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Monograph

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Interactive identification key to all brittle star families (Echinodermata; Ophiuroidea) leads to revised morphological descriptions

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Abstract. Ophiuroidea is the largest class among extant echinoderms, with over 2000 described species assigned to 33 families. Here, the first identification key to the recently revised classification was developed, and revised morphological descriptions were derived from it, expanding the previous short diagnoses. The key was built by analyzing internal and external skeletal characters of predominantly the type species of each family, including at least two mutually exclusive attributes per family. Various numeric and multistate characters were used to create a traditional as well as an interactive key using the DELTA and Xper software programs. Illustrations (SEM and digital photos) are included in the key to facilitate the assessment of character states by users. Not only is it the first identification key to the families, according to the recently proposed new classification and the examined species, but this interactive key also assists users in understanding the family level taxonomy of brittle stars. The interactive key allows new characters and states to be added, when more species will have been analyzed, without the need to reconfigure the complete key (as may be necessary with conventional keys).

Keywords. Morphology, taxonomy, DELTA, interactive key, characters.

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Introduction

Ophiuroidea Gray, 1840 is one of the most diverse classes among extant echinoderms (Stöhr *et al.* 2012), currently including 2096 species (Stöhr *et al.* 2020). Ophiuroids are an ancient group of marine invertebrates with a fossil record dating back to the early Ordovician, about 480 ma (Shackleton 2005). They occupy marine habitats, ranging from the poles to the equator, from intertidal reefs to hadal depths of at least 6500 m (Smith *et al.* 1995; O'Hara *et al.* 2017). From the mid-eighteenth century, there has been a rise in the discovery rate of ophiuroid species, which has remained relatively high (Stöhr *et al.* 2012). Since the early-twentieth century, ophiuroid taxonomy has received more attention, as is evidenced by the production of traditional identification keys for various geographical areas (Mortensen 1927; Clark & Rowe 1971; Paterson 1985; Smirnov *et al.* 2006; Pomory 2007; Martynov 2010a; Gondim *et al.* 2013), but all of these keys are based on a now-outdated classification, which limits their use above the genus level. Matsumoto (1915, 1917) suggested the first comprehensive classification for the whole class, separating it into two subclasses, Myophiuroida Matsumoto, 1915, which possesses ventral arm plates that cover the ambulacral groove, and Oeogophiuroida Matsumoto, 1915, which lacks ventral arm plates. He divided the former into four different orders, Phrynophiurina Matsumoto, 1915, Laemophiurina Matsumoto, 1915, Chilophiurina Matsumoto, 1915, Gnathophiurina Matsumoto, 1915, and 13 families. Matsumoto's (1915, 1917) classification was not universally accepted though, and Mortensen (1927) instead proposed two orders, Euryalae and Ophiurae, based on the articular structures of the vertebrae (streptospondylous vs zygospondylous). He also provided the first traditional dichotomous identification key for 12 families but it was restricted to the British Isles. On the other hand, Murakami (1963) agreed with Matsumoto (1915, 1917), and he identified several new and taxonomically important characters from the examination of dental and oral plates. Fell (1960) included 17 families in his key to the ophiuroid genera, and while it is still useful, users need to be familiar with previous classifications to successfully navigate the key. All of the above-mentioned keys are conventional dichotomous keys. So far, only a single, taxonomically and geographically limited, computerized interactive key for Ophiuroidea is available (Alitto *et al.* 2018). Interactive keys have been created for many other taxa though, e.g. for Australian aquatic invertebrates using the software LUCID (Lucidcentral 2012), and also for various plants and animals using DELTA (Dallwitz 2019), but none includes echinoderms.

Eighty years after Matsumoto's (1915) work, Smith *et al.* (1995) proposed a new phylogeny, based on a cladistic analysis of all Ophiuroidea, including mostly morphological (43 characters) and limited molecular data, proposing 17 families. This study split the Ophiuroidea into the orders Euryalida Lamarck, 1816 and Ophiurida Müller & Troschel, 1840, based on vertebral articulation type, as Mortensen (1927) had done. Although the molecular study provided some support for the morphological tree, it left most of the deep branches unresolved (Smith *et al.* 1995) and was debated for methodological shortcomings (Stöhr 2012). Thanks to the studies on arm spine articulations (Martynov 2010b) and lateral arm plates (Thuy & Stöhr 2011), new phylogenetically informative characters were discovered, which led to a breakthrough with the successful inference of the ophiuroid phylogeny from morphological characters in great congruence with the molecular phylogeny (Thuy & Stöhr 2016), proposed two years earlier (O'Hara *et al.* 2014). At that time, the ophiuroid classification comprised 19–20 families (Thuy & Stöhr 2016). Recently, O'Hara *et al.* (2017) presented a new molecular phylogeny, which resulted in a new and revised classification that increased the number of families to 33 (O'Hara *et al.* 2018). The new phylogeny found several of the previous families to be paraphyletic or polyphyletic (O'Hara *et al.* 2017), which were revised in the new classification, and many genera were transferred to other families than their traditional placement (O'Hara *et al.* 2018). Consequently, existing identification keys to the previous families can no longer be used. One might argue that species identification keys are more useful than family keys, but 1) these are lacking or outdated for the majority of species, 2) they are usually geographically limited, 3) identification to high ranks is useful for an estimate of diversity and can speed up faunal inventory studies, and 4) the new classification differs greatly from all previous ones and a key can make it more

accessible to users. Therefore, the present study aims to develop a new identification key for the currently accepted ophiuroid families (O'Hara *et al.* 2018), while at the same time expanding the short diagnoses provided by O'Hara *et al.* (2018) into detailed descriptions using previously rarely considered characters.

The family level taxa of Ophiuroidea are based on nodes of similar age (± 110 ma) on the recent phylogeny (O'Hara *et al.* 2017), but as ranks in a classification they are of course artificial constructs by and for humans to conceptualize the diversity. During the evolution within a family clade, many changes happened: some genera/species lost the synapomorphies that support the monophyly of each node on the phylogenetic tree, others kept some of them as plesiomorphies, and most evolved novelties/autapomorphies that may or may not need to be included in the family description. Also, the within-family phylogeny has not been analyzed yet, apart from few exceptions (e.g., Ophiocomidae Ljungman, 1867; O'Hara *et al.* 2019), and the support for each family is biased towards molecular data. Previous descriptions of many families no longer reflect the morphological diversity of the included genera, e.g., the family Ophiomyxidae Ljungman, 1867 now includes several genera that were previously assigned to Ophiodermatidae Ljungman, 1867, whereas several former ophiomyxids have been transferred to the resurrected Ophioscolecidae Lütken, 1869 (which is currently paraphyletic). The assemblage of genera included in Ophiomyxidae now share rather few characters. This complicates the identification of family-specific characters that allow the correct familial assignment of all species by morphology, which was emphasized also by O'Hara *et al.* (2018), who limited the family descriptions to a few diagnostic characters based on the type genera. Pending full taxonomic revisions of all families, the present study aims to provide revised descriptions, based on the characters used for the creation of an interactive identification key.

A conventional (often dichotomous) key has a single access point and is fixed in the order in which the characters need to be assessed, and with an increasing number of steps, it quickly becomes unwieldy and imprecise, because the probability of making a wrong decision (and then following the wrong path) increases with the number of decisions to be made. Attempts have been made to better structure excessively long keys (with hundreds of couplets to evaluate), but they still have severe limitations for incomplete specimens and human error, problems that can be overcome with computerized multiple access keys (Walter & Winterton 2007). The main limitation when constructing any kind of key is defining the most suitable characters and states that accurately identify a specific taxon, which can be difficult when the taxa are not sufficiently distinct from each other. To overcome the above-mentioned obstacles, we chose to create a software-based interactive key in which the user chooses/enters the character states of the specimen that can be observed, not limited by a particular order of decisions as in traditional keys, and thus offering multiple access points. The program eliminates taxa to which the chosen character states do not apply, and the process is continued until only one taxon remains (Dallwitz *et al.* 2000). This allows the inclusion of a large number of characters, and species (or incomplete specimens), which lack some of the typical features, can still be identified. Redundancy also ensures that user errors have less impact on the outcome. It should be noted that the characters used in this key were chosen for family identification purposes, not for phylogenetic inference and also not for identification at lower taxonomic levels (genus, species). This means that homoplastic characters (e.g., madreporite shape, branching arms) can be useful for identification when they can narrow down the selection of possible results, and autapomorphies are particularly useful for identification but not for phylogenetic inference. Characters that vary between species (e.g., disc color, number of distal/proximal spines and tentacle scales) were excluded as not useful for the identification of families. Consequently, the character matrix differs considerably from the one used to infer a phylogeny from morphological characters (Thuy & Stöhr 2011) and would not be suitable for that purpose.

Traditionally, ophiuroids have been described based on limited external structures, such as disc scales, arm plates and spines, and oral frame skeleton, among others. Modern descriptions also include microscopic structures, observed by scanning electron microscopy, and internal skeletal structures (Martynov 2010a;

Stöhr 2012; Stöhr & Martynov 2016; Okanishi *et al.* 2017), and many other characters have been re-evaluated (Thuy & Stöhr 2016, 2018). Despite this interest, the terminology used for ophiuroid skeletal elements is not standardized and authors have used different terms, which might lead to confusion for readers. Also, the descriptions of the 33 families in the new classification were limited to a few diagnostic characters (O'Hara *et al.* 2018). Therefore, besides creating the keys, we elaborated on some terminology and expanded the descriptions for each family. These descriptions cannot replace full taxonomic revisions, but since those are time-consuming and will probably not be achieved in the nearest future, the key-derived descriptions are a useful compromise, providing more information than the short diagnoses by O'Hara *et al.* (2018). To evaluate the differences between interactive and conventional keys, and to provide a tool that can be used without a computer, we used the software to export a conventional polychotomous key, which prioritizes external characters to facilitate usage without the need for extensive preparation of the animals.

Material and methods

Primarily, the type species of each family was used to find the features that may distinguish the families. When the type species was not available, another species of the type genus was evaluated, and if no member of the type genus was available, other genera in the family were used. Additional species from most families were used to verify the presence of the chosen characters and to test the key. The species assessed in this study are shown in Table 1. Characters were collected by examining images in publications (Smith *et al.* 1995; Pomory 2007; Gondim *et al.* 2013), preserved specimens collected in the Persian Gulf and in the museum collections of the Royal Belgian Institute of Natural Sciences (RBINS), as well as examining scanning electron microscope images (SEM) and 3D images of museum specimens of the Swedish Museum of Natural History (SMNH) and RBINS. We used 54 external and 22 internal characters, amounting to a total of 77 characters and 190 states (Appendix 1), to create the interactive key. The characters and states were defined partially based on O'Hara *et al.* (2018), modified for the current purpose, and additional characters were selected after specimen/image examination. All characters include at least two mutually exclusive states. The genera included in each family were extracted from O'Hara *et al.* (2018) and verified for possible later changes in Stöhr *et al.* (2020).

The primary software package used to develop a traditional and interactive key was DELTA (DEscription Language for TAXonomy) (Dallwitz *et al.* 2006). It allows the choice of different types of characters such as ordered, unordered, integer, real numeric and text, but we omitted real number characters, e.g., 'disc diameter' as an absolute size, because not only do the animals change size during growth, but also it might not be easy to measure the targeted character precisely while using the key. Instead, using a multiple-choice character with ranges of values or relative size, e.g., 'the arm, is \times times as long as the disc diameter' is more useful. Selected images were uploaded and labeled in the software to enable users to compare to their specimens, to facilitate the choices to be made. To create a key, a great deal of attention must be paid to choose the most powerful characters and states for family discrimination. Regarding character dependency, DELTA has the capability to define dependencies between characters, i.e., if the character 'A' is not present in a taxon, the other dependent characters describing character 'A' cannot be applied (see characters 42 and 43–45 in Appendix 1). On the other hand, missing data for some states were left blank and written as "no data" in the family description. These may be completed in the future as the project progresses and more morphological traits will be included. This is the main advantage of the interactive key, i.e., that it allows new characters to be added without disrupting the existing structure.

