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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, *Ophiomedeia* 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 excluded from the family Ophiacanthidae: *Amphilimna*, *Ophiocymbium*, *Ophiodaces*, *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, Ophiidermatidae, Ophiocomidae, Ophionereididae, Ophiochitonidae, Amphilepididae, Amphiuroidae, 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

использованием сканирующего электронного микроскопа. Отдельно исследована морфология артикуляционных гребней боковых пластинок, несущих иглы – у 178 видов, относящихся к 105 родам и 16 семействам, охватывающие всё основное разнообразие офиур. На такой широкой базе исследование выполняется впервые. Подобное исследование стало возможным в первую очередь благодаря многочисленным сборам глубоководных экспедиций Института Океанологии им. П.П. Ширшова (Москва, Россия). Были выявлены многочисленные таксономические противоречия, вызванные чрезмерным применением в систематике офиур исключительно внешних признаков. Впервые было продемонстрировано, что форма артикуляционных гребней боковых пластинок является очень важным признаком как на уровне семейства, так и на уровне вида. Большинство родов большого семейства Ophiacanthidae были исследованы с целью определения таксономических границ данного семейства. Кроме того, целый ряд родов с неопределённым систематическим положением, включая *Amphilimna*, *Ophiopsila*, *Ophiolimna* и *Ophioconis* был специально изучен с целью определения их семейственной принадлежности. Особое внимание было уделено одной из групп, предположительно промежуточной между семействами Ophiomuxidae и Ophiacanthidae, включающей роды *Ophiocymbium*, *Ophiologimus* и ряд других. Описано четыре новых вида рода *Ophiocymbium*: *O. antarcticus* sp.nov., *O. ninae* sp. nov., *O. rarispinum* sp. nov., *O. tanyae* sp. nov. и представлено детальное переописание типового вида этого рода *O. cavernosum* Lyman, 1880. Описан также близкий к этому роду, новый род и вид *Ophioplexa condita* gen. et sp. nov. и продемонстрирована его, а также родов *Ophiocymbium* и *Ophiologimus* принадлежность к семейству Ophiomuxidae, а не к семейству Ophiacanthidae, как это считалось ранее. Все представители данной группы обитают на значительной глубине в 3000–6000 м. Другой таксон с предположительно переходной морфологией между двумя семействами Ophiomuxidae и Ophiacanthidae, *Ophiorupta* gen.nov. (*Ophiorupta discrepans* (Koehler, 1922) comb. nov.) также рассматривается как представитель семейства офиомиксид. На основании исследования сделан вывод, что два больших семейства офиур, Ophiomuxidae и Ophiacanthidae, в целом, хорошо отличаются друг от друга по строению артикуляционных гребней, зубных и генитальных пластинок и довольно чётко отграничены, хотя и имеется целый ряд родов, демонстрирующих скорее переходную морфологию между этими двумя семействами. Все без исключения исследованные таксоны семейства Ophiacanthidae имеют особый волютообразный завиток на артикуляционном гребне, тогда для офиомиксид характерны гребни более простого строения. Предполагавшаяся ранее полифилия семейства Ophiacanthidae, была обусловлена в первую очередь включением значительного числа родов, относящихся к самым разным, подчас совершенно не родственными семействам (например, *Amphilimna*, *Ophioparte* и мн. др.) только на основании наличия более-менее длинных, многочисленных игл на лучах. Приведены обновленные диагнозы семейств Ophiomuxidae и Ophiacanthidae. На основании данного анализа следующие роды исключены из семейства Ophiacanthidae: *Amphilimna* Verrill, 1899, *Ophiocymbium* Lyman, 1880, *Ophiodaces* Koehler, 1922, *Ophiodelos* Koehler, 1930, *Ophiologimus* H.L. Clark, 1911, *Ophiophrura* H.L. Clark, 1911, *Ophioprium* H.L. Clark, 1915, *Ophioparte* Koehler, 1922.

Проанализированы родственные взаимоотношения между вымершим палеозойским подклассом офиур с открытой амбулакральной бороздой Oegophiurida и современными офиурами. Было обнаружено значительное сходство между артикуляционными гребнями палеозойских эгофиурид и современного представителя семейства Ophiomuxidae *Ophioscolex glacialis* Müller et Troschel, 1842. Кроме того, впервые выявлена гомология между вентральными иглами Oegophiurida и амбулакральными чешуйками современных офиур, на основе положения, формы и наличия переходных случаев, например у *Ophioplexa condita* gen. et sp. nov. Предполагается, что семейство Ophiomuxidae таким образом родственно позднему Oegophiurida, у которых уже имелись слившиеся позвонки. В свете новых данных критически проанализирована систематика высших таксонов класса Ophiuroidea, основанная на строении генитальных пластинок. Предполагается, что вместо ранее выделенных нескольких отрядов и подотрядов офиур, большинство семейств Ophiuroidea близкородственны. Большинство семейств офиур образуют компактную группу, которая включает семейства Ophiomuxidae, Ophiacanthidae, Ophiodermatidae, Ophiocomidae, Ophionereididae, Ophiochitonidae, Amphilepididae, Amphiuridae, Ophiactidae, Ophiolepididae, Hemieuryalidae, Ophiotrichidae). Традиционный отряд Ophiurida Müller et Troschel, 1842, restr., предлагается ограничить единственным семейством Ophiuridae. Анализ микроструктурных морфологических признаков также показал неожиданное близкое сходство внешне очень различных традиционных групп офиур, таких как Euryalida Lamarck, 1816 (семейства Asteronychidae, Asteroschematidae, Gorgonocephalidae, Euryalidae) и Ophiurida Müller et Troschel, 1842 (в ограниченном объеме, см. выше). Предполагается, что группы Euryalida и Ophiurida имеют общее происхождение. Описание любой офиуры предложено сопровождать сведениями по морфологии артикуляционных гребней, а также различных признаков внутреннего строения, полученных с использованием сканирующего электронного микроскопа.

**Ключевые слова:** Ophiuroidea, морфология, систематика, филогения, новые микроструктурные признаки, ревизия семейства Ophiacanthidae на уровне родов, сравнение с близкими таксонами семейства Ophiomuxidae, описание новых глубоководных таксонов, анализ родственных связей палеозойских Oegophiurida и современных Ophiomuxidae.

## Introduction

The Ophiuroidea is a peculiar echinoderm group strikingly different from the other classes, due to acquisition of a particular locomotion using arm movement and corresponding formation of new morphological units, arm segments, possessing articulated vertebrae.

Large, conspicuous shallow-water ophiuroid species received considerable attention from earlier taxonomists. The first ophiuroid species were described from European waters in the middle and second part of the 18<sup>th</sup> century, but placed within the sea-star genus *Asterias* sensu latissimo, for instance *Asterias ophiura* Linnaeus, 1758 (now *Ophiura ophiura*), *Asterias bidentata* Bruzelius, 1805 (now *Ophiacantha bidentata*) or *Asterias nigra* Abildgaard in Müller, 1789 (now *Ophiocomina nigra*). Many of them became type species of large and well-established genera and then families, for instance the Ophiuridae and Ophiacanthidae.

The current ophiuroid taxonomy on family-level was shaped by efforts of few taxonomists, who suggested further differentiation of two families—Astrophytidae and Ophiuridae—encompassing all ophiuroid diversity known in the time of Lyman (1882). Ljungman (1867) created the families Gorgonocephalidae, Ophiomyxidae, Amphiuridae, Ophiotrichidae, Ophiolepididae, Ophiocomidae, Ophiodermatidae, and Ophiacanthidae and Verrill (1899) Asteronychidae, Asteroschematidae and Hemieryalidae. These families constitute the core of ophiuroid taxonomy and their placement has rarely been challenged. Matsumoto (1915; 1917) also added several new families, i.e. Amphilepididae, Ophiactidae and Ophioleucidae, but most of them received a controversial acceptance. Besides advances in Ophiuroidea systematics, numerous regional works appeared, which included descriptions of new species and genera, especially on European (Delle Chiaje 1828; Müller & Troschel 1842; Lütken 1855; 1859; M. Sars 1861) and Indo-West Pacific species (Duncan 1879; 1887; Brock 1888; de Loriol 1893 and others).

Since major ophiuroid diversity occurs in deeper waters, progress in taxonomy of Ophiuroidea relied to a great extent on the technological progress of scientific vessel expeditions. Therefore, after the mid-19<sup>th</sup> century, deep-water studies became one of the important sources in the understanding of ophiuroid diversity. Almost every new deep-water expedition has brought new material that has strongly influenced ophiuroid taxonomy. One of the most important contributions to ophiuroid systematics remains Lyman's monographic report (1882), based on the deep-water collections from the HMS "*Challenger*" cruise around the globe (also Lyman 1878; 1879; 1880). Numerous new ophiuroid taxa were described from the large number of European and American deep-water expeditions (e.g. G.O. Sars 1871; Lyman 1883; Koehler 1896a, b; 1904a; 1907a; 1922a,b; 1930; Lütken & Mortensen 1899; H.L. Clark 1911; 1939; Mortensen 1933a; 1936 and others) in the second half of the 19<sup>th</sup> and earlier 20<sup>th</sup> centuries. Numerous new data were obtained and many of the aberrant or unusual ophiuroid species (including *Perlophiura profundissima* Belyaev & Litvinova, 1972) were discovered by the Russian deep-water program during 1950–1990 (Belyaev & Litvinova 1972; 1976; Litvinova 1975; 1981; 1984 and others). Although some material from these expeditions has already been published, many species remain undescribed. Most recently, a detailed review of the family Ophiacanthidae including descriptions of new genera and species from the bathyal of New Caledonia was published (O'Hara & Stöhr 2006), summarizing data obtained during many French deep-water tropical expeditions of 1980–1990s. In the last decade, several new genera and species have been reported from the relatively well-studied central and northern Atlantic Ocean (Stöhr 2003; Stöhr & Segonzac 2005; Martynov & Litvinova 2008).

Research in the Antarctic region at the end of the 19<sup>th</sup> and earlier 20<sup>th</sup> century resulted in numerous articles and monographic reports on the Antarctic Ophiuroidea (Studer 1876; 1882; Bell 1894; Koehler 1901; 1922b; Hertz 1927a,b; Mortensen 1936; Madsen 1967; Fell 1961; 1962) and in the discovery of several unusual taxa (e.g. *Ophioparte gigas* Koehler, 1922), which are important for the goals of the present study. Taxonomic studies on the Antarctic and subantarctic ophiuroids continue in modern time (Bernasconi & D'Agostino 1975; Smirnov 1977; Guille 1982; Hunter 2007; Martynov & Litvinova 2008 and others).

With the decline of the era of the great deep-sea expeditions in the first half of the 20<sup>th</sup> century, ophiuroid studies switched to the systematics of shallow water species. Numerous reviews dealt with shallow water and shelf ophiuroid species of various regions—Europe (Mortensen 1927), Russia (Dyakonov 1954), Mediterranean (Tortonese 1965), West Africa (Madsen 1970), South Africa (A.M. Clark 1974; Clark AM &



Courtman-Stock 1976), Indo-West Pacific (A.M. Clark & Rowe 1971; Devaney 1970; 1974), Madagascar (Cherbonnier & Guille 1978), Australia (H. L. Clark 1938), Chile (Tommasi 1968; Gonzalo & Alarcon 1968), Brazil (Tommasi 1967; 1970), Belize (Hotchkiss 1982) and others. Some regions were sources of descriptions of several new taxa or new taxonomic considerations. A synoptic key of the ophiuroid genera compiled by Fell (1960) is still of great importance. Further, from Australian and New Zealand waters several interesting ophiacanthid and other brittle-stars were described (Baker 1979; Baker & Devaney 1981), although the taxonomic placement of some of them has been the subject of discussions (Paterson 1985; O'Hara & Stöhr 2006). The Caribbean and adjacent regions have received special attention, as they are traditional research areas for the North American echinoderm taxonomists. Many of Lyman's classical works were based on material collected in the Caribbean (e.g. Lyman, 1869; 1875; 1883); additional papers have been published by H.L. Clark (1901; 1919; 1933 etc.), Verrill (1899) and others. More recently, detailed descriptions of various taxa, including new species of the genera *Ophioderma*, *Ophiolepis*, *Ophionereis*, and others have been published (e.g. Hendler & Miller 1984; Hendler & Turner 1987). One of few recent regional monographs on the class Ophiuroidea was devoted to the Caribbean region (Hendler *et al.* 1995). In a similar way, the Japanese fauna has been specially reviewed in numerous papers of Irimura (e.g. 1969; 1981; 1993), and more recently Fujita *et al.* (1997; 2004), Fujita & Irimura (2005) etc. as well as a synoptic monograph (Irimura 1982) and Museum specimens list (Irimura *et al.* 1995). Most recently, a monograph on Eastern North Pacific (including Canada and Alaska) Ophiuroidea and other echinoderms have appeared (Lambert & Austin 2007). Apart from faunal reviews, several revisions of particular genera have appeared, for instance on the genera *Ophioderma* (Ziesenhenné 1955), tropical American species of the genus *Amphipholis* (Thomas 1966), and *Ophionereis* (A.M. Clark 1953; Thomas 1973). Besides assessing the species diversity, workers attempted to evaluate the taxonomic position of some traditional taxa. Thomas (1967; 1972) had questioned the placement of the genus *Amphilimna* within the family Amphiuroidae. Cherbonnier & Guille (1972) suggested ophiocomid affinities of the genus *Ophiosphaera* instead of the earlier placement within the families Ophitrichidae or Amphiuroidae. Wilkie (1980) transferred the genus *Ophiocomina* from the family Ophiocomidae into Ophiacanthidae, which led to further discussion on the value of internal characters for ophiuroid taxonomy (Baker & Devaney 1981).

After the discovery of a bizarre hot-vent fauna in 1977 (Lonsdale 1977; Corliss *et al.* 1979), deep-water researches focused on a detailed study of a particular localities, often containing hot- or cold seeps, by means of submersibles. This approach led to the discovery of several unusual new ophiuroid genera and species (Stöhr & Segonzac 2005; 2006a, b). Detailed anatomical information by means of SEM was provided for each of these taxa. The brittle-star hot-vent and cold seeps fauna is a promising source for further studies, since the taxonomic position of the newly described taxa are not yet settled.

The 1970s and 1980s became the ecological and physiological rather than taxonomic era of ophiuroid studies. Numerous investigations on spatial distribution, feeding and reproduction featured during this period. Several important ontogenetic studies led to the establishment of new homological patterns of the jaw plates, oral and apical papillae (Hendler 1978; 1988). Investigations of the ontogenetic sequences of several ophiuroid species from different families led to growing understanding of patterns of ontogeny of the class Ophiuroidea (Webb & Tyler 1985; Sumida *et al.* 1998; Stöhr 2005).

Despite undisputable advances in taxonomy at the species level, higher-level taxonomy of the Ophiuroidea remained problematic. A major revision of the Ophiuroidea by Matsumoto (1915; 1917) contained diagnoses of several new orders based on a few internal characters originally used by Lyman (1882). Subsequently, there has been only a single attempt to revise ophiuroid systematics (Smith *et al.* 1995). Mortensen (1927; 1933a) did not agree with Matsumoto's ordinal system and persisted in using the two traditional orders, Euryalida and Ophiurida, which traced back to Müller & Troschel (1842). He did not comment on Matsumoto's system in detail and did not analyse the usefulness of the internal characters. Currently, Mortensen's (1927) system of two ophiuroid orders is most stable taxonomy and utilized in many publications. Lyman's (1882) and Matsumoto's (1915; 1917) suggestions to apply internal characters to ophiuroid taxonomy have receive very scant attention. Internal characters have been used in ophiuroid taxonomy as an exotic addition rather than as valid characters. The only exception was a detailed study of the dental plates and jaws on a broad range material by Murakami (1963). Although numerous species were

involved in the latter study, Matsumoto's system was not critically investigated and dental plates and jaw morphology were used mostly as an additional proof of the validity of that system.

The typical ophiuroid description principally has not changed from Lyman's time to the 20th century. Only a few workers have used jaw and dental plate morphology in the description of every species of a genus, for instance Devaney (1970) in a paper on a revision of the genus *Clarkoma*, Baker and Devaney (1981) in a paper on Australian ophiuroids, Bartsch (1982, 1983, 1987) etc. Most recently for some taxa, spine articulations, jaw shape, and vertebrae morphology were applied (Stöhr & Segonzac 2005; 2006a; O'Hara & Stöhr 2006), but these were also used only as additional characters without an estimation of their taxonomic importance. Adradial genital plate and radial shield articulations have not been investigated since the light microscopic study by Matsumoto (1917). A special study with a broad comparison by SEM of both external and internal ophiuroid characters has never been performed. Although Matsumoto's elaborate ordinal system was largely unaccepted by ophiuroid workers, this system was used in the *Treatise of Invertebrate Paleontology* (Spencer & Wright 1966) and further appeared in some other works (e.g. A.M. Clark & Courtman-Stock 1976; Wilkie 1980). In the sole phylogenetic analysis of the Ophiuroidea (Smith *et al.* 1995), a modified variant of Matsumoto's system was also adopted, but at the same time the validity of the characters was not specially investigated and data were uncritically derived from the light microscopic studies of Matsumoto (1917) and Murakami (1963).

One of the most important problems of current ophiuroid taxonomy is the uncertain delineation between common families. A certain crisis of taxonomy of ophiuroids was noted by Paterson & Baker (1988), Smith *et al.* (1995) and Dearborn *et al.* (1996). For instance, one of the central and largest ophiuroid families, Ophiacanthidae, encompasses more than 30 genera, some of which (*Ophiotoma*, *Ophiotrema*) overlap with the family Ophiomyxidae, whereas other genera (*Ophiolimna*, *Ophiothamnus*) have affinities with definitely different ophiuroid groups, i.e. Ophiodermatidae and Ophiactidae (Martynov 2010).

Paterson (1985) attempted to unravel the Ophiacanthidae, "a taxonomist's nightmare" by his own account (agreeing with Koehler's (1914: 72) opinion that "the classification of Ophiacanthidae now represents actual chaos"), and divided the family into the four subfamilies: Ophiacanthinae, Ophiotominae, Ophioplinthacinae and Ophiohelinae. To support this decision, Paterson (1985) for the first time also suggested to use a novel character — the shape of the arm spine articulations. In the majority of studied ophiacanthid genera, Paterson found possessed peculiar "comma-shape" arm articulations on the lateral arm plate. However, the subfamily Ophiohelinae lacked this distinctive articulation shape. The present study confirms the differences of the Ophiohelinae from other Ophiacanthidae. Moreover further contradictions were discovered: the traditional ophiacanthid genus *Ophiothamnus* appears to have arm spine articulations typical of the Amphiuroidae and Ophiactidae (Martynov 2010). This could mean that either the articulation shape is of lesser systematic importance, or the subfamily Ophiohelinae is not a member of the family Ophiacanthidae. Leaving the testing of the articulation significance to further studies, Paterson at that stage retained the Ophiohelinae as an ophiacanthid taxon. Until recently, the taxonomic importance of the spine articulations was never tested. Most recently, new genera from the hot-vent and seep environments were discovered (Stöhr & Segonzac 2005; 2006a) and considered to be members of the family Ophiacanthidae. However both *Ophienigma spinilimbatum* Stöhr & Segonzac, 2005 and *Ophiolamina eprae* Stöhr & Segonzac, 2006 possess non-ophiacanthid articulations and thus their importance was questioned (Stöhr & Segonzac, 2005, 2006a). The promising suggestion of Paterson (1985) to further subdivide Ophiacanthidae into four subfamilies has also received little attention. Recently, in a monograph on the New Caledonian bathyal ophiacanthids, O'Hara & Stöhr (2006) arranged genera according to these subfamilies, but also suggested that their delineation was not always clear.

Smith's *et al.* (1995) cladistic analysis suggested the paraphyletic origin of the family Ophiacanthidae, however it did not contain a detailed comparison of a large number of ophiacanthid genera. Stöhr and Segonzac (2005) also described a new species of the genus *Ophioscolex* from another family (Ophiomyxidae) and noted its affinities with the ophiacanthid subfamily Ophiotominae. Lyman (1883: 268), when describing the new genus *Ophiotoma*, noted that "The genus may be called an *Ophioscolex* with upper arm plates and hollow arm spines" thus highlighting the strong ophiomyxid affinities of the new genus. Indeed, some

ophiacanthid genera, particularly from the subfamily Ophiotominae, e.g. *Ophiotoma*, *Ophiotrema*, *Ophioprium*, *Ophiophrura* etc., have some ophiomyxid features, including the soft, easily damaged disk and numerous spiniform oral papillae. Whether these structures really indicate a close relationship of the Ophiomyxidae and Ophiacanthidae or merely represent a plesiomorphy or convergence is currently unclear. Despite these obvious problems, the relationship between the ophiacanthid Ophiotominae and the Ophiomyxidae previously has not been investigated and delineation between these two families remains uncertain. Paterson (1985) included the following genera in Ophiotominae: *Amphilimna* Verrill (1899), *Ophiocymbium* Lyman, 1880, *Ophiodaces* Koehler, 1922, *Ophiodelos* Koehler, 1930, *Ophiolimna* Verrill, 1899, *Ophiologimus* H.L. Clark, 1911, *Ophiomedeia* Koehler, 1906, *Ophiophrura* H.L. Clark, 1911, *Ophiopristis* Verrill, 1899, *Ophioprium* Verrill, 1899, *Ophiotoma* Lyman, 1883, *Ophiotrema* Koehler, 1896, *Ophiosparte* Koehler, 1922. Most of these genera until recently had not been studied with modern techniques, including SEM. Their actual family position remains uncertain since at least for *Amphilimna* and *Ophiosparte* alternative taxonomic placements have been suggested, considerably different from the currently accepted ones (e.g. Koehler 1922a, b; Dearborn *et al.* 1996).

Thus, one of the central aims of the present study is the delineation of the families Ophiomyxidae and Ophiacanthidae and an estimation of their relationship. Most of the genera of the subfamily Ophiotominae were reinvestigated using SEM and as many of the species from these genera were included into the study as the material allowed. Except for taxa represented only by type material, the arm spine articulations, vertebrae, radial shield, genital plates, jaws and dental plates for numerous species were investigated. SEM study of type material was restricted to the arm spine articulation and vertebrae.

The testing of the taxonomic reliability of the arm spine articulations and other features in the family Ophiacanthidae would have been impossible without a broad morphological comparative ground across the entire class Ophiuroidea. To accomplish this goal, 178 species from 105 genera and 16 families were examined (ca. 40 % of the total ophiuroid generic diversity considering 255 valid ophiuroid genera according to Fell (1960)), including 52 species from 21 genera, traditionally placed within the family Ophiacanthidae. The patterns of the arm spine articulations have been studied to assess their taxonomic value and in most cases this feature has been found to be a very useful tool for ophiuroid taxonomy and phylogeny (Martynov 2010). In the present study, spine articulations are used for taxonomic reassessment of some poorly known genera and species controversially placed, within the families Ophiacanthidae and Ophiomyxidae. Additionally, other internal features, previously rarely used in ophiuroid systematic are utilized, i.e. jaws, dental plate, articulation surface of the adradial genital plate with the radial shield articulation surface, and vertebrae.

Ophiuroid taxonomy contains so much homoplasy that even apparently distantly related groups may possess a set of similar characters, not only in external but also in internal features, that in turn suggests they need taxonomic reassessment. For example, the genera *Ophiopsila* and *Amphilimna*, originally placed in the family Amphiuroidae and externally similar to amphiuroids, are currently placed in the Ophiocomidae and Ophiacanthidae respectively, without clear explanations. It is also necessary to construct the present study as a general analysis of various features utilized across the entire class Ophiuroidea and not only within Ophiacanthidae and Ophiomyxidae. Only under such an approach is it possible to suggest a reliable framework of morphological structures useful for both taxonomy and phylogeny.

Several new species are described to illustrate the utility of the internal characters. All of them are deep-water taxa discovered in various areas of the world oceans at depths of 3000–6000 m and possess sets of external characters that *prima facie* make it difficult to unambiguously classify them as Ophiomyxidae or Ophiacanthidae. Among these taxa are several new species of the genus *Ophiocymbium*, traditionally placed in Ophiacanthidae. However SEM study of the arm spine articulations, genital plates and dental plate, does not show any similarities with major ophiacanthid genera. Instead, the arm spine articulations are similar to the pattern found in the Ophiomyxidae type genus *Ophiomyxa*, whereas the dental plate does not differ from another ophiomyxid species *Ophioscolex purpureus*. The evaluation of contradictory features in the newly described species and assessing their family placement is thus also an essential part of the present study.

This comprehensive approach helps to highlight the importance of the arm spine articulation pattern for ophiuroid taxonomy in general and for the understanding of the taxonomic placement of the newly discovered

taxa in particular, and shows that in most cases articulations in combination with some internal characters are essential for taxonomic and phylogenetic interpretations of taxa at different levels — from family to species.

## Material and methods

The present study is largely based on the numerous samples collected by the Russian deep-water expeditions. Samples obtained during cruises with different research vessels of the P.P. Shirshov Institute of Oceanology, Moscow (IORAS) from 1954 to 1992 were used (Table 3). Type and other additional specimens from the Zoological Museum of Moscow State University (ZMMU), National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), Museum of Comparative Zoology, Harvard University (MCZ), Muséum National d'Histoire Naturelle, Paris (MNHN), Zoological Institute, St. Petersburg (ZIN RAS), Icelandic Institute and Museum of Natural History, Reykjavik (NI) and Zoological Museum, Danish Museum of Natural History (ZMUC) were also examined. Skeletal elements were isolated by bleaching in domestic bleach (NaOCl), rinsed in water and dried.

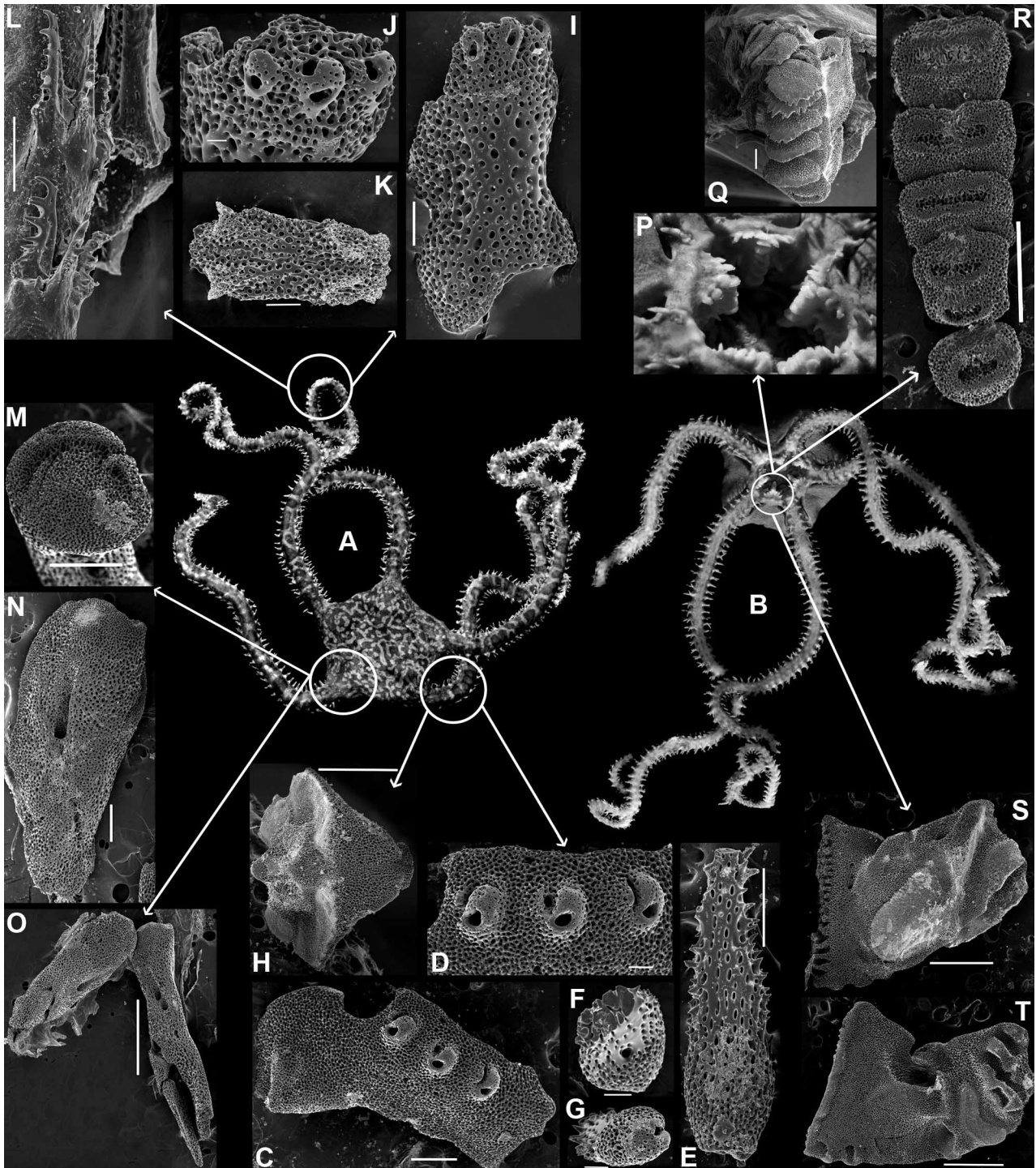
Abbreviations: abg—abradial genital plate; adp—adoral shield papillae; ag—adradial genital plate; cr—connecting ridge (between proximal edge of the spine articulation and lateral arm plate); dap—dorsal arm plate; dd—disk diameter; dp—dental plate; fdap—fragmented dorsal arm plate; gc—adradial genital plate condyle; gr—radial shield groove; grs—grove spines; gra—lateral arm plate area occupied by groove spines; gs—genital slit(s); jw—jaws; lap—lateral arm plate; lr—lateral ridge of the adradial genital plate, attachment area of the abradial genital plate; msr—most proximal arm spine articulations; no—nerve opening of the arm spine articulations or spine ventral side; mo—muscle opening of the arm spine articulations; pb—podial basin (of vertebrae); rc—radial shield condyle; re—radial shield excavation; rsh—radial shield; s—spine; sr—arm spine articulations; th—teeth; ts—tentacle scales; tsa—lateral arm plate area occupied by tentacle scales; vap—ventral arm plate; vbr—vertebrae; vp—ventral processe of the lateral arm plate

## Ophiuroid morphology: traditional and new data

The ophiuroid body is usually divided into a distinct circular or pentagonal central disc and radial rays called arms (Figs 1, 2). These features had already appeared in the Paleozoic Oegophiurida (Fig. 3). This pattern is almost invariable across any ophiuroid species. The number of arms is five in most taxa (rare exceptions in different families include species with arms numbering from six to ten). The first segments of the arms are attached to the distal jaw articulation surface and the arms continued ventrally under the disk. At the junction of arm and disk there are a peculiarly ophiuroid set of ossicles, comprised of a pair of genital plates ventrally and the radial shields dorsally (Figs 1M–O, 2L–N).

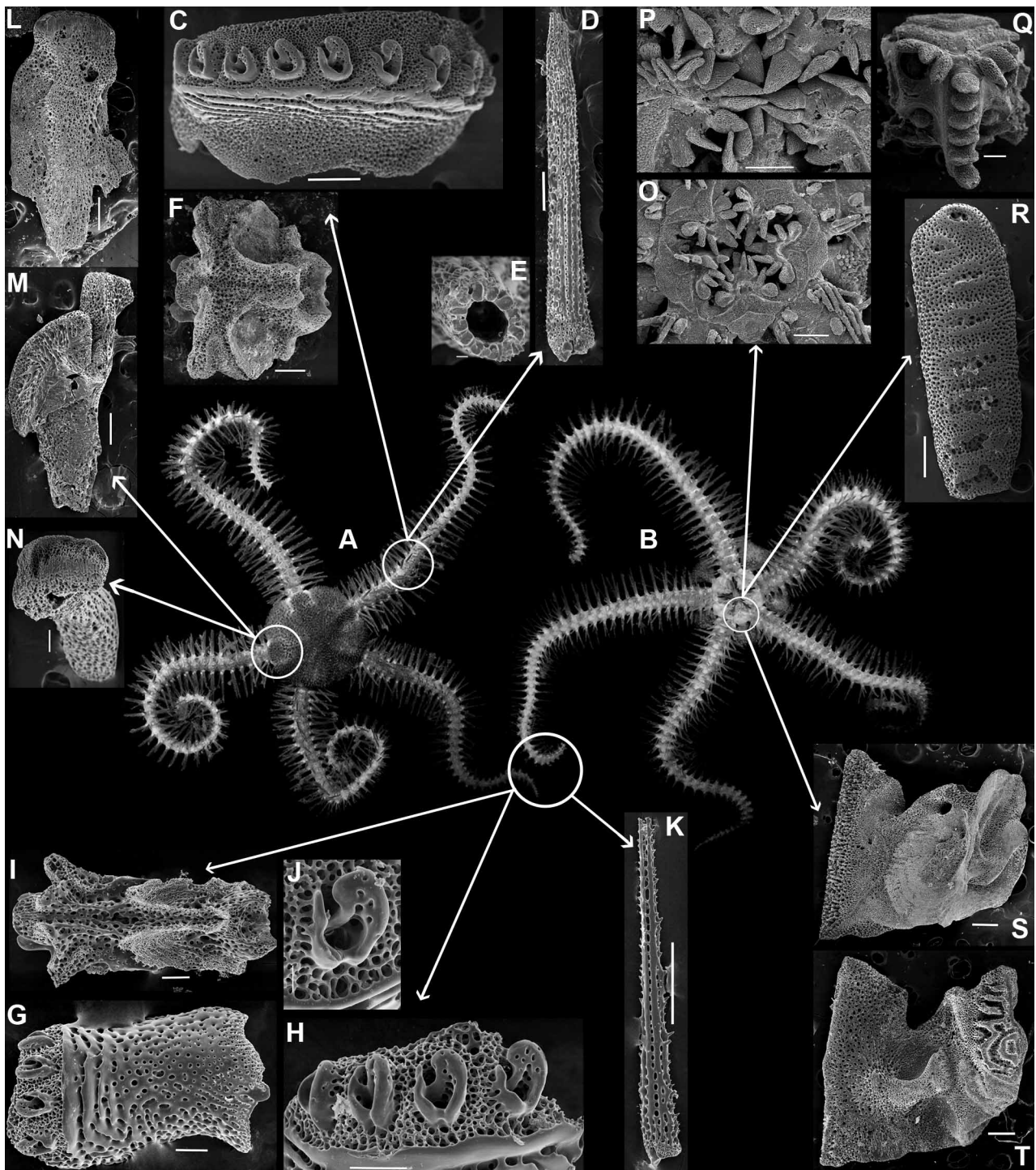
**The genital plates.** The genital plates consist of the more massive and often more elongated adradial plate (=genital plate using Matsumoto's (1917) terminology) and a usually shorter and morphologically simpler abradial genital plate (=genital scale according to Matsumoto). The genital plates border the genital (=bursal) slits, which lead to another peculiarly ophiuroid organs, the bursae, with reproductive and respiratory functions. The genital slits vary from being merely spot-like proximal openings not supported by the genital plates (many euryalids and some ophiomyxids) to well-defined long slits bordered by the genital plates in most other Ophiuroidea. The abradial genital plate articulates with the adradial genital plate in most species by means of a lateral ridge, of various shapes in different taxa (Figs 2M; 4–10). The adradial genital plate has an elaborate surface near its distal edge for articulation with the corresponding ventral surface of the radial shield (Figs 1M, N, 2L, N). The patterns of the articulation between abradial and adradial genital plates and between adradial plate and radial shield have taxonomic importance at the family, genus or species level. The following patterns are indicative for ophiuroid families.





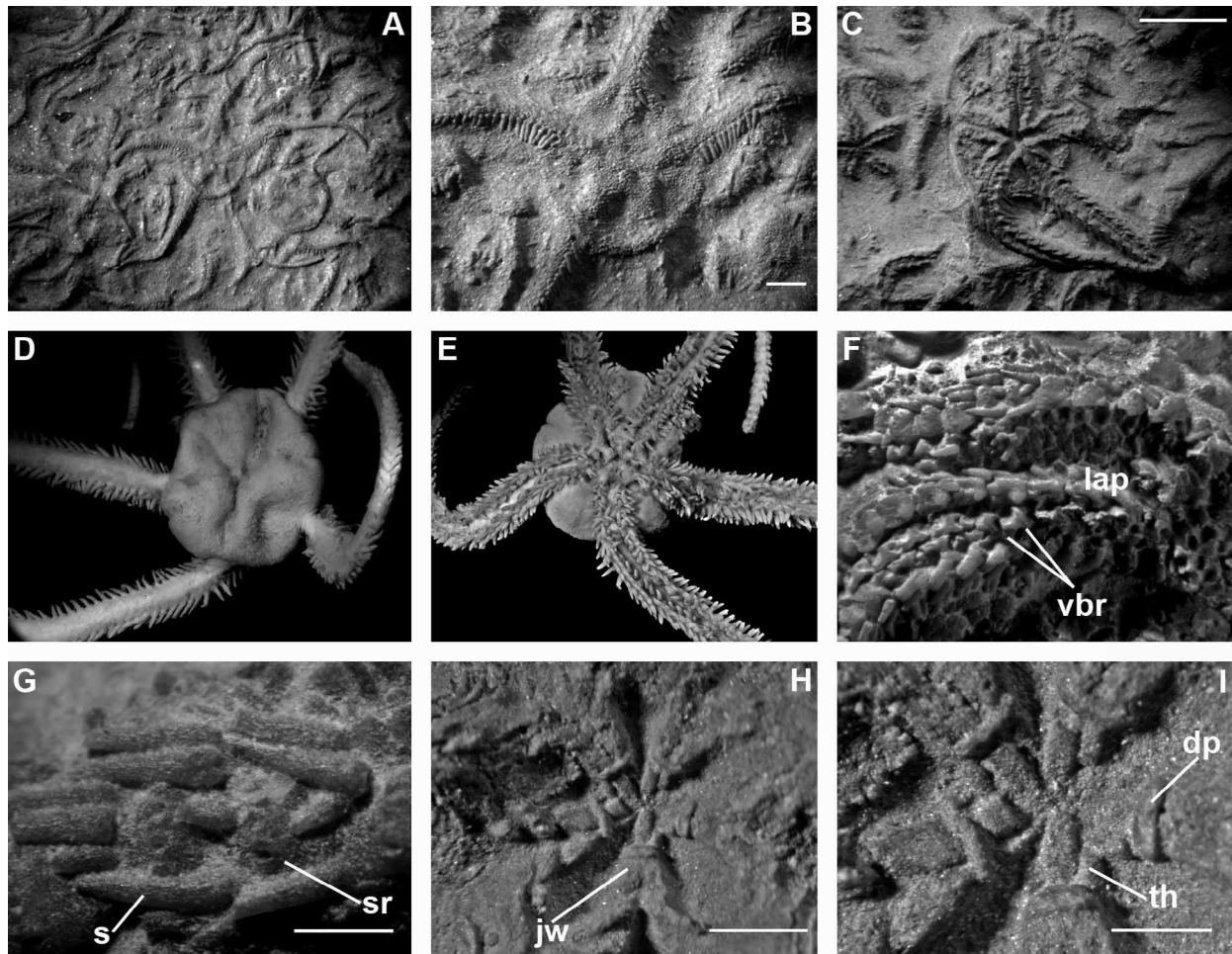
**FIGURE 1.** *Ophiomyxa pentagona* (Lamarck, 1816), ZMMU D-553, 21 mm dd, type species of the genus *Ophiomyxa*, the family Ophiomyxidae. External morphology and microstructural details. A. dorsal view; B. ventral view; C–H, proximal segments: C. lateral arm plate; D, details of arm spine articulations; E. spine; F. solid spine sectioned transversally; G. spine, ventral view; H. vertebra, dorsal view; I–L. distal segments: I. lateral arm plate; J. details of arm spine articulations; K. vertebra, dorsal view; L. distal arm segments in situ showing hooks; M. articulation surface of the adradial genital plate; N. radial shield, ventral view; O. articulating adradial genital plate and radial shield; P. general overview of the oral structures; Q. teeth in situ; R. dental plate; S. jaw, abradial view; T. jaw, adradial view; Scale bars: C, E, I, L–N, Q, 300 µm; D, F, G, K, 100 µm; J, 30 µm; H, O, R–S, 1 mm; P, 600 µm. Photos: A–B Tatiana Korshunova; C–T Alexander Martynov.





**FIGURE 2.** *Ophiacantha bidentata* (Bruzellius, 1805), ZMMU D-750, 8 mm dd, type species of the genus *Ophiacantha*, the family Ophiacanthidae. External morphology and microstructural details. A. dorsal view; B. ventral view; C–E. proximal segments: C. lateral arm plate and spine articulations; D. spine; E. hollow spine sectioned transversally; F. vertebra, dorsal view; G–K, distal segments: G. lateral arm plate; H. details of arm spine articulations; J. single spine articulations; I. vertebra, dorsal view; K. non-hooked spine; L. radial shield, ventral view; M. articulating adradial and abradial genital plates; N. articulation surface of the adradial genital plate; O. general overview of the oral structures; P. details of oral and apical papillae (showing both single and double apical papillae); Q. teeth in situ; R. dental plate; S. jaw, abradial view; T. jaw, adradial view; Scale bars: C–D, F, M–N, R–T, 300  $\mu$ ; E, J, 30  $\mu$ ; O–P, 1 mm. Photos: A–B Sergei Galkin; C–T Alexander Martynov.





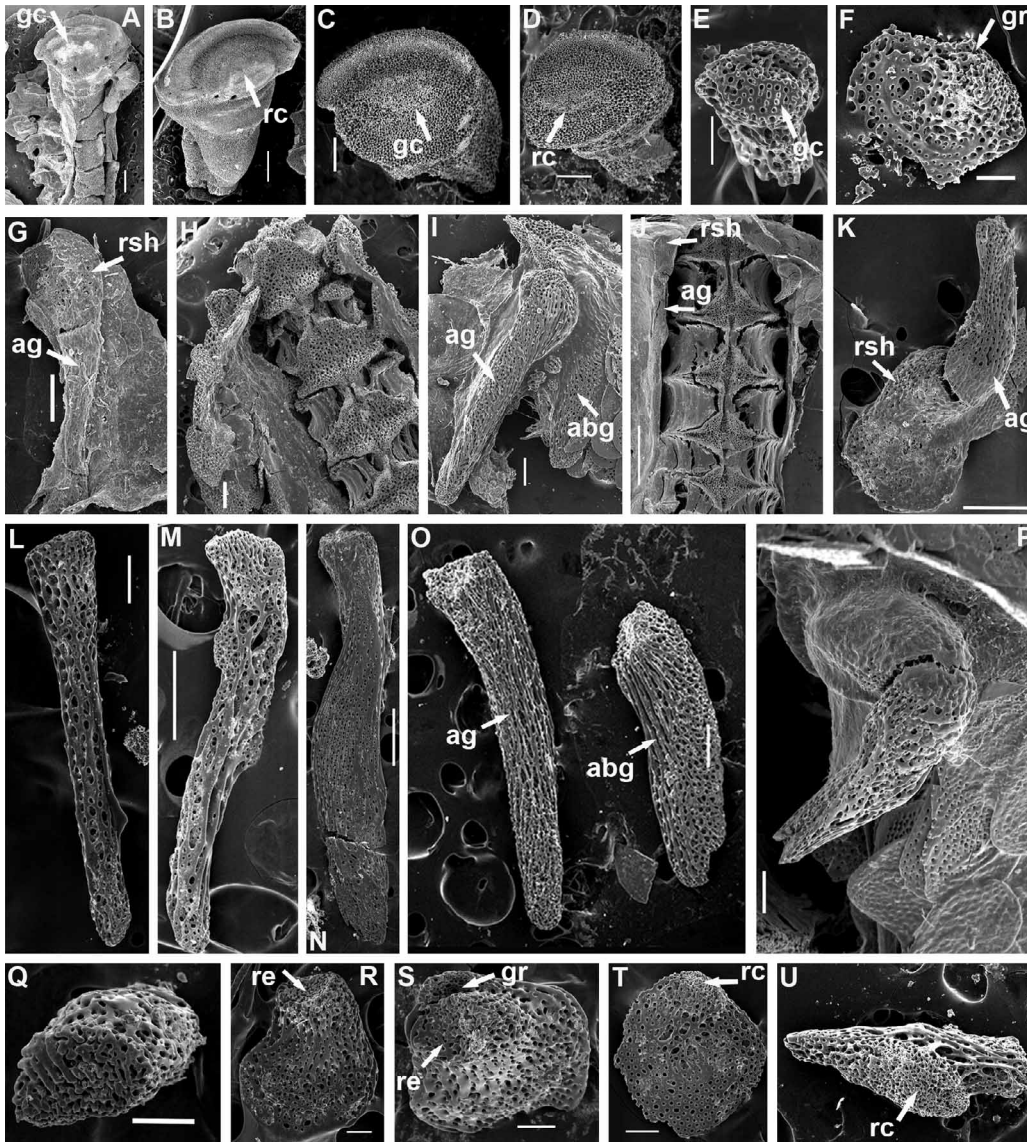
**FIGURE 3.** Representatives of the Paleozoic subclass Oegophiurida. A, *Strataster ohioensis* Kesling & Vasseur, 1971 (Mississippian strata of Ohio), paratype UMMP 58331c; B. same, disk and proximal arms details; C. paratype UMMP 58332a, ventral view; H. holotype UMMP 58329a, jaws and teeth, dorsal view; I. same, details showing dental plates and teeth; F–G, *Eugasterella thorni* Kesling, 1969 (Middle Devonian Arkona Shale, Ontario), paratype UMMP 57479, F. details of arm segments, ventral view showing unfused vertebrae and absence of the ventral arm plate; G. lateral arm plate, details, showing spine and spine articulation; D–E, Recent species of the family Ophiomyxidae, *Ophioscolex glacialis* Müller & Troschel, 1842 ZMMU D-118, 34 mm dd., dorsal and ventral view respectively. Scale bars: B, H, 1 mm; C, 5 mm; G, I, 500  $\mu$ ; Photos: A–C, H–I Daniel Miller; D–E Alexander Martynov.

Euryalida (Gorgonocephalidae, Asteronychidae and Asteroschematidae) (Figs 4A–D): abradial genital plate is considerably smaller than adradial plate, articulating without a special ridge; the articulation faces of both adradial plate and radial shield are very similar, forming a large, moderately elevated condyle.

Ophiomyxidae (Figs 4E–U): both abradial and adradial genital plates are typically considerably reduced and similar in size, though in the Ophiobyrinae they are well-defined. In some other taxa (e.g. *Ophioplexa* **gen. nov.**, *Ophiocymbium*, *Ophiologimus*) abradial genital plates are completely absent (Figs 4G, K, P). In the genus *Ophioscolex* adradial genital plates are without a distinct condyle, whereas in *Ophiomyxa* it is well-defined (Fig. 6A) The genus *Ophiocymbium* possesses a reduced, but distinct condyle (Fig. 4E). Thus, compared with other families, the Ophiomyxidae demonstrate quite a variable pattern of genital plates.

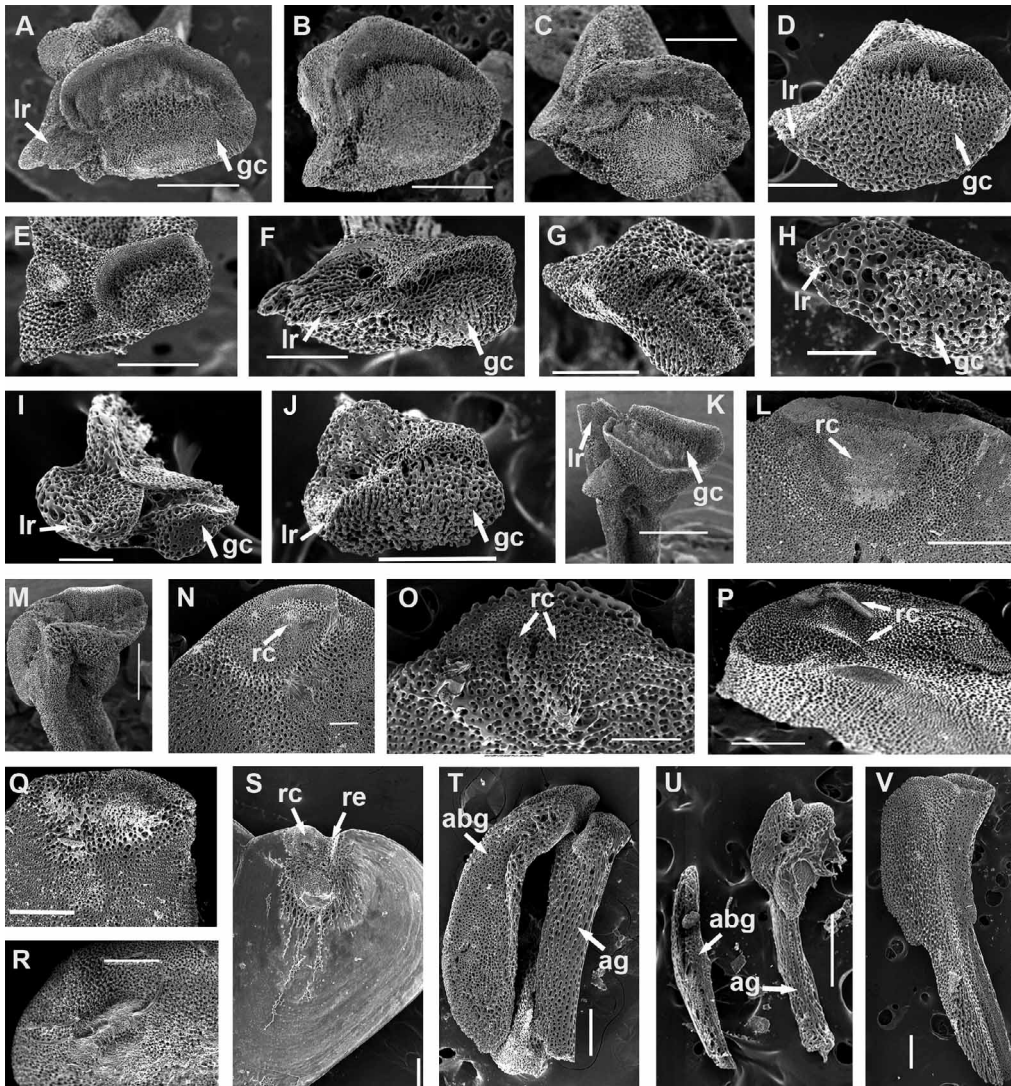
Ophiuridae (Figs 5; 65): the abradial genital plate is similar in size or slightly smaller than the adradial plate; the lateral ridge (articulating area of the abradial genital plate) starts at the same level as the adradial genital plate condyle (e.g. Figs 65H, I) and forms a characteristic lateral prolongation of various length and degree of development in different taxa (Figs 5A–K). The articulation face of the adradial plate has one well-defined condyle, bordered by a rectangular low ridge, the articulation surface of the radial shield varies across taxa, usually with 1–2 slightly conspicuous condyles, but in some groups with well-defined narrow ridges, or lacking distinct condyles.





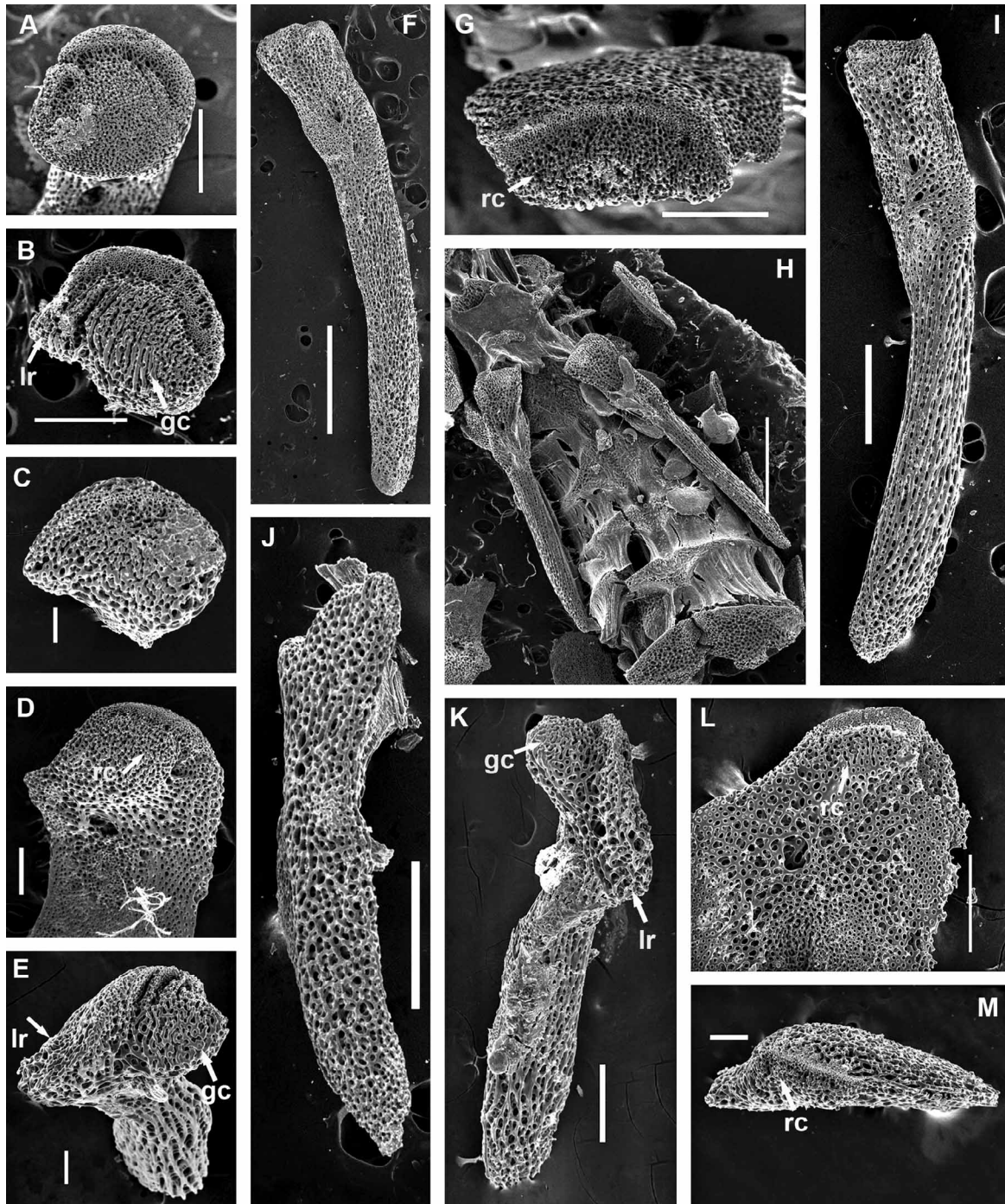
**FIGURE 4.** Genital plates and radial shields of various taxa of the families Asteronychidae, Gorgonocephalidae and Ophiomyxidae. A. *Gorgonocephalus arcticus* Leach, 1819, ZMMU D-613, 39 mm dd, adradial and abradial genital plates in situ, showing articulation surface, dorsal view; B. same, articulation surface of the radial shield, ventral view; C. *Asteronyx loveni* Müller & Troschel, 1842, ZMMU D-833, 17.5 mm dd, articulation surface of the adradial genital plate, dorsal view; D. same, articulation surface of the radial shield, ventral view. E. *Ophiocymbium cavernosum* Lyman, 1880, ZMMU D-794, 9.5 mm dd, articulation surface of the adradial genital plate, dorsal view; F. same, radial shield showing articulation surface, ventral view; G. same, articulating adradial genital plate and radial shield, dorsal view; H. *Ophiocymbium tanya* **sp. nov.**, paratype 11 mm dd, ZMMU D-801, dissected disk showing most proximal vertebrae and absence of the both genital plates and radial shield, dorsal view; I. *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-843, 18 mm dd, adradial and abradial genital plates in situ, ventral view; J. *Ophioplexa condita* **gen. et sp. nov.**, paratype ca. 17 mm dd, ZMMU D-792, dissected disk showing articulating adradial genital plate and radial shield in situ, dorsal view; K. same, separate articulating adradial genital plate and radial shield, dorsal view; L. *Ophiocymbium ninae* **sp. nov.**, paratype 5 mm dd, ZMMU D-804, adradial genital plate, dorsal view; M. *Ophiologimus* cf. *secundus* Koehler, 1914, 4 mm dd, ZMMU D-814, adradial genital plate, dorsal view; N. *Ophioplexa condita* **gen. et sp. nov.**, separate adradial genital plate, dorsal view; O. *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-843, adradial and abradial genital plates, dorsal view; P. *Ophioplexa condita* **gen. et sp. nov.**, separate articulating adradial genital plate and radial shield, dorsal view; Q. articulation surface of the adradial genital plate, dorsal view; R. radial shield, ventral view, showing distally the distinctive excavated articulation surface; S. articulation surface of the radial shield, ventral view; T. *Ophiocymbium ninae* **sp. nov.**, paratype 5 mm dd, radial shield, ventral view; U. *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-843, same, articulation surface of the radial shield, proximal view; Scale bars: A–B, 1 mm; C–D, 300  $\mu$ ; E–F, 100  $\mu$ ; G, 200  $\mu$ ; H, 300  $\mu$ ; I, 200  $\mu$ ; J, 1000  $\mu$ ; K, 300  $\mu$ ; L, 100  $\mu$ ; M, 300  $\mu$ ; N, 300  $\mu$ ; O, 200  $\mu$ ; P, 100  $\mu$ ; Q–T, 100  $\mu$ ; U, 200  $\mu$ . Photos: Alexander Martynov.





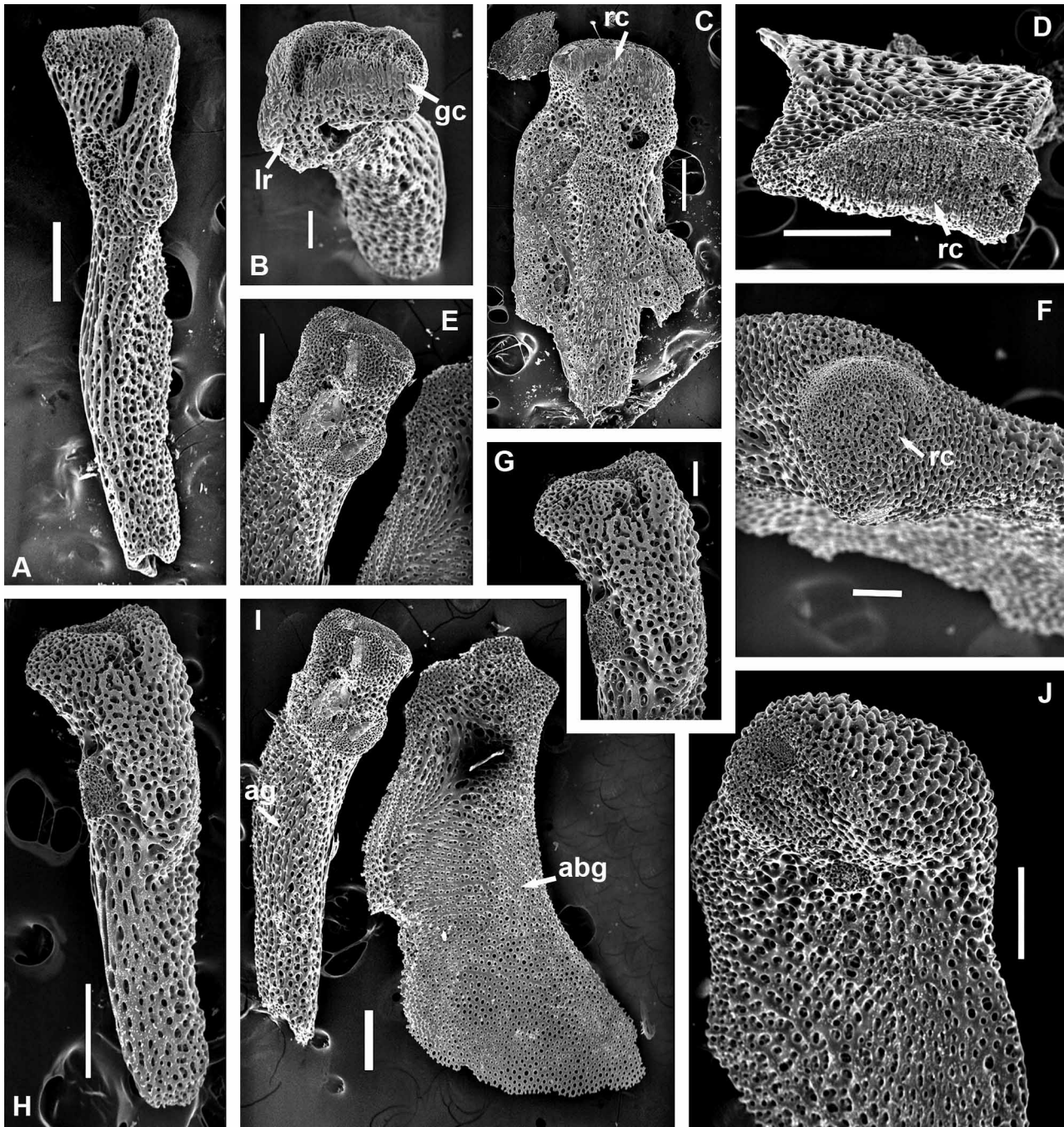
**FIGURE 5.** Genital plates and radial shields of various taxa of the family Ophiuridae. A. *Ophionotus victoriae* Bell, 1902, ZMMU D-131, sta. 888, 34 mm dd, articulation surface of the adradial genital plate, dorsal view; B. *Ophiosparte gigas* Koehler, 1922 ZIN 25/21449, 42 mm dd, articulation surface of the adradial genital plate, dorsal view; C. *Ophiopleura borealis* Danielssen & Koren, 1877, ZMMU D-319, 23 mm dd, articulation surface of the adradial genital plate, dorsal view; D. *Ophioplinthus confragosa* (Lyman, 1878), ZMMU D-733, 12 mm dd, articulation surface of the adradial genital plate, dorsal view; E. *Ophiura sarsii* Lütken, 1855, R/V, ZMMU D-821, 14 mm dd, articulation surface of the adradial genital plate, dorsal view; F. *Ophiocten sericeum*, ZMMU D-167, 9 mm dd, articulation surface of the adradial genital plate, dorsal view; G. *Ophiernus vallincola*, IORAS 13.40, 10 mm dd, articulation surface of the adradial genital plate, dorsal view; H. *Ophiophycis mirabilis* Koehler, 1901, ZMMU D-850, 5.5 mm dd, articulation surface of the adradial genital plate, dorsal view; I. *Ophioleuce* sp., ZMMU D-826, 5.5 mm dd, articulation surface of the adradial genital plate, dorsal view; J. *Ophiura* sp., ZMMU D-823, 7.5 mm dd, articulation surface of the adradial genital plate, dorsal view; K. *Ophionotus victoriae* Bell, 1902, ZMMU D-131, 34 mm dd, articulation surface of the adradial genital plate, dorso-ventral view; L. same, articulation surface of the radial shield, ventral view; M. *Ophiopleura borealis* Danielssen & Koren, 1877, ZMMU D-319, 23 mm dd, articulation surface of the adradial genital plate, ventral view; N. *Ophioplinthus confragosa*, ZMMU D-733, articulation surface of the radial shield, ventral view; O. *Ophiophycis mirabilis* Koehler, 1901, ZMMU D-850, 5.5 mm dd, articulation surface of the radial shield, ventral view; P. *Ophiura sarsii*, ZMMU D-821, articulation surface of the radial shield, distal view; Q. *Ophiura* sp., ZMMU D-823, articulation surface of the radial shield, ventral view; R. *Ophiernus vallincola*, IORAS 13.40, articulation surface of the radial shield, ventral view; S. *Ophioleuce* sp., ZMMU D-826, radial shield, ventral view; T. *Ophiura* sp., ZMMU D-823, articulating adradial and abradial genital plates, lateral view; U. *Ophioleuce* sp., ZMMU D-826, 5.5 mm dd, adradial and abradial genital plates, lateral views; V. *Ophioplinthus confragosa* (Lyman, 1878), ZMMU D-733, 12 mm dd, adradial genital plate, lateral view; Scale bars; A, 800  $\mu$ ; B, 800  $\mu$ ; C, 600  $\mu$ ; D, 300  $\mu$ ; E, 400  $\mu$ ; F, 200  $\mu$ ; G, 300  $\mu$ ; H, 120  $\mu$ ; I, 300  $\mu$ ; J, 300  $\mu$ ; K,L, 1 mm; M, 800  $\mu$ ; N, 300  $\mu$ ; O, 200  $\mu$ ; P, 600  $\mu$ ; Q, 300  $\mu$ ; R, 300  $\mu$ ; S, 300  $\mu$ ; T, 300  $\mu$ ; U, 300  $\mu$ ; V, 300  $\mu$ . Photos: Alexander Martynov.





**FIGURE 6.** Genital plates and radial shields of various taxa of the families Ophiomyxidae and Ophiacanthidae. A. *Ophiomyxa pentagona* (Lamarck, 1816), ZMMU D-553, 21 mm dd, articulation surface of the adradial genital plate, dorsal view; B. *Ophiotoma assimilis* Koehler, 1904, ZMMU D-807, 18.5 mm dd, articulation surface of the adradial genital plate, dorsal view; C. *Ophiotoma alberti* (Koehler, 1896), ZMMU D-810, 12 mm dd, articulation surface of the adradial genital plate, dorsal view; D. same, articulation surface of the radial shield, ventral view; E. *Ophiolimna perfida* (Koehler, 1904), ZMMU D-808, 9 mm dd, articulation surface of the adradial genital plate, dorsal view; F. *Ophiotoma assimilis* Koehler, 1904, ZMMU D-807, adradial genital plate, dorsal view; G. same, articulation surface of the radial shield, distal view; H. *Ophiotoma alberti* (Koehler, 1896), ZMMU D-810, dissected disk showing genital plates in situ in relation to the vertebrae, dorsal view; I. same, adradial genital plate; J. same, abradial genital plate; K. *Ophiolimna perfida* (Koehler, 1904), ZMMU D-808, adradial genital plate, dorsal view; L. same, radial shield showing articulation surface, ventral view; M. same, articulation surface of the radial shield, distal view; Scale bars: A, 300  $\mu$ ; B, 400  $\mu$ ; C–D, 100  $\mu$ ; E, 300  $\mu$ ; F, 100  $\mu$ ; G, 400  $\mu$ ; H, 1 mm; I–J, 500  $\mu$ ; K–L, 300  $\mu$ ; M, 100  $\mu$ . Photos: Alexander Martynov.



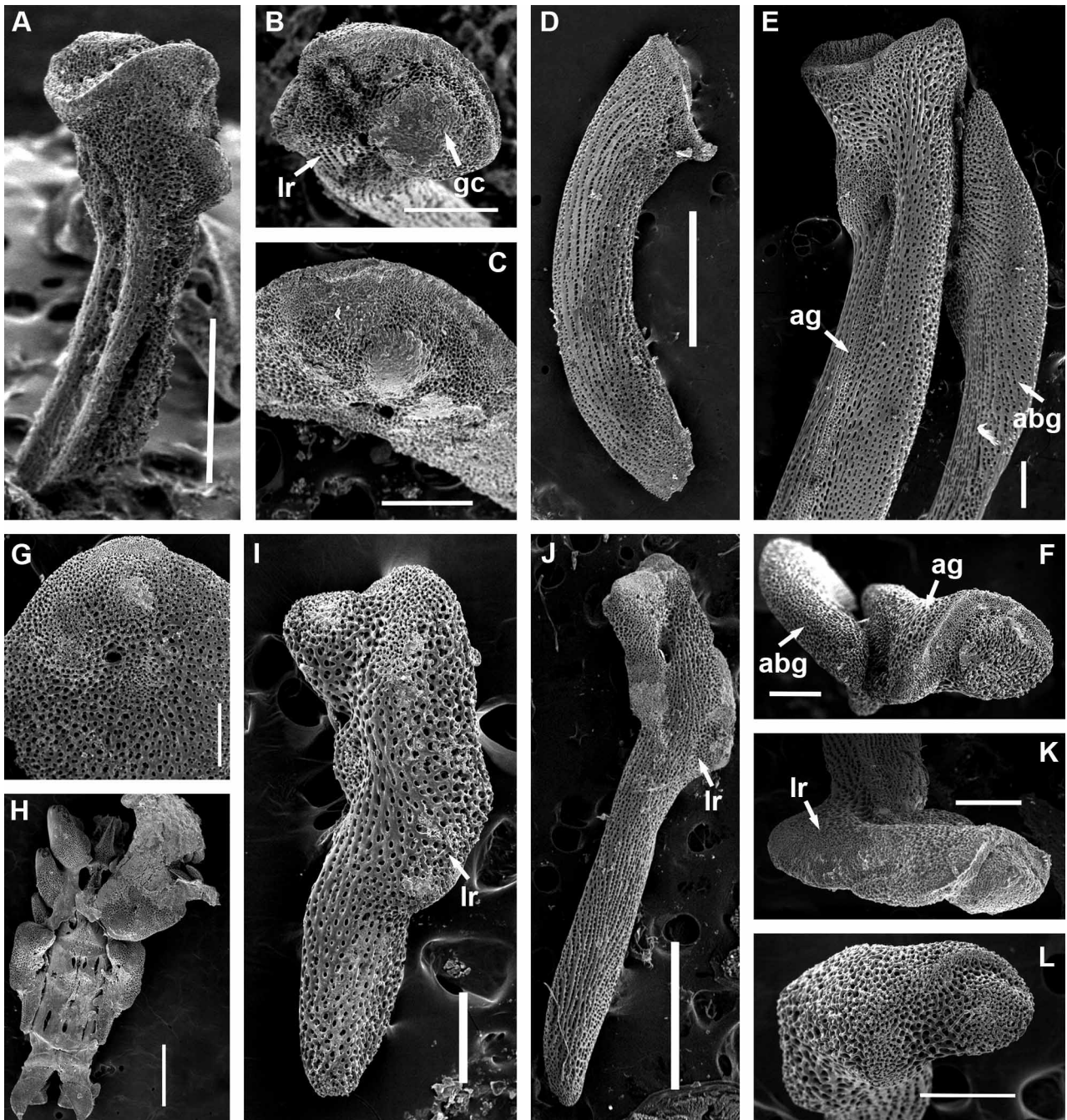


**FIGURE 7.** Genital plates and radial shields of various taxa of the family Ophiacanthidae. A. *Ophiacantha bidentata* (Bruzelius, 1805), ZMMU D-750, 8 mm dd, adradial genital plate, dorsal view; B. same, articulation surface of the adradial genital plate, dorsal view; C. same, radial shield, ventral view; D. same, articulation surface of the radial shield, distal view; E. *Ophiocamax vitrea* Lyman, 1878, ZMMU D-811, 9 mm dd, articulation surface of the adradial genital plate, dorsal view; F. same, radial shield articulation surface, distal view; G. *Ophiomoeris obstricta* (Lyman, 1878), ZMMU D-855, dd 5 mm dd, articulation surface of the adradial genital plate, dorsal view; H. *Ophiomoeris obstricta* (Lyman, 1878), adradial genital plate, dorsal view; I. *Ophiocamax vitrea*, adradial and abradial genital plates, dorsal views; J. *Ophiomoeris obstricta* (Lyman, 1878), ZMMU D-855, articulation surface of the radial shield, ventral view. A, 300  $\mu$ ; B, 100  $\mu$ ; C–E, 300  $\mu$ ; F, 100  $\mu$ ; G–J, 300  $\mu$ . Photos: Alexander Martynov.

Ophiacanthidae (Figs 6; 7; 47G, H; 78G; 82J): abradial genital plate similar in size or slightly smaller than adradial plate and articulating below level of the adradial plate condyle (e.g. 78G); articulation surface of the adradial plate varies from slightly elevated elongated condyle (e.g. *Ophiacantha bidentata*, Fig. 7B;

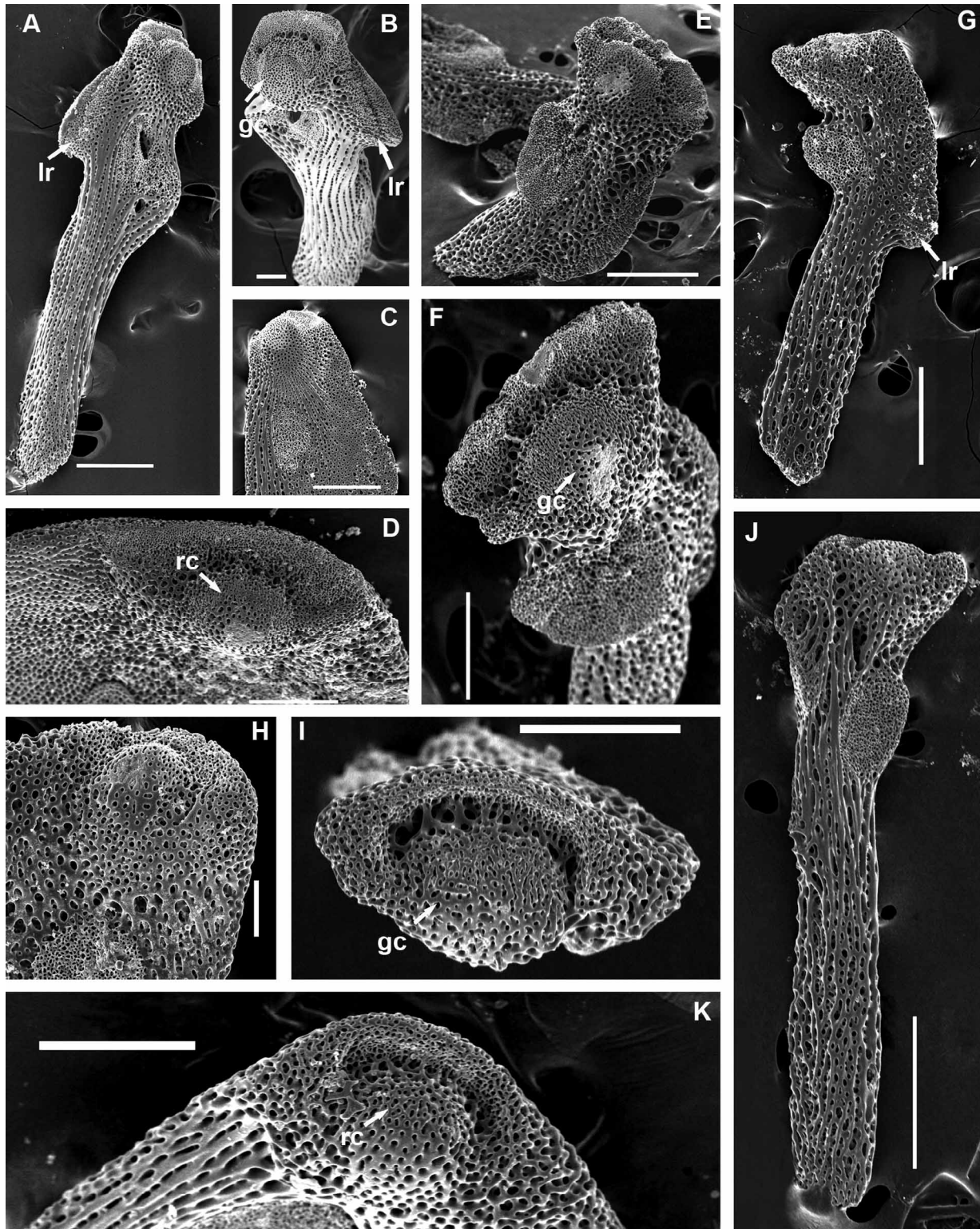


*Ophiolimna bairdi*, Fig. 82J) to well-defined asymmetrically placed condyle (*Ophiolimna perfida*, Fig. 6E, *Ophiotreta larissae*, Fig. 78I). A somewhat intermediate condition was found in *Ophiotrema alberti* and *Ophiotoma assimilis* (Figs 6B, C). Radial shields with a single weakly defined condyle.



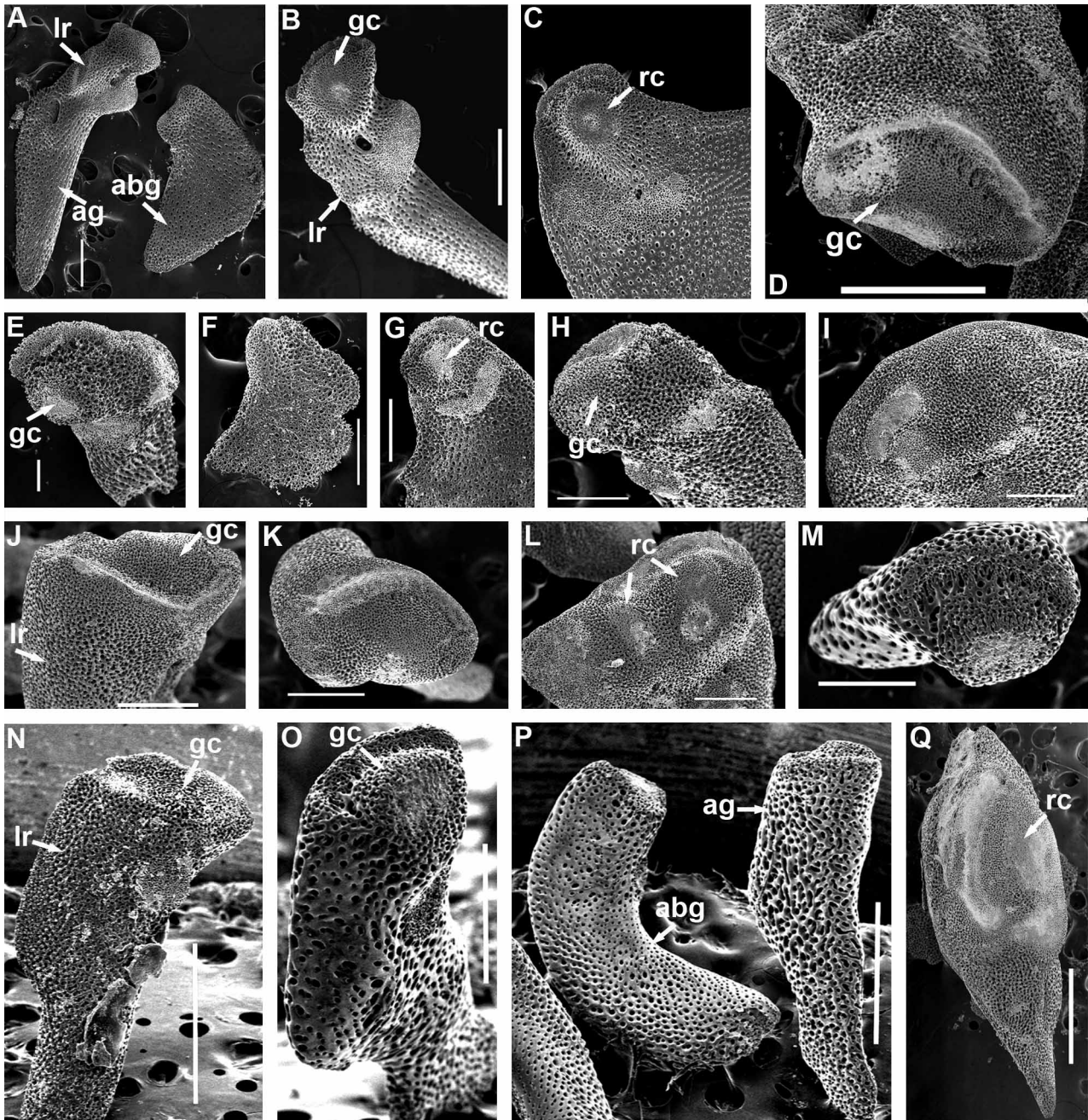
**FIGURE 8.** Genital plates and radial shields of various taxa of the families Ophiocomidae, Ophionereididae and Ophiodermatidae. A. *Ophiocoma pica* Müller & Troschel, 1842, ZMMU D-551, 13.5 mm dd, adradial genital plate, ventral view; B. same, articulation surface of the adradial genital plate, dorsal view; C. same, radial shield articulation surface of the radial shield, distal view; D. same, abradial genital plate, dorsal view; E. *Ophiocomina nigra* (Abildgaard in O.F. Müller, 1789), ZMMU D-309, 17 mm dd, articulating adradial and abradial genital plates, dorsal view; F. same, articulation surface of the adradial genital plate, dorsal view; G. *Ophiopeza spinosa* (Ljungman, 1867), ZMMU D-819, 6 mm dd, articulation surface of the radial shield, ventral view; H. same, adradial genital plate and radial shield in situ, dorsal view; I. same, adradial genital plate, dorsal view; J. *Ophionereis schayeri* (Müller & Troschel, 1844), ZMMU D-820, 12 mm dd, adradial genital plate, dorsal view; K. same, articulation surface of the adradial genital plate, dorsal view; L. *Ophiopeza spinosa*, articulation surface of the adradial genital plate, dorsal view; Scale bars: A, 600  $\mu$ ; B–C, 300  $\mu$ ; D, 800  $\mu$ ; E–F, 300  $\mu$ ; G, 300  $\mu$ ; H, 300  $\mu$ ; I, 300  $\mu$ ; J–L, 300  $\mu$ . Photos: Alexander Martynov.





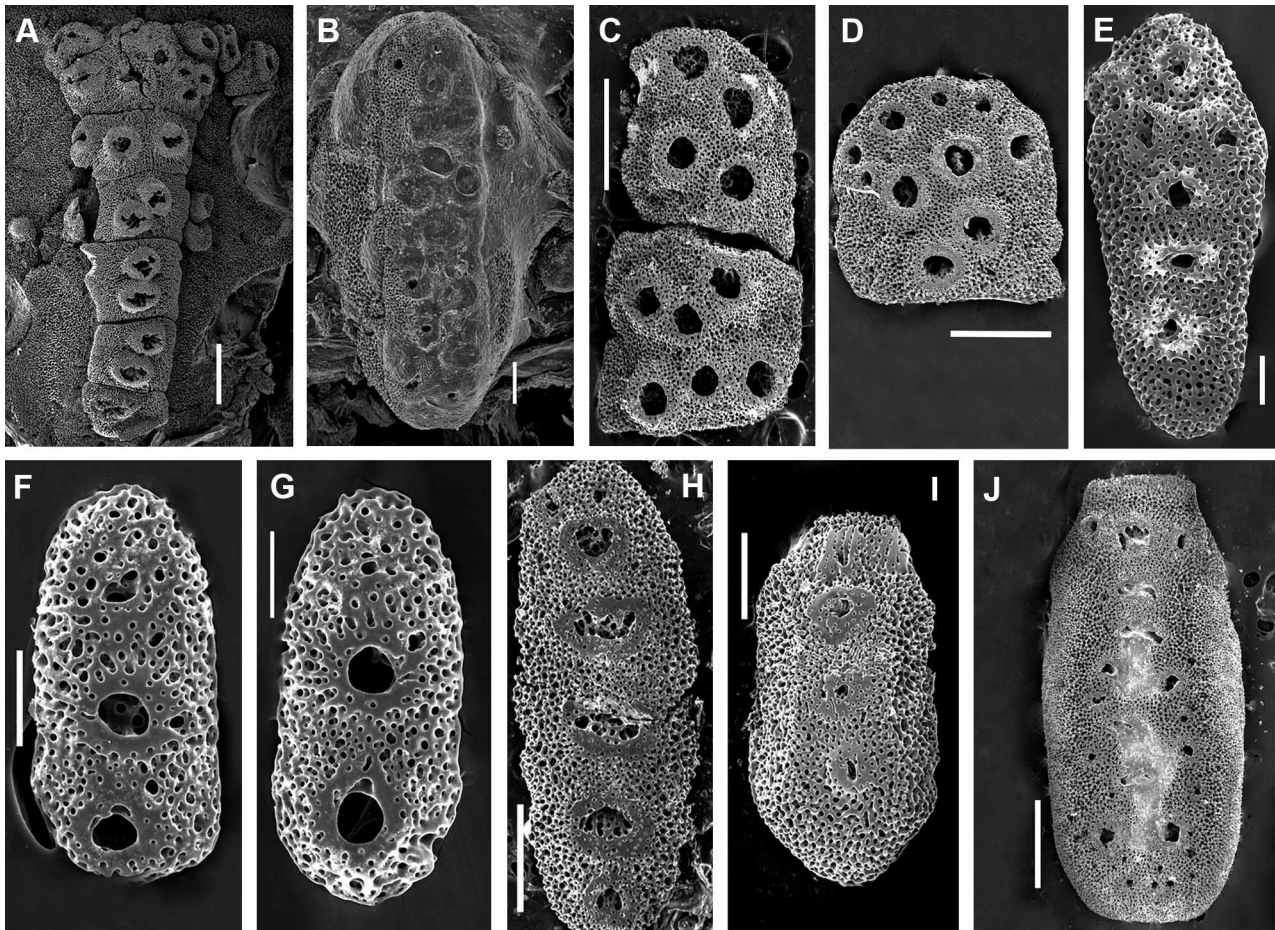
**FIGURE 9.** Genital plates and radial shields of various taxa of the families Amphiuroidae and Ophiactidae. A. *Amphipholis kochii* Lütken, 1872, ZMMU D-142, 8 mm dd, adradial genital plate, dorsal view; B. same, articulation surface of the adradial genital plate, dorsal view; C. same, articulation surface of the radial shield, ventral view; D. *Amphioplus* sp., ZMMU D-849, 6 mm dd, radial shield, distal view; E. same, adradial genital plate, dorsal view; F. same, articulation surface of the adradial genital plate, dorsal view; G. *Histampica duplicata* (Lyman, 1875), ZMMU D-729, 5.5 mm dd, adradial genital plate, dorsal view; H. same, articulation surface of the radial shield, ventral view; I. *Ophiactis abyssicola* (M. Sars, 1861), ZMMU D-631, 6 mm dd, articulation surface of the adradial genital plate, dorsal view; J. same, adradial genital plate, dorsal view; K. same, articulation surface of the radial shield, ventral view. Scale bars: A–D, 300  $\mu$ ; E–F, 200  $\mu$ ; G, 300  $\mu$ ; H, 100  $\mu$ ; I–J, 200  $\mu$ ; K, 40  $\mu$ . Photos: Alexander Martynov.





**FIGURE 10.** Genital plates and radial shields of various taxa of the families Ophiotrichidae, Ophiolepididae and Ophiordermatidae. A. *Ophiothrix fragilis* (Abildgaard, 1789), ZMMU D-827, 8 mm dd, adradial and abradial genital plates, dorsal view; B. same, enlarged adradial genital plate, dorsal view; C. articulation surface of the radial shield, ventral view; D. *Ophioderma* sp., ZMMU D-832, 27 mm dd, articulation surface of the adradial genital plate, dorsal view; E. *Ophiothela danae* Verrill, 1869, ZMMU D-828, 5 mm dd, adradial genital plate, dorsal view; F. same, abradial genital plate, dorsal view; G. same, articulation surface of the radial shield, ventral view; H. *Ophiolepis elegans* Lütken, 1859, IORAS 15.99, 9 mm dd, articulation surface of the adradial genital plate, dorsal view; I. same, articulation surface of the radial shield, ventral view; J. *Ophioplocus imbricatus* (Müller & Troschel, 1842), ZMMU D-20, 18 mm dd, articulation surface of the adradial genital plate, ventral view; K. same, dorsal view; L. same, articulation surface of the radial shield, ventral view; M. *Ophiopenia tetracantha* H.L. Clark, 1911, ZMMU D-580, 8.5 mm dd, articulation surface of the adradial genital plate, dorsal view; N. *Ophiolepis elegans* Lütken, 1859, IORAS 15.99, 9 mm dd, adradial genital plate, dorsal view; O. *Ophiopenia tetracantha*, ZMMU D-580, adradial genital plate, dorsal view; P. same, adradial and abradial genital plates, dorsal view; Q. *Ophioderma* sp., ZMMU D-832, articulation surface of the radial shield, distal view; Scale bars: A-B, 300  $\mu$ ; C, 100  $\mu$ ; D, 1 mm; E, 100  $\mu$ ; F, 300  $\mu$ ; G, 300  $\mu$ ; H, 300  $\mu$ ; I, 400  $\mu$ ; J, 400  $\mu$ ; K, 400  $\mu$ ; L, 400  $\mu$ ; M, 300  $\mu$ ; N, 300  $\mu$ ; O, 200  $\mu$ ; P, 200  $\mu$ ; Q, 1 mm. Photos: Alexander Martynov.





