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A REVISED CLASSIFICATION OF THE DENDROCHIROTE HOLOTHURIANS

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Recent studies on some unusual dendrochirote holothurians and examination of available data on fossil holothurians have led us to conclude that the hitherto accepted classification of the dendrochirote holothurians conceals some important evolutionary trends. In this article a new classification is proposed in which tentacle numbers are abandoned as criteria for diagnosing major taxa; instead, importance is attached to the shape of the calcareous ring, the shape of the tentacles, and the calcareous deposits of the body wall. The reasons for such changes in classification are given in detail elsewhere (Fell and Pawson, in press).

NEW TAXA

Certain genera which were hitherto grouped in the order Dendrochirotida are known to lack the richly branched tentacles which are so characteristic of other genera within that order. These genera with essentially unbranched tentacles also share other important features, which suggest a natural grouping of three families. We therefore propose a new order to accommodate these families.

Order DACTYLOCHIROTIDA nov.

Diagnosis: Tentacles 8-30 in number, not branched but digitiform or digitate, the digits sometimes bifurcate. Body enclosed

in a test comprising imbricate plates. Calcareous ring simple, lacking complex posterior processes.

Included families: Ypsilothuriidae Heding, 1942; Rhopalodinidae Perrier, 1902; and a third family, diagnosed here as new:

Family VANEYELLIDAE nov.

Diagnosis: Anus and mouth at opposite ends of the body, which is U-shaped or fusiform. Plates in the body wall with or without small spires. Tentacles 10-20 in number.

Included extant genera: *Vaneyella* Heding and Panning, 1954 (type genus by tautonymy); *Mitsukuriella* Heding and Panning, 1954.

The order Dendrochirotida as now restricted may be diagnosed as follows:

Order DENDROCHIROTIDA Grube, 1840
(restricted herein)

Diagnosis: Tentacles 10-30 in number, richly branched. Calcareous ring simple or with complex posterior processes. Test sometimes well developed, or reduced to non-contiguous calcareous spicules.

Morphological and paleontological evidence (Fell and Pawson, in press) suggests that this order includes some very primitive extant holothurian genera. These genera seem best assigned to new families; one new genus and two new families are diagnosed here:

Family PLACOTHURIIDAE nov.

Diagnosis: Body completely enclosed in a test of imbricate plates without spires. Sole lacking. Calcareous ring long, slender, with long posterior processes.

Included extant genus: *Placothuria* n.g.

Placothuria n.g.

Diagnosis: Tentacles 10, richly branched. Body U-shaped. Calcareous ring long, with posterior processes composed of a mosaic of small pieces.

Type-species: Stolus huttoni (Dendy) (illustrated in Pawson, 1963, pl. 7).

Etymology: The generic name is derived from the Greek *plax* (a plate) and *Holothuria,* and refers to the test formed by overlapping plates. Gender, feminine.

A second new family within the order Dendrochirotida is proposed:

Family PARACUCUMIDAE nov.

Diagnosis: Body completely invested in a test of imbricate scales with spires. Sole lacking. Calcareous ring simple, lacking posterior processes.

Included extant genus: *Paracucumis* Mortensen, 1925.

A REVISED CLASSIFICATION

The relationships of the orders Dendrochirotida and Dactylochirotida are discussed elsewhere, in the broad context of the inferred evolution of the Holothuroidea (Fell and Pawson, in press). From the new data the following revised classification of holothurians emerges:

Subclass DENDROCHIROTACEA Grube, 1840

(Nomen translatum herein, ex Dendrochirotae Grube, 1840)

Introvert (with retractor muscles) always present. Tubefeet and respiratory trees usually present. Madreporite free in the body cavity. Mesentery of the posterior loop of the intestine in the right or left ventral interradius. Free tentacle ampullae lacking. Gonad in two tufts, one tuft to each side of the dorsal mesentery.

Order DENDROCHIROTIDA Grube, 1840

(restricted herein)

Tentacles richly branched, 10-30 in number.

Key to Included Families

1 (6) Body partly or completely invested by plates.

2 (5) Body enclosed by a test comprising conspicuous imbricate plates; sole lacking.

3 (4) Calcareous ring complex, with long paired posterior processes. ..... Placothuriidae nov. (Included extant genus: *Placothuria* nov.)

4 (3) Calcareous ring simple, lacking posterior processes . . . . . Paracucumidae nov. (Included extant genus: *Paracucumis* Mortensen, 1925)

5 (2) Body invested dorsally by conspicuous plates; sole present . . . . . Psolidae Perrier, 1902 (Included extant genera: *Psolus* Oken, 1815; *Stolinus* Selenka, 1868; *Psolidium* Ludwig, 1886; *Lepidopsolus* Bronn, 1860; *Thyonepsolus* Clark, 1901)

6 (1) Body more or less naked, not enclosed by a test; calcareous deposits small, inconspicuous.

7 (10) Calcareous ring complex, with paired or unpaired posterior processes.

8 (9) Processes composed of a mosaic of small pieces . . . . . Phyllophoridae Ostergren, 1907 (emend. herein). (Included subfamilies: Phyllophorinae Ostergren, 1907; Semperiellinae Heding and Panning, 1954; Thyoninae Panning, 1949).

