks. As noted above, Mueller (1850a; 1850b), Selenka (1867) and Semper (1868) united holothurians with respiratory trees in one taxon opposed to holothurians, in which the respiratory trees were absent. Later lung holothurians were distinctly separated in phylogenetic reconstructions either as one branch (Östergren, 1907; Becher, 1909), or groups of similar branches (Cuénot, 1948), or as a separate clade (Kerr and Kim, 2001). The subclass is well recognized by two characters: respiratory trees (secondary absent in Deimatidae) and table ossicles. In some taxa tables are apparently secondarily absent.

There are a number of various interpretations of the relationships between the orders in the subclass Holothuriacea. Ludwig (1891; 1889–1892) assigned molpadiids to Dendrochirote-branch. In Ludwig's opinion the nearness of molpadiids and dendrochirotids is indicated by the presence of anterior retractor muscles in some molpadiids; presence of processes of the calcareous ring; a similar symmetry of the calcareous ring in most molpadiids and some dendrochirotids; similarity in the morphology of the stone canal. However all these characters could appear independently. Clark (1910) supported the idea of closeness of Molpadiida and Dendrochirotida. Pawson (1982) although assigning Molpadiida to the subclass Apodacea, noted that "Molpadiids show many similarities to dendrochirotids" (p. 817). On the cladogram of the class proposed by Kerr and Kim (2001) molpadiids are a sister group of dendrochirotids.

Östergren (1907) considered molpadiids as being near to aspidochirotids (the latter in Östergren's classification included only the families Stichopodidae and Holothuriidae). In his opinion, these two groups show the presence of free hanging tentacular ampullae and paired muscle strips. Östergren's view was supported by Smirnov (1984). Now I believe that these characters are very likely to have appeared independently.

In my opinion there is one morphological character allowing the assumption of the close relationship between the orders Dendrochirotida and Molpadiida as opposed to the order Aspidochirotida. In the development of holothurians, five primary tentacles later contact with particular radial ambulacral canals. In Dendrochirotida and Molpadiida two primary tentacles are connected with the medioventral radial canal, two with the left dorsal and one with the right dorsal canal (Runnström and Runnström 1919; Runnström, 1927; Inaba, 1930). A similar topography of the arrangement of the primary tentacles is displayed by Synaptida which are secondary lack of radial ambulacral canals (Runnström, 1927). In the order Aspidochirotida two primary tentacles are also connected with the medioventral radial canal, while only one primary tentacle is connected with the left dorsal canal and one tentacle is connected with the left and one with the right ventral radial canal (Edwards, 1909; Runnström, 1927) (Fig. 8).

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[14] Unfortunately there is no detailed description or classification of various types of tables, what makes the use of this morphotype of sclerites difficult for taxonomy. Soodan (1975) attempted the classification of the towers and proposed a system of the parafamily Priscopedatidae, to which he assigned fossil turriform sclerites, based on the morphology of the disc. Apparently, different types of tables appeared and developed independently in different branches (Gilliland, 1993). Nevertheless, it is likely that the ability to develop a spire from several closely spaced 2–4 pillars is typical of all lung holothurians.

[15] *Priscopedatus quinquespinosus* Mostler et Rahimi-Yazd, 1976, from the Upper Permian of northern Iran cannot be considered as a true tower.

Order Aspidochirotida Grube, 1840
[nom. transl. Pawson et Fell, 1965
(ex. Aspidochiroten Grube, 1840)]

Holothuriacea with 10–30 shield-shaped tentacles (genera *Dendrothuria, Scothothuria, Pseudothuria*, and the subgenera *Semperothuria* and *Selenkothuria* of the genus *Holothuria* with dendritiform tentacles). Bilateral symmetry pronounced because of differentiation of bivium and trivium and mouth opening, subventral or ventral. Dorsal feet often modified into papillae. Two primary tentacles connected with medioventral radial canal, one primary tentacle with left dorsal canal, one tentacle is connected with left and one with right ventral radial canal. Stone canal opening into body cavity. Introvert and retractor muscles not developed. Respiratory trees present or secondarily absent (family Deimatidae). *Rete mirabile* of hemal system well-developed (families Stichopodidae and Holothuriidae) and sometimes connected with left branch of the respiratory tree. Mesentery, suspending posterior loop of intestine, anteriorly and medially attached to body wall in right ventral interradius or right dorsal interradius (family Deimatidae). Calcareous ring consists of 10 segments. Radial and interradial segments differ in shape and size. Radial segments usually much larger than interradial, their upper edge can be relatively flat or wavy, but a deep notch for the nerve is in the middle of the segment. Upper margin of interradial segments triangular, with slightly projecting apix. Ossicles: tables, plates, rods, C-shaped bodies, buttons (plate-shaped ossicles with smooth or wavy edge with a few perforations arranged in two parallel rows). Detritophagous with rare exceptions.

The order includes five families: Synallactidae, Stichopodidae, Holothuriidae, Mesothuriidae, and Deimatidae.

Bathysynactites viai – imprint holothurians externally resembling the holothurian order Aspidochirotida, of which, unfortunately, no skeletal elements have remained, described from Muschelkalk, Middle Triassic, of Terragona, Spain (Cherbonnier, 1978). *Collbatothuria danieli* holothurian imprint externally similar to the holothurian order Aspidochirotida, the sclerites of which are not known, and calcareous ring resembling that of aspidochirotids described from the Middle Triassic (Ladinian) of Ciollbató, northen Spain (Smith and Gallemí, 1991).

The table-like sclerites *Tetravirga* n. sp. (Mostler and Rahimi-Yazd, 1976) are somewhat similar to sclerites of the family Synallactidae described from the Upper Permian. Sclerites, most similar to the tables of the extant synallactids (*Priscopedatus triassicus* group of the paragenus *Priscopedatus* and the paragenus *Stichopitella*, parafamily Priscopedatidae), are known beginning from the Middle Triassic (Mostler, 1969; 1972; 1977). Button-like sclerites (paragenus *Calclamna*, parafamily Calclamnidae), which are similar to the buttons of most Holothuriidae, some Stichopodidae and rarely found in Synallactidae known from the Late Jurassic (Gilland, 1993).

Remarks. The families Stichopodidae and Holothuriidae are closely related by most likely similarly original presence in the life cycle of two larval stages: planktotrophic auricularia larva and non-feeding doliolaria larva. These two families show presence of free-hanging tentacle ampullae, radial muscle bands longitudinally subdivided into two, and a well-developed *rete mirabile*. Östergren (1907) included these two families in the order Aspidochirota, and assigned the family Synallactidae to the order Elasipoda. Heding (1940) considered them as the subfamilies Stichopodinae and Holothuriinae in the families Holothuriidae, opposed to the family Synallactidae. However, it is quite possible that such characters as free tentacular ampullae, radial muscle bands longitudinally divided in two, and a well-developed *rete-mirabile* could have developed independently, whereas the life cycle with auricularia stages indicates a close relationship between the two families.