For the creation of the conventional key, of the original 77 characters, 46 characters were found to be sufficient to separate the taxa. We prioritized external characters in the creation of the conventional key as much as possible (without compromising identification accuracy), because these are more easily observed under field conditions. To achieve this, DELTA offers techniques such as weighting and setting reliability values. Weighting in DELTA is not related to weighting in phylogenetic inference. It serves

Table 1 (continued on next page). List of the species assessed to create the identification key to the ophiuroid families. The type species of each family is marked with a “T”, square brackets [] indicate species that could not be assessed due to lack of material, and those with an asterisk (*) were assessed mainly from literature.

Family	Type genus	Species assessed
Amphilepididae	<i>Amphilepis</i> Ljungman, 1867	<i>Amphilepis norvegica</i> (Ljungman, 1865) (T)
Amphilimnidae	<i>Amphilimna</i> Verrill, 1899	<i>Amphilimna olivacea</i> (Lyman, 1869) (T)
Amphiuridae	<i>Amphiura</i> Forbes, 1843	<i>Amphiura chiajei</i> Forbes, 1843 (T) <i>Amphiura atlantidea</i> Madsen, 1970 <i>Amphiura filiformis</i> (O.F. Müller, 1776) <i>Acrocnida brachiata</i> (Montagu, 1804) <i>Amphioplus aurensis</i> A.M. Clark, 1955 <i>Amphioplus congensis</i> (Studer, 1882) <i>Amphipholis nudipora</i> Koehler, 1914 <i>Amphipholis squamata</i> (Delle Chiaje, 1828) <i>Amphipholizona delicata</i> H.L. Clark, 1915 <i>Amphipholizona perplexa</i> (Nielsen, 1932) <i>Ophiophragmus acutispina</i> (Koehler, 1914)
Asteronychidae	<i>Asteronyx</i> Müller & Troschel, 1842	<i>Asteronyx loveni</i> Müller & Troschel, 1842 (T)
Astrophuriidae	<i>Astrophuriura</i> Sladen, 1879	<i>Astrophuriura permira</i> Sladen, 1879 (T) <i>Ophiomisidium tommasii</i> Borges, Monteiro & Amaral, 2006
Clarkcomidae	<i>Clarkcoma</i> Devaney, 1970	<i>Clarkcoma canaliculata</i> (Lütken, 1869) * (T)
Euryalidae	<i>Euryale</i> Lamarck, 1816	<i>Euryale aspera</i> Lamarck, 1816 (T)
Gorgonocephalidae	<i>Gorgonocephalus</i> Leach, 1815	<i>Gorgonocephalus caputmedusae</i> (Linnaeus, 1758) (T)
Hemieuryalidae	<i>Hemieuryale</i> von Martens, 1867	<i>Hemieuryale pustulata</i> v. Martens, 1867 (T) <i>Actinozonella texturata</i> (Lyman, 1883) <i>Ophioplus tuberculatus</i> (Lyman, 1883) <i>Ophiozonella falklandica</i> Mortensen, 1936 <i>Ophiozonella longispina</i> (H.L. Clark, 1908) <i>Sigsbeia lineata</i> Lütken & Mortensen, 1899 <i>Sigsbeia murrhina</i> Lyman, 1878
Ophiacanthidae	<i>Ophiacantha</i> Müller & Troschel, 1842	<i>Ophiacantha bidentata</i> (Bruzelius, 1805) (T) <i>Ophiacantha abyssicola</i> G.O. Sars, 1872 <i>Ophiocanops multispina</i> Stöhr, Conand & Boissin, 2008 <i>Ophiochondrus stelliger</i> Lyman, 1879 <i>Ophiolimna bairdi</i> (Lyman, 1883) <i>Ophiolimna perfida</i> (Koehler, 1904) <i>Ophioplinthaca plicata</i> (Lyman, 1878)
Ophiactidae	<i>Ophiactis</i> Lütken, 1856	<i>Ophiactis savignyi</i> (Müller & Troschel, 1842) (T) <i>Ophiactis abyssicola</i> (M. Sars, 1861)
Ophiernidae	<i>Ophiernus</i> Lyman, 1878	<i>Ophiernus vallincola</i> Lyman, 1878 (T)
Ophiobyrssidae	<i>Ophiobyrssa</i> Lyman, 1878	<i>Ophiobyrssa rudis</i> Lyman, 1878 * (T)
Ophiocamacidae	<i>Ophiocamax</i> Lyman, 1878	<i>Ophiocamax vitrea</i> Lyman, 1878 (T)
Ophiocomidae	<i>Ophiocoma</i> L. Agassiz, 1836	<i>Ophiocoma echinata</i> (Lamarck, 1816) (T) <i>Ophiocoma erinaceus</i> Müller & Troschel, 1842 <i>Ophiocoma scolopendrina</i> (Lamarck, 1816)
Ophiodermatidae	<i>Ophioderma</i> Müller & Troschel, 1840	<i>Ophioderma longicaudum</i> (Bruzelius, 1805) (T)
Ophiohelidae	<i>Ophiohelus</i> Lyman, 1880	[<i>Ophiohelus umbella</i> Lyman, 1880] (T) <i>Ophiomyces delata</i> Koehler, 1904 <i>Ophiotholia spathifer</i> (Lyman, 1879)

Table 1 (continued). List of the species assessed to create the identification key to the ophiuroid families. The type species of each family is marked with a “T”, square brackets [] indicate species that could not be assessed due to lack of material, and those with an asterisk (*) were assessed mainly from literature.

Family	Type genus	Species assessed
Ophiolepididae	<i>Ophiolepis</i> Müller & Troschel, 1840	<i>Ophiolepis superba</i> H.L. Clark, 1915 (T)
Ophiroleucidae	<i>Ophiroleuce</i> Koehler, 1904	<i>Ophiroleuce seminudum</i> Koehler, 1904 (T) <i>Ophiopallas paradoxa</i> Koehler, 1904
Ophiomusaidae	<i>Ophiomusa</i> Hertz, 1927	<i>Ophiomusa lymani</i> (Wyville-Thomson, 1873) (T)
Ophiomyxidae	<i>Ophiomyxa</i> Müller & Troschel, 1842	<i>Ophiomyxa pentagona</i> (Lamarck, 1816) (T) <i>Ophiarachna incrassata</i> (Lamarck, 1816)
Ophionereididae	<i>Ophionereis</i> Lütken, 1859	[<i>Ophionereis reticulata</i> (Say, 1825)] (T) <i>Ophionereis porrecta</i> Lyman, 1860 <i>Ophiochiton fastigatus</i> Lyman, 1878 <i>Ophiodoris malignus</i> Koehler, 1904 <i>Ophioplax lamellosa</i> Matsumoto, 1915
Ophiopezidae	<i>Ophiopeza</i> Peters, 1851	<i>Ophiopeza fallax</i> Peters, 1851 (T) <i>Ophiopeza spinosa</i> (Ljungman, 1867)*
Ophiopholidae	<i>Ophiopholis</i> Müller & Troschel, 1842	<i>Ophiopholis aculeata</i> (Linnaeus, 1767) (T)
Ophiopsilidae	<i>Ophiopsila</i> Forbes, 1843	<i>Ophiopsila aranea</i> Forbes, 1843 (T) <i>Ophiopsila guineensis</i> Koehler, 1914
Ophiopteridae	<i>Ophiopteris</i> E.A. Smith, 1877	<i>Ophiopteris antipodum</i> E.A. Smith, 1877 (T)
Ophiopyrgidae	<i>Ophiopyrgus</i> Lyman, 1878	<i>Ophiopyrgus wyvillethomsoni</i> Lyman, 1878 (T) <i>Ophiopyrgus saccharatus</i> Studer, 1882 <i>Amphiophiura insolita</i> (Koehler, 1904) <i>Amphiophiura latro</i> (Koehler, 1904) <i>Ophiopleura borealis</i> Danielssen & Koren, 1877 <i>Ophioplinthus tessellata</i> (Verrill, 1894) <i>Ophioparte gigas</i> Koehler, 1922
Ophioscolecidae	<i>Ophioscolex</i> Müller & Troschel, 1842	<i>Ophioscolex glacialis</i> Müller & Troschel, 1842 (T) <i>Ophiolycus purpureus</i> (Düben & Koren, 1846)
Ophiosphalmidae	<i>Ophiosphalma</i> H.L. Clark, 1941	[<i>O. planum</i> (Lyman, 1878) = <i>O. armigerum</i> (Lyman, 1878)] (T) <i>Ophiosphalma glabrum</i> (Lütken & Mortensen, 1899)
Ophiothamnidae	<i>Ophiothamnus</i> Lyman, 1869	[<i>Ophiothamnus vicarius</i> Lyman, 1869] (T) <i>Histampica duplicata</i> (Lyman, 1875)
Ophiotomidae	<i>Ophiotoma</i> Lyman, 1883	[<i>Ophiotoma coriacea</i> Lyman, 1883] (T) <i>Ophiocomina nigra</i> (Abildgaard in O.F. Müller, 1789) <i>Ophiocopa spatula</i> Lyman, 1883 <i>Ophiotreta valenciennesi</i> (Lyman, 1879)
Ophiotrichidae	<i>Ophiothrix</i> Müller & Troschel, 1840	<i>Ophiothrix fragilis</i> (Abildgaard in O.F. Müller, 1789) (T) <i>Macrophiothrix elongata</i> H.L. Clark, 1938 <i>Macrophiothrix hirsuta cheneyi</i> (Lyman, 1861)
Ophiuridae	<i>Ophiura</i> Lamarck, 1801	<i>Ophiura ophiura</i> (Linnaeus, 1758) (T) <i>Ophiura carnea skoogi</i> (Koehler, 1923) <i>Ophiura sarsii</i> Lütken, 1855 <i>Ophiocten sericeum</i> (Forbes, 1852)

*citations: Clarkcomidae (Devaney 1970; Hendler 2018), Ophiobysidae (Martynov 2010a; O’Hara *et al.* 2018) and Ophiopezidae (Martynov 2010a).

the purpose of letting characters with high reliability be used more in the key compared to those with lower reliability. Reliable characters are those whose state values can easily be assigned to a specimen and thus most accurately separate the taxa. We used a higher reliability value (8) for external characters and a lower value (1) for internal and difficult characters in the creation of the conventional key. For the interactive key the reliability value was set as the default (5). We assigned weights to characters that are more reliable for identification, which causes them to appear first in the interactive key and increases their likelihood of being used in the creation of the conventional key. As an alternative to DELTA, the same dataset was transferred to Xper2 (desktop application, ver. 2.3.2) and Xper3 (online application), in which we applied character weights (= reliability) ranging between 1 and 5, to create conventional and interactive keys. The character reliability in DELTA for characters 1–77 was as follows: 1,8 2,1 3–8,8 9,1 10–22,8 23–33,1 34,8 35,1 36–45,8 46,1 47–50,8 51–62,1 63,8 64,1 65–67,8 68–77,1, in which the value of each character reliability is next to the character number(s) separated by a comma (e.g., 3–8,8: the value of 8 was assigned to characters 3 to 8). The character weights in Xper were as follows: 1,5 2,1 3–8,5 9,1 10–22,5 23–33,1 34,5 35,1 36–45,5 46,1 47–50,5 51–62,1 63,5 64,1 65–67,5 68–77,1.

Since the terminology used for ophiuroid characters varied between authors and has subsequently caused confusion, we have prepared a glossary that explains the more difficult characters used in the present study.