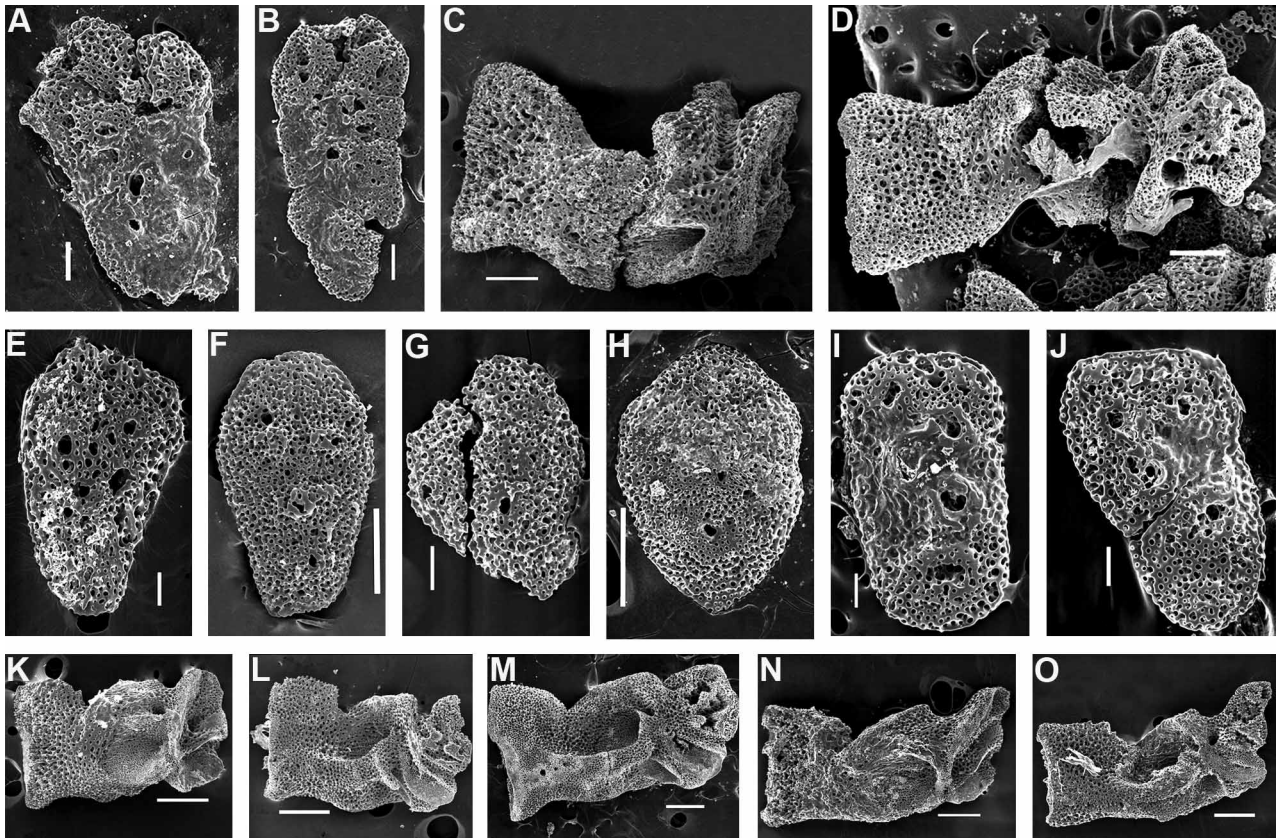
**FIGURE 11.** Dental plates of various taxa of the families Gorgonocephalidae, Asteronychidae, and Ophiuridae. A. *Gorgonocephalus arcticus* Leach, 1819, ZMMU D-613, 39 mm dd, dental plate in situ; B. *Asteronyx loveni* Müller & Troschel, 1842, ZMMU D-833, 17.5 mm dd, dental plate in situ; C. *Asteronyx loveni* Müller & Troschel, 1842, ZMMU D-851, 32 mm dd, part of the dental plate; D. *Ophionotus victoriae* Bell, 1902, ZMMU D-131, 34 mm dd, ventral part of the dental plate; E. *Ophiura* sp., ZMMU D-823; F,G, *Ophioleuce* sp., ZMMU D-826, 5.5 mm dd; H. *Ophiernus vallincola* IORAS 13.40, 10 mm dd; I. *Ophioplinthus confragosa* (Lyman, 1878), ZMMU D-733, 12 mm dd; J. *Ophiopleura borealis* ZMMU D-319, 23 mm dd; Scale bars: A, 1 mm; B, 300 µm; C,D, 600 µm; E–H, 100 µm; J, 1 mm. Photos: Alexander Martynov.

Ophiodermatidae, Ophiocomidae and Ophionereididae (Figs 8; 10D, Q): abradial genital plate similar in size or slightly smaller than adradial plate and articulating below level of the adradial plate condyle (e.g. 8E); the articulation surface of the adradial plate has a characteristic, well-defined, asymmetrically placed condyle (Figs 8B, F, K, L) (the only exception was found in the genus *Ophioderma*—having 1–2 irregular massive condyles, Fig. 10D). Radial shield with single or few weakly defined condyles.

Ophiochitonidae: abradial genital plate similar in size or slightly smaller than adradial plate and articulating below level of the adradial plate condyle; articulation surface of the adradial plate with weakly defined asymmetrically placed condyle (in *Ophiochiton ternispinus*, present study), or distinct prominent condyle (in *Ophiochiton fastigatus*, see Matsumoto, 1917) bordered by a low ridge. Adradial genital plates lie close to each other, but not in contact over the proximal vertebrae. The articulation face of the radial shield has one weakly defined condyle and an excavation.

Amphilepididae: abradial genital plate similar in size or slightly smaller than adradial plate, both weakly developed, articulating below level of the adradial plate condyle; articulation surface of the adradial plate has a weakly defined symmetrically placed condyle bordered by a low ridge. Adradial genital plates over the proximal vertebrae lie close to each other but not in contact. Radial shield with single compact, well-defined condyle.





**FIGURE 12.** Dental plates and jaws of the genera *Ophioscolex*, *Ophiocymbium* and *Ophiologimus*. A–B, *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-843, 18 mm dd, dental plates; C–D, *Ophiocymbium tanyae* sp. nov., paratype 11 mm dd, ZMMU D-801, abradial and adradial views of the jaws respectively; E. same, dental plate; F. *Ophiocymbium ninae* sp. nov., paratype 5 mm dd, ZMMU D-803, dental plate; G. *Ophiocymbium ninae* sp. nov., paratype 5 mm dd, ZMMU D-805, dental plate; H. *Ophiocymbium cavernosum* Lyman, 1880, ZMMU D-794, 9.5 mm dd, dental plate; I–J, *Ophiologimus* cf. *secundus* Koehler, 1914, ZMMU D-815, 4 mm dd, dental plates; K–L, *Ophiocymbium ninae* sp. nov., paratype 5 mm dd, ZMMU D-805, abradial and adradial views of the jaws respectively; M. *Ophiocymbium cavernosum* Lyman, 1880, ZMMU D-794, 9.5 mm dd, jaw, adradial view; N–O, *Ophiologimus* cf. *secundus* Koehler, 1914, ZMMU D-815, 4 mm dd, abradial and adradial views of the jaws respectively; Scale bars: A, 200  $\mu$ ; B, 200  $\mu$ ; C–D, 300  $\mu$ ; E, 100  $\mu$ ; F, 300  $\mu$ ; G, 100  $\mu$ ; H, 300  $\mu$ ; I–J, 100  $\mu$ ; K–L, 300  $\mu$ ; M, 100  $\mu$ ; N–O, 300  $\mu$ . Photos: Alexander Martynov.

Ophiactidae and Amphiuridae (Figs 9; 39I): abradial genital plate similar in size or slightly smaller than adradial plate and articulating below level of the adradial plate condyle (Fig. 9A, B); articulation surface of the adradial plate has a well-defined symmetrically placed condyle bordered by a low ridge. Adradial genital plates over the proximal vertebrae lie in contact to each other (Fig. 39I), forming a characteristic amphiuroid pattern. Radial shield with single, compact, well-defined condyle.

Ophiolipididae (Figs 10H–O): abradial genital plate similar in size or slightly smaller than adradial plate and articulating below level of the adradial plate condyle (Figs 10I, N); articulation face of the adradial plate with weakly defined condyle bordered by a low ridge. Radial shield with 1–2 weakly defined condyles.

Ophiotrichidae (Figs 10A–C, E–G): abradial genital plate similar in size or slightly smaller than adradial plate and articulating below level of the adradial plate condyle (Figs 10A, B); articulation surface of the adradial plate with well-defined condyle, bordered by a low ridge. Radial shield with single compact well-defined condyle.

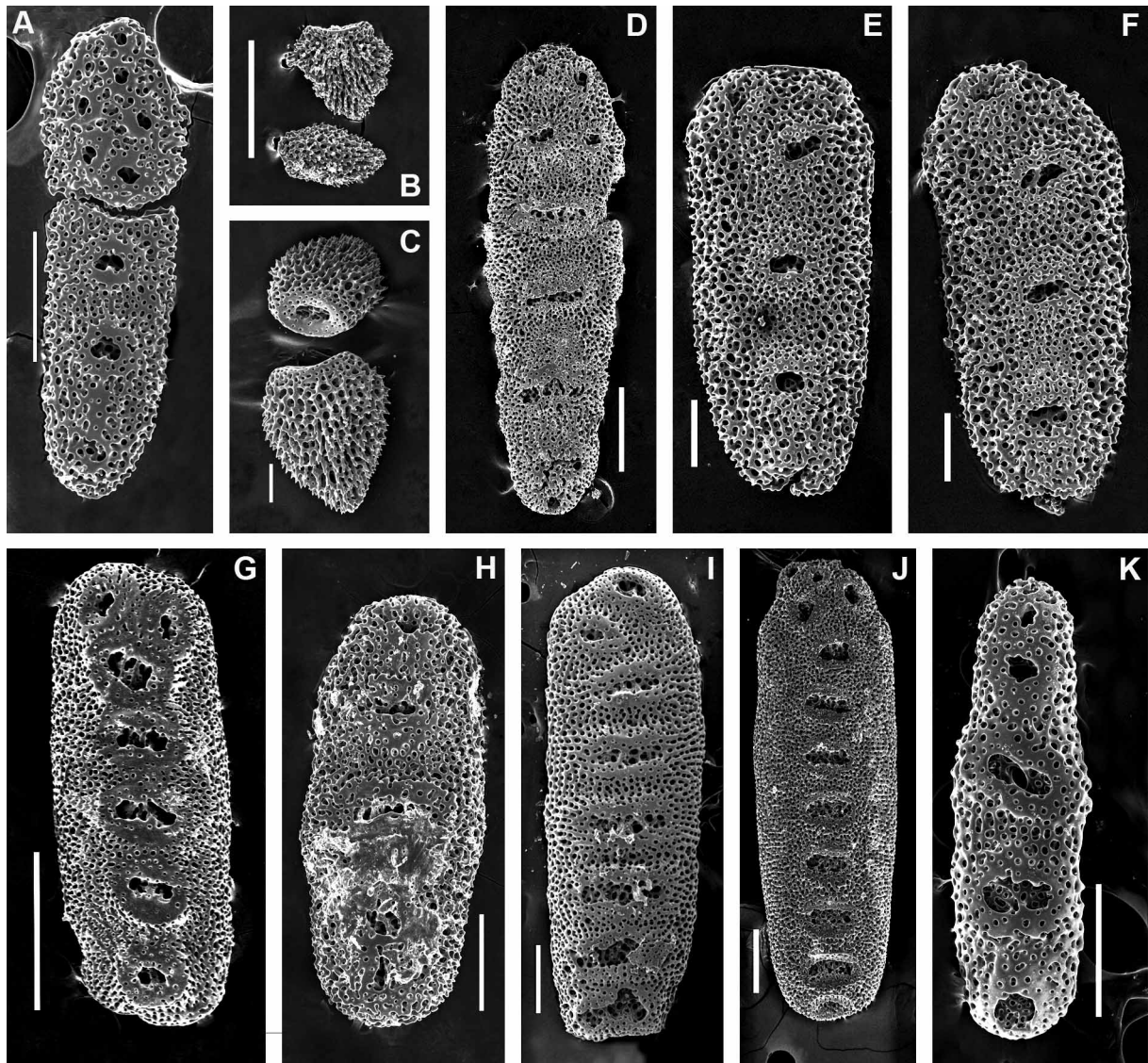
**Disc scales.** Dorsally the disk is covered with varying numbers of scales. The degree of differentiation of the disk scales, their sizes and homo- or heterogeneity are usually characteristic for particular genera and species. Numerous disk scales, which completely obscure the initial postlarval six primary plates rosette (one central and five radial plates), are characteristic of the adult condition in many taxa. Instead, appearance at the

adult stage of a well defined primary plate rosette, which occupies a considerable part of the entire dorsal disk surface is a sign for the pedomorphic origin of a species (Belyaev & Litvinova 1972; Vadon 1990; Martynov unpublished data). Disk scales in turn can be covered with various armouring. These additional structures are traditionally referred to as spines, spinelets (small spines) and granules. Such structures are mosaically distributed within various families, including distantly related ones. Some taxa possess a peculiar pattern of the disk scale covering. For instance, euryalids usually lack disk spinelets, but a few genera have short massive spines dorsally on the radial shields and adjacent regions. Many taxa of the family Ophiacanthidae instead possess well defined spines or spinelets (e.g. *Ophiacantha*), but some have an entirely smooth disk (e.g. *Ophiotoma*) or densely covered with numerous small granules (e.g. *Ophiolimna*) (Fig. 44). Similar granules are a typical condition in most taxa of the families Ophiocomidae and Ophiodermatidae (e.g. Figs 44E; 81C, D). The appearance of a very similar external disk morphology, including densely placed granules, between the distantly related families Ophiuridae (genera *Ophiostriatius*, *Bathylepta* etc.) (Figs 81E, F), Ophiocomidae and Ophiodermatidae, demonstrates one of many restriction of using exclusively external features in Ophiuroidea and thus will be the matter of special attention in the present study. Comparison of granule shape across particular taxa has been attempted by SEM (Irimura 1988), but granule morphology still remains untested as a taxonomically reliable character. Relatively long disk spines have also been found in some taxa of the family Amphiuridae (e.g. *Dougaloplus*) and in most taxa of the family Ophiotrichidae.

**Oral structures.** The inside and ventral part of the central disk are occupied by elaborate oral structures, placed usually in five sets, corresponding to the radius number (or more in few exceptions) (Figs 1B, P, Q; 2B, O, P). Proximal to the first arm vertebrae, structures are modified into paired oral plates or half-jaws (Figs 1–2, S, T). Both vertebrae and jaws are homological to the ambulacral plates of Asteroidea (Hendler 1978). The distal abradial surface of the jaw articulates with the first vertebrae usually forming a rib and few sharp folds. Distal articulation surfaces on the adradial surfaces of each half-jaw of a pair possess an area of low convoluted folds (Figs 1–2, S–T). The pattern of these folds may considerably differ within various taxa, but their taxonomic importance was not investigated in this study. The jaws are variable in shape and relative height. The proportions of the jaws vary within different families (Figs 1S, T; 2S, T; 12C–D, K–O). Generally, in postlarval stages jaws are elongated and distinctly comprised from two pieces, as a clear sign of their origin by fusion of two ambulacral plates (Hendler 1978; 1988; Martynov unpublished data). Adult jaws are usually higher than postlarval ones and traces of the fusion often completely disappear, but in some taxa they remain as a vertical suture. The ventral distal jaw edge bears distinct openings for oral papillae in several unrelated taxa. In some (e.g. *Ophiomyxa*) these openings are bordered with low elevations (Fig. 1T). The pattern and number of oral papillae are traditionally one of the most reliable ophiuroid taxonomic characters. The present study emphasizes the importance of the various internal features, does not discard the usefulness of the oral papillae morphology, but cautions towards a more careful application. Numerous long spiniform oral papillae are characteristic for some euryalids and ophiomyxids (Figs 15A–D) and possibly are plesiomorphic state of this character. Many genera of the ophiacanthid subfamily Ophiotominae also possess spiniform oral papillae, but these are usually shorter. The ancestral state of the oral papillae also implies their homogeneity and similarity in size and shape from the distal to the proximal jaw area. In different families oral papillae are differentiated, distalmost papillae often modified into wider and operculiform shape, proximal papillae narrower. Wide distalmost papillae are characteristic for some ophiacanthids (genus *Ophiolimna*, some species of the genus *Ophiacantha*) (Fig. 44) and for all genera of the families Ophionereididae, Ophiocomidae and Ophiodermatidae. The particular pattern of the oral papillae differentiation is an important taxonomic character for distinguishing genera in the family Amphiuridae. A special case is represented by block-shaped (rectangular, much wider than high) oral papillae. Such papillae (usually one papilla on each jaw edge) are widespread at postlarval and some juvenile stages of various non-related ophiuroids. In presumably pedomorphic taxa, block-shaped paired papillae persist into the adult stage (Vadon 1990; Martynov unpublished data). Therefore, using the block-shaped papillae as an indicator of relationship is problematic, since they can easily appear in taxa with different forms of adult oral papillae belonging to different families. Block-shaped papillae have been found in many small pedomorphic genera of the family Ophiuridae (*Ophiomisidium*, *Opiopyrgus*, *Astrophiura*, *Perlophiura*, and others), but are also known for the relatively



large-sized ophiurid genus *Ophiocten*, in apparently ophiacanthid genera *Ophiocymbium* and *Ophiothamnus*, in many amphiuroids and in some Ophiolepididae. The block-shaped papilla has been specially termed as the buccal scale (Hendler 1978; Stöhr 2005).



**FIGURE 13.** Dental plates and teeth of various taxa of the family Ophiacanthidae. A. *Ophiorupta discrepans* (Koehler, 1922) **comb. nov.**, ZMMU D-806, ca. 7 mm dd, dental plate, the transverse fissure is not natural; B. same, teeth; C. *Ophiotoma alberti* (Koehler, 1896), ZMMU D-810, 12 mm dd, teeth; D. *Ophiotoma assimilis* Koehler, 1904, ZMMU D-807, 18.5 mm dd, teeth; E–F, *Ophiotoma alberti*, ZMMU D-810, dental plates; G. *Ophiolimna bairdi* (Lyman, 1883), ZMMU D-648, 9.5 mm dd, dental plate; H. *Ophiolimna perfida* (Koehler, 1904), ZMMU D-808, 9 mm dd, dental plate; I. *Ophiacantha bidentata* (Bruzelius, 1805), ZMMU D-750, 8 mm dd, dental plate; J. *Ophiocamax vitrea* Lyman, 1878, ZMMU D-811, 9 mm dd, dental plate; K. *Ophiomoeris obstricta* (Lyman, 1878), ZMMU D-855, 5 mm dd; Scale bars: A–B, 300  $\mu$ ; C, 100  $\mu$ ; D–E, 200  $\mu$ ; F, 200  $\mu$ ; G–K, 300  $\mu$ . Photos: Alexander Martynov.

Proximally each jaw pair terminates in a dental plate. The dental plate has several particular patterns in different families, and with some caution it can be used as a taxonomic marker (Murakami 1963; present study). In euryalids, the dental plate is usually fragmented but very long, corresponding to the high jaws (Figs 11A–C). In some ophiomyxids the jaws are low, and correspondingly the dental plate became considerably shorter. As an evidence for this reduction an additional space dorsally at the jaw terminal junction remains, not covered by the dental plate, in some ophiomyxid and apparently ophiacanthid genera – *Ophioscolex* and *Ophiocymbium* (Fig. 15B). According to this pattern, it is possible to suggest therefore that shortened dental

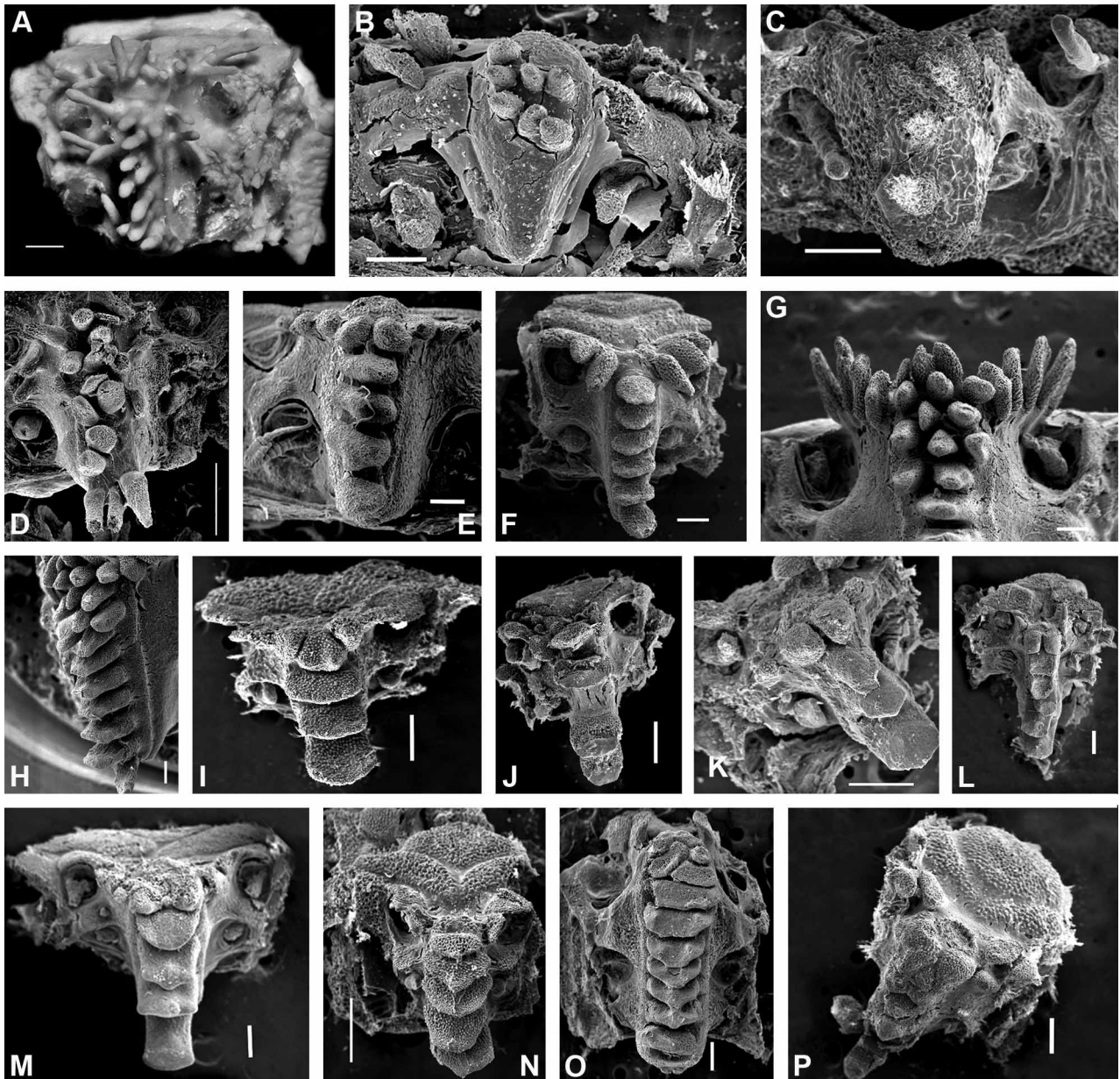


plates in different families correspond only to part of the long and fragmented ancestral dental plate. High jaws are characteristic (with few exceptions) also for Ophiocomidae, Ophionereididae and Amphiuridae, but their long dental plates are never fragmented.



**FIGURE 14.** Dental plates of various ophiuroid taxa. A. *Amphiura* sp., ZMMU D-830, 10.5 mm dd; B. *Amphipholis kochii* Lütken, 1872, ZMMU D-142, 8 mm dd; C. *Amphioplus* sp., ZMMU D-849, 6 mm dd, radial shield; D. *Histampica duplicata*, ZMMU D-729, 5.5 mm dd; E. *Ophiactis abyssicola* (M. Sars, 1861), ZMMU D-631, 6 mm dd; F. *Ophiactis* sp., ZMMU D-831, 6 mm dd; G. *Ophiozonella alba* Lütken, 1899, IORAS 15.109, 7.5 mm dd; H. *Ophiolepis elegans* Lütken, 1859, IORAS 15.99, 9 mm dd; I. *Ophiocomina nigra* (Abildgaard in O.F. Müller, 1789), ZMMU D-309, 18 mm dd; J. *Ophiocoma pica* Müller & Troeschel, 1842, ZMMU D-142, 13.5 mm dd; K. *Ophionereis schayeri* (Müller & Troeschel, 1844), ZMMU D-820, 12 mm dd; L. *Ophiothela danae* Verrill, 1869, ZMMU D-828; M. *Ophiothrix fragilis* (Abildgaard in Müller, 1789), ZMMU D-827, 8 mm dd; N. *Ophioderma* sp, ZMMU D-832, 27 mm dd; O. *Ophiopeza spinosa* (Ljungman, 1867), ZMMU D-819, 6 mm dd; P. *Ophiomyxa pentagona* (Lamarck, 1816), ZMMU D-553, 21 mm dd; Q. *Ophioderma* sp., ZMMU D-832, Cuba, dental plate and teeth in situ; Scale bars: A, 600  $\mu$ ; B, 300  $\mu$ ; C, 400  $\mu$ ; D, 100  $\mu$ ; E, 300  $\mu$ ; F, 100  $\mu$ ; G, 300  $\mu$ ; H, 400  $\mu$ ; I, 300  $\mu$ ; J, 600  $\mu$ ; K, 600  $\mu$ ; L, 100  $\mu$ ; M, 300  $\mu$ ; N, 1 mm; O, 100  $\mu$ ; P, 600  $\mu$ ; Q, 1 mm. Photos: Alexander Martynov.



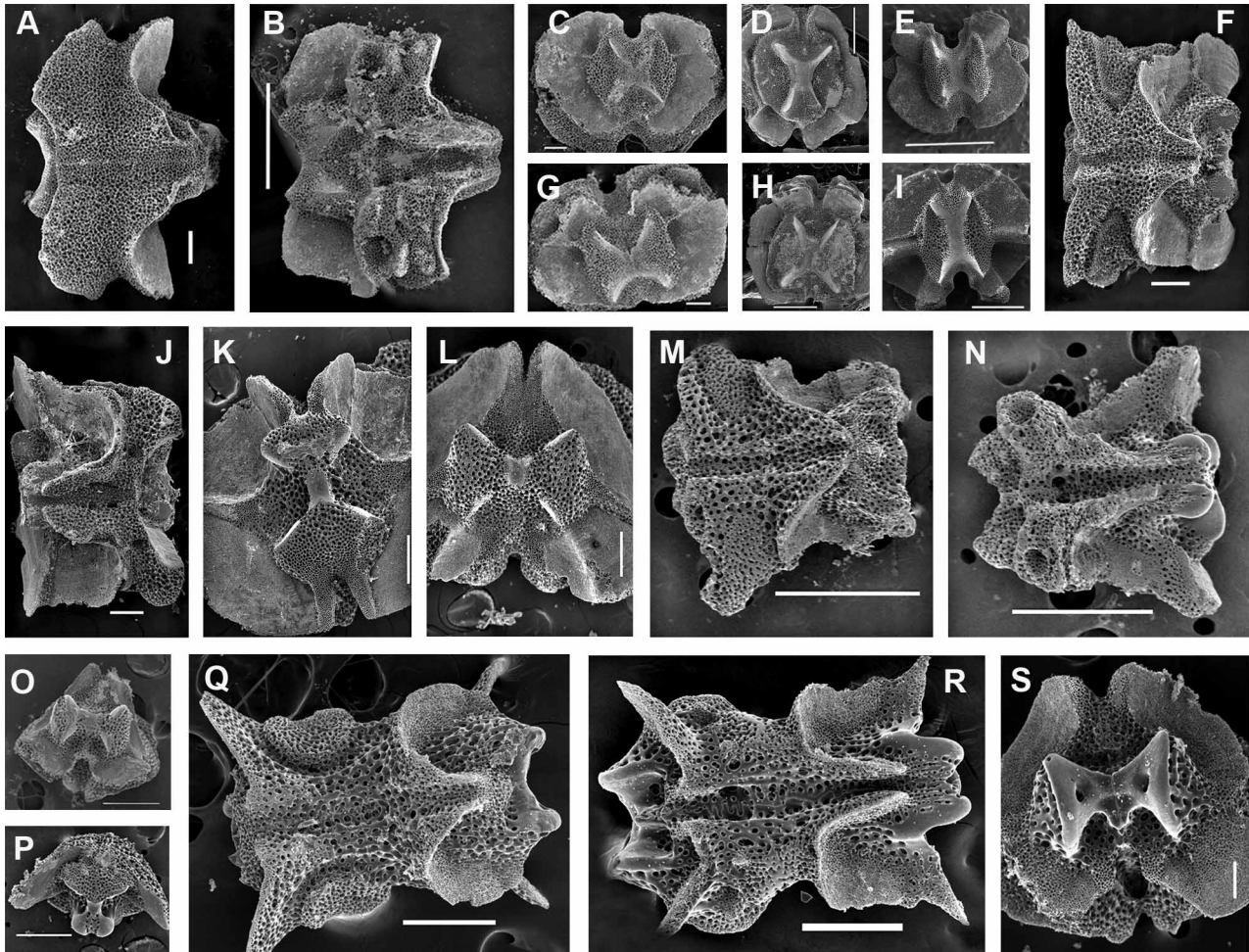


**FIGURE 15.** Inside mouth views of the oral structures of various ophiuroid taxa. A. *Gorgonocephalus arcticus* Leach, 1819, ZMMU D-613, 39 mm dd; B. *Ophiocymbium cavernosum* Lyman, 1880, ZMMU D-794, 9.5 mm dd; C. *Ophiologimus* cf. *secundus* Koehler, 1914, ZMMU D-815, 4 mm dd; D. *Asteronyx loveni* Müller & Troschel, 1842, ZMMU D-833, 17.5 mm dd; E. *Ophiotoma assimilis* Koehler, 1904, ZMMU D-807, 18.5 mm dd; F. *Ophiacantha bidentata* R/V “Sevastopol” sta. 1238, ZMMU D-750; G-H, *Ophiocomina nigra* (Abildgaard in O.F. Müller, 1789), ZMMU D-309, 18 mm dd; I. *Ophiozonella alba* Lütken, 1899, IORAS 15.109, 7.5 mm dd; J. *Ophioconis vivipara* Mortensen, 1925, ZMMU D-834, 6.5 mm dd; K. *Dougaloplus derjugini* (Djakonov, 1949), ZMMU D-838, 9.5 mm dd, inside mouth view; L. *Amphiplus cernuus* (Lyman, 1879), IORAS N. 1.89, 13 mm dd; M. *Amphiura carchara* H.L. Clark, 1911, ZMMU D-835, 5.5 mm dd; N. *Ophiactis abyssicola* (M. Sars, 1861), ZMMU D-631, 6 mm dd; O. *Ophiopholis aculeata* (L., 1767), ZMMU D-559, 15 mm dd; P. *Ophiopenia tetracantha* H.L. Clark, 1911, ZMMU D-580, 8.5 mm dd; Scale bars: A, 1 mm; B, 300  $\mu$ ; B, 300  $\mu$ ; C-H, 300  $\mu$ ; D, 1 mm; I, 300  $\mu$ ; I, 300  $\mu$ ; J, 300  $\mu$ ; K, 300  $\mu$ ; L, 300  $\mu$ ; M, 300  $\mu$ ; N, 300  $\mu$ ; O, 300  $\mu$ ; P, 300  $\mu$ . Photos: Alexander Martynov.

The following patterns of the dental plate have been discovered in various families:

Gorgonocephalidae and Asteronychidae (Figs 11A–C): dental plate fragmented into several irregular pieces; teeth sockets not perforating the plate, small and rounded; teeth are long and spiniform, similar in shape to oral papillae.





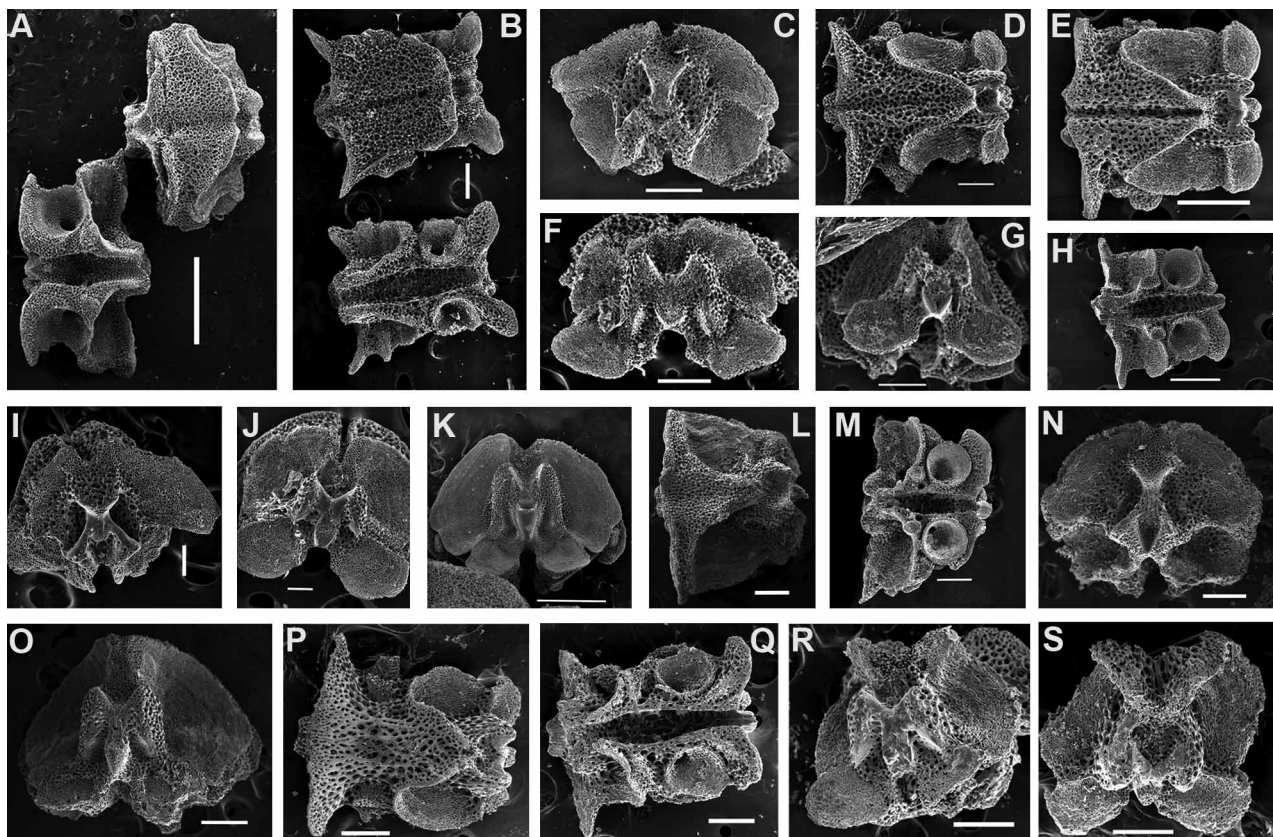
**FIGURE 16.** Vertebrae and streptospondylous vertebral articulation of various ophiuroids. A. *Asteronyx loveni* Müller & Troschel, 1842, ZMMU D-833, 17.5 mm dd, dorsal view; B. same, ventral view; C. same, proximal view; D. same, distal view; E. *Ophiobyrsa rudis* Lyman, 1878, ZMMU D-868, 12.5 mm dd, proximal view; F. *Ophiocamax vitrea* Lyman, 1878, ZMMU D-811, 9 mm dd, dorsal view; G. *Gorgonocephalus arcticus* Leach, 1819, ZMMU D-613, 39 mm dd, proximal view; H. same, distal view; I. *Ophiobyrsa rudis*, distal view; J. *Ophiocamax vitrea*, ventral view; K. *Ophiocamax vitrea*, proximal view; L. same, distal view; M. *Ophiacantha setosa* (Bruzellius, 1805), ZMMU D-688, 6 mm dd, dorsal view; N. same, ventral view; O. same, distal view; P. same, proximal view; Q. *Ophiomoeris obstricta* (Lyman, 1878), ZMMU D-855, 5 mm dd, dorsal view; R. same, ventral view; S. same, distal view; Scale bars: A, 300 ; B, 1000  $\mu$ ; C, 300  $\mu$ ; D, 300  $\mu$ ; E, 1 mm I, 500  $\mu$ ; F, 300  $\mu$ ; G,H, 1 mm; J–L, 300  $\mu$ ; M–N, 600  $\mu$ ; O–P, 400  $\mu$ ; Q,R, 300  $\mu$ ; S, 100  $\mu$ . Photos: Alexander Martynov.

Asteroschematidae: Dental plate entire, with elongate, non-perforating sockets (Murakami, 1963, *Asteroschema yaeyamensis* Murakami, 1944) or sockets almost indistinct (present study, *Asteroschema inornatum* Koehler, 1906).

Ophiuridae (Figs 11D–J; 65O–P; 82I): dental plate entire, but in *Ophioparte* (considered in Martynov 2010 and here as an ophiurid) sutures of fragmentation remain between sockets; teeth sockets typically small perforations, irregularly placed, varying in number from numerous in *Ophioparte* and *Ophionotus* to few in *Ophiura* but in some taxa, e.g. *Ophiernus*, sockets are non-perforating, elongated and placed one after another.

Ophiomyxidae (Figs 12A, B, E–J; 14P): dental plate fragmented or entire. At least two types of fragmentation can be detected: 1) with irregular fragmentation, several irregular, rounded teeth sockets, and spiniform teeth (*Ophiocolex glacialis*) (Figs 12A, B) and *Ophiobyrsa rudis* (Figs 80H, I), or 2) transversally fragmented into similar pieces with elongate, non-perforating teeth sockets and massive teeth (*Ophiomyxa*) (Fig. 14P).





**FIGURE 17.** Vertebrae of various taxa of the family Ophiomyxidae. A. *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-843, 18 mm dd, proximal segments, dorsal and ventral views; B. same, distal segments, dorsal and ventral views; C. same, proximal segments, proximal view; D. *Ophiocymbium cavernosum* Lyman, 1880, ZMMU D-795, 10.5 mm dd, proximal segments, dorsal view; E. *Ophiocymbium ninae* sp. nov., paratype 5 mm dd, ZMMU D-804, proximal segments, dorsal view; F. *Ophioscolex glacialis*, proximal segments, distal view; G. *Ophiocymbium cavernosum* Lyman, 1880, ZMMU D-795, proximal segments, proximal view; H. *Ophiocymbium ninae* sp. nov., paratype 5 mm dd, ZMMU D-804, ventral view; I. same, proximal view; J. same, distal view; K. *Ophiomyxa pentagona*, ZMMU D-553, 21 mm dd, distal view; L. *Ophioplexa condita* gen. et sp. nov., holotype ca. 18 mm dd, ZMMU D-788, proximal segments, dorsal view; M. same, ventral view; N. same, proximal view; O. same, distal view; P. *Ophiocymbium tanyae* sp. nov., holotype 9.5 mm dd, ZMMU D-799, proximal segments, dorsal view; Q. same, ventral view; R. same, distal view; S. same, proximal view. Scale bars: A, 1000  $\mu$ ; B, C, 200  $\mu$ , D, 200  $\mu$ ; E, 300  $\mu$ ; F, 200  $\mu$ ; G, 200  $\mu$ ; H, 300  $\mu$ ; I, 100  $\mu$ ; J, 100  $\mu$ ; K, 1000  $\mu$ ; L–S, 300  $\mu$ . Photos: Alexander Martynov.

Ophiacanthidae (Figs 13; 47C; 78D, E; 82G): dental plate entire, typically with elongate, non-perforating sockets, placed one after another, and massive teeth. In most taxa ventralmost teeth (apical papillae) placed on rounded sockets, which rarely in some taxa, e.g. *Ophiotreta* (Figs 78D, E), may occupy up to half of the dental plate.

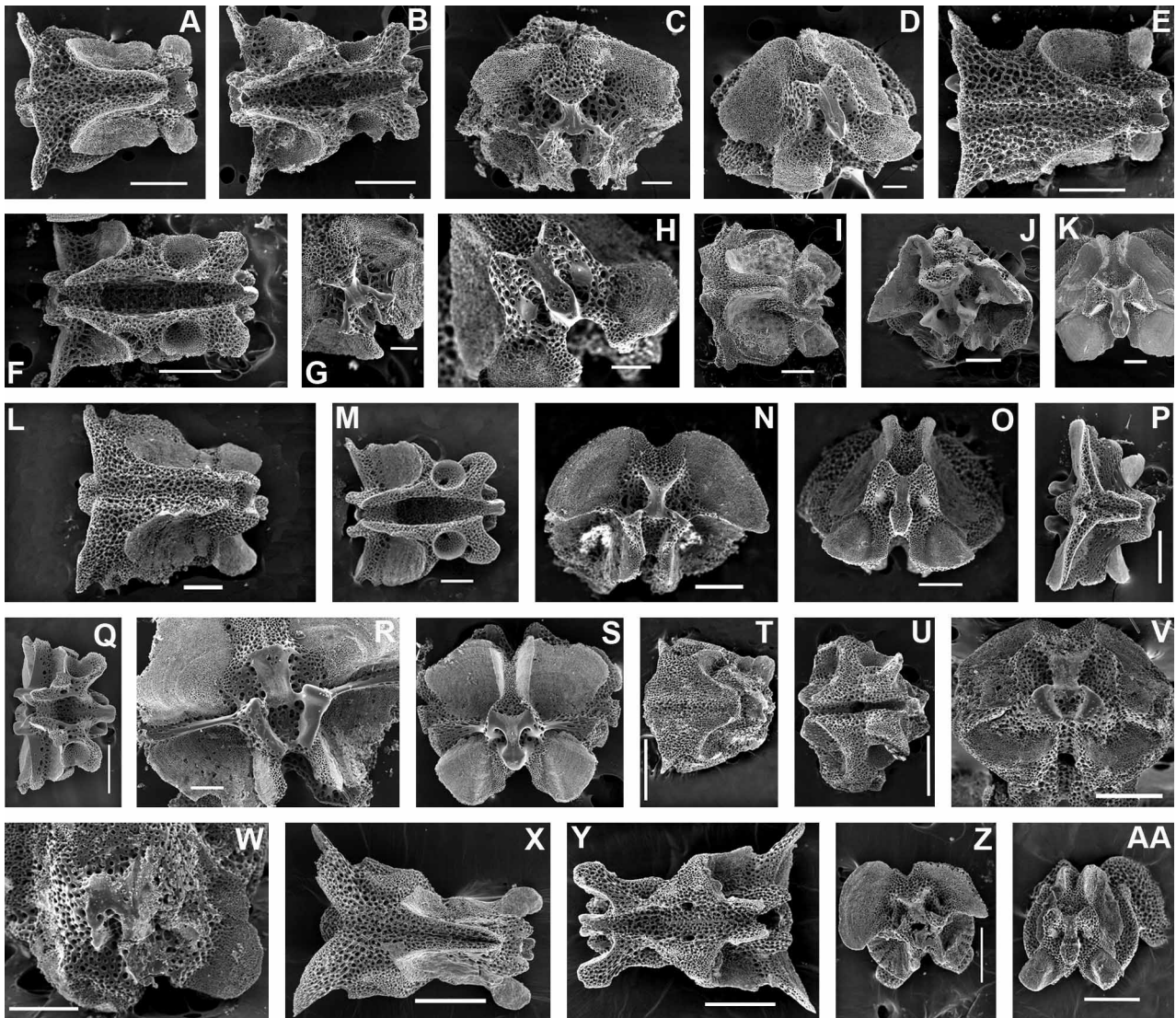
Ophiodermatidae (Figs 14N–O): dental plate typically fragmented transversally into similar pieces having elongate, non-perforating sockets and massive teeth. At least in the genus *Ophiopeza* entire plates were found instead (Fig. 14O).

Ophiocomidae (Figs 14I, J): dental plate entire, with large heart-shaped perforated sockets dorsally (except genus *Ophiocomina*, with non-perforated, elongate sockets), some divided longitudinally by a septum, and numerous well-defined, round sockets ventrally, placed both medially and at the edges, bearing a cluster of the ventralmost teeth (“tooth papillae”) in all representatives, including *Ophiocomina*.

Ophionereididae (Fig. 14K): dental plate entire, with characteristic large heart-shaped perforated sockets dorsally.



Ophiochitonidae: dental plate entire, possibly artificially subdivided into two pieces in *Ophiochiton fastigatus* Lyman, 1878 (Murakami 1963), since according to the present study at least *Ophiochiton ternispinus* Lyman, 1883 has an entire dental plate. Both species possess dental plates with indistinct, elongate, entirely non-perforated sockets (Murakami 1963).



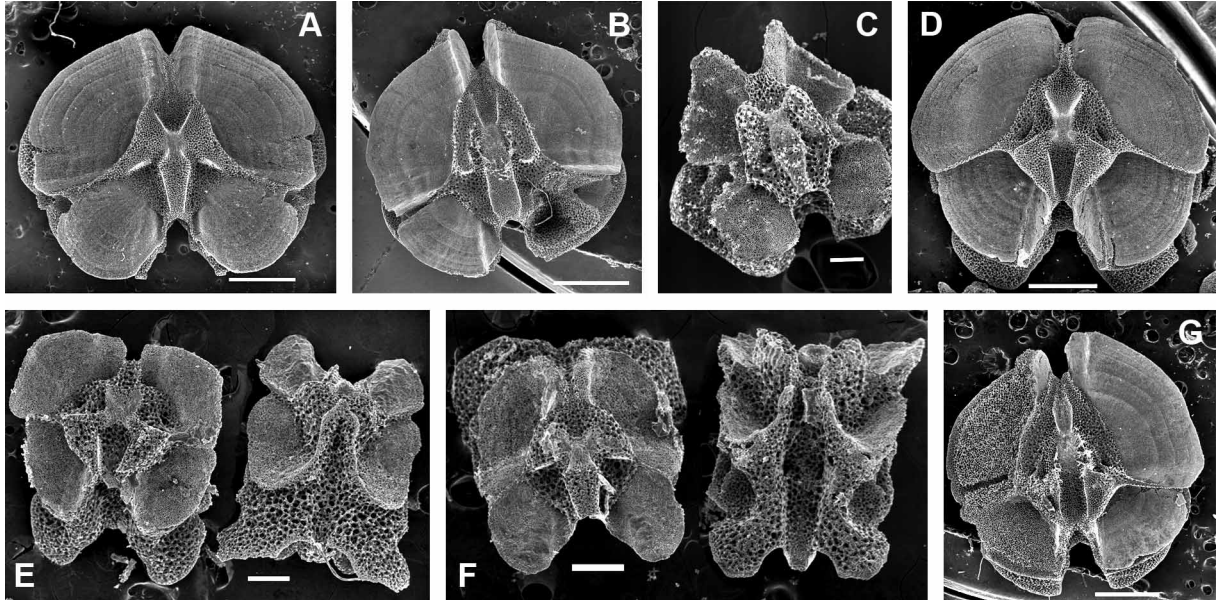
**FIGURE 18.** Vertebrae of various ophiuroid taxa. A. *Ophiologimus* cf. *secundus* Koehler, 1914., ZMMU D-815, 4 mm dd, proximal segments, dorsal view; B, same, ventral view; C, same, proximal view; D, same, distal view; E. *Ophiorupta discrepans* (Koehler, 1922) **comb. nov.**, ZMMU D-806, ca. 7 mm dd, dorsal view; F, same, ventral view; G, same, proximal view; H, same, distal view; I. *Ophiacantha bidentata* (Bruzellius, 1805), ZMMU D-750, 8 mm dd, dorsal view, J, same, proximal view; K, same, distal view; L. *Ophiotoma alberti* (Koehler, 1896), ZMMU D-810, 12 mm dd, dorsal view; M, same, ventral view; N, same, proximal view; O, same, distal view; P. *Amphipholis kochii* Lütken, 1872, ZMMU D-142, 8 mm dd, dorsal view; Q, same, ventral view; R, same, proximal view; S, distal view; T. *Ophiopenia tetracantha* ZMMU D-580, 8.5 mm dd, dorsal view; U, same, ventral view; V, same, proximal view; W, same, distal view; X. *Ophiopeza spinosa* (Ljungman, 1867), ZMMU D-819, 6 mm dd; Y, same, ventral view; Z, same, proximal; AA, distal view; Scale bars: A–B, 300  $\mu$ ; C, 100  $\mu$ ; D, 100  $\mu$ ; E, 300  $\mu$ ; F, 300  $\mu$ ; G, 100  $\mu$ ; H, 100  $\mu$ ; I, 300  $\mu$ ; J, 300  $\mu$ ; K–L, 300  $\mu$ ; M–O, 300  $\mu$ ; P, 300  $\mu$ ; R, 100  $\mu$ ; Q, 300  $\mu$ ; S, 300  $\mu$ ; T, 400  $\mu$ ; U, 400  $\mu$ ; V, 300  $\mu$ ; W, 200  $\mu$ ; X, 300  $\mu$ ; Y, 300  $\mu$ ; Z, 300  $\mu$ ; AA, 300  $\mu$ . Photos: Alexander Martynov.

Amphilepididae: In the present study a pattern of entire dental plate with several narrow, slit-shaped, non-perforating sockets, uniform in shape and size, was discovered in *Amphilepis platytata* H.L. Clark, 1911. Murakami (1963) instead presented for *Amphilepis diastata* Murakami, 1942 dental plate with characteristic large heart-shaped perforating sockets dorsally, some divided longitudinally by a septum. It is not excluding



therefore, that this species belongs to the genus *Amphiura* (and family Amphiuridae, see below), as it was suggested by A.M. Clark (1970).

Amphiuridae (Figs 14A–C): in most taxa the dental plate is entire, with characteristic large heart-shaped perforating sockets dorsally, some divided longitudinally by a septum. In few aberrant taxa, e.g. the genus *Amphilimna* (here considered an amphiurid, see below), dental plate devoid of perforations (Fig. 40B) or fragmented (Fig. 39E, F).



**FIGURE 19.** Vertebrae of various taxa of the family Ophiuridae. A. *Ophiopartea gigas* Koehler, 1922, ZIN 25/21449, 42 mm dd, proximal segments, distal view; B. *Ophiura ophiura* (L., 1758), ZMMU D-518, 25 mm dd, proximal segments, distal view; C. *Ophiura* sp., ZMMU D-823, 7 mm dd, proximal segments, distal view; D. *Ophiopartea gigas* Koehler, 1922, proximal segments, proximal face; E. same, distal segments, proximal and dorsal views; F. same, distal segments, distal and ventral views; G. *Ophiura ophiura* (L., 1758), proximal segments, proximal view; Scale bars: A–B, 1 mm; C, 100  $\mu$ ; D, 1 mm; E, 300  $\mu$ ; F, 300  $\mu$ ; G, 1 mm. Photos: Alexander Martynov.

Ophiactidae (Figs 14D–F): dental plate entire, varying from non-perforated (as in the genus *Histampica*, Fig. 14D) to perforated sockets, typical for the genus *Ophiactis* (Fig. 14E, F). For some *Ophiactis* species heart-shaped perforations almost identical to the Amphiuridae pattern have been reported (Murakami 1963, e.g. *Ophiactis hemiteles* H.L. Clark, 1915).

Ophiolepididae (Figs 14G, H): dental plate entire, varying from perforated (as in the genus *Ophiozonella* (Fig. 14G) to semi-perforated sockets in the genus *Ophiolepis* (Fig. 14H).

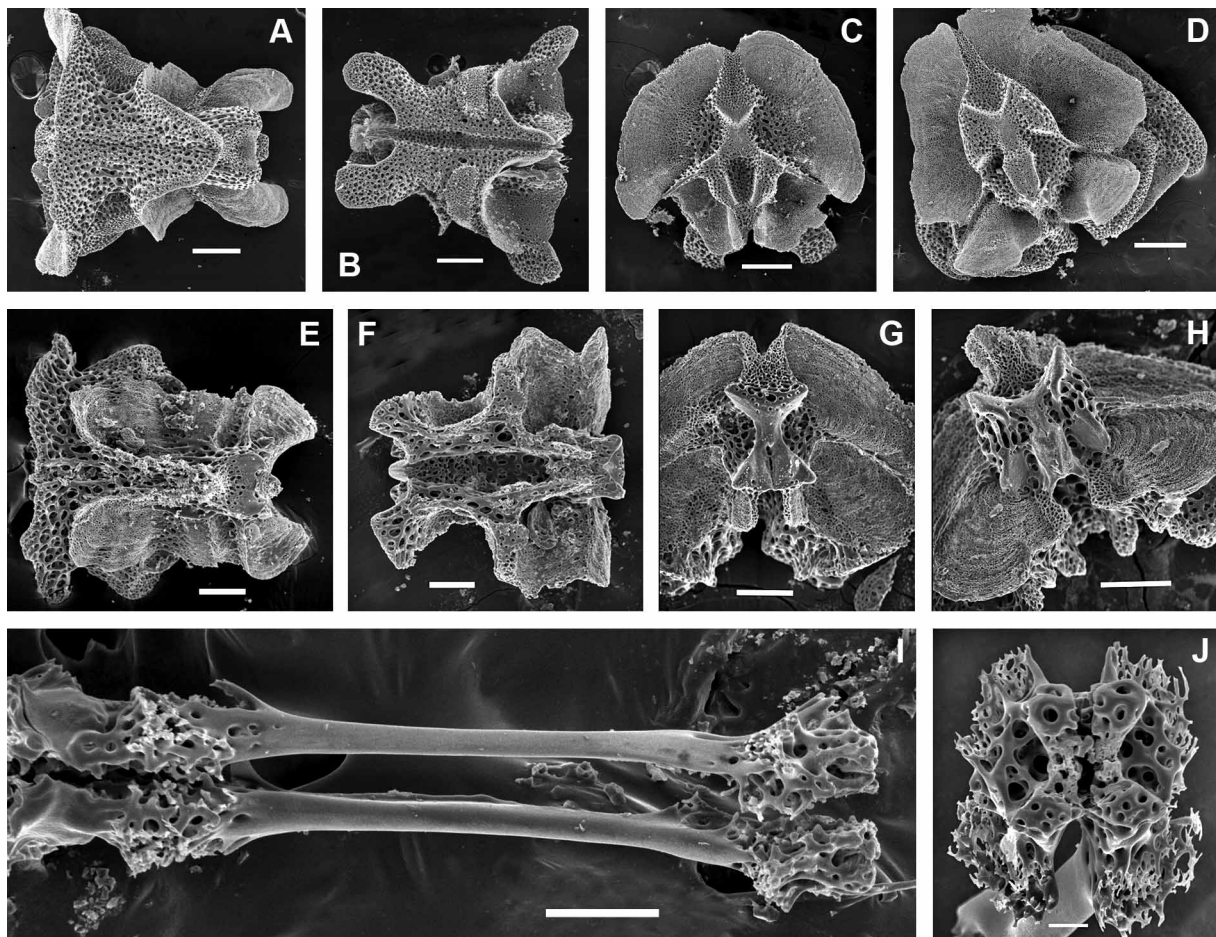
Hemieuryalidae: the genus *Ophiomoeris* (traditionally placed in this family) has an entire dental plate with somewhat oblique elongate non-perforated sockets (Fig. 14K). For the Hemieuryalidae s.str. (e.g. genera *Hemieuryale* and *Sigsbeia*) the dental plate morphology is unknown.

Ophiotrichidae (Figs 14L, M): dental plate entire, with large heart-shaped perforated sockets dorsally and numerous well defined round sockets ventrally, placed only at the edges, a cluster of the ventralmost teeth (“tooth papillae”) originate both at the edge and medially in all representatives.

The dental plate is covered with teeth (Figs 1P, Q; 2Q). The pattern of the sockets correspond to the shape of the teeth. Round small sockets bear spiniform teeth, whereas quadrangular and rounded teeth fit into the elongate slit-shaped sockets (Fig. 1–2, R). Shape of teeth and dental plate sockets are characteristic for apparently related group of genera and families. For instance, the families Ophionereididae, Ophiocomidae, Amphiuridae and Ophiotrichidae possess a characteristic large perforated heart-shaped dorsal sockets (Fig. 14) (united sometimes into the order Gnathophiurida, see Matsumoto 1917; Wilkie 1980). However, many cases of apparently convergent similarities prevent to use this character by itself. In adult stage, most ophiuroids usually bear numerous teeth, whereas postlarval stages and paedomorphic taxa from different

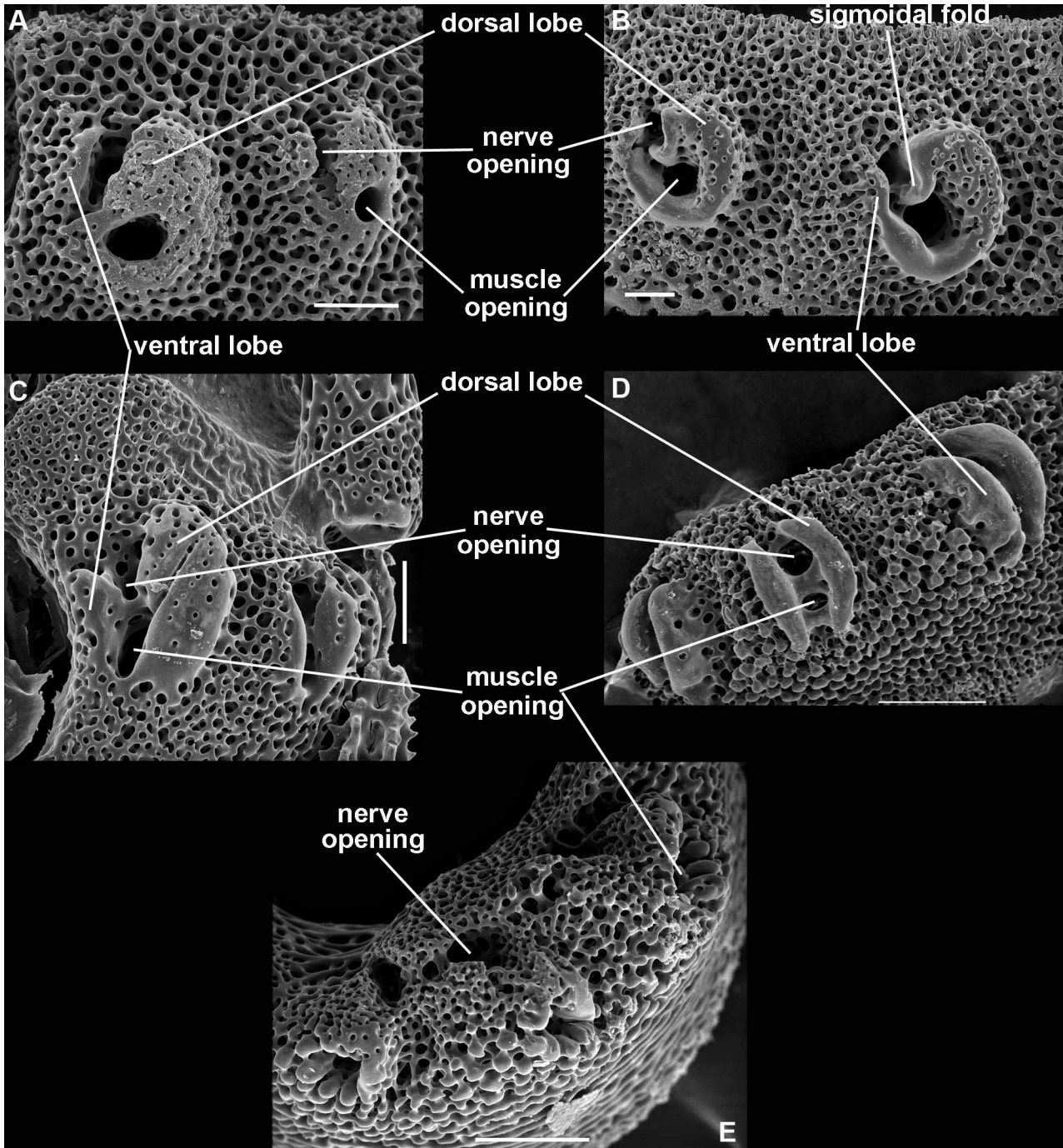
families have only a single or two teeth (Belyaev & Litvinova 1972; Vadon 1990; Martynov unpublished data).

In some taxa, teeth are placed on the dental plate quite irregularly (Gorgonocephalidae, Asteronychidae, most Ophiomyxidae) and there is little difference between dorsal and ventral teeth (Figs 15A–D). In many other families, this pattern is changed to teeth placed regularly one after another (Figs 15 E–P). A few ventralmost teeth usually remain spiniform, other teeth becoming rectangular, and the dorsalmost teeth are usually the longest or most massive. Such differentiation in the teeth occur in most ophiacanthids and ophiidermatids. In the family Ophiocomidae the ventralmost spiniform teeth have undergone a modification into an elaborated cluster, traditionally called tooth papillae (e.g. Fell 1960) (Fig. 15G). They are placed on the dental plate, have teeth sockets (Figs 14I, J) and differ from usual ventralmost teeth mostly in number. Thus there are no obstacles to considering them as a further complication of the ventral teeth. Similarly, in traditional ophiuroid morphology there is a difference in terminology between teeth and apical papillae. According to the present study, the so-called apical papillae are just ventralmost teeth and also placed on the dental plate (Fig. 15). In some smaller groups, especially in the Amphiuroidae, the ventralmost teeth are differentiated into a peculiar paired or triple structure (Figs 15K–M), called sometimes infradental papillae, and often not placed strictly on the dental plate, but rather in-between the dental plate and jaw edges. According to Hendler (1978; 1988) infradental papillae appear during ontogeny at the dental plate and migrate to their final position and thus should also be considered as ventralmost teeth. Amphiuroid-like paired apical papillae sometimes appear in other families, e.g. in Ophiacanthidae, as a variation (e.g. Fig. 2P).



**FIGURE 20.** Vertebrae of various taxa of the family Ophiuridae, proximal segments. A. *Ophioplinthus confragosa* (Lyman, 1878), ZMMU D-733, 12 mm dd, dorsal view; B. same, ventral view; C. same, proximal view; D. same, distal view; E. *Ophioleuce* sp., ZMMU D-826, 5.5. mm dd, dorsal view; F. same, ventral view; G. same, proximal view; H. same, distal view; I. *Perlophiura profundissima* Belyaev & Litvinova, 1972, IORAS 14.352, 3.4 mm dd, dorsal view; J. proximal view. Scale bars: A–D, 300  $\mu$ ; E, 100  $\mu$ ; F–I, 100  $\mu$ ; J, 30  $\mu$ . Photos: Alexander Martynov.



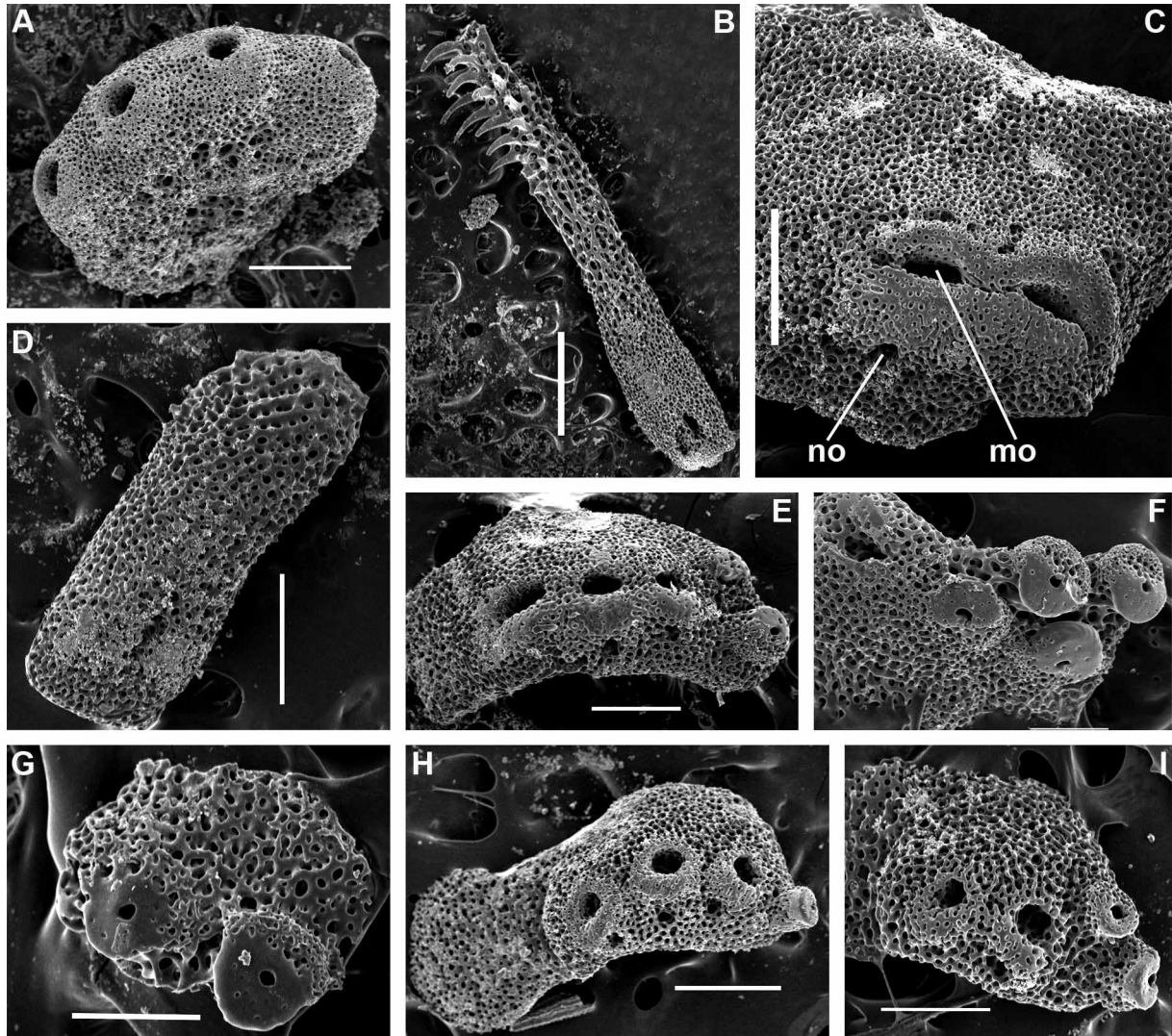


**FIGURE 21.** Arm spine articulations (proximal segments): general terms and homological structures within distantly related ophiuroid families. A. *Ophiomyxa pentagona* (Ophiomyxidae); B. *Ophiotoma paucispina* (Lütken & Mortensen, 1899) (Ophiacanthidae); C. *Ophiolycus purpureus* (Düben & Koren, 1846) (Ophiomyxidae); D. *Amphiodia craterodmeta* H.L. Clark, 1911 (Amphiuridae); E. *Ophiura robusta* (Ayes, 1851) (Ophiuridae). Scale bars: A–C, E, 100  $\mu$ ; D, 120  $\mu$ ; Photos: Alexander Martynov.

Distally the jaws are bordered by two adoral shields, which represent modified lateral arm plates, evident from their ontogeny (Hendler 1978; Sumida *et al.* 1998; Stöhr 2005). The adoral shields in postlarval stages (and in some adult representatives of some genera) bear one or more well-defined spines, which are homologous to the lateral arm plate spines (Hendler 1978). Adoral shield papillae and adjacent oral papillae border the second tentacle pore, often termed oral tentacle scales (Paterson 1985; O'Hara & Stöhr 2006). The teeth, oral papillae, and adoral shield papillae represent an interesting case of similarity deserving more attention and further study. In groups which are presumably closest to an ophiuroid ancestral condition, e.g.



many euryalids, ophiomyxids, in *Ophiosparte* (a genus with yet unclear position, see below), in some ophiacanthids of the subfamily Ophiotominae, the shape and pattern of all above mentioned spiniform oral structures are very similar (Figs 15A; 65B, L; 76H).

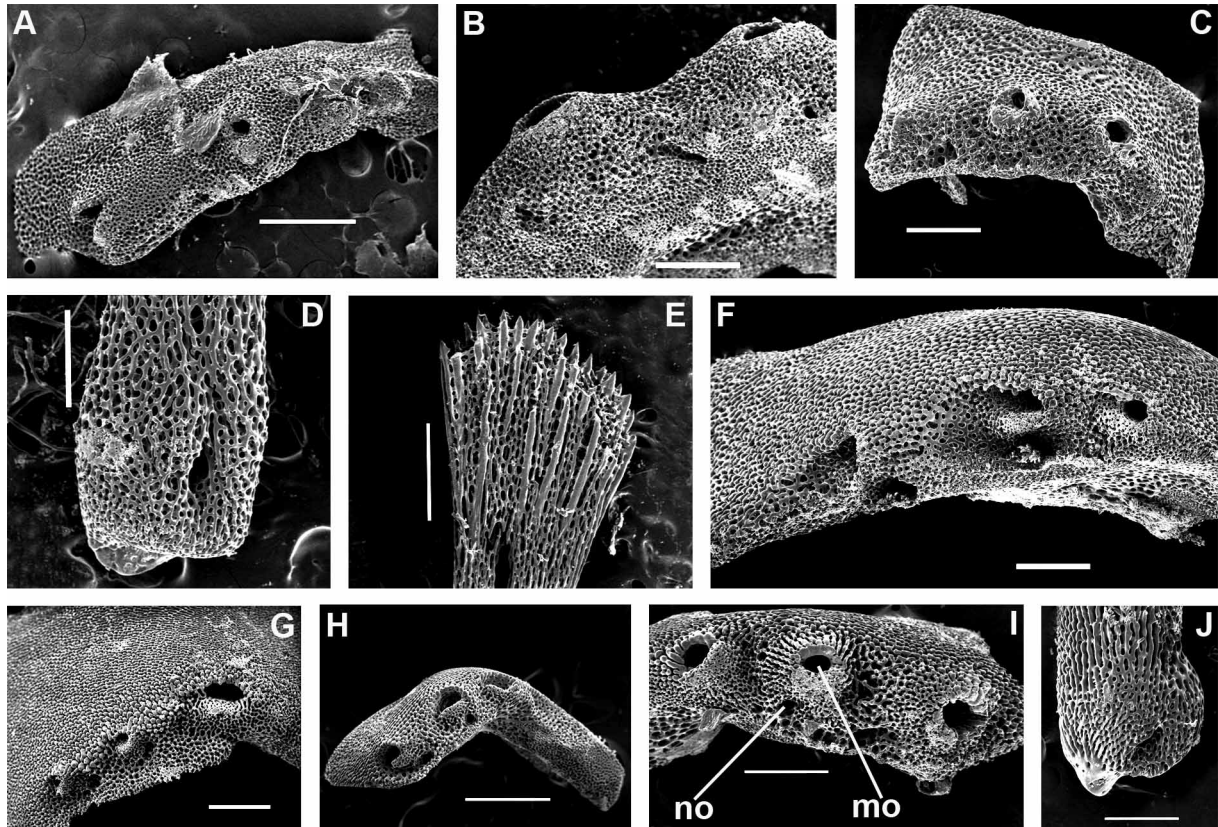


**FIGURE 22.** Arm spine articulations and spines of various taxa of the families Asteronychidae and Gorgonocephalidae. A. *Asteronyx loveni* Müller & Troschel, 1842, ZMMU D-851, 32 mm dd, articulations, proximal segments; B. same, spine, middle segments; C. *Gorgonocephalus arcticus* Leach, 1819, ZMMU D-613, 39 mm dd, articulations, most proximal segments; D. same, spine, proximal segments; E–F. same, articulations, middle segments; G. same, articulations, distal segments; H. *Astrotoma agassizii* Lyman, 1875, ZMMU D-138, 32 mm dd, proximal segments; I. same, distal segments; Scale bars: A, 300  $\mu$ ; B, 600  $\mu$ ; C, 300  $\mu$ ; D, 100  $\mu$ ; E, 300  $\mu$ ; F, 200  $\mu$ ; G, 100  $\mu$ ; H, 300  $\mu$ ; I, 200  $\mu$ . Photos: Alexander Martynov.

Another characteristic ophiuroid skeletal element — the unpaired oral shield—is placed distally to the adoral shields. The shape of the oral shield is widely used in ophiuroid taxonomy, especially for distinguishing species. The Euryalida possess weakly developed oral shields, sometimes almost lacking as a distinct structure but instead integrated within an area of numerous smaller plates. On the contrary, most of the rest Ophiuroidea have well defined oral shields. In this respect Euryalida is also differs from the rest Ophiuroidea: their madreporite is placed in many cases more distally from the adoral shields area (especially in the various genera of the family Gorgonocephalidae, personal observations), i.e. toward to the disk edge. Euryalids' madreporite also clearly differs from the most other Ophiuroidea in having distinctly porous appearance. These facts omitted in classical reviews on ophiuroid morphology and systematics (e.g. Mortensen, 1927; Dyakonov, 1954). Both structure and position of the madreporite of the Euryalida is more



similar to the madreporite in Asteroidea than to the most Ophiuroidea and may imply ancestral condition of the euryalids' madreporite. Compare to the homogeneous structure of the euryalids' madreporite, various ophiurids, including distantly related taxa such as *Ophioscolex* and *Ophioplexa* (Ophiomyxidae), *Ophiopleura* (Ophiuridae), *Ophiocamax* have instead markedly elevated distal madreporic area and flattened proximal/and or marginal zone devoids of the conspicuous pores. Madreporic oral shield of the non-euryalid Ophiuroidea may be therefore a product of the migration of the true madreporite more proximally and its further fusion with one or some plates initially placed closely to the adoral shields (as in modern *Gorgonocephalus* and *Astrochele*). Euryalids also demonstrate another unusual feature: in some taxa there are five madreporites (i.e. one in each interradii, see for instance Dyakonov, 1954; Stewart, 2000) instead of single madreporite. All these unusual euryalid features need further investigations.

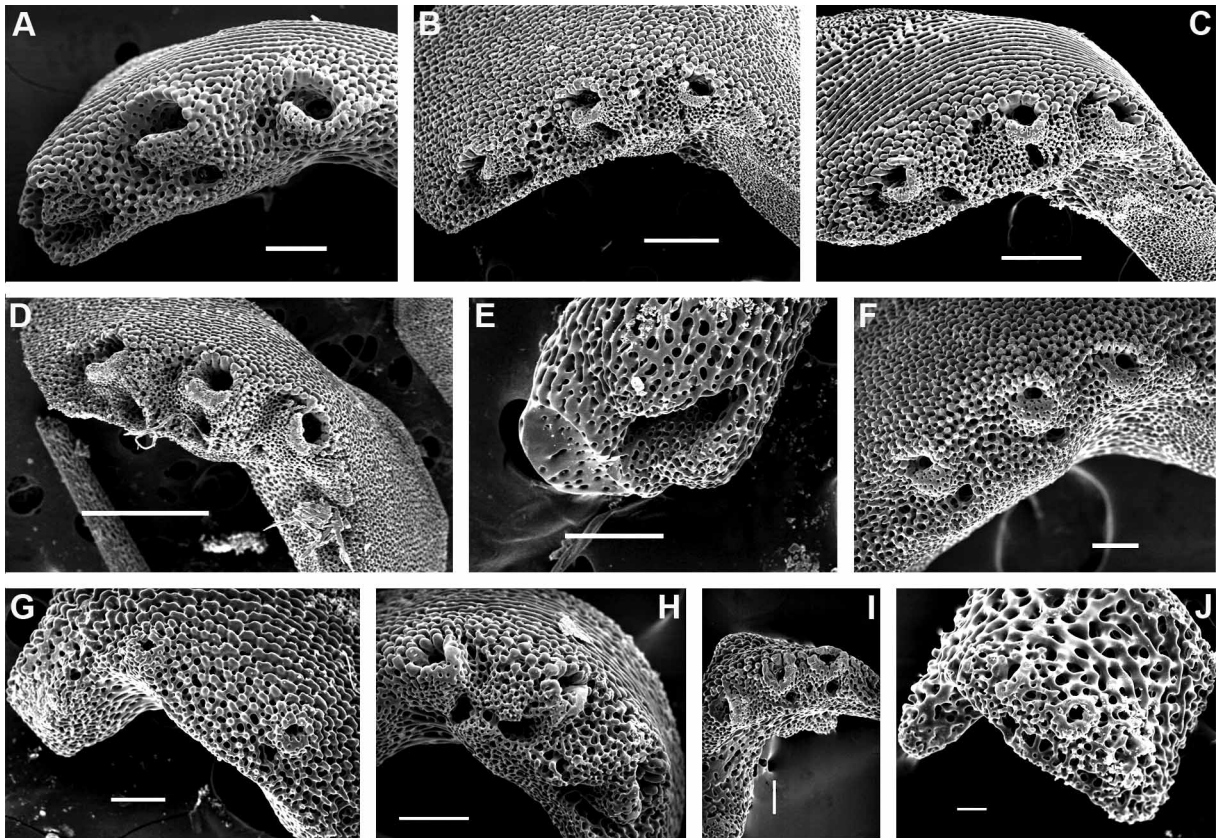


**FIGURE 23.** Arm spine articulations and spines of the various taxa of the family Ophiuridae. A–B, *Ophiosparte gigas* Koehler, 1922, ZIN 25/21449, 42 mm dd, spine articulations, proximal segments; C. same, distal segments; D. same, basal part of the spine, lateral view showing conspicuous nerve opening; E. same, apical part of the spine; F. *Ophiura ophiura* (L., 1758), ZMMU D-518, 25 mm dd, proximal segments; G. *Ophiopleura borealis* Danielssen & Koren, 1877, ZMMU D-319, 23 mm dd, proximal segments; H. same, distal segments; I. *Ophionotus victoriae* Bell, 1902, ZMMU D-131, 34 mm dd, distal segments, spine articulations; J. same, basal part of the spine, lateral view showing conspicuous nerve opening; Scale bars: A, 600  $\mu$ ; B, 400  $\mu$ ; C–D, 300  $\mu$ ; E, 600  $\mu$ ; F–H, 300  $\mu$ ; I, 400  $\mu$ ; J, 200  $\mu$ . Photos: Alexander Martynov.

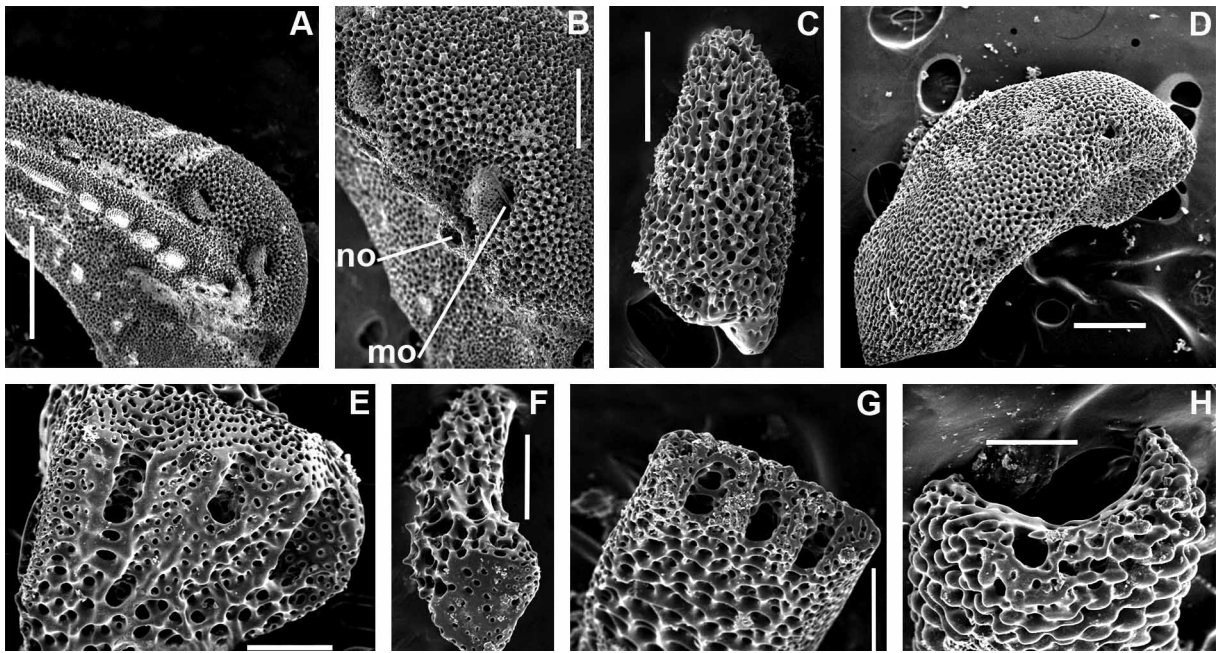
**Arm structures.** Each arm comprises of numerous similarly-constructed segments (Figs 1–2, A–B). In some species the number of segments exceeds one hundred. Generally proximal segments are shorter than wide (Figs 1C–D, H and Figs 2C, F), whereas distal segments are longer than wide (Figs 1 I–K and 2 G, I). Proximal segments are the first segments formed during ontogeny, thus distalmost segments in adult ophiuroids correspond to postlarval and juvenile segments of a given species (H.L. Clark 1914; Litvinova 1989a,b). This general rule does not apply to pedomorphic species: they have considerably elongated (i.e. juvenile) segments proximally, that are even more elongated distally. The number of segments in smaller pedomorphic species is also considerably reduced. Every ossicle, from which each segments are constructed,



is progressively elongated towards the distal arm tip. Arm segments of most ophiuroid taxa consist of a definite number of elements. Most of the inside of a segment is occupied by the vertebrae. The vertebrae are one of the most peculiar ophiuroid ossicles, strongly resembling the non-homologous structure that gave them their name — spinal column bones of vertebrates. Ophiuroid vertebrae are homologous to the asteroid ambulacra (Hendler 1978) and originally consisted of two ossicles, later evolving into a single fused structure. The vertebrae of the extinct subclass Oegophiurida represent the unfused stage of the vertebrae (Fig. 3F, vbr). In the ontogeny of the modern ophiuroid vertebrae also form at first as paired plates (Hendler 1978; Martynov unpublished data). Traces of vertebral fusion persist in most ophiuroids: a mid-longitudinal suture line is evident both dorsally and ventrally (e.g. Fig. 16M). Besides these sutures, the vertebral morphology of some taxa clearly indicates their construction from two halves (Fig. 62D). Further evidence for the fused nature of the vertebrae occurs on the distalmost segments of some non-paedomorphic species and all segments of paedomorphic ophiuroids: their vertebrae are clearly comprised of two halves. Probably one of the most striking examples is the vertebral morphology of the paedomorphic species *Perlophiura profundissima* Belyaev & Litvinova, 1972, which instead of normal vertebrae possesses two weakly connected smooth bars, easily broken apart (Belyaev & Litvinova, 1972; Litvinova 1989a,b; present study) (Fig. 20I). Proximal vertebrae are very narrow, flattened disks, but rapidly transform into an elongate and broadened body distally.



**FIGURE 24.** Arm spine articulations and spines of the genera *Ophiura* and *Ophioctenella*. A. *Ophiura affinis* Lütken, 1858, ZMMU D-465, 7 mm dd, middle segments; B. *Ophiura sarsii* Lütken, 1855, Mareano program, sta. R 48, 11.2 mm dd, middle segments; C. *Ophiura sarsii*, ZMMU D-115, 12 mm dd, proximal segments; D. *Ophiura sarsii*, ZMMU D-136, 15 mm dd, proximal segments, spine articulations; E. same, spine, lateroventral view; F. *Ophiura albida* Forbes 1839, ZMMU D-494, 9 mm dd, proximal segments; G. *Ophiura carnea* Lütken, 1858, Mareano program, sta. R 96 017, 4,2 mm dd, middle segments; H. *Ophiura robusta* (Ayres, 1851), White Sea, 2006, 5 mm dd, proximal segments; I. *Ophiura* sp., ZMMU D-823, 7 mm dd, proximal segments; J. *Ophioctenella acies* Tyler *et al.*, 1995, Serpentine program, sta. 316-07, 3.5 mm dd, proximal segments; Scale bars: A, 100  $\mu$ ; B-C, 300  $\mu$ ; D, 600  $\mu$ ; E, 150  $\mu$ ; F, 100  $\mu$ ; G-I, 100  $\mu$ ; J, 30  $\mu$ . Photos: Alexander Martynov.



**FIGURE 25.** Arm spine articulations and spines of the various taxa of the family Ophiuridae. A-C, *Stegophiura ponderosa* (Lyman, 1878), ZMMU D-582, 34 mm dd, proximal segments; A–B, spine articulation; C, spine, lateral view; D, *Stegophiura nodosa* (Lütken, 1855), ZMMU D-120, 8 mm dd, proximal segments; E, *Ophiophycis mirabilis* Koehler, 1901, ZMMU D-850, 5.5 mm dd, articulations, proximal segments; F, same, spine, lateral view; G, *Astrophisura permira* Sladen, 1879, IORAS 14.178, 7 mm dd, proximal segments; H, *Ophiomisidium irene* Fell, 1952, ZMMU D-864, 2.2 mm dd, proximal segments; Scale bars: A, 1 mm; B, 400  $\mu$ ; C, 200  $\mu$ ; D, 300  $\mu$ ; E–F, 150  $\mu$ ; G, 120  $\mu$ ; H, 80  $\mu$ . Photos: Alexander Martynov.

The dorsal vertebral side has a characteristic pattern for most ophiuroids (except Euryalida and some ophiomyxids) of a distal triangular keel and proximal wings separated medially by a shallow groove (Figs 1H, K; 2F, I). The main functional purpose of the vertebrae is to connect segments along the whole arm. This is attained by special articulation surfaces on both distal and proximal faces of the vertebrae together with attached muscles and connective tissue. Two main types of the vertebral articulation faces – streptospondylous and zygospondylous have been distinguished (Bell 1892; Matsumoto 1917). All modern Euryalida exclusively possess streptospondylous articulations, whereas in other families the zygospondylous articulation dominates. However, in most large families, e.g. Ophiomyxidae and Ophiacanthidae, a few streptospondylous taxa have appeared. Zygospondylous-like structures of the yet unfused surface have been observed in the Palaeozoic Oegophiurida (Kesling 1972). The Carboniferous family Onychasteridae Miller, 1889, apparently related to Euryalida, possessed a zygospondylous articulation (Spencer & Wright 1966). Taken together with the mosaic appearance of some non-Euryalid streptospondylous taxa, the zygospondylous articulation condition is most probably a plesiomorphic feature. Streptospondylous vertebral articulation allows segments to move much more easily in relation to each other (Litvinova 1996), particularly useful for climbing, and can be derived from the zygospondylous form by simple reduction of the middle ventral condyles. There have been repeated attempts to use vertebral morphology as an important taxonomic character, but reliable conclusions on its systematic importance have not yet appeared (see more detailed considerations below). The dorsal and ventral sides of the vertebrae are protected by dorsal and ventral arm plate respectively. The shape of the dorsal and ventral arm plates is an important character for distinguishing species and sometimes genera. The appearance of the ventral arm plate was one in a series of important events in the ophiuroid evolutionary history, which delineated the modern Ophiuroidea from the paleozoic group Oegophiurida. The latter has an open ambulacral groove (i.e. an asteroid feature) (Fig. 3C, F), and vertebrae and tentacles remain largely unprotected. Possibly the protective function was performed by the so-called groove spines in Oegophiurida, which judging from their ventral position around tentacles and their relatively large size might partially have protected the ambulacral groove. Conservatism of the ventral arm plate, which



has persisted across most of the highly diverse Ophiuroidea, probably reflects their functional protective importance. Even in the groups where a dorsal arm plate is lacking or fragmented (Euryalida and Ophiomyxidae) a ventral plate is usually present. The clear morphological trend in the modern Ophiuroidea, from relatively large tentacle pores in the Ophiomyxidae and Ophiotominae to small or almost inconspicuous pores in many other ophiuroids, may also imply a functional decrease of the importance of tentacles and increasing arm movement. Every segment has two tentacle pores. Proximally, the first pore occurs on the lateral side of the jaw, inside the mouth. The second tentacle pore also opens either within the mouth or more superficially on the first arm segment, at the same level with the following tentacle pores. The position of the second tentacle pore is an important traditional character, distinguishing various taxa. The tentacle pores, bordered by lateral and ventral arm plates and the tentacle scales, are underlain by the vertebral podial basins (Fig. 83B), where the tentacles are attached.