Morphology of the calcareous ring and sclerites in the family Deimatidae is more similar to that in aspidochirotids than in elasipodids. The molecular-phylogenetic data also indicate the similarity of these groups. It is possible that Deimatidae lacking respiratory trees and with all three mesenteria attached dorsally, most likely lost their respiratory trees and secondarily acquired dorsal attachment of mesenteria suspending the second descending loop of the intestine.

The family Synallactidae is most-likely a para- or polyphyletic group of the deep-sea aspidochirotids with respiratory trees. Sluiter (1901) noted that this family is artificial. Becher (1909), although considering synallactids as a natural group, has placed the genera constituent this family at different parts on the phylogenetic tree (Fig. 5). Recently the polyphyletic and paraphyletic nature of Synallactidae was noted by Kerr and Kim (2001) and Solís-Marín's (2003).

Family Synallactidae Ludwig, 1894

Aspidochirotida with 10–20 tentacles (suspension feeder members have secondarily dendritiform tentacles). Body cylindrical, or flattened with a distinct sole. The ambulacral dorsal appendages are usually in the shape of papillae. Gonad subdivided into two parts, lying to either side of mediodorsal mesentery. Free-hanging tentacle ampulae are absent. Radial muscle bands undivided. Stone canal attached to the body wall and sometimes opens externally. Calcareous ring can be well-developed, reduced, or altogether absent. Ossicles: tables, rods, sometimes C-shaped bodies, very rarely buttons.

Sclerites, similar to those of Synallactidae are known from the beginning of the Upper Permian and Middle Triassic (see above). The table-like sclerites similar to those of the genera *Synallactes* and *Bathy-*

plotes have recently been described from the Upper Ordovician (see Footnote 4).

References: Ludwig (1894), Östergren (1986), Koehler and Vaney (1905), Ekman (1926), Heding (1940), Imaoka (1978), O'Loughlin (2002), Solís-Marín (2003), Solís-Marín and Laguarda-Figueras (2004), O'Loughlin and Ahearn (2005).

Remarks. Solís-Marín (2003) revised the family and synonymized a number of genera, took nine genera and 1 species out of it and placed them in the group Incertae sedis. In his system the family Synallactidae included 10 genera. Even in such reduced composition, the family Synallactidae is probably not a monophyletic group. It includes such morphologically different genera as *Synallactes* on one hand, and *Pseudostichopus* on the other hand. Apart from morphological differences these two genera are very different in the structure of triterpene glycosides (Silchenko et al., 2002; 2004). Numerous studies showed, that the morphology of the triterpene glycosides could be used as good taxonomic characters, allowing the recognition of species, genera, and groups of related genera. In the order Aspidochirotida the glycosides are taxonomic markers for the groups of closely related species and genera (Stonik, Kalinin, and Avilov, 1999; Kalinin, Avilov, and Stonik, 2000; Kalinin et al., 2005). Recent studies of the genera *Synallactes* (the type genus of the family) and *Pseudostichopus* demonstrated that the structure of triterpene glicosides in these two genera is quite different; therefore *Pseudostichopus* must be removed from the family Synallactidae (Silchenko et. al., 2004; Kalinin et al., 2005). Apparently, this requires additional morphological, molecular-phylogenetic, and chemical studies, but it is quite possible that the family Synallactidae can be subdivided into two subfamilies or two genera groups: "Synallactinae" and "Pseudostichopodinae."

Family Deimatidae Théel, 1882, sensu Ekman, 1926

Aspidochirotida with 15–20 tentacles. The lateroventral ambulacral canals give rise to numerous tube-feet and well-developed lateral papillae, whereas dorsal ambulacral canals give rise to dorsal papillae. Papillae of constant shape because their sclerites arranged with their longitudinal axis, coincident with that of the papillae. No free-hanging tentacle ampullae present. Madreporite attached to body wall without penetrating it. Respiratory trees absent (secondarily). Radial muscle bands undivided. Gonad is subdivided in two parts, each composed of a few sacciform tubules, lying to either side of the mediodorsal mesentery. Calcareous ring slightly calcified. Ossicles: deimatid plates with many perforations (the size of the perforations decreasing from the center to periphery), cross-like plates with expanded and perforated terminations; spatula-shaped rods with perforated terminations, and rods with expanded ends.

Oneirophantites tarrogenensis is a holothurian imprint externally similar to the holothurian family Deimatidae, but unfortunately without sclerites preserved. It is described from the Muschelkalk, Middle Triassic, of Terragona, Spain (Cherbonnier, 1978).

Ludwig (1894), based on the presence or absence of the lateral papillae, subdivided the family Deimatidae Théel, 1882 into two distinct groups. Ekman (1926) recognized the family Laetmogonidae previously assigned to Deimatidae sensu Théel, 1882. Laetmogonidae are very different from Deimatidae *s. str.* and is actually nearer to Elpidiidae than to Deimatidae.

The family Deimatidae is very different from other families in the order Elasipodida, to which it was previously assigned. Morphology of ossicles, presence of lateral papillae, and orientation of ossicles in the lateral and dorsal papillae clearly distinguished deimatids from elasipodids. The longitudinal axis of ossicles in the papillae of Deimatidae is parallel to the longitudinal axis of the papillae, and in the families of elasipodids it is perpendicular to it. Plate-like ossicles, cross-like plates, and spatula-like perforated plates of deimatids are not found in the families of Elasipodida *s. str.* and are more similar to the plates of lung holothurians. Becher (1909, p. 445, fig. 8) indicated the similarity of the perforated plates *Oneirophanta alternata* (=*O. mutabilis mutabilis*) of deimatids and *Synallactes woodmasoni* (=*Amphigymnas multipes*) of synallactids. The morphology of the calcareous ring of deimatids is similar to that of synallactids and other aspidochirotids. The molecular-phylogenetic data (Solís-Marín, 2003) show that the species *Deima validum* of the family Deimatidae is similar to the species *Paroriza prouhoi* and *Benthothuria funebris* that have respiratory trees, what indicates the connection of Deimatidae with lung holothurians.

References: Théel (1882); Ekman (1926); Hansen (1975); Pawson (2002).

Family Stichopodidae Haeckel, 1896

Aspidochirotida with 18–20 tentacles. Body quadrangular or trapezoid. Large papillae on dorsal side. Free hanging tentacle ampullae present. In most Stichopodidae stone canal hangs free into body cavity. *Rete mirabile* well developed. Radial muscles subdivided into two bands. The gonad is subdivided in two parts, each composed of tubules, lying on either side to the mediodorsal mesentery. Calcareous ring well developed. Ossicles: tables, branched rods, C- and S-shaped bodies.