Abbreviations

2AdShSp	=	secondary adoral shield spine
2IPa	=	secondary infradental papillae
AdSh	=	adoral shield
AdShSp	=	adoral shield spine
DP	=	dental plate
IPa	=	infradental papillae
k-plate	=	Keilplatte sensu Ludwig (1899) (meaning wedge plate)
LAP	=	lateral arm plate
LOPa	=	lateral oral papillae
OP	=	oral plate
OSh	=	oral shield
PP	=	primary plate
RS	=	radial shield
TPa	=	tooth papilla
TSc	=	tentacle scale(s)
VAP	=	ventral arm plate
VAP-1	=	first ventral arm plate
vCtP	=	ventral compartment plate

Terminology

Disc (flat/high)

Flat or high stands for the height of the disc relative to the level of the arms; if it is at about the same level as the arms, such as in *Ophiura* Lamarck, 1801, it is considered flat; in e.g., *Amphiophiura* Matsumoto, 1915 it is considered as high. Sac-like refers to a soft, floppy disc that is much higher than wide, e.g., as in *Ophiomyces* Lyman, 1869, where it may be caused by the absence of the radial shields. See character 35 and Fig. 1A–C.

Integument

This is the skin of the whole animal, but in this study, only integument characters of the disc (thick or thin skin) are used. Thick skin is defined by the thickened epidermis and may be compared with thin skin in cross-sectional slides. For practical reasons, if the skin is transparent enough for the plates/scales to

be visible in a stereo microscope, we use the term ‘thin’. If the plates are obscured, the skin is ‘thick’. Granules can be present on both thick and thin skin. Hence, the integument can be described in terms of whether the skin is obscuring the plates (RS, PP, k-plate) or not. See character 36 and Fig. 1D–F.

Scales (thick/thin)

Thin scales are translucent, while thick scales are opaque and often raised. Scales may bear spines/granules or may have tubercles growing out of them. See Fig. 1E–F.

Dorsal disc (granules, tubercles, spines, scales, plates)

Spines and granules are articulating structures on top of the plates/scales, and can be removed mechanically. ‘Tubercles’ are outgrowths of the stereom (non-articulating) and thus part of the scales and plates and can be either macroscopic or microscopic. Generally, we distinguish between macroscopic tubercles that are visible at low magnification, whereas a tuberculous stereom structure is visible at high magnification or by SEM and after removal of the skin (e.g., by bleaching or enzyme treatment). The term ‘plates’ is applied to various ossicles that have a fixed (predictable) position; on the disc, these are the primary plates and radial shields, as well as the k-plate (when present), which separates a pair of radial shields proximally. Other plate-like ossicles are termed ‘scales’, and these do not have a fixed position. Radial shields often differ in covering (with granules/spines) from the rest of the disc and therefore, we apply ‘covering of radial shields’ as separate characters. See characters 37–45 and Fig. 2A–B, D.

Ventral disc

The ventral disc can have spines, granules or none. We created another character for the presence/absence of scales, since their distribution on ventral interradii varies, from covering the whole area of an interradius

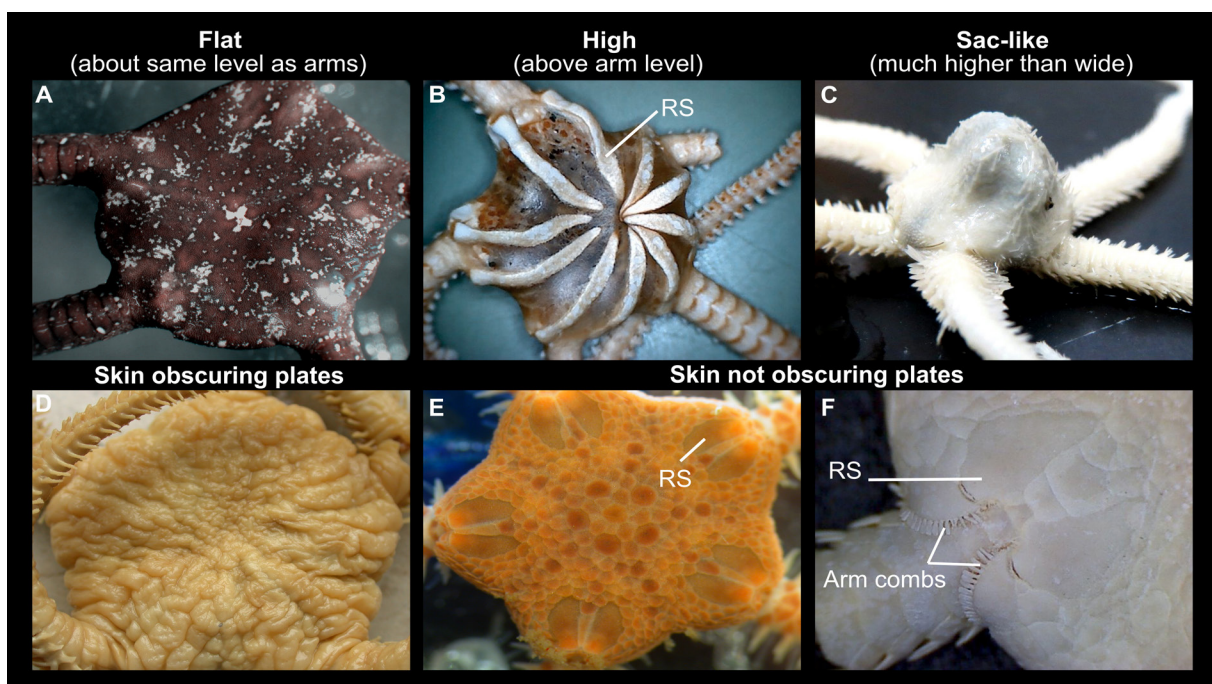


Fig. 1. Dorsal disc shapes and radial shields in brittle stars as defined for the purpose of this study. **A.** Flat (*Ophioderma* sp.). **B.** High, with bar-like radial shields (*Asteronyx loveni* Müller & Troschel, 1842 (dry specimen)). **C.** Sac-like, radial shields absent (*Ophiotholia spathifer* (Lyman, 1879)). **D.** Thick skin obscuring scales and plates (*Ophiosparte gigas* Koehler, 1922). **E.** Flat, radial shield scalene triangular to half circle (*Amphiura chiajei* Forbes, 1843). **F.** Arm combs, radial shields isosceles triangular to pear-shaped (*Ophiura ophiura* (Linnaeus, 1758)).

to half/less than half or none. To estimate the size of the scales, we considered the interradius as a triangle and counted the scales on the H line of the triangle. The state ‘few scales with whole coverage’ implies that the size of the scales is greater than with ‘many scales and whole/half coverage’. See characters 47–49 and Fig. 2C.

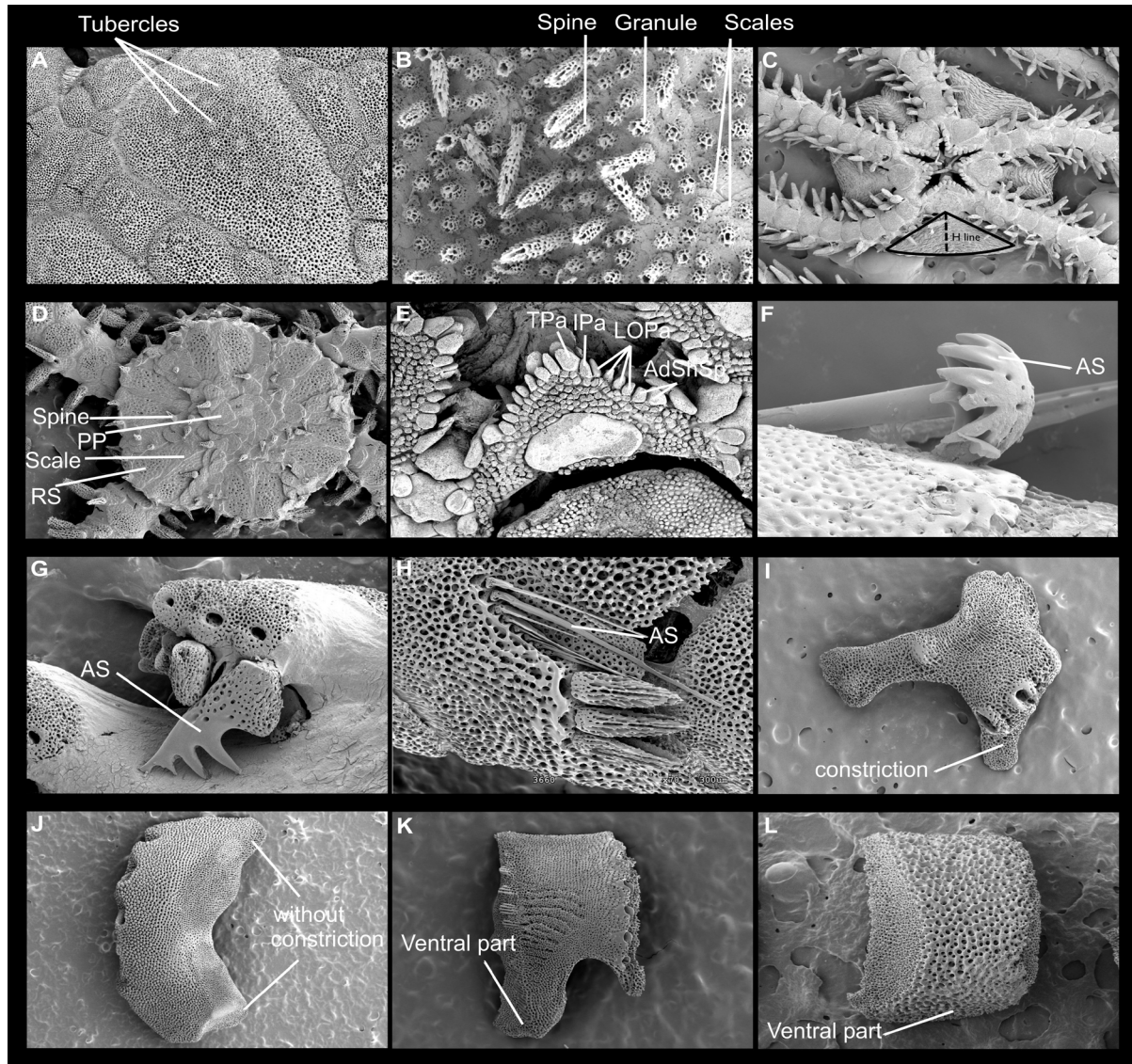


Fig. 2. SEM images of various brittle star ossicles. **A–E.** Disc structures. **A.** Dorsal disc, radial shield with tubercles (*Ophiomusa lymani* (Wyville-Thomson, 1873)). **B.** Dorsal disc (*Ophiolimna bairdi* (Lyman, 1883)). **C.** Ventral disc (*Ophionereis porrecta* Lyman, 1860), the interradius is assumed as a triangle and H gives its height. **D.** Dorsal disc, triangular radial shield (*Ophiactis savignyi* (Müller & Troschel, 1842)). **E.** Ventral disc, mouth (*Ophioderma* sp.). – **F–H.** Atypical arm spines. **F.** Umbrella-shaped arm spine (*Ophiotholia spathifer* (Lyman, 1879)). **G.** Hook-shaped arm spine (*Asteronyx loveni* Müller & Troschel, 1842). **H.** Bristle spines (*Ophiernus vallincola* Lyman, 1878). – **I–L.** Lateral arm plates (LAP). **I.** LAP with constriction (*Ophioscolex glacialis* Müller & Troschel, 1842). **J.** Dorsal and ventral part of LAP without constriction (*Ophiura ophiura* (Linnaeus, 1758)). **K.** Ventral part of LAP projecting ventro-proximalwards (*Ophiopallas paradoxa* Koehler, 1904). **L.** Ventral part of LAP not projecting ventro-proximalwards (*Ophiosphalma fimbriatum* (Koehler, 1922)).