Both sides of each vertebra is covered with a lateral arm plate. These plates are ancient structures and appearing in the Oegophiurida (Fig. 3F, G). The shape of the arm plate varies from rectangular as in the Ophiomyxidae (Fig. 1C) and Ophiotominae, to strongly arched, as in many other ophiacanthids (Fig. 2C).

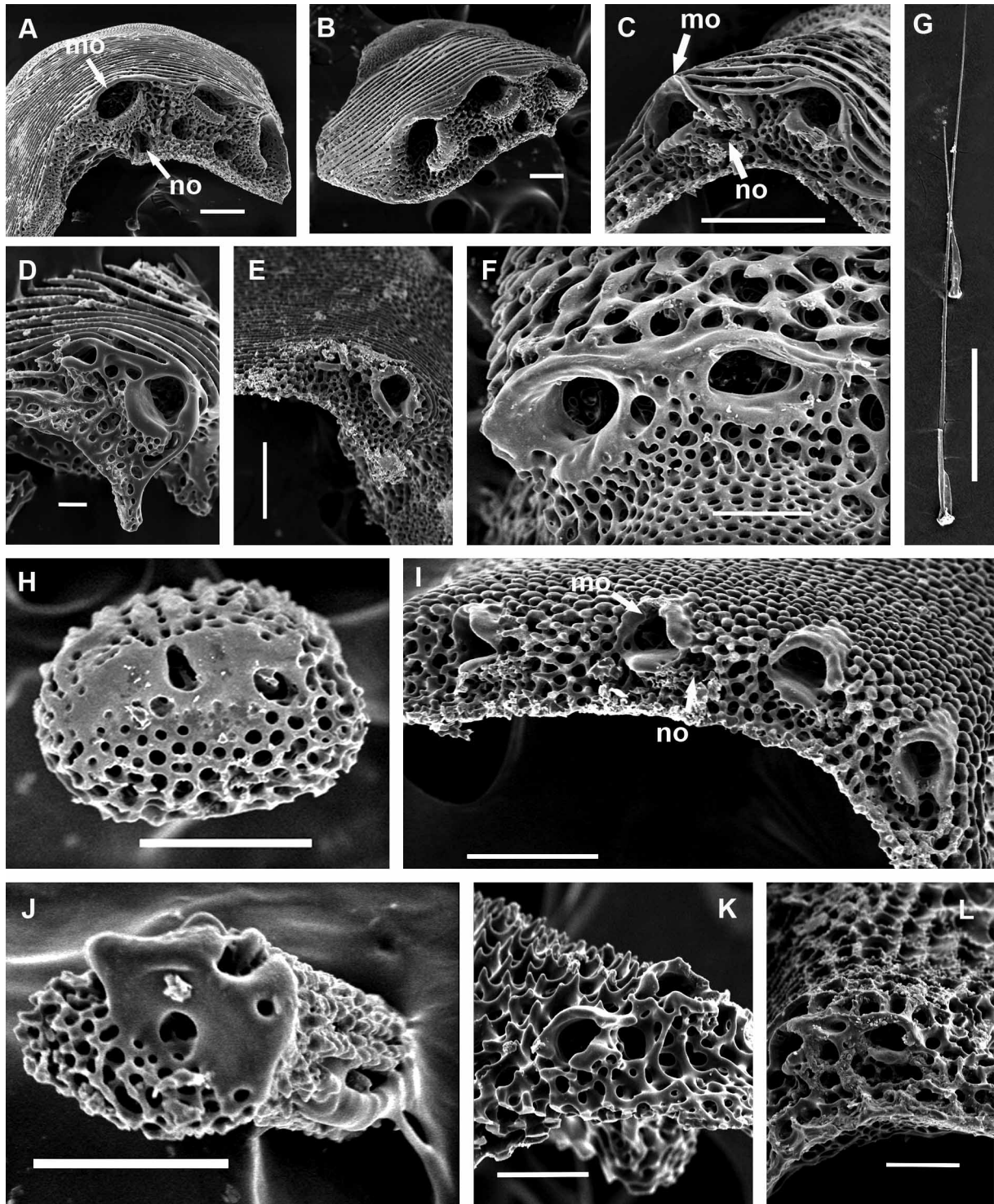
The lateral arm plates in Oegophiurida and all modern Ophiuroidea bear spines. Their shape and size may vary considerably, but even greatly reduced, the spines are always present. It implies their great functional importance, firstly as protective and locomotory structures. In some families there is an increase in the massiveness of the lateral arm plates and corresponding reduction of the spines. This trend is especially characteristic for the family Ophiuridae. Spines may be built from a tightly packed stereom, not leaving any (as in many genera of the family Ophiomyxidae) (e.g. Fig. 1F) or only a small lumen (e.g. as in genus *Ophiolycus*, Fig. 73M) inside. In many other ophiuroids, particularly within the family Ophiacanthidae, the spines became entirely hollow (e.g. Fig. 2E). Spines sit on special elevations of the stereom, here called arm spine articulations. Each of the articulations has two openings – a proximal one for muscle penetration and a distal one for the nerve (Stauber & Märkel 1988; Byrne 1994). Both nerve and muscle openings are bordered by differently shaped stereom protuberances (Fig. 21). The nerve passes through the appropriate articulation ridge opening and enters the base of the spine through one or more small openings. The muscle leaves the articulation opening and attaches to the base of the spine, often to a special condyle. In a minority of the ophiuroid taxa, the muscle and nerve openings are fused (Figs 27A–C), e.g. in the ophiomyxid *Ophioscolex* s.str., and the traditionally ophiacanthid genus *Ophiothamnus*. Fused muscle and nerve openings may be a very ancient feature, since the paleozoic oegophiurid *Eugasterella thorni* Kesling, 1969 possesses a single large opening of the arm spine articulations (Fig. 3G). Ontogenetically, articulations with a single large opening precede the formation of the double-opening ridges, at least in the amphiuroid *Amphipholis squamata* and the ophiurid *Ophiura sarsii* (author's unpublished observations). Simultaneously, this fact may turn a possible secondary appearance of the single-opening ridges in various non-related taxa into a pedomorphic event. In this respect special attention should be paid to particular small features of the articulation (Fig. 21) in order to distinguish superficially similar articulation acquired in different ophiuroid lineages.

Most ophiuroid families, or groups of genera, possess a characteristic shape of arm spine articulations. Their examination delivered the most reliable results for the delineation of the families Ophiomyxidae and Ophiacanthidae in this work.

The following patterns of spine articulations were discovered.

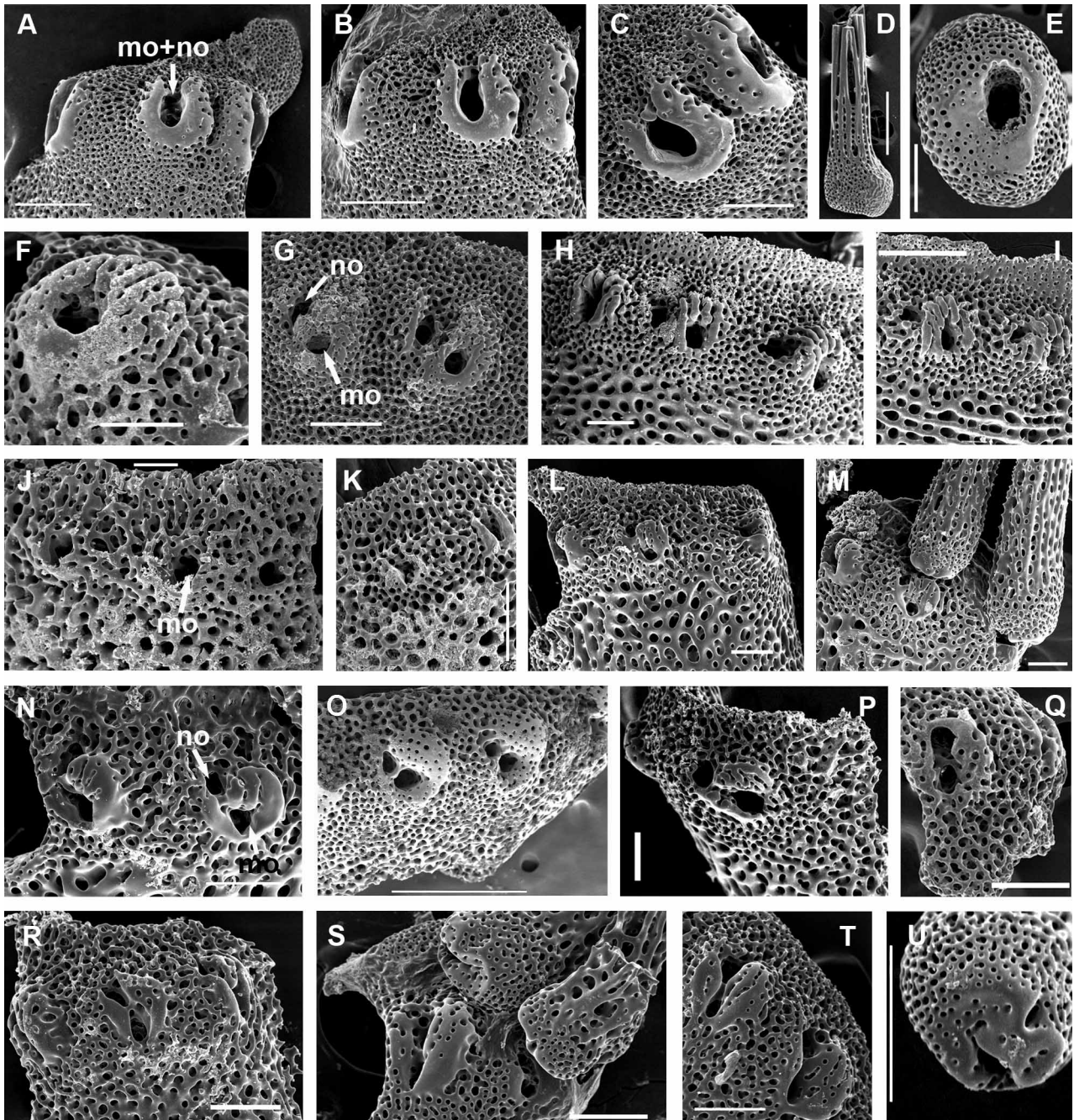
Gorgonocephalidae and Asteronychidae (Fig. 22): a slit-shaped or round, large muscle opening with low border. At some distance from the base of the border there is a small simple nerve opening. There are separate tubercles, each with a single opening for a hook (if any) (Fig. 22E–H).

Ophiuridae (Figs 23; 24; 25; 26): a large irregularly-round muscle opening on an elevation and a nerve opening at the basis of this knob, the dorsalmost articulation is usually placed at an angle in relation to the nerve opening. In some small-sized taxa, e.g. *Ophiophycis*, *Ophiomisidium*, *Astrophiuura* and in the juvenile specimens of some *Ophiura* species, the nerve opening is reduced (Figs 25D, E; G). There is a special variant of the ophiurid articulation pattern within the group “Ophioleucidae” (generally considered either as a separate family or as a subfamily of Ophiuridae) (Fig. 26): irregularly rhombic articulations with high borders, framed large opening for the muscle, elongated in a dorsoventral direction. A small nerve opening is situated ventral to the articulations.



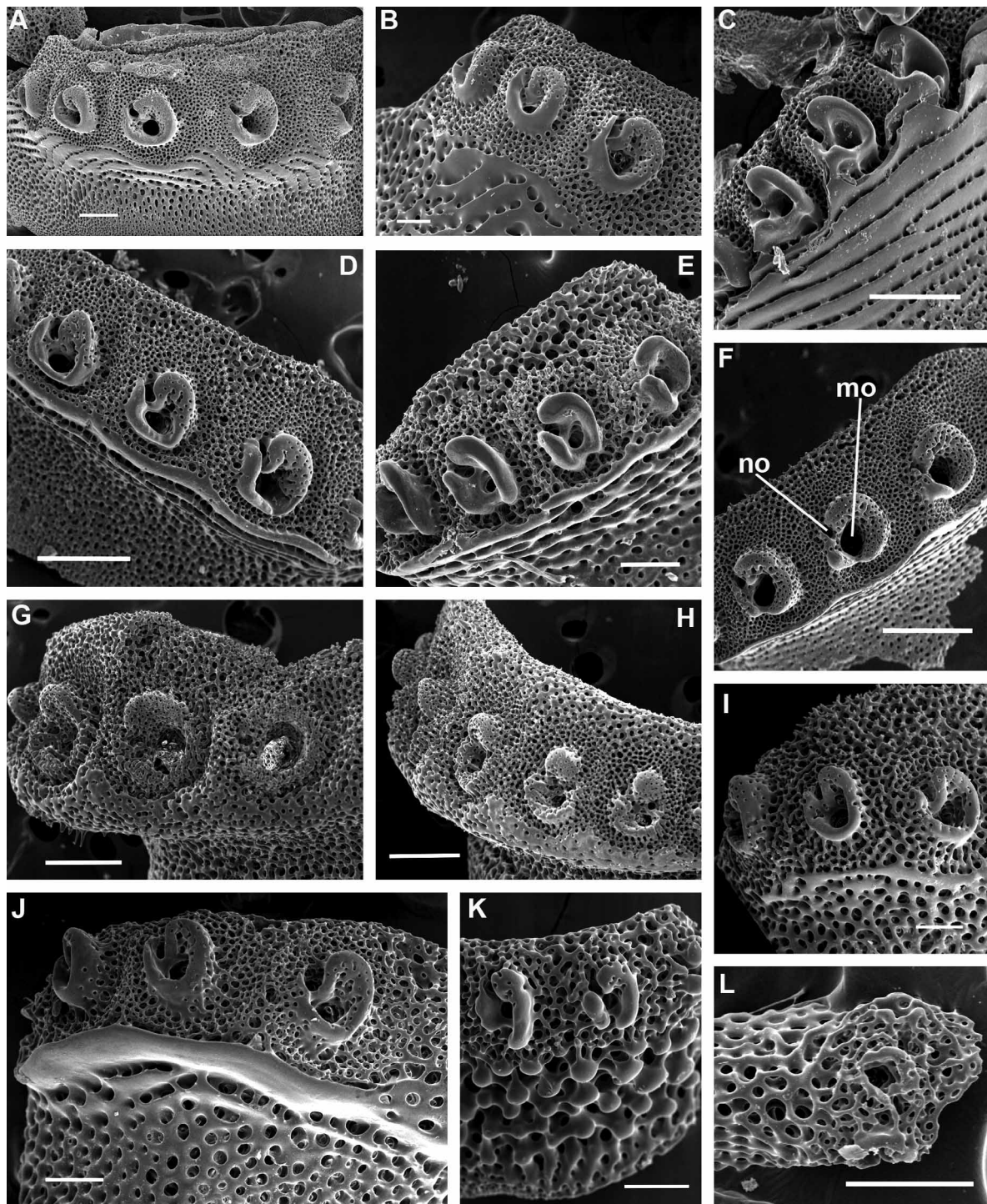
**FIGURE 26.** Arm spine articulations and spines of the family Ophiuridae. A. *Ophiocten sericeum* (Forbes, 1852), ZMMU D-167, 9 mm dd, proximal segments; B. *Ophiocten sericeum*, Holocene, Kara Sea, disarticulated ossicles, proximal segments; C. *Ophiostriatus* sp., ZMMU D-840, 8.5 mm dd, proximal segments; D. *Ophioleuce* sp., ZMMU D-826, 5.5 mm dd, proximal segments; E. *Ophioleuce brevispinum* (H.L. Clark, 1911), IORAS 13.28, 10 mm dd, proximal segments; F-H, *Ophiernus belyaevi* Litvinova, 1975, IORAS N 13.19, 12 mm dd, proximal segments; F. spine articulation; G. modified dorsalmost spines; H. normal spine, ventral view; I-J, *Ophiopallas paradoxa* Koehler, 1904, IORAS N 13.8, proximal segments; I. articulations; J. spine, ventral view; K. *Bathylepta pacifica* Belyaev & Litvinova, 1972, IORAS N 13.1, 4 mm dd, proximal segments; L. *Uriopha ios* Paterson, 1980, IORAS N 13.39, 3 mm dd, proximal segments. Scale bars: A–B, 100  $\mu$ ; C, 200  $\mu$ ; D, 30  $\mu$ ; E, 150  $\mu$ ; F, 80  $\mu$ ; G, 300  $\mu$ ; H, 100  $\mu$ ; I, 120  $\mu$ ; J–L, 60  $\mu$ . Photos: Alexander Martynov.





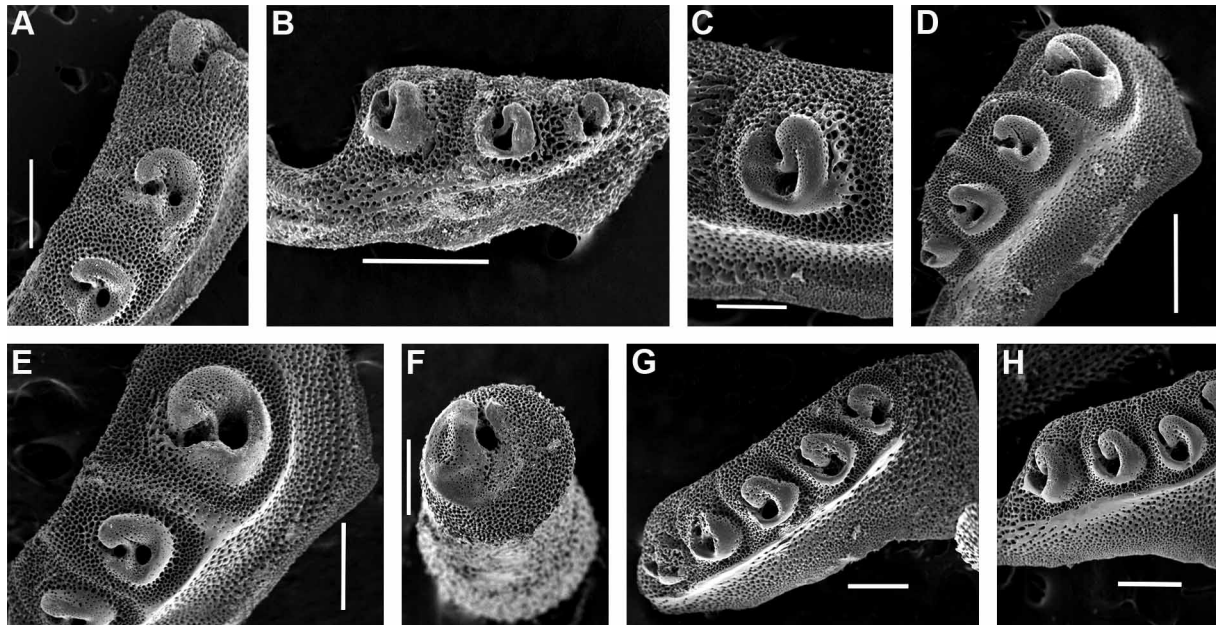
**FIGURE 27.** Arm spine articulations and spines of the various taxa of the family Ophiomyxidae. A–C, *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-817, 27 mm dd; spine articulations of the proximal segments; D, spine, lateral view, E, spine, ventral view showing large nerve opening; F, *Ophiomyxa brevirima* H.L. Clark, 1915, ZMMU D-725, 19 mm dd, distal segments; G, *Ophiomyxa brevirima*, proximal segments; H, *Ophiocymbium cavernosum* Lyman, 1880, ZMMU D-794, 9.5 mm dd, proximal segments; I, *Ophiocymbium cavernosum*, ZMMU D-795, 10.5 mm, proximal segment; J, *Ophiocymbium tanyae* sp. nov., holotype, ZMMU D-799, 9.5 mm dd, proximal segments; K, same, middle segments; L, *Ophiologimus* cf. *secundus* Koehler, 1914, ZMMU D-815, 4 mm dd, proximal segments; M, same a proximal segment with spines; N, same, details of the articulations of the proximal segments; O, *Ophiobyrsa rudis* Lyman, 1878, ZMMU D-868, 12.5 mm dd; P, *Ophiologimus* cf. *secundus*, most proximal segments; Q, *Ophiolycus purpureus* (Düben & Koren, 1846), ZMMU D-845, 5.5 mm dd, most proximal segments; R, same, proximal segments; S, *Ophiolycus nutrix* Mortensen, 1936, ZMMU D-818, 8 mm dd, proximal segments with spines; T, same, other proximal segments; U, same, spine base, ventral view; Scale bars: A–B, 300  $\mu$ ; C, 200  $\mu$ ; D, 400  $\mu$ ; E, 150  $\mu$ ; F, 100  $\mu$ ; G, 150  $\mu$ ; H, 100  $\mu$ ; I, 100  $\mu$ ; J, 100  $\mu$ ; K, 200  $\mu$ ; L, 100  $\mu$ ; M, 100  $\mu$ ; N, 100  $\mu$ ; O, 250  $\mu$ ; P, 100  $\mu$ ; Q, 100  $\mu$ ; R, 100  $\mu$ ; S–T, 120  $\mu$ ; U, 150  $\mu$ . Photos: Alexander Martynov.





**FIGURE 28.** Arm spine articulations of the various taxa of the family Ophiacanthidae. A. *Ophiotoma assimilis* Koehler, 1904, ZMMU D-807, 18.5 mm dd, proximal segments; B. *Ophiotoma alberti* (Koehler, 1896), ZMMU D-810, 12 mm dd, proximal segments; C. *Ophiolimna bairdi* (Lyman, 1883), ZMMU D-648, 9.5 mm dd, proximal segments; D. *Ophiacantha bidentata* (Bruzelius, 1805), ZMMU D-750, 8 mm dd, proximal segments; E. *Ophiacantha abyssicola* G.O.Sars, 1871, ZMMU D-846, 4.8 mm dd, proximal segments; F. *Ophiacantha spectabilis* G.O.Sars, 1871, ZMMU D-660, ca. 11 mm dd proximal segments; G. *Ophiocamax vitrea* Lyman, 1878, ZMMU D-811, 9 mm dd, dorsal spine articulations of the proximal segments; H. same, ventral articulations of the proximal segments; I. *Ophioplinthaca rudis* (Koehler, 1897), ZMMU D-812, 7 mm dd, proximal segments; J. *Ophiosemnotes tylota tuberculata* Dyakonov, 1954, IORAS 3.71, 6 mm dd, proximal segments; K. *Ophiotebes* sp., ZMMU D-847, 5.5 mm dd, proximal segments; L. *Ophiomedeia* sp., ZMMU D-848, 3.5 mm dd, proximal segments. Scale bars: A, 200  $\mu$ ; B, 100  $\mu$ ; C, 200 nm; D, 300  $\mu$ ; E, 100  $\mu$ ; F–H, 300  $\mu$ ; I, 100  $\mu$ ; J, 100  $\mu$ ; K, 100  $\mu$ ; L, 120  $\mu$ . Photos: Alexander Martynov.





**FIGURE 29.** Arm spine articulations and spines of the various taxa of the family Ophiocomidae. A. *Ophiocoma erinacea* Müller & Troschel, 1842, ZMMU D-123, 15 mm dd, proximal segments; B–C, *Ophiocoma pica* Müller & Troschel, 1842, ZMMU D-560, 13.5 mm dd, proximal segments; D–E, *Ophiomastix caryophyllata* Lütken, 1869, ZMMU D-108, 17.5 mm dd, articulations, proximal segments; F. same, dorsalmost club-shaped spine, ventral view; G–H, *Ophiocomina nigra*, ZMMU D-309, 12 mm dd, proximal segments; Scale bars: A–B, 400  $\mu$ ; C, 200  $\mu$ ; D, 600  $\mu$ ; E, 400  $\mu$ ; F–H, 300  $\mu$ . Photos: Alexander Martynov.

Ophiomyxidae (Fig. 27): two main types can be distinguished. First, the double-opening type, somewhat subparallel with a low dorsal lobe in *Ophiolycus* (Figs 21C; 27Q–T), symmetrically elevated in some *Ophiobyrsa* and *Ophiobyrsella*, and with a chelate, asymmetrically elevated knob in the genus *Ophiomyxa* Müller & Troschel, 1842 (Fig. 27G) and in *Ophiobyrsa rudis* Lyman, 1878 (Fig. 27O). Second, the single-opening type, sometimes horseshoe-shaped with a broad low border (e.g. in the genus *Ophioscolex* Müller & Troschel, 1842 s.str., *Ophiogeron*, *Ophiocanops*) (Figs 27A–C). In the genus *Ophiomyxa*, the articulations placed distally on the lateral plate are single-opening (Fig. 27F), similar to the genus *Ophioscolex*. Thus, the distinction between double- and single-opening articulations is not strict within the family Ophiomyxidae and evidently intermediate cases exist.

Ophiacanthidae (Figs 28; 47E, F; 68–70; 78F, H; 82A etc): volute-shaped articulations with a large muscle opening and a small slit-shaped nerve opening. There is a specific bending of the stereom protuberance that makes the lobe appear volute-shaped, for which I propose the term sigmoidal fold (Fig. 21B). This fold is present in the type of the family Ophiacanthidae, *Ophiacantha bidentata*, and without exception, though more or less variable (Fig. 28), in all studied species of the genus *Ophiacantha* and other genera of the subfamilies Ophiacanthinae s.str. and Ophioplinthacinae (Fig. 28). The most regular, rounded volute, with a distinct whorl on the articulations, was discovered in some species of the genus *Ophiotoma* (subfamily Ophiotominae) (Figs 68A, B; 69E–H). In other ophiacanthid genera, the articulations are more elongated (e.g. Fig. 28E, K), proximally closed or semi-closed. On the distal plates the articulations may become more parallel but always retain a volute-shape.

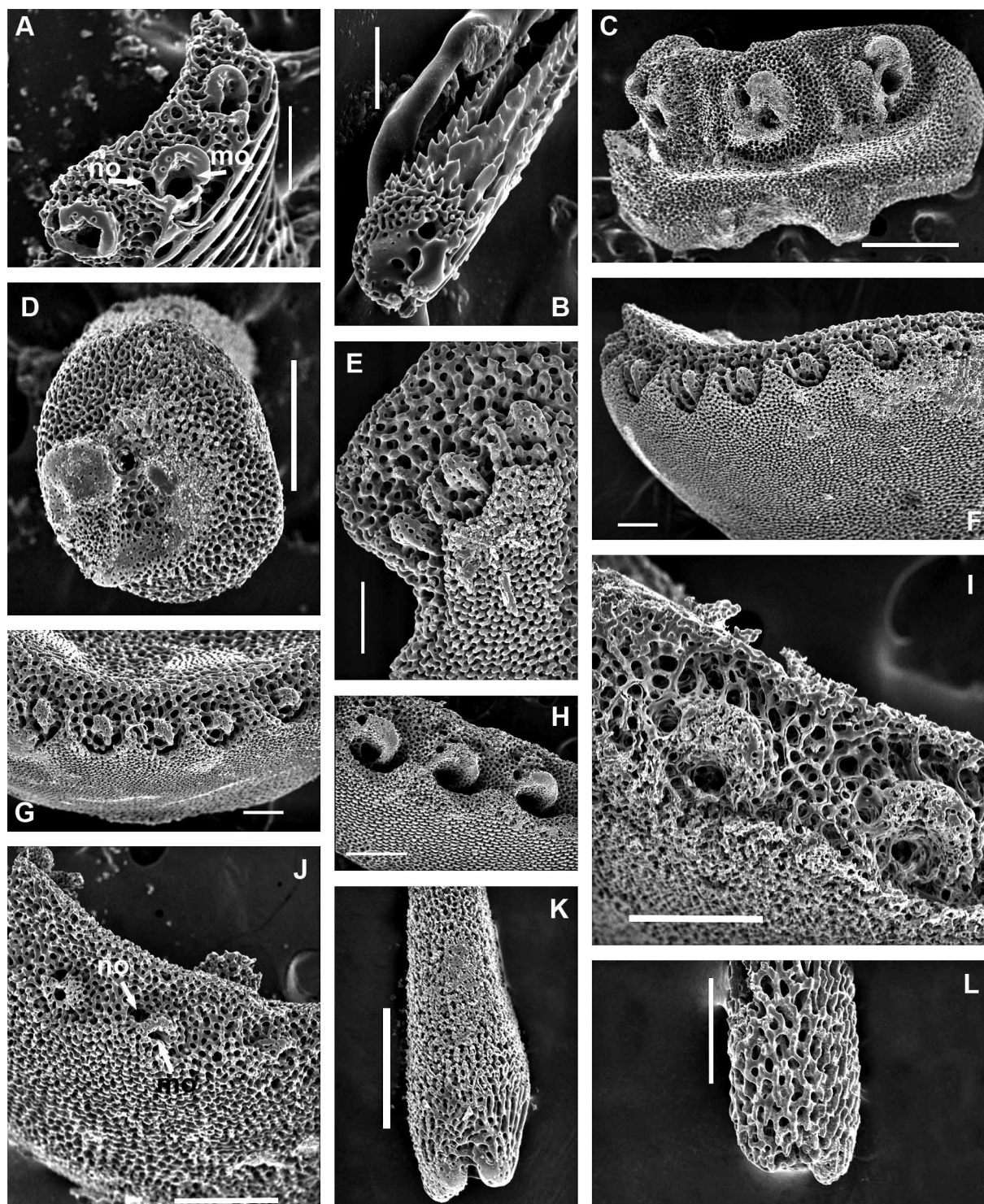
Ophiocomidae (Fig. 29): strong, volute-shaped, always proximally closed articulation slightly depressed on the lateral plate, with two openings nearly equal in size. The sigmoidal fold is always present.

Ophiodermatidae (Fig. 30): articulations with one large curved lobe and a small second lobe, often considerably reduced. There are two openings nearly equal in size. The articulations often are considerably depressed on the lateral plate. The sigmoidal fold is present in many taxa, but often considerably reduced.

Ophiactidae and Amphiuroidae (Figs 31, 32): nearly parallel, quite often slightly curved (especially in Ophiactidae) high ridges, elongated in the proximal-distal direction, framing two openings of nearly equal



size (or sometimes one large opening due to reduction of the septum). The ridges are open at both ends or closed proximally.

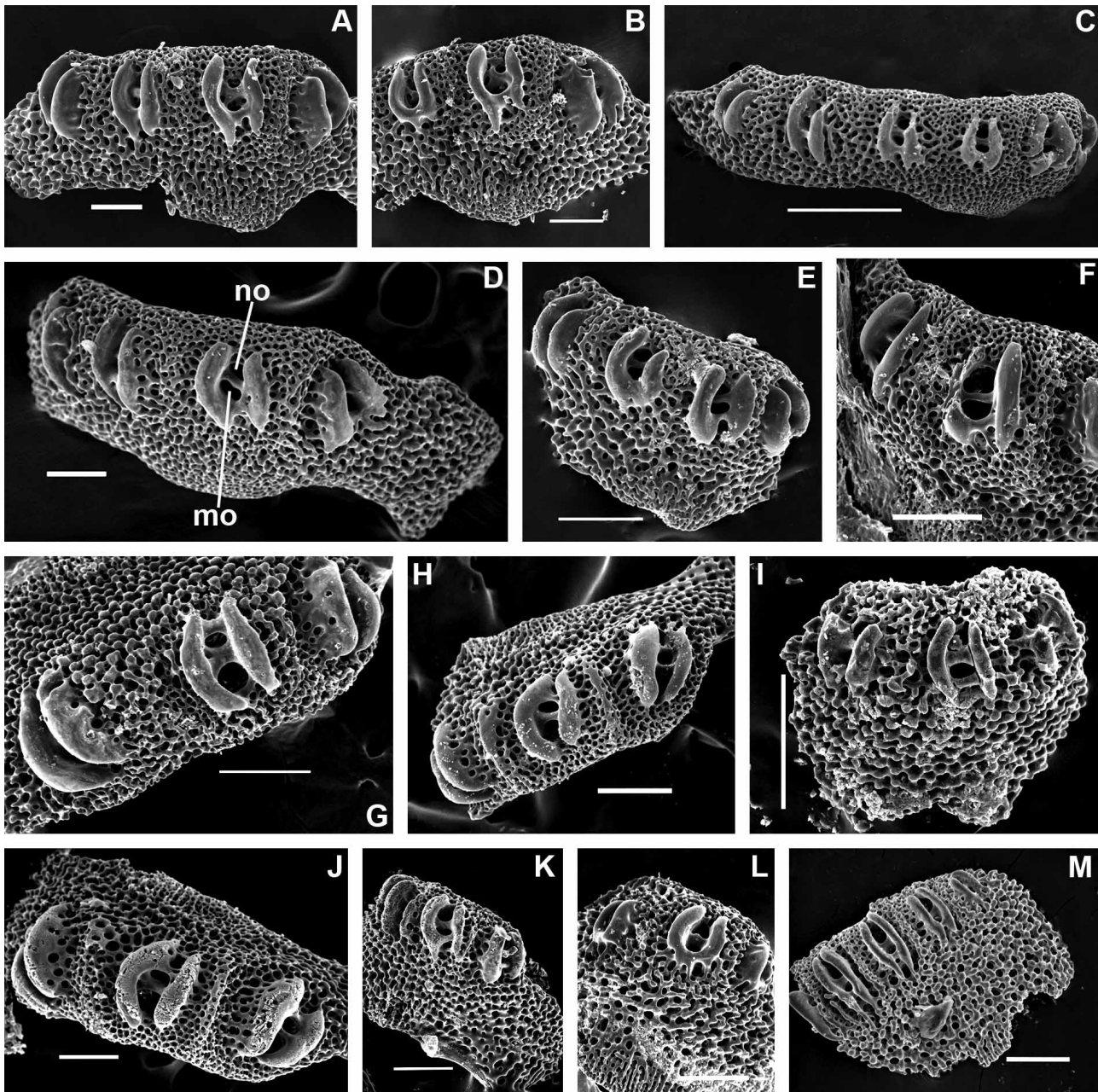


**FIGURE 30.** Arm spine articulations and spines of various taxa of the family Ophiidermatidae. A-B, *Ophioconis* sp., IORAS 8.4, 7 mm dd, proximal segments; A. articulations; B. spine, ventro-lateral view; C-D, *Ophiarachna incrassata* (Lamarck, 1816), ZMMU D-95, 25 mm dd, proximal segments; C. articulations; D. spine, ventral view; E-G, *Ophiopeza spinosa* (Ljungman, 1867), ZMMU D -819, 6 mm dd; E. most proximal segments; F. proximal segments; G. middle segments; H. *Ophiopsammus maculata* (Verrill, 1869), ZMMU D-859, 29 mm dd, middle segments; I. *Ophioderma* sp., ZMMU D-832, 27 mm dd, proximal segments, articulations; J. *Bathypectinura heros* (Lyman, 1879), IORAS 8.1, 19 mm dd, proximal segments; K. *Ophioderma* sp., spine, lateral view; L. *Bathypectinura heros*, spine; Scale bars: A, 60  $\mu$ ; B, 40  $\mu$ ; C, 600  $\mu$ ; D, 300  $\mu$ ; E-G, 100  $\mu$ ; H, 300  $\mu$ ; I, 150  $\mu$ ; J, 400  $\mu$ ; K, 200  $\mu$ ; L, 150  $\mu$ . Photos: Alexander Martynov.



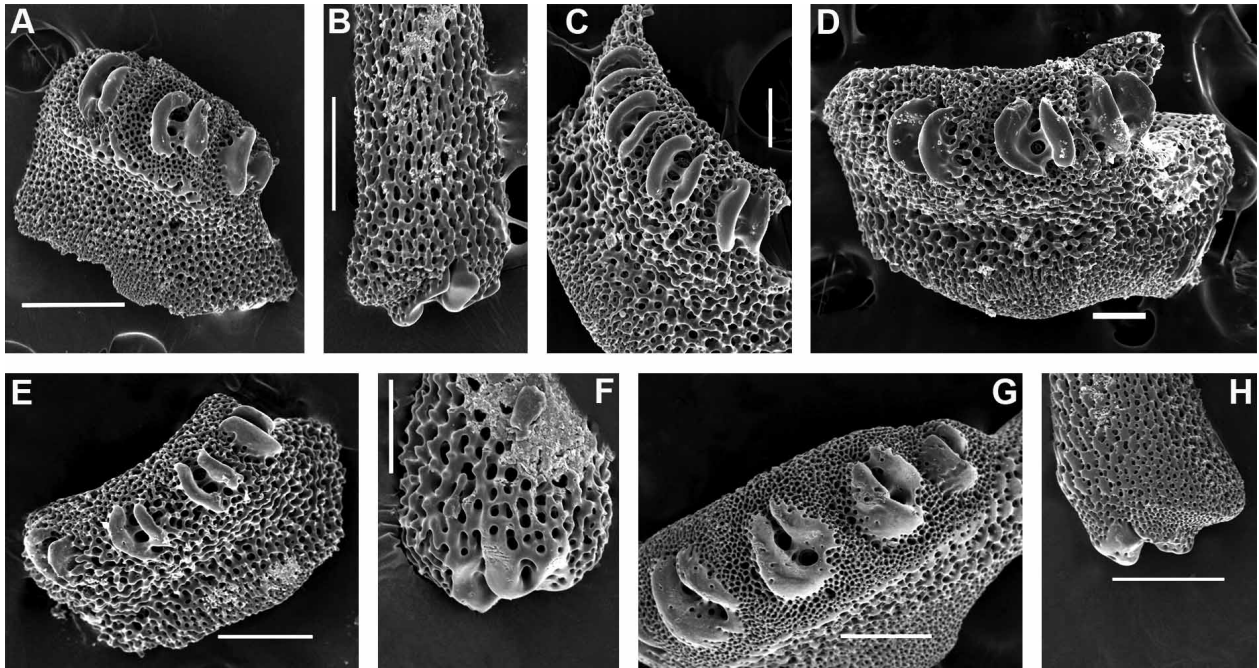
Amphilepididae (Figs 33F, G): semi-parallel to semi-circular ridges proximally, with peculiarly arranged irregular ribs.

Ophionereididae (Figs 33A–C): horseshoe-shaped, proximally closed ridges, with a saddle-shaped area, which is framed by a regular ribbed border, a little depressed on the lateral plate. There are two openings, nearly equal in size.



**FIGURE 31.** Arm spine articulations and spines of various taxa of the family Amphiuroidae. A–B, *Amphiura sundevalli* (Müller & Troschel, 1842), ZMMU D-579, 7 mm dd, proximal segments showing variability of the ridges; C, *Amphiura sundevalli*, ZMMU D-579, proximal segments; D, *Dougaloplus derjugini* (Djakonov, 1949), ZMMU D-836, 8 mm dd; E, *Amphiura borealis* (G.O. Sars, 1871), ZMMU D-767, 3.5 mm dd, proximal segments; F, *Amphiura carchara* H.L. Clark, 1911, ZMMU D-835, 5.5 mm dd, proximal segments; G, *Amphiodia craterodmeta* H.L. Clark, 1911, ZMMU D-578, 5 mm dd, proximal segments; H, *Amphipholis squamata* (Delle Chiaje, 1828), ZMMU D-772, proximal segments, 3.5 mm dd; I, *Amphipholis torelli* Ljungman, 1871, ZMMU D-860, 3 mm dd, proximal segments; J, *Amphipholis kochi*, ZMMU D-142, 8 mm dd, intertidal, proximal segments; K, same, distal segments; L, *Amphioplus cernuus* (Lyman, 1879), ZMMU D-853, 5 mm dd, proximal segments; M, *Ophiosphaera insignis* Brock, 1888, ZMMU D-852, 5 mm dd, proximal segments. Scale bars: A–B, 100  $\mu$ ; C, 300  $\mu$ ; D, 100  $\mu$ ; E, 100  $\mu$ ; F–G, 120  $\mu$ ; H–K, 100  $\mu$ ; L, 120  $\mu$ ; M, 100  $\mu$ . Photos: Alexander Martynov.





**FIGURE 32.** Arm spine articulations and spines of the various taxa of the family Ophiactidae. A. *Ophiactis abyssicola* (M.Sars, 1861), ZMMU D-631, 6 mm dd, articulation ridges, proximal segments; B. same, spine, latero-ventral view, proximal segments; C. *Ophiactis* sp., ZMMU D-831, 6 mm dd; D. *Histampica duplicata* (Lyman, 1875), ZMMU D-729, 5.5 mm dd, proximal segments; E. *Ophiopus arcticus* Ljungman, 1867, ZMMU D-856, 4.5 mm dd, spine articulations; F. same, spine, latero-ventral view; G. *Ophiopholis aculeata* (L., 1767), ZMMU D-134, 18 mm dd, articulations, proximal segments; H. *Ophiopholis aculeata* (L., 1767), 15 mm dd, ZMMU D-615, spine, proximal segments; Scale bars: A, 300  $\mu$ ; B, 200  $\mu$ ; C–D, 100  $\mu$ ; E, 200  $\mu$ ; F, 80  $\mu$ ; G–H, 300  $\mu$ . Photos: Alexander Martynov.

Ophiochitonidae (Figs 33H–I): horseshoe-shaped, not enlarged ridges, closed proximally, without a ribbed border. Muscle openings slightly larger than nerve openings.

Ophiolepididae (Fig. 34): small, in different degrees of reduction, parallel or subparallel ridges open at both ends, framing two openings nearly equal in size. The ridges are considerably depressed on the lateral plate in the genus *Ophiolepis* Müller & Troschel, 1842.

Ophiotrichidae (Fig. 35): nearly parallel slightly curved ridges with a low round border of conspicuously smooth stereom framing two openings nearly equal in size arranged at an angle to each other, elongated in a ventro-dorsal direction. The ridges are open at both ends.

Hemieuryalidae (s.str.) (Figs 36A, B): two parallel ridges placed at an angle to each other, with a single small opening. Inner surfaces of the ridges bear triangular scars – sites of contact with the spine base (Figs 36C, D).

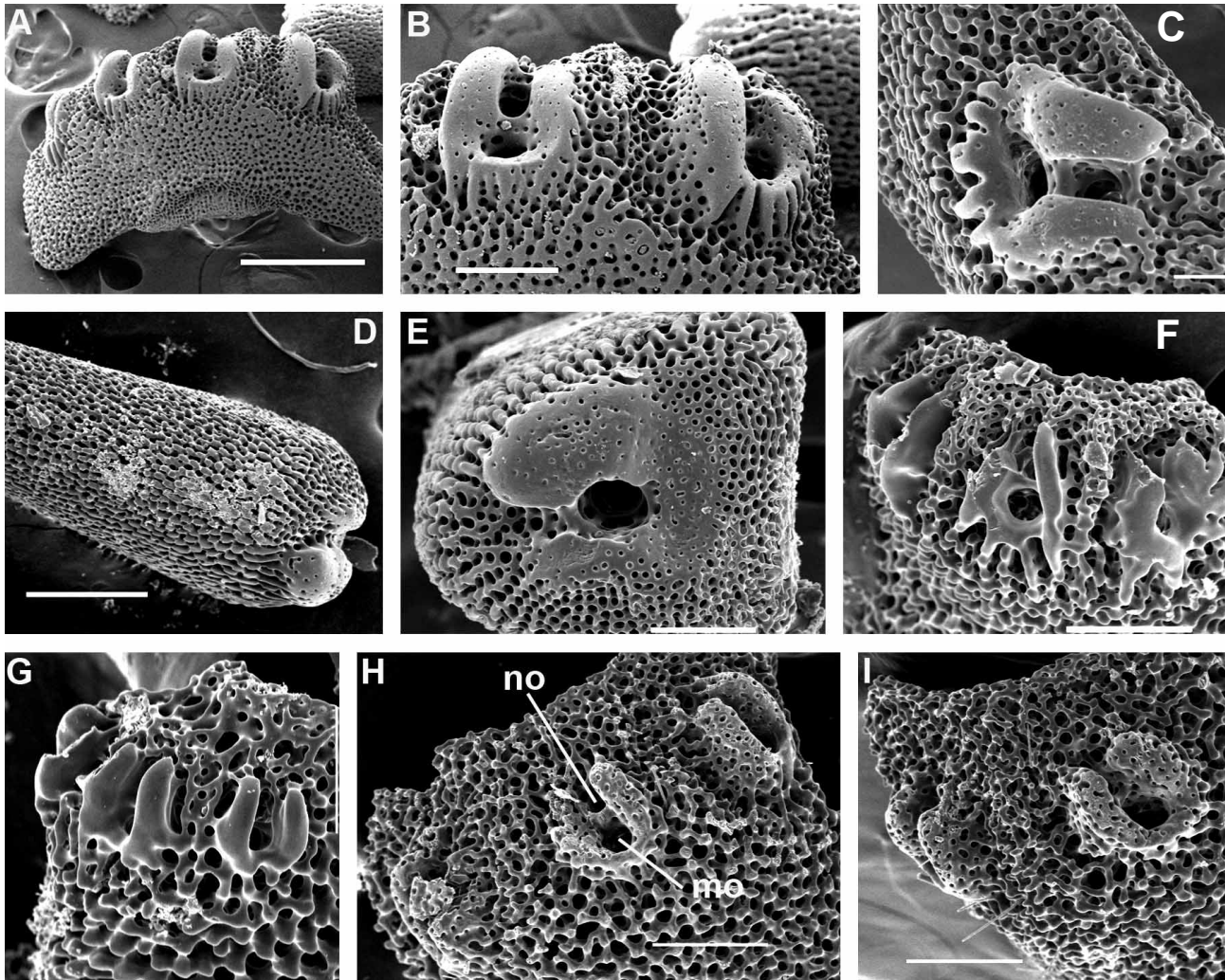
## Class Ophiuroidea

### Family Ophiacanthidae Ljungman, 1867

#### Ophiotominae in the traditional sense and new results

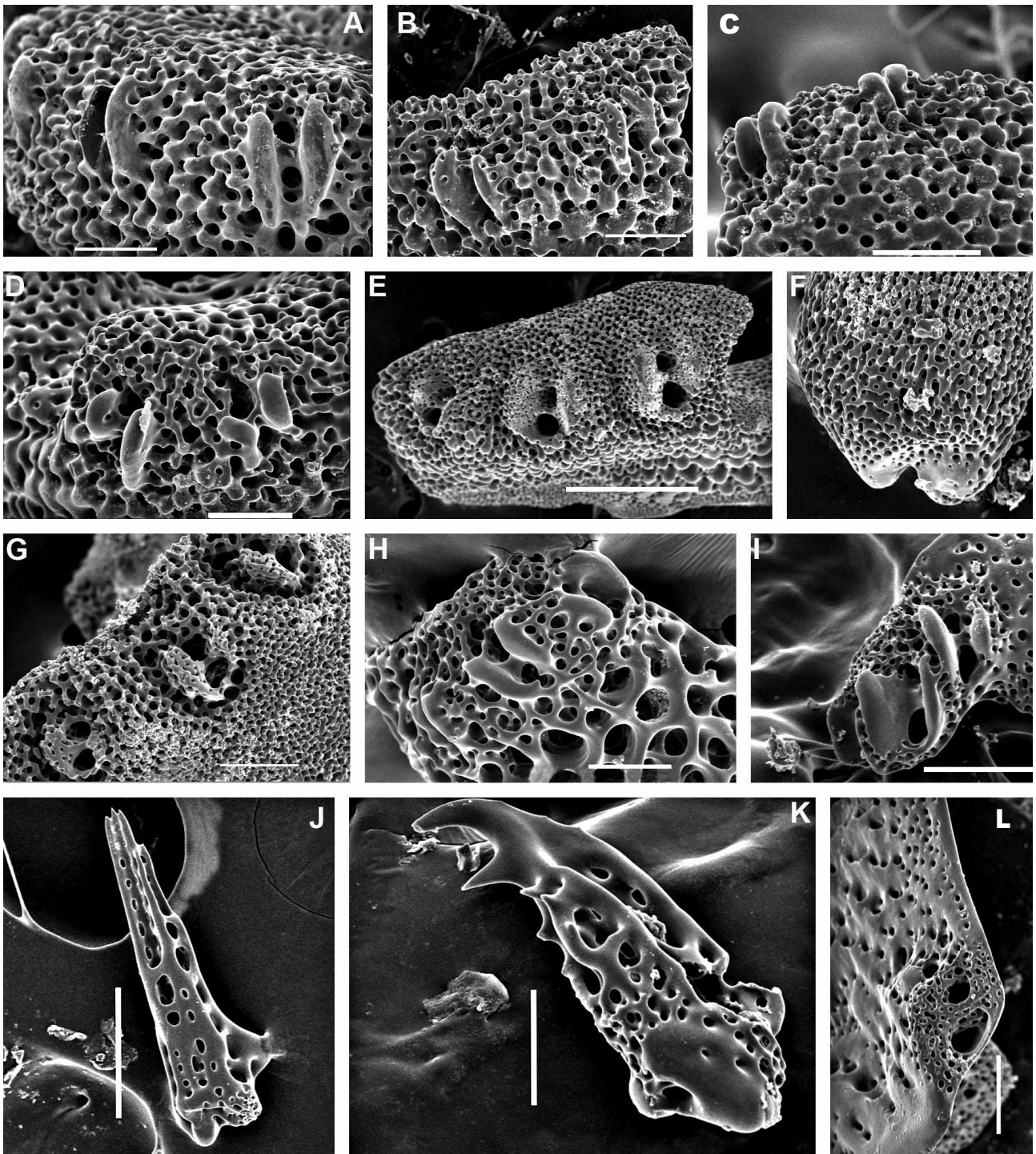
The taxonomy of the family Ophiacanthidae is one of the most complicated within the Ophiuroidea. Some of the representatives of this large family are apparently similar to the Ophiomyxidae (Ophiotominae according to Paterson (1985)), whereas others are similar to other distantly-related brittle-star groups. A genus-level

revision of the family Ophiacanthidae is a desirable, but a not yet completed task. Therefore, the family Ophiacanthidae appeared to be a good candidate to test the usefulness of the internal and microstructural characters for ophiuroid taxonomy and phylogenetic relationships. Herein, a critical review of the genera included in the ophiacanthid subfamily Ophiotominae is presented. Below are listed in alphabetical order, all the genera of the subfamily Ophiotominae, sensu Paterson (1985). For each genus, a diagnosis (including both external and internal characters) and a key for identification of species are provided. Type specimens, as far as were available, were used for diagnosis and keys. Appropriate taxonomic remarks were added, where necessary. A general discussion on the genera of the Ophiotominae and their taxonomic re-evaluation according to the newly obtained results will be presented in separate sections.



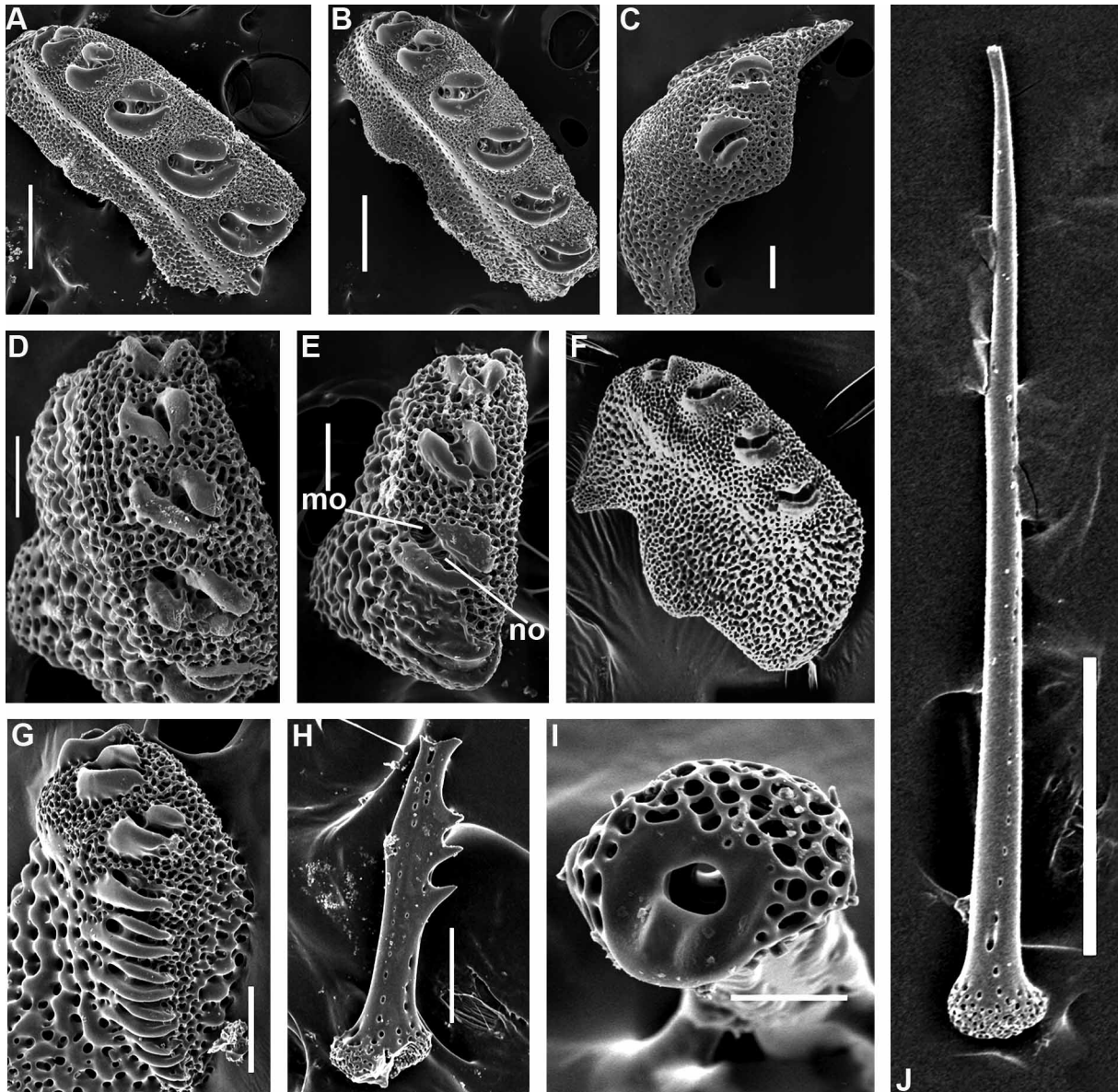
**FIGURE 33.** Arm spine articulations and spines of the various taxa of the families Ophionereididae, Ophiochitonidae and Amphilepididae; A–C, *Ophionereis schayeri* (Müller & Troschel, 1844), ZMMU D-820, 12 mm dd, arm spine articulations, proximal segments; D. same, spine, lateral view of the basal part; E. same, spine, ventral view; F. *Amphilepis platytata* H.L. Clark, 1911, ZMMU D-844, 6.5 mm, proximal segments; G. distal segments; H–I, *Ophiochiton ternispinus* Lyman, 1883, ZMMU D-743, 5.5 mm dd, proximal segments. Scale bars: A, 400  $\mu$ ; B, 150  $\mu$ ; C, 100  $\mu$ ; D, 200  $\mu$ ; E, 100  $\mu$ ; F, 120  $\mu$ ; G, 80  $\mu$ ; H–I, 150  $\mu$ . Photos: Alexander Martynov.





**FIGURE 34.** Arm spine articulations and spines of the various taxa of the family Ophiolepididae. A. *Ophiopenia tetracantha* H.L.Clark, 1911, ZMMU D-580, 8.5 mm dd, proximal segments; B. *Ophiozonella alba* (Lütken & Mortensen, 1899), IORAS 15.109, 7.5 mm dd, proximal segments; C–D, *Ophiozonella* sp., ZMMU D-861, 6 mm dd, proximal segments; E. *Ophioplocus imbricatus* (Müller & Troschel, 1842), ZMMU D-20, articulations, proximal segments; F. same, spine, base lateral view; G. *Ophiolepis elegans* Lütken, 1859, IORAS 15.99, 9 mm dd, proximal segments; H. *Abyssura brevibrachia* Belyaev & Litvinova, 1976, IORAS 14.305, 6 mm dd, proximal segments; I. *Ophiambix aculeatus* Lyman, 1880, ZMMU D-862, 4 mm dd, articulations, middle segments; J. same, spine; K. same, hook-shaped spine; L. *Ophiophyllum nesisii* Martynov & Litvinova, 2008, ZMMU D-746, 7 mm dd, proximal segments; Scale bars: A, 120  $\mu$ ; B, 150  $\mu$ ; C, 120  $\mu$ ; D, 80  $\mu$ ; E, 400  $\mu$ ; F, 120  $\mu$ ; G–H, 100  $\mu$ ; I, 150  $\mu$ ; J, 150  $\mu$ ; K, 60  $\mu$ ; L, 100  $\mu$ ; Photos: Alexander Martynov.





**FIGURE 35.** Arm spine articulations and spines of the various taxa of the family Ophiotrichidae. A–B, *Ophiotrix fragilis* (Abildgaard, 1789), ZMMU D-827, 8 mm dd, proximal segments; C, same, most proximal segment; D, *Ophiopsammium rugosum* Koehler, 1905, ZMMU D-101, 7 mm dd, proximal segments; E, *Ophiothela danae* ZMMU D-828, 5 mm dd, most proximal segments; F, *Gymnolophus obscura* (Ljungman, 1867), ZMMU D-863, 8 mm dd, proximal segments; G, *Ophiopteron elegans* Ludwig, 1888, IORAS 12.4, 5 mm dd, articulation ridges, proximal segments; H, same, normal spine, lateral view, middle segments; I, same, ventral view; J, same, one of the elongated spine, united to a fan, proximal segments; Scale bars: A–B, 300  $\mu$ ; C–D, 100  $\mu$ ; E, 100  $\mu$ ; F, 30  $\mu$ ; G, 120  $\mu$ ; H, 150  $\mu$ ; I, 40  $\mu$ ; J, 400  $\mu$ ; Photos: Alexander Martynov.

### Genus *Amphilimna* Verrill, 1899

Figures 37–39

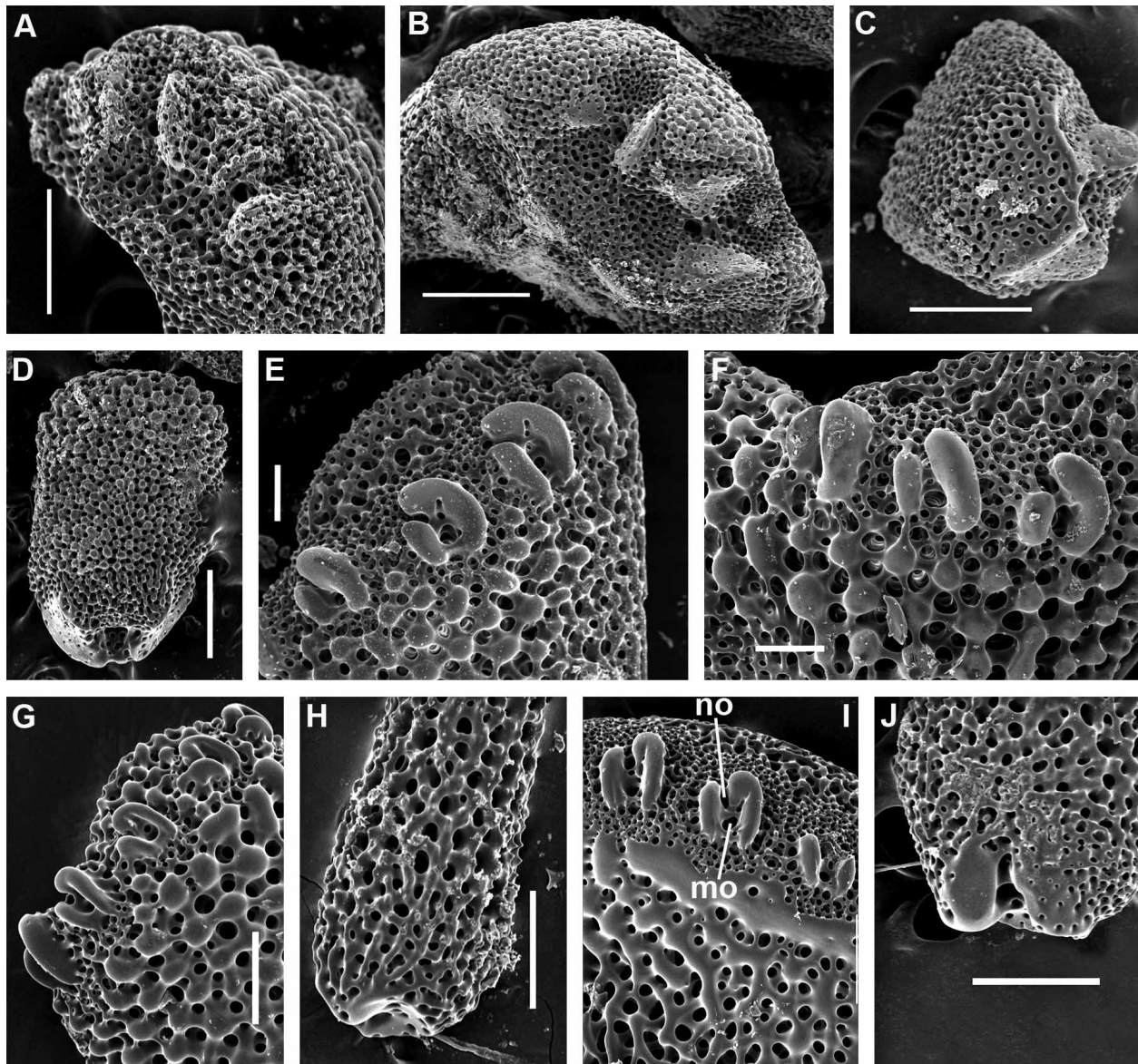
*Amphilimna* Verrill, 1899: 30

Type species: *Ophiocnida olivacea* Lyman, 1869, by original designation

**Diagnosis.** The disk is covered with numerous small, uniform scales. A skin layer is not evident. The dorsal disk surface is covered with numerous long spinelets or granules. The radial shield and adradial genital plate are well defined. The articulation surfaces of both adradial genital plate and radial shield bear a distinct

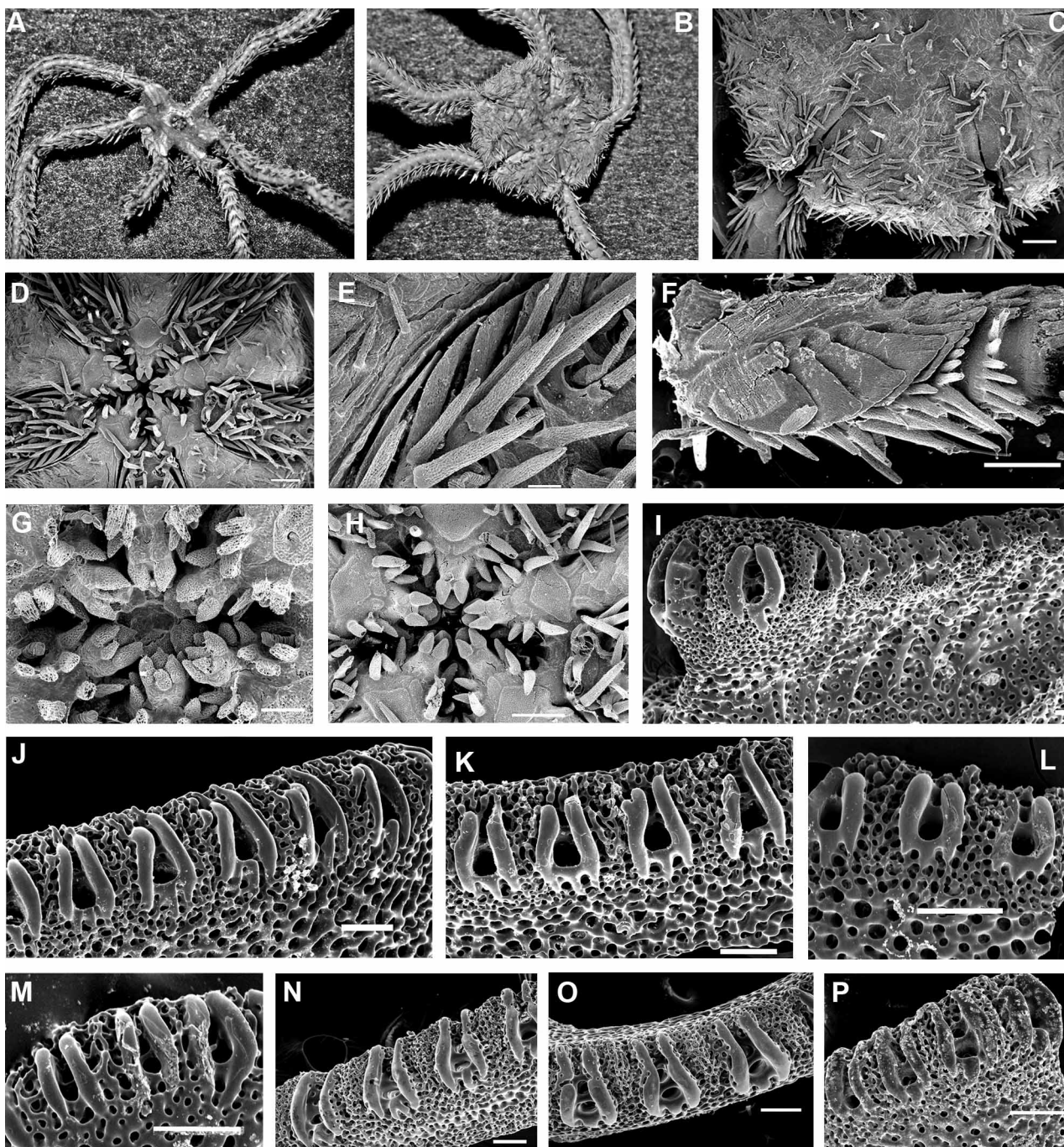


compact ball-like condyle. The abradial genital plate has a peculiar twisted shape. The oral frame bears few spiniform or square papillae, of which the distal (adoral shield papillae) are longer. The apical papillae are paired or tripled and conical. The jaws are moderately short and high. The adradial sides of the jaws distally bear a few sharp straight folds. The dental plate is entire (as in the type species) or transversally fragmented (in *A. multispina*) and bears alternately placed non-perforated sockets. The teeth are rectangular and massive. Dorsal and ventral arm plates are well developed. Tentacle scales are placed on the lateral and ventral arm plates, the former spiniform and distinctly elongate. Arm spine articulations consist of two subparallel ridges each, often tapering and bottle-like distally. The spines are moderately long, not flattened, and solid. Most proximal spines under the disk are characteristically modified into wide scale-like structures. Distal hooks are absent. The vertebrae are distinctly keeled with zygospondylous articulation.



**FIGURE 36.** Arm spine articulations and spines of the various taxa of the families Hemieuryalidae and Ophiacanthidae. A. *Hemieuryale pustulata* Martens, 1867, ZMMU D-857, dd unknown, proximal segments; B. *Sigsbeia murrhina* Lyman, 1878, ZMMU D-858, dd unknown, articulations, proximal segments; C. same, spine, ventral view; D. same, spine, lateral view; E. *Ophiomoeis obstricta* (Lyman, 1878), ZMMU D-855, 5 mm dd, articulation ridges, proximal segments; F. same, most proximal segments; G. same, distal segments; H. spine, proximal segments, latero-ventral view; I. *Ophiochondrus convolutus* Lyman, 1869, USNM 7164, 6.5 mm dd, articulations, proximal segments; J. spine, proximal segments. Scale bars: A, 200  $\mu$ ; B, 300  $\mu$ ; C–D, 200  $\mu$ ; E–H, 100  $\mu$ ; I, 200  $\mu$ ; J, 120  $\mu$ . Photos: Alexander Martynov.





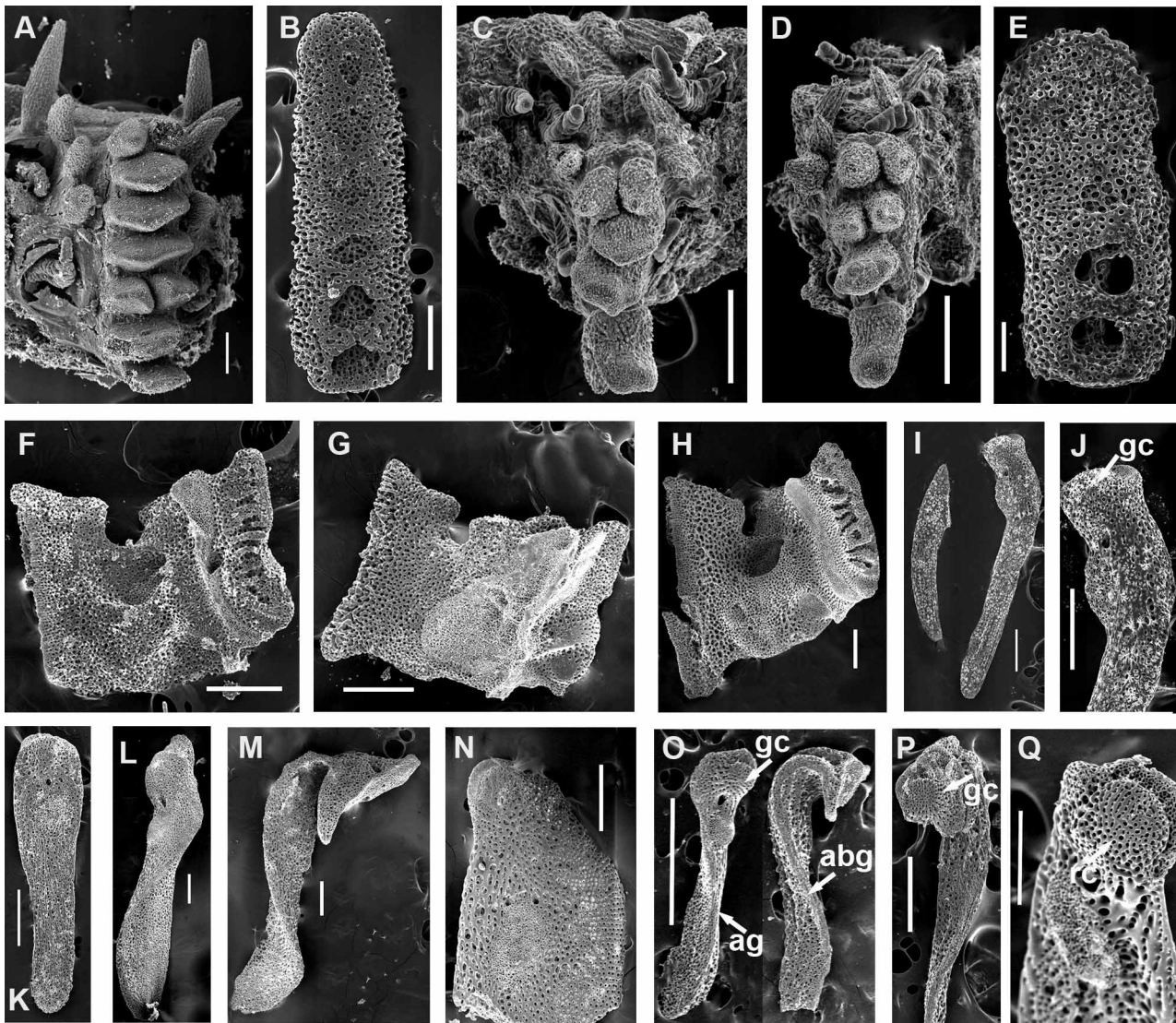
**FIGURE 37.** Genera *Ophiopsila* and *Amphilimna*, external views and details. A. *Ophiopsila bispinosa* A.M. Clark, 1974, ZMMU D-829, 5.5 mm dd, external view, dorsally; B. *Amphilimna olivacea* (Lyman, 1869), ZMMU D-51, 11 mm dd, external view, dorsally; C. same, enlarged part of the disk; D. same, oral frame; E. same, ventral view of some most proximal segments showing the aberrant scale-like arm spine; F. same, removed most proximal arm segments showing aberrant arm spines, lateral view; G. *Ophiopsila bispinosa*, same, oral frame; H. *Amphilimna olivacea*, oral frame enlarged; I. same, lateral arm plate and spine articulation ridges of the most proximal segments (including ridges modified into scars bearing aberrant spines); J, K, same, arm spine articulation ridges, proximal segments; L. same, middle segments; M. *Amphilimna multispina* Koehler, 1922, ZMMU D-841, arm spine articulation ridges, proximal segments; N,O, *Ophiopsila annulosa* (M. Sars, 1857), ZIN 2/17060, dd unknown, arm spine articulation ridges, proximal segments; P. *Ophiopsila bispinosa* A.M. Clark, 1974, ZMMU D-829, arm spine articulation ridges, proximal segments. Scale bars B,E, 300  $\mu$ ; C,D, F, 1 mm; G, 300  $\mu$ ; H, 300  $\mu$ ; I, 100  $\mu$ ; J, 300  $\mu$ ; K, 100  $\mu$ ; L, 120  $\mu$ ; M, 80  $\mu$ ; N,O,P, 100  $\mu$ . Photos: A–B Tatiana Korshunova; C–P Alexander Martynov.



**Remarks.** Verrill (1899), when establishing the genus *Amphilimna*, placed it in the family Amphiuridae. This decision was then supported by Koehler (e.g. 1922a). Thomas (1967; 1975) considered *Amphilimna* within Ophiacanthidae, and Paterson (1985) further placed it in the subfamily Ophiotominae. A detailed discussion on the taxonomic problems of the placement of *Amphilimna* will be presented in a general discussion section below.

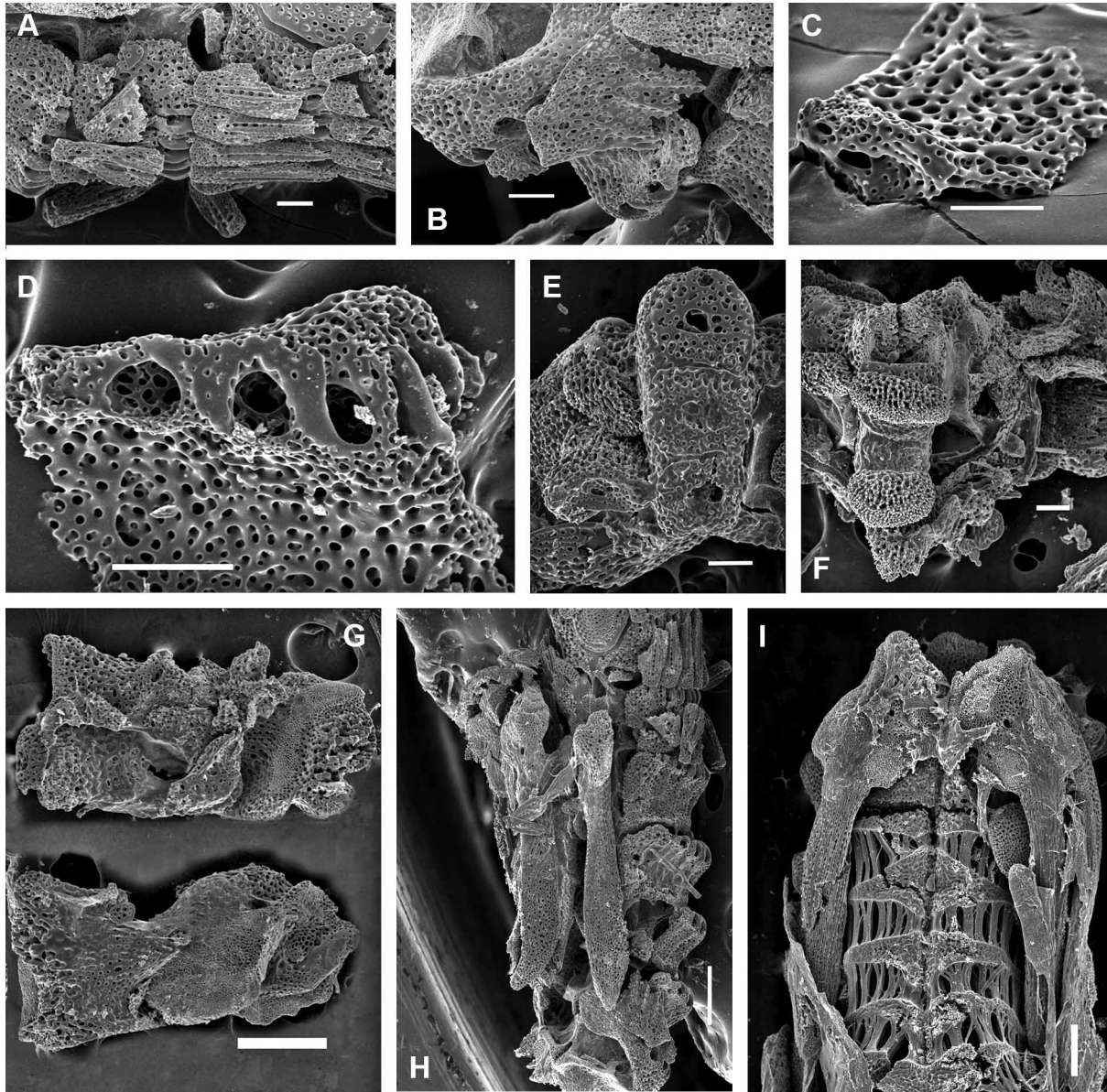
**Material studied.** *Amphilimna olivacea* (Lyman, 1869), ZMMU D-52, 2 specimens (Figs 37B–F; H, I–L); *Amphilimna multispina* Koehler, 1922, 6 paratypes, USNM E00026; ZMMU D-841, D-842, 3 specimens (Figs 37M; 39); *Amphilimna valida* (H.L.Clark, 1939), USNM E42872, 1 specimen.

**Number of species in the genus:** 10.



**FIGURE 38.** Details of the genera *Amphilimna* and *Ophiopsila*. A. *Amphilimna olivacea* (Lyman, 1869), ZMMU D-51, 11 mm dd, inside mouth view of one interradius; B. same, dental plate; C–D, *Ophiopsila bispinosa* A.M. Clark, 1974, ZMMU D-829, 5 mm dd, inside mouth views of two interradii; E. same, dental plate; F. same, jaw, adradial view; G. same, abradial view; H. *Amphilimna olivacea*, ZMMU D-51, jaw, adradial view; I. *Ophiopsila bispinosa* A.M. Clark, 1974, ZMMU D-829, 5.5 mm dd, adradial and abradial genital plates, dorsal view; J. same, enlarged adradial genital plate showing articulation surface, dorsal view; K. radial shield, ventral view; L. *Amphilimna olivacea*, ZMMU D-51, 11 mm, adradial genital plate, dorsal view; M. same, abradial genital plate, lateral view; N. radial shield, ventral view; O. *Amphilimna multispina* Koehler, 1922, ZMMU D-841, 5 mm dd, adradial and abradial genital plates, lateral view; P. same, enlarged adradial genital plate showing articulation surface, dorsal view; Q. same, articulation surface of the radial shield, ventral view; Scale bars: A–B, 300  $\mu$ ; C,D, 300  $\mu$ ; C, 100  $\mu$ ; E, 100  $\mu$ ; F–H, 300  $\mu$ ; I–N, 300  $\mu$ ; O, 600  $\mu$ ; P, 300  $\mu$ ; Q, 150  $\mu$ . Photos: Alexander Martynov.





**FIGURE 39.** *Amphilimna* and *Amphiura*, details. A. *Amphilimna multispina* Koehler, 1922, ZMMU D-841, 5 mm dd, most proximal segments in situ showing both aberrant and normal spines; B. same, most proximal segments in situ, showing aberrant flattened spine and its articulation ridges; C. same, isolated aberrant flattened spine, ventro-lateral view; D. same, aberrant arm spine articulation ridges, most proximal segments; E. same, dental plate in situ, showing natural fragmentation into three pieces, teeth are removed; F. same, dental plate with teeth, ventral piece of the dental plate removed; G. same, jaws, abradial view (above), adradial view (below); H. same, dissected disk showing position of the genital plates in situ, dorsal view; I. *Amphiura chiajei* Forbes, 1843, ZMMU D-776, 5 mm dd, dissected disk showing position of the genital plates in relation to the vertebrae, in situ, dorsal view. Scale bars: A, 100  $\mu$ ; B, 100  $\mu$ ; C, 60  $\mu$ ; D, 80  $\mu$ ; E–F, 100  $\mu$ ; G–I, 300  $\mu$ . Photos: Alexander Martynov.

#### Key to species of the genus *Amphilimna* Verrill, 1899

- 1(8) Tentacle scales on proximal segments long and spiniform
  - 2(7) Disk scales cover only with spinelets
  - 3(6) Up to seven spines on proximal arm segments
  - 4(5) Oral shield rhomboidal.....
- A. *olivacea* (Lyman, 1869), both coasts of the Atlantic Ocean (from Massachusetts to Uruguay and West Africa), at 60–350 m



- 5(4) Oral shield triangular.....  
 .....*A. cribriformis* A.M. Clark, 1974, Atlantic Ocean (South Africa and Mozambique), at 86–200 m
- 6(3) 12–13 spines on proximal arm segments .....  
 ..... *A. polyacantha* Liao, 1983, North Pacific near Hainan Id., at 72–200 m
- 7(2) Disk scales covered with both spinelets and granules .....  
 .....*A. granulosa* Liao, 1989, tropical West Pacific, South Chinese Sea, at 280 m
- 8(1) Tentacle scales on proximal segments rounded, operculiform
- 9(12) Dorsal disk scales bear relatively long spinelets
- 10(11) Six to nine arm spines, oral shield longer than wide.....  
 ..... *A. multispina* Koehler, 1922, Indo–West Pacific (Philippines and East Africa), at 91–357 m
- 11(10) Up to six spines, oral shield wider than long.....  
 .....*A. valida* (H.L. Clark, 1939), Indian Ocean (off Zanzibar), at 238–350 m
- 12(9) Dorsal disk scales bear granules or very short spinelets
- 13(14) Radial shields covered with spinelets and granules .....  
 .....*A. transacta* (Koehler, 1930), Indo–West Pacific, at 300 m
- 14(13) Radial shields uncovered
- 15(20) Radial shields three–four times longer than wide
- 16(17) Ventral disk covered with relatively sparsely placed short spinelets .....  
 .....*A. tanyodes* Devaney, 1974, Indo-West Pacific, at 91–110 m
- 17(16) Ventral disk covered with densely placed granules and tiny spinules
- 18(19) Oral shields as wide as long ..... *A. mirabilis* (H.L. Clark, 1941), Atlantic Ocean (Caribbean), at 320–430 m
- 19(18) Oral shields distinctly wider than long... *A. sinica* Liao, 1989, tropical West Pacific, South Chinese Sea, at 280 m
- 20(15) Radial shields only slightly longer than wide.....  
 .....*A. nike* (Schoener, 1967), tropical Atlantic (Florida to Surinam), at 476–681 m

### Genus *Ophiocymbium* Lyman, 1880

Figures 4E–G, H, L, T; 12C–G; H, M; 15B; 17D, E, G–H, J, P, S; 27H–I; J, K; 40–43; 55 I–N; 67G

*Ophiocymbium* Lyman, 1880: 7

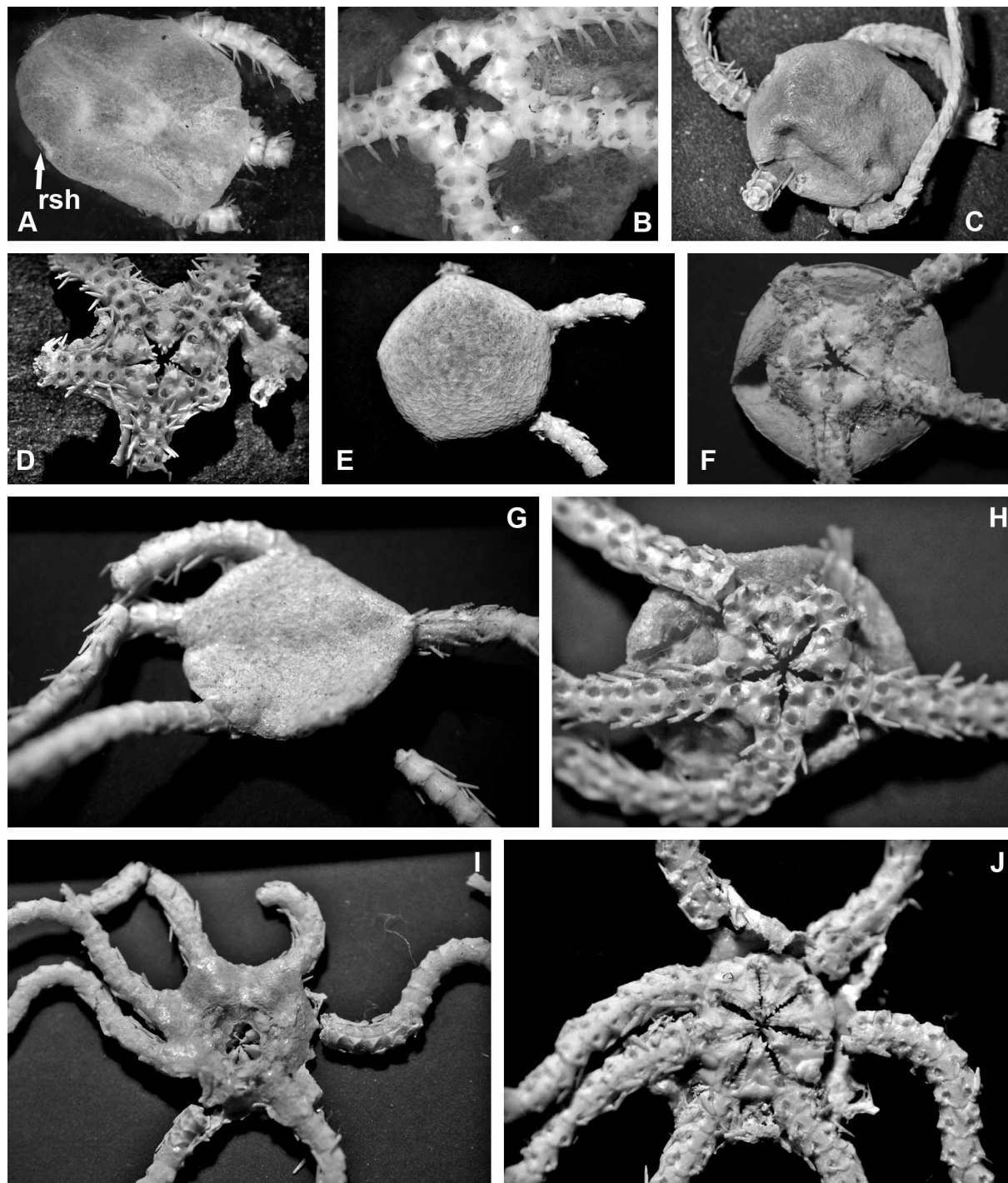
Type species: *Ophiocymbium cavernosum* Lyman, 1880, by monotypy

**Diagnosis.** The disk is covered with numerous small, uniform scales covered by a thin skin layer, not evident when dried. The dorsal disk surface can bear a few sparsely placed spinelets. The radial shield and adradial genital plate are small and externally inconspicuous or totally absent. The articulation surface of the radial shield is distinctly excavated ventrally, distally with a groove. The abradial genital plate is absent. The genital slits are small. The jaws bears a few block-shaped oral papillae. The adoral shield papillae, if any, differ considerably from the oral papillae and are placed around the second tentacle pore. The jaws are slightly elongated. The distal adradial sides of the jaws bear a few sharp straight folds. The dental plate is entire, small, with a few rounded sockets and devoid of folds. The teeth are spiniform and numerous, ventralmost teeth (apical papillae) of similar shape. The dorsal and ventral arm plates are well developed. The tentacles scales are placed on the lateral arm plate, and usually occur only on a few proximal segments. The arm spine articulations are compressed transversally. Some proximal articulations may have a distinct nerve opening. The sigmoidal fold is absent. The arm spines are relatively short and flattened, hollow. Distal hooks absent. The vertebrae with a blunt distal keel and zygospondylous articulation.