References: Clark (1922), Massin et al. (2002), Byrne, Rowe, and Uthicke (2010).

Family Holothuriidae Burmeister, 1837
[ex. Holothuridae Burmeister, 1837]

Aspidochirotida with up to 30 tentacles. Body more or less cylindrical, sometimes with flattened ventral side. Dorsal side with numerous papillae. Free hanging tentacle ampullae present. Stone canal freely hangs into the body cavity. *Rete mirabile* well developed. Radial muscles subdivided into two bands. The gonad is unpaired and composed of one tuft of tubules to the left of the mediodorsal mesentery. Calcareous ring well developed. Ossicles: tables, buttons, rods, rosettes (sometimes only rods present). Many Holothuriidae have Cuvierian organs peculiar to this family only. They represent tubular or filamentous structures, attached to base of respiratory trees, and in some species could occasionally be ejected through cloaca or tear in body wall.

References: Pearson (1913; 1914a; 1914b), Panning (1929; 1934a; 1934b; 1935a; 1935b, 1935c), Deichmann (1958), Rowe (1969), Massin, Mercier, and Hamel (2000), Appeltans (2002), Samyn, Massin (2003), Massin, Samin, and Thandar (2004), Samyn, Appeltans, and Kerr (2005).

Family Mesothuriidae fam. nov.

Aspidochirotida with 20 (13–22) tentacles. Body elongated, rounded or flattened. Tube-feet runs along entire ventral side (genus *Mesothuria*) or only along ventral ambulacra (genus *Zygothuria*). Papillae more or less evenly spread on dorsal surface. No free-hanging tentacle ampullae present. Stone canal attached to the body wall without penetrating it. *Rete mirabile* not developed. Radial muscle bands undivided. The gonad in a single tuft of tubules to the left of the mediodorsal mesentery. Calcareous ring well developed. Ossicles: tables with large laced disc perforated with large holes. Spire is composed of three or four pillars surrounding the central hole.

Type genus *Mesothuria* Ludwig, 1894

This family is distinguished from the families Holothuriidae and Stichopodidae by the absence of free hanging tentacle ampullae, non devided radial muscle bands, madreporite attached to body wall, and not developed *rete mirabile*. It differs from the families Stichopodidae and Synallactidae by a reduced gonad (developed only its part left). It is distinguished from all the families of the order by tables with a laced disc with large holes.

Remarks: Solís-Marín's (2003) morphology-based cladistic analysis of the family Synallactidae indicates that the genera *Mezothuria* and *Zygothuria* are opposite to the remainder of Synallactidae (Solís-Marín, 2003, fig. 6.2). Analysis of molecular data produces a similar result (Solís-Marín, 2003, figs. 6.4, 6.6). Solís-Marín suggested that the family should be divided into two: Synallactidae (*s. str.*), including the genera with a paired gonad, and "Mesothuriidae", including the genera with an unpaired gonad. He further suggested that Synallactidae *s. str.* could have evolved from the family Stichopodidae, whereas "Mesothuriidae" could have evolved from the family Holothuriidae. Both lineages are independently lost free-hanging tentacle ampullae. Over 100 years ago a similar hypothesis was put forward by Sluiter: "*Wenn wir aber eine derartige polyphyletische Abstammung dieser Tiefsee-Formen annehmen, so ist selbstverständlich eine naturliche Gruppe der Synallactinae nicht aufrecht zu halten. Sehr schwierig ist allerdings die Lösung der Frage, wo diese Formen dann einzureihen sind und Gewissheit hieruber wird uns wahrscheinlich wohl fur immer versagt bleiben. Im Allgemeinen scheint mir eine Ableitung der Gattungen: Bathyplotes, Paelopatides, Pseudostichopus, Synallactes und Meseres von fruheren Stichopus-Arten am wahrscheinlichsten, da sie mit dieser Gattung sowohl den ganzen Habitus als auch die 2 Buschel von Gonaden gemein haben. Andrerseits wäre vielleicht Mesothuria eher von einer Holothuria-Art abzuleiten.*" (Sluiter, 1901, p. 4). Becher also connected the genera *Mesothuria* and *Zygothuria* with Holothuriidae, but considered the two genera not as secondarily simplified, but as ancestral for Holothuriidae. In his tree he placed them at the base of the stem of Holothuriidae (Fig. 5). In his opinion, development of tentacular ampullae as well as the accelerated development of the respiratory trees and the development of the *rete mirabile* in Holothuriidae and Stichopodidae were independent (Becher, 1909, pp. 462–463).

In my opinion, regardless of whether the genera *Mesothuria* and *Zygothuria* are ancestral for Holothuriidae or derived, the arguments of Sluiter (1901), Becher (1909) and, particularly, Solís-Marín (2003) indicate that *Mesohuria* and *Zygothuria* are very distinct and can be classified as a separate family Mesothuriidae.

References: Ludwig, 1894; Perrier, 1902; Heding, 1940; Solís-Marín, 2003.

Order Dendrochirotida Grube, 1840
[nom. transl. Pawson et Fell, 1965
(ex. Dendrochiroten Grube, 1840)]

Holothuriacea with 10–30 dendritic tentacles (families Ypsilothuriidae and Rhopalodinidae and some genera with secondarily modified simple tentacles, sometimes with rudimentary branches). Body wall thick and dense. In some taxa, body completely or partially covered with plates forming test which gives body more or less permanent shape. Body from cylindrical to U-like and barrel-like (family Rhopalodinidae) shape. Bilateral symmetry not very prominent, although there is some difference in the number and morphology of feet on the ventral and dorsal surfaces. Tube-feet arranged along radii or scattered over the entire body of holothurians. Dorsal feet not modified into papillae. Introvert (retractile anterior part that can be pulled down into the pharynx by the contraction of the five retractor muscules attached to the radial segments of the calcareous ring) present. Two primary tentacles connected with medioventral radial canal, two—with left dorsal and one—with right dorsal canal. Stone canal with madreporite freely hangs into body cavity. Respiratory trees present. *Rete mirabile* of hemal systems weakly developed and not connected with left branch of the respiratory tree. Mesentery suspending posterior loop of intestine, attached to body wall anteriorly and medially in right ventral interradius near medioventral muscle band or medioventrally. Radial muscle bands undivided. Development without auricularian stage. Calcareous ring consists of 10 segments. Radial segments larger than interradial. Ring segments usually higher than wide. In many dendrochirotids segments are arrow-tip shape. Radial segments on anterior margin have notch for a nerve. In many dendrochirotids, radial segments have posterior projections or processes. Processes can be entire or broken into pieces. Sometimes ring segments also fragmented to produce mosaic pattern. Ossicles: tables, perforated plates, baskets, cups, rods, etc. Suspension-feeders catching prey from surrounding water by branched dendritic tentacles or detritus-feeders feeding on sediment and possessing secondarily simplified tentacles.