Oral papillae sensu lato (according to Hendler 2018)

One angle of the oral frame includes a dental plate (DP), two oral plates (= half-jaws) (OP), two adoral shields (AdSh), and one oral shield (OSh), positioned from proximal towards distal. The terminology for the articulated ossicles situated at the jaws has been clarified by Hendler (2018). Oral papillae sensu lato are small ossicles (papilliform, or spiniform) attached to the edges of the plates (DP, OP, AdSh, VAP-1, and vCtP) around the ophiuroid oral frame. We used the following papillae in the key. Those on the DP (described below) include teeth and tooth papillae. Infradental papillae are only the pair that develops later than others on the DP/OP joint and ultimately articulate with the OP, then move under the ventralmost tooth (situated on the most ventral part of the DP). Secondary infradental papillae (2IPas) appear close to the DP/OP joint. Each new ossicle arises proximal to its predecessor on the OP in the same direction. The adoral shield spine (AdShSp) is mainly positioned on the adoral shield (AdSh). However, the position of the AdShSp can vary during ontogenesis. It may remain on the AdSh (as in *Ophioderma rubicundum* Lütken, 1856), overlap the AdSh and the OP (as in *Ophiolepis paucispina* (Say, 1825)), or articulate with the OP (as in *Ophionereis olivacea* H.L. Clark, 1900). The secondary adoral shield spine (2AdShSp) is homologous with the AdShSp, and both are situated next to each other. The buccal scale, which is a plesiomorphy in Ophiuroidea, but might be homologous within several orders (secondarily absent in some taxa), is situated inside the oral slit and next to the oral plate ridge. Lateral oral papillae (LOPa) are all remaining ossicles not named above that develop on the OP distal to the IPa (Hendler 2018). See characters 50–58 and Figs 2E, 4.

Dental plate

The dental plate sits vertically inside the mouth, covering the proximal edges of two oral plates (half-jaws). We refer to the end closest to the upper/aboral disc as dorsal and the end at the mouth opening, situated below the teeth, as ventral. Since the terms aboral (away from the mouth) and oral (close to the mouth) may be less precise when talking about the mouthparts, ventral/dorsal have been preferred by numerous previous authors, e.g., Hendler (2018) and O'Hara *et al.* (2018), and could be considered the standard terminology in ophiuroid morphology. Dental sockets on the DP are either a depression or a perforation that may be with/without a septum. A foramen (pl. foramina) is a hole perforating the socket on the DP, and a perforation is a smaller hole than a foramen. Perforating holes are divided into two types, one with distinct borders and the other with indistinct borders (e.g., *Ophiolepis superba* H.L. Clark, 1915 and *Ophiactis savignyi* (Müller & Troschel, 1842), respectively). The geometry of the DP (entire/fragmented) varies from equal width all over to ventral or dorsal half widest. To infer the size of dental sockets, we estimated whether their height is less than 50% of their width, equal or wider. Another character to describe the DP is the ratio of teeth to tooth papillae on the DP, i.e., whether there is only a single column of teeth, or with a single column on half of the DP and the other half with tooth papillae (e.g., Ophiotrichidae Ljungman, 1867, Ophiopholidae O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018), or with a single column on $\frac{2}{3}$ of the DP and tooth papillae on $\frac{1}{3}$ of the DP (e.g., Ophiuridae Müller & Troschel, 1840), or covering the entire DP with teeth or tooth papillae evenly (e.g., Gorgonocephalidae Ljungman, 1867). See characters 68–74 and Fig. 3F–I.

Arm spine shape

Considering the 'tip' and 'cross-section' shape, as well as the 'ratio of distal $\frac{1}{3}$ of an arm spine to the maximum proximal thickness' (in a given cross-sectional plane), four states are defined for this study (Fig. 5). Tapering/conical (distally less than half as thick as proximal diameter with round cross-section and tapering tip); flat (distally half as thick as proximal diameter or same with oval cross-section); cylindrical (same thickness at both ends with flat/round tip); pointed (distally half to equally as thick as proximal diameter with round cross-section and pointed tip). See characters 12–17 and Fig. 5.

Tentacle scales

TSc develop later than arm spines and are situated next to the tube foot (= tentacle) pore, often at the LAP, sometimes on the VAP or both. The spines have visible articulations on the LAP, while the TSc has

no articulation (except in *Ophiomyces*). The pores may be visible along the arm or only on the proximal part (e.g., in *Ophiomusa* Hertz, 1927 only the first two are visible, while in *Ophiosphalma* H.L. Clark, 1941 the pores are visible on more than two proximal segments, and in most other genera they are present along the entire arm). We also described the tentacle scale length (compared with the nearest spine) and shape (comparing the length with TSc width) accompanied by the oval/round estimated cross-section. See characters 18–22.

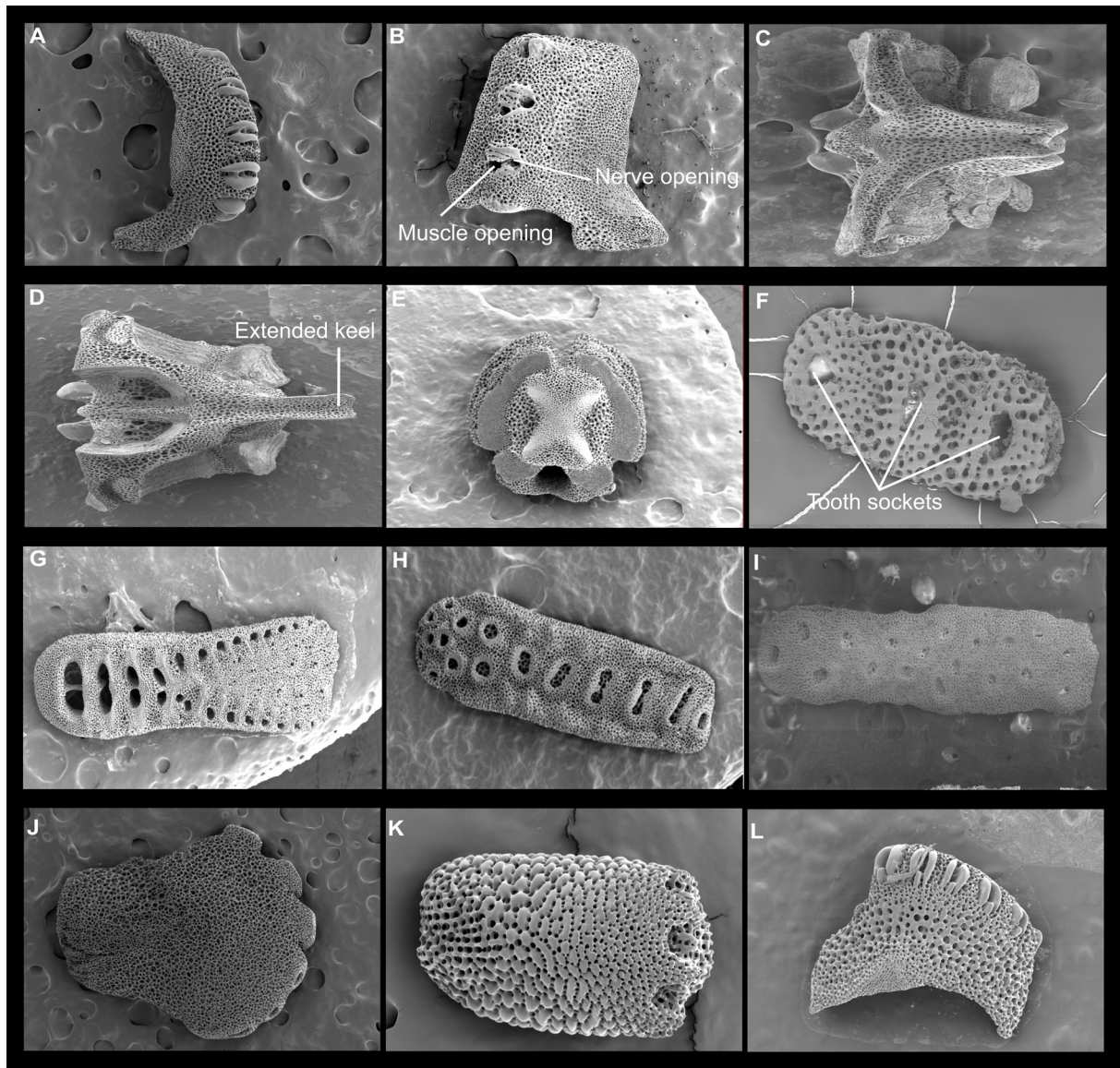


Fig. 3. SEM images of various ossicle structures in brittle stars. **A.** Muscle and nerve opening on LAP separated by small ridge if at all (*Amphiura chiajei* Forbes, 1843). **B.** Muscle and nerve opening on LAP separated by large, prominent ridge or regular stereom (*Ophiolycus purpureus* (Düben & Koren, 1846)). **C.** Non-keeled vertebra (*Amphiura chiajei*). **D.** Keeled vertebra (*Ophiothrix fragilis* Abildgaard, 1789). **E.** Vertebra with oral bridge (*Euryale aspera* Lamarck, 1816). **F.** Sockets indicate teeth and tooth papillae on dental plate as single row (*Amphilepis norvegica* (Ljungman, 1865)). **G.** $\frac{1}{2}$ single row of teeth and $\frac{1}{2}$ tooth papillae (*Ophiothrix fragilis*). **H.** $\frac{2}{3}$ single row of teeth and $\frac{1}{3}$ tooth papillae (*Ophiocamax vitrea* Lyman, 1878). **I.** Sockets on dental plate covering evenly (*Asteronyx loveni* Müller & Troschel, 1842). **J–K.** LAP not arched = position lateral. **L.** LAP arched = wrapped around the arm.

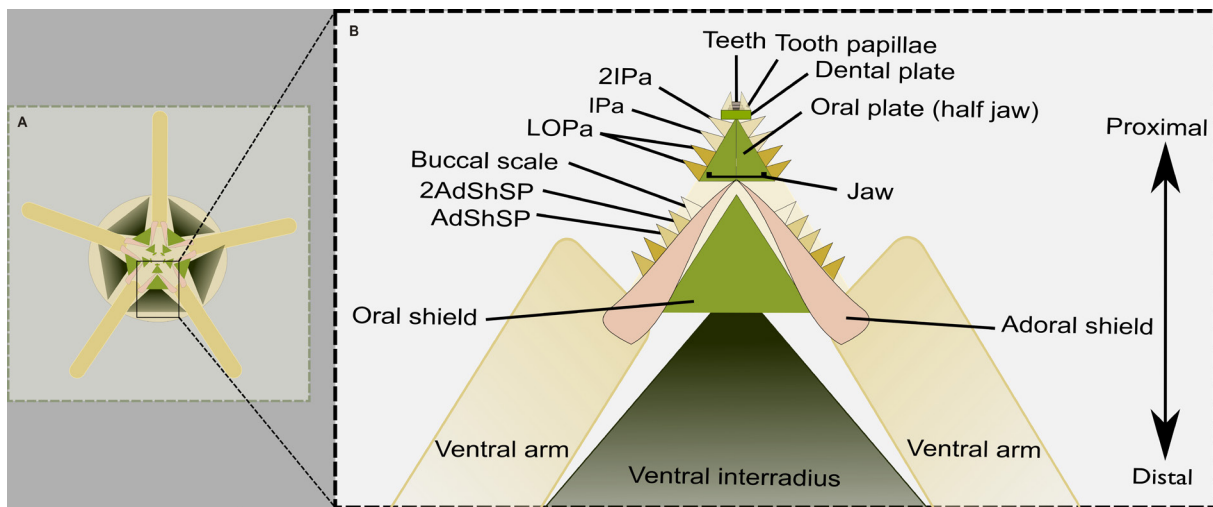


Fig. 4. Oral papillae sensu lato. **A.** Ventral side of a schematic brittle star. **B.** One angle of the oral frame includes a dental plate (DP), two oral plates (= half-jaws) (OP), two adoral shields (AdSh), and one oral shield (OSh), positioned from proximal towards distal. The typical position of teeth, tooth papillae, secondary infradental papillae (2IPa), infradental papillae (IPa), buccal scale, secondary adoral shield spine (2AdShSp), adoral shield spine (AdShSp) on DP, OP and AdSh are illustrated, respectively. The presence/absence, number and shape of each papilla vary among different taxa.