**Remarks.** Until recently, this genus was monotypic (Lyman 1880; Paterson 1985). In the present study four other abyssal and ultra-abyssal new species have been discovered. This facilitates an appropriate discussion on the variability of different features within the genus. The taxonomic placement of *Ophiocymbium* will be evaluated after a general discussion on the taxonomic value of ophiuroid characters. R/V “Akademik Kurchatov” ultra-abyssal sampling in the Sandwich trench discovered another unknown ophiuroid, seemingly belonging to the family Ophiacanthidae, and similar to the genus *Ophiocymbium*. Close examination suggests that it is an undescribed genus and species, named here *Ophioplexa condita* **gen. et sp.**

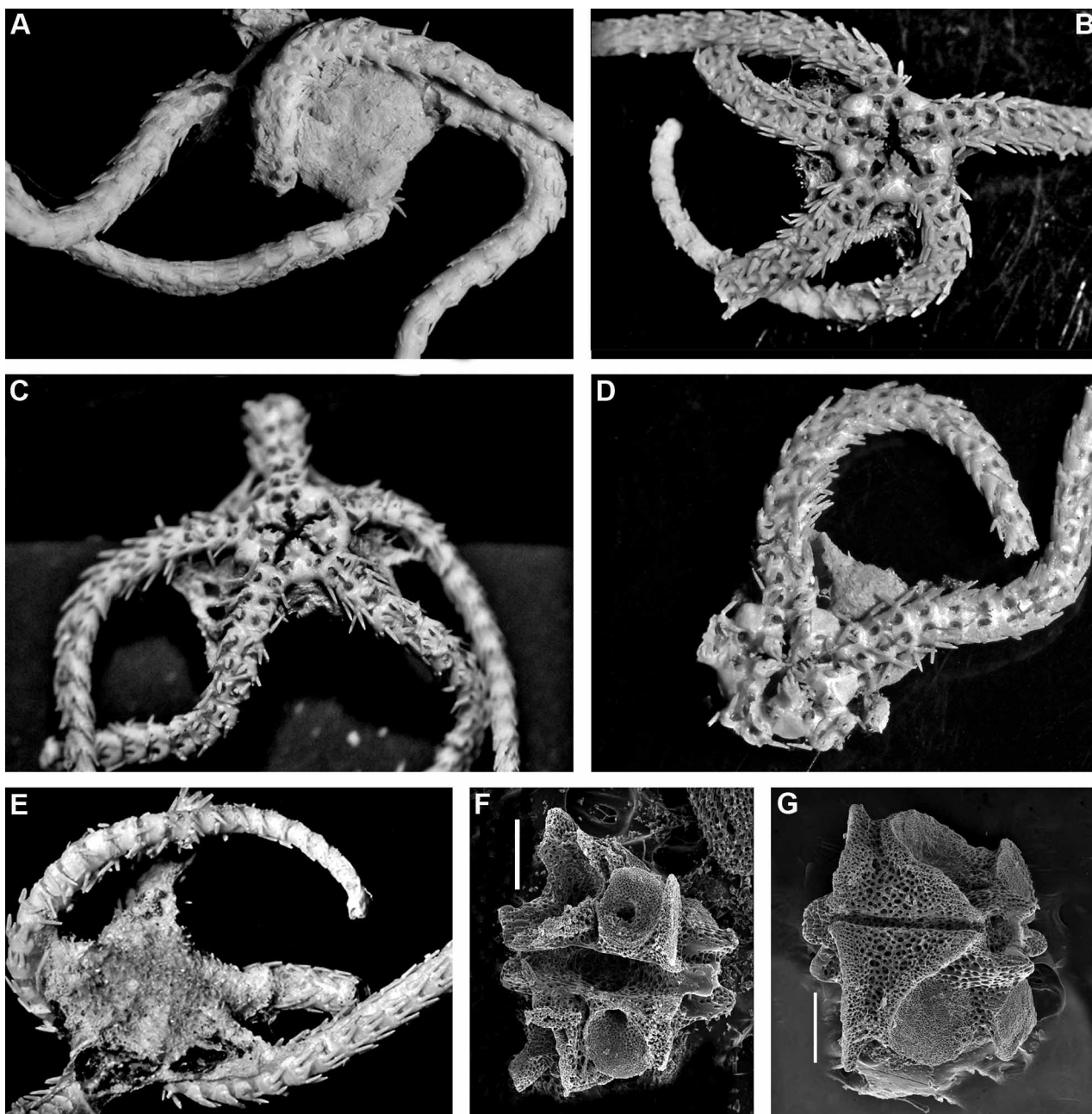
**nov.** It is of importance for the present study since, like *Ophiocymbium*, it apparently belongs in Ophiotominae and simultaneously has affinities to Ophiomyxidae. It will be listed and described below.

Number of species in the genus: 5.



**FIGURE 40.** External views of the genera *Ophiocymbium* and *Ophiologimus*. A. *Ophiocymbium cavernosum* Lyman, 1880, holotype, BMNH 82.12.23.391, 8.3 mm dd, dorsal view; B. same, ventral view; C. *Ophiocymbium cavernosum*, ZMMU D-795, 10.5 mm dd, dorsal view; D. *Ophiocymbium cavernosum*, ZMMU D-795, 8.5 mm dd, ventral view; E. *Ophiocymbium tanyae* sp. nov., holotype 9.5 mm dd, ZMMU D-799; F. same, ventral view; G. *Ophiocymbium rarispinum* sp. nov., holotype 9.2 mm dd, ZMMU D-798, dorsal view; H. same, ventral view; I. *Ophiologimus* cf. *secundus* Koehler, 1914, ZMMU D-814, 8 mm dd, dorsal view; J. same, ventral view. Photos: Tatiana Korshunova.





**FIGURE 41.** External views and vertebrae of *Ophiocymbium ninae* sp. nov. A. paratype, ZMMU D-804, 5.5 mm dd, dorsal view; B. holotype 6.8 mm dd, ZMMU D-802, 6.8 mm dd, ventral view; C. paratype 6.5 mm dd, ZMMU D-803, ventral view; D. paratype, ZMMU D-803, 6.1 mm dd, ventral view; E. holotype, dorsal view, ZMMU D-802, 6.8 mm dd; F. vertebra, ventral view; G. vertebra, dorsal view; Scale bars: F,G, 300  $\mu$ . Photos: A–F Tatiana Korshunova; F–G Alexander Martynov.

### Key to species of the genus *Ophiocymbium* Lyman, 1880

- 1 (6) Disk regular, almost rounded, covered with numerous small distinct scales. Skin is not evident. Tentacle scales absent or evident only at few proximalmost segments, oval
- 2 (5) At the disk edge very small radial shields and genital plate can be recognized. Tentacle scales present only on the first segment of each radius beyond the disk
- 3 (4) Disk scales dorsally completely devoid of spinelets. .... *Ophiocymbium cavernosum* Lyman, 1880
- 4 (3) Dorsal disk scales bear short, sparsely placed spinelets..... *O. rarispinum* sp. nov.

- 5 (2) Radial shields and genital plates completely absent. Tentacle scales present on three most proximal segments.....  
.....*O. tanyae* **sp. nov.**
- 6 (1) Disk irregular, sub-pentagonal. Conspicuous skin layer partially obscures disk scales. Tentacle scales well defined, present on most segments, spiniform or lanceolate, similar in shape to arm plate
- 7 (8) Disk scales covered with numerous short spinelets. Proximalmost tentacle scales elongate-oval with obtuse apical part..... *O. ninae* **sp. nov.**
- 8 (7) Disk scales naked. Proximalmost tentacle scales narrow, spiniform, with sharp pointed apical part.....  
.....*O. antarcticus* **sp. nov.**

An identification key for all known species of the genus *Ophiocymbium*, based exclusively on the spine articulation patterns, has been constructed from the present material. Such keys potentially could be prepared for species of most of genera of Ophiuroidea and are an interesting field for further studies.

- 1(8) At least one articulation per lateral plate is of the double-opening type
- 2(3) Articulations are delineated from main lateral arm plate body by distinct elevated borders of stereom, almost smooth proximally ..... *O. ninae* **sp. nov.** (Figs 55M–N)
- 3(2) Articulations are not clearly delineated from the main lateral arm plate, being an elevated tubercle slightly distinguished from the perforate stereom of the neighbouring lateral arm plate
- 4(5) Articulations are elongated transversally; muscle opening slit-shaped ..... *O. antarcticus* **sp. nov.** (Figs 42E–F)
- 5(4) Articulations and muscle opening rounded
- 6(7) Most of the articulations per lateral plate are of the double-opening type .....  
..... *Ophiocymbium cavernosum* Lyman, 1880 (Figs 27H–I)
- 7(6) Only one articulation per lateral plate is of the double-opening type..... *O. rarispinum* **sp. nov.** (Figs 43A–C)
- 8(1) All articulations are of the single-opening type..... *O. tanyae* **sp. nov.** (Figs 27J–K)

### ***Ophiocymbium cavernosum* Lyman, 1880**

Figures 4E–G;12H,M;15B; 17D, G; 27H–I; 40A–D

*Ophiocymbium cavernosum* Lyman, 1880: 7–8; Lyman, 1882: 163, plate 27, figs 1–3; Paterson, 1985: 59–60, fig. 24

**Material.** Two specimens, ZMMU D-795, R/V “Dmitry Mendeleev”, cruise 16, sta. 1290, 23 January 1976, 54° 33' S 159° 24,0' E, depth 5410–5450 m, Sigsbee trawl. Three specimens, ZMMU D-794, R/V “Akademik Kurchatov”, cruise 11, sta. 870, 29.11.1971, 55° 7' S 25° 2' W – 55° 8' S 25° 1' W, depth 4704–4680 m, Sigsbee trawl. One dried specimen, ZMMU D-796, R/V “Vitayz”, st. 4074, 20.10.1958, 40° 19' N 175° 45' W, depth 6065 m. One ethanol specimen, ZMMU D - 797, R/V “Vitayz”, st. 4074, 20.10.1958, 40° 19' N 175° 45' W, depth 6065 m.

**Description of a specimen from sta. 1290:** The disk, 10.5 mm dd, is rounded, conspicuously, but irregularly swollen (probably artificially) not extending onto the proximal arm segments. The disk plates are numerous, most of them elongate and narrow, irregular-rhomboidal – to polygonal, entirely devoid of spines and granules. Radial shields are elongated plates slightly larger than disk scales, scarcely visible at the edges of the disk (see a detailed radial shield description under paratype variations). The interradii are slightly swollen, ventrally without spinelets. There are no evident genital slits, but between arms and disk a long groove superficially resembles a genital slit. A narrow adradial genital plate articulating with the radial shield can just be seen in the distal part of the ventral side of the disk. There is no abradial genital plate, though a very small elongated scale adjacent to the adradial genital plate similar in structure and shape to the disk scales could be considered its remnant. Each jaw bears a cluster of 3–5 short spiniform teeth apically, which can be termed apical papillae. There is no larger middle apical papilla. Few additional teeth are placed more dorsally on the dental plates, similar in shape and size to the apical papillae. The total number of teeth including apical papillae is 4–8, distributed in a cone-shape tapering dorsalwards. Oral papillae are weakly developed and represent rather 1–3 block-shaped elevations, more like a fringe on the jaw than true papillae. One small spiniform papilla is placed in some interradii laterally to the apical papillae, at the ventral edge of



the dental plate. The adoral shield papillae are long, slightly flattened, similar in size and shape to the arm spines, one papilla placed in the middle of each adoral shield. The oral shield is relatively narrow, triangular with a straight or slightly convex rather long distal edge, conspicuously longer than wide, completely separated from the first lateral arm plate by the adoral shields. Distally the oral shield is adjoined by a supplementary narrow plate or just an elevation formed by adjacent interradiial scales. The madreporite is considerably swollen. The adoral shields are wing-shaped laterally, broadly adjoining the arm, rapidly narrowing towards the jaws, retaining thus only a narrow bar between jaws and oral shield.

True genital slits are inconspicuous small openings under the adoral shields, but a long furrow between the proximalmost arm segments and ventral disk interradius forms a false slit. Arm length is about 1.3 times the disk diameter. On all arms dorsal plates are absent for the proximal 3–4 segments, covered only with thin skin in which few small scales are embedded and the vertebrae are clearly visible, or skin apparently very thin and transparent, exposing the vertebrae. The dorsal arm plates are well developed but rather small, triangular, well separated on all segments (to about half of the length of the dorsal arm plate proximally and twice the length of the dorsal plate distally). All dorsal arm plates have pointed proximal and slightly convex distal edges. Many of the dorsal arm plates have a pit in the middle of the distal edge. Arms have weakly developed nodes, but arm spine articulations are placed on the lateral plates without forming an elevation. Laterally between two adjacent lateral plates there is a narrow space of uncovered soft tissue. On the first arm segment there are two spines, on the most proximal segments under the disk are three, on the proximal free segments four, and distally three spines. All spines are similar in size, flattened, and pointed apically. There are no hook-shaped spines. The first ventral arm plate is broadly triangular; other ventral arm plates have a characteristic pole axe shape throughout the entire arm length, with straight proximal edge and convex distal edge with a small elevation. The ventral plates are separated throughout the length of the arm, except for the first two segments. The tentacle pores are large along the entire arm length. There are no tentacle scales except for the first arm segments; there is a single small scale placed on the inner part of the lateral arm plate, differing from the following arm spines only in size and absence of a defined articulation ridge.

**Variability.** A single specimen, also from sta. 1290, ca 12 mm dd, is similar to the holotype and shows only minor differences. Adoral shield papillae are two in number. Genital slits seem to be entirely absent, but long grooves between disk and arm segments under the disk are very evident. Block-shaped oral papillae are more evident, 2–3 in number. Two paired proximalmost oral papillae are rectangular and pointed. There are 2–3 spines on the most proximal lateral arm plates under the disk, and 4–5 on the proximal lateral plates. The spines are flattened, hollow and apically pointed. No tentacle scales on any segment.

**Internal and microstructural characters.** Radial shield and genital plate articulate very tightly, and have the appearance of an entire plate, broken by a fissure (Fig. 4G). The radial shield is a very small irregular plate, with a slightly elevated articulation surface (Fig. 4F). The articulation surface of the genital plate has a slightly elevated condyle (Fig. 4E). The abradial genital plate is absent. Jaws are slightly elongated. Adradial sides of the jaws bear folds distally (Fig. 12M). The dental plate is large and without folds, with few small rounded sockets (Fig. 12H). Arm spine articulations are well developed and clearly belong to the double-opening type (Figs 27H–I). The muscle opening has a distinct distal lobe within the ribbed area. Nerve opening placed laterally below the level of the muscle opening. Vertebrae rather long, not keeled and with well developed zygospondylous articulation (Figs 17D, G). Vertebral dorsal median groove almost indistinct. Podial basins are large.

**Remarks.** The present material covers a wide geographical range, including southern and northern Pacific and Atlantic Oceans. All studied specimens agree well with the holotype of *O. cavernosum* (Figs 40A–D) in general appearance of the disk, shape of the dorsal and ventral arm plates, presence of the large uncovered tentacle pores, with only very small spiniform tentacle scale on one proximalmost segment. The oral structures of the holotype also agrees well with the present specimens in having a small cluster of spiniform apical papillae, distinctly block-shaped distal oral papillae and 2–4 additional long spiniform papillae on the adoral shield and around the second tentacle pore. The radial shields of the holotype are very small (Fig. 40A, left) articulating with the small bar-shaped genital plate. Similar radial shields and genital plates were discovered in all present specimens (Fig. 4E–F). The abradial genital plate is absent in all studied

specimens. The holotype originated from the Kerguelen Islands region from 3568 m depth, thus relatively close geographically and bathymetrically to some specimens of the present material from the Sandwich trench. Arm spine articulations are essentially similar in both Atlantic and Pacific specimens (Figs 27H and I) and represent a typical ophiomyxid pattern with large ribbed muscle opening and a small opening adjoining it laterally, similar to the genus *Ophiomyxa* (compare Figs 27G and 27H, I). Along a single lateral arm there is a transition from double-opening articulation to single-opening rounded or slightly subparallel ridge. Such variability is also characteristic for ophiomyxid articulations. No signs of the ophiacanthid volute-shaped articulations were found.

***Ophiocymbium tanyae* sp. nov.**

Figures 4H; 12C–E, H; 17P–S; 27J, K; 40E, F

**Material.** Holotype, dried, ZMMU D-799, R/V “Vityaz”, sta. 7407, 29° 18' N 143° 15' E – 29° 17' N 143° 15' E, Izu-Bonin Trench, depth 6740–6850 m, Sigsbee trawl. Four paratypes, ethanol, ZMMU D-800, same sta. as holotype. One paratype, disarticulated and mounted on a SEM stub, ZMMU D-801, same sta. as holotype.

**Etymology.** This species is named in honour of neurophysiologist and my wife Tanya Korshunova (Moscow, Institute of Higher Nervous Activity and Neurophysiology) for her generous assistance and patience.

**Description of the holotype.** The disk measures 9.5 mm dd, rather flattened, pentagonal with rounded angles. Numerous disk plates, most of elongated shape, narrowed, irregular-rhomboidal or polygonal, entirely devoid of spines and granules. Disk scales continue dorsally and extend onto the first arm segment. Skin layer is thin and not conspicuous. Radial shields and both genital plates are absent. The interradii are slightly swollen, ventrally with numerous scales. Each jaw bears one larger spiniform apical papilla and 1–2 smaller adjacent ones. Apical papillae are distinct from the teeth, the latter are narrower and longer and only one in number in most interradii except a single jaw with two teeth. The proximalmost oral papillae are small, spiniform, typically placed in pairs. Three papillae are placed distally on each side of the jaws and characteristically block-shaped, appearing rather as modified, originally spiniform, papillae attached to the jaws over almost their entire length. The distalmost oral papillae are shorter than the middle one, which is rather long and rectangular, but pointed distally, the most proximal block-shaped papilla is more pointed, and in some interradii almost spiniform. The second tentacle pore is covered by two similarly sized, flattened and rounded scales, which are placed on the adoral shield and thus can be equally considered as both adoral shield spines or tentacle scales. The oral shield is wide, triangular or somewhat rhomboidal, with straight or slightly convex distal edge, as long as wide, completely separated from the first lateral arm plate by the adoral shields. Distally the oral shield adjoins a supplementary narrow plate or just an elevation formed by adjacent interradiial scales. The adoral shield is wing-shaped laterally, widely adjoining the arm, narrowing towards the midline of the jaws, retaining a moderately narrow bar between the jaws and oral shield. True genital slits are barely conspicuous small openings under the adoral shields, but long furrows between the most proximal arm segments and the ventral disk interradius form a false slit.

Arm length is almost equal to the disk diameter. The dorsal arm plates are well developed but rather small, triangular, narrowing and turning pentagonal towards the middle of the arm, well separated on all segments (for about the length of the dorsal arm plate proximally and twice the dorsal plate distally). All dorsal arm plates have pointed proximal and straight distal edges. Arms have weakly developed nodes but arm spine articulations are placed on lateral plates without forming an elevation. On the most proximal segments under the disk there are two conical spines, on the proximal and distal segments there are three (rarely four) spines. The second dorsal spine is slightly longer than others. The first ventral arm plate is triangular. Further ventral arm plates have a characteristic pole-axis shape throughout entire arm length. Medially ventral arm plates have a distinct elevation, making the plates somewhat roundly carinate. The proximal edge of the ventral arm plate is straight, whereas the distal edge is convex with a small pit in the middle. Ventral plates throughout the length of the arm are separated, slightly so on the proximal segments, and similar in length distally. The



tentacle pores are large. On the first three arm segments under the disk there are distinct large tentacle scales, placed on the lateral plates. On the first segment there are two flattened rounded tentacle scales, whereas on the second and third segments the scales become more spiniform. The tentacle scales are similar in size to the arm spines and capable of covering a considerable part of the tentacle pore. On the remaining segments tentacle scales are entirely absent. There are no tentacle scales on the ventral arm plates.

**Paratype variations.** A paratype in ethanol, from the same station as the holotype, 12.0 mm dd, is similar to the holotype, but differs in minor ways. The first 1–2 proximal segments near the disk lack dorsal arm plates and small scales, exposing the vertebrae. There are no teeth on any dental plates except for the conspicuous middle apical papilla and 1–2 adjacent smaller apical papillae. Oral shields are smaller than in the holotype, triangular or irregularly oval. The madreporite has lost its usual shape and is markedly swollen. On the most proximal lateral arm plates under the disk there are two spines, on proximal and middle lateral plates three (occasionally four) flattened apically pointed spines.

**Internal and microstructural characters.** Radial shield and both genital plates are absent (Fig. 4H). Jaws are elongated (Figs 12C–D). Adradial sides of the jaws distally irregularly folded (Fig. 12D). Dental plate without folds, with few small rounded sockets (Fig. 12E). Arm spine articulations are poorly developed and clearly belong to the single-opening type (Fig. 27J, K). The unevenly rounded or slightly subparallel muscle opening lacks a ribbed distal area and a distinct lobe. The nerve opening is not evident. Vertebrae rather long, not keeled and with well developed zygospondylous articulation (Fig. 17P, R). Vertebral dorsal median groove absent (Fig. 17P). Podial basins are large (Fig. 17Q).

**Remarks.** *Ophiocymbium tanyae* sp. nov. resembles *O. cavernosum* in general disk appearance but differs from it in several important characters. All arm segments of *O. cavernosum* are entirely devoid of conspicuous tentacle scales (except for the first segment bearing a very small spiniform scale), whereas *Ophiocymbium tanyae* sp. nov. has a conspicuous, wide, flattened tentacle scale on the first three proximal segments. The absence of the tentacle scales in *O. cavernosum* is confirmed in the present study for the holotype and several specimens from the Atlantic and Pacific oceans. Another important difference of *Ophiocymbium tanyae* sp. nov. is the complete absence of adradial and abradial genital plates and the radial shields, confirmed for all studied specimens (Fig. 4H). In contrast, *O. cavernosum* has a small, but evident adradial genital plate and radial shield (Fig. 4G); confirmed also for the holotype.

### *Ophiocymbium ninae* sp. nov.

Figures 4L,T; 12F–G, K–L; 17E, H–J; 41; 55I–N

**Material.** Holotype, ZMMU D-802, R/V “Vityaz”, cruise 45, sta. 6109, 15 May 1969, 56°14,1' N 139° 44,0' W – 56°12,7' N 139° 43,4' W, depth 3450–3460 m, grab dredge “Ocean”. 13 dried paratypes, ZMMU D-803, same sta. as the holotype. 9 dried paratypes, ZMMU D-804, R/V “Vityaz, cruise 29, sta. 4213, 34° 54' N 123° 55' W, depth 4231–4200 m, Sigsbee trawl. 3 ethanol paratypes, ZMMU D-805, R/V “Vityaz, cruise 29, sta. 4213, 34° 54' N 123° 55' W, depth 4231–4200 m, Sigsbee trawl.

**Etymology.** This species is named in honour of ophiuroid taxonomist Nina Litvinova (Moscow, P.P. Shirshov Institute of Oceanology), whose efforts in describing the deep-water Ophiuroidea has elucidated their importance for taxonomy and phylogeny.

**Description of the holotype.** The disk, 6.8 mm dd, is pentagonal. The disk plates are numerous, somewhat obscured by thin wrinkled skin, when dried. Radial shields are very small irregular plates, similar in size to disk scales, placed at the edge of the disk and scarcely visible (see a detailed radial shield description under paratype variations). The whole dorsal side of the disk is covered with short cylindrical or subconical, sparsely placed spinelets. The interradii are slightly swollen, ventrally covered with few spinelets. Each jaw bears apically a cluster of 3–4 spiniform teeth or apical papillae. The 3–6 lateral papillae together with the adoral shield papillae are placed along both edges of each jaw in a characteristic, slightly curved row around the second tentacle pore. The adoral shield papillae are long, flattened, similar in size and shape to the arm spines, 2–3 in number in most interradii, five in one interradius. The paired proximalmost oral papillae are placed laterally. Between lateral oral papillae and second tentacle pore the jaws form a rectangular border,

which is superficially similar to the block-shaped oral papillae. Numerous spiniform teeth are distributed in a cone-shape, tapering dorsalwards. There are approximately 10 teeth (including apical papillae) on each dental plate. The oral shield is wide, triangular with straight or slightly convex, rather long distal edge, as long as wide, completely separated from the first lateral arm plate by the adoral shields. Distally the oral shield adjoins a supplementary narrow elongated plate or just an elevation formed by adjacent interradiial scales. The madreporite has a conspicuous swollen round area occupying a considerable part of its surface. The adoral shield is wing-shaped laterally, widely adjoining the arm, rapidly tapering towards to the midline of the jaws, retaining thus only a narrow bar between jaws and oral shield. True genital slits are barely conspicuous, small openings under the adoral shields, but a long furrow between the most proximal arm segments and the ventral interradius forms a false slit.

Arm length is about 1.7 times the disk diameter. On all arms the most proximal dorsal plates are absent for two-three segments, replaced by a covering of small disc scales. The dorsal arm plates are well developed but rather small, triangular, tapered and increasingly pentagonal towards the middle of the arm, well separated on all segments (for about half of the length of the dorsal arm plate proximally and length of the dorsal plate distally). All dorsal arm plates have pointed proximal and convex distal edges. Arms have weakly developed nodes, but arm spine articulations are placed on lateral plates without forming an elevation. Laterally between two adjacent lateral plates there is a narrow space of uncovered soft tissue. There are two spines on the first arm segment, three on proximal segments under the disk, afterwards four to five and then three distally. The first dorsal spine is slightly longer than the other ones proximally and medially. Spines are flattened, pointed apically. There are no hook-shaped spines. The first ventral arm plate is broadly triangular, the second has straight distal and proximal edges; further ventral arm plates have a characteristic pole-axis shape throughout most of the arm length, with a triangular proximal edge, whereas distally they vary from straight to slightly concave or convex with a small elevation. Ventral plates throughout the length of the arm are contiguous, except for the first two segments. The tentacle pores are large throughout the entire arm length. Basally on the parts of the lateral plate encircling the tentacle pores there are one, or rarely two larger, long, flattened, pointed tentacle scales. On most arm segments there is one tentacle scale. Distally the tentacle scale becomes small and spiniform. The tentacle scales are shorter than arm spines, but conspicuous and capable of covering the whole tentacle pore. Many of the tentacle scales are broken or have fallen off. There are no tentacle scales on the ventral arm plates.

**Paratype variations.** A paratype, from the same station as the holotype, 7.0 mm dd, is similar with the holotype, but has a markedly pentagonal disk and some other minor differences. Numerous disk scales are clearly embedded within a thin skin. Apical papillae (teeth) are less numerous and thinner, up to 7 in number. A single spiniform tooth in the dorsal part of the dental plate is markedly longer than (up to twice) the apical papillae. The distalmost oral papillae are block-shaped, but short. The following two oral papillae are short and spiniform. The first 1–2 proximal segments near the disk have no dorsal plates and are covered with small scales and skin. The madreporic oral shield is similar in shape to the others but with a swollen area in the middle. Genital slits are very short, placed just below adoral shields, a narrow adradial genital plate is evident in the distal part of the ventral side of the disk, but does not support the walls of the genital slits. The abradial genital plate is absent. Radial shields are very small and inconspicuous. On the 1–2 proximal lateral arm plates under the disk there are two flattened, apically pointed spines, on the proximal and middle lateral plates there are 4–5 spines. Although many tentacle scales are missing, three are present on the most proximal arm segments and some second and third segments. The ventralmost of these three scales is placed at the border of lateral and ventral arm plates, but still on the lateral plate.

A small paratype, from the same station as the holotype, 4.0 mm dd, is similar to the holotype, except for the pentagonal disk and some other differences. There are obvious primary plates joined in a flower-shaped structure. Few disk spines are visible. The radial shields are more evident than in the holotype and other paratypes. Dorsal arm plates proximally are almost rhomboid with rounded angles. Medially and distally dorsal arm plates become almost ovoid. The distance between two adjacent dorsal arm plates proximally is about equal to the dorsal plate length, whereas distally it is up to twice the length of the dorsal plate. Apical papillae (teeth) are considerably fewer than in the holotype and there is an obvious larger middle apical papilla



and 1–3 smaller and thinner lateral apical papillae. A single spiniform tooth in the dorsal part of the dental plate is present only in some interradii and is similar in size to the middle apical papilla. The distalmost oral papillae are block-shaped relatively long elevations. The single pair of oral papillae are rectangular and pointed, somewhat similar in shape to the buccal scales of Amphiuroidae and Ophiactidae. The first 1–2 proximal segments near the disk lack dorsal plates and are covered with small scales or almost naked skin exposing the vertebrae. The madreporic oral shield does not differ from the remaining oral shields. Genital slits in most interradii are longer than in the holotype, whereas in one interradius they are small. A narrow adradial genital plate is obvious in the distal part of the ventral side of the disk, but does not support the walls of the genital slits. The abradial genital plate is absent. On the 1–2 proximal lateral arm plates under the disk there are 2–3 flattened, apically pointed spines, on proximal and middle lateral plates four, and distally three spines. Proximally there are 1–2 large, flattened tentacle scales, which become smaller medially and disappear entirely distally. There are no hook-shaped spines.

**Internal and microstructural characters.** The radial shield is a very small irregular plate, with slightly elevated articulation surface (Fig. 4T). The articulation surface of the abradial genital plate does not have any distinct condyles (Fig. 4L). The abradial genital plate is absent. Jaws are slightly elongated (Figs 12K, L). Adradial sides of the jaws distally bear few indistinct straight folds and irregularly-shaped tubercles (Fig. 12L). The dental plate is devoid of folds, with few small rounded sockets (Figs 12F, G). Arm spine articulations are well defined and belong to the double-opening type (Figs 55M, N). The muscle opening is placed on a distinct round or elongated elevation, some articulations are slightly ribbed distally. Nerve opening placed laterally below the level of the muscle opening. Vertebrae rather short, not keeled and with well developed zygospondylous articulation (Figs 41G, 17E, J). Vertebral dorsal median groove is distinct (Figs 41G, 17E). Podial basins are large (Figs 41F, 17H).

**Remarks.** *Ophiocymbium ninae* sp. nov. is clearly distinguished from both *Ophiocymbium cavernosum* and *Ophiocymbium tanyae* sp. nov. by the presence of conspicuous short disk spinelets, less evident distal block-shaped oral papillae, and the shape of the arm spine articulations and vertebrae. *Ophiocymbium tanyae* sp. nov. also differs from *Ophiocymbium ninae* sp. nov. by the absence of the adradial genital plate.

### *Ophiocymbium antarcticus* sp. nov.

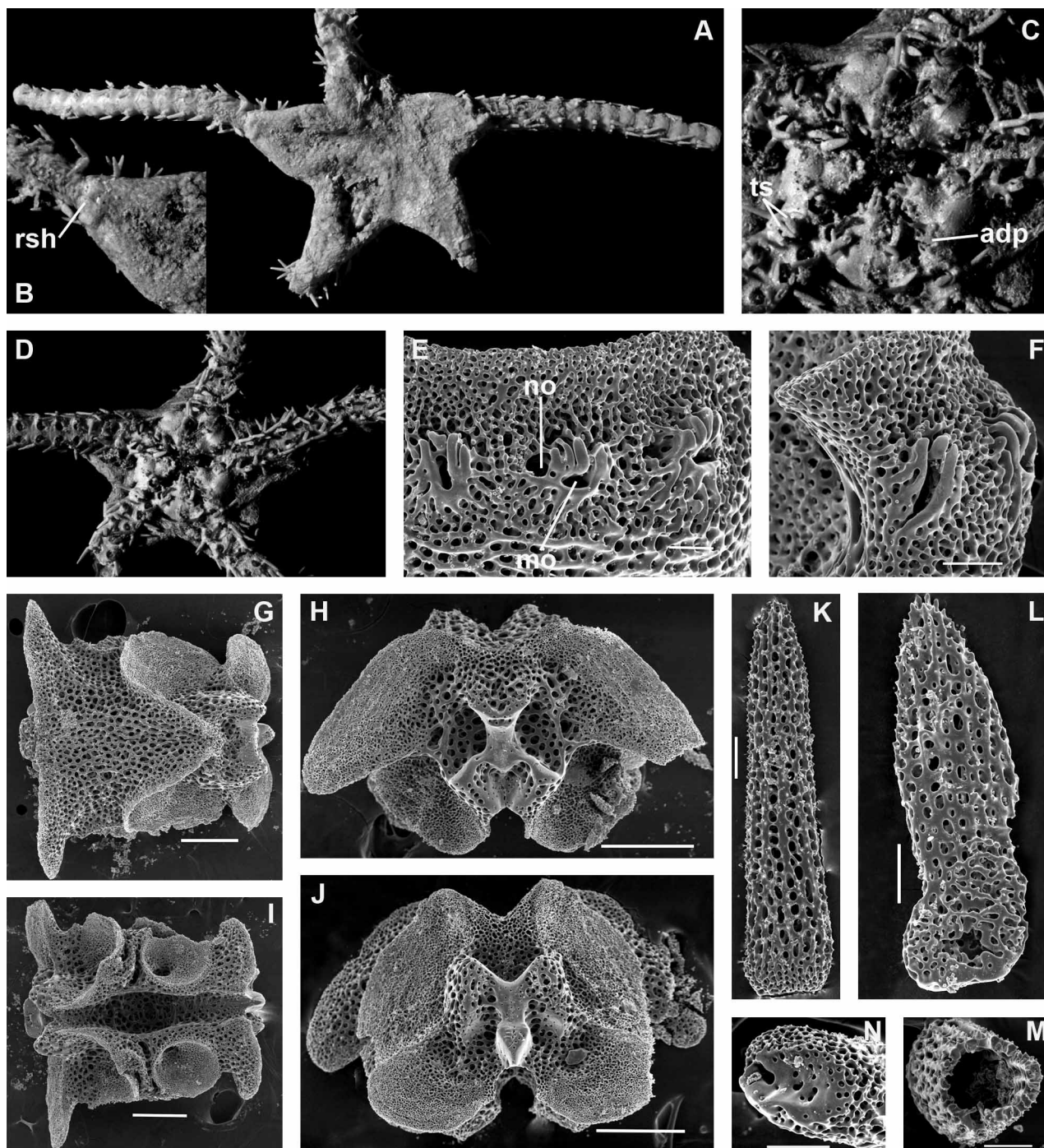
Figure 42

**Material.** Holotype, USNM 1106231, South Atlantic Ocean, Scotia Sea, South Sandwich Islands, NE of Candlemas Island, Cr. 575, sta. 38, 22 May 1975, 57° 00,24' S 26° 10,06' W depth 2740–2757 m, Trawl-Blake. No paratypes.

**Etymology.** This species is named after Antarctic.

**Description of the holotype.** The disk, ca. 13 mm dd, is pentagonal. The disk plates are numerous, somewhat obscured by thin wrinkled skin when dried, extending across the first 1–3 arm segments, substituting for the dorsal arm plates. Radial shields are very small irregular plates, similar in size to disk scales, placed at the edge of the disk and scarcely visible. The whole dorsal side of the disk is devoid of spinelets. The interradii are slightly swollen. Each jaw bears apically a cluster of 4–6 spiniform teeth or apical papillae. The 2–6 lateral oral papillae together with the adoral shield papillae are placed along both edges of a jaw in a characteristic, slightly curved row around the second tentacle pore. The adoral shield papillae are long, slightly flattened or rounded, similar in size and shape to the arm spines, 2–3 in number in most interradii. There is a distinct gap between adoral papillae and apical papillae. Between lateral oral papillae and second tentacle pore the jaws form an indistinct rectangular border, which is superficially similar to the block-shaped oral papillae. Beyond this border deeper on the jaws there is small triangular papilla, not evident in all radii. Numerous spiniform teeth are distributed somewhat irregularly. There are approximately 10–12 teeth (including apical papillae) on each dental plate. The oral shield is wide, with straight or slightly convex distal edge, as long as wide, completely separated from the first lateral arm plate by the adoral shields. The madreporic oral shield has a conspicuous swollen oval area occupying the distal portion. The adoral shield is

poorly developed, laterally having a narrow wing, widely adjoining the arm, rapidly tapering towards to the midline of the jaws, thus retaining only a narrow inconspicuous bar between the jaws and oral shield. Genital slits are long furrows opening widely proximally, not supported by genital plates.



**FIGURE 42.** *Ophiocymbium antarcticus* sp.nov., holotype USNM 1106263, 13 mm dd, external views and details. A. dorsal view; B. dorsal disk view, details showing small radial shields; C. ventral view, details; D. ventral view; E. arm spine articulations, proximal segments; F. slit-shaped ventralmost arm spine articulation, proximal segments; G. proximal vertebra, dorsal view; H. same, proximal view; I. same, ventral view; J. same, distal view; K. spine; L. tentacle scale; M. hollow spine, transversally sectioned; N. spine, ventral view. Scale bars: E–F; G–J, 300  $\mu$ ; K–N, 100  $\mu$ ; Photos: A–D Tatiana Korshunova; E–N Alexander Martynov.

Most arms are broken off. The length of the longest arm piece is 13 mm. On all arms the most proximal dorsal plates are absent for two segments. The dorsal arm plates are well developed but rather small, triangular, well separated on all segments (for about half of the length of the dorsal arm plate proximally and



length of the dorsal plate distally). On most proximal segments the dorsal arm plates are somewhat irregular, and have traces of fusion from several pieces and additional small plate distally. All dorsal arm plates have pointed proximal and convex distal edges. Arms have weakly developed nodes, but arm spine articulations are placed on lateral plates without forming an elevation. Laterally between two adjacent lateral plates there is a narrow space of uncovered soft tissue. There are two spines on the first arm segment, three to four on most proximal segments under the disk, five on the proximal free segments, and distally four to three spines. The first dorsal spine is slightly longer than the other ones proximally and medially. Spines are slightly flattened to round, hollow, pointed apically. There are no hook-shaped spines. The first ventral arm plate is broadly triangular, the second has straight distal and proximal edges; further ventral arm plates have a characteristic pole-axe shape throughout most of the arm length, with an almost straight proximal and slightly convex distal edge. Ventral plates throughout the length of the arm are contiguous. The tentacle pores are large throughout the entire arm length. Basally on the parts of the lateral plate encircling the tentacle pores, there are two long, subequal, flattened, pointed tentacle scales, only slightly shorter than the adjacent arm spines. Two tentacle scales persist for at least the three most proximal segments. On most arm segments there is one tentacle scale. Distally the tentacle scale gradually decreases in size. The tentacle scales are shorter than arm spines, but conspicuous and capable of covering the whole tentacle pore. Many of the tentacle scales are broken or have fallen off. There are no tentacle scales on the ventral arm plates.

**Internal and microstructural characters.** The radial shield is a small sub-rounded plate. The adradial genital plate is absent. Arm spine articulations are well defined and belong to the double-opening type (Fig. 42E). The muscle opening is on a distinct round or elongated elevation, some articulations are slightly ribbed distally. The nerve opening is placed laterally below level of the muscle opening. The ventralmost articulations have a peculiar oblique slit-shaped shape (Fig. 42F). Vertebrae are rather short, not keeled, with well developed zygospondylous articulation (Fig. 42G–H). The vertebral dorsal median groove is not distinct. Podial basins are large (Fig. 42I).

**Remarks.** *Ophiocymbium antarcticus* sp. nov. is clearly distinguished from both *Ophiocymbium cavernosum* and *Ophiocymbium tanyae* sp. nov. by the presence of a distinctly pentagonal disk, less evident distal block-shaped oral papillae, and the shape of the arm spine articulations and vertebrae. *Ophiocymbium antarcticus* sp. nov. is somewhat similar to *Ophiocymbium ninae* sp. nov. but differs in lacking disk spinelets, the shape of the tentacle scales and the arm spine articulation details. The disk of *Ophiocymbium antarcticus* sp. nov. is almost twice as larger as the largest known example (7 mm dd) of 26 known *O. ninae* sp. nov. specimens.

***Ophiocymbium rarispinum* sp. nov.**

Figure 40G, H; 43; 67G

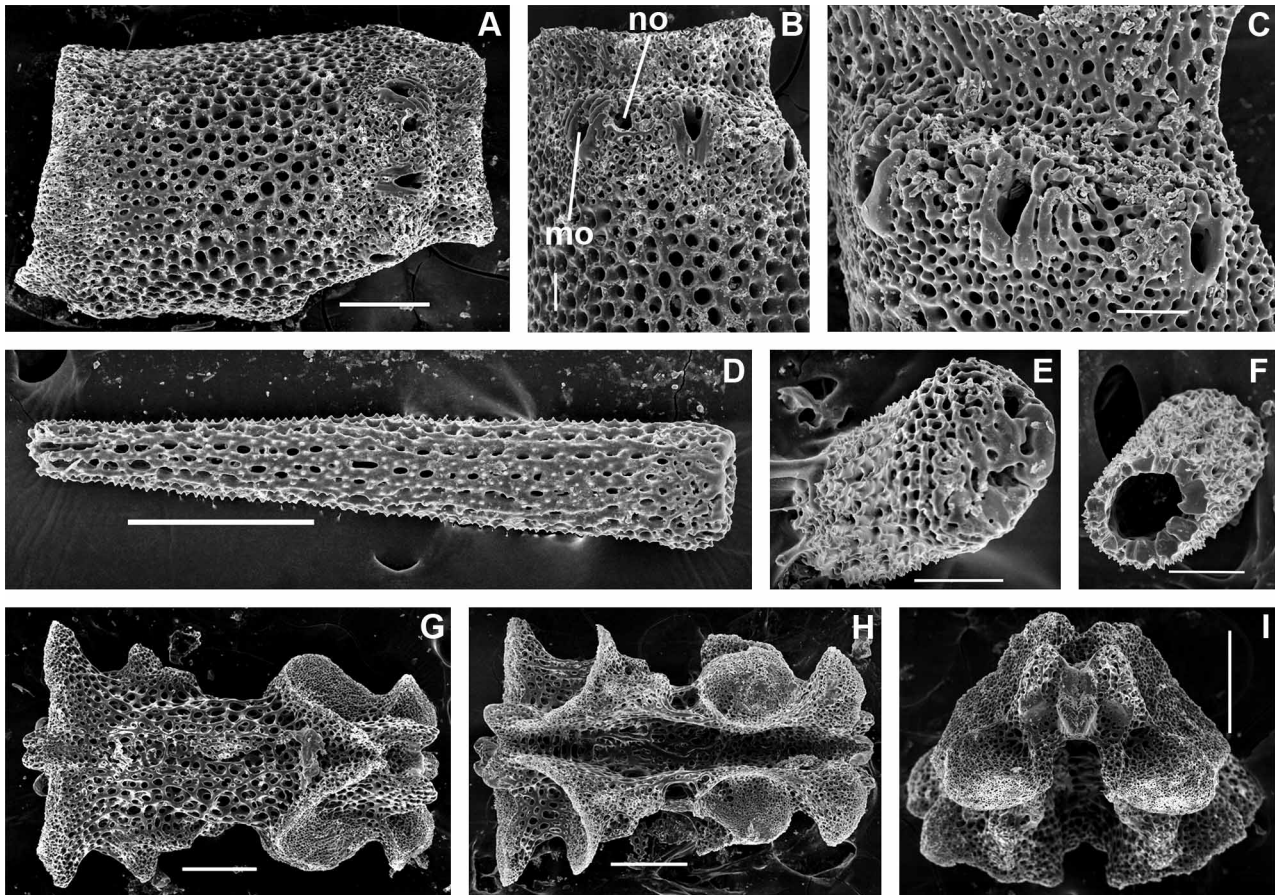
**Material.** Holotype, dried, ZMMU D-798, R/V “Vityaz”, sta. 7407, 29° 18' N 143° 15' E – 29° 17' N 143° 15' E, Izu-Bonin Trench, depth 6740–6850 m, Sigsbee trawl.

**Etymology.** From Latin *rarus* (rare, few) and *spina* (spine), in reference to few short scattered disk spinelets.

**Description of the holotype.** The disk, 9.2 mm dd, is flattened and rather rounded, not extending onto the proximal arm segments. The disk is covered by numerous small scales, slightly obscured by thin skin, giving the disk a wrinkled appearance. Few short spinelets are very sparsely placed in some areas of the dorsal disk. Radial shields are very small but conspicuous at the edges of the disk. Distally part of the articulating genital plate is also evident. The interradii are flattened, ventrally not covered with spinelets. There are no evident genital slits, but between arms and disk a long groove is present, which is superficially similar to the genital slit. A narrow adradial genital plate articulating with the radial shield is evident in the distal part of the ventral side of the disk, but does not support the walls of the genital slits. There is no abradial genital plate.

Each jaw bears a cluster of 4–6 short papillae apically. There is no larger middle apical papilla. Few other teeth are placed more dorsally on the dental plates, similar in shape and size to the apical papillae. The total number of teeth including apical papillae is 8–10, distributed in a dorsalwards tapering cone-shaped pattern.

The oral papillae are represented by two well-defined block-shaped elevations. The third distalmost oral papilla is short and rounded. 1–2 small spiniform papillae also placed in some interradii lateral to the apical papillae, at the ventral edge of the dental plate. The adoral shield papillae are long, slightly flattened, very similar in size and shape to the arm spines, one papilla is placed in the middle of each adoral shield.



**FIGURE 43.** *Ophiocymbium rarispinum* sp. nov., holotype, ZMMU D-798, 9.2 mm dd, details. A. proximal lateral arm plate showing spine articulations; B–C, spine articulations, proximal segments; D. proximal spine; E. same, ventral view; F. hollow proximal spine, sectioned transversally; G. proximal vertebra, dorsal view; H. same, ventral view; I. same, distal view. Scale bars: A, D, G–I, 300 ; B–C, E–F, 100  $\mu$ . Photos: Alexander Martynov.

The oral shield is relatively narrow, triangular with straight or slightly convex rather long distal side, conspicuously longer than wide, completely separated from the first lateral arm plate by the adoral shields. Distally the oral shield adjoins a supplementary oral shield in form of a narrow elongated plate or just an elevation formed by adjacent interradii scales. The madreporic oral shield is considerably swollen. Adoral shield wing-shaped laterally, widely adjoining the arm, rapidly narrowing towards the mid-line of the jaws, retaining thus only a narrow bar between jaws and oral shield. True genital slits are barely conspicuous small openings under the adoral shields, but a long furrow between the most proximal arm segments and the ventral disk interradius forms a false slit.

Arm length is about 1.5 times the disk diameter. On all arms the most proximal dorsal plates are absent for 3–4 segments, covered only with thin skin, in which few small scales are embedded; vertebrae are clearly visible through translucent skin, or skin entirely absent exposing the vertebrae. The dorsal arm plates are well developed but rather small, triangular, well separated on all segments (for about half of the length of the dorsal arm plate proximally and twice the length of the dorsal plate distally). All dorsal arm plates have pointed proximal and slightly convex distal edges. Many of the dorsal arm plates have a pit in the middle of the distal edge. Arms have weakly developed nodes but arm spine articulations are placed on lateral plates without forming an elevation. Between two adjacent lateral plates there is a narrow space of uncovered soft tissue.



There are two flattened, apically pointed arm spines on the first arm segment, four on most proximal segments under the disk, four on the proximal free segments, and three distally. All spines are similar in size. There are no hook-shaped spines. The first ventral arm plate is broadly triangular, most further ventral arm plates have a characteristic pole axe shape throughout the entire arm length with straight proximal edge and convex distal edge with a small elevation. Ventral plates throughout the length of the arm are separated, except for first two segments. The tentacle pores are large throughout the entire arm length. There are no tentacle scales except for the first arm segments, where there is a single small scale placed on the inner part of the lateral arm plate, differing from the following arm spines only in size and absence of the defined articulation ridge.

**Internal and microstructural characters.** The radial shield is a small sub-rounded plate. The adradial genital plate is absent. Arm spine articulation belongs to the double-opening type (Figs 43A–C). The muscle opening is placed on a distinct round or elongated elevation, some articulations slightly ribbed distally. The nerve opening is placed laterally below the level of the muscle opening. Ventralmost spine articulations have a rounded shape (Fig. 43C). Vertebrae rather long proximally, not keeled and with well developed zygospondylous articulation (Fig. 43I). The vertebral dorsal median groove is slightly distinct. Podial basins are large (Fig. 43H).

**Remarks.** *Ophiocymbium rarispinum* sp. nov. has a similar arm spine articulations shape to *O. cavernosum*, but differs in having visible radial shields and small sparsely-placed disk spinelets.

### Discussion on the genus *Ophiocymbium*

Initially this genus and its type species were described among other unique deep-water ophiuroids without specified family placement (Lyman, 1880). Perrier (1891) to whom usually erroneously referred authorship of the Ophiacanthidae did not include *Ophiocymbium* in this family, and in further reviews of this family (Verrill, 1899; Koehler, 1914) the genus *Ophiocymbium* was also not considered. The genus was assigned to the family Ophiacanthidae for the first time by Matsumoto (1915, 1917); supported by Fell (1960). Paterson (1985) reported that *Ophiocymbium cavernosum* possessed “comma-shaped” arm spine articulations and thus supported considering of this species as an ophiacanthid. However, an investigation of all five different species of the genus *Ophiocymbium* studied here (including variability within type species *O. cavernosum* from different oceans) has failed to demonstrate any similarity to the ophiacanthid articulation (e.g. Figs 27H–K). Instead there is a basic similarity to the type genus of the family Ophiomyxidae, *Ophiomyxa* (Figs 27G and Figs 27H–I). Besides spine articulations shape, the genus *Ophiocymbium* has following characters which significantly differ from the family Ophiacanthidae and point to the ophiomyxid relationship: poorly developed (or absent) genital plates, very small (or entirely reduced) radial shields and lateral arm plates without characteristic nodes. Paterson (1985) figured articulations of *Ophiocymbium cavernosum* without mentioning the exact locality of the specimen he studied. The articulation in his specimen, although generally similar to *O. cavernosum*, clearly differs in having a wider, partially imperforate smooth border, and in the lateral arm plate showing a distinct striation, not discovered in any specimens used in the present study, including the holotype. This pattern also differs considerably from typical ophiacanthid pattern (Figs 21B; 28). The specimen described by Paterson belongs to another ophiomyxid taxon, most likely to *Ophiophrura tripapillata* (Stöhr & Segonzac, 2005) **comb.nov.** (see below). Both *Ophiocymbium cavernosum* sensu Paterson, 1985 (part., only the SEM image) and *Ophiophrura tripapillata* share very similar arm spine articulations and striated stereom of the lateral arm plates (compare Fig. 13C in Paterson (1985) and Figs 53A–E in the present study).

Further discussion of the placement and relationship of the genus *Ophiocymbium* will be discussed below.

### Genus *Ophiodaces* Koehler, 1922

*Ophiodaces* Koehler, 1922b: 24

Type and only species: *Ophiodaces inanis* Koehler, 1922, by monotypy

*Ophiodaces inutilis* (lapsus calami): Koehler, 1922b: 89, legend to Plate 78, figs 6–8

Non *Ophiodaces sensu* Fell, 1960: 15

**Diagnosis.** The disk scales are obscured by a moderately developed skin layer. The radial shields are very large, partially concealed by skin in some interradii. The genital plates (judged from external morphology) are well developed. The genital slits are long, genital plates possibly bordering almost the entire length of the slits. The jaw bears numerous spiniform oral papillae similar in shape to the small cluster of ventralmost teeth. Two pairs of the adoral shield papillae are massive, conical, markedly different in shape and length (approximately 2 times longer than the oral papillae), placed around the second tentacle pore. The teeth are spiniform, which suggests that the dental plate should have small rounded sockets. All teeth are similar in shape. The oral shield is strongly convex distally and markedly triangular proximally, no distinct distal lobe. The adoral shields are similar in size distally and proximally. Dorsal and ventral arm plates are well developed. The dorsal arm plates are oval, with straight edges both distally and proximally, contiguous. The dorsal arm plates are entire proximally. The ventral arm plates are contiguous, with a convex distal and straight proximal edge. The spines are relatively short, conical. One small conical tentacle scale is placed on the lateral arm plate.

**Remarks.** The type of *Ophiodaces inanis* Koehler, 1922 was not examined (according to Rowe, Pawson, 1977, is in the Australian Museum). Fell (1961) discovered a smaller specimen that he identified as *Ophiodaces inanis*, but this specimen differs considerably from Koehler's (1922b) description in having a small rounded radial shield, inconspicuous skin on the disk and other features. It is unlikely that it is conspecific with the type specimen. Fell (1961) also suggested that the entire taxon *Ophiodaces inanis* was possibly only a juvenile stage of *Ophiosparte gigas*. But Fell's relatively-large specimen (6.5 mm) has small sub-rounded radial shields, a hardly evident skin layer and conical arm spines. All these features preclude this specimen being identified as *Ophiosparte gigas*, which has strong, long radial shields, a thick skin layer and apically spatulate arm spines (Figs 65B–C). However, their features suggest that both the real *Ophiodaces inanis* as well as Fell's specimen may actually be related to the family Ophiuridae instead of Ophiacanthidae.

The single specimen of *Ophiodaces* available for study from the Smithsonian Institution, identified as *Ophiodaces cf. inanis* (USNM 1106231) did not show any similarity to the description, including photographs of the features of both dorsal and ventral sides (Koehler 1922b). It possesses tiny, hardly conspicuous radial shields, a very different pattern of the oral frame and adoral shield papillae, long proximally paired tentacle scales, and a different shape of the dorsal and ventral arm plates (Fig. 42). All these features and the morphology of the arm spine articulations of the present specimen correspond well to the genus *Ophiocymbium*, but do not meet with any known species from this genus. Therefore, this well-preserved specimen is described in the present study as another new species of the genus, *Ophiocymbium antarcticus* **sp. nov.**

Fell (1960) listed *Ophiodaces* as a synonym of *Ophiodictys*, and “*inanis* Koehler, 1922” as the type species of *Ophiodictys*. These are both errors (Fell 1961). The genus *Ophiodictys*, with the type species *O. uncinatus* Koehler, 1922 is an entirely different taxon, closely related to the genus *Ophioplinthaca* (Koehler 1922b; O'Hara & Stöhr 2006).

### Genus *Ophidelos* Koehler, 1930

*Ophidelos* Koehler, 1930: 93–94

Type species: *Ophidelos insignis* Koehler, 1930, by monotypy

**Diagnosis.** This genus has a very peculiar external appearance, because of very short arms, which rapidly taper distalwards. The dorsal disk consists of numerous small disk scales covered with small granules, some of which extend onto the dorsal arm surface. A skin layer is not evident. The radial shields are very small, hardly conspicuous. The genital slits are conspicuous. The jaw bears several small square or rounded oral papillae. The teeth are spiniform and few in number. The adoral shield papillae do not differ from the other



oral papillae. Judging from the spiniform teeth, the dental plate should have small rounded sockets. The oral (possibly triangular) and adoral shields concealed by skin. The adoral shields are considerably elongated. The dorsal and ventral arm plates are well developed. The dorsal arm plates are triangular, with a convex distal edge, contiguous. The ventral arm plates are contiguous, with a convex distal edge and straight proximal edge. The spines are flattened and ribbed. One long spiniform tentacle scale is placed on the lateral arm plate.

**Remarks.** The general shape of the genus *Ophiodelos* makes it a very aberrant ophiuroid, hardly comparable with any other ophiacanthid genus. There is only a single taxon of the class Ophiuroidea, which closely resembles *Ophiodelos*, the aberrant genus *Ophiambix*, which has been placed in three different families (Paterson & Baker 1988). According to the latter study, this genus should be placed within the family Ophiuridae, however, the arm spine articulations of *Ophiambix* point to Ophiolepididae affinities (Martynov 2010). Very short arms, rapidly tapering distally, very small disk covered with small granules continuing onto the dorsal arm plates, inconspicuous radial shields, strong flattened spines with ribs – all these features are shared by both genera *Ophiodelos* and *Ophiambix*. *Ophiodelos insignis* differs considerably from described species of the genus *Ophiambix* (Bartsch 1983; Paterson 1985; Paterson & Baker 1988), because of the presence of only a single long spiniform tentacle scale and the weak dorsal granular covering of the disk and arms. This does however not exclude the possibility that *Ophiodelos insignis* should be placed in *Ophiambix*. The holotype of *Ophiodelos insignis* was not examined; therefore a definite conclusion on its placement cannot be made now.

### Genus *Ophiolimna* Verrill, 1899

Figures 44A–D; 45A–C; G–J; 46A–D; 47; 81A–B; 82A–E, G, J

*Ophiolimna* Verrill, 1899: 40, 44

Type species: *Ophiacantha bairdi* Lyman, 1883, by original designation

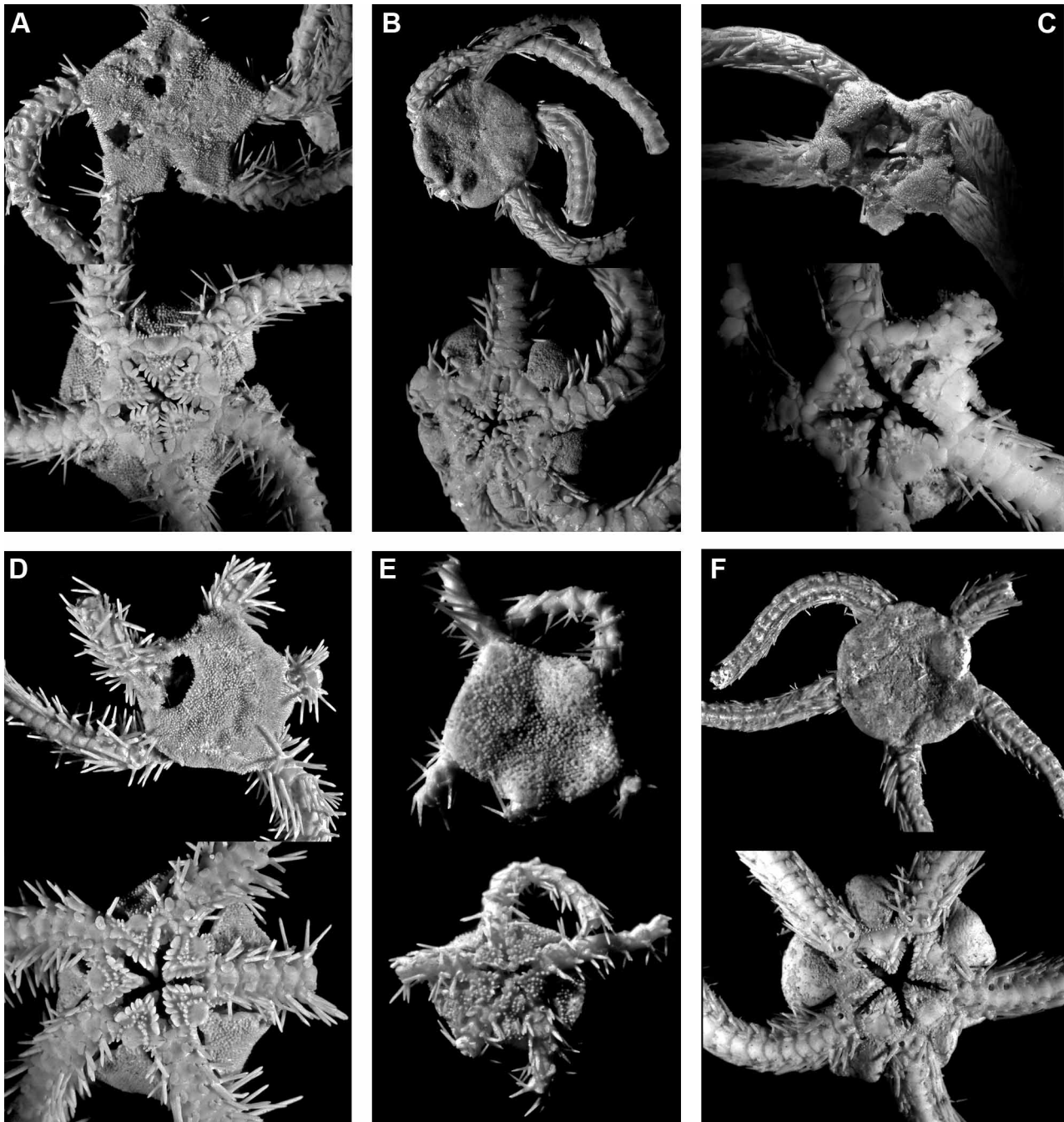
**Diagnosis.** The disk is covered with numerous small, uniform scales, completely concealed by thin skin and small densely placed granules (in some species with the addition of few spinelets), both dorsally and ventrally. The radial shields are completely or partially concealed by the granules, well defined, but relatively small, rounded or elongated. Both genital plates are well defined. The genital slits are long and conspicuous, about half their length lined by the genital plates. The jaw bears several short square, rounded or conical oral papillae similar in shape to the single (or double) apical papillae. The distalmost oral papillae are wide, rounded, operculiform, considerably different from other oral papillae. The jaws are slightly longer than high. The adradial sides of the half-jaws bear a few convoluted folds distally. The adradial sides of the half-jaws distally bear a few sharp straight folds. The dental plate is elongated, not fragmented, without folds, and with few elongate sockets, alternately placed. The teeth are broad, conical, few in number. Generally all teeth are similar in shape, but the dorsalmost teeth are usually longer. The oral shield is broadly triangular or oval, without distinct distal lobe. The adoral shields with distal wings, proximally tapered. The junction area of the adoral shields and the edges of the oral shield are covered with granules or small papillae. Dorsal and ventral arm plates are well developed. The arm spine articulations are placed distinctly at an angle or almost transversally in relation to the lateral plate. The muscle opening is larger than the nerve opening. There is a volute-shaped smooth lobe, occupying the dorsal and distal part of the articulations. The sigmoidal fold is well-defined. The proximal edge of the spine articulation has an incision and connects with the main part of the lateral arm plate by a characteristic short connecting ridge. The arm spines are relatively long, rounded, hollow over almost their entire length, not hooked distally. A single broad tentacle scale is placed on the lateral arm plates. The vertebrae have a narrow keel and are abruptly truncated distally, the dorsal medial furrow is moderately expressed. The articulation is zygospondylous. The podial basins are small.

**Material studied.** *Ophiolimna bairdi* (Lyman, 1883), 2 paratypes MCZ 1917; ZMMU D-648, 9 specimens (Figs 44A; 81A); *Ophiolimna antarctica* (Lyman, 1879), 5 specimens, ZMMU D-868 (Figs 47A–E, F–K); *Ophiolimna perfida* (Koehler, 1904), paratype MCZ 3212 of *Ophiacantha lambda* H.L. Clark, 1911; ZMMU D-808, 3 specimens (Figs 44C; 47F); *Ophiolimna papillata* (H.L. Clark, 1911), paratype MCZ 2984

(Fig. 44D); *Ophiolimna diastata* (H.L. Clark, 1911), paratype USNM 26210; paratype MCZ 2983 (Figs 44B; 45A–C; G, J).

**Remarks.** The genus has a long and convoluted taxonomic history. See details in Discussion.

**Number of species:** 6.



**FIGURE 44.** *Ophiolimna* and *Ophioconis*, external views. A. *Ophiolimna bairdi* (Lyman, 1883), paratype MCZ 1917, R/V “Blake”, sta. 308, 10 mm dd; B. *Ophiolimna diastata* (H.L. Clark, 1911), paratype MCZ 2983, 9 mm dd; C. *Ophiolimna perfida* (Koehler, 1904), (paratype *Ophiacantha lambda* H.L. Clark, 1911, MCZ 3212), 10 mm dd; D. *Ophiolimna papillata* (H. L. Clark, 1911), paratype MCZ 2984, 9.5 mm dd; E. *Ophioconis cincta* Brock, 1888 USNM E42554, 3 mm dd; F. *Ophioconis miliaria* Lyman, 1878, holotype MCZ 167, 8 mm dd. Photos: Tatiana Korshunova.

#### Key to species of the genus *Ophiolimna* Verrill, 1899

- 1(10) Radial shields concealed under disk scales and granules
- 2(7) Disk is irregular in appearance, subpentagonal and often considerably damaged dorsally



- 3(6) Distalmost oral papilla of moderate size, approximately 2 times wider than other oral papillae
- 4(5) Oral frame granules concentrated at adoral shields junction and between oral papillae; no granules at oral shield lateral edges; oral shield is broadly triangular with obtuse angles.....  
.....*O. bairdi* (Lyman, 1883), North Atlantic, at 620–2600 m
- 5(4) Oral frame granules distinctly placed both between oral papillae and bordering the oral shield from almost all sides; oral shield is oval to rhomboidal.....*O. papillata* (H. L. Clark, 1911), North Pacific, at 140–700 m
- 6(3) Distalmost oral papilla very wide, approximately 3 times wider than other oral papillae; oral frame bears (if any) few indistinct granules.....*O. opercularis* Koehler, 1907, North Atlantic, at 6035 m
- 7(2) Disk rounded, usually intact dorsally
- 8(9) Disk covers with ganules of a moderate size; adoral shield papillae (distalmost oral papillae) are not considerably larger (1.5–2 times) than the rest.....  
.....*O. antarctica* (Lyman, 1879), Antarctic waters, circumpolar, subantarctic, reaches New Zealand and New Caledonia (the range of this species should be checked since other *Ophiolimna* species considered here as valid (e.g. *O. papillata*) sometimes have been included into its synonymy), at 180–1006 m
- 9(8) Disk covers with extremely small granules; adoral shield papillae (distalmost oral papillae) are considerably larger (2–3 times) than the rest.....*O. diastata* (H.L. Clark, 1911), off Japan, at 445–460 m
- 10 (1) Radial shields exposed
- 11 (12) Dorsal arm plates with distinctly elevated distal edge; disk granules with crown-shaped top.....  
.....*O. placentigera* (Lyman, 1880), South Pacific at Fiji and New Caledonia, at 1618–2511 m
- 12 (11) Distal edge of dorsal arm plates not elevated; disk granules obtuse conical at their top.....  
.....*O. perfida* (Koehler, 1904), Pacific Ocean from Japan to New Caledonia, at 411–1280 m

### Genus *Ophiologimus* H.L. Clark, 1911

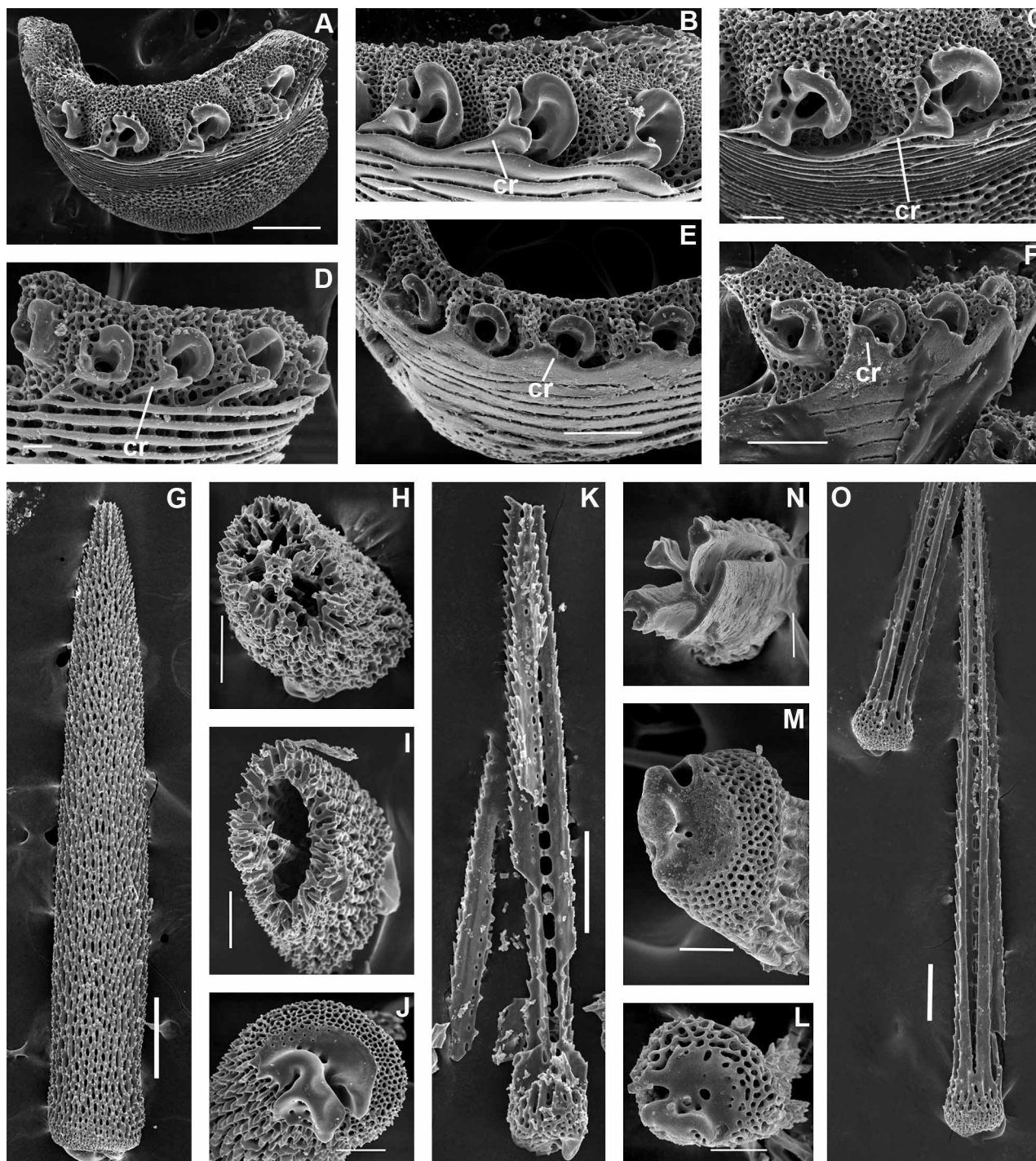
Figures 4M; 27 L–N; 40 I–J; 48; 49

*Ophiologimus* H.L. Clark, 1911: 252

Type species: *Ophiologimus hexactis* H.L. Clark, 1911, by original designation

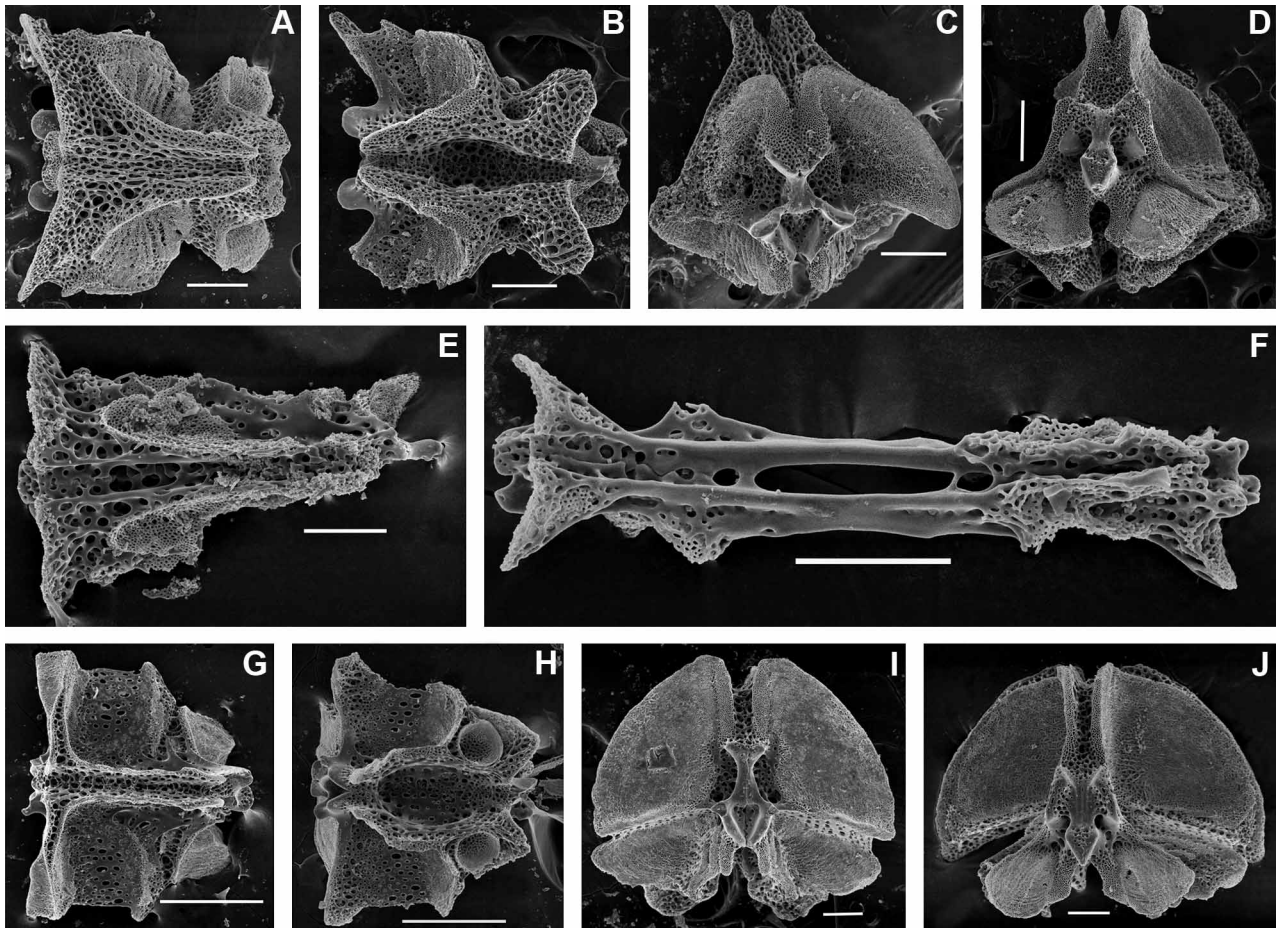
**Diagnosis.** The disk is covered with numerous small, uniform scales, and a thin skin layer, evident when dried. The radial shields are completely concealed by skin, small rounded plates hardly conspicuous in dried specimens in most species (including the type species). The adradial genital plate is poorly developed and the abradial genital plate is absent in most species. The genital slits are long and conspicuous, genital plate(s) lining approximately half of the slits. The jaw bears numerous very short, square or rounded oral papillae, considerably different from the 2–3 ventralmost teeth. The adoral shield papillae are very short and do not differ from other oral papillae, placed around the second tentacle pore. The half-jaws are elongate, very low. The adradial sides of the half-jaws bear a few sharp straight folds distally. The dental plate is small, elongated, without folds, with few rounded sockets, alternately placed. The teeth are spiniform and few in number (besides apical papillae there are 4–5 teeth). All teeth are of similar shape. The oral shield is broadly triangular, without distinct distal lobe, except for the madreporite. The adoral shields have distal bilobed wings, proximally tapering. The dorsal and ventral arm plates are well developed. The arm spine articulations are placed distinctly at an angle or almost transversally in relation to the lateral plate. Muscle and nerve openings are similar in size. There is a prominent perforated lobe, occupying the dorsal and distal part of the articulations. The sigmoidal fold is absent. The spines are relatively long, flattened, hollow over almost their entire length, hooked distally. Two or one flattened tentacles scales with pointed ends are placed on the lateral arm plate. The vertebrae have a rounded distal keel, the dorsal medial suture is indistinct. The articulation is zygospondylous. The podial basins are large.

**Remarks.** The genus *Ophiologimus*, traditionally placed within the family Ophiacanthidae externally similar to one of the ophiomyxid genus, *Ophyolycus*, which is in turn often considered as just a synonym of the genus *Ophioscolex* (see below). *Ophiologimus* distinguishes from the *Ophyolycus* by the short oral and oral shield papillae, all similar in size (*Ophyolycus* has long spiniform oral shield papillae), well defined dorsal arm plate throughout the arm length (*Ophyolycus* possesses well defined dorsal arm plates only proximally) and entirely hollow arm spines (*Ophyolycus* has almost solid spines with small holes).



**FIGURE 45.** *Ophiolimna* and *Ophioconis*, spine articulations and spines. A–C, G–J, *Ophiolimna diastata* (H.L. Clark, 1911), paratype USNM 26210, 6.7 mm dd. A. lateral arm plate showing spine articulation; B–C, details of spine articulations, proximal segments; G. proximal spine; H. proximal spine, sectioned transversally in the basal part showing semi-solid structure; I. same, hollow spine sectioned transversally in the middle part showing a ridge inside; J. same, ventral view; D, K–L, *Ophioconis cincta* USNM E42554, 3 mm dd. D. details of spine articulations, proximal segments; K. solid proximal spine showing distinct ribs; L. same, ventral view; E–F, M–O, *Ophioconis cupida*, Koehler, 1905, USNM E 42555, 5 mm dd. E. proximal lateral arm plate showing spine articulation; F. same; M. proximal spine, ventral view; N. solid spine sectioned transversally showing distinct ribs; O. proximal spines. Scale bars: A, G, 300  $\mu$ . B, C, H–J, K, E–F, O, 100  $\mu$ ; D, L, M–N, 30  $\mu$ . Photos: Alexander Martynov.





**FIGURE 46.** *Ophiolimna* and *Ophiocnida*, vertebrae. A–D, *Ophiolimna diastata* (H.L. Clark, 1911), paratype USNM 26210, 6.7 mm dd. A. proximal vertebra, dorsal view; B. same, ventral view; C. same, proximal view; D. same, distal view. E–F, *Ophiocnida cincta* USNM E42554, 3 mm dd. E. middle vertebra, dorsal view; F. distal vertebra, dorsal view; G–J, *Ophiocnida cupida*, USNM E 42555, 5 mm dd. G. proximal vertebra, dorsal view; H. same, ventral view; I. same, proximal view; J. same, distal view. Scale bars: A–D, G–H, 300  $\mu$ ; E–F, I–J, 100  $\mu$ . Photos: Alexander Martynov.

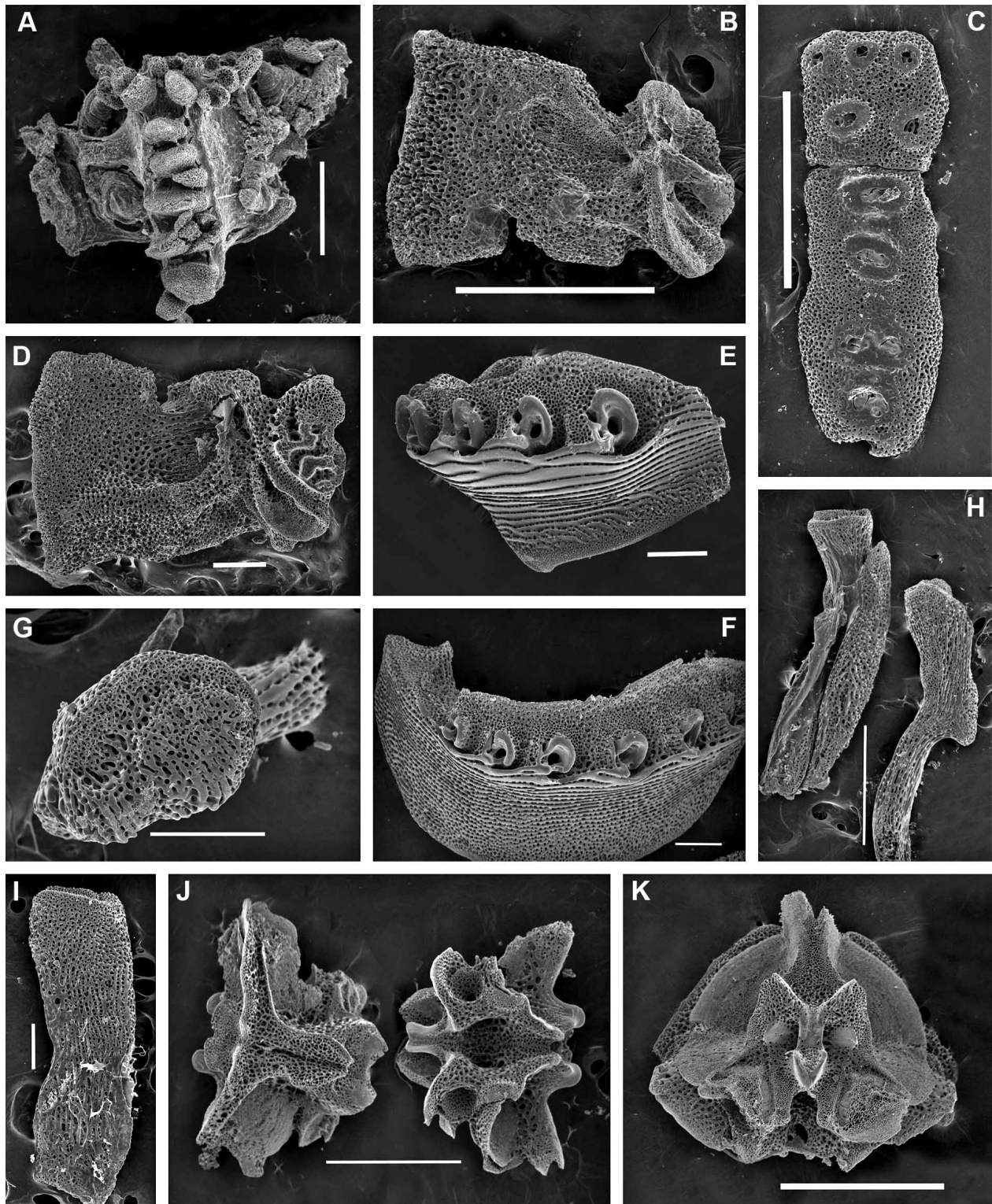
**Material studied.** *Ophiologimus hexactis* H.L. Clark, 1911, holotype USNM 25724 (Fig. 48); *Ophiologimus quadrispinus* H.L. Clark, 1925, USNM E 06912, 4 specimens, USNM E 06911, one specimen (Fig. 49); *Ophiologimus secundus* Koehler, 1914, 4 syntypes USNM 032302; *Ophiologimus* cf. *secundus*, ZMMU D-814, one specimen, ZMMU D-814, 4 specimens (Figs 4M; 27L–N; 40I–J)

**Number of species:** 4.

#### Key to species of the genus *Ophiologimus* H.L. Clark, 1911

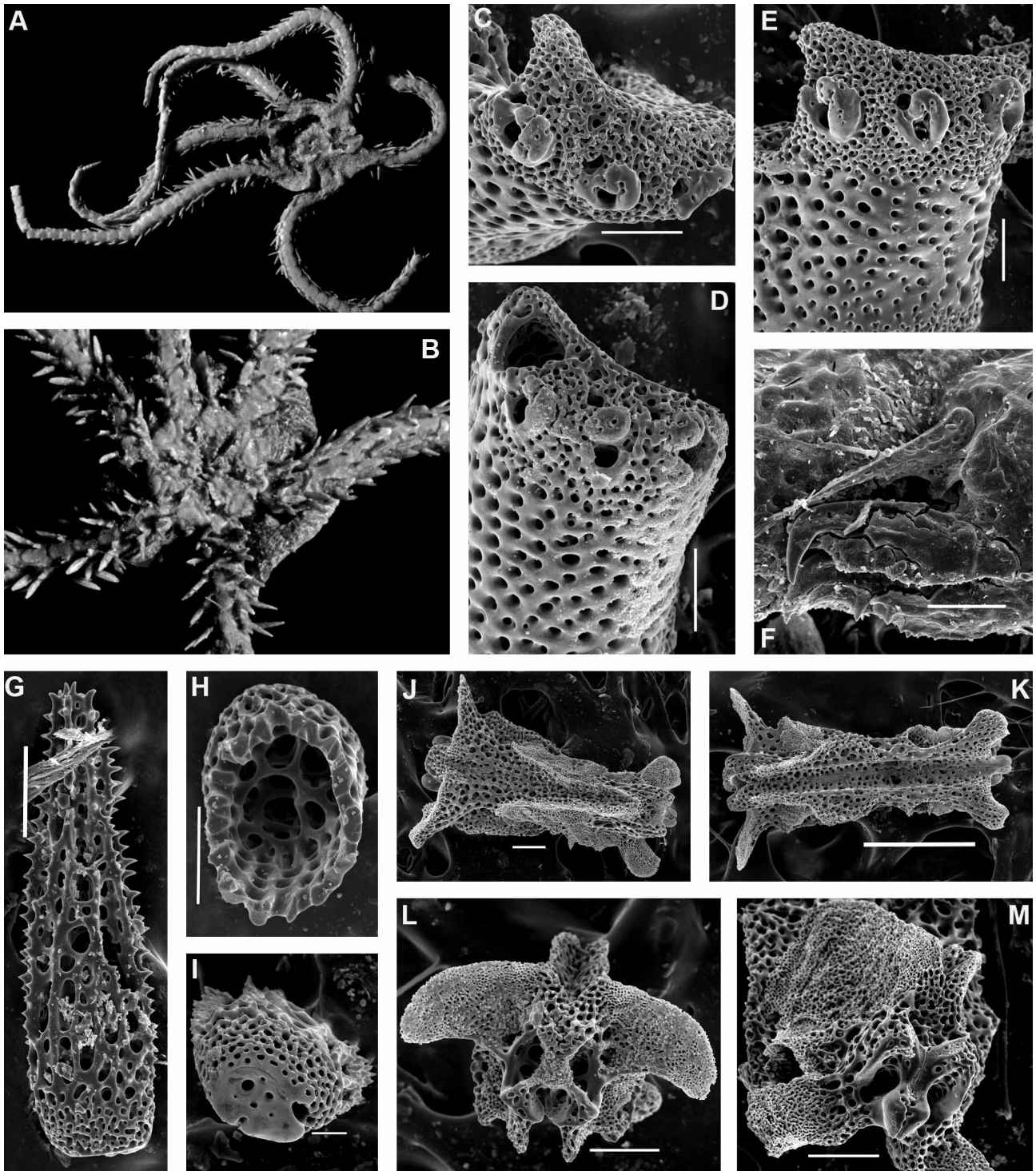
- 1(6) Six or more arms; radial shields very small, hardly conspicuous, rounded
- 2(3) Two tentacle scales..... *O. hexactis* H.L. Clark, 1911, North Pacific (Honshu, Japan), at 151–287 m
- 3(2) Single tentacle scale
- 4(5) Dorsal arm plates polygonal, proximally contiguous; oral shield broadly triangular.....  
.....*O. prolifer* (Studer, 1882), South Pacific, off New Zealand, at 1086 m
- 5(4) Dorsal arm plates triangular, proximally separated; oral shield rhomboidal.....  
.....*O. secundus* Koehler, 1914, North Atlantic (off Florida), at 535 m
- 6(1) Five arms; radial shields (concealed by skin) relatively large, elongated.....  
.....*O. quadrispinus* H.L. Clark, 1925, Pacific Ocean (Hawaii and New Caledonia), 238–675 m





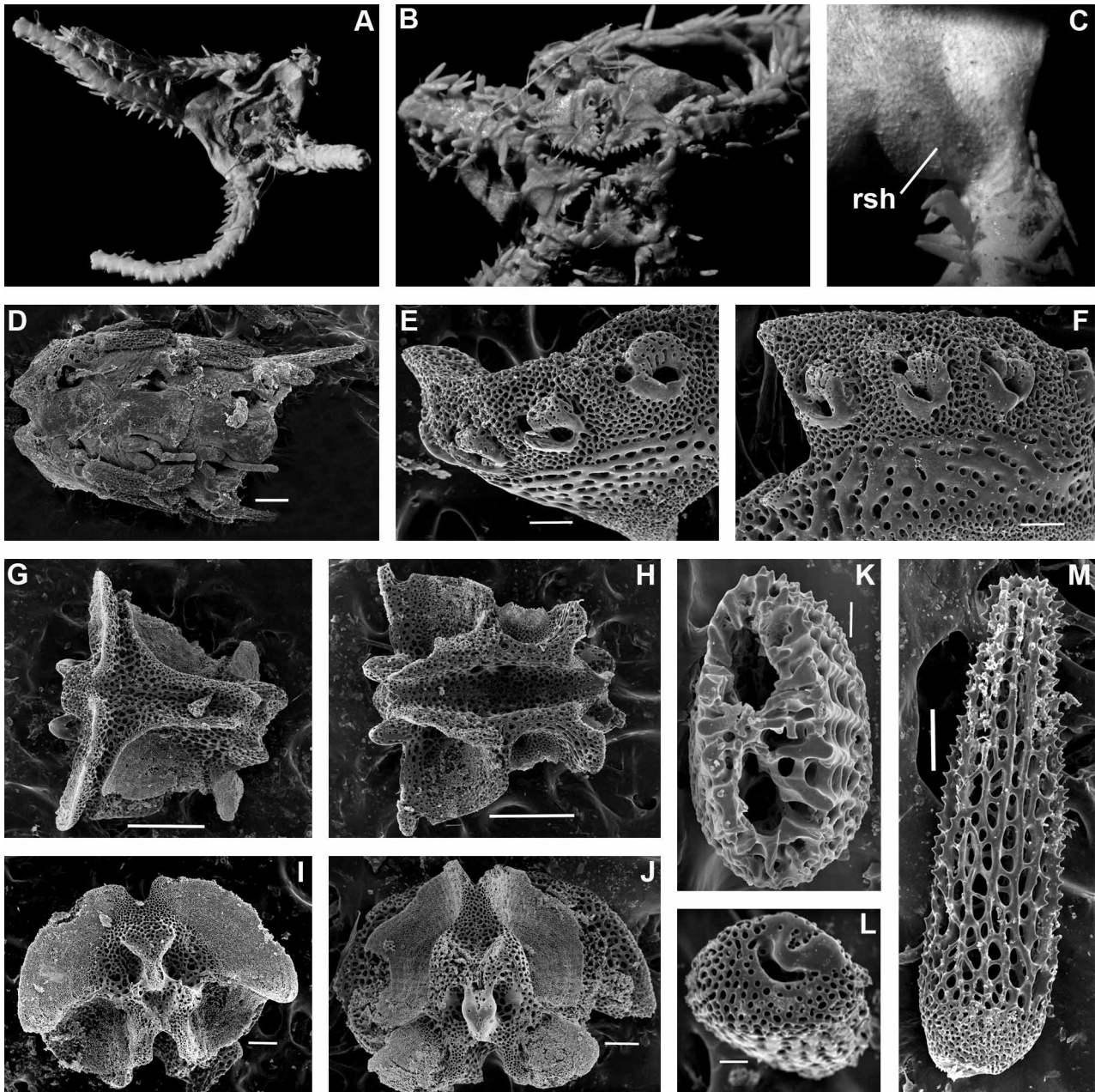
**FIGURE 47.** *Ophiolimna antarctica* (Lyman, 1879), ZMMU D-868, 10 mm dd, details (A–E, F–K) and *Ophiolimna perfida* (Koehler, 1904), ZMMU D-808 (F). A. *Ophiolimna antarctica*, inside mouth view of one interradius; B. same, jaw, abradial view; C. same, dental plate, damaged; D. same, jaw, adradial view; E. same, arm spine articulations, proximal segments; F. *Ophiolimna perfida* (Koehler, 1904), ZMMU D-808, proximal segments, arm spine articulations, proximal segments; G. *Ophiolimna antarctica* articulation surface of the adradial genital plate; H. same, articulating adradial and abradial genital plates and isolated adradial genital plate respectively, dorsal view; I. same, radial shield, ventral view; J. same, vertebrae, dorsal and ventral views respectively; K. same, distal view. Scale bars: A–C, 1 mm; D–G, 300  $\mu$ ; H, 1 mm; I, 300 ; J–K, 1 mm. Photos: Alexander Martynov.