Unfortunately, because tables, perforated plates and other kinds of ossicles occurring in dendrochirotids are also found in other holothurian orders, whereas plates can also be found among other classes of Echinodermata, it is very difficult to establish which sclerites belonged to dendrochiroids. It is likely that button shaped and plate-shaped sclerites (paragenus *Binoculites*, parafamily Calclamnidae) from the Middle Triassic (Gilliland, 1992; 1993), e.g., *Binoculites terquemi* Deflandre-Rigaud, 1952 belong to Dendrochirotida although it is possible that they could belong to the order Aspidochirotida.

The order includes 14 extant families: Cladolabidae, Phyllophoridae, Rhopalodinidae, Sclerothyonidae, Sclerodactylidae, Placothuriidae, Thyonidae, Cucumariidae, Psolidae, Ypsilothuriidae, Paracucumidae, Heterothyonidae, Thyonidiidae, and Cucumellidae, and the extinct family Monilipsolidae.

References: Panning (1949), Heding and Panning (1954), Pawson and Fell (1965), Pawson (1970).

Remarks. Semper (1868) subdivided the family Dendrochirotae into three subfamilies: (1) Stichopoda, in which tube-feet are arranged along radii; (2) Gastropoda, in which tube-feet are arranged only on a strictly limited ventral side, and tube-feet are absent on the dorsal surface; (3) Sporadipoda, in which tube-feet scattered over the entire body of holothurians. This system was accepted by Théel (1886). Théel placed the genus *Rhopalodina* in a separate family Rhopalodinidae. In Östergren's (1907) system, the order Dendrochirota was subdivided into two families, Cucumariidae and Rhapolodinidae. The family Cucumariidae was subdivided into three 3 subfamilies: Psolinae, holothurians with a prominent sole, Cucumariinae, holothurians with ten tentacles, and Polyphorinae with many tentacles. The modern system of the order is based on the works of Panning (Panning, 1949; Heding and Panning, 1954). Panning traditionally subdivided the order Dendrochirota into three families: Psolidae, which he did not study, Cucumariidae with 10 tentacles, and Phyllophoridae with more than 10 tentacles. Panning based his subdivision of the family Cucumariidae and Phyllophoridae into subfamilies on the calcareous ring morphology. He subdivided the subfamilies into genera mainly based on ossicles and their combinations. According to Panning, the evolution of these families was parallel, and each subfamily of Cucumariidae corresponded to a subfamily within Phyllophoridae, with a similar morphology of the calcareous ring (Panning, 1949, p. 407). Pawson and Fell (1965) continued working on the systems of dendrochirotids. They rejected using the number of tentacles as one of the major characters and logically complete Panning's system, by using a characters suggested by Panning, i.e., calcareous ring morphology, as one of the major characters for the system. The composition of the two main large families of dendrochirotids, Cucumariidae and Phyllophoridae, was changed based on this character. The subfamily Thyoninae, that includes holothurians with 10 tentacles, but with a mosaic calcareous ring, was transferred from Cucumariidae to Phyllophoridae, while the subfamily Thyonidiinae, with numerous tentacles, but with a simple undivided calcareous ring, similar to that of Cucumariinae, they transferred from Phyllophoridae to Cucumariidae. They considered the subfamily Sclerodactylinae, previously included in the Cucumariidae, as a family and included in it the subfamily Cladolabinae, previously classified in the Phyllophoridae. Apart from the morphology of the calcareous ring, Pawson and Fell considered the presence of a test and simple digitate tentacles to be very important characters. In my opinion, these characters originated repeatedly in various branches of the order (see the above discussion on the significance of these characters in the systematics of dendrochirotids). Pawson and Fell recognized the new families Placothuriidae and Paracucumidae within dendrochirotids. The families Ypsilothuriidae, Rhopalodinidae, and the new family Vaneyellidae, these authors united in the new order Dactylochitrotida. Later Pawson (1970) recognized one more family, Heterothyonidae within the Dendrochirotida.

In my opinion, the order Dactylochirotida is polyphyletic and should be abolished, whereas the families, previously assigned to it, should be included in the order Dendrochirotida (see above). The composition of many families in the Dendrochirotida should be revised, as well as the system of the order itself.

Family Cladolabidae (Heding et Panning, 1954), status nov.

Dendrochirotida with 15–20 tentacles, arranged in two or three circles (10 + 5, 10 + 10, 10 + 5 + 5). Tube-feet arranged along radii or scattered over entire body. Segments of calcareous ring entire, high, not subdivided into pieces, radial segments with forked processes. Processes medium sized or short, entire or subdivided into a few pieces. In the latter case the processes are usually very short. Sometimes short forked processes also developed on interradial segments. Ossicles: tables with two pillars (disc of the tables with a few perforations, sometimes the disc is reduced and the table acquires a rod-like appearance), simple, convex, cross-like, spined plates, and rosettes.

References: Heding and Panning (1954), Thandar (1989).

Remarks. Heding and Panning (1954) assigned their new family to the multitentacular phyllophorids. Pawson and Fell (1965) considered cladolabids as a subfamily within the family Sclerodactylidae. Cladolabidae are distinguished from the families Sclerothyonidae and Sclerodactylidae by relatively short and usually entire, forked processes of radial segments. Based on the sclerite morphology, the genera placed in the family are very different from each other, and it is quite possible that the family is polyphyletic.

Family Phyllophoridae (Ostergren, 1907), sensu nov.

Dendrochirotida with 15, 20 or 25 (usually 20) tentacles arranged in two or three circles (10 + 5 or 10 + 5 + 5). Tube-feet usually scattered over the entire body of holothurians. Segments of the calcareous ring are medium-high, entire or, sometimes, in the lower part of the radial segments subdivided into several large pieces; radial segments with forked processes subdivided into a few large pieces; the length of processes greater than height of ring. Ossicles: tables with 4 pillars and their derivatives, sometimes rosettes present.

References: Heding and Panning (1954), Thandar (1990).