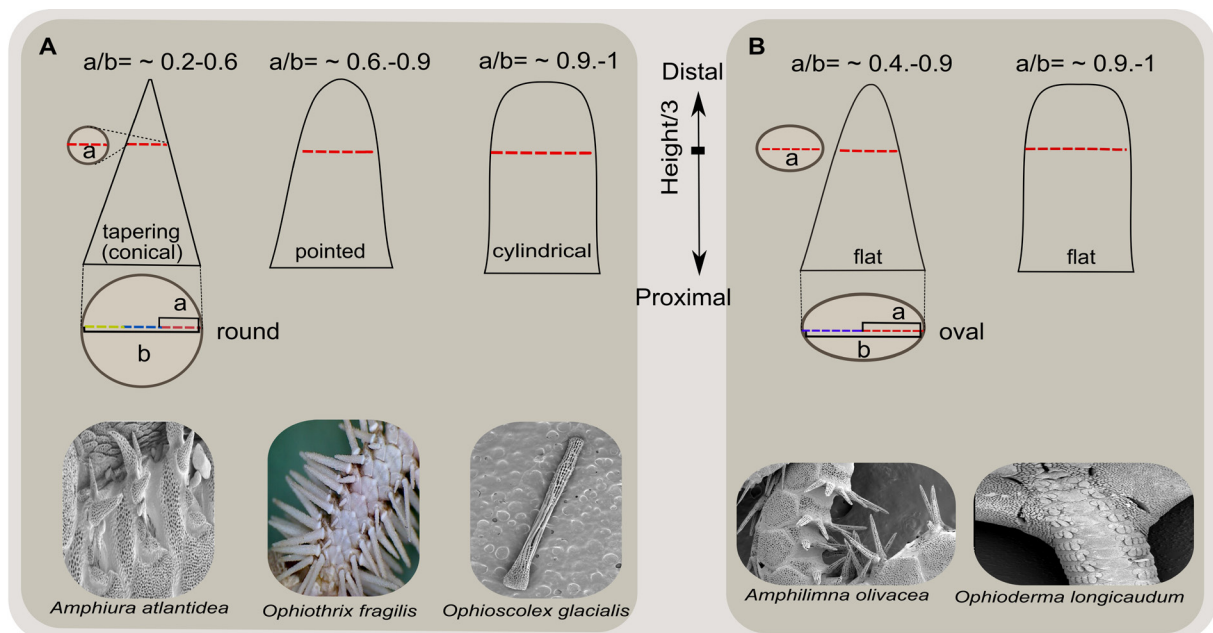


Fig. 5. Typical arm spine shape. **A.** Tapering (conical): distally $\frac{1}{3}$ as thick as proximal diameter with a round cross-section; Pointed: distally half as thick as proximal diameter with a round cross-section; Cylindrical: same thickness at both ends with flat/round tip. **B.** Flat: distally half as thick as proximal diameter with oval cross-section. Red dashed lines show the $\frac{1}{3}$ distal cross-section. The letters ‘a’ and ‘b’ illustrate the diameter of $\frac{1}{3}$ distal and basal cross-sections, respectively. ‘a/b’ shows the approximate ratio of these diameters.

Keel

A keel is a longitudinal, median and often raised structure on the dorso-distal part of the vertebrae. The vertebral keel was originally introduced by LeClair (1996) as the structure projecting distally from the dorsal groove of the vertebrae, extending beyond the length of the articulating structures and matched by a large depression (socket) on the proximal face of the adjacent vertebra. It is only found in Ophiotrichidae, Ophionereididae Ljungman, 1867 and Ophiopholidae. This definition was applied by most later authors (LeClair & LaBarbera 1997; O'Hara *et al.* 2018;), whereas Martynov *et al.* (2015) used a broader definition, including short structures protruding from the dorso-distal part of the vertebrae in Ophiacanthidae Ljungman, 1867 and forming an arrow-shaped structure, but not extending beyond the articulating structures and not matched by a proximal deep socket. The latter broader definition reduces the taxonomic value of the keel and is rejected here. To avoid misunderstandings, we modified the term to 'extended keel', meaning the original definition of a long distal process with matching proximal socket. See character 76 and Fig. 3C–D.

Results

This study resulted in traditional and interactive keys for the families of Ophiuroidea, based on the classification proposed by O'Hara *et al.* (2018) and the examined species listed in Table 1. The key is based on a limited number of species and only on adult specimens, which may limit its usefulness for other species and juvenile stages. Although we assigned highest and lowest weight to the same characters in DELTA and Xper, the resulting keys were different. Giving lower scores to some characters increased the length of the conventional key on both platforms. The interactive keys are available as a DELTA file package (<https://zenodo.org/record/4563203>) and as an Xper3 online application (<http://xper3.fr/xper3GeneratedFiles/publish/identification/7495441984259574364/>). Below we present the conventional key created by DELTA. In Appendix 2, a condensed tabular key is available; its full text version is provided as [Supp. file 1](#). The full character and item matrix (tabular key) is provided as [Supp. file 2](#). The conventional key produced by Xper 3 is available as [Supp. file 3](#). A comparison of both software programs and their features is provided in [Supp. file 4](#).

Below, all 33 families are described as we understand them by the examined species. The descriptions were generated with the aid of DELTA Intkey (Dallwitz *et al.* 2000) and edited manually.

Interactive Key in DELTA format

We recommend the usage of the CSIRO version of DELTA Intkey for better performance and compatibility. When the interactive key is running, the characters are listed on the left (it is also possible to ask the software to show all or the best characters to separate the taxa). In addition, on the upper right, all taxa, and on the lower half, only eliminated ones are shown (Fig. 6). By clicking on a character, the states will be shown to choose from and images can be requested to distinguish the states precisely. After selecting the states, the software eliminates some taxa. The remaining taxa are then shown in the upper right half of the window. The user can continue the identification process based on the characters that are possible to observe on the specimen and narrow the identification until one taxon remains. Moreover, characters can be used in any sequence. Some family characters may not be present or ambiguous in some species. Therefore, it is possible to skip ahead, facilitating faster identification.

The screenshot displays the DELTA interactive key workspace with the following components:

- Best Characters (71):** A list of 71 characters, with character 1.71 highlighted in blue. The list includes:
 - 1.71 arm spine articulation (size)
 - 1.62 longest arm spines (relative length)
 - 1.54 teeth (shape)
 - 1.44 teeth on DP arranged as (the ratio of teeth and tooth papillae on dental plate)
 - 1.35 distance between spine articulations
 - 1.34 oral shield (shape)
 - 1.30 ventral interradial (cover)
 - 1.28 ventral scales (length)
 - 1.26 dental plate (geometry)
 - 1.20 arm (relative length)
 - 1.17 radial shield (length)
 - 1.07 radial shield (covering)
 - 0.99 ventro-distal tip of LAF (projecting ventralwards e.g. Ophiopallas)
 - 0.99 integument (skin obscuring plates)
 - 0.99 buccal scales on DP (absence/presence)
 - 0.92 nerve opening (size-related to arm spine articulation)
 - 0.92 lateral oral papillae (absence/presence)
 - 0.89 scales on DP as (depression/perforation-with/without septum)
 - 0.80 radial shield (shape)
 - 0.87 scales on ventral interradial (covering: from disc edge)
 - 0.87 Ventral teeth (the number of oral papillae sensu lato on DP)
 - 0.85 the ratio of distal 1/3 an arm spine to maximum thickness (in a given cross-sectional plane) (arm spine)
 - 0.83 arm spine articulation (with/without sigmoidal fold)
 - 0.82 disc (flat/high)
 - 0.81 adoral shield (separated or meeting in front of oral shield)
 - 0.77 arm spines (direction)
 - 0.75 dorsal disc (cover-granules)
 - 0.74 dorsal disc (cover - primary plates)
 - 0.74 dorsal disc (cover-shapes)
 - 0.69 dorsal disc (cover-spines)
 - 0.68 adoral shield spine (absence/presence)
 - 0.68 Lyman's ossicle (absence/presence)
 - 0.67 dorsal and/or ventral edge(s) of LAFs (with/without constriction=concave)
 - 0.67 vertebrae (streptospondylous/zygospondylous)
 - 0.66 ventral scales (oval/round)
- Remaining Taxa (22):** A list of 22 taxa names enclosed in a green box:
 - Amphilepididae
 - Amphimimidae
 - Amphuridae
 - Clarkomidae
 - Gergonocephalidae
 - Hemiseuryllidae
 - Ophiactidae
 - Ophiobryidae
 - Ophiociridae
 - Ophiocnemidae
 - Ophiocnemulidae
 - Ophiocrotidae
 - Ophiocrotulidae
 - Ophiocrotulidae
 - Ophiocrotulidae
 - Ophiocrotulidae
 - Ophiocrotulidae
 - Ophiocrotulidae
 - Ophiocrotulidae
 - Ophiocrotulidae
 - Ophiocrotulidae
- Eliminated Taxa (11):** A list of 11 taxa names enclosed in a red box:
 - (1) Asterozoididae
 - (1) Astrophuridae
 - (1) Bryidae
 - (1) Ophiocrotulidae
 - (1) Ophiocrotulidae
 - (1) Ophiocrotulidae
 - (1) Ophiocrotulidae
 - (1) Ophiocrotulidae
 - (1) Ophiocrotulidae
 - (1) Ophiocrotulidae
 - (1) Ophiocrotulidae
- Used Characters (1):** A list containing one character:
 - ventral position of LAF projecting ventro-proximallywards

Fig. 6. DELTA interactive key workspace. The software window shows: available characters (blue box), used characters (grey), remaining taxa (green) and eliminated taxa (red).

Conventional identification key to the families of the Ophiuroidea with respect to the species listed in Table 1

1.	Longest arm spines shorter than half a segment	2
–	Longest arm spines between half and one segment long	12
–	Longest arm spines between one and two segments long	20
–	Longest arm spines longer than two segments	32
2(1).	Arm spines tapering (conical) (Fig. 5)	3
–	Arm spines flat (Fig. 5)	Ophiodermatidae Ljungman, 1867 [p. 34]
–	Arm spines cylindrical (Fig. 5)	4
–	Arm spines pointed (Fig. 5)	6
3(2).	Arm combs present (Fig. 1F); dorsal arm plate present; spines all similar in shape (Fig. 5); arm spines mainly lateral	Ophiopyrgidae Perrier, 1893 [p. 25]
–	Arm combs absent; dorsal arm plate absent; spines not all similar in shape (Fig. 2F–H); arm spines at proximal segments only on ventral side of arms	Asteronychidae Ljungman, 1867 [p. 19]
4(2).	Radial shield scalene (oblique) triangular (Fig. 1E)	Astrophiuridae Sladen, 1879 [p. 24]
–	Radial shield isosceles (mirror-symmetric) triangular to pear-shaped (Fig. 1F).....	5
–	Radial shield bar-like (Fig. 1B)	Euryalidae Gray, 1840 [p. 20]
5(4).	Arm combs present (Fig. 1F); arm spines mainly lateral; tentacle scales more than two times as long as wide; dorsal disc scale/plate without tubercles (Fig. 2B–D)	Ophiopyrgidae Perrier, 1893 [p. 25]
–	Arm combs absent; arm spines at proximal segments only on ventral side of arms; tentacle scales nearly as long as wide; dorsal disc scale/plate with tubercles (Fig. 2A)	Hemieuryalidae Verrill, 1899 [p. 40]
6(2).	Tentacle scales nearly as long as wide	7
–	Tentacle scales slightly longer than wide	8
–	Tentacle scales more than two times as long as wide	10
7(6).	Tentacle scales shorter than the spine nearby; tentacle scales cross section round; disc pentagonal; dorsal disc with spines (Fig. 2B–D)	Ophiosphalmidae O’Hara <i>et al.</i> , 2018 [p. 22]
–	Tentacle scales as long as the spine nearby; tentacle scales cross section oval; disc circular; dorsal disc without spines (Fig. 1A–B, D–F)	Astrophiuridae Sladen, 1879 [p. 24]
8(6).	Accessory dorsal arm plate present; dorsal disc with obvious primary plates (Fig. 2D); adoral shield meeting in front of the oral shield; distance between spine articulations dorsalwards increasing	Ophiolepididae Ljungman, 1867 [p. 39]
–	Accessory dorsal arm plate absent; dorsal disc with concealed primary plates (Fig. 1A–D); adoral shield separated (Fig. 4); distance between spine articulations equal	9
9(8).	Arm spines predominantly parallel to arm axis (adpressed); integument obscuring plates (Fig. 1D); dorsal disc without scales; dorsal disc with spines (Fig 2B, D)	Ophiopezidae O’Hara <i>et al.</i> , 2018 [p. 35]
–	Arm spines predominantly erect, standing perpendicular to arm axis; integument not obscuring plates (Fig. 1E–F); dorsal disc with scales (Fig. 2B, D); dorsal disc without spines (Fig.1A–B, D–F)	Ophiomyxidae Ljungman, 1867 [p. 36]