**FIGURE 48.** *Ophiologimus hexactis* H.L. Clark, 1911, holotype USNM 25724, 5 mm dd, external views and details. A. dorsal view; B. ventral view; C–D, arm spine articulations, distal segments; E. arm spine articulations, proximal segments; F. distal segments, hooks; G. spine, proximal segments; H. hollow spine, transversally sectioned; I. spine, ventral view; J. proximal vertebra, dorsal view; K. same, ventral view; L. same, proximal view; M. same, distal view. Scale bars: C–H, J, L–M, 100  $\mu$ ; I, 30  $\mu$ .; K, 300  $\mu$ . Photos: A–B Tatiana Korshunova; C–M Alexander Martynov.





**FIGURE 49.** *Ophiologinus quadrispinus* H.L. Clark, 1925, USNM E06912, 5.5 mm dd, external views and details. A. dorsal view; B. ventral view; C. details of dorsal disk showing moderately well developed radial shields concealed under the skin; D. proximal arm segments, ventral view; E. proximal lateral arm plate showing spine articulations; F. spine articulations, details; G. proximal vertebra, dorsal view; H. same, ventral view; I. same, proximal view; J. same, distal view; K. hollow proximal spine, sectioned transversally, showing two large holes separate by a septa; L. same, ventral view; M. proximal spine. Scale bars: D, G–H, 300  $\mu$ ; E–F, I–J, M, 100  $\mu$ ; K, L, 30  $\mu$ . Photos: A–B Tatiana Korshunova; C–M Alexander Martynov.

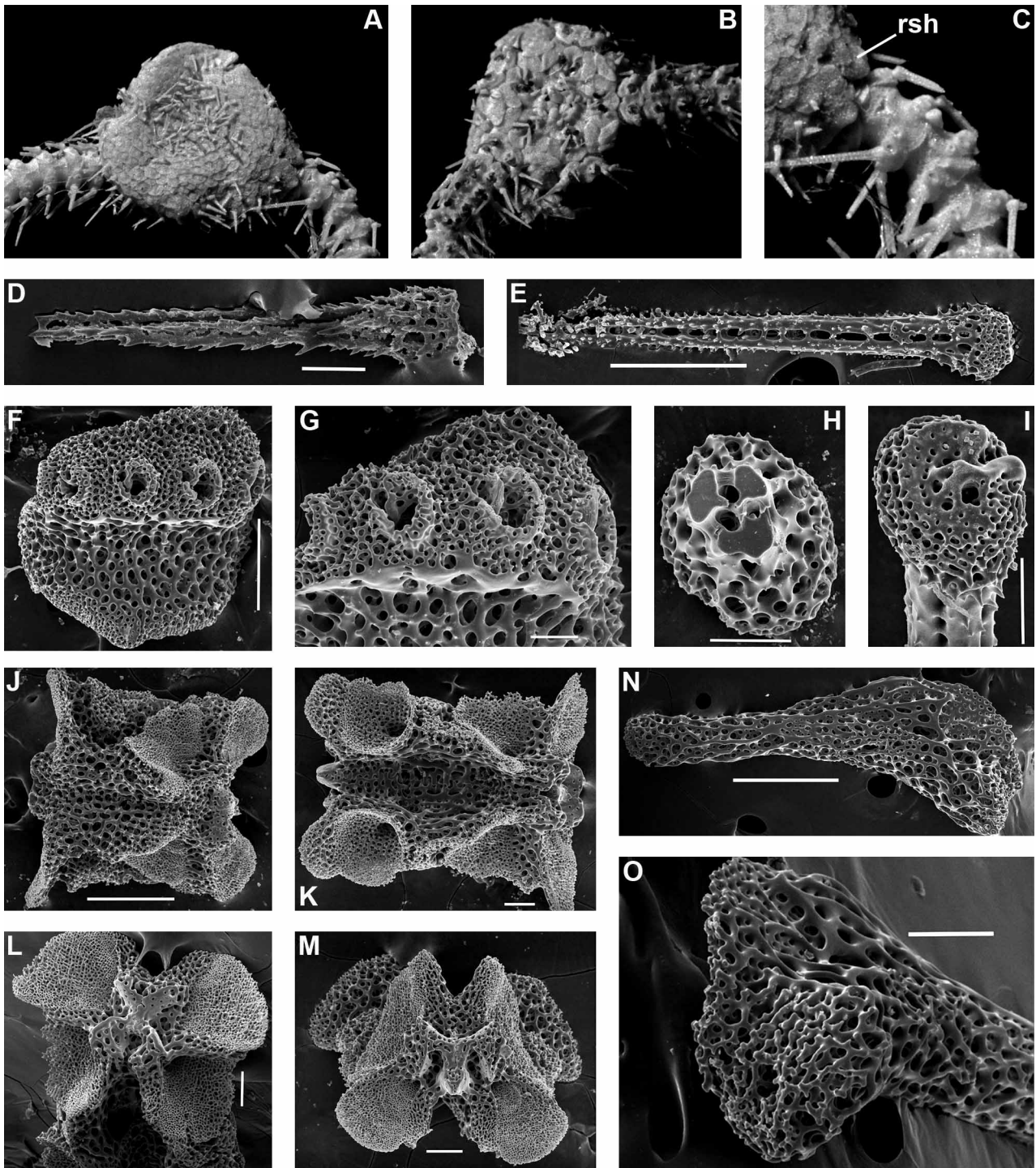
### Genus *Ophiomedeia* Koehler, 1906

Figure 50

*Ophiomedeia* Koehler, 1906:19

Type and single species: *Ophiomedeia duplicata* Koehler, 1906, by monotypy





**FIGURE 50.** *Ophiomedea duplicata* Koehler, 1906, holotype MNHN EcOs 20426, 4.6 mm dd, external view and details. A. dorsal view; B. ventral view; C. dorsal view showing small radial shields and proximal arm segments; D. dorsal disk spine; E. spine, proximal segments; F. lateral arm plate and spine articulations, proximal segments; G. arm spine articulations, details; H. spine section showing small cavities; I. spine, ventral view; J. proximal vertebra, dorsal view; K. same, ventral view; L. same, proximal view; M. same, distal view; N. adradial genital plate, dorsal view; O. adradial genital plate, articulation surface. Scale bars: D, G–H, J–L, N, 100  $\mu$ ; E–F, I, M, 300  $\mu$ . Photos: A–C Tatiana Korshunova; D–N Alexander Martynov.

**Diagnosis.** The disk is covered with numerous small, uniform scales, not concealed by a skin layer. Both dorsal and ventral sides of the disk are covered with numerous relatively long spinelets. The radial shields are small, triangular, hardly conspicuous plates. The adradial genital plate has well-defined lateral wing, and a

small but distinct condyle separated by a shallow groove. Abradial genital plate not detected. The genital slits are short and only slightly evident. The jaw bears three or four pairs of spiniform oral papillae, very different from the shape of the massive, wide, single ventralmost tooth. There is the pair of long spiniform adoral shield papillae, 2–3 times longer and markedly different from the other oral papillae, placed around the second tentacle pore. The dental plate, judged from the massive teeth morphology should bear few slit-shaped sockets. The oral shield is markedly wider than long, oval, with a small proximal and a more or less distinct distal lobe. The adoral shields are broad bands, of uniform shape throughout. The dorsal and ventral arm plates well developed. The dorsal arm plates are small, triangular, with almost straight distal edge, and contiguous. The muscle opening is larger than the nerve opening. There is a volute-shaped, perforated lobe, occupying the dorsal and distal parts of the articulations. The sigmoidal fold is well-defined. The spines are relatively long, rounded, contain small lumens inside, not hooked distally. The tentacle scales are small and conical, one or two in number, placed both on the lateral and ventral plates, or absent. The tentacle pores are relatively large.

**Material studied.** *Ophiomedea duplicata* Koehler, 1906, holotype MNHN, EcOs 20426 (Fig. 50).

**Remarks.** Koehler (1922a) has included into the genus *Ophiomedea* two other species, one initially described within a separate genus *Ophiophrura* H.L. Clark, 1911 (with type species *O. liodisca* H.L. Clark, 1911) and *Ophiomedea discrepans* Koehler, 1922, an abyssal species from the Philippine region. Holotypes of both *Ophiophrura liodisca* and “*Ophiomedea*” *discrepans* were examined (Figs 51 and 63) and compared with the holotype of *Ophiomedea duplicata* Koehler, 1906 (EcOs 20426) (Fig. 50). It was revealed that all three taxa differ considerably from each other and do not show any close similarity. *Ophiomedea duplicata* is a true ophiacanthid, with spine articulations possessing a volute-shaped lobe (Figs 50F, G) and the sigmoidal fold and massive wide teeth, whereas both *Ophiophrura liodisca* and “*Ophiomedea*” *discrepans* show non-ophiacanthid articulation and spiniform teeth (Figs 51H, I; 63G, H).

*Ophiomedea duplicata* is currently known only from a single specimen from the type locality in the North Eastern Atlantic, off Canary Ids, at 2075 m.

### Genus *Ophiophrura* H.L. Clark, 1911

Figures 51, 52, 53

*Ophiophrura* H.L. Clark, 1911: 249

*Ophiophrura* (lapsus calami), Paterson, 1985: 52

Type species: *Ophiophrura liodisca* H.L. Clark, 1911, by monotypy

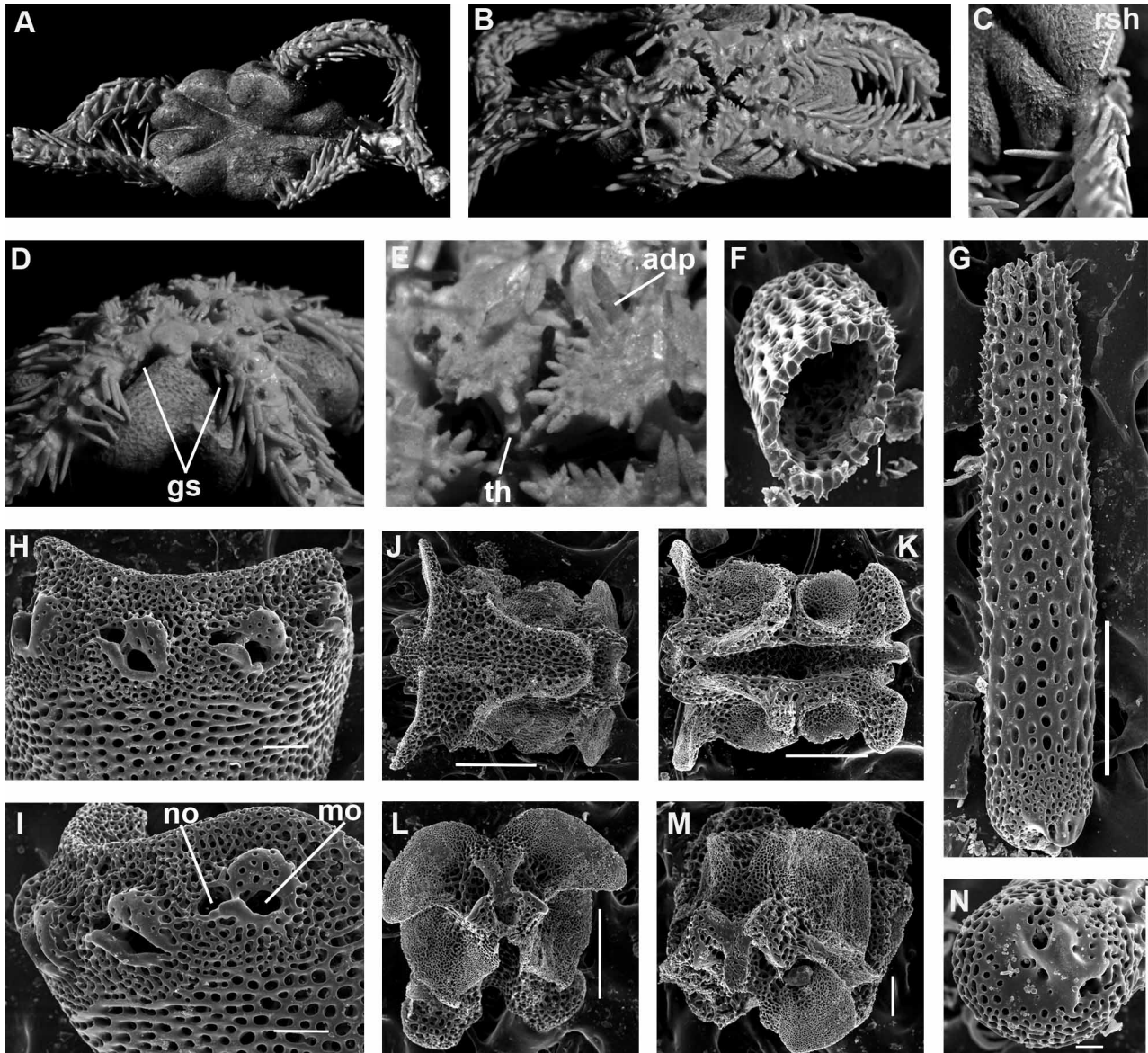
**Diagnosis.** The disk is covered with numerous small, uniform scales, and a thin skin layer, evident when dried. The radial shields are small rounded plates, hardly conspicuous in dried specimens. The adradial genital plate is poorly developed, tightly articulated with the radial shield, proximally slightly curved. The abradial genital plate is very short and externally slightly conspicuous. Details of the articulations of genital plates and radial shields are unknown. The genital slits are long and conspicuous, but genital plates border only a distal third of the slits. The jaw bears numerous spiniform oral papillae, similar in shape to the small cluster of 3–4 ventralmost teeth. Two adoral shield papillae and one adjacent oral papilla of each jaw are somewhat club-shaped and flattened, 2–3 times longer and thicker than the oral papillae; they are placed around the second tentacle pore. The dental plate is small and elongated, without folds and with few rounded sockets, alternately placed. The teeth are spiniform and few in number (besides the ventralmost ones there are 4–5 teeth). All teeth are of similar shape. The oral shield is rhomboidal with a distinct distal lobe. The adoral shields have distal bilobed wings, proximally tapered. Dorsal and ventral arm plates are well developed. Arm spine articulations are placed distinctly at an angle in relation to the lateral arm plate. Muscle and nerve openings are similar in size or the muscle opening is slightly larger. There is a prominent perforated distal lobe occupying the dorsal part of the articulation. The sigmoidal fold is absent. The arm spines are relatively long, club-shaped or slightly flattened, hollow over almost their entire length, not hooked distally. Two elongated tentacle scales with pointed ends are placed on the lateral arm plate and one or two on the ventral plate, forming a



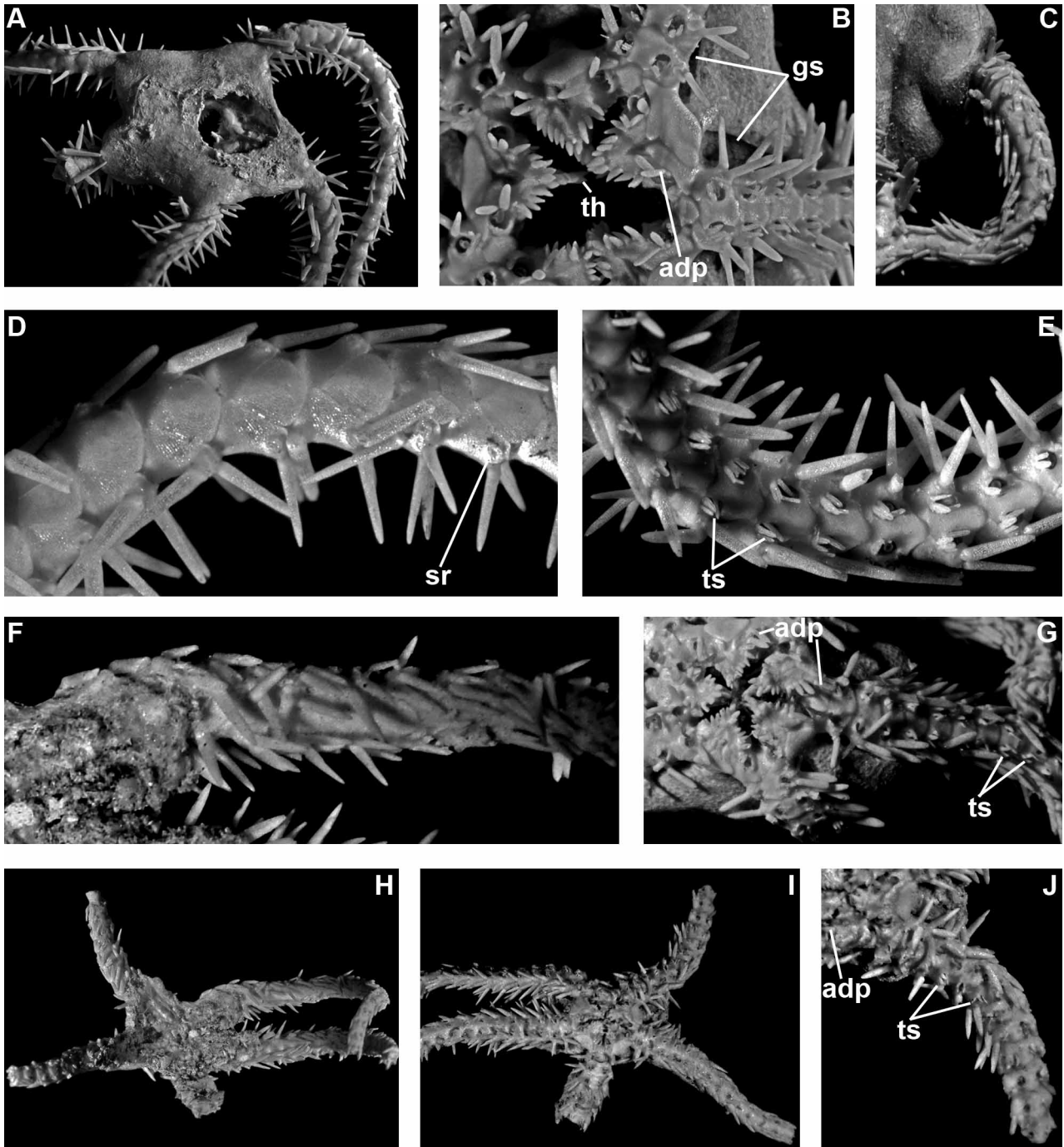
characteristic pattern. The vertebrae have a rounded distal keel; the dorsal medial suture is indistinct. The articulation is zygospondylous. The podial basins are large.

**Material studied.** *Ophiophrura liodisca* H.L. Clark, 1911, Holotype USNM 25672 (Figs 51; 52C, G); *Ophioprium imperfectum* H.L. Clark, 1915, Holotype MCZ 2167 (Figs 52F, H–J); *Ophioscolex tripapillatus* Stöhr & Segonzac, 2005, Paratype NI-1016 (Fig. 53).

**Remarks.** Previously, only few specimens of the type and only species, *Ophiophrura liodisca*, were known. An additional specimen recently described by O'Hara and Stöhr (2006) differs from the type specimen. For instance, H.L. Clark (1911) described spiniform “oral tentacle scales”, whereas in the specimen described by O'Hara and Stöhr (2006) these papillae are flattened and spatulate. In this respect this specimen possibly represents a separate undescribed species.



**FIGURE 51.** *Ophiophrura liodisca* H.L. Clark, 1911, holotype USNM 25672, 8 mm dd, external views and details. A. dorsal view; B. ventral view; C. details of the disk showing small radial shields (rsh); D. ventro-lateral view showing long genital slits; E. close up of oral frame showing long club-shaped adoral shield papillae and spiniform teeth; F. hollow proximal spine, transversally sectioned; G. spine; H–I, arm spine articulations, proximal segments; J. proximal vertebra, dorsal view; K. same, ventral view; L. same, proximal view; M. same, distal view; N. spine, ventral view. Scale bars: F, 30  $\mu$ ; H–I, 100  $\mu$ ; J–L, 300  $\mu$ ; M, 100  $\mu$ ; N, 30  $\mu$ . Photos: A–E Tatiana Korshunova; F–N Alexander Martynov.



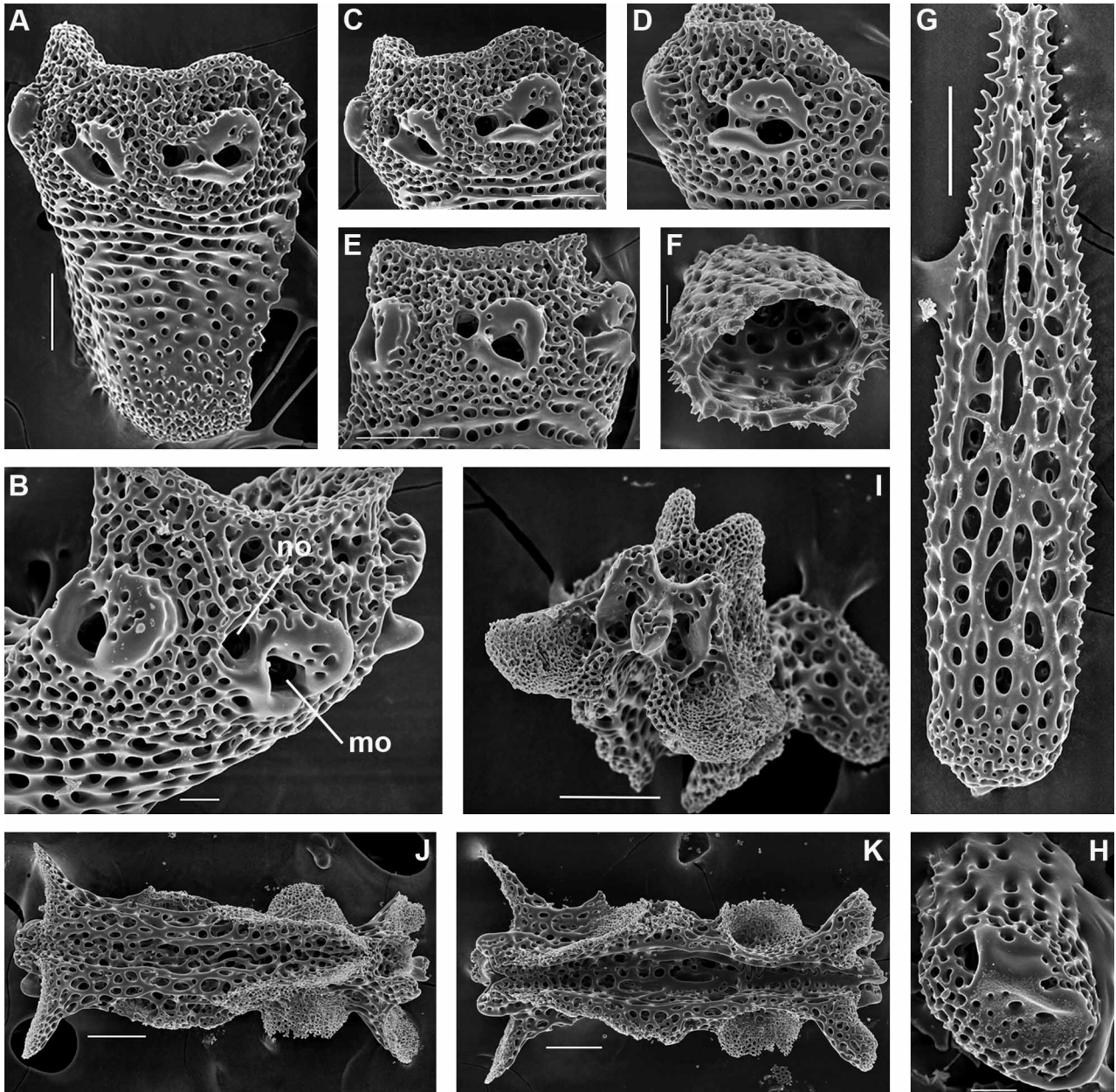
**FIGURE 52.** *Ophiophrura tripapillata* (Stöhr & Segonzac, 2005) **comb.nov.** (A–B, D–E, holotype MNHN EcOs 22795, 10 mm dd), *Ophiophrura imperfecta* (H.L. Clark, 1915) **comb.nov.** (F, H–J, holotype MSZ 2167, ca. 7 mm dd), and *Ophiophrura liodisca* H.L. Clark, 1911, holotype USNM 25672, 8 mm dd (C, G). A, H, dorsal view; B, G, I, ventral views; C, F, dorsal disk details; D–E, G, J, arm segments, ventral views, details showing pattern of several tentacle scales. A–B, D–E Sabine Stöhr; C, G Tatiana Korshunova; F, H, I–J Alexander Martynov.

“*Ophioprium*” *imperfectum* H.L. Clark, 1915 is very different from the type species of the genus *Ophioprium*, *O. cervicornis*, as was already mentioned by Clark (1915). In the present study, *O. liodisca* was examined in detail (Fig. 51). *Ophiophrura* is characterized by two pairs of well-defined adoral shield papillae, spiniform teeth, three to four spiniform tentacle scales and hollow spines. All these features are present in the holotype (MCZ 2167) of “*Ophioprium*” *imperfectum* H.L. Clark, 1915 (Figs 52F, H–J), which is therefore considered as second species of the *Ophiophrura*. The recently described *Ophioscolex tripapillatus* Stöhr & Segonzac, 2005 differs considerably from the type species of both genera *Ophioscolex* s.str. and *Ophiolycus*



(see the diagnoses below) in having hollow spines, 3–4 elongate tentacle scales, well-defined dorsal arm plates (including proximalmost segments), flattened adoral shield papillae and a lack of hooked distal arm spines (Figs 52A–B; D–E; 53). All these characters corresponded well with the type species of the genus *Ophiophrura*, according to the re-examination of the type material of *O. liodisca*. Spine articulations of *Ophioscolex tripapillatus* are not ophiacanthid (Stöhr & Segonzac, 2005; present study, Figs 53A–E) and differ greatly from the types species of both genera *Ophioscolex* and *Ophiolycus* but are similar to *Ophiophrura liodisca*. According to the present SEM study of an *Ophioscolex tripapillatus* paratype, the spine articulations possess a conspicuous distal lobe and are similar to *Ophiophrura liodisca* articulation pattern (compare Figs 51H–I and 53A–E). *Ophioscolex tripapillatus* is therefore considered to be within the genus *Ophiophrura*.

**Number of species:** 3.



**FIGURE 53.** *Ophiophrura tripapillata* (Stöhr & Segonzac, 2005) **comb. nov.**, paratype NI-1016, 4 mm dd, details. A. lateral arm plate, middle segments, showing arm spine articulations; B–E, arm spine articulations, middle segments, details; F. hollow middle spine, transversally sectioned; G. spine; H. same, ventral view; I. middle vertebra, distal view; J. same, dorsal view; K. same, ventral view. Scale bars: A, C, E, G, I–K, 100  $\mu$ ; B, F, H, 30  $\mu$ . Photos: Alexander Martynov.

**Key to species of the genus *Ophiophrura***

- 1(2) Oral shields have distinct distal lobe; oral shield proximal edge triangular.....  
 ..... *O. lioDISca* H.L. Clark, 1911, North Pacific, off Japan, at 864–919 m
- 2(1) Oral shields without distinct distal lobe
- 3(4) Oral shield broadly triangular, distal edge almost straight, proximal edge convex.....  
 ..... *O. imperfecta* (H.L. Clark, 1915) **comb. nov.**, Caribbean, off St. Vincent, at 771 m
- 4(3) Oral shields elongated lozenge-shaped.....  
 ..... *O. tripapillata* (Stöhr & Segonzac, 2005) **comb. nov.**, North Atlantic, at 1015–1400 m

***Ophioplexa* gen. nov.**

**Diagnosis.** The disk covered with numerous small, uniform scales covered by a thin skin layer, not evident when dried. The radial shield and adradial genital plate are small and externally inconspicuous. The articulation surface of the radial shield is distinctly excavated ventrally, distally with a groove. The abradial genital plate is absent. The genital slits are small. The oral frame bears numerous oral papillae similar in shape to the cluster of the ventralmost teeth (apical papillae). Several adoral shield papillae, which do not differ considerably from the oral papillae, are placed around the second tentacle pore. The jaws are slightly elongated. The adradial sides of the jaws distally bear a few sharp straight folds. The dental plate is large with rounded sockets and irregular folds. The teeth are spiniform and numerous, ventralmost teeth of similar shape. The dorsal and ventral arm plates are well developed. The arm spine articulations are compressed transversally. Some proximal articulations may have a distinct nerve opening. The sigmoidal fold is absent. The arm spines are hollow, relatively short and flattened, not hooked distally. The vertebrae are distinctly keeled and with zygospondylous articulation.

**Etymology.** *Ophio-* (after ophiuroid) and *plexus* (Latin, noun, feminine), braided, in current usage meaning also a complicated combination of elements in a system, in reference to an intricate relationship of the new genus combining traits of both ophiomyxids and ophiacanthids.

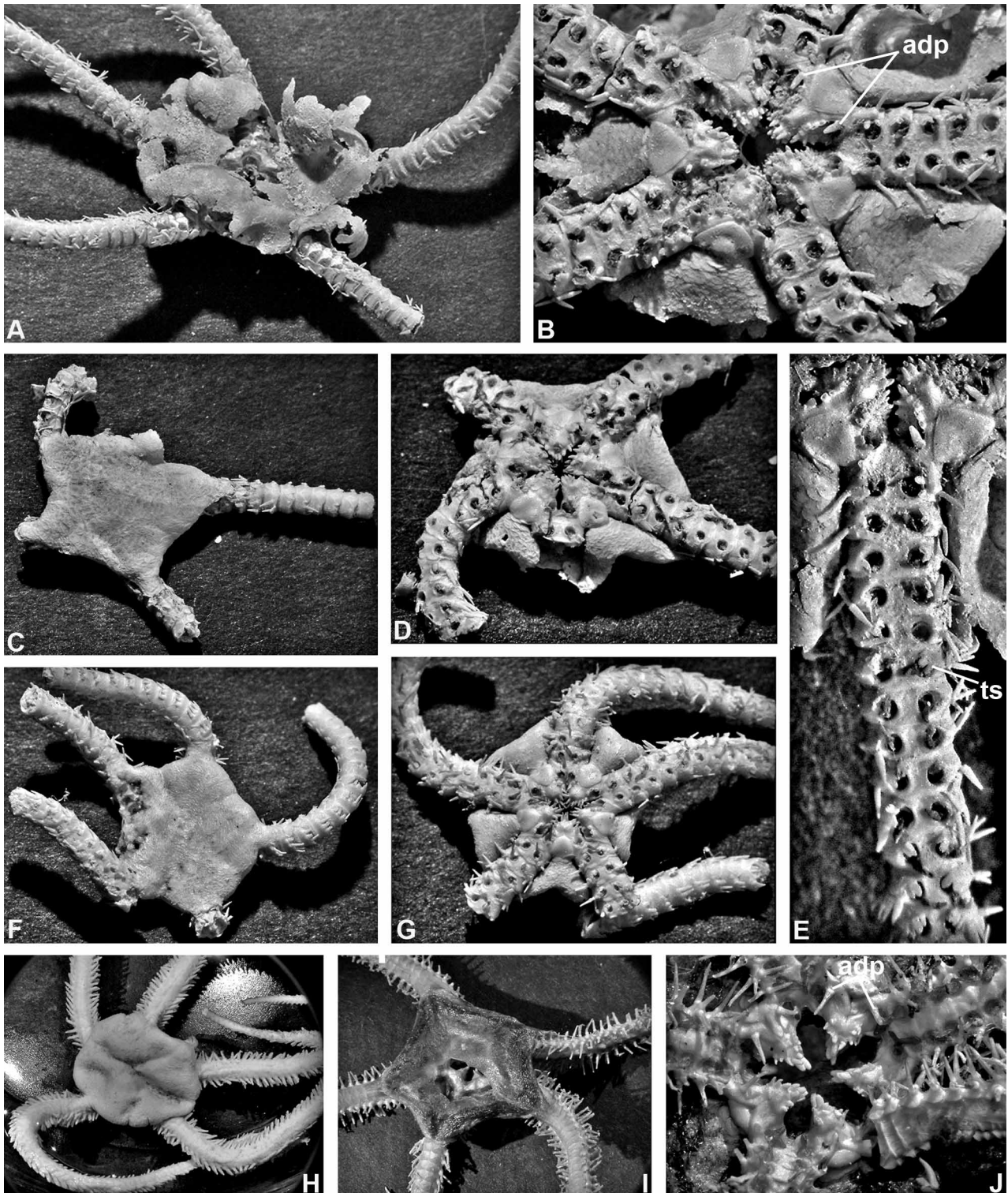
**Remarks.** (see also under Discussion below). The new genus shows some similarities to the genus *Ophiocymbium* in the presence of a poorly developed adradial genital plate and radial shield, but possesses several important differences. The genus *Ophiocymbium* has distinct block-shaped distal oral papillae as adult and few apical papillae, whereas *Ophioplexa* **gen. nov.** is characterized by numerous spiniform oral papillae, both proximally and distally. The numerous apical papillae of *Ophioplexa* **gen. nov.** are placed in a dense cluster, whereas *Ophiocymbium* has only a few apical papillae. The arm spine articulations of *Ophioplexa* **gen. nov.** are dorso-ventrally compressed with distinct nerve and muscle openings, whereas *Ophiocymbium* has a typical rounded muscle opening, but the nerve opening, if conspicuous, has a different appearance. The dental plate of *Ophioplexa* **gen. nov.** has a remarkable appearance, with a combination of several articulations and numerous small openings (Fig. 55M–N), whereas the dental plate of *Ophiocymbium* has a few round openings and completely lacks articulation (Fig. 12E–H).

***Ophioplexa condita* gen. et sp. nov.**

Figures 4J, K, N, P–S; 17L–O; 54A–E; 55A–H; 56; 67F

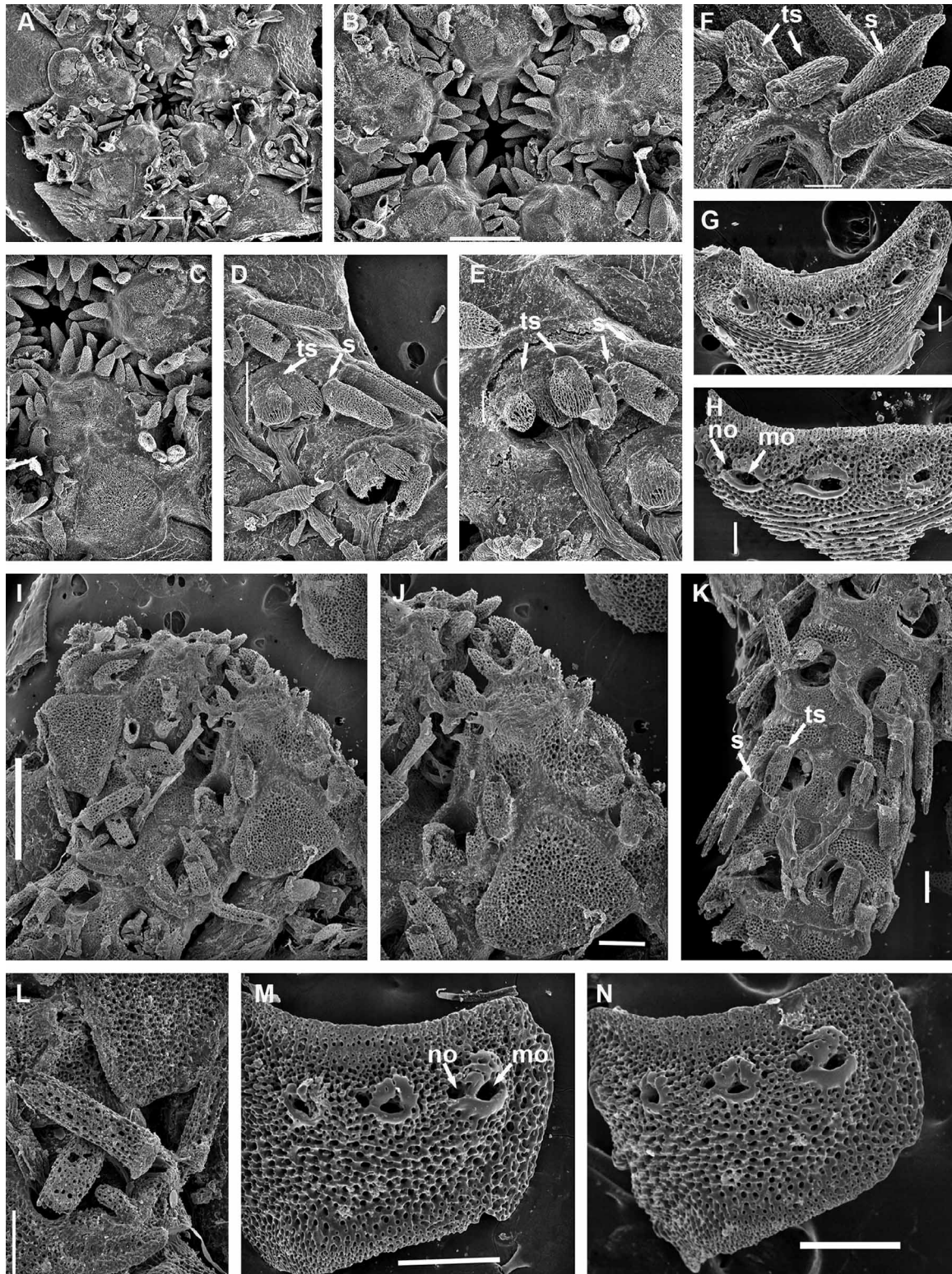
**Material.** Holotype, dried, ZMMU D-788, R/V “Akademik Kurchatov”, cruise 11, sta. 896, 05.12.1971, 56° 52' S 24° 59' W – 56° 51' S 24° 59' W, depth 5651–5530 m, Sigsbee trawl. One paratype, dried, ZMMU D-789, same sta. as holotype. One paratype, ethanol, ZMMU D-790, same sta. as holotype. One paratype, mounted on SEM stub, ZMMU D-791, same sta. as holotype. One paratype disarticulated and mounted on SEM stub, ZMMU D-792, same sta. as holotype. Two paratypes, dried, ZMMU D-793, R/V “Akademik Kurchatov”, cruise 11, sta. 870, 29.11.1971, 55° 7' S 25° 2' W – 55° 8' S 25° 1' W, depth 4704–4680 m, Sigsbee trawl.





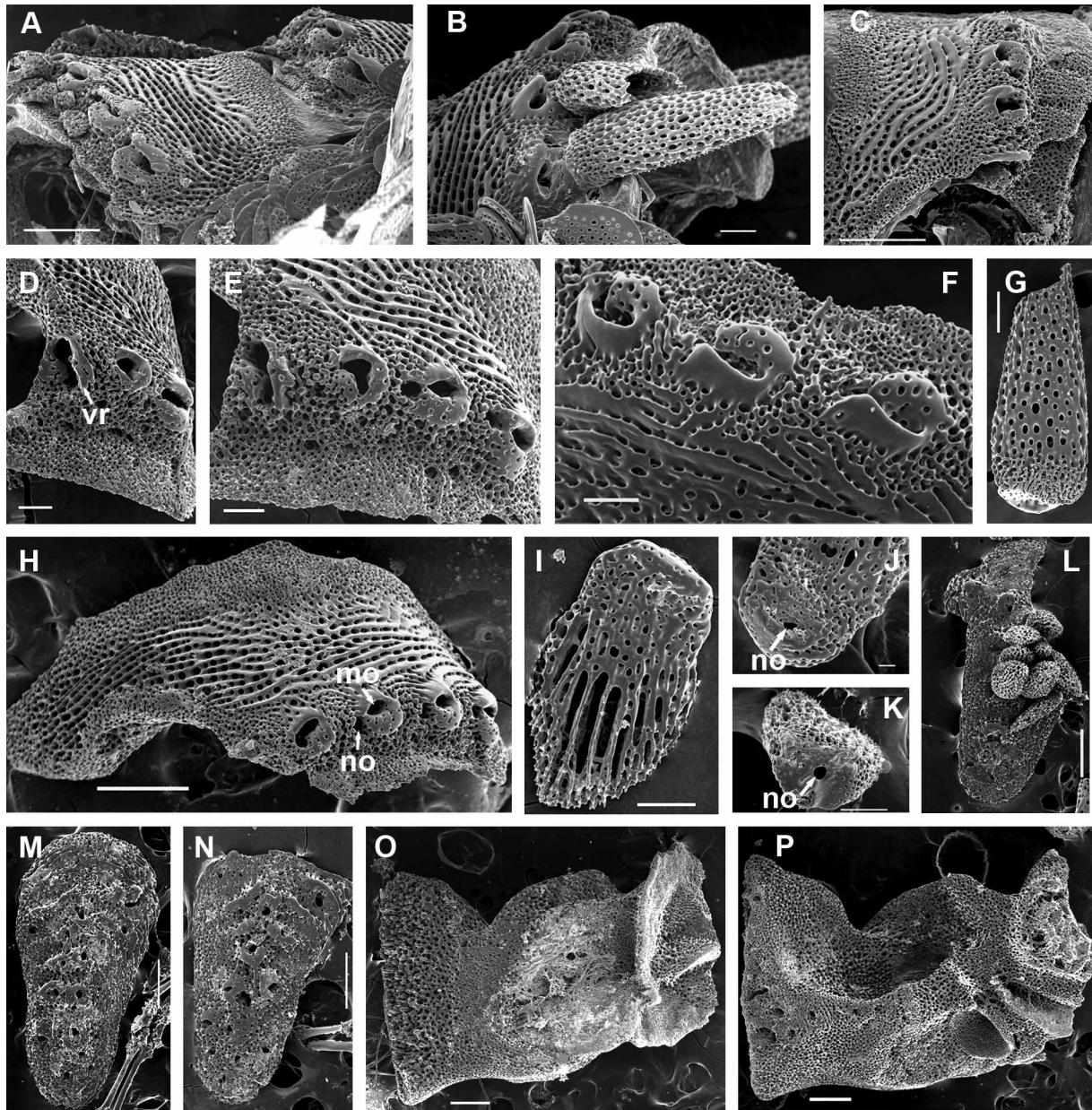
**FIGURE 54.** *Ophioplexa condita* gen. nov., sp. nov. and *Ophioscolex glacialis* Müller & Troschel, 1842, external views. A. *Ophioplexa condita* gen. nov., sp. nov., external view of the holotype ca. 18 mm dd, dorsal, ZMMU D-788, B. same ventral; C. a paratype 11.8 mm dd, dorsal view, ZMMU D-789; D. same, ventral view; E. holotype, ventral view of the arm; F. a paratype 8 mm dd, dorsal view, ZMMU D-793; G. same ventral; H. *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-118, ethanol specimen 34 mm dd; I. *Ophioscolex glacialis*, ZMMU D-866, dried specimen 22 mm dd, showing changing in the external appearance compare to living and ethanol specimens; J. same, oral frame. Photos: Tatiana Korshunova.





**FIGURE 55.** *Ophioplexa condita* gen. nov., sp. nov. and *Ophiocymbium ninae* sp. nov., details. A. *Ophioplexa condita* gen. nov., sp. nov., paratype 19 mm dd, ZMMU D-791, disk ventral view; B. same oral frame showing clusters of the ventral teeth (apical papillae); C. same, one interradius showing apical, oral and adoral shield papillae; D-F, same, most proximal arm segments showing tentacle scales and spines; G-H, arm spine articulations, distal segments; I. *Ophiocymbium ninae* sp. nov., paratype 5 mm dd, ZMMU D-803, details, part of the oral frame and ventral arm side; J. same, jaw and oral papillae, one interradius; K. ventral arm view showing spines and tentacle scales; L. most proximal segments showing details of tentacle scales and spines; M-N, arm spine articulations, proximal segments; Scale bars: A–B, 1 mm; C–D, 500  $\mu$ ; E–F, 200  $\mu$ ; G–H, 100  $\mu$ ; I, 1 mm; J–N, 300  $\mu$ . Photos: Alexander Martynov.





**FIGURE 56.** *Ophioplexa condita* gen. nov., sp. nov. Arm spine articulations, spines, tentacle scales, dental plates and jaws of a paratype of ca. 17 mm dd, ZMMU D-792. A. two proximal arm segments adjoining disk; B. same, showing hollow spines; C. ventral view of the articulations of the most proximal segments under the disk in situ including attaching area of the tentacle scales; D. separate lateral arm plate of the most proximal segments showing distinct shape of the ventralmost ridge; E. same, showing variability of following articulation; F. articulations of a middle segment; G. spine of a middle segment; H. separate lateral arm plate of the proximal segment showing more typical pattern of the articulation; I. a separate tentacle scale of the most proximal segment; J. same, basal part showing a small opening, presumably for nerve; K. basal part of a spine showing an opening for nerve; L. dental plate with several teeth; M, N, dental plates; O. jaw, abradial view; P. jaw, adradial view. Scale bars: A, 300 ; B, 100  $\mu$ ; C, 300  $\mu$ ; D, 100  $\mu$ ; E, 100  $\mu$ ; F,G, 100  $\mu$ ; H, 300  $\mu$ ; I,J, 100  $\mu$ ; K, 30  $\mu$ ; L–P, 300  $\mu$ . Photos: Alexander Martynov.

**Etymology.** from Latin *conditus*, hide, concealed, in reference to some morphological (small concealed radial shields and genital plates) and ecological (abyssal environment) features of the new species.

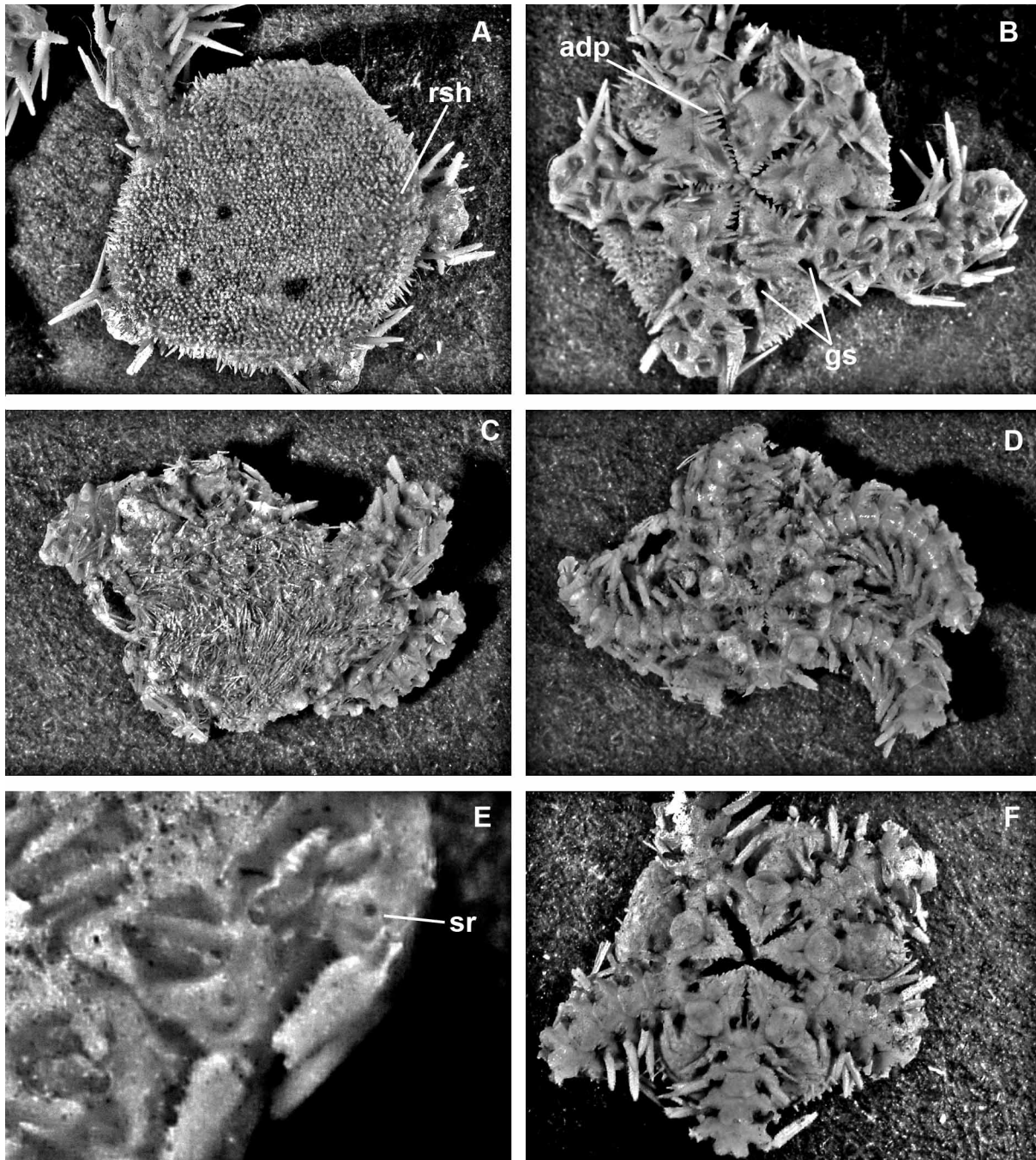
**Description of the holotype.** The disk is damaged, approximately 18 mm dd, presumably flattened when alive, round and not indented interradially. The disk plates are numerous, most of them elongated and narrow, irregular-rhomboidal and polygonal, entirely devoid of spines and granules. There is a thin skin layer, which is conspicuous in ethanol specimens, but almost undetectable when dried. Radial shields are very small and

entirely concealed under disc scales (see a detailed radial shield description under internal and other characters below). The interradii are slightly swollen, ventrally covered with numerous scales similar to the dorsal ones. Each jaw bears three to five irregularly placed, narrow, spiniform ventralmost teeth, which are not distinguished from more dorsally placed teeth, nor from adjacent lateral oral papillae. Distal oral papillae and adoral shield papillae are similar in size and shape, and placed along both edges of a jaw in a characteristic slightly curved row around the second tentacle pore, approximately 5–6 in number (including 2–3 adoral papillae in the strict sense). Thus there is a continuous series of papillae from the teeth to the adoral shield papillae. Deeper in the mouth opening on the jaws there is a distinct group of papillae, placed laterally to the other oral papillae, 2–4 in number. Numerous spiniform teeth are arranged in a dorsalwards tapering cone-shape on the dental plate. There are 17–20 teeth (including “apical papillae”). The oral shield is wide, triangular, with straight or slightly convex, distal edge, about as long as wide, completely separated from the first lateral arm plate by the adoral shields. Distally the oral shield is contiguous with a supplementary oral shield in form of a narrow elongated plate or just an elevation formed by adjacent interradii scales. The madreporite is similar in shape to the others, but slightly larger and has a swollen round area in the middle, conspicuously smaller than the entire shield. Adoral shields wing-like laterally, widely adjoining the arm, rapidly narrowing towards the jaws, thus retaining only a narrow bar between jaws and oral shield. True genital slits are small openings under the adoral shields, but long furrows between the proximalmost arm segments and the ventral disk interradius form false slits. Arm length is about 1.4 times the disk diameter.

The dorsal arm plates are well developed but thin, fan-shaped, moderate in size. Few proximal plates are wide, rapidly narrowing towards the middle of the arm, contiguous along most of the arm length. The proximal edge of the dorsal arm plate is almost straight throughout the length of the arm, but triangular on the basal segments. A few proximal dorsal plates have a pointed proximal angle, whereas the majority of them possess a short straight proximal edge. Two arms show irregular bands of numerous elongated scales intermingled with the lateral and dorsal plates. These proximal scales are similar to dorsal disk scales. The second dorsal arm plate near the disk is narrow, elongated transversally, bar-shaped or oval. On two arms the proximalmost dorsal plates are absent for 4–5 segments, whereas in one arm small scales almost entirely conceal the first two proximal segments. Arms are weakly noded and form a low lateral ridge on which the arm spine articulations are placed. There are two or four arm spines on the most proximal segments under the disk, six to seven rather adpressed spines on the free proximal and middle segments, and five distally. Dorsal and ventral spines are similar in size. Arm spines are flattened, pointed apically. The proximal edge of the ventral arm plate is straight, whereas the distal edge is convex with a small pit in the middle. Ventral plates throughout the length of the arm are contiguous. The tentacle pores are larger and more conspicuous proximally than towards the distal end of the arm. Basally on the part of the lateral plate that encircles the tentacle pores, three flattened, apically rounded tentacle scales are placed. The tentacle scales are shorter than the arm spines, but conspicuous and large enough to cover the whole tentacle pore. Many of the tentacle scales are broken or have fallen off. Towards the distal end of the arm the number of tentacle scales is reduced to two, and the inner scale is shorter than the outer one. The ventral arm plates do not bear any tentacle scales.

**Paratype variations.** A paratype, from sta. 870, 8 mm dd, differs from the holotype in having an almost undamaged irregularly-pentagonal disk, evenly covered with numerous, mostly elongated scales, which continue dorsally onto 1–2 proximal arm segments. Almost all dorsal arm plates, except for the 1–2 most proximal, have a pointed, narrowly triangular proximal edge, and are separated by lateral plates, to a small degree proximally, but up to half of the dorsal plate length distally. The pattern of the oral papillae is similar to the holotype, but the papillae are significantly fewer, and the curved row of oral papillae around the second tentacle pore is evident only in some interradii. Numerous spiniform teeth do not differ from the 3–4 apical papillae. Two, rarely three papillae on the adoral shield. Oral shields are more lengthened than in the holotype, and the madreporite is just an inconspicuous spot within the oral shield. Most of the oral shields have a remarkable feature of one or two rather conspicuous scales overlapping the shield distally, as a continuation of the supplementary oral shield – several scales adjacent distally to the oral shield. In other characters the paratype is similar to the holotype.





**FIGURE 57.** Genera *Ophioprium* and *Ophiopristis*, external views. A-B, *Ophioprium cervicornis* (Lyman, 1883), holotype MCZ 2043, 10 mm dd, dorsal and ventral views respectively; C-D, *Ophiopristis hirsuta* (Lyman, 1875), holotype MCZ 1950, 5.8 mm dd, dorsal and ventral views respectively; E, *Ophioprium cervicornis* (Lyman, 1883), holotype MCZ 2043, arm spine articulations, proximal segments; F, *Ophiopristis hirsuta* (Lyman, 1875), paratype MCZ 1951, 5 mm dd, ventral view. Photos: Alexander Martynov.

Another paratype, also from sta. 870, 5.5 mm dd, differs from the holotype and other paratype in size, an irregularly pentagonal disk, evenly covered with numerous polygonal and oval scales, which are continued dorsally on 2–3 proximal arm segments. The pattern of the oral papillae is also distinct from the holotype and from the paratype from the same station (870), but these differences clearly reflect the juvenile nature of the present specimen. The papillae are significantly smaller in number, and the curved row of oral papillae around the second tentacle pore is indistinct and can be traced only in two interradii. One or two distalmost oral papillae are block shaped. At least one papilla on the adoral shields is present in one interradius, whereas in

the other interradii it has most probably fallen off. Oral shields are more elongated in length than in the holotype, and the madreporite is just an inconspicuous spot within one oral shield. Most of the oral shields are overlapped by a conspicuous scale distally. On the most proximal lateral arm plates under the disk there are 2 spines, on the proximal lateral plates 4–5 spines, towards the middle 5–6. Spines are flattened, all similar in size. Tentacle scales are similar to the holotype, but many are broken or have fallen off. In the middle part of the arm the number of tentacle scales is reduced to two.

**Internal and microstructural characters.** Radial shield and genital plate articulate very tightly, unlike most extant ophiuroids, and have the appearance of an entire plate broken by a fissure (Figs 4J, K, P). The articulation surface of the radial shield is distinctly excavated ventrally, with a distal groove (Figs 4R, S). The articulation surface of the adradial genital plate lacks distinct condyles (Fig. 4Q). The abradial genital scale is absent. Jaws are slightly elongated (Figs 56O, P). Adradial sides of the jaws distally bear few sharp straight folds (Fig. 56P). The dental plate is large with rounded sockets and irregular folds (Figs 56M, N). Arm spine articulations compressed transversally (Figs 55G–H; 56A–H). Some proximal articulations may have a distinct nerve opening (Figs 56D–E). Few ventralmost articulations on the proximalmost segments have a distinctive slit-shaped appearance (Figs 56C–E). Vertebrae short, distinctly keeled and with well developed zygospondylous articulation (Figs 17L–O). Vertebral dorsal median groove almost indistinct (Fig. 17L). Podial basins are large (Fig. 17M).

### Genus *Ophiopristis* Verrill, 1899

Figures 57C–D, F; 58–60

*Ophiopristis* Verrill, 1899: 39, 40

Type species: *Ophiacantha hirsuta* Lyman, 1875, by original designation

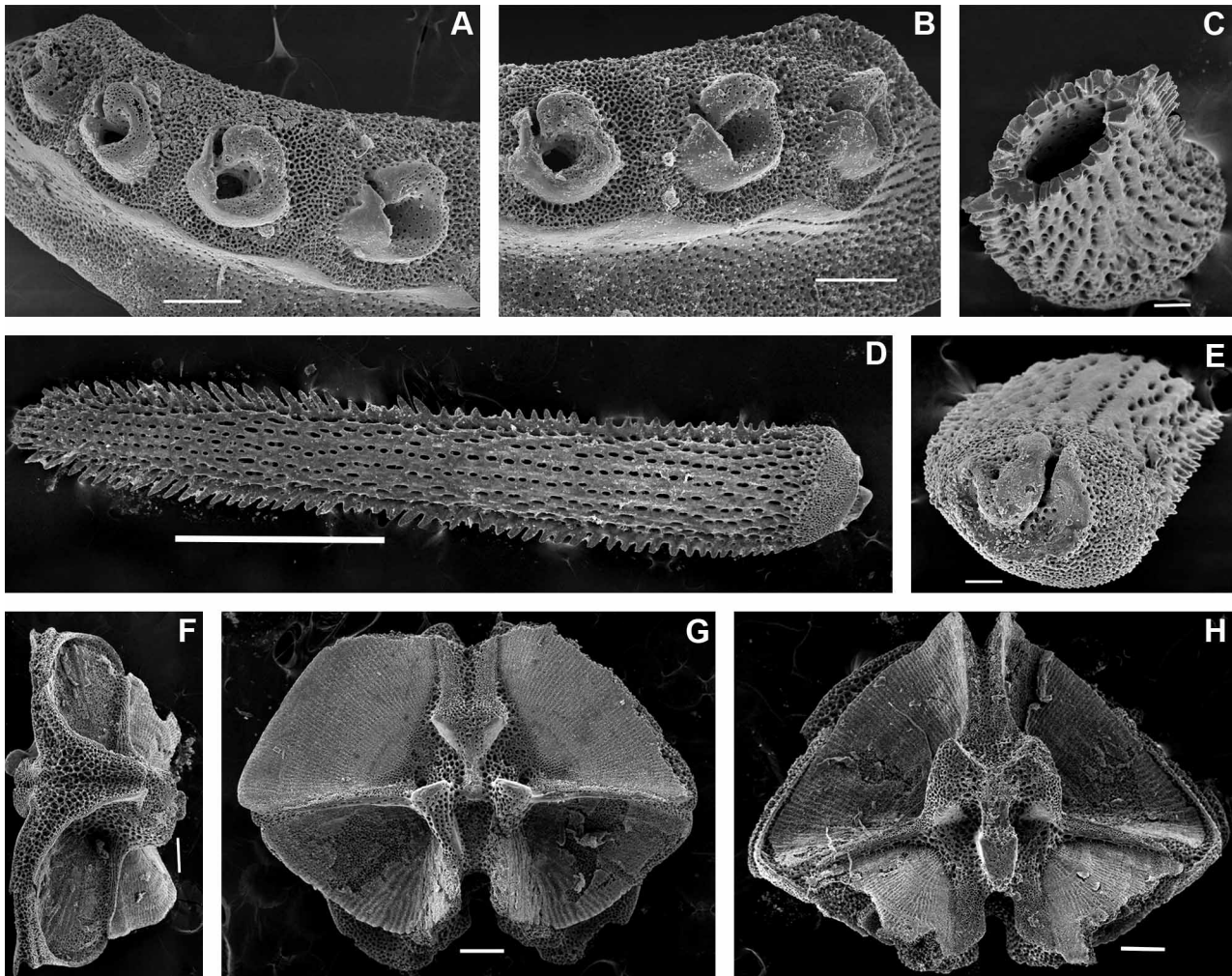
**Diagnosis.** The disk is covered with numerous small, uniform scales; a skin layer is not evident. The dorsal disk surface is covered with long, densely spaced spinelets. The radial shields are well-defined, elongated, but concealed under the disk plates. The adradial and abradial genital plates are well-defined. The genital slits are long and conspicuous, genital plates border approximately half of the slits. The articulation surface of the radial shield is a broad, low elevation. The jaw bears numerous short conical oral papillae similar in shape to the single (or double) apical papillae. The adoral shield papillae and adjacent oral papillae are slightly longer than other oral papillae. The half-jaws are relatively low. The adradial sides of the half-jaws distally bear a few convoluted folds. The dental plate is elongated without folds and with few elongate narrow slit-shaped sockets, alternately placed. The sockets for the apical papillae are similar in shape to all others. The teeth are broad, conical to rectangular. There are 1–2 ventralmost teeth. Generally all teeth are similar in shape, but the dorsalmost teeth are usually longer. The oral shield is broadly arrow-shaped with a short distal lobe. The adoral shields have distal wings, proximally tapered. Dorsal and ventral arm plates are well developed. The arm spine articulations are placed at a small angle in relation to the lateral plate. The muscle opening is larger than the nerve opening. There is a volute-shaped perforated lobe occupying the dorsal and distal part of the articulation. The sigmoidal fold is well-defined. The proximal edge of the spine articulation is entire but connected with the main part of the lateral arm plate by a short ridge. The arm spines are relatively long, rounded, hollow over almost their entire length, not hooked distally. Tentacle scales are well-defined, oval or lanceolate, single or double. The tentacle pores of moderate size. The vertebrae have a narrow keel that is distally abruptly truncated; the dorsal medial furrow is moderately expressed. The articulation is zygospondylous. Podial basins are moderate in size.

**Material studied.** *Ophiopristis hirsuta* (Lyman, 1875), Holotype MCZ 1950 (Figs 57C–D, F); USNM 6429, 1 specimen (Fig. 58); *Ophiopristis luctosa* (Koehler, 1904), MNHN EcOs 22978–22979, 2 specimens (Fig. 59); *Ophiopristis procera* (Koehler, 1904), Syntype EcOs 20406 (Fig. 60); *Ophiopristis dissidens* (Koehler, 1905), MNHN EcOs 22478, 4 specimens.

**Remarks.** O'Hara & Stöhr (2006) recently reviewed the genus *Ophiopristis* and further delineated it from other ophiacanthid genera, initially suggested by Paterson (1985). Among the species included into this genus,



a small Australian species *O. axiologus* differs considerably from all previously known species by bottle-shaped arm spines, disk covered with short stellate stumps instead of relatively long spinelets and possibly represents another genus (O'Hara & Stöhr 2006). *Ophiopristis axiologus* is therefore not included in the key below.



**FIGURE 58.** *Ophiopristis hirsuta* (Lyman, 1875), USNM 6429, 10 mm dd, details. A. arm spine articulations, proximal segments; B. same, details; C. hollow spine transversally sectioned; D. spine; E. same, ventral view; F. proximal vertebra, dorsal view; G. same, proximal view; H. same, distal view. Scale bars: A–B, F–H, 300  $\mu$ ; C, E, 100  $\mu$ ; D, 1 mm. Photos: Alexander Martynov.

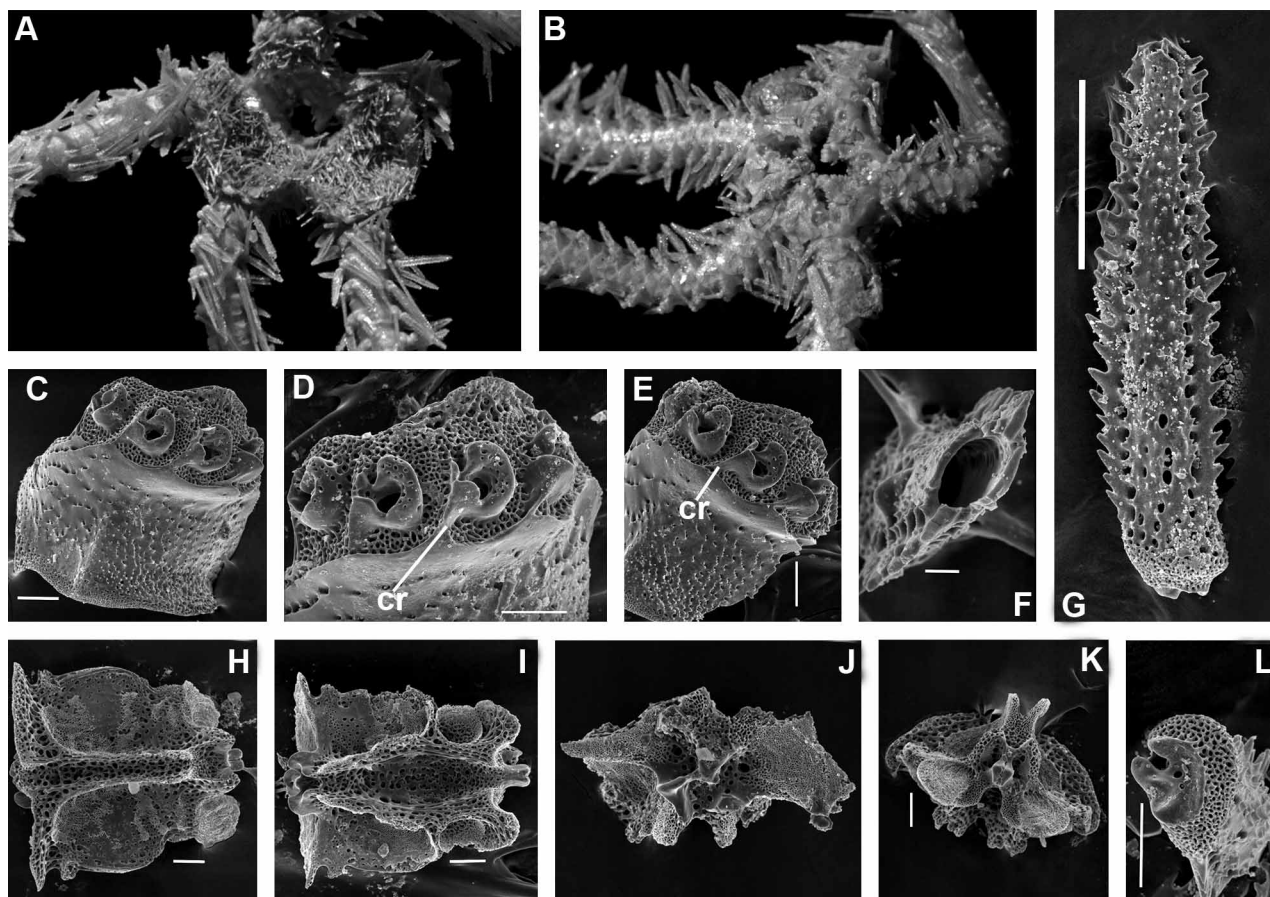
There are a number of species of the genus *Ophiacantha*, which possess characters similar to *Ophiopristis*, including long numerous spinelets and the pattern of the oral papillae, for instance *O. hylacantha* H.L. Clark, 1911 or *O. atopostoma* H.L. Clark, 1911. H.L. Clark (1915), while creating *Ophioprium* and delineating it from Verrill's *Ophiopristis*, noted that the former differs considerably from other ophiacanthids, whereas *Ophiopristis* should be considered as a synonym of *Ophiacantha*. The situation needs further study, involving delineation of the more than 130 currently known *Ophiacantha* species from some other ophiacanthid genera.

**Number of species: 8.**

#### Key to species of the genus *Ophiopristis* Verrill, 1899

- 1(12) Disk covered with spinelets
- 2(5) 2–3 tentacle scales on all arm segments

- 3(4) Ventral arm plate triangular with convex distal edge.....*O. hirsuta* (Lyman, 1875), Caribbean, at 182–436 m  
 4(3) Ventral arm plates rectangular with almost straight distal edge .....  
 ..... *O. dissidens* (Koehler, 1905), Indo-West Pacific, at 11–250 m  
 5(2) One tentacle scale (except proximalmost segments, where sometimes 2)  
 6(9) Tentacle scales oval; oral shields covered distally with spinelets  
 7(8) Arm spines slightly serrated .....*O. luctosa* (Koehler, 1904), Indo-West Pacific, at 216–460 m  
 8(7) Arm spines distinctly serrated.....*O. procera* (Koehler, 1904), Indo-West Pacific, at 595 m  
 9(6) Tentacle scales lanceolate; oral shields naked distally  
 10(11) Arm spines distinctly thorny..... *O. mitsuii* (Murakami, 1942), off Japan  
 11(10) Arm spines finer.....*O. vestita* (Koehler, 1898), Indo-West Pacific, at 354–382 m  
 12(1) Disk covered with spinelets and granules  
 13(14) Disk spinelets very short; 5 arm spines .....*O. ensifera* Verrill, 1899, Caribbean, at 200–477 m  
 14(13) Disk spinelets relatively long; 7 arm spines..... *O. sertata* (Lyman, 1869), Caribbean, at 365–615 m



**FIGURE 59.** *Ophiopristis luctosa* (Koehler, 1904), MNHN EcOs 22978, 4.5 mm dd, external view and details. A. dorsal view; B. ventral view; C. lateral arm plate and spine articulations, proximal segments; D–E, arm spine articulations, details; F. hollow spine transversally sectioned; G. spine, proximal segments; H. proximal vertebra, dorsal view; I. same, ventral view; J. same, proximal view; K. same, distal view; L. spine, ventral view. Scale bars: C–E, H–K, 100  $\mu$ ; F, 30  $\mu$ ; L, 300  $\mu$ . A–B Tatiana Korshunova; C–M Alexander Martynov.

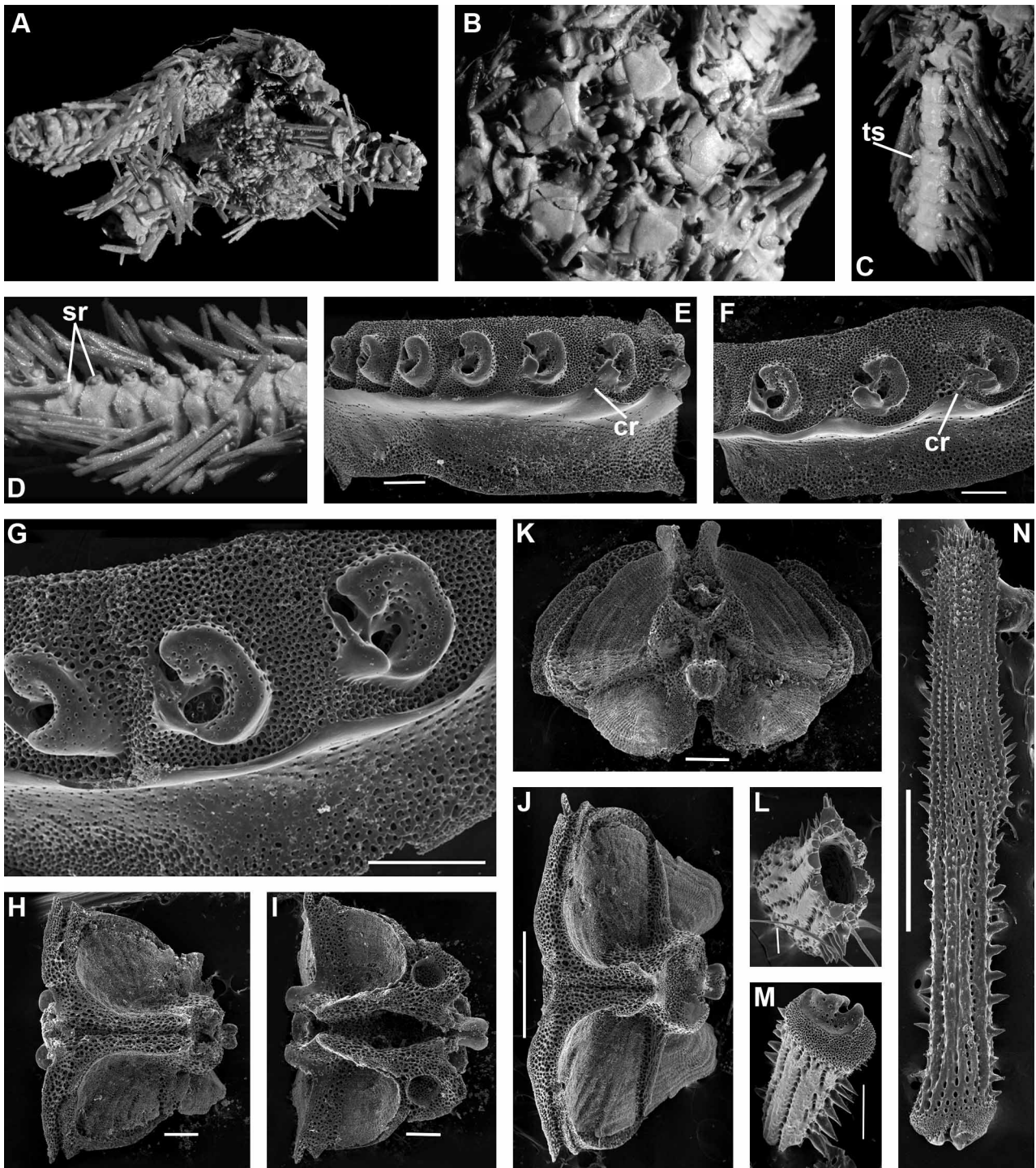
### Genus *Ophioprium* H.L. Clark, 1915

Figures 57A, B; 61–62

*Ophioprium* H.L. Clark, 1915: 214–215

Type species: *Ophiacantha cervicornis* Lyman, 1883, by original designation

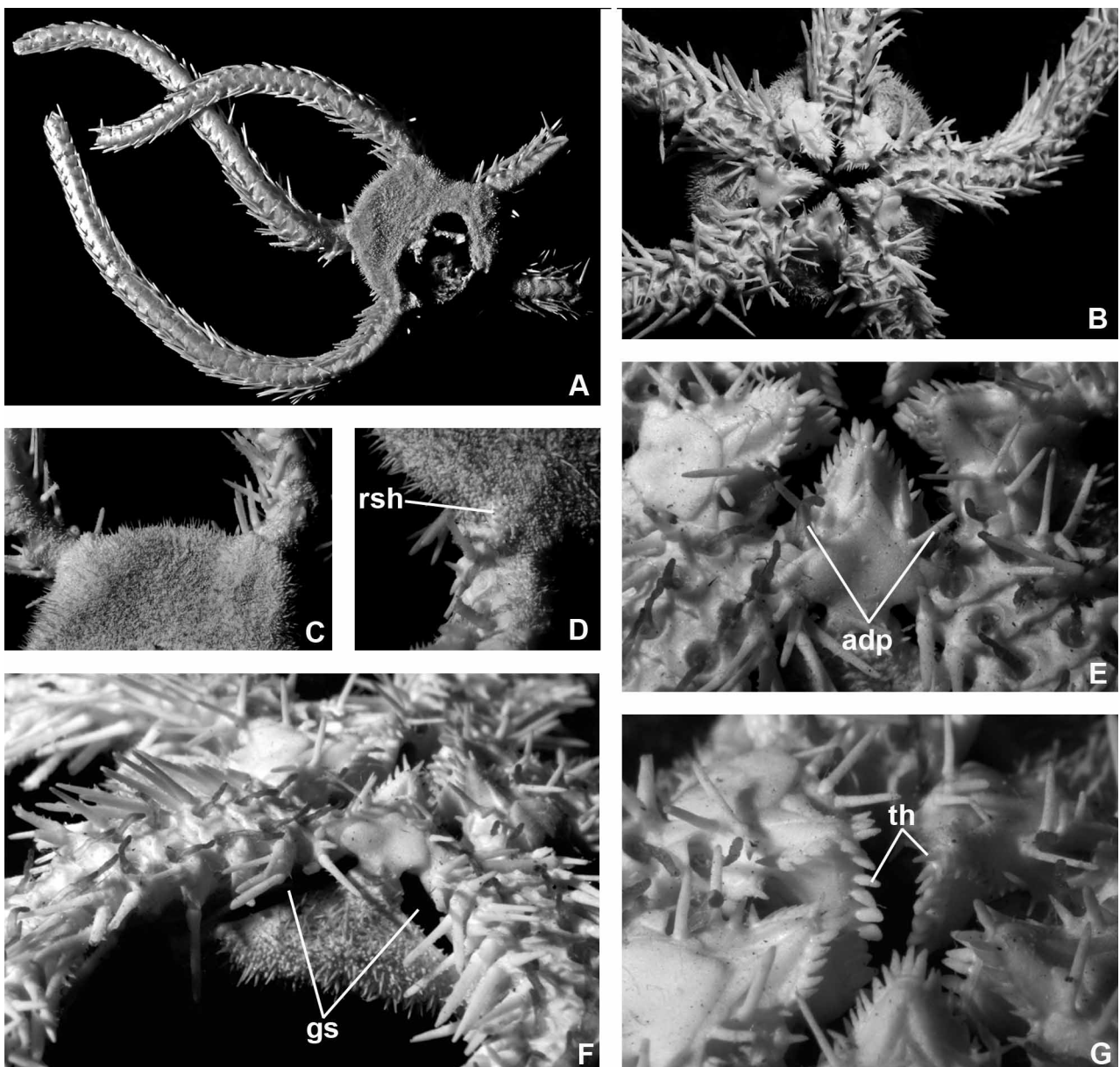




**FIGURE 60.** *Ophiopristis procera* (Koehler, 1904), syntype MNHN EcOs 20406, 12 mm dd, external view and details. A. dorsal view; B. ventral view; C. proximal arm segments, ventral view showing oval tentacle scales; D. same, dorsal view, showing arm spine articulations and spines; E–F, lateral arm plate and spine articulations, proximal segments; G. same, details; H. distal vertebra, dorsal view; I. same, ventral view; J. proximal vertebra, dorsal view; K. same, distal view; L. hollow proximal spine transversally sectioned; M. proximal spine, ventral view; N. proximal spine. Scale bars: E–I, 100  $\mu$ ; J, N, 1 mm; K, M 300  $\mu$ ; L, 100  $\mu$ . A–C Tatiana Korshunova; D–N Alexander Martynov.

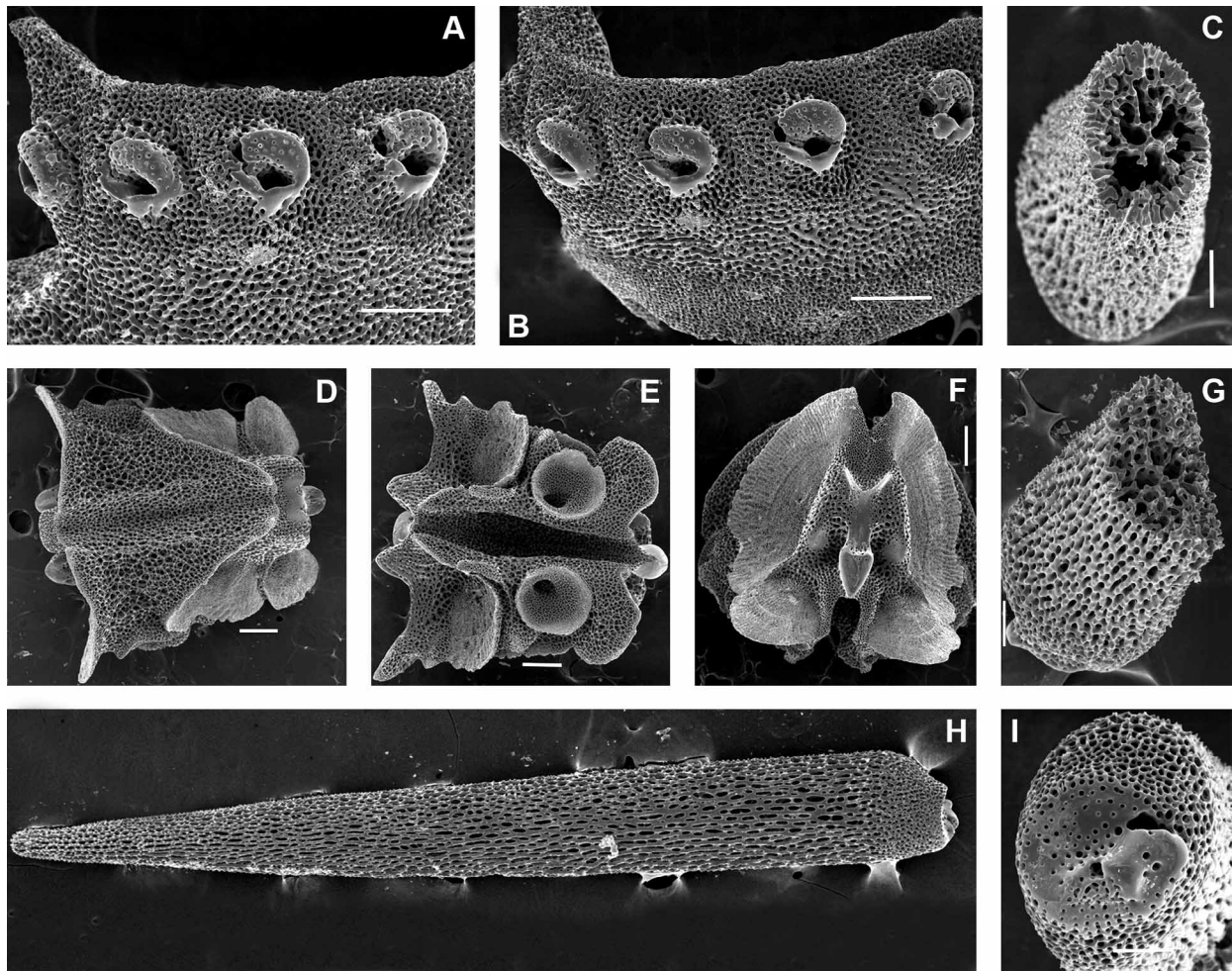
**Diagnosis.** The disk is covered with numerous small, uniform scales and a thin skin layer. The radial shields are small, rounded, hardly conspicuous in dried specimens. The adradial and abradial genital plates are well defined. Details of the articulations of genital plates and radial shields are unknown. The genital slits are long and conspicuous, genital plates border more than half of the slits. The jaw bears numerous spiniform oral

papillae, similar in shape to the small cluster of ventralmost teeth. Two adoral shield papillae and one adjacent oral papilla of each jaw are narrow, spiniform, 3–4 times longer than the oral papillae, placed around the second tentacle pore. The half-jaws, judged from the length of the dental plate, are high. The dental plate is small and elongated, without folds and with few rounded sockets, alternately placed. The teeth are spiniform and few in number (besides the apical papillae there are 4–5 teeth). All teeth are similar in shape. The oral shield is lozenge-shaped with a distinct distal lobe. The adoral shields have distal bilobed wings, proximally tapered. Dorsal and ventral arm plates are well developed. The arm spine articulations are placed almost transversally in relation to the lateral plate. The muscle opening is larger than the nerve opening. A prominent distal perforated lobe occupies the distal part of the articulation. The sigmoidal fold is absent. The arm spines are long, flattened, solid over most of their length but contain some holes of various sizes, not hooked distally. The tentacles scales are thin, spiniform, placed on both lateral and ventral arm plates. The tentacles pores are large. The vertebrae have a rounded distal keel, with deep dorsal medial furrow. The articulation is zygospondylous. The podial basins are large.



**FIGURE 61.** *Ophioprium permixtum* (Koehler, 1914), USNM E 05300, 15 mm dd, external views. A. dorsal view; B. ventral view; C. dorsal disk, details; D. dorsal disk, details showing small radial shields; E. ventral view, details oral and adoral shield papillae; F. interradian view showing long wide genital slits; G. ventral view, showing details of the teeth. Photos: Tatiana Korshunova.





**FIGURE 62.** *Ophioprium permixtum* (Koehler, 1914), USNM E 05300, 15 mm dd, details. A–B, lateral plate and spine articulations, proximal segments; C, G, proximal spine, section showing small cavities; D, proximal vertebra, dorsal view; E, same, ventral view; F, same, distal view; H, proximal spine; I, proximal spine, ventral view. Scale bars: A–B, D–F, 300  $\mu$ ; C, G, K, 100  $\mu$ ; I, 1 mm. Photos: Alexander Martynov.