Remarks. The family was established by Östergren (1907) as a subfamily within the family Cucumariidae and united multitentacled taxa. Heding and Panning (1954) subdivided it into several subfamilies and in their system, the type subfamily Phyllophorinae was a compact, clearly delineated group. Pawson and Fell (1965), based on the similarity in the calcareous ring, assigned the subfamilies Phyllophorinae, Semperiellinae, and Thyoninae in the family Phyllophoridae. However, based on the structure of the calcareous ring, Phyllophorinae on one hand and Thyoninae and Semperiellinae on the other hand are very different, and, therefore, I consider them as two separate families: Phyllophoridae and Thyonidae. In Thyonidae, the ring is usually tubular, whereas radial and interradial segments and their processes are subdivided into many pieces and the ring is mosaic; processes of the radial segments are long. In Phyllophoridae, the ring is not tubular, the interradial segments are entire, while the radial segments are either entire, or subdivided basally into a few (usually 2–3) large pieces; processes of the radial segments are medium-long and are subdivided into a few pieces, so that the ring in Phyllophoridae *s. str.* does not appear mosaic. In the system proposed Phyllophoridae *s. str.* corresponds to the subfamily Phyllophorinae in Heding and Panning's system.

Family Rhopalodinidae Théel, 1886
(=Ordo Decacrenidia Bronn, 1860;
Class Diplostomidea Semper, 1868)

Dendrochirotida of pear-shaped or bottle-shaped form with 10–30 and more tentacles, arranged in one or two circles. Body composed of two parts: a lower soft spherical part, and an extended hard part, the proboscis. Dorsal surface strongly reduced. Mouth and anus lying at the tip of proboscis, with a gonopore in between. Calcareous ring has bilateral symmetry, medium-high. Segments of calcareous ring entire, undivided; radial segments with entire short rudimentary forked processes much shorter than segments. Ossicles: tables with four pillars and plates. Body almost entirely buried in substrate, above which only long proboscis protrudes.

References: Panning (1936), Heding (1937), Heding and Panning (1954), Thandar (2001).

Remarks. Because of their unusual shape and pseudodecaradial symmetry these dendrochirotids even been separated in an independent class. Heding and Panning considered rhopalodinids as a subfamily in the family Phyllophoridae *s. lato*, while Pawson and Fell assigned this family to the order Dactylochirtotidae. Thandar (2001) in his revision of the family indicated that it was close to the family Phyllophoridae sensu Pawson et Fell, 1965. The calcareous ring of rhopalodinids somewhat resembles the ring of some Cladolabidae, whereas tables with four pillars are similar to those of Thyonidiidae and Phyllophoridae.

Family Sclerothyonidae Thandar, 1989, status nov.

Dendrochirotida with 10 tentacles, the two ventral of which strongly reduced. Tube-feet lying along radii in two rows. Segments of calcareous ring low, radial segments with long forked processes, with length considerably higher than ring segment height. Ring segments entire, with processes subdivided into pieces. Ossicles: tables with two pillars, forming arched spire, and irregularly shaped disc with 6–8 perforations or disc with 4 perforations, and plates with numerous perforations.

References: Thandar (1989).

Remarks. This family was established by Thandar as a subfamily in the family Sclerodactylidae. It is distinguished from the latter in the calcareous ring, which segments are low, whereas the ring resembles that of Cucumariidae. However, radial segments have prominent forked processes subdivided into pieces. The latter character is similar in Sclerothyonidae and Sclerodactylidae.

Family Sclerodactylidae Panning, 1949, sensu nov.

Dendrochirotida with 10 tentacles. Tube-feet can be lying along radii, and arranged interradially, sometimes having papilla-like shape. Calcareous ring segments entire, high; radial and interradial segments connecting to one another along almost entire height; radial segments with forked processes medium-sized, usually subdivided into three-four large pieces. Ossicles: tables with two or four 4 pillars or plates, sometimes baskets.

References: Panning (1949), Thandar (1989).

Remarks. The subfamily was established by Panning within the family Cucumariidae based on the calcareous ring morphology. Pawson and Fell included in it the subfamily Cladolabinae, which I here consider as a separate family. Thandar, based on the calcareous ring morphology, recognized within it the subfamily Sclerothyoninae, which I here consider as separate family.

Family Placothuriidae Pawson et Fell, 1965

Dendrochirotida with 10 tentacles. Body U-shaped, completely covered by a test consisting of overlapping tables. Segments of calcareous ring high; and radial and interradial segments subdivided into several large pieces arranged in one row one above another; both radial and interradial segments possessing long forked processes, which are also subdivided into several pieces arranged in one row one above another. Ossicles: tables.

The family includes one genus *Placothuria* Pawson et Fell, 1965.

References: Pawson (1963), Pawson and Fell (1965).

Family Thyonidae Panning, 1949, sensu nov.

Dendrochirotida with 10–20 tentacles. Tube-feet scattered all over body, or lying along radii. Calcareous ring segments high. Ring often tubular, forked processes of radial segments long, prominent. Interradial segments often strongly elongated basally fused with processes of radial segments; both calcareous ring segments, and processes subdivided into many pieces. Ring mosaic. Ossicles: tables with 2 or 4 pillars and/or plates; sometimes baskets present.

The family includes two subfamilies: Thyoninae and Semperiellinae.

References: Panning (1949), Heding and Panning (1954), Pawson and Fell (1965), Thandar (1990).

Remarks. A subfamily Thyonidae for 10-tentacular dendrochirotids with mosaic calcareous ring was established by Panning (1949). Later Heding and Panning (1954) separated multitentacular dendrochirotids with a mosaic calcareous ring in the subfamily Semperiellinae. Pawson and Fell (1965) included these two subfamilies along with the subfamily Phyllophorinae in the family Phyllophoridae.

Subfamily Thyoninae Panning, 1949

Thyonidae with 10 tentacles, 2 ventral tentacles reduced. Tube-feet scattered over entire body. Ossicles: tables, with 2 or 4 pillars and/or plates, sometimes cups.

Remarks. In contrast to other Thyoninae, the genus *Hemithyone* Pawson, 1967 (Pawson, 1967a) does not have a mosaic calcareous ring, but has processes of the radial segments subdivided into a few fragments, whereas the interradial segments are subdivided into the upper and lower regions. It is possible that the genus does not belong to Thyonidae.

Subfamily Semperiellinae Heding et Panning, 1954

Thyonidae with 15–20 tentacles. Tube-feet lying along radii or scattered over entire body. Ossicles: tables with 4 or 2 pillars, or, in genus *Cladolella*, rods terminating into spines (modified tables).

References: Hansen, McKenzie (1991).

Suborder Cucumariina Al. Smirnov, subordo nov.

Cucumariida with calcareous ring of sinusoidal appearance which has the following structure: ring segments with a high central part and low lateral parts; the upper lateral parts of segments, corresponding to the excavations for attachment of tentacular ampullae, are reduced; the lower edge of segments with a small central depression, lacks processes or with short processes; neither the ring segments, nor the processes are subdivided; the segments are connected by their lateral sides, corresponding to the lower part of the lateral sides of the ring of other dendrochirotids.