- 10(6). Arm combs present (Fig. 1F); disc circular; genital papillae present; distance between spine articulations dorsalwards increasing..... **Ophiopyrgidae** Perrier, 1893 [p. 25]
 – Arm combs absent; disc pentagonal; genital papillae absent; distance between spine articulations equal 11
- 11(10). Arm spines predominantly parallel to arm axis (adpressed); tentacle scales longer than the spine nearby; tentacle pores visible only on proximal arm; dorsal disc with obvious primary plates (Fig. 2D) **Ophiomusaidae** O’Hara *et al.*, 2018 [p. 23]
 – Arm spines predominantly erect, standing perpendicular to arm axis; tentacle scales shorter than the spine nearby; tentacle pores visible along most of the arm; dorsal disc with concealed primary plates (Fig. 1B–D) **Ophiomyxidae** Ljungman, 1867 [p. 36]
- 12(1). Arm spines predominantly parallel to arm axis (adpressed) 13
 – Arm spines predominantly erect, standing perpendicular to arm axis 16
- 13(12). Tentacle scales nearly as long as wide 14
 – Tentacle scales slightly longer than wide 15
 – Tentacle scales more than two times as long as wide **Ophiopyrgidae** Perrier, 1893 [p. 25]
- 14(13). Arm spines cylindrical (Fig. 5); radial shield isosceles (mirror-symmetric) triangular to pear-shaped (Fig. 1F); the ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.9–1 (Fig. 5); arm spines at proximal segments only on ventral side of arms **Hemieuryalidae** Verrill, 1899 [p. 40]
 – Arm spines pointed (Fig. 5); radial shield scalene (oblique) triangular (Fig. 1F); the ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9 (Fig. 5); arm spines mainly lateral **Ophioleucidae** Matsumoto, 1915 [p. 38]
- 15(13). Arm combs present (Fig. 1F); spines all similar in shape; arm spine cross section round (Fig. 5); integument not obscuring plates (Fig. 1E–F) **Ophiuridae** Müller & Troschel, 1840 [p. 24]
 – Arm combs absent; spines not all similar in shape (Fig. 2F–H); arm spine cross section oval (Fig. 5); integument obscuring plates (Fig. 1D) **Ophiernidae** O’Hara *et al.*, 2018 [p. 37]
- 16(12). Integument not obscuring plates (Fig. 1E–F); nerve opening approximately as large as muscle opening 17
 – Integument obscuring plates (Fig. 1D); nerve opening smaller than muscle opening 18
- 17(16). Tentacle scales nearly as long as wide; radial shield length between one third and half of the disc radius; arm spine articulation ventralwards increasing in size
 **Amphiuridae** Ljungman, 1867 [p. 44]
 – Tentacle scales slightly longer than wide; radial shield length more than half of the disc radius; arm spine articulation larger in middle of arm **Ophiactidae** Matsumoto, 1915 [p. 46]
- 18(16). Arm covering without granules/spines/tubercles; arm spine cross section round (Fig. 5); arm spines mainly lateral; genital slit longer than half the length of an interradius 19
 – Arm covering with granules; arm spine cross section oval (Fig. 5); arm spines at proximal segments only on ventral side of arms; genital slit shorter than half the length of an interradius **Gorgonocephalidae** Ljungman, 1867 [p. 21]
- 19(18). Tentacle scales present; dorsal disc with scales (Fig. 2B, D); radial shield without granules/spines (Fig. 1B); ventral teeth single (Fig. 4) **Ophionereididae** Ljungman, 1867 [p. 42]
 – Tentacle scales absent; dorsal disc without scales; radial shield with granules (Fig. 1A); ventral teeth several (tooth papillae) (Fig. 4) **Ophiobysidae** Matsumoto, 1915 [p. 29]

20(1).	Integument not obscuring plates (Fig. 1E–F)	21
–	Integument obscuring plates (Fig. 1D)	26
21(20).	Radial shield length between one third and half of the disc radius	22
–	Radial shield length more than half of the disc radius	25
22(21).	Arm combs present (Fig. 1F); arm spines predominantly parallel to arm axis (adpressed); tentacle scales slightly longer than wide; ventral teeth several (tooth papillae) (Fig. 4)	
 Ophiuridae Müller & Troschel, 1840 [p. 24]	
–	Arm combs absent; arm spines predominantly erect, standing perpendicular to arm axis; tentacle scales nearly as long as wide; ventral teeth single (Fig. 4)	23
23(22).	Accessory dorsal arm plate present; accessory ventral arm plate present; spines not all similar in shape (Fig. 2F–H); dorsal and/or ventral edge(s) of LAPs with constriction (Fig. 2I)	
 Ophiopholidae O’Hara <i>et al.</i> , 2018 [p. 47]	
–	Accessory dorsal arm plate absent; accessory ventral arm plate absent; spines all similar in shape; dorsal and/or ventral edge(s) of LAPs without constriction (Fig. 2J)	24
24(23).	The number of scales on H line (Fig. 2C) of an interradius about 7–14; arm spine articulation larger in middle of arm; dental plate ventral half widest; dental sockets less than 50% of the width	
 Ophiothamnidae O’Hara <i>et al.</i> , 2018 [p. 46]	
–	The number of scales on H line (Fig. 2C) of an interradius about 14–21; arm spine articulation ventralwards increasing in size; dental plate dorsal half widest; dental sockets equal to or more than 50% of the width	Amphiuridae Ljungman, 1867 [p. 44]
25(21).	Tentacle scales present; dorsal disc with spines (Fig. 2B, D); arm spine articulation larger in middle of arm; nerve opening approximately as large as muscle opening	
 Ophiactidae Matsumoto, 1915 [p. 46]	
–	Tentacle scales absent; dorsal disc without spines (Fig. 1A–B, D–F); arm spine articulation ventralwards increasing in size; nerve opening smaller than muscle opening	
 Amphilepididae Matsumoto, 1915 [p. 45]	
26(20).	Tentacle scales nearly as long as wide	27
–	Tentacle scales slightly longer than wide	28
–	Tentacle scales more than two times as long as wide	30
27(26).	Arm spines flat; the number of scales on H line (Fig. 2C) of an interradius more than 21; arm spine cross section oval (Fig. 5); ventral teeth several (tooth papillae) (Fig. 4)	
 Ophiotomidae Paterson, 1985 [p. 30]	
–	Arm spines pointed (Fig. 5); the number of scales on H line (Fig. 2C) of an interradius about 7–14; arm spine cross section round (Fig. 5); ventral teeth single (Fig. 4)	
 Ophiacanthidae Ljungman, 1867 [p. 33]	
28(26).	Arm spines predominantly parallel to arm axis (adpressed); radial shield absent (Fig. 1C); ventral interradii with spines; ventro-distal tip of LAP projecting ventralwards (Fig. 2K)	
 Ophiohelidae Perrier, 1893 [p. 27]	
–	Arm spines predominantly erect, standing perpendicular to arm axis; radial shield present; ventral interradii with granules; ventro-distal tip of LAP not projecting ventralwards (Fig. 2L)	29

- 29(28). Radial shield scalene (oblique) triangular; the number of scales on H line (Fig. 2C) of an interradius more than 21; arm spine cross section oval (Fig. 5); radial shield with granules
 **Ophiotomidae** Paterson, 1985 [p. 30]
- Radial shield isosceles (mirror-symmetric) triangular to pear-shaped (Fig. 1F); the number of scales on H line (Fig. 2C) of an interradius about 14–21; arm spine cross section round (Fig. 5); radial shield without granules/spines (Fig. 1B) **Ophionereididae** Ljungman, 1867 [p. 42]
- 30(26). Tentacle scales shorter than the spine nearby; the number of scales on H line (Fig. 2C) of an interradius about 14–21; oral shield covering less than one third of interradius; at least one socket on DP as depression or perforation without septum 31
- Tentacle scales longer than the spine nearby; the number of scales on H line (Fig. 2C) of an interradius more than 21; oral shield covering more than one third of the length of an interradius; at least one socket on DP as perforation with septum
 **Ophiopsilidae** Matsumoto, 1915 [p. 43]
- 31(30). Arm spine cross section round (Fig. 5); tentacle scales cross section oval; radial shield absent (Fig. 1C); ventral interradii without granules/spines **Ophioscolecidae** Lütken, 1869 [p. 28]
- Arm spine cross section oval (Fig. 5); tentacle scales cross section round; radial shield present (Fig. 1C); ventral interradii with spines **Amphilimnidae** O'Hara *et al.*, 2018 [p. 41]
- 32(1). Radial shield length less than one third of the disc radius 33
- Radial shield length between one third and half of the disc radius 35
- Radial shield length more than half of the disc radius 36
- 33(32). Radial shield scalene (oblique) triangular (Fig. 1E); arm spine cross section oval (Fig. 5); integument obscuring plates (Fig. 1D); radial shield with granules (Fig. 1A) 34
- Radial shield isosceles (mirror-symmetric) triangular to pear-shaped (Fig. 1F); arm spine cross section round (Fig. 5); integument not obscuring plates (Fig. 1E–F); radial shield without granules/spines (Fig. 1B) **Ophiomyxidae** Ljungman, 1867 [p. 36]
- 34(33). Adoral shield separated; ventral position of LAP projecting ventro-proximalwards (Fig. 2K); disc flat (about same level as arms); lateral oral papillae multiple rows of lateral papillae
 **Ophiocomidae** Ljungman, 1867 [p. 36]
- Adoral shield meeting in front of the oral shield; ventral position of LAP not projecting ventro-proximalwards (Fig. 2L); disc high (above arm level); lateral oral papillae single row of lateral papillae (Fig. 2E) **Ophiotomidae** Paterson, 1985 [p. 30]
- 35(32). Arm covering without granules/spines/tubercles; arm spines pointed (Fig. 5); tentacle scales nearly as long as wide; integument obscuring plates (Fig. 1D)
 **Ophiacanthidae** Ljungman, 1867 [p. 33]
- Arm covering with tubercles grown out of scales/plates; arm spines cylindrical (Fig. 5); tentacle scales slightly longer than wide; integument not obscuring plates (Fig. 1E–F)
 **Ophiocamacidae** O'Hara *et al.*, 2018 [p. 29]
- 36(32). Tentacle scales nearly as long as wide 37
- Tentacle scales more than two times as long as wide 38
- 37(36). Accessory ventral arm plate present; tentacle scales cross section round; scales on ventral interradii absent; ventral teeth several (tooth papillae) (Fig. 4)
 **Ophiopteridae** O'Hara *et al.*, 2018 [p. 31]
- Accessory ventral arm plate absent; tentacle scales cross section oval; scales on ventral interradii covering the whole area of an interradius; ventral teeth single (Fig. 4)
 **Ophiacanthidae** Ljungman, 1867 [p. 33]

- 38(36). Arm spines flat (Fig. 5); tentacle scales shorter than the spine nearby; arm spine cross section oval (Fig. 5); tentacle scales cross section oval**Clarkcomidae** O'Hara *et al.*, 2018 [p. 32]
– Arm spines pointed (Fig. 5); tentacle scales as long as the spine nearby; arm spine cross section round (Fig. 5); tentacle scales cross section round **Ophiotrichidae** Ljungman, 1867 [p. 48]

Morphological descriptions of each family with respect to the species listed in Table 1

In total, there are 33 characters for the arm, 29 for the ventral part of the disc, including the oral frame, 12 for the dorsal disc, and three characters for vertebrae. The language is software generated, slightly human-modified.