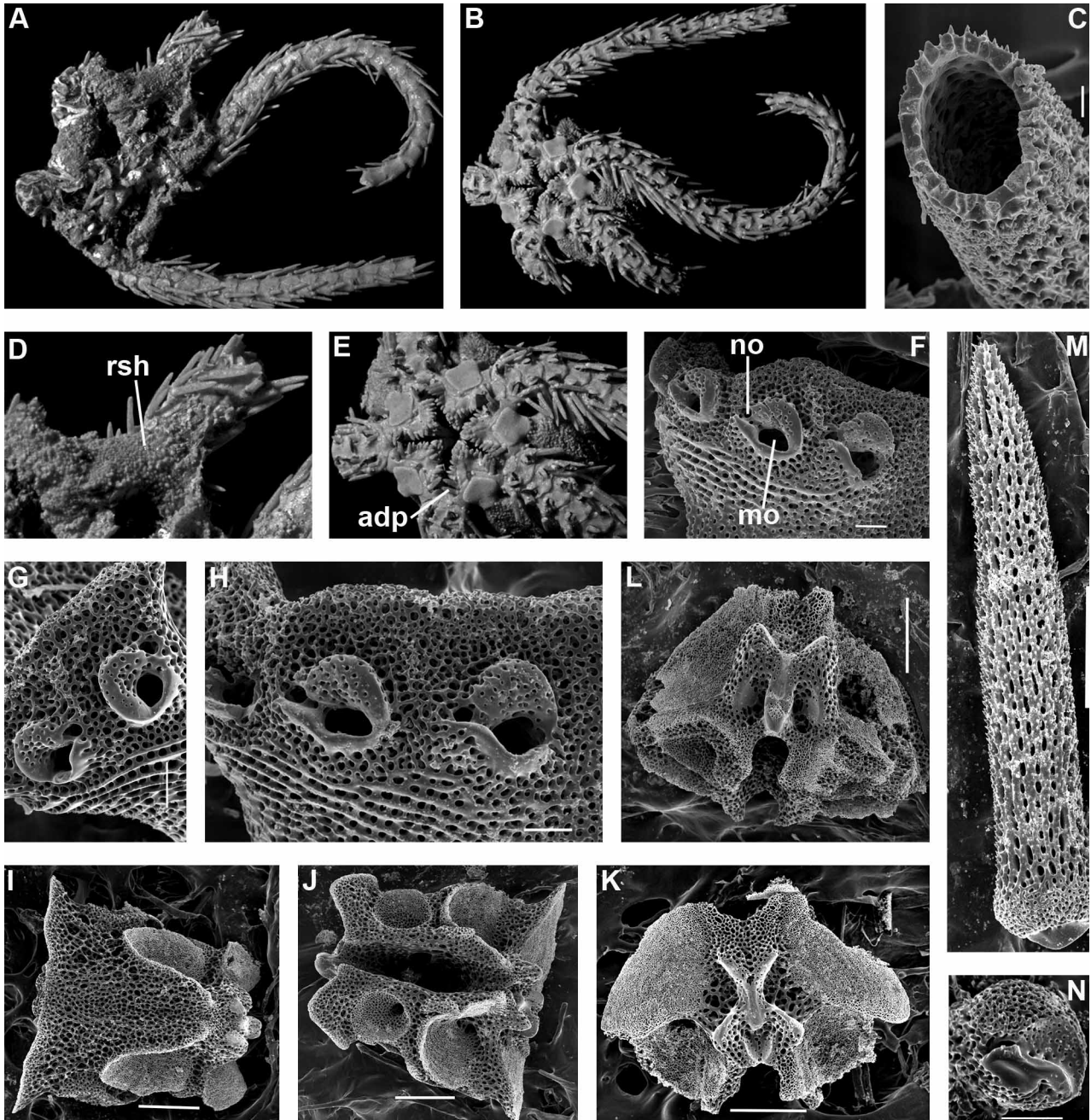
**Remarks.** Several different species have been included in the genus *Ophioprium* (H.L. Clark 1915; Baker 1979; Baker & Devaney 1981). Paterson (1985) excluded from this genus *Ophioprium larissae* Baker, 1979, *O. kapalae* Baker, 1979, *O. axiologus* (H.L. Clark, 1909) and *O. rosea* (Lyman, 1878) but retained *O. imperfectum* H.L. Clark, 1915. Re-examination of the holotype of *O. imperfectum* (Figs 52F, H–J) during the present study reveals considerable differences from the type species of the genus *Ophioprium*. Thus, only two species remain within the genus. Both species are very similar and their taxonomy needs further study. Verrill's authorship of the genus *Ophioprium* was incorrectly listed by Paterson (1985).

**Material studied.** *Ophioprium cervicornis* (Lyman, 1883), Holotype MCZ 2043 (Figs 57A, B); *Ophioprium permixtum* (Koehler, 1914), Holotype USNM 032296; one specimen USNM E 05300 (Figs 61; 62).

#### Key to species of the genus *Ophioprium* H.L. Clark, 1915

- 1(2) Most proximal segments completely lack tentacle scales on the ventral plate; three adoral and adjacent oral papillae are markedly longer, approximately 3–4 times that of other oral papillae; distal oral shield lobe is well defined .....  
.....*O. permixtum* (Koehler, 1914), North Western Atlantic, off Florida, 615 m
- 2(1) Most proximal segments possess distinct tentacle scales on the ventral plate; three adoral and adjacent oral papillae are slightly longer, approximately 2 times than other oral papillae; the distal oral shield lobe is poorly defined .....  
.....*O. cervicornis* (Lyman, 1883), Caribbean, 378–1042 m





**FIGURE 63.** *Ophiorupta discrepans* (Koehler, 1922) *comb.nov.*, holotype USNM 41196, 5 mm dd, external view and details. A. dorsal view; B. ventral view; C. hollow proximal spine, sectioned transversally; D. disk details showing small radial shields, concealed by granules; E. ventral views, details of oral structures; F. spine articulations, proximal segments; G. same, details of ventralmost articulations; H. same, details of dorsalmost articulations; I. proximal vertebra, dorsal view; J. same, ventral view; K. same, proximal view; L. same, distal view; M, proximal spine; N, same, ventral view. Scale bars: C, 30  $\mu$ ; F–H, N, 100  $\mu$ ; I–L, 300  $\mu$ . Photos: A–B, D–E Tatiana Korshunova; C, F–N Alexander Martynov.

### *Ophiorupta* gen. nov.

Type species: *Ophiomedeia discrepans* Koehler, 1922

**Diagnosis.** The disk plates are concealed by numerous small granules. Radial shields are small and concealed under disc scales. Genital slits are long. Each jaw bears several spiniform apical papillae. The latter are clearly distinguished at least from the dorsally placed teeth, which are elongated and more massive. The adjacent 3–4



lateral oral papillae are similar to the ventralmost teeth (apical papillae) and together form a row of similar spiniform papillae. Between the lateral and adoral papillae there is a more or less clear gap, which is however in some interradii almost indistinguishable. The adoral papillae are 2–3 times larger than the 3–4 lateral papillae. The oral shield is wide, arrow-shaped with small narrow distal lobe. The dorsal arm plates are well developed. Arms have more or less conspicuous nodes and lateral arm plates have a low lateral ridge, on which the large spine articulations are placed. Spines are flattened, pointed apically. The first ventral arm plate is irregularly trapezoid. Succeeding ventral arm plates have a characteristic pole-axe shape throughout the entire arm length. The tentacle pores are larger and more conspicuous proximally than towards the distal end of the arm. Two first proximal segments bear three large elongated, flattened, slightly apically pointed tentacle scales, two on the lateral arm plates and one opposite to the others on the ventral plate. Further segments lack the third tentacle scale and bear only two scales on the lateral plates. The tentacle scales are shorter the arm spines but conspicuous and capable of covering the whole tentacle pore.

Jaws are slightly elongated. Dental plate is without folds, with few small rounded sockets in the ventral part and few elongated ones dorsally. Arm spine articulations are well developed and represent the double-opening type, but the second opening is not always distinct. The muscle opening is placed within the somewhat transversally compressed and elongated ridge, with a distinct distal lobe. The sigmoidal fold is absent. The nerve opening is placed laterally and distally from the muscle opening, but indistinct. Vertebrae are rather long, not keeled and with well developed zygospondylous articulation. Vertebral dorsal median groove is indistinct, but broad. Podial basins are large.

**Etymology.** *Ophio-* (after ophiuroid) and *ruptus* (Latin), break, in reference to the easily damaged disk.

**Remarks.** The “Vityaz” specimen of *Ophiorupta discrepans* **comb. nov.** was found 40 years later after Koehler’s work (1922a) near the type locality at similar depths and essentially agrees with the first description. In addition, the holotype of *Ophiomedea discrepans* Koehler, 1922 (USNM 41196) was examined, including SEM investigation of the arm spine articulations, spines and vertebrae (Fig. 63) and no reliable differences from the “Vityaz” specimen (Fig. 64) were found.

Koehler (1922a) considered *O. discrepans* within his genus *Ophiomedea* based on some similarities of the oral structures (long adoral shield papillae) and the presence of several tentacle scales both on lateral and ventral arm plates in both *O. discrepans* and the type species, *Ophiomedea duplicata* Koehler, 1906. However these features are not restricted only to the genus *Ophiomedea*; instead several different ophiomyxids and ophiacanthids possess these characters. The type species of the genus *Ophiomedea*, *O. duplicata* has a single massive, wide ventralmost tooth, thus differs significantly from *O. discrepans*, which possesses a cluster of narrow teeth instead of the apical papilla. In addition, the disk of *Ophiomedea* is covered by long spinelets, whereas in *Ophiorupta* **gen. nov.** there are small numerous granules. The taxonomic position of *O. duplicata* was unclear and it has never been recorded after the first description, which mentioned only the small, possibly juvenile specimen of 4 mm dd. In the present study the holotype of *Ophiomedea duplicata* (MNHN EcOs 20426) has been re-investigated (Fig. 50). The features mentioned above are confirmed. The rounded, regular disk without evident skin layer, covered with numerous long spines and massive teeth (both ventral and dorsal) are clearly different from “*Ophiomedea*” *discrepans*. In addition, arm spine articulations of the *Ophiomedea duplicata* holotype reveal the presence of a well-defined ophiacanthid volute, including the sigmoidal fold (Figs 50F–G). “*Ophiomedea*” *discrepans* in turn does not possess typical ophiacanthid volute-shaped articulation and the sigmoidal fold is definitely absent (Figs 63F, G–H; 64H–P). In this respect the current placement of “*Ophiomedea*” *discrepans* within the family Ophiacanthidae is questioned. Paterson (1985) indicated that juveniles of *Ophiotrema alberti* are quite similar to *Ophiomedea duplicata*. This did not exclude the possibility that *Ophiomedea duplicata* may be only a juvenile stage of a larger ophiacanthid species. The question whether *Ophiomedea duplicata* is a paedomorphic adult species or just an ontogenetic stage of an ophiacanthid taxon requires further investigation. However, it is possible to conclude that various features of *Ophiomedea*, including distinctly noded arms (Figs 50C, F, G) are not similar with the proximal and distal segments of any species of the genus *Ophiotoma* (Figs 66–70).

Apparently most closely related to *Ophiorupta* **gen. nov.** is the genus *Ophiophrura* H.L. Clark, 1911. Koehler (1922a) questioned the synonymy of the genera *Ophiomedea* and *Ophiophrura*, and O’Hara and

Stöhr (2006) used the binomen *Ophiomedeia liodisca* (H.L. Clark, 1911). *Ophiomedeia*, *Ophiophrura* and *Ophiorupta* **gen. nov.** share similar oral frames and the presence of several tentacles scales. However, these characters are typical for almost all taxa of the ophiacanthid subfamily Ophiotominae and also for some ophiomyxid taxa. The holotype of *Ophiophrura liodisca* (USNM 25672) was examined, including SEM study of the arm spine articulations, spines and vertebrae (Fig. 51). There are several characters that distinguish the genera *Ophiophrura* and *Ophiorupta* **gen. nov.**: reasonable well-defined radial shields, massive dorsalmost teeth, a cluster of the spiniform teeth, arm spine articulations with large muscle opening and very distinct distal lobe (Fig. 63H) occur in *Ophiorupta*. *Ophiophrura* has subparallel arm spine articulations (Fig. 51H). In addition, dorsal disk is covered with a dense coat of granules in *Ophiorupta* **gen. nov.** (Figs 63–64A, B) and a thin but evident skin layer in *Ophiophrura* (Figs 51A–C).

The new genus clearly differs from the ophiacanthid genus *Ophiotoma*, in the general disk and oral frame appearance (compare Figs 63–64 and 66–70), shape of the arm spine articulations and dental plate. The genus *Ophiopristis* differs considerably from *Ophiorupta* **gen. nov.** in the general oral frame appearance, presence of the typical ophiacanthid massive teeth over most of the dental plate length, and typical ophiacanthid sigmoidal fold of the spine articulations (Figs 57–60). Various species of the genus *Ophiopristis*, including the type species, also have a peculiar appearance due to the presence of numerous densely placed long disk spinelets, thus clearly differing from *Ophiorupta* **gen. nov.** The genus *Ophioprium* is somewhat similar to *Ophiorupta* **gen. nov.** in having long spiniform adoral shield papillae. For comparison, the holotype of *Ophioprium cervicornis* (Lyman, 1883) from MCZ and an additional specimen of *Ophioprium permixtum* (Koehler, 1914) were studied, including SEM-preparation of lateral arm plates and vertebrae (Figs 61–62). *Ophiorupta* **gen. nov.** clearly differs from the genus *Ophioprium* in a number of important characters, including the presence of numerous ventralmost teeth covering about half of the dental plate. Although the oral papillae in *Ophioprium* are similar in shape and size to the apical papillae, they are distinguished from the latter, forming a distinct long regular row along the jaw. Unlike the genus *Ophioprium*, oral papillae of *Ophiorupta* **gen. nov.** are hardly distinct from the apical papillae. In addition, there is an indistinct gap between the apical and oral papillae and the adoral shield papillae of *Ophiorupta* **gen. nov.** Adoral shield papillae of the genus *Ophioprium* and *Ophiorupta* **gen. nov.** are markedly different – the former genus has long spiniform papillae, whereas the adoral papillae of *Ophiorupta* **gen. nov.** are considerably flattened. Arm spine articulations of both *Ophiorupta* **gen. nov.** and *Ophioprium*, though, belong to the non-ophiacanthid type, lacking a sigmoidal fold (Figs 62A–B and 63F–G, H, 64H–P).

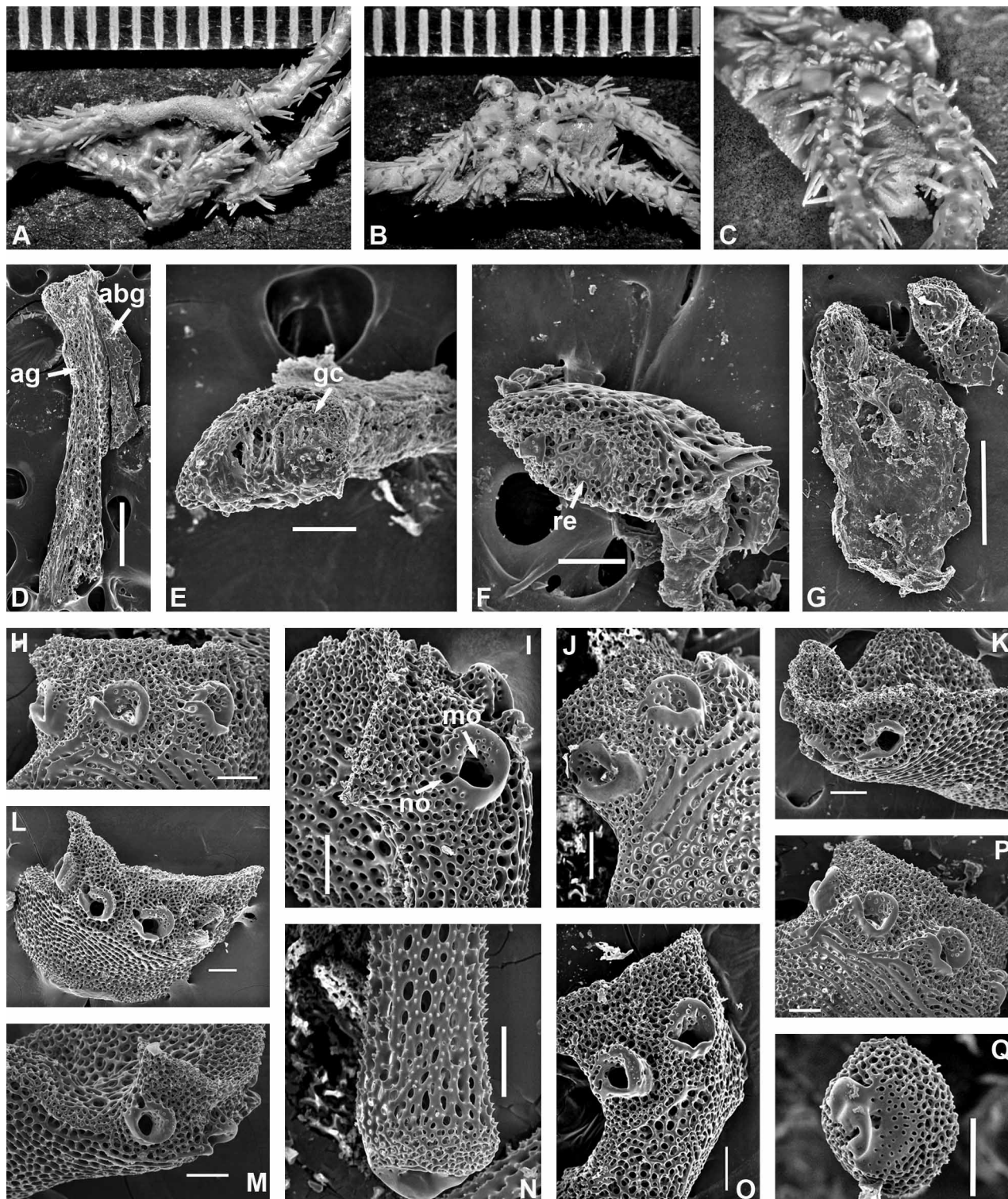
The dental plate morphology is of special interest, since it combines several small rounded openings (typical for the family Ophiomyxidae) with a few elongated sockets (characteristic for Ophiacanthidae) (Fig. 13A). Murakami (1963) studied the dental plate of *Ophiophrura liodisca* and found a few small, round sockets, arranged in a way that is considerably different from *Ophiorupta discrepans* **comb. nov.** – ventral teeth cluster and correspond to irregularly placed sockets, and dorsally there are a few slightly elongate imperforate sockets. The present study of the holotype of *Ophiophrura liodisca* confirmed the presence of a short dental plate covered with a few alternately placed spiniform teeth (Fig. 51E). The number of parallel cases and exceptions from different ophiuroid families (see below for discussion) does not allow using the dental plate shape alone for taxonomic placement.

Finally, an ophiacanthid species reported by Paterson (1985) from the North Atlantic under the name *Ophiotrema* *cf. tertium* clearly does not belong to that genus (O'Hara & Stöhr 2006). The general disk appearance, numerous apical papillae, scarcely distinguished from the oral papillae, and an indistinct gap between adoral and other papillae suggest that it may belong to *Ophiorupta* **gen. nov.** Moreover, “*Ophiotrema cf. tertium*” inhabits similar depths (ca. 5000 m) as *Ophiorupta* **gen. nov.** Thus, although *Ophiorupta discrepans* (Koehler, 1922) **comb. nov.** is known only from two specimens, it represents an important case of possibly transitional morphology between the families Ophiomyxidae and Ophiacanthidae. The relationships of these two large ophiuroid families will be discussed below.



*Ophiorupta discrepans* (Koehler, 1922) comb. nov.

Figures 13A–B; 18E–H; 63; 64

*Ophiomedeia discrepans* Koehler, 1922a: 95–98, plate 26, figs 1–4

**FIGURE 64.** *Ophiorupta discrepans* (Koehler, 1922) comb. nov., ZMMU D-806, ca. 7 mm dd, external views and details; A–C, external views; D, articulating adradial and abradial genital plates, dorsal view; E, articulation surface of the adradial genital plate, dorsal view; F, articulation surface of the radial shield, distal view; G, radial shield, ventral view; H, J, P proximal segments; I, L, O, most proximal segments; K, M, distal segments; N, spine, proximal segments, lateral view; Q, same, ventral view; Scale bars: D, 300  $\mu$ ; E, 100  $\mu$ ; F, 100  $\mu$ ; G, 300  $\mu$ ; H–Q, 100  $\mu$ . Photos: A–C Tatiana Korshunova; D–Q Alexander Martynov.

**Material.** Holotype USNM 41196, dried, R/V “Albatros”, sta. 5359, depth 4160 m; ZMMU D-806, R/V “Vityaz”, sta. 5028, 7° 43,3' N 120° 20,1' E, depth 4110–4111 m.

**Description of the specimen from sta. 5028.** The disk is damaged and ca. 7 mm in dd, not indented interradially. The disk plates are almost entirely concealed by numerous small granules. Radial shields are small and concealed under disc scales. The interradii are slightly swollen, ventrally covered with numerous small granules. Areas adjacent to the genital slits are almost entirely devoid of granules. Genital slits are long, proximally bordered by a well-defined abradial genital plate. Each jaw bears five to seven irregularly placed narrow spiniform apical papillae. The latter are clearly distinguished at least from the dorsally placed teeth, which are elongated and more massive. The adjacent 3–4 lateral oral papillae are similar to the ventralmost teeth (apical papillae) and together form a row of similar spiniform papillae. Between the lateral and adoral papillae there is a more or less clear gap, which is however in some interradii almost indistinguishable. The adoral papillae are 2–3 times larger than the 3–4 lateral papillae. Two of the adoral shield papillae are properly placed on the adoral shield whereas 1–2, similar in shape to the adoral papillae, are placed on the jaw. The ventralmost teeth are numerous (ca. 12 in number) and distributed in a cone-shape tapering dorsalwards; the dorsal teeth instead are more massive, elongated and placed one by one. The oral shield is wide, arrow-shaped with small narrow distal lobe and large triangular proximal part, about as wide as long, completely separated from the first lateral arm plate by the adoral shields. The madreporic oral shield is slightly but evenly swollen, the distal lobe is not clearly separated from the rest of the shield and its general shape is a regular lozenge. The adoral shield is narrow wing-shaped laterally, widely adjoining the arm, slightly narrowing towards the mid-line of the jaws, thus retaining only a narrow bar between jaws and oral shield.

The arm length is about two times the disk diameter. The dorsal arm plates are well developed but thin, triangular, relatively small, rather narrow even on the proximal segments, gradually narrowing further toward the distal part of the arm, slightly separated on few proximal segments and widely (up to 2/3 of the dorsal arm plate length) distally. The distal edge of the dorsal arm plate is slightly convex throughout the length of the arm. About two proximal arm segments lack the normal dorsal arm plates and bear instead few small rounded scales, which are dorsal disk scales including granulation. Arms have more or less conspicuous nodes and lateral arm plates have a low lateral ridge, on which the large spine articulations are placed. There are two spines on the first segment, three on the other segments under the disk, three to four moderately erect spines on the free proximal and middle segments, and three distally. The dorsalmost spines on the proximal segments are the longest, up to length of two segments. Spines are flattened, pointed apically.

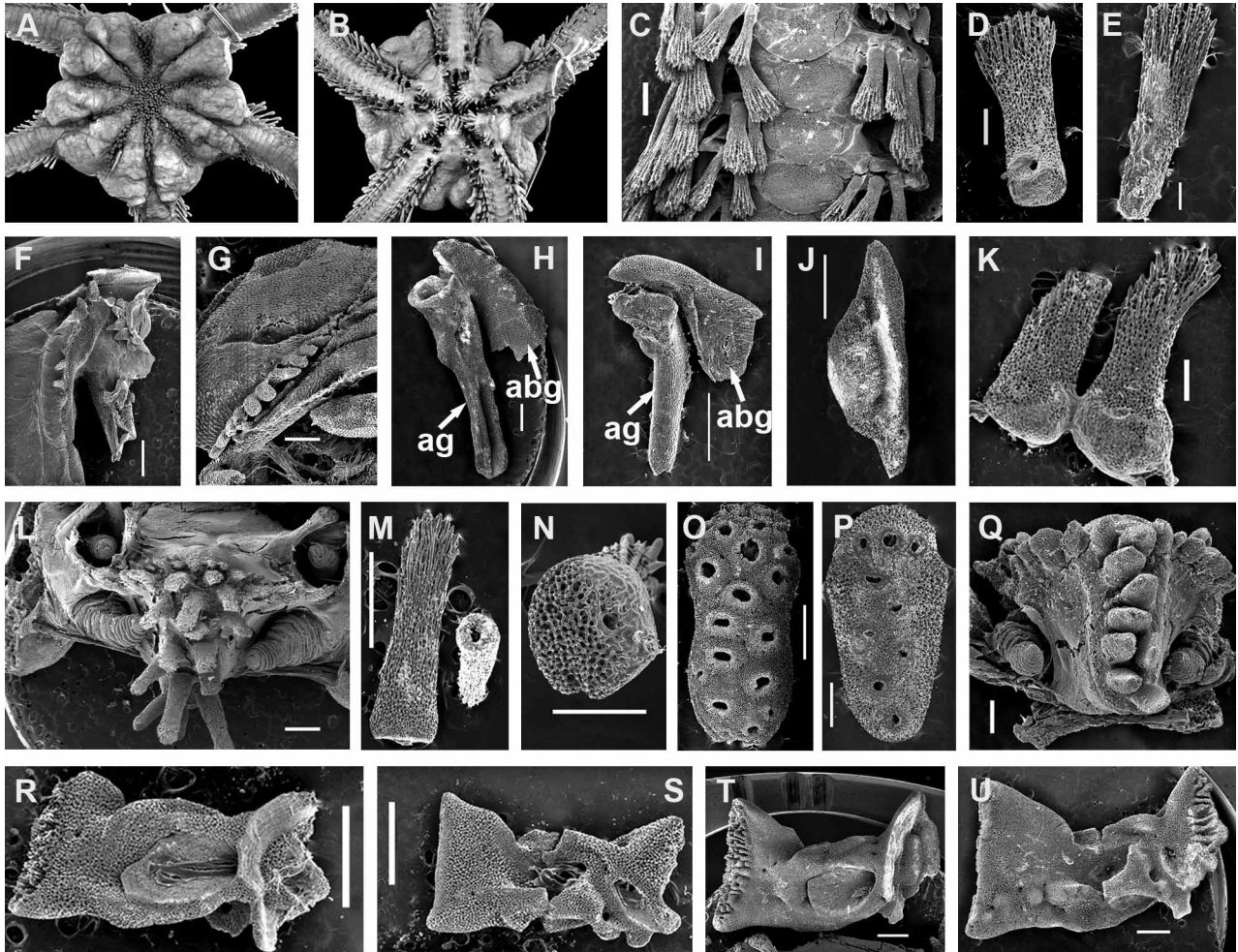
The first ventral arm plate is irregularly trapezoid. Succeeding ventral arm plates have a characteristic pole-axe shape throughout the entire arm length. The proximal edge of the ventral arm plate is slightly concave or straight on the first 2–4 proximal segments, whereas the distal edge is convex. On distal segments the proximal edge of the ventral arm plate is triangular. Ventral plates are contiguous on the first 4–5 segments and separated on further segments for up to half of their length. The tentacle pores are larger and more conspicuous proximally than towards the distal end of the arm. Two first proximal segments bear three large elongated, flattened, slightly apically pointed tentacle scales, two on the lateral arm plates and one opposite to the others on the ventral plate. Further segments lack the third tentacle scale and bear only two scales on the lateral plates. The tentacle scales are shorter the arm spines but conspicuous and capable of covering the whole tentacle pore. Distally there are also two scales, but considerably reduced in size.

**Internal and microstructural characters.** The study was limited, because only a single specimen was available. Jaws are slightly elongated. Dental plate is without folds, with few small rounded sockets in the ventral part and few elongated ones dorsally (Fig. 13A). Arm spine articulations are well developed and represent the double-opening type, but the second opening is not always distinct (Figs 63F–G, H; 64H–P). The muscle opening is placed within the somewhat transversally compressed and elongated ridge, with a distinct distal lobe. The sigmoidal fold is absent. The nerve opening is placed laterally and distally from the muscle opening, but indistinct. Vertebrae are rather long, not keeled and with well developed zygospondylous articulation (Figs 18E, H). Vertebral dorsal median groove is indistinct, but broad (Fig. 18E). Podial basins are large (Fig. 18F).



Genus *Ophiosparte* Koehler, 1922

## Figure 65

*Ophiosparte* Koehler, 1922b: 21Type and single species: *Ophiosparte gigas* Koehler, 1922, by monotypy

**FIGURE 65.** *Ophiosparte gigas* Koehler, 1922 and *Ophiura sarsii* Lütken, 1855, details. A–B, *Ophiosparte gigas* Koehler, 1922, MCZ 6805, 57 mm dd, external views, dorsal and ventral sides respectively; C. *Ophiosparte gigas*, ZIN 25/21449, 42 mm dd, proximal segments showing tentacle scales and spines; D. same, tentacle scale of the second tentacle pore, lateral view, showing conspicuous nerve opening; E. same, tentacle scale of the proximal segments; F. same, arm comb papillae; G. *Ophiura sarsii*, ZMMU D-865, 14 mm dd, arm comb papillae; H. *Ophiosparte gigas*, ZIN 25/21449, articulating adradial and abradial genital plates, dorsal view; I. *Ophiura sarsii*, ZMMU D-865, articulating adradial and abradial genital plates, dorsal view; J. *Ophiosparte gigas*, ZIN 25/21449, articulation surface of the radial shield, distal view; K. same, ventral teeth, lateral view; L. same, inside mouth view of one interradius; M. same, dorsal teeth, lateral and ventral views respectively; N. same, ventral tooth, ventral view; O. same, dental plate; P. *Ophiura sarsii*, ZMMU D-865, dental plate; Q. same, inside mouth view of one interradius; R. same, jaw, abradial view; S. same, adradial view; T. *Ophiosparte gigas*, ZIN 25/21449, jaw, abradial view; U. same, jaw, adradial view; Scale bars: A–B, 300  $\mu$ ; C, 1 mm; D–E, 300  $\mu$ ; F, 1 mm; G, 300  $\mu$ ; H–J, 1 mm; K–M, 1 mm; N, 300  $\mu$ ; O, 1 mm; P, 300  $\mu$ ; Q, 300  $\mu$ ; R–U, 1 mm. Photos: Alexander Martynov.

**Diagnosis.** The disk scales are obscured by a strong skin layer. The radial shields are large, largely concealed by skin. The genital plates are well developed. The strong adradial genital plate is almost straight and has a well-defined articulation surface with a short lateral ridge. The abradial genital plate articulates with the adradial genital plate at the level of the articulation surface and is broad, flattened. The genital slits are long and genital plates line almost the entire length of the slits. There are arm comb papillae on the genital plates. The jaw bears numerous spiniform oral papillae similar in shape to the large cluster of the ventralmost teeth.

Oral papillae, teeth and spines have a specific shape, widened apically. Three pairs of the adoral shield and adjacent oral papillae are placed around the tentacle scale, similar in shape to the teeth and lateral arm spines. The teeth are spiniform. All teeth are of similar shape. The dental plate possesses numerous irregularly placed rounded sockets, with several strong folds in-between. The oral shield is strongly convex distally, sometimes with a weak lobe, and slightly triangular proximally. The adoral shields are obscured by skin, both ends are of similar size. The dorsal and ventral arm plates are well developed. The dorsal arm plates are oval, with straight edges both distally and proximally, contiguous, unfragmented even proximally. The arm spine articulations possess a large rounded muscle opening bordered by a low elevation, and, at considerable distance from it, a small nerve opening. Correspondingly, the basal part of the spine has a nerve opening not strictly ventrally, but laterally. The ventral arm plates are contiguous, with convex distal and straight proximal edge. The arm spines are long, solid, widened apically, not hooked distally. Several tentacle scales, similar in shape and size to the spines, are placed on the lateral arm plate. The vertebrae have a well-defined median keel and are blunt distally. The articulation is a special variant of the zygospondylous type, known as the “comb-shaped” type (see Litvinova, 1989a, b). The podial basins are moderate in size.

**Material studied.** MCZ 6805(27081), 1 specimen; ZIN 25/21449, 1 specimen (Fig. 65); MNHN, EcOs 10761, 1 specimen.

**Remarks.** *Ophiosparte gigas* is a well-known Antarctic taxon, inhabiting the shelf zone. However its exact systematic position is still unresolved. Until recently its initial taxonomic placement within the family Ophiacanthidae (Koehler 1922b) was challenged only in a single study (Dearborn *et al.* 1996), who suggested an ophiomyxid relationship. Paterson (1985) included *Ophiosparte* in the ophiacanthid subfamily Ophiotominae, and therefore it bears a special interest for the present study. The type material of *Ophiosparte gigas* is in the Australian Museum (Rowe, Pawson, 1977).

### Genus *Ophiotoma* Lyman, 1883

Figures 66–70

*Ophiotoma* Lyman, 1883: 268

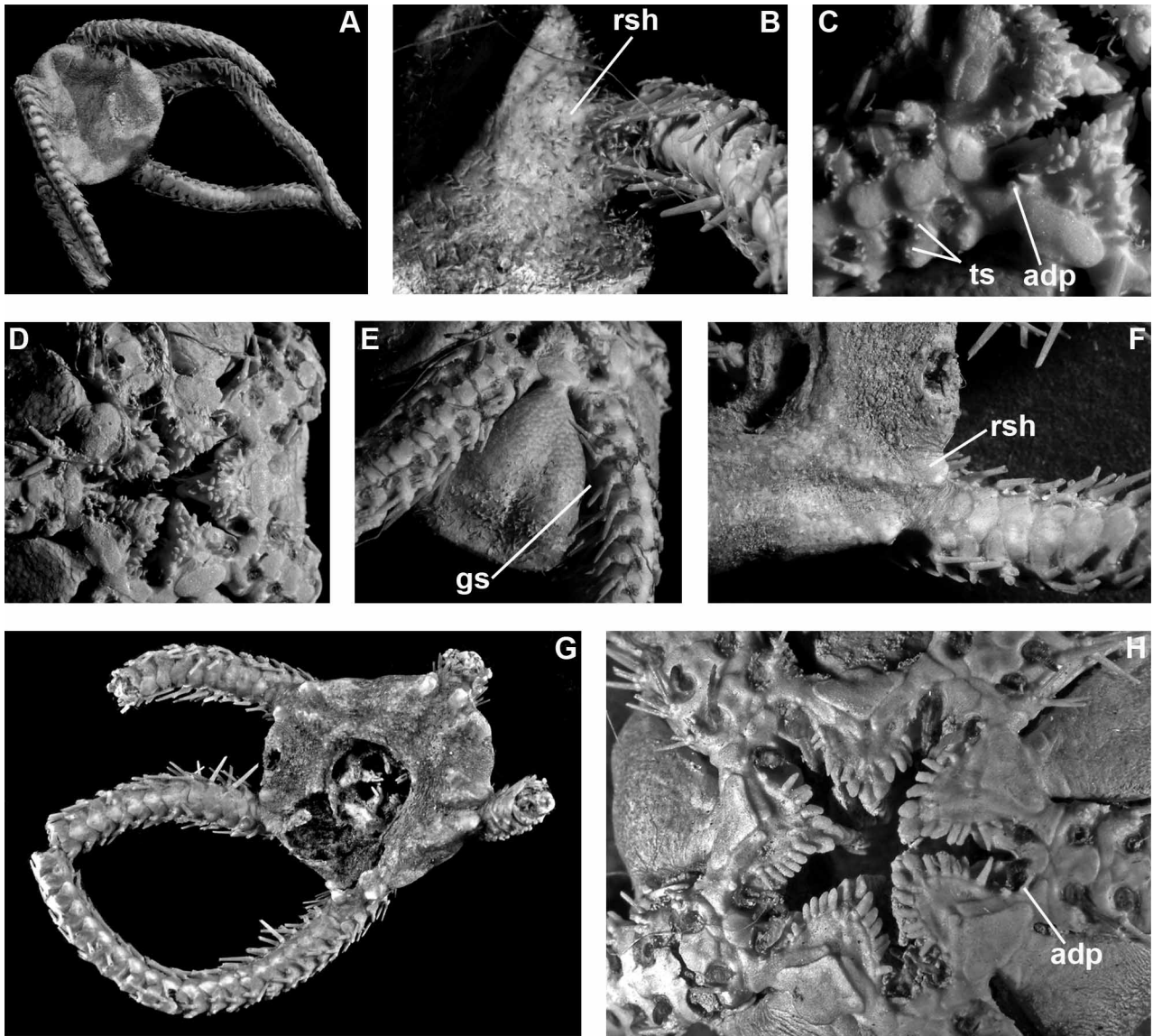
*Ophiotrema* Koehler, 1896b (type species *Ophiotrema alberti* Koehler, 1896): 251

*Ophiopora* Verrill, 1899 (type species *Ophiacantha bartletti* Lyman, 1883): 39, 43

Type species: *Ophiotoma coriacea* Lyman, 1883, by monotypy

**Diagnosis.** The disk is covered with numerous small, uniform scales, obscured by a moderately developed skin layer. The dorsal disk surface is usually covered with spinelets of various lengths, rarely naked. The radial shields are well-defined, elongated, but concealed under a thin skin layer. The adradial and abradial genital plates are well-defined. The genital slits are long and conspicuous, the genital plates border about half of the slits. The articulation surface of the radial shield is a broad, low elevation. The jaw bears numerous short conical oral papillae similar in shape to the single (or double) apical papillae. The adoral shield papillae and adjacent oral papillae are slightly longer than other oral papillae and not separated by a gap. The half-jaws are relatively high. The adradial sides of the jaws bear a few convoluted folds distally. The dental plate is elongated, without folds, and with a few elongate narrow slit-shaped sockets, placed alternately. The sockets for apical papillae are small and rounded. The teeth are broad, conical to rectangular. There are 1–2 ventralmost teeth. Generally all teeth are similar in shape, but the dorsalmost teeth are usually longer. The oral shield is broadly arrow-shaped with a short distal lobe. The adoral shields have distal wings, proximally tapered. Dorsal and ventral arm plates are well developed. The arm spine articulations are placed at a small angle in relation to the lateral plate. The muscle opening is larger than the nerve opening. There is a volute-shaped perforate lobe, occupying the dorsal and distal part of the articulation. The sigmoidal fold is well-defined. The proximal edge of the spine articulation is entire and does not connect with the main part of the lateral arm plate. The spines are relatively long, rounded, contain small lumens inside, not hooked distally. Several small thin tentacle scales are placed both on the lateral and ventral plates, or absent. The tentacle pores are large. The vertebrae have a narrow keel, abruptly truncated distally; a dorsal medial furrow moderately expressed. The articulation is zygospondylous. The podial basins are of a moderate size.



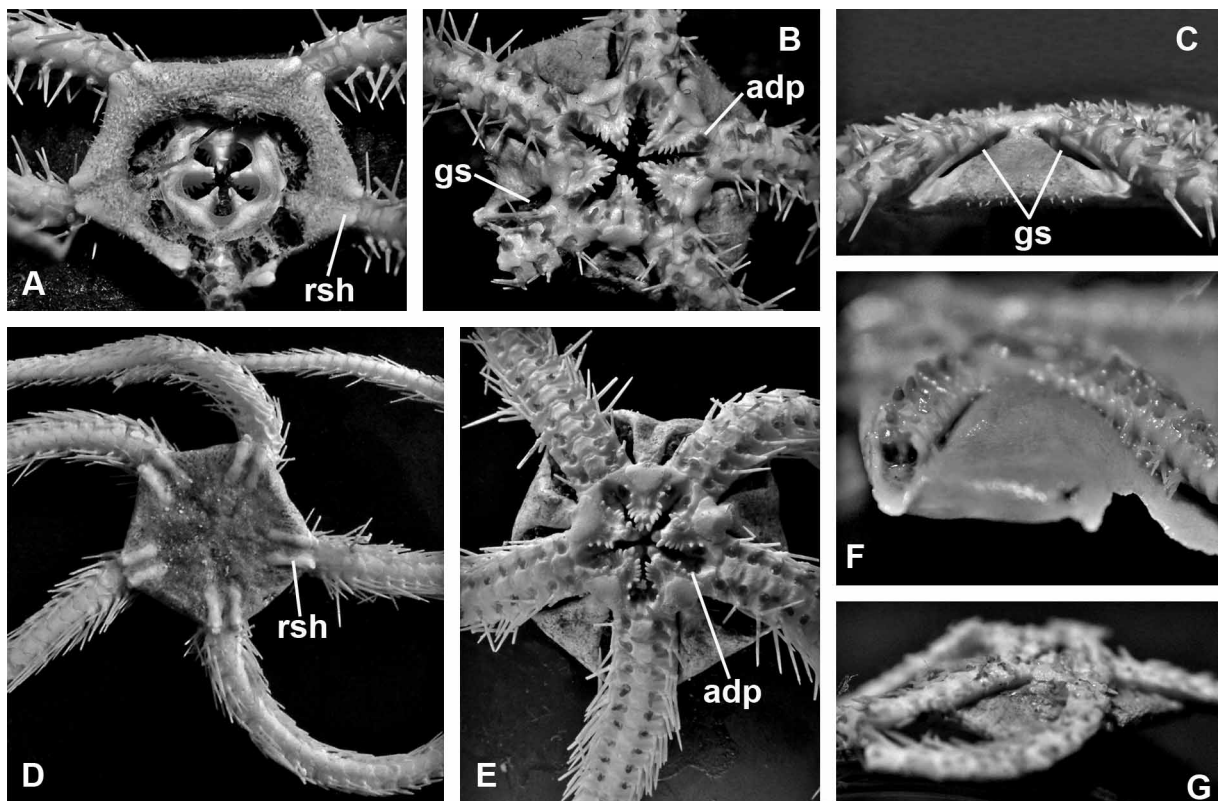


**FIGURE 66.** *Ophiotoma alberti* (Koehler, 1896), A–E, syntype MNHN EcOs 20383, 18 mm dd, external views. A. dorsal view; B. dorsal disk, details, showing moderately well-defined radial shields concealed by the skin; C. ventral view, details showing several small tentacle scales and oral papillae; D. ventral view; E. inerradial view, showing long genital slits; F–H, *Ophiotoma coriacea* Lyman, 1883, holotype MCZ 2143, 16 mm dd. F. dorsal disk, details showing moderately well-defined radial shields; G. dorsal view; H. ventral view. Photos: A–E Tatiana Korshunova; F–H Alexander Martynov.

**Material studied.** *Ophiotoma coriacea* Lyman, 1883, holotype MCZ 2143 (Figs 66F, G–H); *Ophiotrema alberti* Koehler, 1896, 3 syntypes MNHN Ec Os 10380 and 20383 (Figs 66A–E; 68); ZMMU D–809 and D–810, one specimen (Figs 6H–J; 13E, F; 18L–O; 28B; 67A–C); *Ophiotrema gracilis* Koehler, 1914, holotype USNM 032301; *Ophiotrema tertium* Koehler, 1922, holotype USNM 41150; *Ophiotoma bartletti* (Lyman, 1883), USNM 14675, one specimen, identified by R. Koehler (Fig. 69); *Ophiotoma paucispina* (Lütken & Mortensen, 1899), USNM E 00699, one specimen, identified by H.L. Clark (Fig. 70); *Ophiotoma assimilis* Koehler, 1904, ZMMU D-807, 16 specimens (Figs 6F–G; 13D; 28A; 67D–E); *Ophiotoma megatreta* (H.L. Clark, 1911) holotype USNM 25596; *Ophiotrema* sp., 2 specimens MNHN EcOs 22484 and 22485.

**Remarks.** The composition of this genus has been contentious. H.L. Clark (1915) did not distinguish the genus *Ophiotrema*, already described by Koehler (1896b), and considered all species within the genus *Ophiotoma*, whereas Koehler (1914; 1922a), Paterson (1985) and O’Hara & Stöhr (2006) accepted both genera. In the present study, appropriate type material of the type species of both *Ophiotoma* (*O. coriacea*

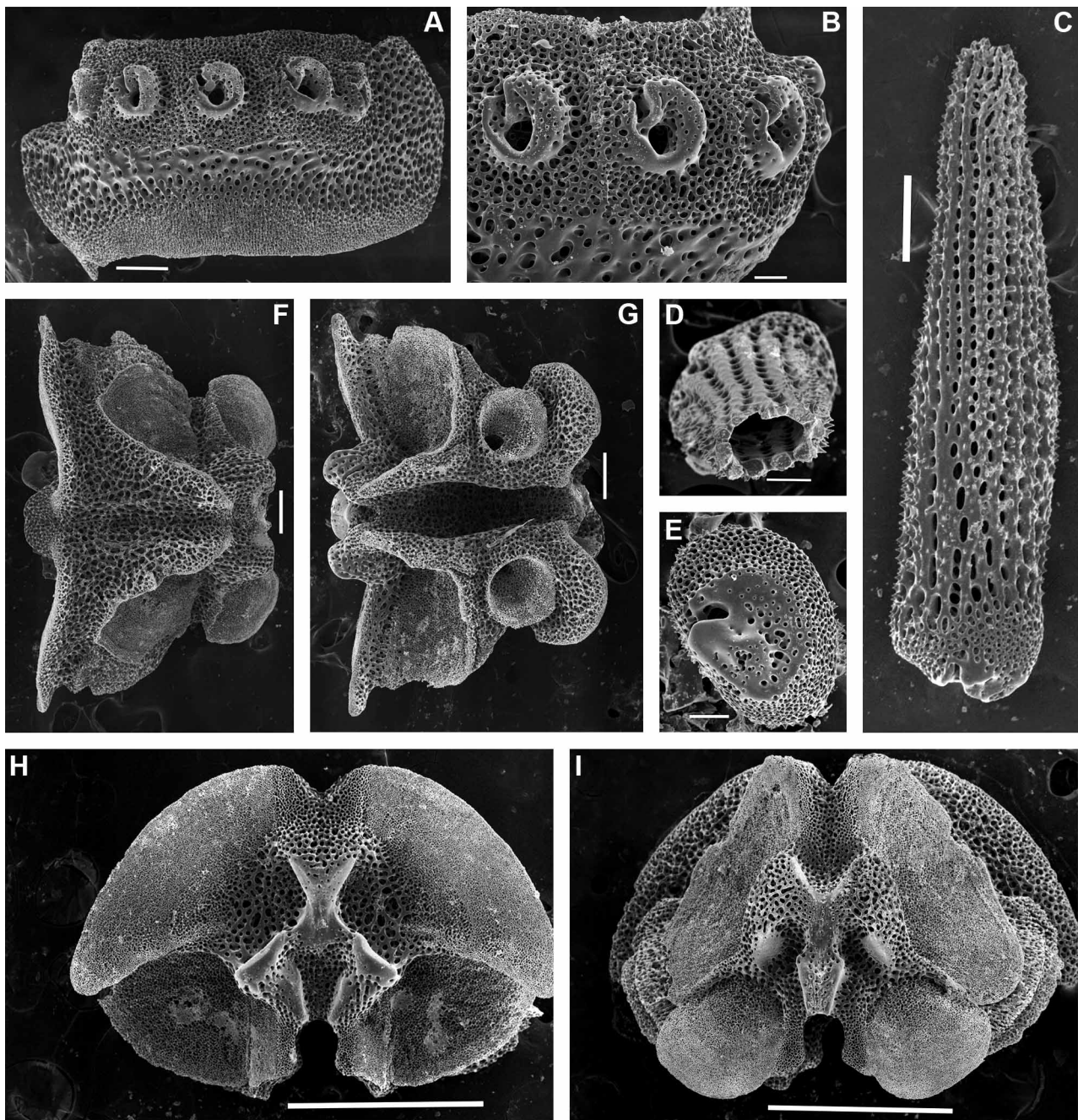
Lyman, 1883) and *Ophiotrema* (*O. alberti* Koehler, 1896) were studied, but no reliable differences were found. Both *O. coriacea* and *O. alberti* share a very similar external appearance. They are both large-sized ophiuroids, with their disks covered by a considerable amount of skin and with embedded oval to elongate radial shields (Fig. 66). The disk of *O. alberti* is covered with numerous conspicuous spinelets, whereas *O. coriacea* possesses very small, hardly conspicuous spinelets, but these differences cannot be considered as generic. The oral frames of both species are also very similar, having the adoral shield and adjacent papillae slightly longer or similar in size to the rest of the oral papillae (Figs 66D, H). The dental plates of both syntypes of *O. alberti* and *O. coriacea* are long, with several large massive teeth. One of the most pronounced differences between *O. coriacea* and *O. alberti* is the presence of several small spiniform tentacle scales in the former, placed both on lateral and ventral plates (Fig. 66C). However, as has already been indicated, the number of tentacle scales of *O. alberti* varies from 5 to 0 (Paterson, 1985). The ZMMU specimen of *Ophiotrema alberti*, otherwise very similar to the MNHN syntypes, completely lacks tentacles scales, except for an ambiguous single small tubercle on the proximalmost segments (Fig. 67B).



**FIGURE 67.** External views of various taxa of the families Ophiacanthidae and Ophiomyxidae. A. *Ophiotoma alberti* (Koehler, 1896), ZMMU D-810, 12 mm dd, dorsal view showing ventral teeth, soft disk damaged in centre after fixation; B. same, ventral view; C. same, ventro-lateral view showing long genital slits bordered by well-defined genital plates; D. *Ophiotoma assimilis* Koehler, 1904, ZMMU D-807, 18.5 mm dd, dorsal view; E. same, ventral view; F. *Ophioplexa condita* gen. nov., sp. nov., paratype 19 mm dd, ZMMU D-790, ventro-lateral view, the grooves between arm bases are not the genital slits, genital plates are not evident; G. *Ophiocymbium rarispinum* sp. nov., holotype 9.2 mm dd, ZMMU D-798, 9.2 mm dd. Photos: Tatiana Korshunova.

Another species, considered within the genus *Ophiotoma*, *O. assimilis* Koehler, 1904 has a smooth disk without spinelets, but also a small single tentacle scale throughout the arms (Figs 67D, E). The holotype of *Ophiacantha megatreta* H.L. Clark, 1911 is now considered within *Ophiotoma*, although it lacks the disk, but additional specimens mentioned by Matsumoto 1917, (see also O'Hara & Stöhr 2006) apparently possess numerous disk spinelets. The arm spine articulations of both *Ophiotoma assimilis* and *O. alberti* are similar (Figs 28A–B). Thus, there are no reliable characters to distinguish these two genera and *Ophiotrema* is considered as a synonym of the genus *Ophiotoma*.





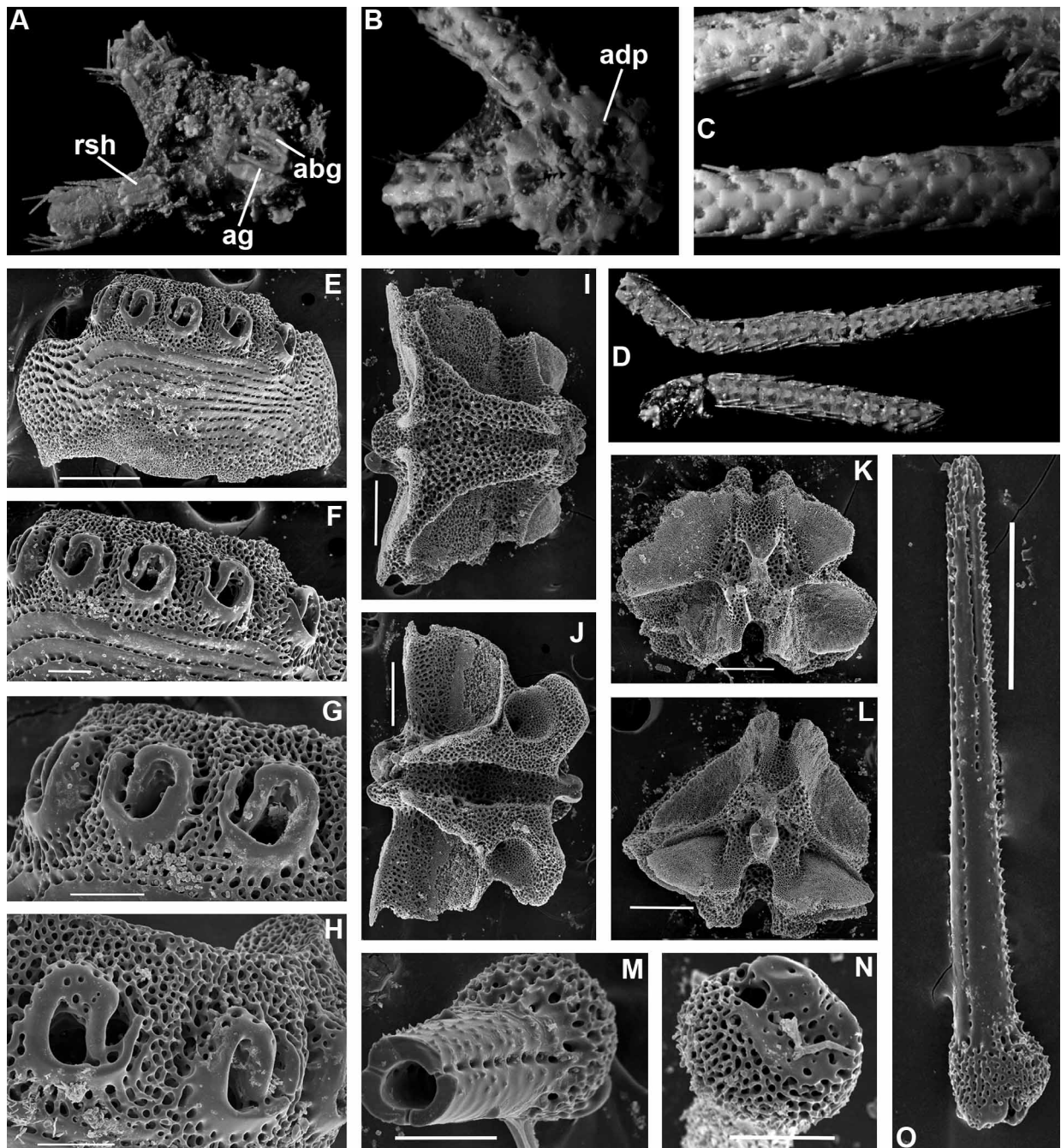
**FIGURE 68.** *Ophiotoma alberti* (Koehler, 1896), syntype MNHN EcOs 20383, 18 mm dd. A. lateral arm plate and spine articulations, proximal segments; B. same, details; C. proximal spine; D. hollow proximal spine, sectioned transversally; E. same, ventral view; F. proximal vertebra, dorsal view; G. same, ventral view; H. same, proximal view; I. same, distal view. Scale bars: A, C, F–G, 300  $\mu$ m; B, D–E, 100  $\mu$ m; H–I, 1 mm. Photos: Alexander Martynov.

*Ophiacantha bartletti* Lyman, 1883 was considered to be a synonym of the type species of the genus *Ophiotoma*, *O. coriacea* by H.L. Clark (1915). But this decision was not supported by Koehler (1922a) and Mortensen (1933a). Verrill (1899) suggested the separate genus *Ophiopora* for *O. bartletti*. Type specimens of *O. bartletti* appear not to have been preserved, since the only “*Ophiacantha bartletti*” present in the MCZ, is the holotype of the true *Ophiotoma coriacea* Lyman, 1883, subsequently, and incorrectly renamed by H.L. Clark as “*Ophiotoma bartletti*” (Figs 66F–H). According to the type description (Lyman, 1883), *Ophiacantha bartletti* has well-defined, relatively long spinelets both on dorsal and ventral sides, a sub-rhomboidal oral shield and apparently lacks the tentacle scales. The first two features differ considerably from *Ophiotoma coriacea* and thus a synonymy with *O. bartletti* is highly unlikely. Based on the presence of well-defined disk



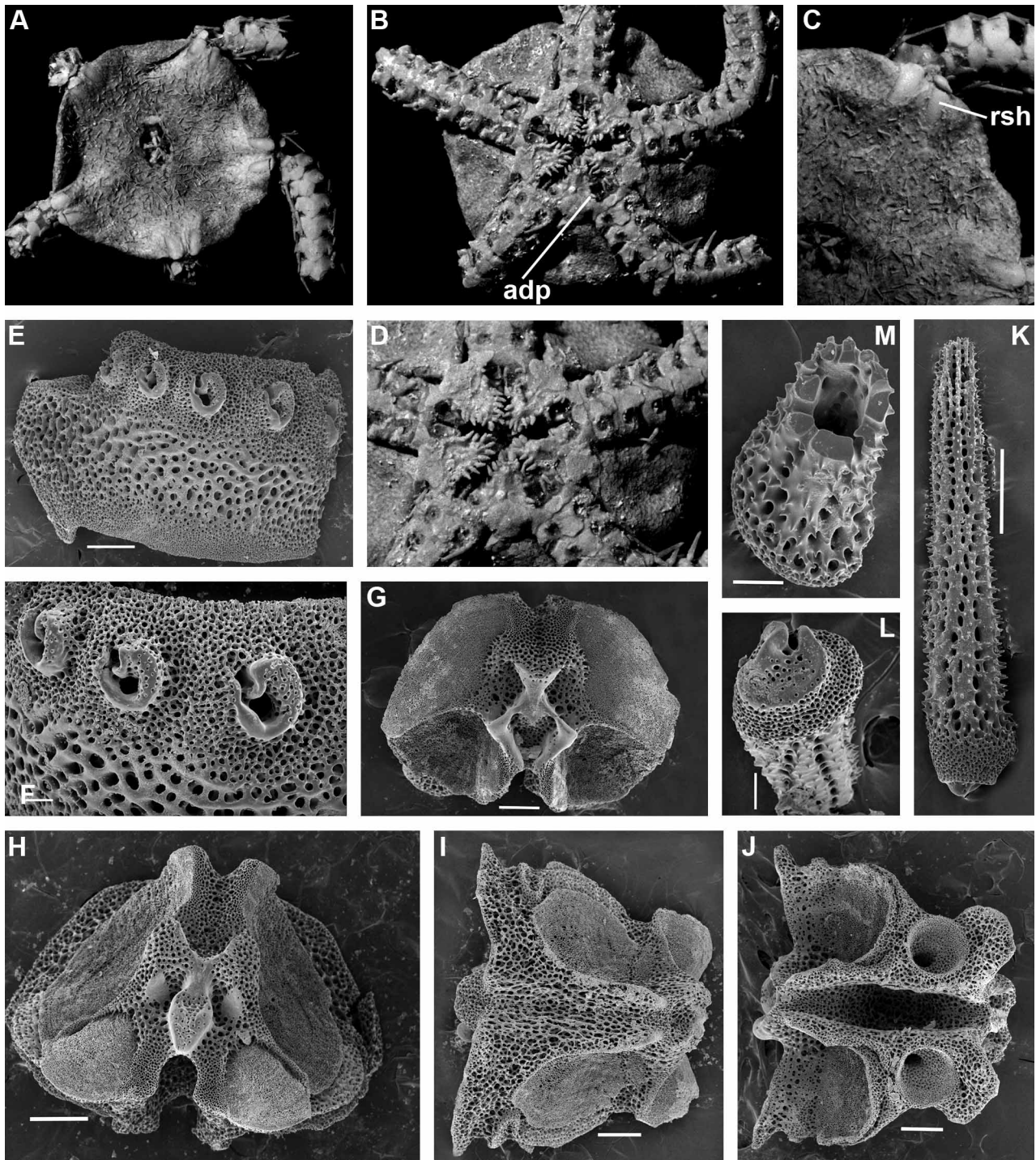
spinelets and some minor features of the oral frame, *Ophiacantha bartletti* is somewhat similar to the type species of *Ophiotrema*, *O. alberti*. Other characters, including arm segments and spine shape are also very different from both *O. coriacea* and *O. alberti* (Fig. 66). In the present study a single available non-type, partially damaged specimen of *O. bartletti* (USNM 14675), identified by R. Koehler, was examined. The general appearance of the oral shields and arms is similar to the first description by Lyman (1883). The studied arm spine articulations show a typical ophiacanthid pattern, although they differ from *O. alberti* and *O. assimillis* (Fig. 69). Thus, according to both external and microstructural characters *O. bartletti* is a well-established species.

**Number of species: 8.**



**FIGURE 69.** *Ophiotoma bartletti* (Lyman, 1883), USNM 14675, ca. 6 mm, external view and details. A. dorsal view; B. ventral view; C. middle arm segments, details; D. arms; E. lateral plate and spine articulations, proximal segments; F–H, same, details; I. proximal vertebra, dorsal view; J. same, ventral view; K. same, proximal view; L. same, distal view; M. hollow spine, sectioned transversally; N. spine, ventral view; O. proximal spine. Scale bars: E, I–K, O, 300 ; F–H, M–N, 100  $\mu$ . Photos: A–D Tatiana Korshunova; E–O Alexander Martynov.





**FIGURE 70.** *Ophiotoma paucispina* (Lütken & Mortensen, 1899), USNM E00699, 14 mm dd, external view and details. A. dorsal view; B. ventral view; C. disk details showing reasonably well-defined radial shields; D. ventral views, details of mouth structures; E. lateral plate and spine articulations, proximal segments; F. same, details; G. proximal vertebra, proximal view; H. same, distal view; I. same, dorsal view; J. same, ventral view; K. proximal spine; L. same, ventral view; M. hollow proximal spine, sectioned transversally. Scale bars: G–J, M, 300  $\mu$ ; E, K–L, 100  $\mu$ . Photos: A–C Tatiana Korshunova; E–M Alexander Martynov.

### Key to species of the genus *Ophiotoma* Lyman, 1883

- 1(12) Disk covered with numerous conspicuous spinelets
- 2(9) Oral shield wider than long

- 3(8) Adoral shield papillae shorter or similar in size to the oral papillae
- 4(5) Oral shield broadly triangular with almost straight distal edge.....  
..... *O. tertium* (Koehler, 1922) **comb. nov.**, Indo-West Pacific, off Philippines, at 1335 m
- 5(4) Oral shield oval with convex distal edge
- 6(7) Dorsal arm plates approx. twice as wide as long, almost contiguous .....  
..... *O. alberti* (Koehler, 1896), North Eastern Atlantic, at 1862–4252 m
- 7(6) Dorsal arm plates similar in width and length, well separated already at proximal segments.....  
..... *O. paucispina* (Lütken & Mortensen, 1899), Eastern Pacific, at 2138–4647 m
- 8(3) Adoral shield papillae differ markedly from the oral papillae, about twice as long; oral shields arrow-shaped .....  
..... *O. gracilis* (Koehler, 1914) **comb. nov.**, Caribbean, at 1250 m
- 9(2) Oral shields similar in width and length
- 10(11) Oral shields irregularly polygonal ... *O. megatreta* (H.L. Clark, 1911), North Pacific, off Japan, at 1068—1716 m
- 11(10) Oral shields arrow-shaped ..... *O. bartletti* (Lyman, 1883), Caribbean, at 529 m
- 12(1) Disk naked or with very small, hardly conspicuous spinelets
- 13(14) Radial shields hardly visible under skin layer, mainly distal part exposed; adoral and adjacent oral papillae spiniform, slightly longer than the other oral papillae; very small spinelets on disk.....  
..... *O. coriacea* Lyman, 1883, North Atlantic, at 1242–4106 m
- 14(13) Radial shields distinctly visible through disk skin layer; adoral and adjacent oral papillae tubercle-shaped, considerably shorter than the other oral papillae; disk naked .....  
..... *O. assimilis* Koehler, 1904, Indo-West Pacific, at 402–1033 m

## Family Ophiomyxidae Ljungman, 1867

### Taxa of the family Ophiomyxidae that have been questioned for ophiacanthid affinity

Paterson (1985) mentioned a close similarity between the ophiotomin *Ophiotoma alberti* and the ophiomyxid *Ophioscolex purpureus* Düben & Koren, 1846. The latter species has been treated together with few others as a separate subgenus *Ophiolycus* Mortensen, 1933 (Mortensen, 1933b, 1936). McKnight (2003) elevated *Ophiolycus* to genus rank, but this decision remained largely undiscussed. Besides the presence of distal hooks, *Ophiolycus* has a number of differences from the type species of the genus *Ophioscolex*, *O. glacialis* Müller & Troschel, 1842: reasonably defined dorsal arm plates (except at proximal segments), elongated well-developed radial shield, thin skin layer, numerous disk scales, and arm spine articulations of the double opening type with a lateral lobe. Therefore *Ophiolycus* is here also accepted as a separate genus. Stöhr & Segonzac (2005) have indicated that the ophiacanthid subfamily Ophiotominae and the genus *Ophioscolex* Müller & Troschel, 1842 of the family Ophiomyxidae is distinguished only by a few characters, but pending a revision they did not provide details. In order to compare and analyze these questioned taxa, diagnoses of both *Ophioscolex* and *Ophiolycus* are provided below.

### Genus *Ophiolycus* Mortensen, 1933

Figures 27Q–U; 71–74

*Ophiolycus* (as subgenus of *Ophioscolex*): Mortensen, 1933b: 315

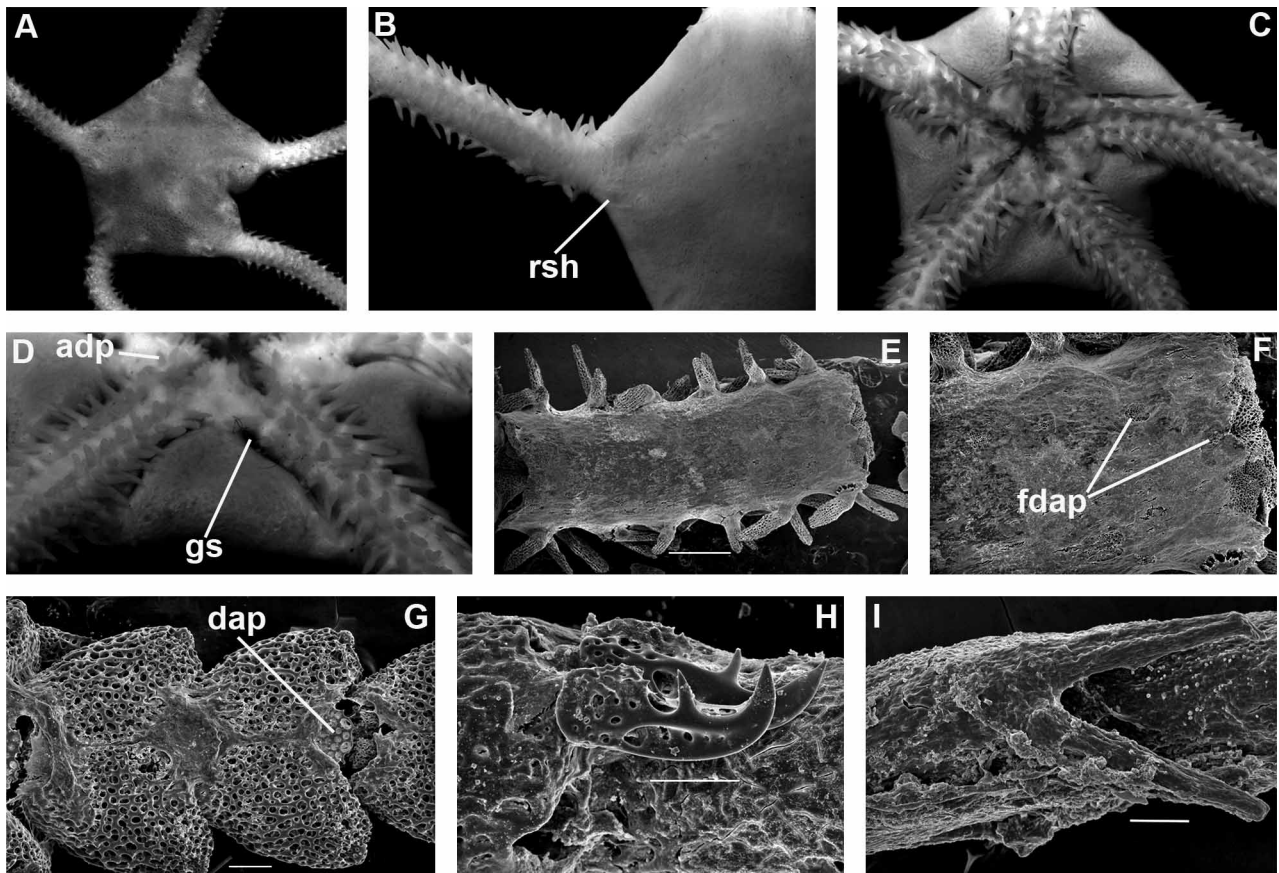
Type species: *Ophioscolex dentatus* Lyman, 1878, by original designation

**Diagnosis.** The disk is covered with numerous small, uniform scales, conspicuous when dried, covered by a thin skin layer. The radial shields are moderately developed, elongated, visible in dried specimens. The adradial genital plate is well developed, tightly articulating with the radial shield, proximally slightly curved. The abradial genital plate is short and externally only slightly conspicuous. The articulation surface of the adradial genital plate is an elongate elevation with a small pit dorsally. The articulation surface of the radial shield is a slightly prominent elevation with distinct proximal groove. The genital slits are long; genital plates



bordering about two thirds of the slits. The jaw bears numerous spiniform oral papillae, similar in shape to the cluster of the 3–4 ventralmost teeth. Two adoral shield papillae and one adjacent oral papilla of each jaw are spiniform, approximately 2 times as long as the oral papillae, placed around the second tentacle pore. The half-jaws are slightly elongated. The adradial sides of the jaws bear a few sharp straight folds distally. The dental plate is small, elongated, entire, without folds and with few rounded sockets, alternately placed. The teeth are spiniform and few in number (besides the apical papillae there are 4–5 teeth). All teeth are of similar shape. The oral shield is rhomboidal, almost devoid of a distinct distal lobe. The adoral shields have distal bilobed wings and are proximally very narrow bars. Dorsal arm plates are moderately developed in some segments but fragmented proximally. Ventral arm plate is well defined. The arm spine articulations are placed almost parallel in relation to the lateral plate. The muscle and nerve openings are similar in size. A low perforated lobe occupies the dorsal part of the articulations. The sigmoidal fold is absent. The spines are relatively long, flattened, solid over almost their entire length, containing only a small lumen. Distally the dorsal and middle arm spines transform into hooks. One small spiniform tentacle scale is placed on the lateral arm plate. The vertebrae have a broad dorsal keel, with a blunt end; the dorsal medial suture is indistinct. The articulation is zygospondylous. The podial basins are large.

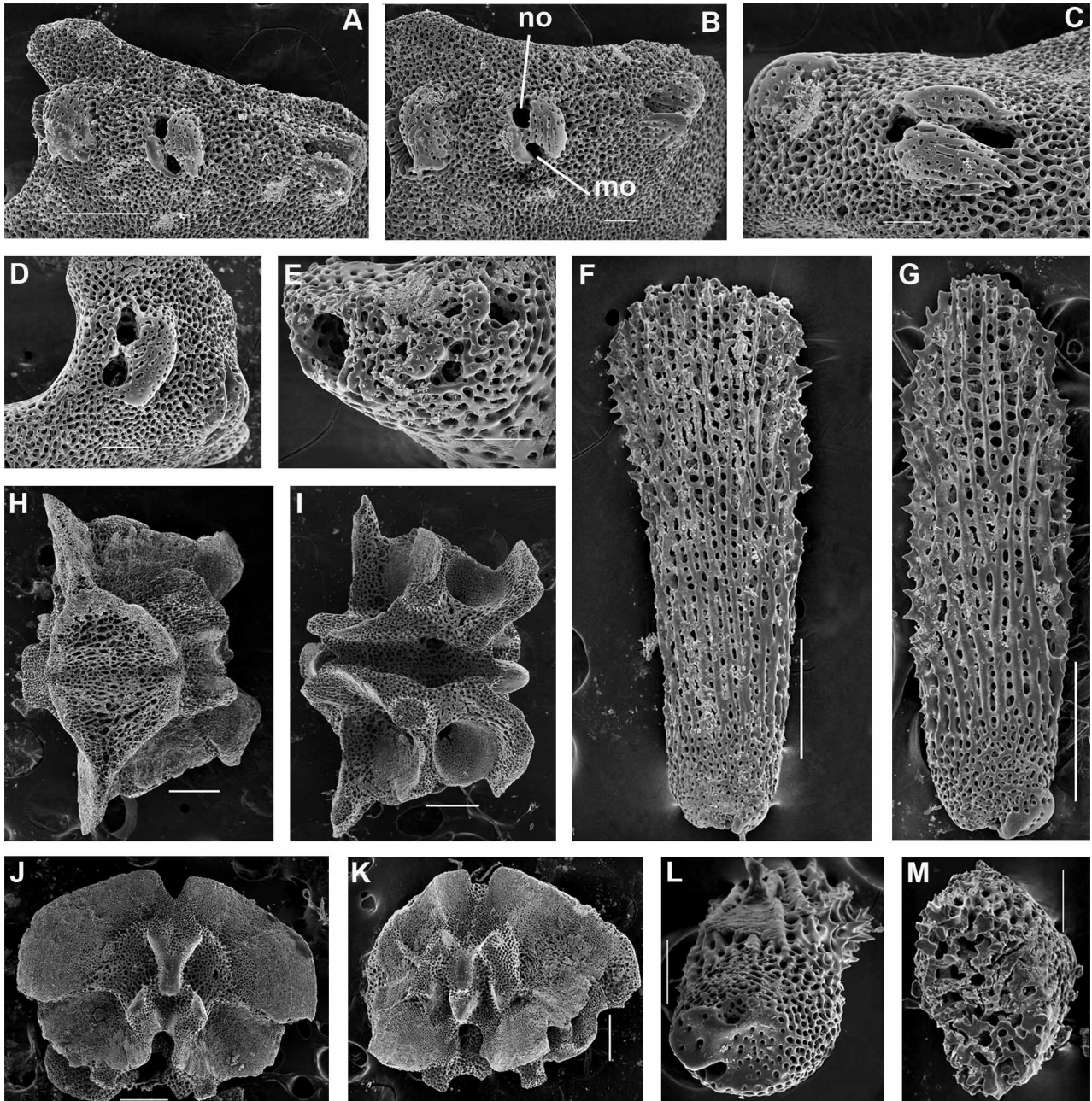
**Material studied.** *Ophiolycus dentatus* (Lyman, 1878), ZMUC, 3 specimens (Figs 71–72); *Ophiolycus purpureus*, ZMMU D-845, 11 specimens; Mareano, 3 specimens (Figs 73–74); *Ophiolycus nutrix* Mortensen, 1936, ZMMU D-818, 2 specimens (Figs 27S–U).



**FIGURE 71.** *Ophiolycus dentatus* (Lyman, 1878), ZMUC, 19.5 mm dd, external views and details (A–H). A. dorsal view; B. disk details showing small radial shields concealed under the skin; C. ventral view; D. ventral view showing genital slits; E. proximal arm segments in situ; F. same, details showing fragmented dorsal arm plates concealed under the skin; G. distal arm segments in situ showing entire dorsal arm plates; H. distal segments, hooks; lateral plate and spine articulations, proximal segments; proximal vertebra, proximal view; I. *Ophioscolex glacialis*, distal segments, hook-shaped spines. Scale bars: E, 1 mm; F, 300  $\mu$ ; G, H–I, 100  $\mu$ ; Photos: A–C Tatiana Korshunova; E–I Alexander Martynov.



**Remarks.** One of the characteristic external features of the genus *Ophiolycus* was the presence of hooks on the distal arm segments (Mortensen 1933b; 1936) (Figs 71H; 73J), whereas the type species of the genus *Ophiocollex*, *O. glacialis* does not possess hook-shaped spines on the distal segments. However, well-defined hooks on the distal arm segments are apparently widely distributed within various distantly-related taxa of the family Ophiomyxidae. In the present study, true distal hooks were detected in the genera *Ophiomyxa* and *Ophiobyrsa* (Figs 1L; 79J). *Ophiosyzygus disacanthus* H.L. Clark, 1911, also has on the distalmost segments small hook-shaped spines (Figs 71I; 75J), somewhat different from the typical hooks of *Ophiomyxa* and *Ophiobyrsa*. Thus, the hooks or hook-shaped spines are clearly a convergent feature. Besides hook-shaped spines, the genus *Ophiolycus* is well distinguished from the genus *Ophiocollex*, and the restricted diagnosis of both genera are given above.

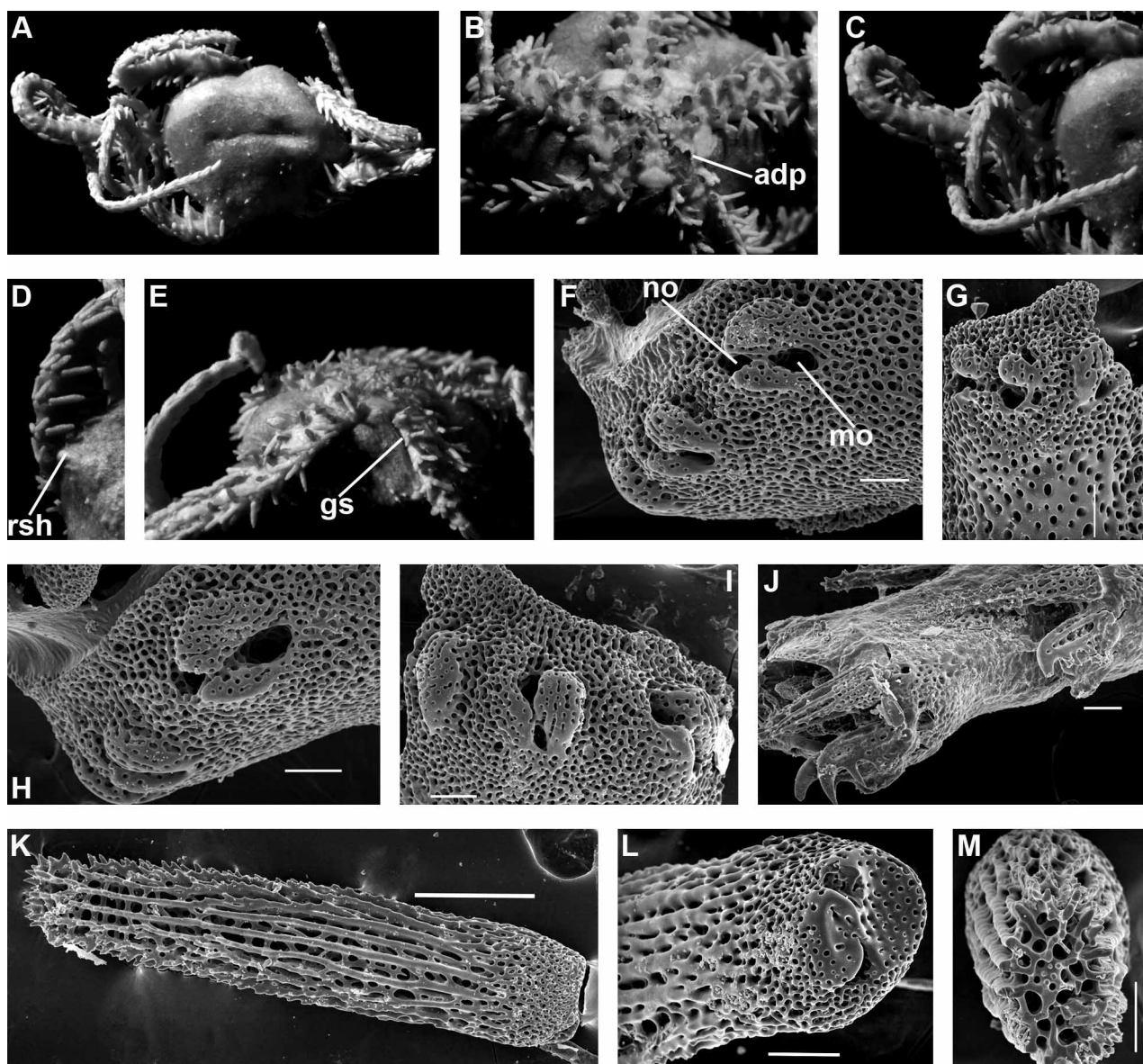


**FIGURE 72.** *Ophiolycus dentatus* (Lyman, 1878), ZMUC, details. A–B, arm spine articulations, proximal segments; C. same, dorsalmost articulation details; D. same, ventralmost articulation details; E. arm spine articulation, distal segments; F. dorsalmost spine; G. spine; H. proximal vertebra, dorsal view; I. same, ventral view; J. same, proximal view; K. same, distal view; L. spine, ventral view; M. solid proximal spine, sectioned transversally showing only small cavities. Scale bars: A, F, G–K, 300  $\mu$ ; B–E, L, M, 100  $\mu$ ; Photos: Alexander Martynov



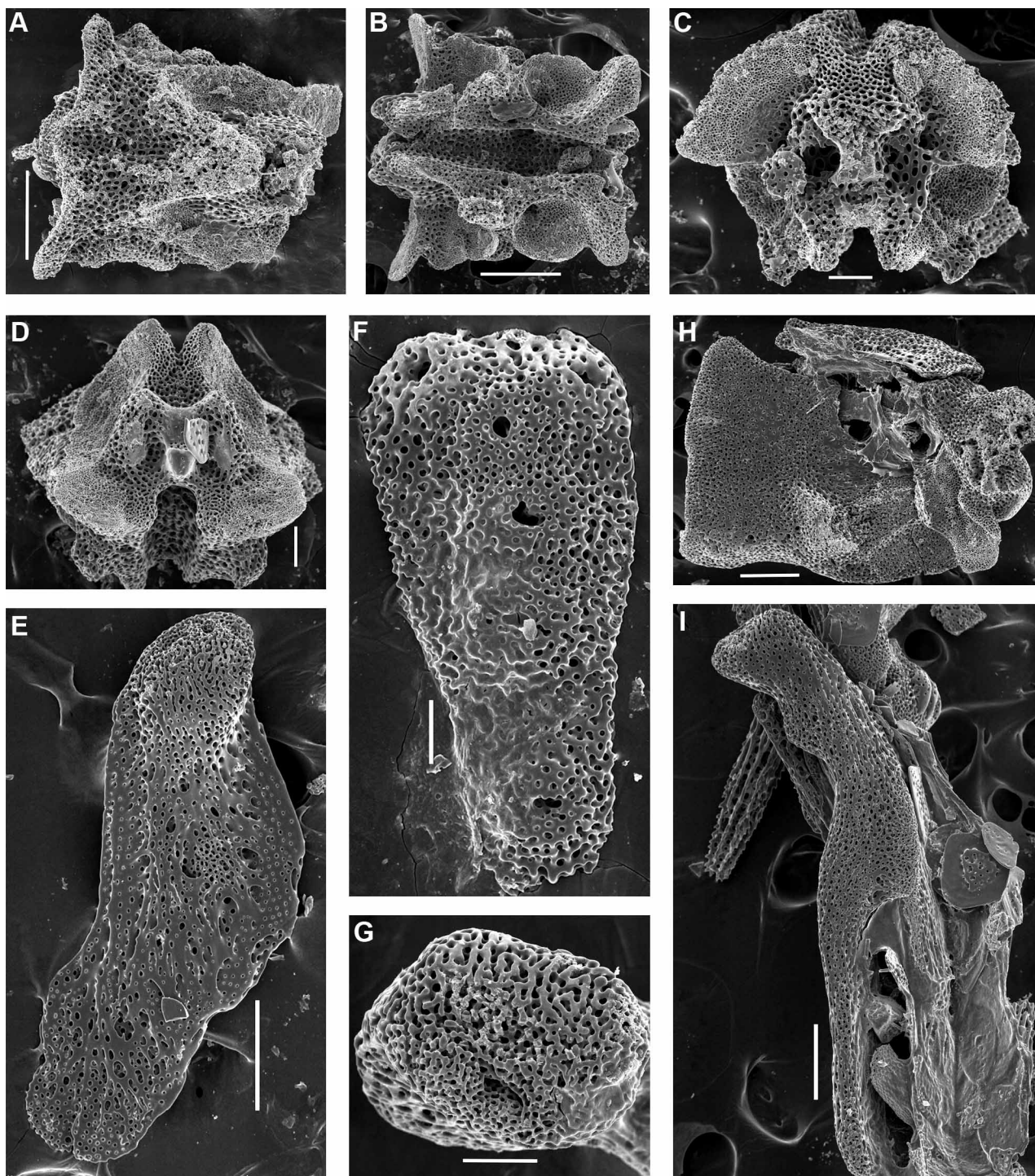
O'Hara (pers. comm.) suggested that *Ophiolycus farquhari* McKnight, 2003 may be a synonym of *Ophiologimus quadrispinus* H.L. Clark, 1925. *Ophiolycus farquhari* is externally similar to *Ophiologimus quadrispinus* in general appearance of the disk and arms, elongate radial shields and absence of the long adoral shield papillae. The latter feature is diagnostic for all species of the genus *Ophiolycus*. McKnight (2003) mentioned the distalmost spines as “weakly hooked at the tip”. Both the type species of the genus *Ophiologimus*, *O. hexactis* (Fig. 48F), and other studied material of *O. quadrispinus* reveal the presence of well-defined hooks. “*Ophiolycus*” *farquhari* therefore is not included into the genus *Ophiolycus* here, but until a complete revision of the genus *Ophiologimus* will be performed, it is retained as a species of doubtful status.

Number of species: 3.



**FIGURE 73.** *Ophiolycus purpureus* (Düben & Koren, 1846), Mareano program, 8 mm dd, external views and details. A; dorsal view; B. ventral view; C. dorsal view showing distal arm segments with hooks; D. dorsal disk view, details showing small radial shields; E. interradian view showing long genital slits; F. arm spine articulations, proximal segments; G. arm spine articulation bear hooks, distal segments; H. proximalmost segments showing large distinct dorsalmost articulations; I. arm spine articulations, proximal segments; J. distal segments, hooks; K. spine; L. same, ventral view; M. spine section showing only small cavities. Scale bars: F-H, J-M, 100  $\mu$ ; I, 300  $\mu$ . Photos: A–E Tatiana Korshunova; F–M Alexander Martynov.





**FIGURE 74.** *Ophiolycus purpureus* (Düben & Koren, 1846), Mareano program, 8 mm dd, details. A. proximal vertebra, dorsal view; B. same, ventral view; C. same, proximal view; D. same, distal view; E. radial shield, ventral view; F. dental plate; G. adradial genital plate, articulation surface; H. jaw, adradial view; I. adradial and abradial genital plates in situ. Scale bars: A–B, E, H, I, 300  $\mu$ ; C, D, F–G, 100  $\mu$ . Photos: Alexander Martynov.