Type-family Cucumariidae Ludwig, 1894.

Suborder includes 8 families: Cucumariidae, Psolidae, Monilipsolidae, Ypsilothuriidae, Paracucumidae, Heterothyonidae and, with question, Thyonidiidae and Cucumellidae.

Remarks. Families Cucumariidae, Psolidae, Monilipsolidae, Ypsilothuriidae, Paracucumidae, Heterothyonidae characterized by the absence of tables ossicles whereas Thyonidiidae, and Cucumellidae characterized by typical tables ossicles. It is impossible to say exactly without a new morphological and molecular-phylogenetic studies are the last two families really belong to new suborder or they acquired the similar structure of calcareous ring independently.

Family Cucumariidae Ludwig, 1894

Cucumariina with 10 tentacles. Tube-feet are most commonly restricted to the radii, or may also be scattered in the dorsal interradii. Calcareous ring low, without posterior processes, or at most medium high with short undivided processes. Ossicles: perforated plates and sometimes baskets.

Remarks. The family Cucumariidae (subfamily Cucumariinae) contains the genera *Staurocucumis* and *Psolicucumis*. I also assign to it a closely related (as shown by Hansen (1988)) genus *Echinocucumis*. I assign to this family the genera *Vaneyella* and *Mitsukuriella*, which were previously assigned to the family Vaneyellidae (order Dactylochirotida), whereas the family Vaneyellidae Pawson et Fell, 1965 is synonymized under Cucumariidae Ludwig, 1894.

Reich (2003a) described a new paragenus *Tripuscucumis* from the Upper Cretaceous of the Baltic Sea Region. These sclerites resemble sclerites of the extant genus *Echinocucumis*. Because this genus had previously been assigned to the family Ypsilothuriidae, Reich assigned his new paragenus to Ypsilothuriidae. Since I assign *Echinocucumis* to the family Cucumariidae, and the paragenus *Tripuscucumis* should also be assigned to this family.

The family includes two subfamilies Cucumariinae and Colochirinae.

References: Panning (1955; 1957; 1963; 1964; 1966; 1971), O'Loughlin and Alcock (2000); Reich (2003a).

Subfamily Cucumariinae Ludwig, 1894, sensu Panning, 1949

Cucumariidae with only plate ossicles.

Subfamily Colochirinae Panning, 1949

Cucumariidae with plate and basket ossicles.

Family Psolidae Burmeister, 1837

Cucumariina with 10 tentacles. Body laterally and dorsally covered with large overlapping scales. Ventral surface lacking scales and modified into sole, using which holothurians attach to substrate. Mouth and anus displaced to dorsal surface and usually covered by large orals or interradials scales. Tube-feet on ventral surface arranged in three rows (in genus *Psolus* medioventral row often reduced). Dorsal tube-feet reduced or, in the genus *Psolus*, completely absent. The segments of calcareous ring without processes. Ossicles: mono- and multi-layered plates, baskets and ball-like laced ossicles formed by developing of additional cross-bars and processes on the plate surface.

References: Bell (1882), Pawson (1967b; 1971; 1982), O'Loughlin and Maric (2008), O'Loughlin and Ahearn (2008).

Remarks. In the structure of the calcareous ring and ossicles, the family is similar to the family Cucumariidae. In my opinion, it cannot be considered as a sister group for the "order Dactylochirotida," to which it is similar only in the presence of large overlapping scales on the dorsal and lateral surfaces. It has been thought for a long time that the name of the subfamily Psolinae based on the generic name *Psolus*, was proposed by Perrier (1902). O'Loughlin and Maric (2008) established that the family Psolidae with the genus *Psolus* Oken, 1815 was established by Forbes (1841). Indeed some time earlier the Psolidae with the genera *Psolus* and *Cuvieria* was proposed by Burmeister (1837, p. 471): "23. (59.) Fam. Psolidae. Die gestielten Füßchen stehen bloß an der flachen Bauchseite; Leib dick, oben gewölbt und hinten verschmächtigt; die Haut sehr hart, rauh. Tentakeln verästelt."

Family Monilipsolidae Smith et Gallemí, 1991, status nov.

Body oval in outline and flattened and fully plated with differentiated dorsal and ventral plating. Double ring of stout, perforated bead-like ossicles around the periphery of strongly calcified sole. Mouth displaced dorsally, no oral valve plates. Anus displaced dorsally at the end of the short tail. The calcareous ring resembles that of Psolidae. Radials with well developed anterior notch. Sclerites represented by scales sometimes with perforation for tube-feet and slightly elongate large bead-like ossicles with large pores. Exterior opening of this pore is directed laterally and slightly ventrally, the interior opening lies within the body cavity, inside the plated mesoderm (after Smith and Gallemí, 1991).

A monotypic family containing *Monilipsolus mirabilis* Smith et Gallemí, 1991 from the Middle Triassic (Ladinian) of Ciollbató, northern Spain.

Remarks. Smith and Gallemí (1991), who described *M. mirabilis* proposed the subfamily Monilipsolinae within the family Psolidae to accommodate their species. *Monilipsolus* is similar to Psolidae in the presence of well-developed sole and in the dorsal position of the mouth and anus. This indicates that *Monilipsolus* was most likely a suspension feeder and lived attached to hard substrate. At the same time, the presence of a rim along the sole formed by bead-like sclerites and a sole covered by tables distinguish *Monilipsolus* from the extant Psolidae. This allows consideration of the subfamily described by Smith and Gallemí as a family.

Family Ypsilothuriidae Heding, 1942

Cucumariina with 8–10 simple tentacles. Body spherical or U-shaped, covered with test composed of scales. Tube-feet restricted to the radii. The segments of calcareous ring without processes. Ossicles: multilayered plates with central or eccentric vertical process, developed from a secondarily upward growing meshwork of plates, and multilayered plates lacking vertical process.

This family may include the sclerites *Palaeoypsilus liassicus* Gilliland, 1992 from the Lower Jurassic of southern Britain.

References: Heding (1942), Panning (1949), Pawson and Fell (1965).

