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Reassessment of the classification of the Ophiuroidea (Echinodermata), based on morphological characters. I. General character evaluation and delineation of the families Ophiomyxidae and Ophiacanthidae

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Abstract

Most of the taxonomically reliable internal and microstructural characters (e.g. jaws, dental plate, genital plates, vertebrae) of the recent Ophiuroidea are studied using SEM on a broad comparative basis for the first time, including examination of the arm spine articulation shape in 178 species from 105 genera and 16 families encompassing all major ophiuroid generic diversity. Numerous taxonomic contradictions caused by "over-applying" of external characters to traditional ophiuroid systematics are found and analyzed. Among newly applied microstructural characters, the shape of the arm spine articulations is found to be of great importance for ophiuroid taxonomy at all levels, from order to species. An identification key of the ophiuroid families based exclusively on the shape of the arm spine articulations is presented. Major genera of Ophiacanthidae were studied in order to delineate this family. The group of taxa, traditionally known as the ophiacanthid subfamily Ophiotominae (Paterson, 1985) that was apparently intermediate between Ophiomyxidae and Ophiacanthidae, including the genera *Amphilimna* Verrill, 1899, *Ophiocymbium* Lyman, 1880, *Ophiodaces* Koehler, 1922, *Ophiodelos* Koehler, 1930, *Ophiolimna* Verrill, 1899, *Ophiologimus* H.L. Clark, 1911, *Ophiomedea* Koehler, 1906, *Ophiophrura* H.L. Clark, 1911, *Ophiopristis* Verrill, 1899, *Ophioprium* H.L. Clark, 1915, *Ophiosparte* Koehler, 1922, *Ophiotoma* Lyman, 1883, *Ophiotrema* Koehler, 1896 was studied in detail using most of available type specimens. In order to study interspecific variability and usefulness as a taxonomic marker of the arm spine articulations, four new species of the apparently ophiotomin genus *Ophiocymbium* are described: ***O. antarcticus* sp. nov.**, ***O. ninae* sp. nov.**, ***O. tanyae* sp. nov.** and ***O. rarispinum* sp. nov.** A new genus and species, which has affinities to Ophiotominae, ***Ophioplexa condita* gen. et sp. nov.** is described. It is demonstrated that many of the genera traditionally included in the subfamily Ophiotominae, e.g. the genera *Ophiocymbium*, *Ophiologimus*, *Ophiophrura*, *Ophioprium* and ***Ophioplexa condita* gen. et sp. nov.,** belong to the family Ophiomyxidae instead of Ophiacanthidae. Another apparently intermediate taxon, ***Ophiorupta discrepans* (Koehler, 1922) comb. nov.** is also considered as an ophiomyxid. Several further genera with disputed taxonomic placement, e.g. *Amphilimna*, *Ophiopsila*, *Ophiolimna*, *Ophioconis*, were studied especially and their revised placement is proposed. The following genera are exluded from the family Ophiacanthidae: *Amphilimna*, *Ophiocymbium*, *Opiodaces*, *Ophiodelos*, *Ophiologimus*, *Ophiophrura*, *Ophioprium* and *Ophiosparte*. The previously proposed paraphyly of the family Ophiacanthidae (Smith *et al.*, 1995) was to a great extent caused by including a number of genera from distantly related families. The relationship between extinct Oegophiurida and recent ophiuroids was analyzed. A remarkable similarity between arm spine articulations of some Paleozoic oegophiurids and the recent ophiomyxid *Ophioscolex glacialis* Müller & Troschel, 1842 was discovered. Oegophiurid groove spines are suggested to be homologous with the tentacle scales of the remaining Ophiuroidea. It is suggested that the family Ophiomyxidae thus may be related to some crown Oegophiurida that had already acquired fused vertebrae. The higher ophiuroid taxonomy, based on the genital plate patterns, is critically analyzed in the light of the present data. It is suggested that instead of earlier proposed numerous ophiuroid subgroups most ophiuroid families are closely related. It is suggested, that most of the ophiuroid families (includes Ophiomyxidae, Ophiacanthidae, Ophiodermatidae, Ophiocomidae, Ophionereididae, Ophiochitonidae, Amphilepididae, Amphiuridae, Ophiactidae, Ophiolepididae, Hemieuryalidae, Ophiotrichidae) form a compact group with numerous intermediate taxa even between apparently very different families, whereas the family Ophiuridae and the traditional order Euryalida are more distantly related to the rest of Ophiuroidea. An appropriate name for this higher ophiuroid group will be suggested after a detailed analysis of other ophiuroid groups, which will be made in further publications of this series.

Key words: Ophiuroidea, morphology, taxonomy, phylogeny, inter-family relationships, new microstructural characters, families Ophiacanthidae and Ophiomyxidae, revision, descriptions of the new deep-water taxa, Paleozoic Oegophiurida, relationship to modern Ophiomyxidae

Резюме

Несмотря на значительный прогресс в таксономии офиур на видовом уровне, систематика семейств и других высших таксонов класса Ophiuroidea до сих пор остаётся противоречивой и основывается почти исключительно на внешних признаках. Неопределённые границы между даже хорошо известными семействами офиур не являются чем-то исключительным, а напротив, представляют собой типичную проблему таксономии Ophiuroidea. Ряд ранее предпринятых попыток в какой-то мере исправить это положение, и использовать различные признаки внутреннего строения, не прижились, и в целом, никак не повлияли на практическую систематику офиур. В единственном доступном филогенетическом анализе 1995 года (Smith et al., 1995) были использованы данные по строению офиур, полученные еще в начале 20-го века с применением светового микроскопа, и с тех пор критически не переисследованные и не переосмысленные. Всё это привело к тому, что в настоящее время систематика и филогенетика офиур в целом чрезвычайно запущена и несовершенна. В данной работе проанализировано строение большинства доступных внешних и внутренних признаков современных представителей класса Ophiuroidea, включая позвонки, генитальные пластинки, челюсти и зубные пластинки с

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