**Key to species of the genus *Ophiolycus* Mortensen, 1933**

- 1(4) Disk covered with few scattered granules or lacking it
- 2(3) Adoral shields and adjacent oral papillae club-shaped, markedly longer than other oral papillae .....  
..... *O. dentatus* (Lyman, 1878), South Atlantic off South Africa, at 163–409 m



- 3(2) Adoral shields and adjacent oral papillae are conical, slightly longer than other oral papillae .....  
 ..... *O. purpureus* (Düben & Koren, 1846), North Atlantic, at 75–1480 m  
 4(1) Disk covered with numerous evident spinelets ..... *O. nutrix* Mortensen, 1936, South Atlantic, at 151–434 m

### Genus *Ophioscolex* Müller & Troschel, 1842

Figures 3D–E; 4I, O; 17A–B; 27A–E; 54H–J; 71I; 75–76

*Ophioscolex*: Müller & Troschel, 1842: 84, 109

Type species: *Ophioscolex glacialis* Müller & Troschel, 1842, by monotypy

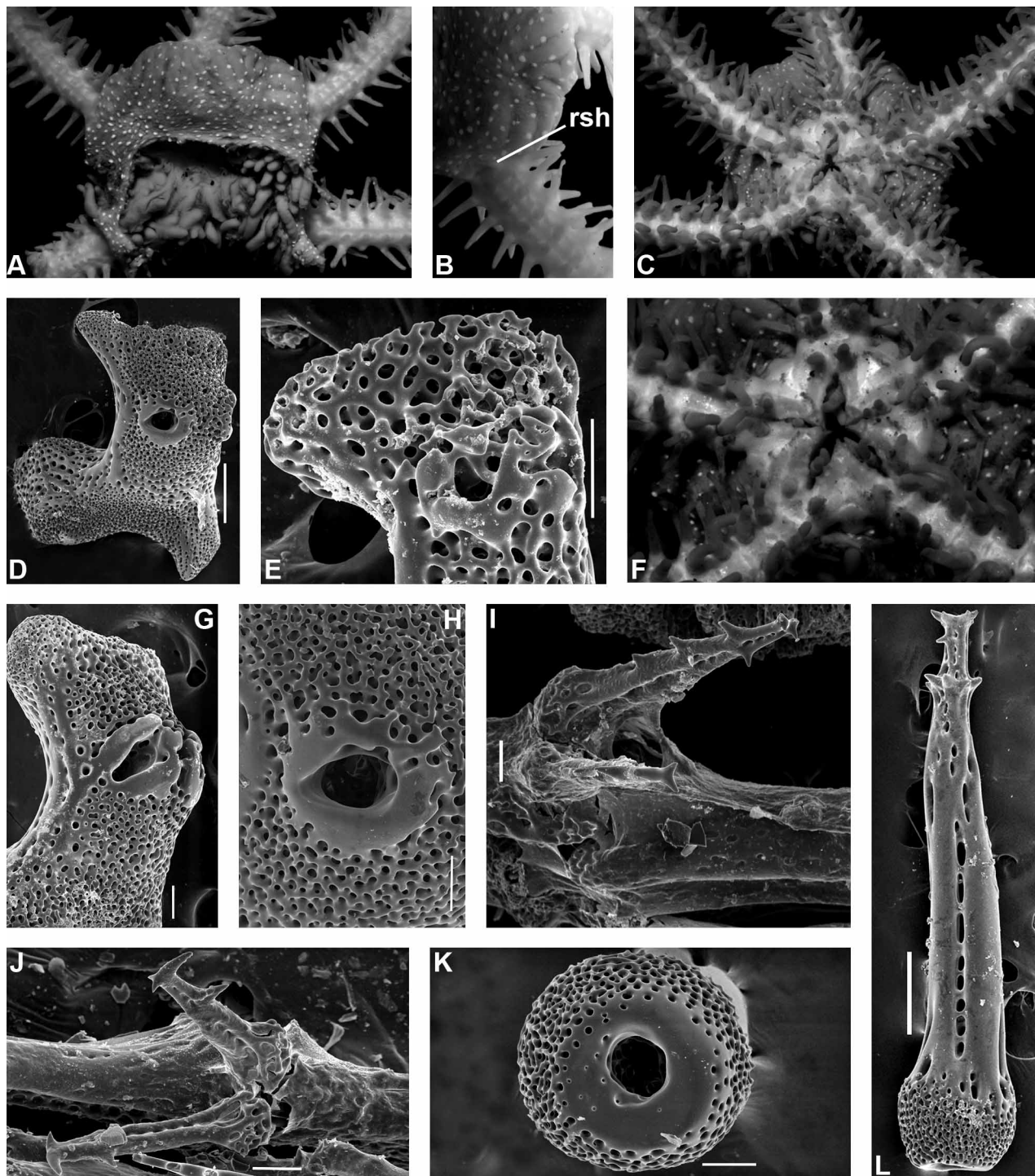
**Diagnosis.** The disk is covered with a thick skin layer, small scales visible within when dried. The radial shields are small, triangular, hardly conspicuous even in dried specimens. The adradial genital plate is poorly developed, slightly curved, elongated, tightly articulated with the radial shield. The abradial genital plate is short and externally slightly conspicuous. The articulation surface of the adradial genital plate is without elevation. The articulation surface of the radial shield has a well-defined elevation but lacks a distinct proximal groove. The genital slits are long and conspicuous, but genital plates border only the small distalmost part. The jaw bears several spiniform oral papillae, similar in shape to the small cluster of ventralmost teeth. A pair of long spiniform adoral shield papillae, approximately 3–4 times as long as the oral papillae, is present only in the type species of the genus. The half-jaws are elongated, low. The adradial sides of the half-jaws lack distal folds. The dental plate is small, entire or consisting of a few not-completely separated irregular plates, elongated, without folds (or with traces of fusion of the smaller plates) and with few rounded sockets, irregularly placed. The teeth are spiniform and few in number. All teeth are similar in shape. The oral shield varies in shape, with or without distinct distal lobe. The adoral shield parts are similar in size, being only slightly widened distally. The dorsal arm plates are only conspicuous in one species (*O. inermis*). The ventral arm plates are well-defined. The arm spine articulations are large, of the single-opening type, encircled by a low, perforated, elevated border. The sigmoidal fold is absent. The arm spines are relatively long, conical in most species when covered in skin, completely entire, but remarkably comprised from several rods. Distal segments without hooks or with somewhat hook-shaped spines. Tentacle scales are completely absent in some species, including the type, whereas others have a small oval or spiniform scale on the lateral arm plate. The vertebrae are not distinctly widened distally; the dorsal medial suture is well-defined. The articulation is zygospondylous. The podial basins are large.

**Material studied.** *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-817, D-843, D-866, ca. 100 specimens (Figs 3D–E; 4I, O; 17A–B; 27A–E; 54H–J); *Ophiosyzygus disacanthus* H.L. Clark, 1911, ZMMU D-875, 1 specimen (Figs 75–76)

**Remarks.** H.L. Clark (1911) described three monotypic genera of the family Ophiomyxidae bearing close external resemblance to the genus *Ophioscolex* s.str: *Ophiocynodus*, *Ophiosyzygus* and *Ophioleptoplax*. Only one taxon, the genus *Ophiocynodus* (with the type species *O. corynetes* H.L. Clark, 1911) has been evaluated (Mortensen 1933b) and considered as synonym of the genus *Ophioscolex*. For *Ophiosyzygus disacanthus* H.L. Clark, 1911 a revised diagnosis has been suggested and the absence of the radial shields claimed in the first description was considered as incorrect (Turner & Heyman 1995). A specimen of *Ophiosyzygus disacanthus*, closely similar to the first description and from the same geographical region (Asian Western Pacific) was examined in the present study both externally and internally (Figs 75–76). Few very large arm spine articulations of the single-opening type, small triangular radial shields, very low jaws and a dental plate with few small rounded openings (Figs 75D–H; 76D–J), are all features essentially similar to those in the type species of the genus *Ophioscolex*, *O. glacialis* (Figs 3D–E; 4I, O; 17A–B; 54H–J). Externally these species are also very similar. Most species of *Ophioscolex*, like *Ophiosyzygus disacanthus*, also lack the adoral shield papillae. The only striking difference between *O. disacanthus* and *O. glacialis*, is the streptospondylous vertebral articulation in the former (Figs 76B–C). Considering the great variability and an easy shift from strepto- to zygospondyly in different ophiuroid taxa, for instance within the genera *Ophiacantha* and *Ophiocamax*, this difference appears as non-generic. *Ophiosyzygus*, therefore, is very similar to of the genus

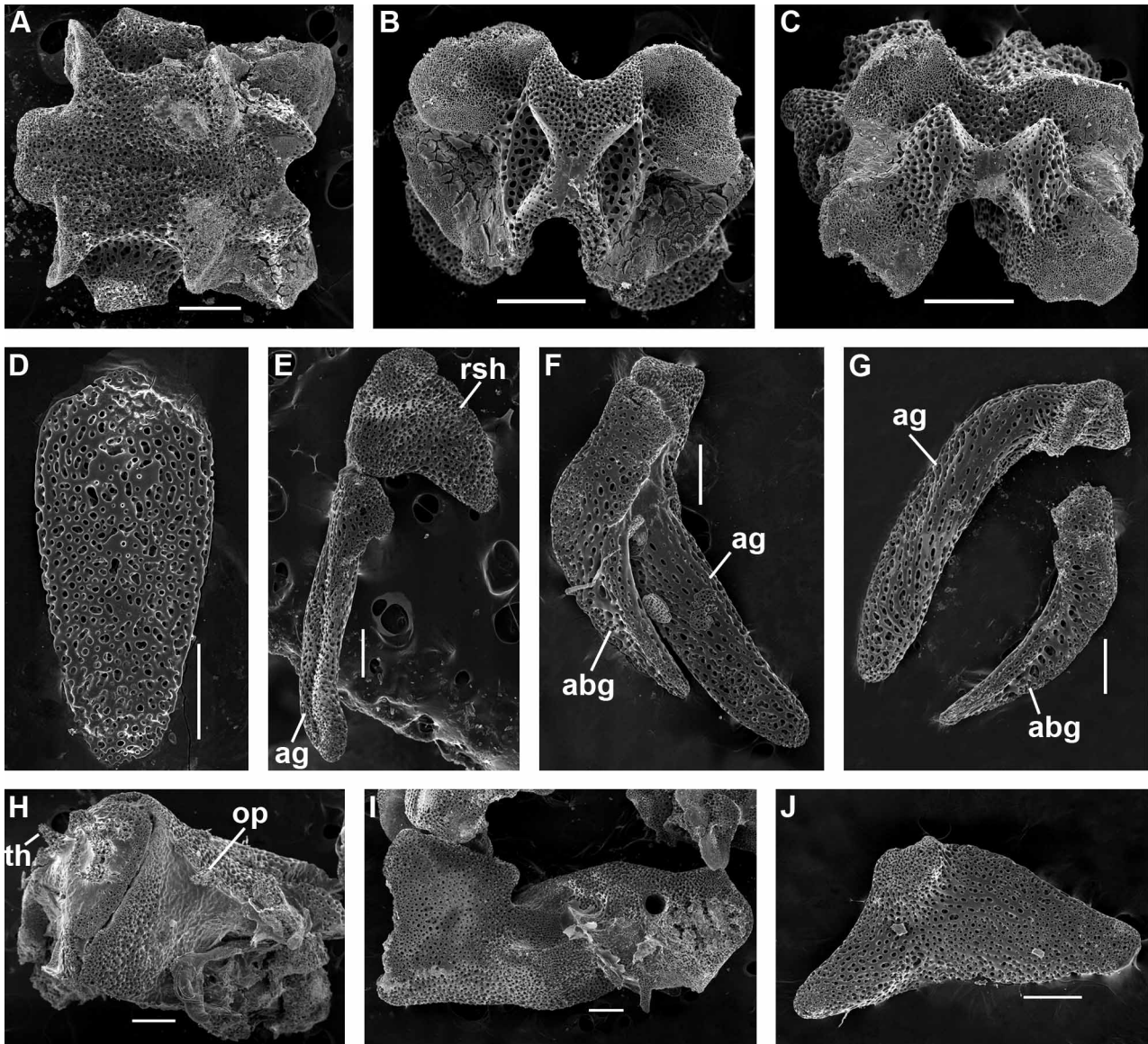
*Ophioscolex* s.str., but pending a detailed revision of the latter they are not formally synonymized. The genus *Ophioleptoplax* has thin evident dorsal arm plates, and thus differs from most species of *Ophioscolex* s.str. (excluding *O. inermis* Mortensen, 1933). The apparent absence of the radial shields (H.L. Clark 1911) in *Ophioleptoplax* is doubtful. The genus needs further investigation.

Number of species: 7.



**FIGURE 75.** *Ophiosyzygus disacanthus* H.L. Clark, 1911, ZMMU D-875, 12 mm dd, external view and details. A. dorsal view; B, same, details showing small radial shields and proximal arm segments; C. ventral view; D. lateral plate and spine articulations, proximal segments; E. spine articulations, distal segments; F. ventral view, details showing mouth parts; G. ventralmost spine articulation, mostproximal segments; H. spine articulation, details, proximal segments; I. distal segments with the spines in situ; J. further distal segments showing modification of the dorsal spine into a hook-shaped structure; K. proximal spine, ventral view; L. proximal spine. Scale bars: D, L, 300  $\mu$ ; E-K, 100  $\mu$ . Photos: A–C, F, Tatiana Korshunova; D–E; G–L Alexander Martynov.





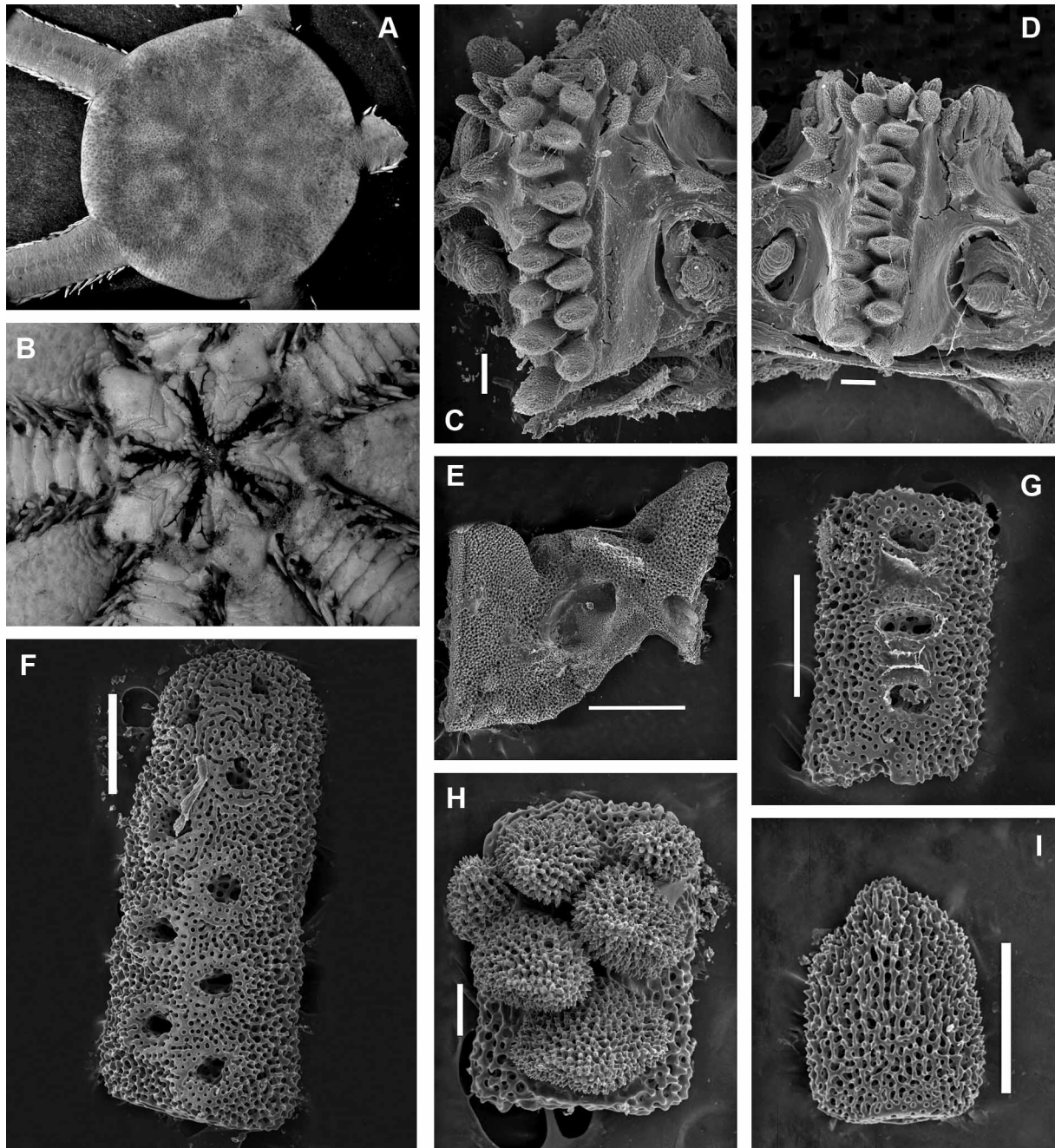
**FIGURE 76.** *Ophiosyzygus disacanthus* H.L. Clark, 1911, ZMMU D-875, 12 mm dd, details. A. proximal vertebra, dorsal view; B. same, proximal view; C. same, distal view; D. dental plate; E. articulated radial shield and adradial genital plate; F. abradial genital plate (left) articulated in situ with the adradial plate; G. same, disarticulated (right, abradial, left adradial genital plate); H. dental plate in teeth in situ on the jaws; I. jaw, adradial view; J. radial shield, ventral view showing articulation surface; Scale bars: A-J, 300  $\mu$ . Photos: Alexander Martynov.

**Key to species of the genus *Ophioscolex* Müller & Troschel, 1842**

- 1(12) Arm spines conical, not serrated
- 2(3) Adoral shields bear a pair of long well-defined spines .....  
.....*O. glacialis* Müller & Troschel, 1842, Arctic and North Atlantic, at 37–2727 m
- 3(2) Adoral shield papillae absent
- 4(9) Tentacle scales present
- 5(6) Disk covered with sparse short spinelets .....*O. marionis* Mortensen, 1936, South Atlantic, at 99–113 m
- 6(5) Disk smooth
- 7(8) Tentacle scale short, pointed, not covering tentacle pore.....  
*O. pertinax* Koehler, 1904, Indo-West Pacific, at 404 m (according to O’Hara (pers. comm.) this species possesses distal hooks and probably belongs to the genus *Ophiolycus*)

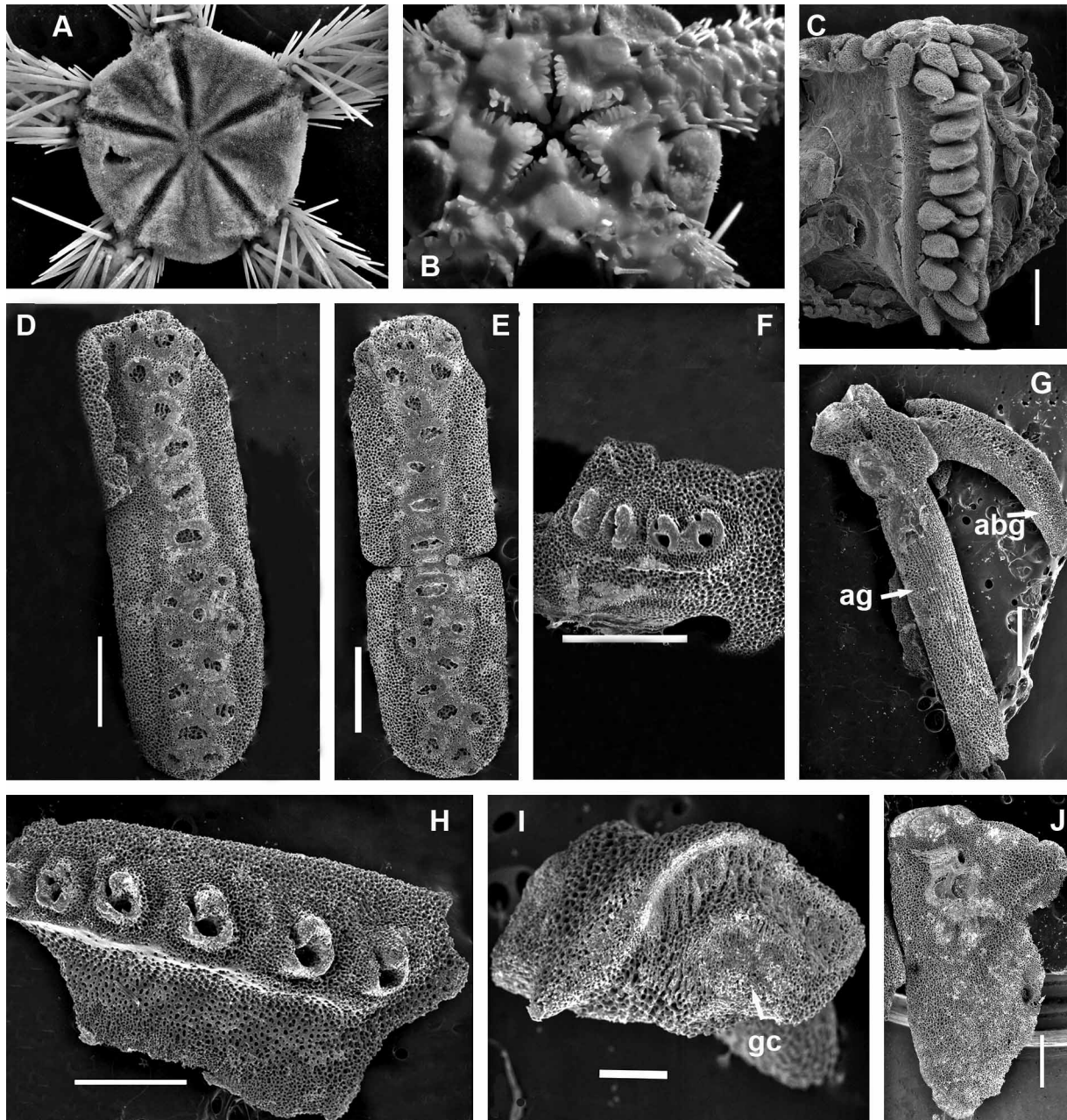


- 8(7) Tentacle scale relatively long, oval, covers the tentacle pore entirely .....  
..... *O. tropicus* Lyman, 1878, Caribbean, at 710 m
- 9(4) Tentacle scales absent
- 10(11) Dorsal arm plate not evident; oral shield longer than wide, with distal lobe .....  
..... *O. corynetes* (H.L. Clark, 1911), North Pacific, off North American coast, at 627–1246 m
- 11(10) Thin dorsal arm plate present; oral shield wider than long, without distal lobe.....  
..... *O. inermis* Mortensen, 1933, inhabits the Indian Ocean, off South Africa, at 409 m
- 12(1) Arm spines flattened, strongly serrate..... *O. serratus* H.L. Clark, 1901, Caribbean, at 166 m



**FIGURE 77.** *Ophionotus victoriae* Bell, 1902, external views and details. A-B, ZMMU D-131, 34 mm dd, external views, dorsal and ventral sides respectively; C-D, inside mouth views of two interradia, ZMMU D-867, 12 mm dd; E. same, jaw, adradial view; same, F. dental plate, partially; G. ZMMU D-867, 7 mm dd, dental plate, partially; H. same, part of the dental plate with teeth; I. same, tooth; C–D, 300  $\mu$ ; E, 1000  $\mu$ ; F–G, 300  $\mu$ ; H, 100  $\mu$ ; I, 300  $\mu$ . Photos: A–B Tatiana Korshunova; C–I Alexander Martynov.





**FIGURE 78.** *Ophiotreta larissae* (Baker, 1979), ZMMU D-680, 21 mm dd, external views and details. A. dorsal view; B. ventral view; C. inside mouth view of one interradius; D-E, dental plates (one possibly naturally fragmented into two pieces); F. arm spine articulations, most proximal segments; G. articulating adradial and abradial genital plates, dorsal view; H. arm spine articulations, proximal segments; I. articulation surface of the adradial genital plate; J. radial shield, ventral side. Scale bars: C-H, 1 mm; I, 300  $\mu$ ; J, 300  $\mu$ . Photos: A-B Tatiana Korshunova; C-J Alexander Martynov.

### Discussion on the taxonomic importance of the internal and microstructural ophiuroid characters

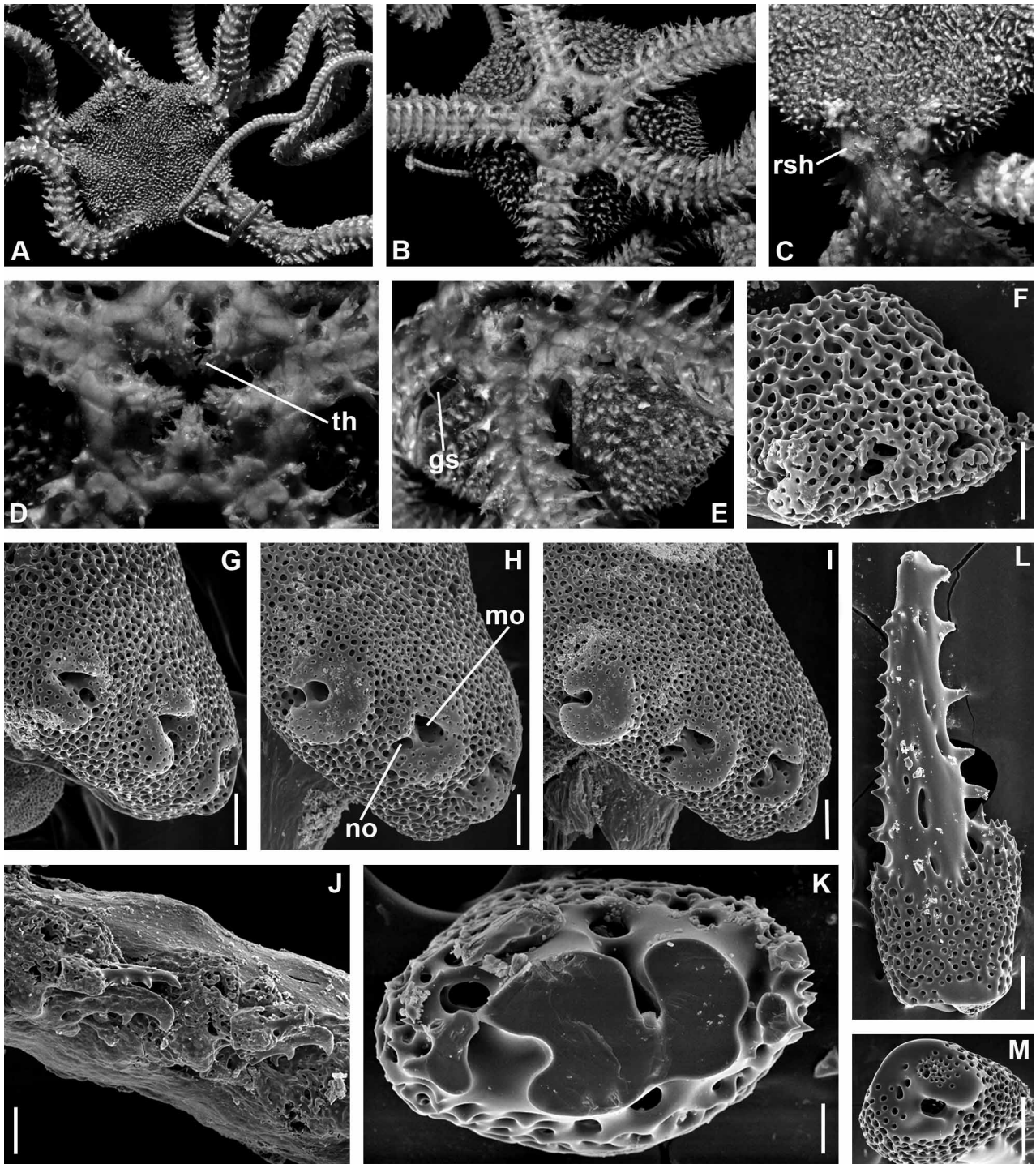
**Vertebrae.** Two main types of the vertebral articulation, streptospondylous and zygospondylous have been recognized (Bell 1892; Matsumoto 1917). However, both patterns have been discovered in distantly related, obviously different groups, e.g. Euryalida (Figs 16C–D, G–H), the ophiomyxid genus *Ophiobyrsa* (Figs 16E, I), various taxa of the family Ophiacanthidae (Figs 16K–L; O–P, S), the family Hemieuryalidae, the supposedly ophiuroid genus *Abyssura* and others. This extremely broad distribution of two main types of the vertebral articulation within the class Ophiuroidea hardly allowed taxonomic implications. For instance,

examination of species of the ophiacanthid subfamily Ophiotominae (including genera *Ophiotrema*, ***Ophiorupta* gen. nov.**, *Ophiolimna*, Figs 18G–H, N–O; 46D; 47K) revealed the presence of the zygospondylous articulation, whereas species of the genus *Ophiocamax* have the streptospondylous type (Figs 16K–L). Even within species of a single ophiacanthid genus, *Ophiacantha*, some species (e.g. *O. bidentata* (Bruzelius, 1805), Figs 18J, K) possess the zygospondylous type, others (*O. setosa* (Bruzelius, 1805), Figs 16O–P) the streptospondylous type. It should be noted that Bell (1892) has applied a different definition of the term “streptospondylous” compared to current usage. His group “Streptophiuræ” encompassing mostly the family Ophiomyxidae, with addition of Hemieuryalidae and Ophiohelinae, possessed a “simple ball-and-socket” vertebral articulation, whereas Euryalida were separated into another group, Astrophysiuræ (Cladophysiuræ), with “hourglass-shaped surfaces”. Thus under the term “streptospondylous” Bell understood a variant of the zygospondylous type, whereas the current meaning of the term “streptospondylous” traces back to Matsumoto (1917), who criticized Bell’s system. The present study shows the presence of the zygospondylous articulation type in various Ophiomyxidae taxa (Figs 17; 18C, D).

Litvinova in a series of papers (1989a,b; 1994; 1996) attempted to further differentiate the two main types of the vertebral articulation. The zygospondylous articulation type was divided into several separate categories, e.g. “comb-shaped”, “universal” and “aberrant”. It was the first attempt to analyse vertebral diversity using SEM, but the main stress was put on ecological characteristics of the ophiuroid vertebrae and some important taxonomic considerations were omitted. For instance Litvinova for the first time discovered a special pattern of the vertebral articulation in many species of the family Ophiuridae, in which the distal articular median condyle is distinctly elongated, often in the shape of a narrow lozenge (Fig. 19). Independently, but without a broad comparison within various ophiurid species and separation into distinct types, ophiurid articulations of the vertebrae were mentioned by Paterson and Baker (1988). Although not all species of the family Ophiuridae possess a “comb-shaped” vertebral articulation type, for many ophiurid taxa, including the *Ophiosparte gigas* Koehler, 1922, this type was revealed (Figs 19A, D, E, F) and thus serves as an additional character that characterizes that family. In contrast, the “universal” vertebral articulation type was shown in various unrelated taxa and thus has little taxonomic importance. LeClair (1996) pointed to the distinction between two main characteristic types of the vertebral dorsal surface, i.e. keeled vertebrae with a narrow distal dorsal process, and non-keeled, and considered them a conservative feature at the family level. However, keeled vertebrae were discovered within several different families some, e.g. Amphiuroidae and Ophiionereididae, sharing also other characters, whereas Ophiidermatidae does not display any similarities with the former two (Fig. 18). LeClair (1996) mentioned transitional stages between keeled and non-keeled vertebrae, even within arms in some species. Instead, keeled vertebrae are also present in the ophiomyxid ***Ophioplexa* gen. nov.**, and the ophiacanthid genera *Ophiacantha*, *Ophiotoma* and *Ophiolimna* (Figs 17L; 18I, L; 47J). Thus the distinction between keeled and non-keeled vertebrae has little taxonomic importance or possibly suggests a common ancestry of many of the recent ophiuroid families.

Irimua & Fujita (2003) have studied vertebral morphology in a number of ophiuroid species from different families and proposed several new vertebral characters, e.g. curved grooves on the dorsal vertebral surface in some ophiacanthid species and shape of the dorsal median groove. This study added to our knowledge several new vertebral features, but their importance for general ophiuroid taxonomy remains uncertain. For instance, the curved grooves, apparently characteristic for the family Ophiacanthidae, are absent in the genus *Ophiotoma* (Fig. 18L) that according to most other characters (see below) clearly belongs to ophiacanthids. Thus the application of the vertebral morphology in ophiuroid taxonomy is highly controversial and definite vertebral features that allow unambiguous taxonomic conclusions at the family and higher levels are scarcely known. For instance the group Euryalida besides having exclusively streptospondylous articulations, also characteristically completely lacks the distal keel (Fig. 16A). However, some ophiomyxid taxa, e.g. *Ophioscolex glacialis* Müller & Troschel, 1842 and apparently the ophiurid *Abysura*, also have vertebrae similar to the euryalid shape (Figs 17A, B). In contrast, vertebral peculiarities are useful for genus and species level taxonomy.



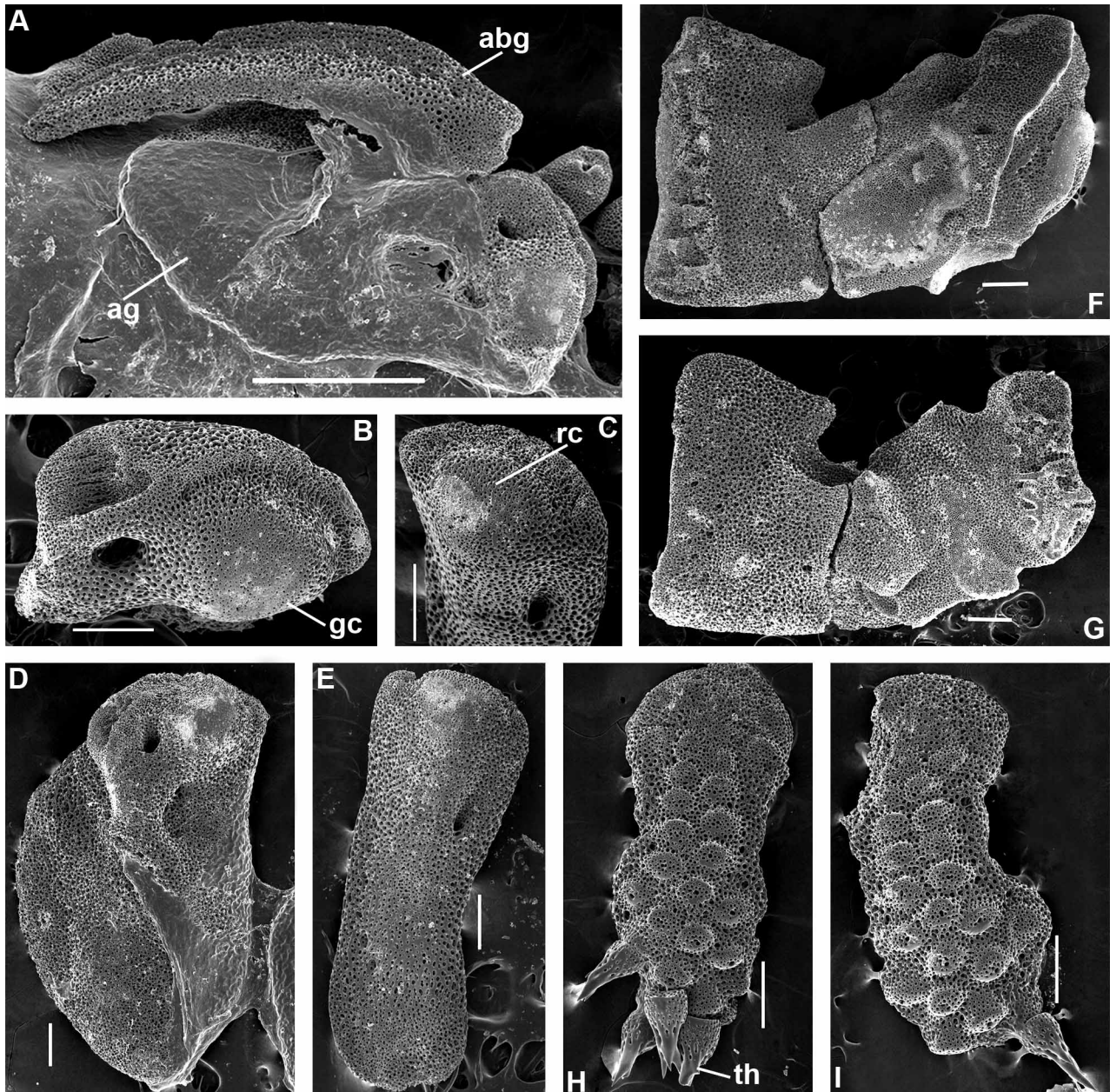


**FIGURE 79.** *Ophiobursa rudis* Lyman, 1878, ZMMU D-868, 12.5 mm dd, external views and details. A. dorsal view; B. ventral view; C. disk, dorsal view, details showing moderately defined radial shields; D. ventral view, details, E. interradian view, showing long genital slits; F. spine articulations, distal segments; G–H, spine articulations, most proximal segments; I. spine articulation, proximal segments, note massive curved lobe of the dorsalmost articulation; J. distal segments showing hooks; K. solid proximal spine, sectioned transversally; L. proximal spine; M. same, ventral view. Scale bars: F–M, 100  $\mu$ . Photos: A–E Tatiana Korshunova; F–M Alexander Martynov.

**Jaws and dental plates.** A detailed study of the ophiuroid jaws and dental plates by Murakami (1963), including analysis of a number of species from different families, discovered several promising patterns of potentially significant taxonomic importance. In this respect the dental plates of the families Amphiuroidae, Ophiocomidae, Ophionereididae and Ophiotrichidae can be mentioned, having similar large heart-shaped

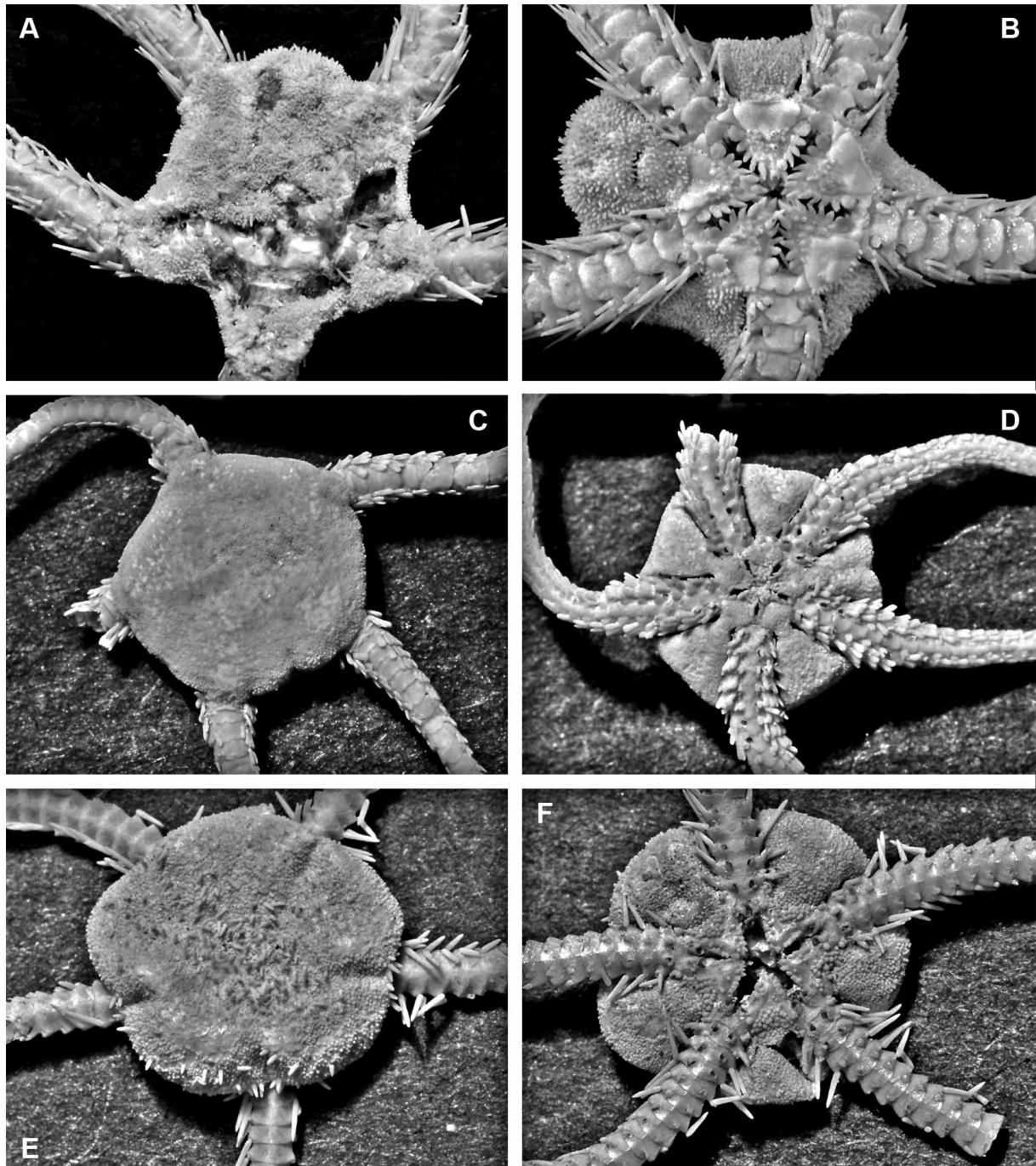


holes in the dorsal section (Fig. 14). Dental plate and jaw morphology was further used in some taxonomic works (Devaney 1970; 1974; A.M. Clark 1974; Baker & Devaney 1981; Bartsch 1982; 1983; 1987; Dearborn *et al.* 1996) and for a phylogenetic analysis (Smith *et al.* 1995), but like other ophiuroid internal features it remained only an addition to the main description, based on external features, and their taxonomic importance was never critically revised. The only exception became Wilkie (1980), who investigated dental plates and jaws of some ophiacanthids, ophiocomids, ophiodermatids and other taxa on comparative grounds and considered *Ophiocomina nigra* as belonging to the family Ophiacanthidae. Baker and Devaney (1981) did not agree with Wilkie's decision and transferred *Ophiocomina* back to Ophiocomidae.



**FIGURE 80.** *Ophiobyrsa rudis* Lyman, 1878, ZMMU D-868, 12.5 mm dd, details. A. articulated abradial and adradial genital plate in situ; B. articulation surface of the adradial genital plate, distal view; C. articulation surface of the radial shield, ventral view; D. adradial genital plate, dorsal view; E. radial shield, ventral view; F. jaw, abradial view; G. jaw, adradial view; H–I, two dental plates with few remaining teeth, showing variability. Scale bars: A, 1 mm; B–I, 300  $\mu$ . Photos: Alexander Martynov.





**FIGURE 81.** External views of the genera *Ophiolimna*, *Ophioconis* and *Ophiostritatus*. A-B, *Ophiolimna bairdi* (Lyman, 1883), ZMMU D-648, 9.5 mm dd; C-D, *Ophioconis vivipara* Mortensen, 1925, ZMMU D-834, 6.5 mm dd; E-F, *Ophiostritatus* sp., ZMMU D-839, 9 mm dd; For all species both dorsal and ventral views are given. Photos: Tatiana Korshunova.

The application of the dental plate shape is considerably limited by an underlying morphological similarity across the class and a number of convergences between apparently distantly related taxa, as evidenced by the taxa examined here. A striking example is the similarity of the dental plates between the genus *Ophiernus* (Fig. 11H) and various genera of the family Ophiacanthidae (Fig. 13). Ophiacanthids have been postulated to have an imperforate dental plate with elongated slit-shaped sockets (Murakami 1963; Bartsch 1987; Smith *et al.* 1995), which can now be confirmed for various ophiacanthid genera, including *Ophiotoma* and *Ophiotrema* (Fig. 13). Ophiacanthid elongated sockets correspond to the massive elongated

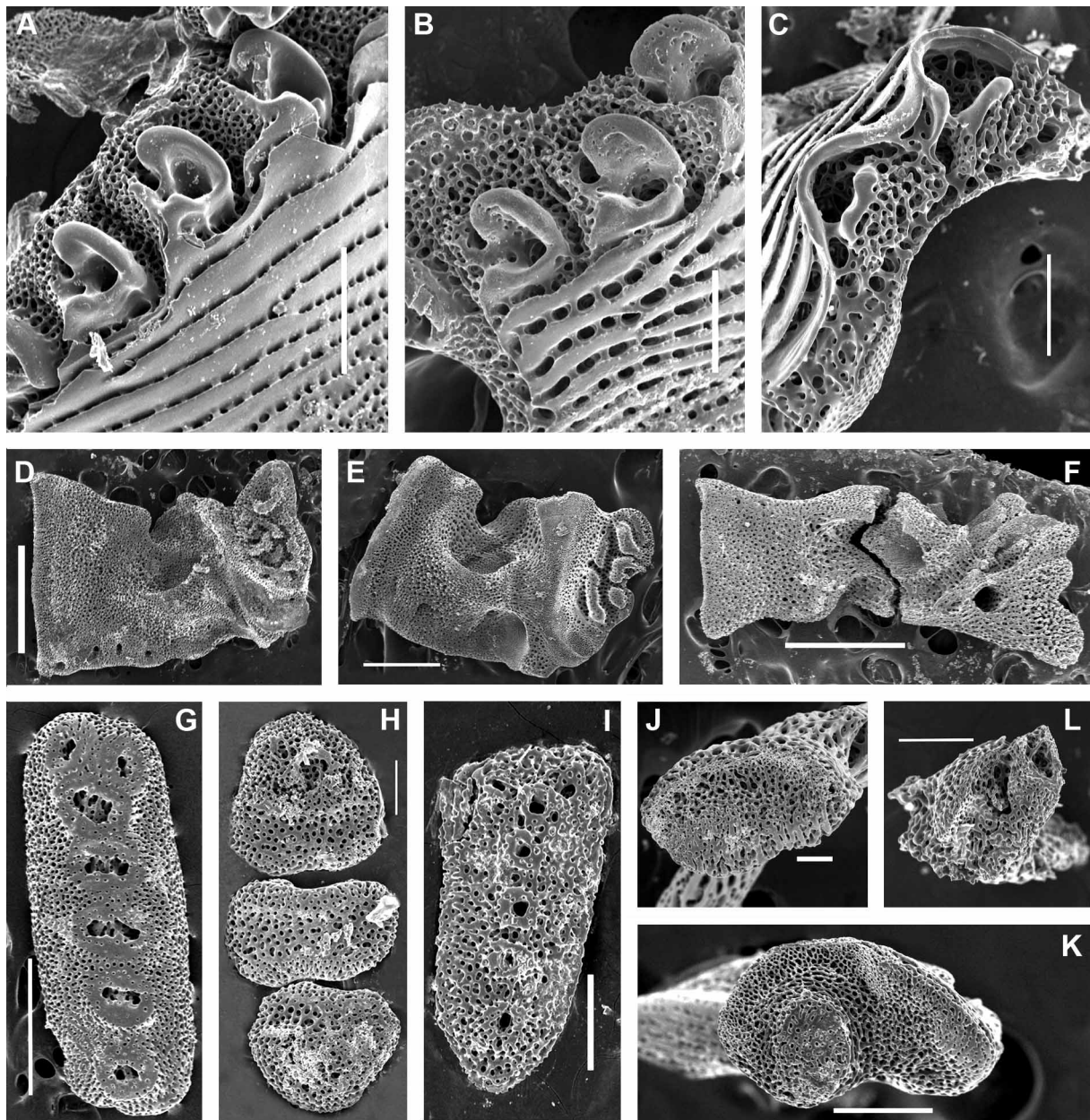
(not spiniform) teeth (Figs 15E–F). The genus *Ophiernus* has been considered to belong to the separate family Ophioleucidae (Matsumoto 1917; Fell 1960). Madsen (1983) has demonstrated a close relationship between Ophioleucidae and Ophiuridae and devaluated the former to subfamilial rank. My data do not support the Ophioleucidae at subfamilial level equal to the diverse Ophiurinae, since they are closely related to the ophiuroid genus *Ophiecten* (see below). A clear convergent nature of the dental plate of the *Ophiernus* species (Fig. 11H) is confirmed by the presence of the so called ophioleucid-group dental plate (with several irregularly placed small rounded sockets and narrow spiniform teeth) in other genera (Figs 11F, G; 82I). The pattern of the dental plate sockets thus depends to a considerable degree on the shape of the teeth. Conical, spiniform teeth require small rounded sockets, whereas more massive teeth need elongated sockets. Exceptionally massive, large quadrangular dorsal teeth of the families Amphiuroidae, Ophionereididae, Ophiocomidae, Ophitrichidae (Figs 15K–M, P) require in turn very large perforate sockets typically formed with heart-shaped openings (Figs 14A–M). Within Euryalida some taxa possess dental plates with several small rounded sockets, bearing numerous spiniform teeth (Figs 11A–C; 15A, D), e.g. species of the genera *Gorgonocephalus*, *Astrotoma*, *Asteronyx* (Murakami 1963; Bartsch 1982; present study), whereas some others, among them *Asteroschema inornatum* Koehler, 1906, have almost indistinct elongated sockets for massive teeth. Murakami (1963) has described well-developed elongated sockets for *Asteroschema yaeyamensis* Murakami, 1944 similar to *Ophiacantha* species.

The group of the ophiotomins in question including the genera *Ophioplexa* **gen. nov.**, *Ophiocymbium*, *Ophiologimus*, have dental plates characterized by rounded sockets (Figs 56M, N; 12E–J; 15B, C), whereas the nominal ophiotomin genus *Ophiotoma* (with ophiomyxid appearance of a soft, easily damaged disk) has the typical ophiacanthid elongated sockets (Figs 13D–F) and also well-defined ophiacanthid spine articulations. Thus, different representatives of both groups Euryalida and Ophiurida may possess quite similar dental teeth sockets, which generally fall into two main types – rounded and elongated. It is suggested that both elongated and rounded socket types appeared relatively early in the ophiuroid evolution, and all modern ophiuroids have inherited the potential for the appearance of both types. For instance, the dental plate of the large Antarctic ophiuroid *Ophionotus victoriae* Bell, 1902 has numerous spiniform teeth ventrally, and correspondingly a dental plate with numerous rounded sockets (Figs 11D; 77C, D, F), however there can be elongated sockets and more massive teeth in the middle of the plate, especially well defined in the juvenile stage of 7 mm dd (Figs 77H–G). Recently Stöhr (2005) showed that juvenile specimens of species of Ophiacanthidae and Ophiomyxidae have spiniform teeth. Earlier, Medeiros-Bergen (1996) has suggested that tooth type is a rather homoplastic character. These facts may further suggest the possibility of transformation of dental plates with the round sockets into the plates with elongated sockets, according to changes in the teeth shape.

Fragmented dental plates have been reported mostly within the groups Euryalida and Ophiomyxidae (here demonstrated for *Gorgonocephalus*, *Ophioscolex* and *Ophiomyxa*) (Figs 11A; 12A, B; 14P), but actually represent several different constructions. *Gorgonocephalus*, for instance has very irregularly fragmented dental plates, some of the separate plates placed even laterally (Fig. 11A), whereas *Ophiomyxa* possesses subequally fragmented regular pieces of the dental plate (Fig. 14P), similar to distantly related ophiidermatids (Fig. 14N). In *Gorgonocephalus*, the numerous teeth do not differ significantly from the oral papillae, and they have a tendency to be placed on separate irregular pieces (Fig. 15A). *Asteronyx* instead has an almost entire plate, but still appears to preserve traces of fusion of separate plates (Figs 11B, C). The genera *Ophioplexa* **gen. nov.** and *Ophiosparte* apparently also have these traces of plate fusion (Figs 56M–N; 65O). The type species of the genus *Ophioscolex*, *O. glacialis* has a somewhat intermediate condition, with a seemingly entire dental plate, but with clear traces of incomplete fusion (Figs 12A, B). The type species of the genus *Ophiobyrsa*, *O. rudis* has an entire plate, but irregular in outline, with numerous teeth on elevated sockets (Figs 80H, I), also similar to euryalids. Thus, due to their presence in two distantly related groups with other apparently ancestral features (e.g. thick skin layer), Ophiomyxidae and Euryalida, completely or partially fragmented dental plates are most likely a plesiomorphic condition. Fragmented dental plates have also been reported for other ophiuroids, e.g. ophiidermatids (Murakami 1963; present study), but compared to euryalids their dental plates are divided regularly (Fig. 14N). Fragmented plates are also present in *Amphilimna multispina* (Figs 39E, F) a taxon of controversial affinities. Some of the dental plates of



*Ophiotreta larissae* may sometimes be slightly subdivided into two pieces (Fig. 78E). These facts suggest an easy appearance of fragmented dental plates within advanced ophiuroids.

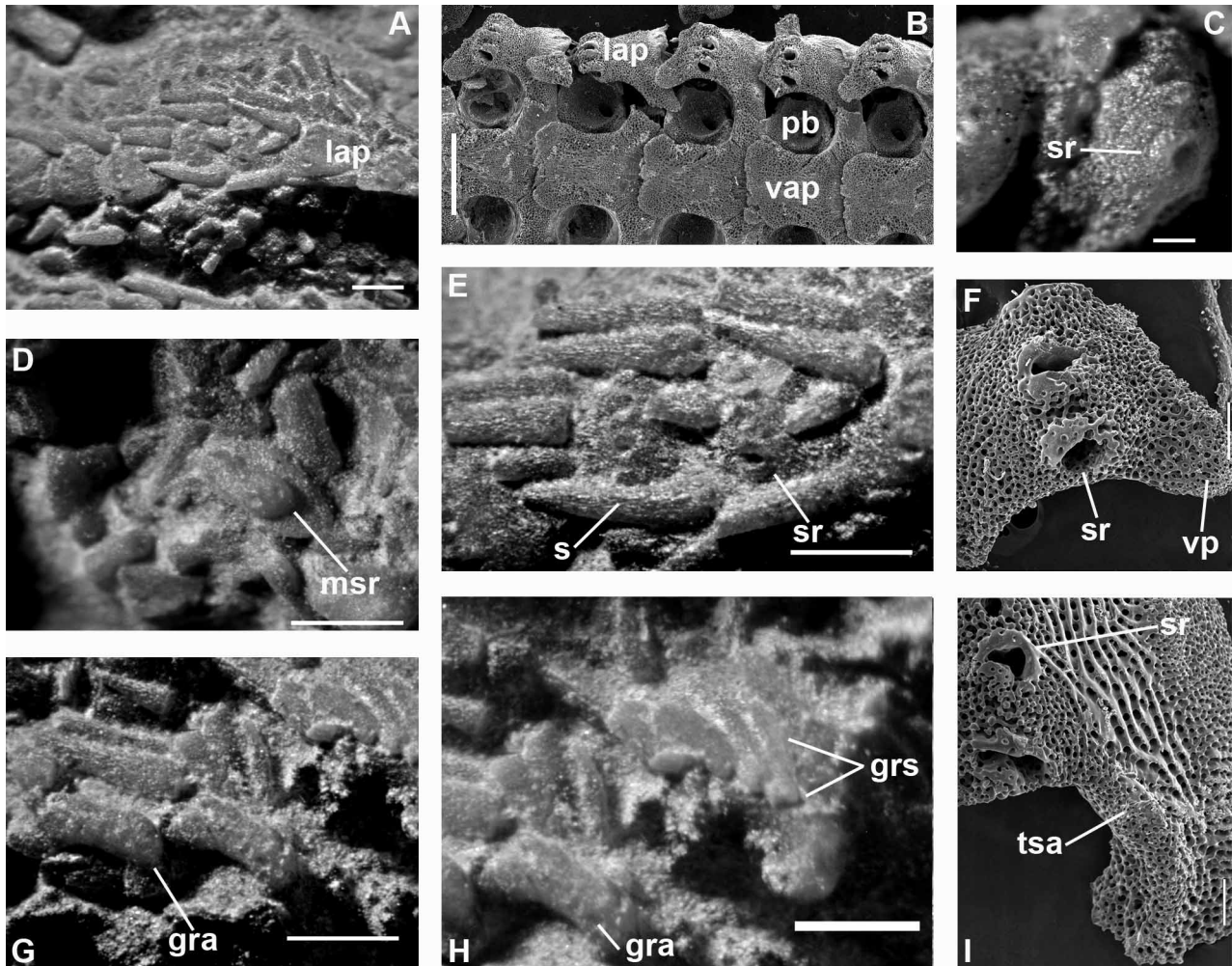


**FIGURE 82.** Details of the species of the genera *Ophiolimna*, *Ophioconis* and *Ophiostriatus*. A-C, Arm spine articulations; A. *Ophiolimna bairdi* (Lyman, 1883), ZMMU D-648, 9.5 mm dd; B. *Ophioconis vivipara* Mortensen, 1925, ZMMU D-834, 6.5 mm dd; C. *Ophiostriatus* sp., ZMMU D-840, 8.5 mm dd; D-F, Jaw, adradial view; D. *Ophiolimna bairdi* (Lyman, 1883); E. *Ophioconis vivipara*; F. *Ophiostriatus* sp., ZMMU D-840; G-I, Dental plate; G. *Ophiolimna bairdi* (Lyman, 1883), ZMMU D-648; H. *Ophioconis vivipara*, ZMMU D-834; I. *Ophiostriatus* sp., ZMMU D-840; J-L, Articulation surface of the adradial genital plate, dorsal view; J. *Ophiolimna bairdi*, ZMMU D-648; K. *Ophioconis vivipara*, ZMMU D-834; L. *Ophiostriatus* sp., ZMMU D-840, 9 mm dd. A, 200  $\mu$ ; B, 100  $\mu$ ; C, 300  $\mu$ ; D, 1 mm; E-G, 100  $\mu$ ; H, 120  $\mu$ ; 80  $\mu$ ; J-L, 100  $\mu$ . Photos: Alexander Martynov.

Some ophiacanthid species may even combine both elongated and rounded teeth sockets, since the ventral teeth, traditionally named in ophiuroid taxonomy as “apical papillae”, sometimes have a spiniform shape, e.g. in the genera *Ophiotoma*, *Ophiotreta*, *Ophiocamax*. In this case, the major part of the dental plate is occupied by elongated sockets, whereas ventrally there are a few rounded openings bearing apical papillae (Figs 13D, J). This feature is significantly more pronounced in the species of the family Ophiocomidae, where rounded sockets bearing apical papillae can reach almost half of the entire dental plate (Figs 14I, J; 15G). In



*Ophiorupta* **gen. nov.** about half of the dental plate is occupied by rounded sockets bearing spiniform ventral teeth, whereas dorsally the sockets are elongated and bear more massive and more typically ophiacanthid teeth (Figs 13A, B). Finally, in a species of the genus *Ophiotreta*, *O. larissae*, which was never considered within the Ophiotominae, but instead placed sometimes (e.g. Fell, 1960) in the genus *Ophiacantha*, clusters of spiniform teeth were found not only ventrally, but also dorsally (Fig. 78C), with few more elongated sockets in between (Figs 78D, E). Clusters of the ventral teeth and apical papillae have been reported also for the species of the ophiacanthid genus *Ophiocamax*, however their dental plates remain typically ophiacanthid (Fig. 13J). The general appearance of the oral frame of the genus *Ophiotreta* and dental plate morphology are rather similar to the nominal ophiotomin genus *Ophiotoma* (Figs 67B, E and 78B). In contrast, the numerous ventral teeth of the family Ophiotrichidae have definite sockets only at the edge of the dental plate (Figs 14L, M).



**FIGURE 83.** *Eugasterella thorni* Kesling, 1969 (Middle Devonian Arkona Shale, Ontario), representative of the Paleozoic subclass Oegophiurida (A, E, G–H, paratype UMMP 57479; C–D, paratype UMMP 57478a) and Recent species of the family Ophiomyxidae, *Ophioscolex glacialis* Müller & Troschel, 1842, ZMMU D-843, 18 mm dd (B, F) and *Ophioplexa condita* **gen et sp. nov.**, paratype ZMMU D-792, 17 mm dd, (I), details. A–B, E, ventro-lateral view of arm segments; C, F, arm spine articulations (of single-opening type), details; D, mostproximal articulation, presumably of double-opening type; G–I, ventro-lateral ridge bears groove spines (G, H) or tentacle scales (I). Scale bars: A, 500  $\mu$ ; B, 1 mm; C, I, 100  $\mu$ ; D–E, G–H, 500  $\mu$ ; F, 500  $\mu$ . Photos: A, C–E, G–H, Daniel Miller; B, F–I Alexander Martynov.

Despite the potential possibility of similar dental plates appearing within different taxa, in various families there are particular trends of dental plate morphology. For instance, within the large family Ophiuridae, small often irregularly placed sockets and corresponding spiniform teeth dominate. The family Ophiodermatidae has a dental plate predominantly fragmented into several plates with elongated sockets (Fig.



14N) (although *Ophiopeza spinosa* evidently has an entire dental plate (Fig. 14O). Fragmented plates have also been reported for various euryalid taxa (e.g. Fig. 11A), but compared to Ophiidermatidae they are evidently irregular. Heart-shaped dental plate dorsal holes have almost invariably been found in the various genera of the families Ophiocomidae, Ophionereididae, Amphiuridae and Ophiotrichidae (Fig. 14). At the same time absence of such holes in an amphiuroid genus, e.g. *Amphilimna* (Fig. 38B), can not be a reason for excluding it from the family Amphiuridae, since all other characters (general appearance of the disk and arm, oral frame morphology, shape of the arm spine articulations, jaw morphology, peculiarities of the genital plate and radial shield articulation surface, see below) (Figs 37–39) can be considered as amphiuroid features. Similarly, the dental plate of the genus *Ophiernus*, with elongated narrow sockets, does not suggest ophiacanthid affinities of the latter genus, nor a lesser general importance of the dental plate morphology for ophiacanthid systematics, since all other characters of species of the genus *Ophiernus*, including arm spine articulations clearly indicate that it is an aberrant member of the family Ophiuridae with an unusual dental plate. Thus, morphology of the dental plate on one hand should be used with caution in ophiuroid systematics, but in some cases it is a useful additional tool for understanding relationships between various groups. On the other hand, the shape of the spine articulations as suggested below is more conservative and therefore more useful for ophiuroid taxonomy, both at family and species levels, than the dental plate or jaw morphology.

**Arm spine articulations.** Arm spine articulation pattern, were initially suggested as an additional character to define the family Ophiacanthidae (Paterson 1985), but omitted in a phylogenetic analysis of the Ophiuroidea (Smith *et al.* 1995). Hess (1960 and further works) and recently Jagt and Kutscher (1998), Jagt (2000) and Kutscher and Jagt (2000) presented a SEM study of numerous ophiuroid species from late cretaceous deposits, suggesting utilization of the shape of the lateral arm plates including arm spine articulations in paleontological investigations. However without broad comparison with extant species the application of this character remained ambiguous. For instance, lateral arm plates of a species identified as *Ophioscolex? cretaceous* Kutscher and Jagt, 2000 according to the data of the present study in turn are identical with species of the genus *Ophiomyxa*. Thus, although arm spine articulation ridge shape is potentially a promising feature for ophiuroid taxonomy, a detailed analysis including most species from all ophiuroid families and groups of genera is needed to test its practical use.

In order to evaluate the taxonomic importance of the arm spine articulations it is necessary to estimate the consistency within already well-established ophiuroid families, whose monophyly or at least morphological homogeneity has never been challenged. One such family is the Amphiuridae containing more than 400 species. For the goals of the present study it is important that despite a considerable diversity, this family is rather uniform and possesses distinctive oral structures - two closely placed apical papillae (often called infradental papillae), confirmed with some minor exceptions for most amphiuroid genera and species (Figs 15K–M). Apart from two apical papillae, the general appearance of the oral structures is also similar across the family, the shape and position of the radial shields, and especially the general shape of the arms. Previous studies of the internal amphiuroid characters also have revealed several particular patterns. Matsumoto (1917) reported for various amphiuroid taxa, special winged jaws and a ball-like condyle of the adradial genital plate articulation surface. Murakami (1963) demonstrated that different amphiuroid species have a similar dental plate structure — few heart-shaped holes in the dorsal part of the plate and some depressions of the same shape towards the lower part of the plate. The dorsal holes are often divided by a narrow, median longitudinal septum. Although this feature was reported also for the families Ophionereididae, Ophiocomidae and Ophiotrichidae, it remained important evidence for a possibly close relationship of all these families because of its unique shape. Ecologically many amphiuroids also have a similar burrowing mode of life. Thus, the Amphiuridae, being a large, but rather uniform family, both in external and internal characters, may represent a good example for testing of the taxonomic value of the spine articulations. However, despite a general agreement, Thomas (1967) claimed that the paired infradental papillae are not always a reliable character and reported them also for the genus *Ophiopsila* (placed by Matsumoto 1915 within the family Ophiocomidae) and within two small families – the Ophiochitonidae and Amphilepididae.

Thomas (1967) studied the genus *Amphilimna* and found that the dental plate is imperforate and thus similar to the family Ophiacanthidae instead of Amphiuridae. Verrill (1899), when establishing the genus

*Amphilimna*, and further Koehler (1922a), instead considered this genus to be an amphiuroid. External ophiacanthid-like characters included slender spines, large tentacle pores bordered by slender scales, long oral papillae and a disc covered by elongated spines. In a further paper Thomas (1975) re-examined the ophiacanthid *Ophioprium cervicornis* (Lyman, 1883), which has long oral papillae, and considered *Ophioprium* and *Amphilimna* to be closely related genera. Based on this decision Paterson (1985) included *Amphilimna* into the ophiacanthid subfamily Ophiotominae. Thomas (1975) and Thomas & Schoener (1972) have added several species to the genus *Amphilimna*, including Indo-West Pacific species. Liao (1983) created the genus *Sinophiura* for one of these, *Amphilimna multispina* Koehler, 1922 and concluded that it belongs to the family Ophiuridae, because its genital plate is neither an ophiacanthid nor amphiuroid, but of an ophiurid type. Thus this case perfectly highlights the problems in ophiuroid taxonomy. In the absence of defined characters, every new discovered feature, even those that contradict most other characters, leads to significant changes of taxonomy.

Externally, *Amphilimna* (including “*Sinophiura multispina*”) is a typical amphiuroid, including the shape of the radial shields and their position within the disk (Figs 37B, C). The incisions of the radial shield area are very similar to those reported for the amphiuroid genus *Ophionephthys* (A.M. Clark & Rowe 1971) and form a pattern especially characteristic for amphiuroids (Fig. 37C). The general appearance of the oral structures (Figs 37D, H) is also essentially amphiuroid-like, not ophiacanthid- or ophiurid-like. It is especially evident in smaller specimens that have two characteristic amphiuroid apical papillae (Thomas & Schoener 1972). The presence of additional apical papillae (up to four) in the different species of the genus *Amphilimna* is not unique for the Amphiuroidae. Some species of *Amphioplus* clearly have three apical papillae (A.M. Clark 1970; personal observations). Elongated oral papillae of the type species of the genus, *Amphilimna olivacea* are shorter (and more typical for Amphiuroidae) even within a growth series of this and other species of the genus *Amphilimna*, e.g. *A. nike* (Schoener, 1967). Furthermore, elongated oral papillae are known for genera and species, whose position within Amphiuroidae has never been challenged, e.g. for *Dougaloplus derjugini* (Dyakonov, 1949) (Fig. 15L). Relatively long distal oral papillae in turn are not so unusual in different species of the genus *Amphiura* (e.g. *Amphiura otteri* Ljungman, 1872; *A. abyssorum* Norman, 1876, *A. sundevalli* (Müller et Troschel, 1842) and others). The large tentacle pores are especially not a reliable character, since the number of various taxa from distantly related ophiuroid families (e.g. Ophiomyxidae—most of the genera, Ophiacanthidae—*Ophioprium*, *Ophiotoma*, *Ophiotrema*, Ophiuridae—*Ophioleuce*, *Ophiernus*, as well as some genera with questionable family placement—*Abyssura*, *Ophiambix*, *Ophiophyllum*) have similar large pores. Within Amphiuroidae relatively large tentacle pores are also not an exceptional character. They have been reported for different species of the genera *Amphiura*, *Ophiocnida*, and *Amphioplus* (for example, *Amphiura borealis* (G.O. Sars, 1871), *Amphiura otteri* Ljungman, 1872, *Amphioplus cernuus*, *A. verrilli* (Lyman, 1879). Therefore this feature cannot be used as an indication of the relationship over large phylogenetic distances.

Another character suggested as an “ophiacanthid” feature for the genus *Amphilimna* are disk spines. Similarly to the large tentacles pores, the quite distinct disk spines are known, not only for the various genera of the family Ophiacanthidae, but also for several obviously unrelated groups, e.g. for some species of the genus *Ophiura* (Ophiuridae), some species of the genus *Ophiactis* (Ophiactidae), *Ophiomastix* (Ophiocomidae), and even for some ophiomyxids (*Ophiostyracium*) and euryalids (e.g. *Ophiocreas*). Within amphiuroids some genera also possess a variable degree of disk spine covering, for instance *Ophiocentrus* and *Amphiacantha*, and thus *Amphilimna* again does not represent a unique case. Thus, the only *Amphilimna* character that disagrees with other Amphiuroidae is the imperforate dental plate, lacking the characteristic dorsal heart-shaped holes, that was one of the main reasons for Thomas’ (1967) decision to place *Amphilimna* in the Ophiacanthidae. The current examination of the congeneric *Amphilimna multispina* Koehler, 1922 sheds some more light on the relationships of the genus. Surprisingly, unlike *A. olivacea*, the dental plate of *A. multispina* is fragmented and composed of three quite small pieces, each with relatively large perforated sockets (Figs 39E, F). This pattern is distinct from the typical dental plates of both Ophiacanthidae and Ophiuridae and represents a specialization of *Amphilimna multispina*. The dental plate of *Amphilimna olivacea*, although imperforate, is also not similar to Ophiacanthidae. Instead of ophiacanthid elongated



sockets, the holes in the dental plate of *A. olivacea* rather represent large amphiuroid-like structures that secondarily have become non-perforating (Fig. 38B). A similar process likely happened in the family Ophiolopidae, where some genera (e.g. *Ophiozonella*, *Ophiopenia*) (Fig. 14G) have dental plates with heart-shaped holes very similar to Amphiuroidae, whereas others (e.g. *Ophiolopis*) have depressed sockets (Fig. 14H). It should be noted that Liao (1983) was also incorrect in considering the genital plates of *Amphilimna multispina* as having features characteristic of the family Ophiuridae. The abradial genital plate of *A. multispina* is unusually twisted and the adradial genital plate has a distinct ball-like condyle (Figs 38O, P), similar to those already reported for the family Amphiuroidae (Matsumoto 1917). *Amphilimna olivacea*, the type species of the genus, also has a similar twisted genital scale (Fig. 38M) and thus the relationship of both species is evident. Unlike *Amphilimna*, members of the family Ophiuridae have a remarkable lateral ridge fused with the articulation surface of the adradial genital plate (Fig. 5). Finally, all known species of the genus *Amphilimna* (including *A. multispina*, “*Sinophiura*”) have a unique feature, not reported previously for any other ophiuroids — several special large, flattened arm spines on the most proximal segments under the disk have a somewhat fish gill-like appearance (Figs 37D-F; 39A-C). The aberrant shape of the abradial genital plate is most probably caused by these very broad scale-like spines.

Thus, the study of the spine articulations within the Amphiuroidae is especially important for resolving such highly problematic cases as the placement of the genus *Amphilimna*. Several closely as well as distantly related amphiuroid species from the genera *Amphiura*, *Amphiodia*, *Dougaloplus*, *Amphilimna*, and *Amphioplus* were used in the present study. These chosen genera cover most of the amphiuroid species diversity previously arranged in few informal groups, e.g. the *Amphiura*-, *Amphipholis*- and *Amphiodia*-groups (Fell 1960; A.M. Clark 1970). It was discovered that all these taxa have essentially similar arm spine articulations, which, generally can be described as subparallel ridges with two openings, usually similar in size (Fig. 31). Some taxa, e.g. *Dougaloplus derjugini* and *Amphilimna olivacea* (Figs 31D and 37J-L) have a muscle opening distinctly larger than the nerve opening. Some genera and species have ridges open on both ends (e.g. *Amphiura*, *Amphiodia*, *Amphilimna multispina*) whereas others have ridges closed proximally (e.g. *Amphiura sundevalli* and *Amphioplus*). Since the closing of the ridges may occur within a single genus (i.e. *Amphiura*) this variation is considered here as part of the amphiuroid arm spine articulation ridge pattern. Most importantly, the genus *Amphilimna*, with controversial taxonomic placement, clearly possesses an amphiuroid articulation pattern along with other above-mentioned amphiuroid features (compare Figs 31 and 37J-M).

Closely connected to the previous *Amphilimna*-case is another genus with a problematic placement, *Ophiopsila* Forbes, 1843. Traditionally this genus was placed within the family Amphiuroidae (e.g. Koehler 1907b), but since Matsumoto (1915; 1917) placed it in the family Ophiocomidae, based on studies of the internal morphology and the numerous “dental papillae”, its taxonomic position has never been discussed. Some *Ophiopsila* species, e.g. *O. aranea* Forbes, 1843, are actually somewhat similar to ophiocomid taxa in having a cluster of numerous apical papillae. However, other external features of the *Ophiopsila* species, i.e. disk appearance and very long arms, differ from the Ophiocomidae and rather point to Amphiuroidae. In the present study, two species of the genus *Ophiopsila* were examined, including for internal features (Figs 37A, G, N-P; 38C-E, I-K). The arm spine articulation ridges of both *Ophiopsila bispinosa* A.M. Clark, 1974 and *O. annulosa* (M. Sars, 1857) have a subparallel appearance, proximally with a ribbed area, distally with a peculiar constriction (Figs 37N-O), and do not display any similarities with other ophiocomid taxa, which have massive volute-shaped articulations of the ophiacanthid type (Fig. 29). The dental plate of *Ophiopsila bispinosa* has few heart-shaped holes dorsally, but lacks sockets for apical papillae ventrally (Fig. 38E). As was already mentioned, heart-shaped dental plate sockets are shared by several different ophiuroid families, i.e. Amphiuroidae, Ophionereididae, Ophiocomidae and Ophiotrichidae, and thus can not be evidence of the relationship of *Ophiopsila* and Ophiocomidae. The Ophiocomidae possess remarkable ventral sockets for the apical papillae (Figs 14I, J; 15G, H), which are absent in *Ophiopsila* (Figs 38C, D). Adradial genital plate and radial shield articulation surfaces of the *Ophiopsila* species have a ball-like condyle, which in turn differs from the asymmetrically placed condyle of the Ophiocomidae (compare Figs 38J and 8B). Thus, *Ophiopsila* and Ophiocomidae do not share any similarities. Instead, the arm spine articulation ridges of *Ophiopsila* are remarkably similar in shape to *Amphilimna olivacea*, type species of the genus *Amphilimna* (Figs 37K-P) and

both belong to the amphiuroid type. The oral frames of *Ophiopsila bispinosa* (varying from several apical papillae to paired amphiuroid-like, Figs 37G, 38C, D) and *Amphilimna olivacea* are also very similar (Figs 37D, H; 38A) and in turn very close to the amphiuroid *Dougaloplus derjugini* (Fig. 15L). The genera *Amphilimna* and *Ophiopsila* thus share several unique characters, including long spiniform tentacle scales (Figs 37D, E) and are closely related. Both these genera thus are proposed as aberrant amphiuroids with unique jaw and dental plate morphology, but typical amphiuroid disk and arm appearance and shape of the arm spine articulations.

Although most amphiuroid taxa have uniformly constructed apical papillae, there are a few remarkable androphorous aberrant taxa with a not so family-specific oral frame. Some of these genera, e.g. *Ophiopholis* Koehler, 1930, are rather clearly placed within amphiuroids since at least the females have more or less evident paired apical papillae (Koehler 1930; Mortensen 1933d), whereas others, first of all the genus *Ophiopsphaera*, have very modified oral structures, irregularly shaped pointed papillae and teeth and their relationship to the Amphiuroidae is therefore obscure. Despite having principally different oral and apical papilla patterns, the shape of the disk and proportions of the radial shields and general appearance of the arms is more similar to those of amphiuroids. Due to its ambiguous external appearance, *Ophiopsphaera* has been placed within three different families. Koehler (1904b) and H.L. Clark (1915) referred this genus to the family Ophiotrichidae, and Fell (1960) agreed with them. A.M. Clark & Rowe (1970) placed *Ophiopsphaera* within Amphiuroidae together with two other androphorous genera. Finally, Cherbonnier & Guille (1972) argued that *Ophiopsphaera* belongs in the family Ophiocomidae. The familial placement of *Ophiopsphaera* was not extensively discussed in that paper, which only mentioned that the structure of the oral papillae and the shape of the spines allowed placing this genus within Ophiocomidae, close to the genus *Ophiarthrum*. As already mentioned, *Ophiopsphaera insignis* has a similar shape of disc and arms to the Amphiuroidae, but has greatly modified oral papillae. Thus, the morphology of other structures is important for resolving the relationships of this genus. Arm spine articulations of the genus *Ophiopsphaera* (Fig. 31M) are essentially similar to those of the amphiuroid taxa and this aberrant genus should therefore be placed within the family Amphiuroidae.

The close relationship of the families Amphiuroidae and Ophiactidae, indicated by their almost indistinguishable articulation ridge patterns, has been suggested in the literature (e.g. Matsumoto 1915; 1917; A.M. Clark 1970) and ophiactids initially were considered as a subfamily of the Amphiuroidae (Matsumoto 1917). In some amphiuroids (e.g. in species of the genus *Amphioplus*) a tricuspid ophiactid single apical papilla may form as a variation. A somewhat unusual ophiactid, the genus *Ophiopholis*, has an irregular apical papilla, which can be single, double, or triple (Fig. 15O). In contrast, a suggestion by Smith *et al.* (1995) that *Ophiopholis* may belong in the family Ophionereididae is not supported by the current data. *Ophiopholis aculeata* arm spine articulations are despite their massiveness essentially similar to the other ophiactid genera (Fig. 32G). The relationship of the Amphiuroidae, Ophiactidae and other related groups will be the subject of further publications in the present series.

The large predominantly tropical family Ophiotrichidae is also of special interest for the present study, since all of the more than 100 species of this family share the quite unique feature of numerous ventral teeth (“dental papillae”) together with a complete lack of oral papillae. For some species similar dental plates and adradial genital plate-radial shield articulation have also been reported (Matsumoto 1917; Murakami 1963; present study: Figs 14L, M; 10A–G). Particular emphasis was put on examining several unrelated taxa of the family Ophiotrichidae, e.g. the common European *Ophiotrix fragilis* (Abildgaard in Müller, 1789) with typical ophiotrichid morphology, and several different genera, including species of the genera *Gymnolophus* and *Ophiothela*. All genera and species of the family Ophiotrichidae investigated in the present study have a special pattern of the arm spine articulations – obliquely placed ridges with peculiar smooth stereom at their borders (Figs 35A–G). Thus, the morphologically homogenous and most likely monophyletic family Ophiotrichidae also possess a great similarity of the articulation ridges across genera.

The particular shape of the articulations in “ophioleucid” species is somewhat different from the other Ophiuridae and in this respect family status may be warranted. However, articulations were discovered in all species of the genus *Ophiecten* (Figs 26A, B) which were essentially similar with the “Ophioleucidae”. The only principal difference between the ophioleucid and *Ophiecten* articulations is the position of the nerve



opening – laterally in the “Ophioleucidae” and distally in *Ophiocten*. However, *Ophiostriatius* shows an evident intermediate case between *Ophiocten* and ophioleucids (Fig. 26C). Remarkably, before the creation of a separate genus *Ophioleuce* Koehler, 1904 and the family Ophioleucidae (Matsumoto 1915; 1917), some species were originally described within the genus *Ophiocten* (for instance *Ophioleuce depressum* (Lyman, 1869)). In some ophioleucids (i.e. species of the genera *Ophioleuce* and *Ophiernus*) external similarity in the general disk and arm shape is evident even without arm spine articulation analysis. On the one hand, dental plates show great variability (e.g. several small irregularly placed sockets as in the genus *Ophiostriatius*, similar to the family Ophiuridae, or instead narrow, elongated, imperforate sockets of *Ophiernus*, similar to the family Ophiacanthidae), on the other hand the greatly elongated jaws of all ophioleucids are similar to most ophiurid taxa (Fig. 82F). The only reliable difference remains the position of the second tentacle pore – outside of the mouth in *Ophiocten* and within the mouth in ophioleucids. However, various species of the family Ophiuridae have been reported as having the second tentacle pore within the mouth, for instance *Ophionotus victoriae* (Fig. 77B), whose position within Ophiuridae has never been challenged. Furthermore, Paterson (1980) has described an aberrant, seemingly paedomorphic new genus and species *Uriopha ios* with both ophiurid and ophioleucid affinities. Based on the position of the second tentacle pore outside of the mouth, Paterson considered *Uriopha* and *Bathylepta pacifica* Belyaev & Litvinova, 1972 as belonging to the subfamily Ophiurinae instead of Ophioleucinae. *Uriopha* and *Bathylepta* both possess ophioleucid-type spine articulations, though considerably reduced due to the small size of the species. (Figs 26K, L).

Thus the position of the second tentacle pore is not a reliable character for distinguishing these families, and Ophioleucidae should be synonymized with Ophiuridae. Retaining ophioleucids as a subfamily of Ophiuridae, as was suggested by Madsen (1983), is also problematic since the entire ophioleucid group is closely similar to the ophiurid genus *Ophiocten*, especially evident from spine articulations pattern (Fig. 26). Moreover, although most studied species of the family Ophiuridae have a rounded muscle opening (Figs 24B–J), the type species of the genus *Ophiura*, *O. ophiura* Lamarck, 1816 (Fig. 23F), and *Ophiopleura borealis* Danielssen & Koren, 1877 (Fig. 23G), have angulated articulations somewhat similar to *Ophiocten*. *Ophiocten affinis* (Lütken, 1858) also has similar pattern (Fig. 24A), a species which has been transferred from the genus *Ophiura* to *Ophiocten* by Sumida *et al.* (1998). However, *O. affinis* rather shows a transitional morphology between the genera *Ophiura* and *Ophiocten* according to both external features and arm spine articulation ridge shape. Thus a close relationship is revealed of the genera *Ophiura* and *Ophiocten* with the ophioleucid group, and the synonymy of the latter with the family Ophiuridae is supported.

Traditionally the family Hemieuryalidae includes 11 morphologically heterogeneous genera. Matsumoto (1915; 1917) separated the subfamily Ophiochondrinae and Mortensen (1927) suggested that the genus *Ophiochondrus* may belong to the family Ophiacanthidae. But hemieuryalid taxonomy was never challenged. The heterogeneity of the family Hemieuryalidae is confirmed by the data presented here — the genera *Hemieuryale* and *Sigsbeia* have peculiar ridges differing from all other ophiuroid spine articulations (Fig. 36A, B), whereas the genera *Ophiochondrus* and *Ophiomoeris* possess typical ophiacanthid volute-shaped articulations (Figs 36E, F, G). The dental plate of the genus *Ophiomoeris* corresponds well with the ophiacanthid elongated non-perforating sockets (Fig. 13K). Thus, only genera closely related to the genus *Hemieuryale* should be retained in the family Hemieuryalidae, whereas at least *Ophiochondrus* and *Ophiomoeris* belong to the family Ophiacanthidae, being possibly closely related to Ophioplinthacinae, with more massive disk scales and lateral arm plates. According to their articulations and oral structures, the family Hemieuryalidae is rather similar to the Ophiolepididae (compare Figs 34D and 36A, B). For instance, some *Ophiozonella* species (e.g. Fig. 34D) have shortened ridges situated at an angle to each other. Further ophiolepidid evolution towards massive disk and arm plates and streptospondylous vertebral articulation may have led to the appearance of the hemieuryalid taxa.

Further support for the importance of the arm spine articulations for ophiuroid taxonomy will be presented by comparison of the families Ophiomyxidae and Ophiacanthidae and a special case of three genera from three apparently distantly related families, Ophiacanthidae, Ophiodermatidae and Ophiuridae.

As one of the important results of the present study, the key for identifications of the ophiuroid families or groups of families by patterns of the arm spine articulations. It is the first identification key of the ophiuroid

families using the arm spine articulations alone and therefore can not be completely free from flawless. Further accumulation of the information on the arm spine articulations of particular taxa will lead to improve of this key as well.

- 1(4) Arm spine articulations do not form a single unit — nerve opening placed separately and more ventrally in relation to the muscle opening. Spine nerve opening placed laterally
- 2(3) The small nerve opening placed immediately under the large muscle opening; muscle opening slit-shaped or round, with simple low border; distinct tubercles for hooks accompany spine articulation in many taxa ..... Euryalida (families Euryalidae, Asteronychidae, Asteroschematidae and Gorgonocephalidae)
- 3(2) The small nerve opening typically placed on the distinct angle in relation to the nerve opening on the dorsalmost articulation; muscle opening is rounded or slightly elongated with variously expressed lobes, sometimes curved; in small taxa nerve opening often indistinguishable; tubercles for hooks are always absent ..... Ophiuridae
- 4(1) Arm spine articulations form compact spine attachment units comprised of muscle and nerve openings of the double-opening type (in few cases the septum between muscle and nerve opening is reduced and the articulations secondarily single-opening)
- 5(10) Articulations are volute-shaped with distinct sigmoidal fold
- 6(7) Articulations are usually not immersed into the stereom ..... Ophiacanthidae
- 7(6) Articulations are usually immersed into the stereom considerably, placed within conspicuous depressions
- 8(9) The proximal border of the articulations are well separated from the lateral arm plate body; the volute-shaped lobe and the sigmoidal fold of the articulations are always well-defined ..... Ophiocomidae
- 9(8) The proximal border of the articulations are well integrated into the lateral arm plate body; the volute-shaped lobe and the sigmoidal fold of the articulations demonstrate various degree of a gradual reduction, from relatively well-defined in some taxa (e.g. *Ophioconis*, *Ophiopeza*) up to merely a small elevation (*Ophioderma*, *Bathypectinura*) ..... Ophiodermatidae
- 10(5) Articulations are not volute-shaped and the sigmoidal fold is lacking
- 11(12) Articulation shape is subrounded or somewhat indistinctly subparallel (e.g. genera *Ophiolycus*, *Ophiologimus*, *Ophiophrura*, *Ophiobyrsa*); in the latter case the dorsal lobe is considerably large compared to the almost indistinguishable ventral one ..... Ophiomyxidae
- 12(11) Articulation comprised from two distinct subparallel ridges (sometimes somewhat curved) both ventral and dorsal lobes are similar in size, either united proximally or not
- 13(14) Articulations possess single small indistinct opening, presumably muscle one; inside ridges borders bear strong triangular scars, the places of contact with the spine bases of corresponding shape ..... Hemieuryalidae
- 14(13) Articulations possess both well-defined nerve and muscle openings (in few cases septa between the openings reduced and resulting opening single and very large); inside ridges borders do not bear strong triangular scars, the places of contact of the spine base, which is also not triangular
- 15(16) Articulations usually placed within a distinct depression on the lateral arm plate or considerably reduced, left only vestiges of subparallel ridges ..... Ophiolepididae
- 16(15) No distinct depressions on the lateral arm plates articulation area
- 17(20) Articulation borders comprised from a considerably perforated stereom
- 18(19) Proximal articulation area distinctly depressed forming a saddle-shaped area; proximal border comprised from conspicuous riblets ..... Ophionereididae
- 19(18) Proximal articulation simply rounded, without depression and riblets ..... Ophiochitonidae
- 20(17) Articulation borders comprised from almost smooth stereom, in some taxa bearing very few scattered perforations
- 21(24) Articulations placed almost parallel to each other
- 22(23) Proximal articulation border comprised from wide array of irregular riblets; muscle opening distinctly larger than nerve one ..... Amphilepididae
- 23(22) Proximal articulation border (if any) is simply rounded or comprised from few regularly placed riblets, occupying narrow area; muscle opening similar in size to the nerve one ..... Amphieuridae and Ophiactidae
- 24(21) Articulations on the lateral arm plate placed at a distinct angle to each other ..... Ophiotrichidae



## Delineation of the families Ophiomyxidae and Ophiacanthidae with using of the newly applied characters

### The family Ophiacanthidae — traditional definitions and newly applied characters

The family Ophiacanthidae is one of the largest among Ophiuroidea and externally characterized by a disk covered with various spinelets in most species, often quite densely placed, long numerous arm spines, and oral papillae arranged without a gap in relation to the apical papilla; the latter typically is relatively narrow and conical (Koehler 1914; Fell 1960). Few taxa have been studied internally and have been reported to possess a dental plate with non-perforating, elongated, narrow tooth sockets (Murakami 1963; Bartsch 1982, 1987), relatively short jaws (Murakami 1963) and well developed adradial and abradial genital plates, and simple articulation surfaces of the adradial genital plate and radial shield in form of a low elongated elevation (Matsumoto 1917). Paterson (1985) has added to the diagnosis of the family a particular shape of the spine arm articulations with a distinct volute-shaped lobe dorsal to the muscle opening. However, his study was based on few ophiacanthid species and has not until now been supplemented by additional taxa. The genera *Ophiocymbium* and *Ophiomyces*, having a clearly different pattern of the articulations from the other ophiacanthid taxa, were nevertheless retained within the family Ophiacanthidae (Paterson 1985). Although the characteristic shape of the spine articulations is a promising feature for testing the monophyly of the Ophiacanthidae, further study (Smith *et al.* 1995) suggested parphyly of this family.

This study shows that most species from the well-known ophiacanthid genera, i.e. *Ophiacantha*, *Ophiolebes*, *Ophiosemmotes*, *Ophiocamax*, *Ophioplinthaca* and others, all have essentially similar articulations with a distinct distal volute-shaped lobe and the sigmoidal fold (Figs 28A–L; 45A–C; 47E–F; 50F–G; 58A–B; 59C–E; 60F–G; 68A–B; 69E–H; 70E–F; 78F, H). Although each of the listed taxa has peculiarities in the shape of the articulation ridge, general constructions are basically the same in all studied species. For instance, within eight studied species of the genus *Ophiacantha*, *O. spectabilis* G.O. Sars, 1871 (Fig. 28F) is characterized by a more circular shape of the articulations with closed proximal edge, whereas in *O. abyssicola* G.O. Sars, 1871 (Fig. 28E) they are more elongated with partially open proximal edge, but all species have a volute-shaped distal lobe.