Phylum Echinodermata Bruguière, 1791
Subphylum Asterozoa von Zittel, 1895
Class Ophiuroidea Gray, 1840
Subclass Myophiuroidea Matsumoto, 1915
Infraclass Metophiurida Matsumoto, 1913
Superorder Euryophiurida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Order Euryalida Lamarck, 1816

Family **Asteronychidae** Ljungman, 1867

Type genus

Asteronyx Müller & Troschel, 1842

Other genera

Astrodia Verrill, 1899; *Astronebris* Downey, 1967; *Ophioschiza* H.L. Clark, 1911.

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate absent. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines not all similar in shape (Fig. 2F–H). The atypical spines are hook-shaped (Fig. 2G). Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.2–0.6. Arm spines tapering (conical); at proximal segments only on ventral side of arms; predominantly erect, standing perpendicular to arm axis. Longest arm spines shorter than half a segment. Tentacle scales absent. Position of lateral arm plate (LAP) only lateral (Fig. 3J–K). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards (Fig. 2L). Arm spine articulation without dorsal and ventral lobes; arranged over entire distal LAP edge; all similar. Distance between spine articulations ventralwards increasing. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc pentagonal to circular; high (above arm level). Integument obscuring plates. Dorsal disc without granules; with concealed primary plates; without scales (*A. loveni* Müller & Troschel, 1842) or a few (O'Hara *et al.* 2018); without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length more than half of the disc radius; bar-like.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate absent. Buccal scales on OP absent. Accessory oral papillae on OP present. Lateral oral papillae on OP absent. Adoral shield spine absent. Lyman's ossicle absent. Oral shield covering less than one third of interradius; about

as long as wide. Madreporite one; with numerous pores. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit shorter than half interradius. Genital papillae absent. Dental plate of equal width all over; entire (single plate). Dental sockets slit-shaped to circular; less than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth spine-shaped. Teeth on DP arranged as covering the entire dental plate evenly.

VERTEBRAE. Vertebrae hourglass-shaped (streptospondylous); beyond segment 5 with short keel (Fig. 3C, E); without oral bridge.

Family **Euryalidae** Gray, 1840

Type genus

Euryale Lamarck, 1816.

Other genera

Asteromorpha Lütken, 1869; *Asteroschema* Örstedt & Lütken, 1856; *Asterostegus* Mortensen, 1933; *Astrobrachion* Döderlein, 1927; *Astroceras* Lyman, 1879; *Astrocharis* Koehler, 1904; *Ophiocreas* Lyman, 1869; *Squamophis* Okanishi Okanishi, O'Hara & Fujita, 2011; *Sthenocephalus* Koehler, 1898; *Trichaster* Agassiz, 1836.

Description

ARM. Arm shape branched; length more than 4× disc diameter; covering with granules. Arm combs absent. Dorsal arm plate absent. Accessory dorsal arm plate absent. Ventral arm plate present or absent. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines not all similar in shape. Atypical arm spines are hook-shaped. Arm spine cross section round. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.9–1. Arm spines cylindrical; at proximal segments only on ventral side of arms; predominantly erect, standing perpendicular to arm axis. Longest arm spines shorter than half a segment. Tentacle scales present; pores visible along the arm; nearly as long as wide; shorter than the spine nearby; cross section round. Position of lateral arm plate (LAP) only lateral. Dorsal and/or ventral edge(s) of LAPs without constriction (Fig. 2J). Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation without dorsal and ventral lobes; restricted to (the ventral or central) portion of the distal edge; all similar. Distance between spine articulations not applicable (two spine articulation). Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening approximately as large as muscle opening (Fig. 3A–B).

DORSAL DISC. Disc pentagonal; flat (about same level as arms). Integument not obscuring plates. Dorsal disc with granules; with concealed primary plates; without scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; with tubercles grown out of plate; length more than half of the disc radius; bar-like.

VENTRAL DISC. Gonads not restricted to the disc (extending into the basal portion of the arms) or restricted to the disc (*Asteroschema*). Ventral interradii without granules/spines. Scales on ventral interradii absent. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine absent. Lyman's ossicle absent. Oral shield covering less than one third of interradius; about as long as wide. Madreporite multiple; with one pore, or with numerous pores. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit shorter than half interradius. Genital

papillae absent. Dental plate of equal width all over; fragmented. Dental sockets slit-shaped; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae hourglass-shaped (streptospondylous); beyond segment 5 non-keeled; with oral bridge (Fig. 3E).

Family **Gorgonocephalidae** Ljungman, 1867

Type genus

Gorgonocephalus Leach, 1815.

Other genera

Asteropora Örstedt & Lütken, 1856; *Astracme* Döderlein, 1927; *Astroboa* Döderlein, 1911; *Astrocanium* Döderlein, 1911; *Astrochalcis* Koehler, 1905; *Astrochele* Verrill, 1878; *Astrochlamys* Koehler, 1912; *Astrocladus* Verrill, 1899; *Astroclon* Lyman, 1879; *Astrocnida* Lyman, 1872; *Astrocrius* Döderlein, 1927; *Astrocyclus* Döderlein, 1911; *Astrodendrum* Döderlein, 1911; *Astrodictyum* Döderlein, 1927; *Astroglymma* Döderlein, 1927; *Astrogomphus* Lyman, 1869; *Astrogordius* Döderlein, 1911; *Astrohamma* Döderlein, 1930; *Astrohelix* Döderlein, 1930; *Astroniwa* McKnight, 2000; *Astrophyton* Fleming, 1828; *Astroplegma* Döderlein, 1927; *Astrosierra* Baker, 1980; *Astrospartus* Döderlein, 1911; *Astrothamnus* Matsumoto, 1915; *Astrothorax* Döderlein, 1911; *Astrothrombus* H.L. Clark, 1909; *Astrotoma* Lyman, 1875; *Astrozona* Döderlein, 1930; *Conocladus* H.L. Clark, 1909; *Ophiocrene* Bell, 1894; *Ophiozeta* Koehler, 1930; *Schizostella* A.H. Clark, 1952.

Description

ARM. Arm shape unbranched, or shape branched; length more than 4× disc diameter; covering with granules. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms present (*Gorgonocephalus caputmedusae* (Linnaeus, 1758)) or absent in some genera. Spines all similar in shape. Arm spine cross section oval. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.9–1. Arm spines flat; at proximal segments only on ventral side of arms; predominantly erect, standing perpendicular to arm axis. Longest arm spines between half and one segment long. Tentacle scales present; pores visible along the arm; slightly longer than wide; shorter than the spine nearby; cross section round. Position of lateral arm plate (LAP) only lateral. Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation without dorsal and ventral lobes; restricted to (the ventral or central) portion of the distal edge; all similar. Distance between spine articulations ventralwards increasing. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; with/without granules; length more than half of the disc radius; bar-like.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with granules. Scales on ventral interradii absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate absent. Buccal scales on OP absent. Accessory oral papillae on OP present. Lateral oral papillae on OP absent. Adoral shield spine absent. Lyman's ossicle absent. Oral shield covering less than one third of interradius; much wider than long. Madreporite one; with numerous pores. Adoral shield meeting in front of the oral shield. Abradial

genital plate not twisted. Number of genital slits one per bursa. Genital slit shorter than half interradius. Genital papillae absent. Dental plate of equal width all over; fragmented. Dental sockets circular; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth spine-shaped. Teeth on DP arranged as covering the entire dental plate evenly.

VERTEBRAE. Vertebrae hourglass-shaped (streptospondylous); beyond segment 5 with short keel; without oral bridge.

Order Ophiurida Müller & Troschel, 1840, restricted sensu O'Hara *et al.* (2017)

Suborder Ophiomusina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Family **Ophiosphalmidae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Ophiosphalma H.L. Clark, 1941.

Other genera

Ophiolipus Lyman, 1878; *Ophiomusium* Lyman, 1869.

Description

ARM. Arm shape unbranched; length 3–4× disc diameter; covering with spines distal to the genital slit around the disc margin but without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar. Arm spine cross section round. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly parallel to arm axis (adpressed). Longest arm spines shorter than half a segment. Tentacle scales present; pores visible only on proximal arm; nearly as long as wide; shorter than the spine nearby; cross section round. Position of lateral arm plate (LAP) arched (wrapped around the arm) (Fig. 3L). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation without dorsal and ventral lobes; arranged over entire distal LAP edge; ventralwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc pentagonal; flat (about same level as arms). Integument not obscuring plates. Dorsal disc without granules; with obvious primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length more than half of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius fewer than 7. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle absent. Oral shield covering less than one third of interradius; much longer than wide. Madreporite no data. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae present. Dental plate of equal width all over; entire (single plate). Dental sockets slit-shaped; equal to or more than 50% of the width. At least one socket on DP as depression or

perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophiomusaidae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Ophiomusa Hertz, 1927. (No other genera)

Description

ARM. Arm shape unbranched; length $3 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate absent or present in some species on a few proximal arm joints only (O'Hara *et al.* 2018). Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly parallel to arm axis (addressed). Longest arm spines shorter than half a segment. Tentacle scales present; pores visible only on proximal arm; more than two times as long as wide; longer than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation without dorsal and ventral lobes; arranged over entire distal LAP edge; all similar. Distance between spine articulations equal. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc pentagonal; high (above arm level). Integument not obscuring plates. Dorsal disc without granules; with obvious primary plates; with scales; without spines. Dorsal disc scale/plate with tubercles. Radial shield present; with tubercles, without granules/spines; length more than half of the disc radius; isosceles (mirror-symmetric) triangular to pear-shaped.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius fewer than 7. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle absent. Oral shield covering more than one third of the length of an interradius; much longer than wide. Madreporite no data. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit shorter than half interradius. Genital papillae absent. Dental plate dorsal half widest; entire (single plate). Dental sockets slit-shaped and circular; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Suborder Ophiurina Müller & Troschel, 1840 sensu O'Hara *et al.* (2017)

Family **Astrophiuridae** Sladen, 1879

Type genus

Astrophiura Sladen, 1879.

Other genera

Ophiomisidium Koehler, 1914; *Ophiophycis* Koehler, 1901.

Description

ARM. Arm shape unbranched; length less than $2 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9, or 0.9–1. Arm spines cylindrical or pointed; mainly lateral; predominantly parallel to arm axis (addressed). Longest arm spines shorter than half a segment. Tentacle scales present; pores visible only on proximal arm; nearly as long as wide; as long as the spine nearby; cross section oval. Position of lateral arm plate (LAP) only lateral. Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation without dorsal and ventral lobes, or with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; all similar. Distance between spine articulations equal. Nerve and muscle openings separated by small ridge if at all.

DORSAL DISC. Disc circular; high (above arm level). Integument not obscuring plates. Dorsal disc without granules; with obvious primary plates; without scales or with a few scales (O'Hara *et al.* 2018); without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length between one third and half of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of lateral papillae; block-shaped and spiniform. Adoral shield spine present. Lyman's ossicle absent. Oral shield covering less than one third of interradius; much wider than long. Madreporite no data. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate and teeth no data.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophiuridae** Müller & Troschel, 1840, restricted sensu O'Hara *et al.* (2017)

Type genus

Ophiura Lamarck, 1801.