9 (8) Processes entire . . . . . Sclerodactylidae Panning, 1949 (Nomen translatum herein, ex Sclerodactylinae Panning, 1949). (Included subfamilies: Sclerodactylinae Panning, 1949; Cladolabinae Heding and Panning, 1954).

10 (7) Calcareous ring simple, lacking posterior processes . . . . . Cucumariidae Ludwig, 1894 (emend. herein). (Included subfamilies: Cucumariinae Ludwig, 1894; Colochirinae Panning, 1949 [partim?]; Thyonidiinae Heding and Panning, 1954).

Order DACTYLOCHIROTIDA nov.

Tentacles digitiform or digitate, the digits sometimes bifurcate, 8-30 in number. Body enclosed by a test comprising imbricate plates. Calcareous ring simple, lacking complex posterior processes.

Key to Included Families

1 (4) Anus and mouth at opposite ends of the body, which is fusiform or U-shaped.

2 (3) Plates with a prominent spire. Tentacles 8-10 in number . . . . . Ypsilothuriidae Heding, 1942 (Included extant genera: *Ypsilothuria* Perrier, 1886; *Echinocucumis* Sars, 1895; *Ypsilocucumis* Panning, 1949)

3 (2) Plates with small spires, or none. Tentacles 10-20 in number. . . . . Vaneyellidae nov. (Included extant genera: *Vaneyella* Heding and Panning, 1954; *Mitsukuriella* Heding and Panning, 1954)

4 (1) Anus and mouth opening close together, body flask-shaped . . . . . Rhopalodinidae Perrier, 1902 (Included

extant genera: *Rhopalodina* Gray, 1853; *Rhopalodinopsis* Heding, 1937).

The above arrangement of taxa is believed to reflect phylogenetic relationships more satisfactorily than that currently employed.

Of the fossil holothurian families defined by Frizzell and Exline (1955), the Calclamnidae (including genus *Thuroholia*) and some members of the Stichopitidae and Priscopedatidae should be included within this subclass.

OTHER HOLOTHURIAN GROUPS

In view of the above proposed revision of the Dendrochirotida, it is desirable to consider briefly the arrangement of the remaining holothurian orders, the Aspidochirotida, Elasipodida, Apodida and Molpadida.

Aspidochirotida and Elasipodida

Both the aspidochirotes and elasipods have tentacles which terminate in an approximately circular disc. The body is usually bilaterally symmetrical in both groups, with the dorsal tubefeet modified into papillae or warts (Aspidochirotida) or into elongate sensory processes (Elasipodida). The two groups are distinguishable on the basis of some anatomical features, but both may be conveniently placed into a single subclass, as follows:

Subclass ASPIDOCHIROTACEA Grube, 1840

(Nomen translatum herein, ex Aspidochirotae Grube, 1840)

Diagnosis: Tubefeet present, tentacles shield-shaped, 10-30 in number. No introvert, hence retractor muscles lacking. Body with conspicuous bilateral symmetry.

Key to Included Orders

1 (2) Respiratory trees present. Mesentery of posterior loop of intestine attached to right ventral interradius ..... Aspidochirotida Grube, 1840

2 (1) Respiratory trees lacking. Mesentery of posterior loop of intestine attached to right dorsal interradius ..... Elasipodida Theel, 1882

Theel (1882) has discussed the possible antiquity of the elasipod holothurians and concluded that they are certainly not representative of an ancestral holothurian stock; rather they are secondarily adapted to deep-sea life. In elasipods, and in some aspidochirotes, the madreporite opens to the exterior, and does not hang free in the body cavity. This can be regarded, not as a primitive feature, but as a logical compensatory consequence of the absence of respiratory trees. The extremely fragile calcareous ring in elasipods is apparently secondarily reduced.

Within this subclass should be placed some representatives of the fossil families Priscopedatidae and Theelidae as defined by Frizzell and Exline (1955).

Apodida and Molpadida

The important character shared by adopids 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.

Subclass APODACEA Brandt, 1835

(Nomen translatum herein, ex Apodes Brandt, 1835)

Diagnosis: Tentacles simple, digitate or pinnate. Tubefeet markedly reduced, or, more usually, lacking altogether. No introvert, hence retractor muscles lacking. Deposits may include anchors and anchor plates.

Key to Included Orders

1 (2) Body cylindrical. Respiratory trees and anal papillae lacking. Deposits often include wheels ..... Apodida Brandt, 1835

2 (1) Body fusiform, often with tapering caudal portion. Respiratory trees and anal papillae present. Wheels lacking ..... Molpadida Haeckel, 1896

It is remarkable that some members of both Apodida and Molpadida have anchors and anchor plates in the body wall. The anchors and their plates differ morphologically in the two orders, but presumably have the same functional significance as accessory locomotor organs, since the anchors project through the body wall.

The fossil family Achistridae and some members of the fossil families Stichopitidae, Theelidae, Synaptitidae and Calcanoridae as defined by Frizzell and Exline (1955) may be included in this subclass.

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