Most of the genera of the subfamily Ophiotominae, including the type genus of the subfamily — *Ophiotoma*, and a genus that has recently been placed in the subfamily in question — *Ophiolimna*, were investigated in the present study. Some of these genera have not only the typical ophiacanthid articulation and sigmoidal fold, but also unfragmented dental plates with elongated slit-shaped sockets, holding relatively broad and massive teeth, for instance *Ophiotoma assimilis* Koehler, 1904 and *Ophiotoma alberti* (Koehler, 1896) (Figs 13D–F). Nevertheless, at least one internal character of *Ophiotoma assimilis* — a massive rounded articulation surface of the adradial genital plate — suggests an ophiomyxid appearance (compare Figs 6 A and B). Thus according to some important characters, i.e. spine articulations and dental plate, some of the studied ophiotomin taxa clearly belong to the family Ophiacanthidae, whereas the soft disk, large tentacle pores and shape of the genital plate articulation surface are possibly plesiomorphic characters indicating an ophiomyxid relationship.

In contrast, within the subfamily Ophiotominae there is another group of genera that is characterized by the disk covered with numerous small scales, without spinelets nor granules dorsally or ventrally. The dorsal arm plates are well-developed, apical papillae usually spiniform and forming a small cluster. Oral papillae differ between various genera of this group, for instance in *Ophiologimus* they are numerous and rather spiniform (Figs 48B; 49B), whereas *Ophiocymbium* has distinctly block-shaped distal oral papillae (Figs 40B, D). The present study has added to the characteristics of both genera, a poorly developed adradial genital plate and absence of the abradial genital plate (Figs 4G, H).

The position of these genera within the family Ophiacanthidae has never been challenged. This study has examined this group of genera for both arm spine articulations and other internal characters. At least all species of the genera *Ophiocymbium* and *Ophiologimus* do not possess any characters that would allow them being included in the family Ophiacanthidae. For instance, spine articulations in both *Ophiocymbium* and *Ophiologimus* lack the volute-shaped appearance and the sigmoidal fold characteristic of the family

Ophiacanthidae (including subfamily Ophiotominae). Instead, these two genera possess rounded or slightly elongated articulations with no nerve opening or a nerve opening at a small distance near the muscle opening (Figs 27H–N). Dental plates of both *Ophiocymbium* and *Ophiologimus* have few round sockets, bearing spiniform teeth (Figs 12E–J; 15B, C), and thus clearly differ from the relatively massive ophiacanthid teeth placed on the narrowly elongated sockets (including the type genus of the subfamily Ophiotominae, *Ophiotoma*) (Fig. 13). All Ophiacanthidae (including Ophiotominae s.str.) have a well-developed adradial genital plate with distinct abradial genital plate (Figs 6, 7; 47H; 67C; 78G), whereas *Ophiocymbium* and *Ophiologimus* have a poorly developed adradial genital plate (sometimes entirely reduced) without abradial genital plate (Figs 4G–H). Thus, at least *Ophiocymbium* and *Ophiologimus* should be excluded from the family Ophiacanthidae and placed in the family Ophiomyxidae, because they share with the latter similar spine articulations, dental plate, radial shield and genital plate. It is important to note that the articulations of the type species of the genus *Ophiocymbium*, *O. cavernosum*, are essentially similar to the articulations of *Ophiomyxa*, the type genus of the family Ophiomyxidae (compare Figs 27H and 27G).

Some ophiomyxid genera (e.g. *Ophioscolex*) also have poorly developed radial shield, adradial and abradial genital plates, as shown above for the type species, *O. glacialis* Müller & Troschel, 1842 (Figs 4I, U). The genus *Ophiocymbium* clearly has some similarities with *Ophioplexa* **gen. nov.** in general disk appearance: very small genital slits under the adoral shields, slit-like grooves between the proximalmost parts of the arms and the ventral disk, and poorly developed genital plate and radial shield. Unlike most genera of the subfamily Ophiotominae, the newly discovered *Ophioplexa* **gen. nov.**, despite presenting some superficial ophiacanthid features, e.g. numerous small disk scales without evident radial shields, combined with well defined dorsal arm plates, lacks any characters of true ophiacanthids (including subfamily Ophiotominae), i.e. the ophiacanthid sigmoidal fold, dental plate with regularly placed elongated sockets and well-developed genital plates and radial shield. Instead, the new genus has narrowly elongated arm spine articulations (Figs 56A–H), a distinct dental plate with several articulations and irregularly placed, small, rounded sockets, holding numerous spiniform teeth (Figs 56M–N), and extremely poorly developed adradial genital plate and radial shield (including total absence of the abradial genital plate) (Figs 4J, K, P).

### Relationships of the family Ophiomyxidae and predecessors of the family Ophiacanthidae

The family Ophiomyxidae encompasses a wide array of different genera and unlike many other ophiuroid families is quite hard to define. Most of the ophiomyxid genera are characterized by a soft disk and arms, poorly developed dorsal arm plates and large tentacle pores. At the same time, other characters vary considerably, e.g. some taxa have large conspicuous radial shields, i.e. *Ophiobyrsa* and *Ophiophrixus*, whereas *Ophioscolex* and *Ophiomyxa* have small radial shields, almost inconspicuous in the type species of the former genus, *O. glacialis*. Many ophiomyxid genera possess spiniform oral papillae and teeth (*Ophiobyrsa*, *Ophioscolex* and many others), whereas the type genus of the family, *Ophiomyxa*, has wide dentate oral papillae and teeth. The genera with questionable placement, e.g. *Ophiologimus* and *Ophiocymbium*, have always been placed in the family Ophiacanthidae instead of Ophiomyxidae, mostly because of their numerous well-defined disk scales and distinct arm plates (Matsumoto 1917; Koehler 1914; Paterson 1985). However, within species traditionally placed in the genus *Ophioscolex*, there is a special group of species, sometimes named as separate subgenus or genus, *Ophiolycus*, with similar characters to *Ophiologimus* and *Ophiocymbium*, including well defined disk scales and distinct, at least at some segments, dorsal arm plates.

In contrast to many other families of Ophiuroidea, the family Ophiomyxidae has a rather "unstable" morphology that can be referred to several apparently ancestral traits of this family. For instance, various genera of the family Ophiomyxidae may or may not have disk scales, or dorsal and ventral arm plates (as in Paleozoic Oegophiurida with an open ambulacral groove). Arm spine articulations are generally highly conservative within different ophiuroid families. In the family Ophiomyxidae they demonstrate a significant variability, but nevertheless fall into two major groups—double-opening and single-opening articulations (Fig. 27). Double-opening type clearly dominates within different apparently distantly related genera, e.g. *Ophiomyxa*, *Ophiolycus*, *Ophiobyrsa*, all possess double-opening articulations (Figs 27G–T), whereas others,



e.g. *Ophioscolex* s.str., have single-opening articulation (Figs 27A–C). However even the genus *Ophiomyxa* has the single-opening type of articulation distally (Fig. 27F). Some ophiomyxid genera however, possess both types of articulations, e.g. *Ophioplexa* **gen. nov.**, *Ophiocymbium* and *Ophiologimus*.

The apparently unusual conservatism of the volute-shaped articulation with sigmoidal fold found across approximately 30 ophiacanthid genera can be explained in this light as one of many already existing traits of Ophiomyxidae, which for some adaptive or constructive reasons became more successful than others. According to my results, the goal to delineate these traditionally well-defined families, Ophiomyxidae and Ophiacanthidae (Fell 1960; Paterson, 1985) is much more complicated than it may appear. Not only that a group of prima facie ophiacanthid genera, i.e. *Ophiocymbium*, *Ophiologimus*, *Ophiophrura*, *Ophioplexa* **gen. nov.**, share both ophiomyxid (dental plate with few round sockets, poorly developed radial shields and genital plates, arm spine articulations of different shape, but always without the volute-shaped appearance lacking the sigmoidal fold) (Figs 27G–T; 42E; 43A–C; 48C–E; 49E–F; 51H, I; 53A–F; 56A–H) and ophiacanthid (well-defined dorsal arm plate, hollow spines), but also the traditional ophiomyxid genus *Ophiolycus* (which in most recent publications is not distinguished from *Ophioscolex*) possesses what can be considered as ophiacanthid features (moderately defined dorsal arm plate and reduced amount of skin on the disk and arms) (Figs 71–74), features. However spines of the genus *Ophiolycus* are not hollow, almost solid and merely contain a very small lumen inside (Figs 72M; 73M). The genus *Ophioprium*, whose position within the family Ophiacanthidae has been never challenged (though H.L. Clark, 1915 has noted considerable differences of that genus from the rest of the ophiacanthids), according to the new results has in turn almost solid spines with small lumen, reasonably similar to the genus *Ophiolycus* and spiniform teeth, which undoubtedly should be sitting on small rounded sockets, and non-volute shaped arm spine articulations without sigmoidal fold, i.e. all ophiomyxid features (Figs 62A–B; C, G). Adoral shield papillae and adjacent oral papillae are remarkably long in *Ophiolycus*, *Ophiophrura*, *Ophiorupta* **gen. nov.** and *Ophioprium*. In this respect, it is necessary to define characters that can be named responsible for delineation of Ophiacanthidae as a group. The morphology of the hypothetical ophiacanthid ancestor thus implies the acquisition of the sigmoidal fold of the arm spine articulations, an entire dental plate with a reduced cluster of apical papillae and narrow, slit-shaped teeth sockets, well-defined adradial and abradial genital plates, fully formed dorsal and ventral arm plates, and reduced adoral shield papillae. Taken together, these characters are diagnostic for the family Ophiacanthidae, however most of them are already present in Ophiomyxidae, but as features scattered within different genera.

Reasonably well-defined genital plates are present in the genera *Ophiomyxa* and *Ophiolycus* (Figs 10, N; 74I), and a broad adradial genital plates were discovered in *Ophiobyrsa rudis* (Figs 80A–E), even more strongly developed than in many other ophiuroids. Slit-shaped teeth sockets are present on the fragmented dental plate in *Ophiomyxa*. Hollow spines, one of the most well-established features of the family Ophiacanthidae (Verrill 1899; Koehler 1914), is present in the genera *Ophiocymbium* and *Ophiologimus*, which otherwise have no shared features with the ophiacanthids. The genus *Ophiolycus*, which possesses reasonably well-defined dorsal (especially more distally) and ventral arm plates (Figs 71G; 73A, C) and a widened lobe for the arm spine articulations, especially in those placed dorsalmost (Figs 72A–D; 73F, I), however has almost solid spines. In addition, species of the genus *Ophiolycus* have thick disk skin, similar to the genus *Ophioscolex*, well-defined adoral shield papillae and narrow spiniform teeth. The articulations of the genus *Ophiolycus* also lack the sigmoidal fold (Figs 21C; 72A–D; 73F–I), one the most characteristic features of the family Ophiacanthidae (Fig. 21B). The dental plate of both *Ophiolycus purpureus* and *O. nutrix* possesses several irregularly placed small rounded sockets, very similar to the type species of the genus *Ophioscolex*, *O. glacialis* (Figs 12A–B; 74F). *Ophioprium*, *Ophiophrura* and *Ophiorupta*, genera traditionally assigned to the subfamily Ophiotominae, completely lack this sigmoidal ophiacanthid fold (Figs 51H, I; 53A–E; 62A–B; 63F–H; 64H–P). Other characters that disagree with the family Ophiacanthidae, are spiniform teeth and well-defined long adoral shield papillae of both *Ophioprium* and *Ophiophrura* (Figs 51E; 61E, G). The general appearance of *Ophiophrura liodisca* is very similar to *Ophiolycus* species and they have tiny, hardly conspicuous radial shields (Figs 51A, C; 73A, D). The articulations of *Ophiophrura liodisca* are somewhat subparallel in appearance and also similar to species of the genus *Ophiolycus* (Figs 51H, I; 73H, I), except with a broader lobe.

Thus, according to the new results, the majority of the Ophiotominae genera are not members of the family Ophiacanthidae, as defined above. On the contrary, other species, including the type of the genus *Ophiotoma* (type genus of the subfamily Ophiotominae) possess most of the “typical” ophiacanthid features, i.e. volute-shaped articulation with the sigmoidal fold, dental plate with narrow sockets, well-defined genital plates and considerably reduced adoral shield papillae.

Before reassessing the taxonomic position of the traditional Ophiotominae genera, it is necessary to discuss the general usefulness of the suggested internal characters for higher taxonomy of Ophiuroidea, because, as was already demonstrated throughout this paper, ophiuroid taxonomy can be understood only under such a general approach.

### General conclusions on ophiuroid taxonomy and the value of traditional and new characters

A significant part of Matsumoto’s definitions of the ophiuroid orders was based on the peculiarities of the adradial genital plate and radial shield articulation. For instance, Euryalida have been united with the family Ophiomyxidae in the order Phrynophiurida, characterized by an articulation “by simple face or a transverse ridge of either plate”, whereas the family Ophiacanthidae together with the family Hemieuryalidae were included in the separate order Laemophiurida, which has a very similar diagnosis as the order Phrynophiurida, distinguished mostly by well developed lateral and dorsal arm plates. Somewhat paradoxically, but well in agreement with the data of the present study, in the phylogenetic chapter of Matsumoto’s (1917: 372) monograph, he considered that “the gap between the Ophiomyxidae and Ophiacanthidae is rather not very important”. Byrne and Hendler (1989) and Byrne (1994) have argued for the validity of the group Phrynophiurida based on soft tissue characters but barely specified them. As shown here, the morphology of the hard structures is crucial for the ophiuroid taxonomy and Ophiomyxidae and Euryalida, for instance, do not share characters allowing unification of these groups. The presence of a large amount of skin on the disk and arms in all euryalids and some ophiomyxids (e.g. Figs 3D–E) is probably a plesiomorphic, asteroid feature, traced to the Oegophiurida as well (Figs 3A–B), whereas the peculiarity of the adradial genital plate-radial shield articulation and the shape of the arm spine articulations are different in these groups.

The strict distinction between a) simple genital plate - radial shield articulation without well developed condyles and sockets of the families Ophiomyxidae and Ophiacanthidae and b) well developed condyle(s) and pit of the more advanced ophiuroids (Matsumoto 1915, 1917; Smith *et al.* 1995) does not reflect a real diversity of these ossicles. For instance, the undoubtedly ophiacanthid genus *Ophiocamax* has a small but distinct ball-shaped elevation of the genital plate, corresponding to the similar socket on the radial shield (Figs 7E, F), despite the usually postulated presence of such a condyle only in more advanced ophiuroids of the orders Gnathophiurida and Chilophiurida. Adradial genital plate-radial shield articulations of the *Ophioplexa* **gen. nov.** and *Ophiocymbium* also can not be considered as having a simple surface; instead the radial shield has a peculiar excavation ventrally, corresponding to the genital plate distal edge and distally a fold and groove (Figs 4R, S) or an elevated condyle (Fig. 4E). They are, however, particular cases, whereas generally when describing the patterns of the adradial genital plate-radial shield articulation, Matsumoto (1917) missed the important fact that already both groups Euryalida and Ophiomyxidae had acquired a condyle-like elevation of the genital plate articulation surface (Figs 4A–E), which also appeared in different modifications and degree of development in various ophiuroids.

One of the largest ophiuroid groups is contained in Matsumoto’s order Chilophiurida, characterized as having “radial shield and genital plate... articulate each other by means of two articular condyles and one pit on both the plates”. Originally the Chilophiurida included the families Ophiolepididae (s.l., including Ophiuridae), Ophioleucidae, Ophiodermatidae, Ophiocomidae and Ophiochitonidae. Smith *et al.* (1995) restricted the Chilophiurina (as an infraorder) to include only the family Ophiuridae, whereas other former families of the order were distributed between three other infraorders. Matsumoto’s original characteristic of all these families “two condyles and one pit” was however retained in the character list in the Smith *et al.* (1995) paper and thus used in the cladistic analysis. In the present study, the adradial genital plate-radial shield articulation surface was examined by SEM in different taxa of every family for the first time. Three



different patterns of the adradial genital plate-radial shield articulation surface have been discovered, but generally they can not be described as “two condyles and pit on each plate”. Instead, all these groups have a single condyle on the adradial genital plate in different degrees of development, bordered by a groove and various numbers (usually 0–3) of folds, grooves and elevations on the radial shield.

Most of the studied taxa of the family Ophiuridae (including the Ophioleucidae), having a variety of external appearances, including *Ophionotus*, *Ophiopleura*, *Ophiura*, *Ophiocten*, always possess a distinctive ridge on the adradial genital plate lateral to the articulation surface (Figs 5A–K, M). This ridge serves for the attachment of the massive abradial genital plate (Figs 5T; 65H, I), articulating with the adradial genital plate in the family Ophiuridae and thus at the same level or above the articulation surface compared to most other ophiuroids. General appearance and corresponding portions that occupy the lateral ridge and condyle differ among ophiurid taxa, e.g. *Ophionotus*, *Ophiopleura* and *Ophioplinthus* have a very broad condyle and narrow lateral ridge (Figs 5A–D), whereas species of the genera *Ophiura* and *Ophiocten* have a short condyle and long lateral ridge (Figs 5E–I). Even in the diminutive ophiurid species *Ophiophyscis mirabilis*, the lateral ridge is still distinct from a small, elevated condyle (Fig. 5H). However in some *Ophiura* species the lateral ridge and condyle have almost fused forming a single articulated area (Fig. 5J).

Some taxa in the ophioleucid group (e.g. *Ophiostriatus* sp., *Ophioleuce* sp.) have a modified variant of the typical ophiurid articulation with strongly elevated condyle, distinctly bordered by a deep, curved groove (Figs 5I; 82L). However, the ophioleucid genus *Ophiernus* has instead the usual ophiurid pattern (Fig. 5G). Unlike the adradial genital plate, the ophiurid radial shield articulation surface has a principally different appearance in different taxa. *Ophiopleura* and *Ophioplinthus* have a single indistinct broad elevation bordered by a shallow groove (Figs 5L, N). *Ophiura sarsii* and *Ophiernus vallincola* both have two very distinct folds and corresponding distinct grooves between them (Figs 5P, R). Similar folds are also found on the radial shield articulation surface of *Ophiophyscis mirabilis* but orientated longitudinally instead of transversally (Fig. 5O). *Ophiura* sp. has one distinct and one unclear elevation with a shallow pit between them (Fig. 5Q). The most remarkable articulation surface is found in the radial shield of an *Ophioleuce* species, forming a deep excavation and corresponding indentation at the distal shield border (Fig. 5S). The compact articulation condyle of the adradial genital plate (Fig. 5I) corresponds well to this excavation of the radial shield. Thus, ophiurid adradial genital plate-radial shield articulation surfaces have a complicated structure including the presence of the lateral ridge fused with the adradial genital plate articulation surface, a feature possibly unique for the family, but do not fit within the strict definition of “two condyles and one pit”.

All studied species of the families Ophiidermatidae, Ophiocomidae and Ophionereididae possess very similar patterns of the adradial genital plate articulation surface — a single asymmetrically placed ball-like condyle forming a peculiar curve together with the adjacent plate border (Figs 8B, F, K, L). Abradial genital plates in species of these families are attached below the level of the articulation surface (Fig. 8E, F) and the attachment area (lateral ridge) is not fused with the articulation surface. The radial shield articulation surface forms a single distinct ball-like condyle in *Ophiocoma pica* and two indistinct condyles in *Ophiopeza spinosa*.

Species of the family Ophiolepididae possess massive genital plates and radial shields. The articulation surface of the adradial genital plate is represented by a broad, more or less distinct, condyle and bordered by a distinct groove (Figs 10J–O). The lateral ridge is poorly defined. The ophiolepidid radial shield articulation surface has either one well-developed and one indistinct condyle (Fig. 10I) or few unclear elevations (Fig. 10L). Thus other “chilophiurid” families also have different patterns of the genital plate-radial shield articulation hardly fitting with Matsumoto’s definition.

Strict utilization of the system suggested by Matsumoto or its modified variants by Fell (1962) and Smith *et al.* (1995) are even more contradictory in light of the present arm spine articulations analysis. For instance, according to Smith *et al.* (1995), the families Ophiocomidae and Ophiidermatidae have been included in two different infraorders, Gnathophiurina and Ophiidermatina respectively, whereas Matsumoto included both families together with Ophiuridae (under the name Ophiolepididae) and Ophiochitonidae in the order Chilophiurida. However the present study discovered for both Ophiocomidae and Ophiidermatidae spine articulations of the ophiacanthid type, although often in a considerably reduced variant in many ophiidermatids (Figs 29, 30). Further, *Ophiocoma nigra* belongs to the family Ophiocomidae according to

external characters, but lacks a typical ophiocomid-amphiurid dental plate with large heart-shaped holes (Fig. 14I), and is thus more similar in this character to Ophiacanthidae (Fig. 13). This fact has been used as a reason to include the genus *Ophiocomina* in the family Ophiacanthidae (Wilkie, 1980). However this decision is highly inconsistent with most other characters (including numerous dental papillae (Figs 15G–H)) that *Ophiocomina* shares with Ophiocomidae. Instead, the presence of the dental plate with the narrow, elongated sockets (Fig. 14I) and simultaneously numerous dental papillae in *Ophiocomina* make a relationship of Ophiacanthidae and Ophiocomidae more likely. Both Ophiocomidae and Ophiodermatidae in turn share a specific shape of the articulation surface of the genital plate — an asymmetrically placed ball-like condyle forming together with the adjacent edge of the genital plate a peculiar curve (Figs 8B, F, L; 82K). Members of the family Ophiacanthidae, even when they possess a weakly developed condyle as in the genus *Ophiocamax*, usually do not have the above mentioned peculiar pattern (e.g. Fig. 7B). However, as discussed above, a pattern of the adradial genital plate articulation surface somewhat similar to the Ophiodermatidae and Ophiacanthidae was discovered in the taxon with questionable placement *Ophiorupta discrepans* **comb. nov.** (Fig. 64E), ophiacanthid species *Ophiotoma alberti*, *Ophiolimna antarctica* (Fig. 47G) and especially in *Ophiolimna perfida* (Fig. 6E). In contrast, the ophiodermatid *Ophioderma* does not possess a clearly defined asymmetrical ball (Fig. 10D).

Smith *et al.* (1995) modified Matsumoto's system and separated Ophiomyxidae into the suborder Ophiomyxina, earlier proposed by Fell (1962), whereas Ophiacanthidae was united together with other ophiuroids in the suborder Ophiurina, but as a “paraphyletic complex” of unclear status. Most likely, a para- or polyphyletic status of the family Ophiacanthidae was caused first of all by inclusion of various genera, which actually belong to other, often distantly related families. As it was shown throughout the present paper, it is especially hard to delineate the families Ophiomyxidae and Ophiacanthidae and their separation into two orders is not warranted either.

### **Ophiacanthid genus *Ophiolimna* and their relationship to the family Ophiodermatidae: the strongest controversy of the ophiuroid taxonomy**

The following case of three externally similar genera currently considered within three different families highlights problems in ophiuroid taxonomy in general and elucidates the relationship of the families Ophiacanthidae and Ophiodermatidae. There are several genera with externally similar appearance, including fine dorsal granules, granules on ventral interradii and similar granules covering the adoral and/or oral shields, which have puzzled taxonomists through the history of ophiuroid systematics. These genera are *Ophiolimna* Verrill, 1899 (currently a member of the subfamily Ophiotominae) and *Ophioconis* Lütken, 1869, which, although currently considered within two different families (Ophiacanthidae and Ophiodermatidae respectively), have a long history of taxonomic association with each other (Figs 81A–D). Lyman (1878, 1882) described species belonging to both, in modern sense, genera *Ophiolimna* and *Ophioconis*, under the same generic name, *Ophioconis*. At the same time, the type species of the genus *Ophiolimna*, *O. bairdi*, was described by Lyman (1883) within the genus *Ophiacantha*.

Verrill (1899) created the genus *Ophiolimna* within the family Ophiacanthidae, but included only two species and did not discuss the relationship with *Ophioconis* and the Ophiodermatidae. H.L. Clark (1911) already suspected that some species of the genus *Ophioconis* really belong to the family Ophiacanthidae, and especially emphasized the similarity between *Ophiacantha* and his species *Ophioconis papillata*. Despite this, the genus *Ophioconis* was placed by him within the family Ophiodermatidae, at the beginning of the classification, thus separate from ophiacanthids. Simultaneously in the same work, Clark placed *O. bairdi* (Lyman, 1883) and *O. lambda* (H.L. Clark, 1911) within the genus *Ophiacantha* (and referred the family Ophiacanthidae close to the end of the classification), but a close resemblance to *Ophioconis* was mentioned. Clark (1911: 230) even stated that “This species is very near *Ophioconis*, and it is virtually impossible to find any character which would warrant their being placed in separate families...”. Matsumoto (1917) for the first time clearly distinguished the genera *Ophioconis*, which he referred to the Ophiodermatidae, and *Ophiolimna*, which he considered within Ophiacanthidae. Matsumoto also further divided *Ophioconis* into three genera,



*Ophioconis* s. str., *Ophiuroconis*, and *Ophiurodon*. The latter two genera he placed into the subfamily Ophiarachninae, whereas *Ophioconis* s. str. was placed into Ophiidermatinae s. str. In the phylogenetic part of his work, most interestingly, Matsumoto considered Ophiarachninae as a very close taxon to the family Ophiacanthidae.

Almost half a century later, Dyakonov (1954) created the genus and species *Toporkovia fragilis* based on a single small imperfect specimen and placed it within the family Ophiidermatidae. Further this genus was included by Fell (1960) into his "Synoptic keys..." in the family Ophiidermatidae, thus supporting Dyakonov's decision. Soon afterwards, Fell (1961) considered the Antarctic species *Ophioconis antarctica* (Lyman, 1878) as a member of the genus *Toporkovia*, as illustration of the idea of bipolarity. Stöhr & O'Hara (2003) mentioned the great similarity as well as the differences between *Ophiolimna antarctica*, previously considered as Ophiidermatidae, and *O. bairdi*, which was always considered as a member of the family Ophiacanthidae. O'Hara and Stöhr (2006) gave a detailed taxonomic history of the genus *Ophiolimna* (including *O. antarctica* and *O. papillata*) considering it as member of the family Ophiacanthidae, and finally considered *Toporkovia* as synonym of this genus. However, until now there are no definite conclusions on the relationship between *Ophioconis*, currently placed in the Ophiidermatidae, and *Ophiolimna*, currently in Ophiacanthidae. Besides some minor differences in arm spines, tentacle scales etc., the presumably ophiidermatid *Ophioconis* is well distinguished from *Ophiolimna* by the presence of strong, very wide hyaline teeth. However, some species, e.g. *Ophioconis miliaria* Lyman, 1878 do not possess such teeth, at least in a well-defined condition. It may therefore be that *Ophiuroconis* is distinguished from *Ophioconis* by the triangular and pointed instead of widened teeth. In contrast, *Ophiurodon* Matsumoto, 1915 is currently recognized as a synonym (or genus with doubtful status) of *Ophioconis* (A.M. Clark 1965; A.M. Clark & Rowe 1971; Baker & Devaney 1981).

Besides the above mentioned taxa, there is another group, some genera of which are externally very similar to the genera *Ophioconis* and *Ophiolimna*, but have never been considered close to the latter or synonymized with it. It is the ophioleucid group of the family Ophiuridae. The external similarity between some ophioleucids, e.g. *Ophiostriatus* from one hand and *Ophioconis* and *Ophiolimna* from another (Fig. 81), is remarkable and includes dorsal and ventral fine granulation, dorsal spinelets intermingled with granules, and striations on the lateral arm plates (Stöhr & O'Hara 2003; O'Hara & Stöhr 2006; present study). The genus *Ophiostriatus* was placed within the group Ophioleucidae (e.g. Madsen 1983), and therefore at least formally was never considered as an ophiacanthid or ophiidermatid. Thus, these three genera, *Ophiolimna*, *Ophioconis* and *Ophiostriatus*, represent a very interesting case, because they have an exceptionally similar external appearance, but are currently considered within three different families. Obviously it is necessary to use additional characters to enlighten the relationship of these three genera. Conclusions of such an investigation may serve as a test for the validity of the spine articulations as a character as well. In the present study many of the microstructural characters of *Ophiolimna bairdi*, *O. antarctica*, *Ophiolimna perfida*, *Ophioconis vivipara* Mortensen, 1925, *Ophioconis permixta* Koehler, 1905, *Ophioconis cf. cincta* Brock, 1888, *Ophioconis cupida* Koehler, 1905, *Ophioconis* sp., *Ophiostriatus striatus* (Mortensen, 1933) and an undescribed species of the genus *Ophiostriatus* were used. The shape of the jaws is very similar between *Ophiolimna* and *Ophioconis* in proportions and especially in the presence of a peculiar folded area on the proximal adradial surface (Figs 82D, E). In contrast, the shape of the jaws of *Ophiostriatus* is greatly different from both *Ophiolimna* and *Ophioconis*: it is very elongated and without proximal folds (Fig. 82F). The dental plate of *Ophiolimna* is entire, imperforate, with regular elongated grooves (Fig. 82G). *Ophioconis* also has an imperforate dental plate, with very weakly developed regular transverse grooves, however the dental plate is naturally fragmented into three pieces (Figs 82H; 15J). The dental plate of *Ophiostriatus* is entire, but perforated by several small round holes, arranged quite irregularly, in single, two or three rows (Fig. 82I). The articulation between adradial genital plate and radial shield differs between all three genera. The articulation surface of the adradial genital plate in *Ophiolimna bairdi* has an elongated, ill-defined elevated ridge (Fig. 82J), *Ophioconis* possesses a well developed asymmetrically placed ball-like condyle, which is clearly separated from the remaining articulation area (Fig. 82K), whereas *Ophiolimna antarctica* (Fig. 47G) and *O. perfida* (Fig. 6E) have an intermediate condition between *O. bairdi* and *Ophioconis*. Finally, *Ophiostriatus*

has a quite complicated structure appearing as a horseshoe-shaped deep groove around the small but distinct condyle (Fig. 82L).

On the articulation surface of the radial shield in *Ophiolimna* there is an elongated elevated ridge (Figs 6M; 47I), in *Ophioconis* several indistinct longitudinal folds, in *Ophiostriatus* also a quite complicated structure with two separate pits and with a condyle in between. The spine articulations of *Ophiolimna* and *Ophioconis* are very similar, both volute-shaped with large muscle opening and small nerve opening (Figs 82A, B). The differences are mainly in the larger and more defined lobe of the articulation in *Ophioconis*, with a more round nerve opening than a rather slit-shaped one in *Ophiolimna*. In other species of *Ophioconis*, *Ophioconis* sp., this lobe is even more developed, whereas the opposite walls of the articulations are more reduced, a condition that is very similar to some “advanced” ophiodermatids (Fig. 30A). Unlike *Ophiolimna* and *Ophioconis*, the articulations of *Ophiostriatus* are very different in having a peculiar irregularly rhomboid shape comprised of a very large muscle and small nerve openings (Fig. 82C). Other special features of the articulations of *Ophiostriatus* include the characteristically curved distal wall fused with the edge of the lateral plate. Considering all above listed characters, *Ophiolimna* is a member of the family Ophiacanthidae. *Ophioconis* is similar to *Ophiolimna* not only in the external characters, but also in the shape of the jaws, the presence of folds on the adradial surface, and an imperforate dental plate with elongated sockets. However, *Ophioconis* has a peculiar character of the family Ophiodermatidae, the fragmented dental plate. Also the hylenated teeth of the genus *Ophioconis* are notable. The articulation surface of the adradial genital plate of *Ophioconis* has a well-developed asymmetrical ball-like condyle and is also more similar to the Ophiodermatidae than to Ophiacanthidae. At the same time, the arm spine articulations of *Ophioconis* are very similar and not distinguishable from *Ophiolimna*. All internal characters of the genus *Ophiostriatus* are very different from *Ophiolimna* and *Ophioconis*. The shape of the jaws and dental plate of *Ophiostriatus* are typical for the family Ophiuridae and the ophiroleucid group. The articulations of *Ophiostriatus* are essentially concurrent with that group too. Thus, considering these three genera, it is possible to conclude that the significant similarity of *Ophiostriatus* on the one hand and *Ophiolimna* and *Ophioconis* on the other hand is clearly a remarkable case of convergence. The external similarity between *Ophiolimna* and *Ophioconis* is well supported by the shape of the articulation tubercles and partially supported by internal characters. The similarity includes small details, essentially alike between all studied species of *Ophiolimna*, and several species of *Ophioconis* (having a fragmented ophiodermatid dental plate and very wide hyaline teeth), including the general appearance of the articulations, which have a peculiar bridge of narrow stereom strips connecting the proximal border of the articulation with the striated stereom structure at a considerable angle (Figs 45A–F; 82A–B) (connecting ridge). A presupposition that such structures, similar in several complicated details, have evolved independently is hardly plausible. Whereas all external and internal characters of *Ophiolimna* do not contradict those known for the family Ophiacanthidae, the fragmented dental plate and genital plate articulation surface of the genus *Ophioconis* are shared with the family Ophiodermatidae. A fragmented dental plate, being a plesiomorphic feature, has also reappeared within some other advanced ophiuroid families, e.g. Amphiuroidae (*Amphilimna multispina*, present study). Thus, the genus *Ophioconis* is an intermediate taxon between two large, well-defined traditional families Ophiacanthidae and Ophiodermatidae.

The presence of a similar articulation surface of the adradial genital plate in other *Ophiolimna* species, *O. antarctica* (Fig. 47G), *O. perfida* (Fig. 6E) and some other ophiotomin ophiacanthids (e.g. *Ophiotoma*) (Fig. 6C) make the limits between Ophiacanthidae and Ophiodermatidae even more uncertain. It is also one of the reasons for the long taxonomic association and confusion between the species now considered within *Ophiolimna* and *Ophioconis*. Therefore, phylogenetically, the large and well-defined, mostly tropical family Ophiodermatidae is rooted within the deep and cold water genus *Ophiolimna* of the family Ophiacanthidae. At least one studied ophiodermatid, e.g. *Ophiopeza spinosa*, has an entire dental plate (Fig. 14O) and thus, even with regard to this character, these families are poorly distinguished. Another consequence of this conclusion is that one of the peculiar characters of almost all ophiodermatids, the fine granulations of both the dorsal and ventral sides (including oral and adoral shields) are similar to the finely granulated disk surface and several papilla-like tubercles on the oral shields of the genus *Ophiolimna*. The similarity of the spine



articulation between the genera *Ophiolimna* and *Ophioconis* agrees with the similarity of other internal characters and therefore can be used as an indication of the relationship. Thus, three large ophiuroid families, one predominantly deep-water—Ophiacanthidae—and two tropical shallow-water—Ophiodermatidae and Ophiocomidae—are closely related and have some intermediate genera. Separation of these families into different orders, infraorders or even superfamilies is highly artificial.

Other families assigned to the different superfamilies of the infraorder Gnathophiurida, i.e. superfamily Gnathophiuroidea (families Amphiuridae, Ophiactidae and Ophiotrichidae) on the one hand and the superfamily Ophiocomoidea (families Ophiocomidae and Ophionereididae) on the other (Smith *et al.* 1995) have a clearly intermediate group, the family Ophionereididae, externally still very similar to the family Ophiocomidae, but with respect to the jaw morphology and the arm spine articulation ridge pattern similar to the family Amphiuridae (compare Figs 33A–C and 31). The family Ophiolpididae considered by Matsumoto (1917) (in broad sense together with the taxa of the family Ophiuridae) within the order Chilophiurida and separated by Smith *et al.* (1995) into an independent infraorder, has an almost typical amphiuroid-ophiactid dental plate (especially in the genus *Ophiozonella*) and subparallel reduced articulations (Figs 34B–D), and appears part of the Amphiuridae-Ophionereididae line.

### The genus *Ophiosparte* and higher ophiuroid taxonomy

There are more examples showing that situations with "ambiguous" boundaries between apparently distantly related families are quite usual within ophiuroids. In this respect the conservative suggestion of Mortensen (1927), to use only two groups (orders) for all recent Ophiuroidea — Euryalida and Ophiurida —, i.e. Müller and Troschel's (1842) system, agrees better with the results of the present study. However, even if according to most characters euryalids are well distinguished from other Ophiuroidea, the arm spine articulation analysis discovered an essential similarity of the family Ophiuridae with euryalids. Smith *et al.* (1995) suggested a possible relationship between the Euryalida and the ophiomyxid subfamily Ophiobyrinae, which, however, was not supported by additional characters, and the latter group was retained as an incertae sedis. Lateral arm plates, including spine articulations, figured by Byrne and Hendler (1988) in *Ophiobyrsa* and *OphiobyrSELLA*, typically have ophiomyxid double-opening articulation. This is confirmed in the present study for the type species of the genus *Ophiobyrsa*, *O. rudis* Lyman, 1878 (Figs 79F–H). The subfamily Ophiobyrinae is similar to Euryalida due to a convergence in the streptospondylous vertebral articulation. However, under Mortensen's and Fell's (1960) system, most ophiuroid families are still only defined by external characters, which has led to the numerous mistakes in assignment of various genera to a particular family that are repeatedly mentioned in the present paper.

The family Ophiuridae that gave its name to the order Ophiurida has similar arm spine articulations to the order Euryalida. Externally, euryalids and ophiurids are very different. *Ophiosparte* Koehler, 1922, an enigmatic taxon early referred either to Ophiacanthidae (Koehler 1922a; Paterson 1985) or to Ophiomyxidae (Dearborn *et al.* 1996) is especially interesting in this regard. However, a number of characters, i.e. true arm comb (papillae placed on the genital plates (Figs 65F, G), arm spine articulations, spines, genital plates and radial shield, and also a set of numerous comb-like tentacle scales (Fig. 65), suggest that *Ophiosparte* is a member of the family Ophiuridae. The special pattern of the *Ophiosparte* vertebral articulation surface ("comb"-shaped) (Figs 19A, D–F), a variant of the zygospondylous articulation, also clearly place it in the Ophiuridae, since that state is not found beyond this family. Somewhat similar small papillae bordering the genital slits in the species of the genus *Ophionereis* are clearly a convergent feature, because in both *Ophiosparte* and Ophiuridae, and unlike *Ophionereis*, the arm comb papillae sit on the genital plates and form a peculiar incision laterally to the insertion of the most proximal arm segments. *Ophionereis* papillae are always placed only along the borders of the genital slits and never on the genital plates near the insertion of the arm into the disk. The arm spine articulations of *Ophiosparte gigas* are clearly a euryalid feature with the distantly placed nerve opening on the lateral plate and a spine nerve opening correspondingly shifted to the latero-ventral side of the spine (Figs 23A–E). Massive well-developed condyles on both adradial genital plate and radial shield articulation surfaces (Fig. 5B) are also similar to the euryalid condition (Figs 4A–D). The

numerous long, spiniform teeth of *O. gigas* do not differ from the adjacent oral papillae (Figs 65L–N) and are very similar to some euryalids, e.g. the genus *Gorgonocephalus* (Fig. 15A). However, the genus *Ophiosparte* also has all the synapomorphies of the family Ophiuridae, including the true arm-comb (compare arm combs in *Ophiosparte*, Fig. 65F and in *Ophiura sarsii*, Fig. 65G) and lateral ridge of the adradial genital plate, fused with the articulation surface (Figs 5B; 65H, I), present in most ophiurid taxa in various degree of development (Figs 5A–K, Ir). In this respect *Ophiosparte* may be considered as an earlier offshoot of an ancestral group common with a euryalid, before acquiring the streptospondylous vertebral articulation and other arm features allowing a climbing mode of life. Thus *Ophiosparte gigas* appears to be an intermediate between the Ophiuridae and Euryalida.

Most of the other ophiuroid families (including Ophiomyxidae, Ophiacanthidae, Ophiodermatidae, Ophiocomidae, Ophionereididae, Ophiochitonidae, Amphilepididae, Amphiuroidae, Ophiactidae, Ophiolepididae, Hemieuryalidae, Ophiotrichidae) form a compact group with numerous intermediate taxa even between apparently very different families as for instance Ophiomyxidae and Ophiacanthidae (genera *Ophioplexa* **gen. nov.**, *Ophioprium*, *Ophiorupta* **gen. nov.** and others) or Ophiacanthidae and Ophiodermatidae (*Ophiolimna* and *Ophioconis*). The intermediate status of these genera, as confirmed by complicated microstructural features of the spine articulations compared to peculiarities of the external morphology, taken together makes the independent evolution of these features hardly possible. An appropriate name for this higher ophiuroid group will be suggested after a detailed analysis of other ophiuroid groups, which will be presented in further publications of this series.

### Renewed diagnoses of the families Ophiomyxidae and Ophiacanthidae and conclusions on their generic composition

According to the results of the present study, the ophiacanthid subfamily Ophiotominae as proposed by Paterson (1985) is a highly heterogeneous group. This is caused not only by the complications in distinguishing the Ophiotominae from the family Ophiomyxidae, but principally by a number of previously included genera from distantly related families. Paterson (1985) listed the following genera within Ophiotominae: *Amphilimna* Verrill, 1899, *Ophiocymbium* Lyman, 1880, *Ophiodaces* Koehler, 1922, *Ophiodelos* Koehler, 1930, *Ophiolimna* Verrill, 1899, *Ophiologimus* H.L. Clark, 1911, *Ophiomedeia* Koehler, 1906, *Ophiophrura* H.L. Clark, 1911, *Ophiopristis* Verrill, 1899, *Ophioprium* Verrill, 1899, *Ophiosparte* Koehler, 1922, *Ophiotoma* Lyman, 1883, and *Ophiotrema* Koehler, 1896. *Ophiocymbium* and *Ophiologimus* do not possess any ophiacanthid characters and should be transferred to the family Ophiomyxidae. The genus *Amphilimna* clearly belongs to the family Amphiuroidae, as suggested already by Verrill (1899), despite having an atypical imperforate dental plate. The genus *Ophiosparte* appears to be an archaic extant taxon of the family Ophiuridae (present study; Martynov, 2010).

The type genus of Ophiotominae, *Ophiotoma*, and the type species of *Ophiotrema* show an ophiacanthid relationship as discussed above. The genus *Ophiodaces* possesses many features that indicate both non-ophiotomin and even non-ophiacanthid relationships: large evident radial shields, general shape of the arms and spines, general appearance of the oral frame and pattern of the adoral shield papillae. The genus *Ophiodelos*, represented by a single known species, *O. insignis* Koehler, 1930, was described based on a single, very small specimen of 4 mm dd. Compared to any other Ophiacanthidae, it clearly has an aberrant morphology of very short arms (only about twice as long as the disk diameter), rapidly tapering distally, superficially similar to some species of the genus *Ophiambix* (a genus with an uncertain family placement). Flattened ribbed spines are also not a usual ophiacanthid feature. Further genera *Ophiophrura*, *Ophioplexa* **gen. nov.**, *Ophioprium* and *Ophiorupta* **gen. nov.**, are not members of the family Ophiacanthidae according to results of the present study, but instead are ophiomyxids. Thus, in the subfamily Ophiotominae of the family Ophiacanthidae unequivocally only three genera could be retained, the type genus, *Ophiotoma* (= *Ophiotrema*), *Ophiopristis* and *Ophiomedeia*. The latter genus, represented only by the type specimen, possesses a number of special features (Fig. 50) that can hardly be compared with the genus *Ophiotoma*.



The genera *Ophiotoma* and *Ophiopristis* in turn do not possess characters that clearly delineate them from the Ophiacanthinae s.str. In addition, the ophiacanthin genus *Ophiotreta* demonstrates a transitional morphology to the Ophiotominae in the pattern of the oral frame (Figs 78B–C). Similarly, the genus *Ophiolimna*, originally included in the Ophiotominae, has affinities not only with the Ophiacanthinae s.str., but also with the family Ophiodermatidae (see above). The well-defined indented proximal edge of the arm spine articulations of all species of the traditional ophiacanthid genus *Ophiolimna* and ophiodermatid *Ophioconis* (Figs 45A–F) is absent in all studied species of the genus *Ophiotoma*, but present in some *Ophiacantha* species, e.g. *O. abyssicola* and *O. pentagona*, and sometimes, as in *O. bidentata*, only on the distal segments (Fig. 28E). Therefore, there are no reasons to consider the genus *Ophiolimna* as closely related to the genus *Ophiotoma*. The special ridge between distal border of the arm spine articulation area and the main lateral arm plate has been discovered to be well-defined not only in the genera *Ophiolimna* and *Ophioconis*, but also in three studied species of the genus *Ophiopristis* – *O. hirsuta*, *O. procera* and *O. luctosa* (Figs 59C–E; 60E–F). Thus the special similarity between *Ophiopristis* and *Ophioconis* is not limited to the articulation shape. There is a remarkable resemblance between vertebrae of *Ophiopristis luctosa* and *Ophioconis cupida* in the exceptionally narrow median dorsal keel and a wide flattened lower lateral area (Figs 59H, I and 46G, H). Similar vertebrae are present also in *Ophiopristis hirsuta* and *O. procera*, especially distally (Figs 58F; 60H, J). The ophiacanthid genera *Ophiopristis* and *Ophiolimna*, despite currently being placed in the subfamily Ophiotominae, are not immediately similar to species of the genus *Ophiotoma*. Instead, both spine articulations pattern and vertebral shape of *Ophiotoma* (including different, large- and small-sized species, as *O. assimilis* and *O. bartletti*) (Figs 28A; 69E–H) and *Ophiolimna* and *Ophiopristis* are quite different. At the same time, the oral frames are very different between *Ophiolimna* and *Ophiopristis* (Figs 44A–F; 59B–E; 60B–F). Further, arm spine articulations very similar to the traditionally ophiotomin genus *Ophiolimna* also have been described for *Ophiocopa spatula* Lyman, 1883 which is currently placed within the ophiacanthid subfamily Ophioplinthacinae (O'Hara & Stöhr 2006). The monotypic genus *Ophiocopa* also shares with *Ophiolimna* similar widened distalmost oral papillae and disk granules, and with the genus *Ophiopristis* the shape of the spine articulations. These newly discovered facts further suggest that subfamily subdivisions within the Ophiacanthidae are unnecessary. After the restrictions and clarifications have been made in the course of the present study within the subfamily Ophiotominae s.str. only the single genus *Ophiotoma* remains. All these data indicate that besides the taxonomic delineation of the families Ophiomyxidae and Ophiacanthidae and the generic revision of the traditional subfamily Ophiotominae, both aims of the present study, a broad taxonomic revision and a phylogenetic analysis of all ophiacanthid genera is still necessary.

A preliminary analysis of the Ophiohelinae group, also considered within Ophiacanthidae has showed spine articulation ridges similar to the Amphiuroidae and Ophiactidae (Martynov 2010). Earlier Paterson (1985) also considered Ophiohelinae articulation ridges as non-ophiacanthid. A detailed investigation of the latter case will be the subject of further publications of the present series.

Below is given renewed diagnoses of both Ophiomyxidae and Ophiacanthidae and new genera lists.

### Family Ophiomyxidae Ljungman, 1867

**Diagnosis.** Disk usually soft, covered with a thick layer of naked skin, usually with a few, small, inconspicuous, embedded scales, but in some taxa disk scales are larger and skin reduced. Radial shields are small, placed at the disk edge. Genital plates in many taxa are poorly developed, in some genera the abradial plate is completely reduced. The articulation surface of the adradial genital plate has a more or less elevated condyle, quite evident in some taxa, but missing entirely in others. The articulation surface of the radial shield has a conspicuous excavation in some taxa, a distal groove or an elongated condyle. Oral papillae usually spiniform, but in *Ophiomyxa* they are clearly widened with a dentate edge. Apical papillae (ventralmost teeth) usually spiniform and forming a small cluster, but in *Ophioplexa* **gen. nov.** the cluster is composed of numerous papillae, and in *Ophiomyxa* there is a single wide apical papilla. The following teeth are also in most cases spiniform. The dental plate has usually several small, round, perforating sockets, but in

*Ophiomyxa* they are elongated and non-perforating. Jaws are relatively short. Adoral shields are distinctively widened, wing-like distally in many taxa, including *Ophioscolex* and *Ophioplexa* **gen. nov.** Oral shields are variable in size.

Dorsal arm plates are usually either fragmented or absent and concealed by a thick skin, but in some genera, including *Ophiocymbium* and *Ophioplexa* **gen. nov.**, they are entire, well-defined with a very thin skin layer. Arm spine articulations are never volute-shaped and lack the sigmoidal fold, and in most taxa, including *Ophiomyxa* and *Ophiobyrsa*, are of the double-opening type. Around the muscle opening there is often a ribbed or folded area. In some taxa, including *Ophioscolex* and *Ophiogeron*, articulations are of the single-opening type, with a large muscle opening and a massive border. Single-opening articulations are present also in some species of the genus *Ophiocymbium*. Arm spines in most taxa, including *Ophiomyxa*, *Ophioscolex* and *Ophiobyrsa* are solid, having a distinctive long base, flattened ventrally and devoid of condyles, but in some taxa, e.g. *Ophiolycus* and *Ophiocymbium*, this base is not evident. In most taxa the vertebrae have a zygospondylous articulation, but in *Ophiobyrsa* and related genera the articulation is streptospondylous.

The family includes the genera: *Astrogeron* Verrill, 1899, *Astrogymnotes* H.L. Clark, 1914, *Neoplax* Bell, 1884, *Ophiobyrsa* Lyman, 1878, *Ophiobyrsella* Verrill, 1899, *Ophioblenna* Lütken, 1859, *Ophiobrachion* Lyman, 1883, *Ophiocanops* Koehler, 1922, *Ophiocymbium* Lyman, 1880, *Ophiogeron* Lyman, 1878, *Ophiohyalus* Matsumoto, 1915, *Ophiohymen* H.L. Clark, 1911, *Ophioleptoplax* H.L. Clark, 1911, *Ophiologimus* H.L. Clark, 1911, *Ophiolycus* Mortensen, 1933, *Ophiomyxa* Müller & Troschel, 1840, *Ophiophrixus* H.L. Clark, 1911, *Ophiophrura* H.L. Clark, 1911, ***Ophioplexa* gen. nov.**, *Ophioprium* H.L. Clark, 1915, ***Ophiorupta* gen. nov.**, *Ophiosciasma* Lyman, 1878, *Ophioscolex* Müller & Troschel, 1840, *Ophiosmilax* Matsumoto, 1915, *Ophiostiba* Matsumoto, 1915, *Ophiostyracium* H.L. Clark, 1911, *Ophiosyzygus* H.L. Clark, 1911 and *Ophiovesta* Koehler, 1930.

### Family Ophiacanthidae Ljungman, 1867

**Diagnosis.** Disk usually covered with numerous small scales and numerous spinelets, but in some taxa (e.g. *Ophiotoma*) the skin is conspicuous. Radial shields are large, exposed or concealed by disc scales, usually occupied a considerable part of the disk. Genital plates in all taxa are well developed, the abradial plate is always present. Articulation surface of the adradial genital plate with a more or less elevated, often elongated condyle, evident in most taxa. Articulation surface of the radial shield in some taxa with a rather inconspicuous elevation, whereas in others (e.g. *Ophiocamax*) with a compact condyle. Oral papillae usually somewhat flattened and rounded. Apical papilla (ventralmost tooth) typically single, wide and massive, but in some taxa there is a cluster of papillae (*Ophiocamax*). Dorsal teeth are also in most cases massive and placed one after the other (including *Ophiocamax*). Dental plate entire and in most cases with elongated non-perforating sockets (including *Ophiotoma*). Jaws typically relatively short. Adoral shields relatively short, but in some genera distally wing-like widened (e.g. *Ophiotoma*). Oral shield variable in size. Dorsal arm plates always well defined. Arm spine articulations always distinctly volute-shaped appearance and with sigmoidal fold, even in reduced (including *Ophiomoeris*, *Ophiochondrus*, *Ophiolebes*) or somewhat modified variants (e.g. *Ophiocamax*) and in all taxa they are of the double-opening type. Arm spines in most taxa with distinct compact ventral condyle, articulating with the volute-shaped lobe. Vertebrae in most taxa probably with zygospondylous articulation (including *Ophiotoma*, *Ophiolimna*, some *Ophiacantha* species), but in *Ophiocamax*, some *Ophiacantha* species, *Ophiomoeris* the articulation is streptospondylous.

The family includes the genera: *Ophiacantha* Müller & Troschel, 1842, *Ophiacanthella* Verrill, 1899, *Ophiochondrus* Lyman, 1869, *Ophialcaea* Verrill, 1899, *Ophientrema* Verrill, 1899, *Ophiocamax* Lyman, 1878, *Ophiochondrus* Lyman, 1869, *Ophiocopa* Lyman, 1883; *Ophiodictys* Koehler, 1922, *Ophiogema* Koehler, 1922, *Ophiohamus* O'Hara & Stöhr, 2006, *Ophiolebes* Lyman, 1878, *Ophiolimna* Verrill, 1899, *Ophiomedeia* Koehler, 1906, *Ophiomitra* Lyman, 1869, *Ophiomitrella* Verrill, 1899, *Ophiomoeris* Koehler, 1904, "*Ophiophthalmus*" Matsumoto, 1917 (see Paterson, 1985 for discussion of the nomenclature of the genus *Ophiophthalmus*), *Ophioplinthaca* Verrill, 1899, *Ophiopristis* Verrill, 1899, *Ophioripa* Koehler, 1922,



*Ophiurothamnus* Matsumoto, 1917, *Ophiosemmotes* Matsumoto, 1917; *Ophiotoma* Lyman, 1883, *Ophiotreta* Verrill, 1899.

The following genera *Glaciacantha* Fell, 1961, *Microphiura* Mortensen, 1911, *Ophienigma* Stöhr & Segonzac, 2005, *Ophiochytra* Lyman, 1880, *Ophiohelus* Lyman, 1878, *Ophiolamina* Stöhr & Segonzac, 2006, *Ophiomyces* Lyman, 1869, *Ophioparva* Guille, 1982, *Ophiothauma* H.L. Clark, 1938, *Ophiotholia* Lyman, 1880 traditionally included into the family Ophiacanthidae according to author's published (Martynov 2010) and unpublished data belong to another ophiuroid families. Their detailed descriptions and exact systematic position will be subject of the following papers of the present series.

### The extinct subclass Oegophiurida and their relationship to the recent family Ophiomyxidae

One of the important outcomes of the present study is the potential to assess the relationship of modern Ophiuroidea with closed ambulacral groove and the Paleozoic fossil Oegophiurida which differs in having a largely unprotected ambulacral groove.

The extinct subclass Oegophiurida differs from all recent Ophiuroidea in several features, which point more to a relationship with the class Asteroidea than to the true Ophiuroidea. Among them are the unfused vertebrae, absence of the ventral arm plates, absence of genital plates and radial shields (Spencer & Wright 1966; present study) (Figs 3A–C, F–I). Despite these asteroidean features, some important characters suggest an ophiuroid relationship: a well-formed distinct central disk, the general appearance of the vertebrae, albeit unfused (Fig. 3F), the structure of the jaws, and the presence of the dental plate (Fig. 3H–I). The latter feature is especially characteristic of both Oegophiurida and Ophiuroidea and not found beyond these two groups, even within Paleozoic Asteroidea, contemporaries of the extinct Oegophiurida (Shackleton 2005). The crown groups of Oegophiurida are even more similar to the recent ophiuroids in having opposite vertebrae, similar in general appearance to the fused vertebrae of the Ophiuroidea.

Few attempts have been made to detect which of the recent Ophiuroidea is most closely related to the extinct subclass Oegophiurida or even included in it. Both Mortensen (1933c) and Fell (1962) argued that the aberrant shallow water tropical taxon *Ophiocanops fugiens* was the single Recent representative of the Oegophiurida. This species, which climbs on anthipatharian corals and is described only on few specimens, has partially unfused vertebrae, gonads penetrating into the proximal arms, and a seemingly absent oral shield. However, Hotchkiss (1977) suggested that *Ophiocanops fugiens* is characterized by rather reduced features and should be placed in the Recent subclass Ophiuroidea near the family Ophiomyxidae, as already suggested in the first description of this taxon (Koehler 1922a). Recently, more specimens of *Ophiocanops fugiens* were discovered (Pearse *et al.* 1998) and revealed the presence of the typical ophiuroid fused vertebrae. Most recently a new species of the genus *Ophiocanops* was described from Reunion Island shallow waters (Stöhr *et al.* 2008), highlighting the reduced nature of this taxon, and the genus *Ophiocanops* was finally placed in the family Ophiomyxidae. Thus, the single recent taxon that was questioned as a member of the extinct subclass Oegophiurida is actually a genus of the extant family Ophiomyxidae.

In the recent ophiuroid fauna there are no taxa, which unambiguously display the specific features of the extinct Oegophiurida, i.e. unfused vertebrae within an open ambulacral groove. However, although it is impossible to find a taxon with a general oegophiurid appearance, it is nevertheless possible to analyze whether oegophiurid characters can be detected in various recent genera of the family Ophiomyxidae. For instance, one such feature that has still not been investigated in comparison of Oegophiurida and Ophiuroidea is the pattern of the lateral arm plates, including arm spine articulations and other features. Several oegophiurid species with outstanding preservation have been described from the Devonian deposits of North America (Kesling 1969; 1970; 1972; Kesling & Vasseur 1971). Detailed photographs of the lateral arm plates have been published of *Eugasterella thorni* Kesling, 1969, which allow the identification of the exact shape of the arm spine articulations and pattern of their placement. In the present study, type specimens of *Eugasterella thorni* were reinvestigated (Fig. 83). Spine articulations are placed on the lateral arm plate in two sets, one round or slightly subparallel, large, with well defined articulations, placed latero-dorsally, bearing large conical spines, and a second set of faint scar-shaped articulations, placed ventrally and holding smaller

flattened aboral spines (groove spines) (Figs 83G, H). This distinction between lateral and groove spines is a characteristic feature described for various oegophiurid taxa (Spencer & Wright 1966; Kesling 1969; 1972; Shackleton 2005). While lateral spines are usually thought to be homologous to the lateral arm plate spines of the recent Ophiuroidea, the flattened oegophiurid groove arm spines have never been investigated. Since the groove arm spines are a characteristic feature of the subclass Oegophiurida, their homology with the Recent Ophiuroidea may be an important argument for a relationship between these groups. Although they share the thick skin layer on the disk and arms with the Paleozoic oegophiurids, modern Euryalida possess strictly different arm spine articulations and lack groove spine structures. Many euryalids have a set of additional hooks placed on separate stub-like structures (Figs 22E–I), but they are placed dorsally, not ventrally, and are clearly not homologous to the oegophiurid groove arm spines. In addition, euryalid arm spine articulations have reduced borders unlike the well-developed ridge borders of the Oegophiurida.

Most of the Recent Ophiuroidea have a rather complicated structure of the arm spine articulations, either volute-shaped, as in the families Ophiacanthidae and Ophiidermatidae, or subparallel as in the families Ophionereididae, Amphiuridae and Ophiactidae (Figs 28–36), but they differ significantly from the oegophiurid articulations. The pattern of the arm spine articulations is very conservative, and many ophiuroid families or groups of genera have a specific shape of articulation. Exceptions mostly concern some species with very small, reduced spines and massive arms (e.g. *Ophiotypa simplex*), although even taxa with massive arms, e.g. species of the genera *Amphiophiura*, *Ophiomusium*, *Ophioplocus* and many ophiidermatids, still have remnants of the ridge structure typical for their respective families that could be detected by a careful SEM examination (Figs 25D; 30; 34B–G). As shown above, the only family of the Recent Ophiuroidea possessing a wide array of patterns of the articulation is Ophiomyxidae, in which both the single-opening and the two-openings types occur. A somewhat intermediate type of articulation was found in the genera *Ophiocymbium* and *Ophiologimus*, now placed in the Ophiomyxidae. The pattern of spine articulations most similar to the extinct Oegophiurida was discovered in the Recent species *Ophioscolex glacialis*, having large subcircular or slightly subparallel single-opening articulations (compare Figs 83C, E and Figs 83B, F). Besides the articulation similarity, *Ophioscolex glacialis* shares with *Eugasterella thorni* the presence of a short distal process on the lateral arm plate (compare Figs 83B, F and Fig 83G). Externally, *Ophioscolex glacialis*, having a thick skin layer on the disk and arm (Figs 3D, E), is also similar to the Paleozoic oegophiurids, which were also heavily covered by skin (Figs 3A–C). *Ophioplexa* **gen. nov.** has an even more notable pattern of the arm spine articulations, which are generally elongated, compressed in a proximal to distal direction, with well defined borders (Figs 56A, F, H). However, on the most proximal segments under the disk, a particular articulation was discovered, which differs greatly from the articulation on most other segments. They are large, subparallel or tapering, and sometimes divided into two parts by weak septa (Figs 56C–E). Almost the same shape of the ventralmost articulation can be detected on the lateral arm plates of the oegophiurid *Eugasterella thorni* (Fig. 83E), whereas the more dorsally placed articulations of this oegophiurid species have a shape very similar to the extant species *Ophioscolex glacialis* (Figs 83B, F). The peculiar ventralmost spines in this oegophiurid follow after these aberrant enlarged articulations. In full agreement with this oegophiurid pattern, the new genus has an aberrant enlarged ridge following three large flattened spines, which occupy the position where usually in the most extant Ophiuroidea the spines called tentacle scales are placed (Figs 55D–F). However these flattened spines of *Ophioplexa* **gen. nov.** differ from the typical ophiuroid tentacle scales in having a more arm spine appearance rather than a simplified scale-like shape and, what is more important, a small opening on their ventral surface (Fig. 56J). Such an opening is very similar to the nerve openings of the typical lateral arm plate spines of most ophiuroids (e.g. Figs 22B, D; 23D, J; 27E, U; 29F; 30B; 32B; 33E; 35I). Three species of the genus *Ophiophrura*, including *O. tripapillata* (Stöhr & Segonzac, 2005), have tentacle scales quite similar to *Ophioplexa* **gen. nov.**, though they are considerably narrower and less spine-shaped. However, in contrast to *Ophioplexa* **gen. nov.**, one to two of the tentacle scales of some “*Ophioscolex*” species are placed on the ventral arm plates, whereas in *Ophioplexa* **gen. nov.** these ventral spines (“tentacle scales”) are placed strictly on the lateral arm plates, i.e. as in the Oegophiurida. Several spiniform tentacle scales are found also in *O. ninae* **sp. nov.** (Figs 55I, K) and in some former ophiotomin species, e.g. *Ophiotoma tertium* (Koehler, 1922), *Ophioprium cervicornis*, *Ophiorupta*



**gen. nov.**, and also a number of other ophiuroid taxa from distantly related families, i.e. Ophiuridae and Ophiolepididae (genus *Ophiambix*). These tentacle scales are either very flattened or spiniform but usually do not have a massive base with a nerve opening, as in *Ophioplexa* **gen. nov.** *Ophiocymbium tanyae* **sp. nov.** also has tentacle scales similar to *Ophioplexa*, but only proximally.

Another example of preservation of the typical oegophiurid pattern of the ventral arm spines is the genus *Ophiosparte* in the family Ophiuridae, which has several large flattened tentacle scales (Figs 65B–E), corresponding to the oegophiurid ventral spines. Further evolution of the family Ophiuridae was mostly in modification and reduction of the characters well developed in the genus *Ophiosparte*. For instance, in the same Antarctic region as *Ophiosparte gigas*, the ophiurid genus *Ophionotus* occurs, which is somewhat similar to the former in general disk appearance, essentially similar in the dental plate and genital plate morphology (Figs 5A, K), but has short reduced oral papillae, tentacle scales and spines, like most other ophiurid taxa (Figs 77A–D). The family Ophiuridae became one of the most successful and prolific ophiuroid lines, including a number of paedomorphic taxa, for instance *Perlophiura profundissima*, which has none of the apomorphies of the family and possesses vertebrae of a postlarval type (Figs 20I, J). The distinctive pattern of the well developed tentacle scales, essentially similar to the arm spines in the genus *Ophiosparte* (Fig. 65C), is found to different degrees in numerous species of the genera *Ophiura*, *Amphiophiura*, and *Stegophiura*.

The common features that are shared by *Ophiosparte* and *Ophioplexa* **gen. nov.**, including numerous spiniform teeth and apical papillae, long adoral shield papillae and several evident tentacle scales, are probably plesiomorphic, since other characters, e.g. the pattern of the radial shield-genital plate articulation, the shape of the articulations and spine, and the pattern of vertebral articulation, differ greatly.

Thus the tentacle scales of all recent Ophiuroidea are homologous to the Oegophiurida groove arm spines. Some taxa, e.g. *Ophioplexa* **gen. nov.** and *Ophiosparte*, still retain tentacle scales very similar in shape and position to the oegophiurid groove arm spines, whereas most other Ophiuroidea possess modified, either spiniform or flattened, tentacle scales. The pattern of the numerous comb-shaped tentacle-scales is so conservative within the family Ophiuridae, that many taxa of that family possess it at least proximally. Earlier Ludwig (1901), Mortensen (1927) and Hyman (1955) considered the ophiuroid tentacle scale as a modified spine, but without much discussion. The homology between oegophiurid groove spines and ophiuroid tentacle scales was not considered prior to this study.

Byrne & Hendler (1988) have reviewed soft-tissue characters in some species of the Ophiomyxidae and concluded that the mode of locomotion of *Ophiogeron supinus* Lyman, 1883, using large tube feet and with restricted arm mobility, may be similar to those of the paleozoic oegophiurid. The arm spine articulations of *Ophiogeron supinus* are large, of single-opening type (Byrne & Hendler, 1988; own observations) and very similar to those in *Ophioscolex* (Figs 83B, F) and the Paleozoic (*Eugasterella*) (Figs 83C, E) oegophiurid, thus supporting the data of soft-tissue morphology and suggesting a possible close similarity between some Recent ophiomyxid and Paleozoic ophiuroids.

Among most important conclusions of the present study thus can be a possibility to reconstruct the most ancestral condition of the Ophiuroidea. As it already well-established, most of the modern ophiuroid species passed during individual development through a peculiar stage with six primary plates arranged in a particular flower pattern and without large skin amount, i.e. the postlarval stereom appears as almost uncovered (e.g. Sumida *et al.*, 1998; Stöhr, 2005; author's unpublished data). And the important fact is that such postlarval pattern already has existed among Devonian oegophiurids (Hotchkiss, 1980). It may therefore imply the great importance of consideration of the entire ontogenetic (life) cycle features and not only the mature stage. Under this approach quite senseless to speak about just “plesiomorphic” or “apomorphic” states, e.g. are ancestral ophiuroids had thick skin or not. Instead much more productively to specify that common ophiuroid *ancestral juvenile* condition (i.e. *juvenile plesiomorphic* state) is the 6 primary plates without conspicuous amount of the skin and *ancestral adult* condition is numerous disk plates heavily covered with thick skin (i.e. *adult plesiomorphic* state). Further heterochronic shifts towards *juvenilization* of the adult morphology might produce similar juvenile adult morphology many times independently in different families, strongly underlined by the common ancestral ontogenetic cycle and it is well supported by structure of the arm spine articulations as unique morphological markers.

**TABLE 1.** Summary of proposed taxonomic changes of the generic placement.

Genus	Current family placement	Proposed family placement
<i>Amphilimna</i> Verrill, 1899	Ophiacanthidae	Amphiuridae
<i>Ophiochondrus</i> Lyman, 1869	Hemieuryalidae	Ophiacanthidae
<i>Ophiocymbium</i> Lyman, 1880	Ophiacanthidae	Ophiomyxidae
<i>Ophiodaces</i> Koehler, 1922	Ophiacanthidae	? Ophiuridae
<i>Ophiodelos</i> Koehler, 1930	Ophiacanthidae	? <i>Ophiambix</i> -relationship
<i>Ophiologimus</i> H.L. Clark, 1911	Ophiacanthidae	Ophiomyxidae
<i>Ophiomoeris</i> Koehler, 1904	Hemieuryalidae	Ophiacanthidae
<i>Ophiophrura</i> H. L. Clark, 1911	Ophiacanthidae	Ophiomyxidae
<i>Ophioprimum</i> H.L. Clark, 1915	Ophiacanthidae	Ophiomyxidae
<i>Ophiopsila</i> M. Sars, 1859	Ophiocomidae	Amphiuridae
<i>Ophioparte</i> Koehler, 1922	Ophiacanthidae, Ophiomyxidae	Ophiuridae
<i>Ophiophaera</i> Brock, 1888	Ophiocomidae	Amphiuridae

**TABLE 2.** Summary of proposed new taxa and new taxa combinations.

New taxa	New combinations	New synonyms
<i>Ophioplexa condita</i> <b>gen. et sp. nov.</b>	<i>Ophiorupta discrepans</i> (Koehler, 1922) <b>comb. nov.</b>	<i>Sinophiura</i> Liao, 1983 <b>syn.nov.</b> (= <i>Amphilimna</i> Verrill, 1899)
<i>Ophiorupta</i> <b>gen.nov.</b>	<i>Ophiophrura tripapillata</i> (Stöhr & Segonzac, 2005) <b>comb. nov.</b>	<i>Ophiotrema</i> Koehler, 1896 <b>syn.nov.</b> (= <i>Ophiotoma</i> Lyman, 1883)
<i>Ophiocymbium antarcticus</i> <b>sp. nov.</b>	<i>Ophiophrura imperfecta</i> (H.L. Clark, 1915) <b>comb.nov.</b> <i>Ophiotoma tertium</i> (Koehler, 1922) <b>comb. nov.</b>	
<i>Ophiocymbium ninae</i> <b>sp. nov.</b>	<i>Ophiotoma gracilis</i> (Koehler, 1914) <b>comb. nov.</b>	
<i>Ophiocymbium rarispinum</i> <b>sp. nov.</b>		
<i>Ophiocymbium tanyae</i> <b>sp. nov.</b>		

**TABLE 3.** Collecting data of the studied ophiuroid specimens. BMNH, British Museum, Natural History, London; IORAS, P.P. Shirshov Institute of Oceanology, Moscow; MCZ, Museum of Comparative Zoology, Harvard University; USNM, National Museum of Natural History, Smithsonian Institution; ZIN, Zoological Institute, St. Petersburg; ZMMU, Zoological Museum of Moscow State University; ZMUC, Zoological Museum, Danish Museum of Natural History.

Museum number	Vessel/ Expedition	Station	Date	Coordinates or locality start		Coordinates stop		Depth [m]	
				Lat.	Long.	Lat.	Long.	Start	Stop
ZMMU D-20				Samoa					
ZMMU D-51	USFC	-	-	Off Martha's Vineyard				155	228
ZMMU D-95	-	-	-	Samoa					-
ZMMU D-101	-	-	1902	Bushir					
ZMMU D-115	"Plavmornin"	23	24.07.1921	73°00' N	50°45' E			200	
ZMMU D-118	"Plavmornin"	88	26.08.1923	74°22' N	41°00' E			260	
ZMMU D-120	"Plavmornin"	140	28.07.1924	69°21' N	56°20' E			15	
ZMMU D-123	-	-	07.05.1902	Bahrain					Coral reefs
ZMMU D-131	"Akademik Kurchatov"	888	03.12.1971	57°06'S	26°44' W			318	

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TABLE 3. (continued)

Museum number	Vessel/ Expedition	Station	Date	Coordinates or locality start		Coordinates stop		Depth [m]	
				Lat.	Long.	Lat.	Long.	Start	Stop
ZMMU D-134	“Odyssey”	-	06.01.1985	Kurile Ids, Simushir Id.				135	145
ZMMU D-136	“Odyssey”	-	06.01.1985	Kurile Ids., Simushir Id.				135	145
ZMMU D-138	“Akademik Kurchatov”	265	10.11.1968	32°18'1 S	71°50'5 W			600	700
ZMMU D-142	-	-	17.04.1893	Peter the Great Bay, Japan Sea				inter-tidal	
ZMMU D-167	“Northern Pole 22” (“SP 22”)	45	01.04.1980	78°22' N	153°01' E			68	
ZMMU D-309	“Sevastopol”	1089	16.07.1957	62°3' N	7°48' W			150	
ZMMU D-319	“Northern Pole 22”	18	01.02.1980	77°48' N	153°54' E			66	
ZMMU D-465	“Sevastopol”	1100	18.07.1957	61°00' N	01°36' W			140	
ZMMU D-494	“Sevastopol”	2588	12.12.1959	62°03' N	07°00' W			95	
ZMMU D-518	“Sevastopol”	1766	15.10.1958	65°13' N	10°00' W			730	
ZMMU D-551				Yemen, Hodeida					
ZMMU D-553	-	-	19.05.1951	Albania, Valona Bay				30	40
ZMMU D-559	-	-	01.07.1955	White Sea, Kandalakshsky Bay, Velikaya Salma Strait				10-20	
ZMMU D-560	-	-	26.06.1910	Sudan, Port Sudan				Coral reefs	
ZMMU D-578-580	“Gidrobiolog”	2/88	11.08.1988	60°04' 3 N	169°03'9 E			100	
ZMMU D-582	“Gidrobiolog”	44		Kurile Ids., Onekotan Id.					
ZMMU D-613-615	-	-	04.1998	White Sea, Kandalakshsky Bay				40	50
ZMMU D-631	“Akademik Mstislav Keldysh”	464	03.09.1982	58°21'1 N	31°36'9 W	58°21'0 N	31°35'6 W	1670	1750
ZMMU D-648	“Akademik Mstislav Keldysh”	499	09.09.1982	58°03' N	30°26' W	58°04'0 N	30°17' 2' W	2440	2429
ZMMU D-660	“Akademik Mstislav Keldysh”	464	03.09.1982	58°21'1 N	31°35'6 W	58°21'0 N	31°36'9 W	1670	1750
ZMMU D-680	“Dmitry Mendeleev”	1255	01.01.1976	29°30' S	167°52' E			500	
ZMMU D-688	“Moskovsky Universitet”	9	06.02.1991	22°51' N	17°02,5' W			90	
ZMMU D-725	“Dmitry Mendeleev”	1255	10.09.1966	29°30' S	167°52' E			500	
ZMMU D-729	“Akademik Mstislav Keldysh”	445	31.08.1982	58°21'1 N	31°35'1 W	58 21'7 N	31°33'0 W	1650	1680
ZMMU D-733	“Akademik Kurchatov”	928	17.12.1971	52°15' S	56°51' W			1105	
ZMMU D-743	“Akademik Mstislav Keldysh”	445	31.08.1982	58°21'1 N	31°35'1 W	58 21'7 N	31°33'0 W	1650	1680
ZMMU D-746	“Akademik Mstislav Keldysh”	464	03.09.1982	58°21'1 N	31°35'6 W	58°21'0 N	31°36'9 W	1670	1750
ZMMU D-750	“Sevastopol”	1238	10.08.1957	71°00' N	12°56' W			380	

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TABLE 3. (continued)

Museum number	Vessel/ Expedition	Station	Date	Coordinates or locality start		Coordinates stop		Depth [m]	
				Lat.	Long.	Lat.	Long.	Start	Stop
ZMMU D-767	“Tunez”	105/17	30.06.1978	72°05' N	15°00' E			602	
ZMMU D-772	“Sevastopol”	1411	06.04.1958	61°05' N	1°45' W			185	
ZMMU D-776	“Sevastopol”	1108	09.07.1957	60°35' N	3°27' W			295	
ZMMU D-788-792	“Akademik Kurchatov”	896	05.12.1971	56° 52' S	24° 59' W	56° 51' S	24° 59' W	5651	5530
ZMMU D-793-794	“Akademik Kurchatov”	870	29.11.1971	55° 7' S	25° 2' W	55° 8' S	25° 1' W	4704	4680
ZMMU D-795	“Dmitry Mendeleev”	1290	23.01.1976	54° 33' S	159° 24,0' E			5410	5450
ZMMU D-796-797	“Vityaz”	4074	20.10.1958	40° 19' N	175° 45' W			6065	
ZMMU D-798-801	“Vityaz”	7407	11.05.1975	29° 18' N	143° 15' E	29° 17' N	143° 15' E	6740	6850
ZMMU D-802-803	“Vityaz”	6109	15.05. 1969	56°14,1' N	139° 44,0' W	56°12,7' N	139° 43,4' W	3450	3460
ZMMU D-804-805	“Vityaz”	4213	16.12.1958	34° 54' N	123° 55' W			4231	4200
ZMMU D-806	“Vityaz”	5028	04.03.1961	7° 43,3' N	120° 20,1' E			4110	4111
ZMMU D-807-808	“Vityaz”	4564	01.12.1959	23°57' S	112°16' E			820	
ZMMU D-810	“Akademik Mstislav Keldysh”	275	02.08.1982	58°30'3 N	31°29'4 W			1684	
ZMMU D-811	“Vityaz”	3541	02.09.1955	30°48'4 N	127° 46'3 E			151	152
ZMMU D-812	“Vityaz”	3539	01.09.1955	30° 37'2 N	128° 41'7 E			700	701
ZMMU D-814-815	“Akademik Kurchatov”	1239	13.03.1973	19° 35'2 N	80° 29'5 W			990	1050
ZMMU D-817	“Akademik Sergei Vavilov”	1201	14.09.1998	77° 59' N	41°01' E			35	
ZMMU D-818	“Akademik Kurchatov”	930	18.12.1971	51°56' S	57°35' W	51°57' S	57°37' W	401	
ZMMU D-819	“Ob”	143	03.06.1956	Seyshelles				40	
ZMMU D-820				Australia, Sydney				3	
ZMMU D-821	“Vityaz”	2766	22.05.1954	Japan Sea				106	
ZMMU D-823	“Meteor”	Tvg 153	2002	10° 00' N	86°11' W			2258	2263
ZMMU D-826	“Akademik Mstislav Keldysh”, “Mir-2”	2793	16.06.1992	59°51'48 N	31°29'43 W			829	844
ZMMU D-827	“Sevastopol”	2587	12.12.1958	62°00' N	6°12' E			120	
ZMMU D-828	-	-	10.05.2007	Vietnam, Fukuok				5-15	
ZMMU D-829	“Vityaz-II”	2634	25.11.1988	25°5,7' S	34°44'	25°5,9' S	34°42'6 E	88	95
ZMMU D-830	“Akademik Kurchatov”	1471	03.03.1974	07°50' S	80°59' W			2400	2600
ZMMU D-831	“Dmitry Mendeleev”	1347	21.02.1976	44°06' S	145°56' E			1800	1820
ZMMU D-832	-	-	-	Cuba				-	
ZMMU D-833	“Sevastopol”	2508	17.11.1959	65°45' N	08°03' W			420	
ZMMU D-834	“Moskovsky Universitet”	16	09.02.1991	25°11'28 N	15° 37' 68' W			80	
ZMMU D-835	“Vityaz”	6105	12.05.1969	58°55' N	142°03' W			2980	2970

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TABLE 3. (continued)

Museum number	Vessel/ Expedition	Station	Date	Coordinates or locality start		Coordinates stop		Depth [m]	
				Lat.	Long.	Lat.	Long.	Start	Stop
ZMMU D-836	“Vityaz”	3578	11.05.1957	38°35' N	142°53' E			1641	
ZMMU D-838	“Vityaz”	3443	14.09.1955	40°24,3' N	143°18,3' E			1406	
ZMMU D-839-840	“Akademik Kurchatov”	898	05.12.1971	56°47' S	24°56' W	56° 46' S	24° 57' W	6150	6052
ZMMU D-841	“Vityaz-II”	2634	25.11.1988	25° 5,7' S	34° 44' E	25° 5,9' S	34° 42'6 E	88	95
ZMMU D-843	“Sevastopol”	2461	07.11.1959	70°3' N	9°29' W			782	
ZMMU D-844	“Vityaz”		6105	12.05.1969	58°55' N	142°03' W		2980	2970
ZMMU D-845	“Sevastopol”	1166	01.08.1957	66°01' N	30°17' W			400	
ZMMU D-846	“Thalasia”	4807	1968	North Atlantic					
ZMMU D-847	“Akademik Oparin”	89		Okhotsk Sea				494	
ZMMU D-848	“Vityaz”	6359-2	24.08.1970	19°03' N	171°09' E			1270	1320
ZMMU D-849	“Vityaz”	6135	09.06.1969	53°32' N	163°22' W			2880	2930
ZMMU D-850	“Akademik Mstislav Keldysh”	478	06.09.82	58°27'03 N	31°45'00 W	58°26'09 N	31°44'01 W	1800	1780
ZMMU D-851	“Vityaz”	6101	11.05.1969	59°10'2 N	142°01'0 E			798	756
ZMMU D-852	“Ob”	143	03.06.1956	Seyshelles				40	
ZMMU D-853	“Vityaz”	6138	11.06.69	53°11'0 N	163°12'0 W			5595	5660
ZMMU D-855				Sunda Islands					
ZMMU D-857-858	“Blake”			Lesser Antilles					
ZMMU D-859	-	-	-	New Zealand				-	
ZMMU D-860	“Tunez”	105/20	04.07.1958	73°01' N	22°00' E			445	
ZMMU D-861	“Vityaz”	7274	23.03.1975	02°30' S	128°51' E			1330	
ZMMU D-863	-	-	-	Vietnam, Fukuok				5-15 m	
ZMMU D-864	“Dmitry Mendeleev”	1269	12.01.1976	44°26' S	174°29' E			710	720
ZMMU D-865	“Sevastopol”	1245	11.08.1957	70°53' N	07°53' W			255	
ZMMU D-866	“North Pole 22”	72	07.01.1979	74°35' N	164°00' E			795	
ZMMU D-867	Bendex		25.11.2003	54°31'51 S	03°13'06 E			370	
ZMMU D-868	-	Slope 49	27.07.1986	off Freycinet Peninsula, Tasmania				200	
ZMMU D-875	“Vityaz”	3541	02.09.1955	30°48'4 N	127°46'3 E			151	152
ZIN 25/21449	13th Soviet Antarctic Expedition	7	07.12.1967	Davis Sea				40-45	
IORAS 1.89	“Vityaz”	5617	06.08.1966	45°32' N	153°46' E			6710	6675
IORAS 12.4	“Vityaz”	7246	02.03.1975	07°23' N	116°34'			76	
IORAS 13.1	“Vityaz”	3655	20.07.1957	05°49' S	152°53' E			6290	7657
IORAS 13.19	“Dmitry Mendeleev”	544	30.07.1972	09°56' S	79°26' W			1060	
IORAS 13.28	“Professor Shtokman”	1970	01.05.1987	25°34' S	89°09' W			538	548
IORAS 13.39	“Discovery” Investigations	8524#1		20°46' N	22°42' W			4412	
IORAS 13.40	“Akademik Mstislav Keldysh”	445	31.08.1982	58° 21'1 N	31° 35'1 W	58° 21'7 N	31° 33'0 W	1650	1680

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TABLE 3. (continued)

Museum number	Vessel/ Expedition	Station	Date	Coordinates or locality start		Coordinates stop		Depth [m]	
				Lat.	Long.	Lat.	Long.	Start	Stop
IORAS 13.8	“Vityaz-II”	2626	22.11.1988	24°42' S	35°31' E			320	
IORAS 14.178	Skif	1061/ 150	01.01.1971	48°12' S	68°39' E			177	169
IORAS 14.352	“Akademik Kurchatov”	4893	26.12.1985	36°12' S	49°09' W			4630	
IORAS 15.99	“Akademik Kurchatov”	1197	02.1973	10°52' N	64°10' W			20	
IORAS 15.109	“Akademik Kurchatov”	220	00°25' S	85°00' W				2265	
IORAS 3.71	“Vityaz”	2078	11.05.1953	44°09' N	148°38' E			1060	
IORAS 8.1	“Vityaz”	4792	26.10.1960	13°50' N	50°40' W			2529	2530
IORAS 8.4	“Vityaz”	7246	02.03.1975	07°23' N	116°34' E			76	
BMNH 82.12.23.391	HMS “Challenger”	157	03.03.1874	53°55' S	108°35' E			3566	
MCZ 167	“Blake”			Off Havana				260	819
MCZ 1917	“Blake”	108	1880	41°24'45 N	65°35'30 E			2260	
MCZ 1950	-	-	-	Off Sombbrero Key, Florida				439	
MCZ 1951	Hassler Expedition	-	-	Off Barbados				183	
MCZ 2043	“Blake”	227	-	Off St. Vincent				1048	
MCZ 2143	“Blake”	108	1880	41°24'45 N	65°35'30 E			2260	
MCZ 2167	“Blake”	226	-	Off St. Vincent				771	
MCZ 2983	“Albatross”	4968	1906	33°25'10 N	135°37'20 E			460	
MCZ 2984	“Albatross”	2842	1900	54°15' N	166°03' W			131	
MCZ 3212	“Albatross”	4957	1906	Bungo Channel, Japan				795	
MCZ 6805	“Hidrografia Naval”	27081	01.1967	63°24' S	56°59' W			40	320
MNHN EcOs 10380	“Travailleur et Talisman”	134		NE Azores				4010	
MNHN EcOs 10761		12	02.1987	Atarctic, Adelie Land				30	
MNHN EcOs 20406	-	-	-	Sunda Islands	-			-	
MNHN EcOs 20383	“Travailleur et Talisman”	134	24.08.1883	42°19' N	23°36' W			4050	
MNHN EcOs 20426	“Travailleur et Talisman”	43	25.07.1883	29°52' N	14°04' W			2075	
MNHN EcOs 22478	BIOCAL DW 64		03.09.1985	24°47'93'S	168°9'12'E			250	
MNHN EcOs 22484	MUSORSTOM 5	CP 324	14.10.1986	21°15'01S	157°51'33E			970	
MNHN EcOs 22485	MUSORSTOM 5	DC321	14.10.1986	21°20'04S	158°02'26E			1000	
MNHN EcOs 22795	DIVANAUT 1	PL904- 12	20.05.1994	37°50'94 N	31°30'63 W			1015	
MNHN EcOs 22928	MUSORSTOM 6	DW 392	13.02.1989	20°47'32S	167°04'06E			340	
MNHN EcOs 22930	MUSORSTOM 6	DW 398	13.02.1989	20°47'19S	167°05'65E			370	

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TABLE 3. (continued)

Museum number	Vessel/ Expedition	Station	Date	Coordinates or locality start		Coordinates stop		Depth [m]	
				Lat.	Long.	Lat.	Long.	Start	Stop
MNHN EcOs 22978	MUSORSTOM 6	DW 393	13.02.1989	20°48'29S	167°09'54E			420	
MNHN EcOs 22979	MUSORSTOM 6	DW 406	15.02.1989	20°40'06S	167°06'08E			373	
NI-1016	BIOIce	2907		65°16'N	28°50'W			1311	
USNM E00026	“Albatross”	5221	24.04.1908		Philippines, Marin- duque Island, San Andreas Point			353	
USNM E00699	“Albatross”	4647	09.11.1904	04°33'00 S	87°42'30 N			3667	
USNM E05300	“Caroline” Johnson-Smithso- nian Expedition		1933	Off Puerto Rico					
USNM E06911	“Albatross”	4096	22.07.1902	21°09'30 N	156°35'05W			497	523
USNM E06912	“Albatross”	4100	23.07.1902	21°05'30 N	156°40'30W			238	276
USNM 6429	“Blake”		10.02.1879	Caribbean, off Martinique					311
USNM 7164	“Albatross”	2152	30.04.1884	23°2' N	82°4' W			708	
USNM 14675	“Albatross”	-	1886	Bahamas	-			-	
USNM 25596	“Albatross”	4969	29.08.1906	Pacific Ocean, Honshu Island, Shiono Misaki				1073	
USNM 25672	“Albatross”	5079	19.10.1906	34°15' N	138°00' E			869	923
USNM 25724	“Albatross”	3749	19.05.1900	34°55' N	139°55' E			152	289
USNM 26210	“Albatross”	4968	29.08.1906	33°24'50 N	135°38'40 E			463	
USNM 41150	“Albatross”	5349	27.12.1908	Philippines, Pal- awan Island, Off NW Coast				1335	
USNM 41196	“Albatross”	5359	09.01.1909	08°12'45 N	120°37'15 E			4160	
USNM 42554	“Anton Bruun”	269-C	03.13.1963	Indian Ocean Arabian Sea, Gulf of Oman				121	124
USNM E42555	“Anton Bruun”	29	28.03.1963	Indian Ocean Andaman Sea				40	55
USNM E42872	“Anton Bruun”	390-E	08.09.1964	South Africa, Natal				350	
USNM 032296	“Albatross”	2665	04.05.1886	Atlantic Ocean, St. Augustine				481	
USNM 032301	“Albatross”	2751	28.11.1887	Caribbean Sea, Montserrat				1256	
USNM 032302	“Albatross”	2666	05.05.1886	Atlantic Ocean ,Cumberland Island				494	
USNM 1106231	“Islas Orcadas”	38	22.05.1975	57°00'24 S	26°10'06 W			2740	2757
ZMUC	“Pickle”		18.12.1929	34°21 S	17°57'E			326	

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