Remarks. Heding (1942) included two genera *Ypsilothuria* and *Echinocucumis* in this family. Panning (1949) considered it as a subfamily of the family Cucumariidae and assigned to it apart from these two genera a new genus *Ypsilocucumis* and the genera *Ekmocucumis, Abyssocucumis*, and *Staurocucumis*. Newertheless, he noted the artificial nature of the subfamily Ypsilothuriinae and indicated considerable differences between the genera *Echinocucumis* and *Ypsilothuria*. Pawson and Fell (1965) considered Ypsilothuriidae as an independent family and placed it in their new order Dactylochirotida. They assigned to it the genera *Ypsylothuria, Ypsilocucumis*, and *Echinocucumis*. Hansen (1988) showed that the genus *Echinocucumis* is similar to the genera *Staurocucumis* and *Psolicucumis* from the subfamily Cucumariinae. Thus, the family Ypsilothuriidae contains only two genera *Ypsylothuria* and *Ypsilocucumis*. The genus *Ypsilocucumis* contains only type-species. Two other species assigned by Panning to this genus are currently assigned to other genera of the family Paracucumidae.

Family Paracucumidae Pawson et Fell, 1965

Cucumariina with 12–15 tentacles. Body completely covered by test composed overlapping scales. Tube-feet reduced. The segments of calcareous ring without processes. Ossicles: plates with centrally or slightly eccentrically positioned vertical process, developed because of the growing upwards of the secondarily meshwork of the plate.

References: Mortensen (1925), Pawson and Fell (1965), Pawson (1982).

Remarks. The family was established for the monotypic genus and species *Paracucumaria antarctica* Mortensen, 1925. O'Loughlin (2002) synonymized this species under *Thyone turricata* Vaney, 1906. The unusual ossicles shaped as plates with a central or slightly eccentric vertical process, developed because of the growing upwards of the secondarily meshwork of the plate, and calcareous ring make *Paracucumis turricata*, the type species of the family Paracucumidae, very close to the genus *Ypsilothuria*. It is quite possible that these species should be included in the family Ypsilothuriidae, and the family Paracucumidae should be considered its junior synonym.

Family Heterothyonidae Pawson, 1970

Cucumariina with 10 tentacles. U-shaped body completely covered by a test consisting of overlapping scales. The segments of calcareous ring with shot processes. Ossicles: plates and baskets. The family includes one extant genus *Heterothyone* with two species *H. alba* and *H. ocnoides,* and the extinct genus and species *Strobilothyone rogentii*, from the Middle Triassic (Ladinian) of Ciollbató, northern Spain (Smith, Gallemí, 1991).

References: Panning (1966), Pawson (1970; 1982), Smith, Gallemí (1991).

Remarks. The genus *Heterothyone* was previously assigned to the subfamily Colochirinae in the family Cucumariidae, to which it is apparently related.

Family Thyonidiidae (Heding et Panning, 1954), status nov.

Cucumariina with 15–25 tentacles. The segments of calcareous ring without processes. Ossicles: tables with 2, 3 or 4 pillars or plates (genus *Parathyonidium*), or reduced (genera *Patallus* and *Athyonidium*).

References: Heding and Panning (1954), Pawson and Fell (1965), Hansen and McKenzie (1991).

Remarks. Heding and Panning (1954) placed their new subfamily into multitentacular phyllophorids. Pawson and Fell (1965) considered thyonidiids as a subfamily within the family Cucumariidae. The family differs from Cucumariidae *s. str.* and other families of Cucumariina by the assemble of characters including multitentacularity and tables ossicles. Based on the sclerite morphology, the genera placed in the family are very different from each other, and it is quite possible that the family is polyphyletic. The genera *Parathyonidium, Patallus*, and *Athyonidium* are most likely not connected with the genera having tables.

Family Cucumellidae, Thandar, 2011

Cucumariina with 12 tentacles. Calcareous ring without processes. Ossicles: simple tables with a trilocular to multilocular, smooth disc and a solid spire ending in 2–3 smooth, diverging processes/teeth (after Thandar, 2011).

The family is monotypic and containing only type-genus *Cucumella* with species *Cucumella triplex* Ludwig et Heding, 1935 (type species) and *C. triperforata* Thandar, 2011.

Remarks. Thandar (2011) assigned the new family to the order Dactylochirotida based on the presence of simple tentacles. As shown above, the order Dactylochirotida is artificial and has been synonymised with the order Dendrochirotida. Thus, I place the family Cucumellidae in the order Dendrochirotida near the family Thyonidiidae. It should be noted that some species, previously assigned to the genus *Cucumella,* were moved by Thandar to the genus *Neoamphycyclus* of the family Thionidiidae.

Ordo Molpadiida Haeckel, 1896
[nomen transl. Pawson, 1982
(ex. Molpadonia Haeckel, 1896]

Holothuriacea with 10–15 digitate or secondarily modified simple tentacles. Body with elongated caudal part or with clearly delineated tail. Tube-feet absent. Anal opening usually surrounded by anal papillae connected with radial ambulacral canals. Two primary tentacles connected with medioventral radial canal, two with left dorsal canal and one with right dorsal canal. Stone canal either opens externally or blindly terminates in body wall, or opens into body cavity. Introvert and retractor muscles not present. Respiratory trees present, but *rete mirabile* not developed. Mesentery, suspending posterior loop of intestine, anteriorly and medially attached to body wall in right ventral interradius. Calcareous ring massive, consists of 10 segments. Radial segments on upper margin notched, and usually with well developed posterior process, subdivided into two (reduced in species of small size). Ossicles: tables, spindle-shaped plates, rocket-shaped plates, caudinid cups. Development known only for *Paracaudina ransonnettii*, in which doliolaria develops without stage of auricularia. Infaunal forms inhabit burrowing into the ground. Detritus-feeders.

Calcareous ring segments similar to those of the extant Molpadiida described from the Early Jurassic of southern Britain (Gilliland, 1992, Calcareous ring Type I) and Late Urassic (Oxfordian) of Switzerland (Hess, 1975). Tables with 3 pillars similar to those of Molpadiida (paragenus *Priscularites*, parafamily Priscopedatidae) are known from the Late Urassic (Oxfordian) (Deflandre-Rigaud, 1962) and Upper Cretaceous (Reich, 2003d).

Order includes 3 families: Molpadiidae, Caudinidae, and Eupyrgidae.

References: Clark (1908), Heding (1931a, 1935), Ludwig, Heding (1935); Deichmann (1936a; 1936b; 1938a; 1938b; 1940), Pawson (1970; 1977; 1982), Pawson and Liao (1992), Pawson, Vance, and Ahearn (2001).

Family Molpadiidae J. Mueller, 1850

Molpadiida with 13–15 tentacles with 1-3 pairs of lateral processes and central process or tentacles simple. Posterior part of the body has a shape of short narrow tail, clearly delineated from the remainder of the body. Free hanging tentacle ampullae usually well developed. Stone canal opens externally. Radial muscle bands paired or, less commonly, undivided. Radial calcareous ring segments with processes and usually with perforation or notch for radial nerve. Ossicles: tables with spire of three fused pillars, sometimes modified into molpadiid anchor, plates, racket-shaped and spindle-shaped plates. In most species, body wall posesses oval yellow, brown, or red phosphate bodies responsible for brown, red, or violet-red color of the animal. Number of these bodies increases with age.

Table sclerites with three pillars similar to those of the extant Molpadiidae (paragenus *Dictyothurites*, parafamily Priscopedatidae) described from the Oligocene of Schleswig-Holstein, Germany (Deflandre-Rigaud, 1959). Racket-shaped plates (paragenus *Calcligula*, parafamily Stichopitidae), which can be assigned to ossicles of extant Molpadiidae, are known beginning from the Lower Cretaceous (Gilliland, 1993; Reich, 2003d). One occurrence of molpadiid anchor *Calcancorella spectabilis* (parafamily Calcancorellidae) is known from the Oligocene of Schleswig-Holstein, Germany (Deflandre-Rigaud, 1959). Fusiform rods of the paragenus *Calclamnella* (parafamily Calclamnidae) similar to those of Molpadiidae are known from the Oligocene, Rupelian of northwestern Poland – *Calclamnella* sp. (Górka and Łuszczewska, 1969) and Oligocene of Schleswig-Holstein, Germany – *C. fusiformis* (Deflandre-Rigaud, 1959). Apparently, Molpadiidae also include fusiform rods of the paragenus *Priscolongatus* from the Upper Cretaceous (Maastrichtian) of Isle of Rugen, northeastern Germany (Reich, 2003d) and from the Oligocene of northwestern Poland (Gorka and Luszczewska, 1969).

References: Reich (2003d).

Family Caudinidae Heding, 1931

Molpadiida with 10 or 15 tentacles with 1 or 2 pairs of lateral processes, central process not developed or tentacles simple. Body usually terminates in strongly elongated or short tail, not delineated from main body, sometimes tail not pronounced (genus *Acaudina*). Free hanging tentacle ampullae usually well developed. Stone canal opens into body cavity. Radial muscle bands subdivided into two. Radial calcareous ring segments with processes, lacking radial nerve perforation. Ossicles: tables with spire consisting of four pillars, cross-like caudinid cups, and plates.

Sclerites similar to caudinid cups, *Pedartopriscus pinguis* (parafamily Exlinellidae) are known from the Upper Jurassic (Deflandre-Rigaud, 1962; Gilliland, 1993).

Family Eupyrgidae Semper, 1868

Molpadiida with 15 simple tentacles with no processes. Barrel-shaped body, short tail, not clearly delineated from the rest of the body. Free hanging tentacle ampullae not developed. Stone canal blindly terminates in body wall and lacking connection with the exterior. Radial muscle bands undivided. Radial calcareous ring segments with rudimentary posterior processes and perforation for a nerve. Ossicles: tables with quadrangular multiperforated disc and spire consisting of three spiny pillars. Family includes one genus *Eupyrgus*.

References: Semper (1868), Östergren (1905), Madsen and Hansen (1994).

Remarks. Apparently neothenal holothurian. Madsen and Hansen (1994) assigned the genus *Eupyrgus* to the family Caudinidae. *Eupyrgus* has undivided muscle bands and no free hanging tentacle ampullae, whereas the calcareous ring lacks processes, although, apparently, their rudiments are present. Absence of such derived characters as subdivision of muscle bands into two, and absence of free hanging tentacular ampullae are described for other molpadiids: *Paratrochostoma spiniferum* Heding, 1935 (=*Molpadia blakei* Théel, 1886) and *Cherbonniera utriculus* Sibuet, 1974 from the family Molpadiidae. Therefore, it is very likely that these characters in *Eupyrgus* are secondary and their appearance is explained by that the *Eupyrgus* is a small-sized neothenal holothurian. At the same time the specific nature of sclerites in *Eupyrgus* allows their recognition as a separate family.

Order Gephyrothuriida Heding, 1935
[nomen transl. ex. Gephyrothurioidea Heding, 1935]

Holothuriacea with 15 forked tentacles with 2–3 pairs of processes, upper pair of processes the largest. Body elongated, cylindrical. Tube-feet reduced and modified into long filamentous papillae with ampullae occurring along dorsal interradii (genus *Gephyrothuria*), or into small papillae lying along dorsal and lateroventral interradii (genus *Hadalothuria*). Free hanging tentacle ampullae absent. Stone canal opens into body cavity. Introvert and retractor muscles absent. Respiratory trees are in the form of two unbranched tubes. Radial muscle bands undivided. The calcareous ring is simple, processes on the segments are absent. The radial segments have a notch for the nerve on the anterior margin. Ossicles are absent.

The order includes one family Gephyrothuriidae.

References: Koehler and Vaney (1905), Clark (1908), Hérouard (1923), Deichmann (1930; 1940), Heding (1935; 1940), Hansen, 1956, O'Loughlin (1998).

Remarks. The placement of this group in the system of Holothuroidea has been variously interpreted. Koehler and Vaney (1905) assigned their new family to Aspidochirotes, whereas Clark (1908) did not accept Gephyrothuriidae as an independent family and assigned gephyrothuriids to Molpadiidae. Hérouard (1923) assigned the genus *Gephyrothuria* to the family Synallactidae. Heding (1935) assigned a number of synalactid taxa to Gephyrothuriidae, e.g., the genus *Pseudostichopus*, and recognized Gephyrothuriidae *s. lato* as a separate order Gephyrothurioidea. However, soon after this (Heding, 1940) discontinued the recognition of Gephyrothuriidae as a separate order and placed Gephyrothuriidae *s. lato* in the order Aspidochirota. Deichmann (1940) assigned to the family Gephyrothuriidae *s. str.* only the genus *Gephyrotyhuria*, and placed the family in the order Molpadonia. O'Loughlin (1998) gave a detailed description of the history of studies of gephyrothuriids. Hansen (1956) described a genus and species *Hadalothuria wolfii*, which he assigned to the family Gephyrothuridae *s. str.* and to the order Miolpadonia. This interpretation of the family was accepted by Pawson (1982) and substantiated by O'Loughlin (1998). In my opinion, the family Gephyrothuriidae *s. str.* should be recognized as a separate order (Smirnov, 1984). This is supported by the morphology of the calcareous ring, which lacks processes or their rudiments, tentacles with dominant upper pair processes, absence of free-hanging tentacular ampullae, and undivided muscle bands. This assembly of characters distinguished gephyrothuriids both from Molpadiida and Aspidochirotida.

Family Gephyrothuriidae Koehler et Vaney, 1905

Diagnosis as for the order.

The family includes two monotypic genera *Gephyrothuria* Koehler et Vaney, 1905 and *Hadalothuria* Hansen, 1956.

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