Other genera

Ophiocrossota H.L. Clark, 1928; *Ophiocten* Lütken, 1855; *Ophioctenella* Tyler, Paterson, Sibuet, Guille, Murton & Segonzac, 1995; *Ophionotus* Bell, 1902.

Description

ARM. Arm shape unbranched; length $3 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs present. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral and at proximal segments only on ventral side of arms; predominantly parallel to arm axis (adpressed). Longest arm spines between half and one segment long, or between one and two segments long (*Ophiura sarsii* Lütken, 1855). Tentacle scales present or absent; pores visible along most of the arm; slightly longer than wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation without dorsal and ventral lobes; restricted to (the ventral or central) portion of the distal edge; all similar. Distance between spine articulations ventralwards increasing. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc circular; flat (at arm level). Integument not obscuring plates. Dorsal disc without granules; with obvious primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length between one third and half of the disc radius; isosceles (mirror-symmetric) triangular to pear-shaped.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius fewer than 7, or 7–14 (*Ophiecten*). Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle absent. Oral shield covering more than one third of the length of an interradius; much longer than wide or about as long as wide (*Ophiecten*). Madreporite one; with one pore or with numerous pores. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae present. Dental plate of equal width all over, or ventral half widest (*Ophiura sarsii*, *Ophiecten*); entire (single plate). Dental sockets circular; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as a single row on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate (two rows in *Ophiecten*).

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophiopyrgidae** Perrier, 1893

Type genus

Ophiopyrgus Lyman, 1878.

Other genera

Amphiophiura Matsumoto, 1915; *Aspidophiura* Matsumoto, 1915; *Dictenophiura* H.L. Clark, 1923; *Euvondrea* Fell, 1961; *Glaciacantha* Fell, 1961; *Gymnophiura* Lütken & Mortensen, 1899; *Ophiogona* Studer, 1876; *Ophiomages* Koehler, 1923; *Ophioperla* Koehler, 1912; *Ophiopleura* Danielssen & Koren, 1877; *Ophioplinthus* Lyman, 1878; *Ophiosparte* Koehler, 1922; *Ophiosteira* Bell, 1902; *Ophiuroglypha* Hertz, 1927; *Spinophiura* Stöhr & Segonzac, 2006; *Stegophiura* Matsumoto, 1915.

Description

ARM. Arm shape unbranched; length $3 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs present. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round (*Amphiophiura*, *Ophioplinthus*), or oval (*Ophiosparte*). The ratio of distal $1/3$ an arm spine to maximum thickness (in a given cross-sectional plane) 0.2–0.6, or 0.6–0.9 (*Amphiophiura*), or 0.9–1 (*Ophiosparte*, *Ophioplinthus*). Arm spines tapering (conical), or cylindrical (*Ophiosparte*), or pointed; mainly lateral; predominantly parallel to arm axis (addressed). Longest arm spines shorter than half a segment (*Amphiophiura*, *Ophioplinthus*, *Ophiopleura*), or between half and one segment (*Ophiosparte*). Tentacle scales present; pores visible along most of the arm; more than two times as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation without dorsal and ventral lobes; arranged over entire distal LAP edge; ventralwards increasing in size (*Amphiophiura*), or all similar (*Ophiosparte*, *Ophiopyrgus*, *Ophioplinthus*). Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc circular; high (above arm level). Integument not obscuring plates (*Amphiophiura*, *Ophiopyrgus*, *Ophioplinthus*, *Ophiopleura*), or skin obscuring plates (*Ophiosparte*). Dorsal disc without granules; with obvious primary plates (*Amphiophiura*, *Ophioplinthus*), or with concealed primary plates (*Ophiosparte*, *Ophiopleura*); with scales (the scales are covered by thickened skin in *Ophiosparte* and embedded in thickened skin in *Ophiopleura*) without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length less than one third of the disc radius, or length between one third and half of the disc radius (*Ophiopyrgus*), or length more than half of the disc radius (*Ophiopleura*); isosceles (mirror-symmetric) triangular to pear-shaped.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius, or absent (*Ophiosparte*, *Ophiopleura*). The number of scales on H line of an interradius about less than 7. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP present. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle absent. Oral shield covering less than one third of interradius; much longer than wide or about as long as wide (e.g., *Ophioplinthus tessellata* (Verrill, 1894) and *Ophiopleura borealis* Danielssen & Koren, 1877). Madreporite no data. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius (or about equal). Genital papillae present. Dental plate ventral half widest; entire (single plate). Dental sockets circular; less than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth spine-shaped. Teeth on DP arranged as a single row on $2/3$ and a cluster of tooth papillae on $1/3$ of dental plate (*Ophioplinthus*).

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Superorder Ophintegrida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Order Ophioscolecida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Family **Ophiohelidae** Perrier, 1893

Type genus

Ophiohelus Lyman, 1880.

Other genera

Ophiomyces Lyman, 1869; *Ophiothauma* H.L. Clark, 1938; *Ophiotholia* Lyman, 1880.

Description

ARM. Arm shape unbranched; length $3 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar (*Ophiomyces*) or not similar in shape. The atypical spines are umbrella-shaped (*Ophiotholia* and *Ophiohelus*) (Fig. 2F). Arm spine cross section round (*Ophiotholia*), or oval (*Ophiomyces*). The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.2–0.6, or 0.9–1. Arm spines tapering (conical), or flat (*Ophiomyces*), or cylindrical (*Ophiotholia*); mainly lateral; predominantly parallel to arm axis (addressed). Longest arm spines between one and two segments long. Tentacle scales present; pores visible along most of the arm; slightly longer than wide; shorter than the spine nearby. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs with constriction (*Ophiotholia*), or without constriction (*Ophiomyces*). Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards (Fig. 2K). Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; ventralwards increasing in size. Distance between spine articulations equal. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc circular; a sac-like shape (much higher than wide). Integument obscuring plates. Dorsal disc without granules; with concealed primary plates; with scales; with spines. Dorsal disc scale/plate without tubercles. Radial shield absent.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradial without granules/spines (*Ophiotholia*), or with spines (*Ophiomyces*). Scales on ventral interradial absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; multiple rows of lateral papillae; paddle-shaped. Adoral shield spine absent. Lyman's ossicle absent. Oral shield covering less than one third of interradius; much longer than wide. Madreporite no data. Adoral shield separated. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate ventral half widest; entire (single plate). Dental sockets circular; less than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as a single row on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophioscolecidae** Lütken, 1869

Type genus

Ophioscolex Müller & Troschel, 1842.

Other genera

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; *Ophiophrura* H.L. Clark, 1911; *Ophioplexa* Martynov, 2010; *Ophioprium* H.L. Clark, 1915; *Ophiorupta* Martynov, 2010; *Ophiosyzygus* H.L. Clark, 1911; *Ophiuroconis* Matsumoto, 1915.

Description

ARM. Arm shape unbranched; length 3–4× disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar, or not all similar in shape (*Ophiolycus*). The atypical spines are hook-shaped. Arm spine cross section round. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.2–0.6, or 0.9–1 (*Ophiolycus*). Arm spines cylindrical (*Ophiolycus*) or tapering (conical); mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between one and two segments long. Tentacle scales present (*Ophiolycus*) or absent; pores visible along most of the arm; more than two times as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs with constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; dorsalwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc without granules; with concealed primary plates; with or without scales; without spines. However, in some species with granules and spines (O'Hara *et al.* 2018). Dorsal disc scale/plate without tubercles. Radial shield absent.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius about 14–21. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP present. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle absent. Oral shield covering less than one third of interradius; much wider than long. Madreporite one or multiple; with one pore or with numerous pores. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate ventral half widest; entire (single plate). Dental sockets circular; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth spine-shaped. Teeth on DP arranged as a single row on half of dental plate and other half with a cluster of tooth papillae (ventral cluster), or a single row on 2/3 and a cluster of tooth papillae on 1/3 of dental plate (*Ophiolycus*).

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Order Ophiacanthida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Suborder Ophiacanthina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Family **Ophiobysidae** Matsumoto, 1915

Type genus

Ophiobysa Lyman, 1878.

Other genera

Ophiobysella Verrill, 1899; *Ophiophrixus* H.L. Clark, 1911; *Ophiosmilax* Matsumoto, 1915.

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between half and one segment long. Tentacle scales absent. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs with constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; ventralwards increasing in size. Distance between spine articulations equal. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; without scales; with spines. Dorsal disc scale/plate without tubercles. Radial shield present; with granules.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; about as long as wide. Madreporite no data. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over; entire (single plate). Dental sockets circular; less than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth spine-shaped. Teeth on DP arranged as covering the entire dental plate evenly.

VERTEBRAE. Vertebrae hourglass-shaped (streptospondylous); beyond segment 5 with short keel; without oral bridge.

Family **Ophiocamacidae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Ophiocamax Lyman, 1878. (No other genera)

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering tubercles grown out of scales/plates. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.9–1. Arm spines cylindrical; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines longer than two segments. Tentacle scales present; pores visible along most of the arm; slightly longer than wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) only lateral. Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; dorsalwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms). Integument not obscuring plates. Dorsal disc without granules; with concealed primary plates; with scales; with spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length between one third and half of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with spines. Scales on ventral interradii absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; multiple rows of lateral papillae; spiniform. Adoral shield spine present. Lyman's ossicle present. Oral shield covering more than one third of the length of an interradius; much wider than long. Madreporite one; with numerous pores. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over; entire (single plate). Dental sockets slit-shaped and circular; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth spine-shaped. Teeth on DP arranged as a single row on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate.

VERTEBRAE. Vertebrae hourglass-shaped (streptospondylous); beyond segment 5 with short keel; without oral bridge.

Family Ophiotomidae Paterson, 1985

Type genus

Ophiotoma Lyman, 1883.

Other genera

Ophiocomina Koehler in Mortensen, 1920; *Ophiocopa* Lyman, 1883; *Ophiomitra* Lyman, 1869; *Ophiopristis* Verrill, 1899; *Ophiotreta* Verrill, 1899.

Description

ARM. Arm shape unbranched; length $3\text{--}4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section oval. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness

(in a given cross-sectional plane) 0.6–0.9 to 0.9–1 (in *Ophiocopa* more pointed than in *Ophiotreta*). Arm spines flat; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between one and two segments long, or longer than two segments (*Ophiocopa*). Tentacle scales present; pores visible along most of the arm; nearly as long as wide (*Ophiotreta*), or slightly longer than wide (*Ophiocomina*); shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; with a fully developed sigmoidal fold; arranged over entire distal LAP edge; dorsalwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc circular; high (above arm level). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; with scales; with spines. Dorsal disc scale/plate without tubercles. Radial shield present; with granules; length less than one third of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with granules. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius more than 21. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of lateral papillae; rounded (*Ophiotreta*) or spiniform (*Ophiocomina*). Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; about as long as wide (*Ophiotreta*), or much wider than long (*Ophiocomina*). Madreporite one; with one pore. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate ventral half widest; entire (*Ophiocomina*) or fragmented (*Ophiotreta*, *Ophiocopa*). Dental sockets slit-shaped and circular; less than 50% of the width or equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth spine-shaped. Teeth on DP arranged as a single row on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophiopteridae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Ophiopteris E.A. Smith, 1877. (No other genera)

Description

ARM. Arm shape unbranched; length 3–4× disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate present. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round, or oval. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.9–1. Arm spines flat or cylindrical; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines longer than two segments. Tentacle scales present; pores visible along most of the arm; nearly as long as wide; shorter than the spine nearby; cross section round. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; with a fully developed sigmoidal fold; arranged over entire distal LAP edge; larger

in middle of arm. Distance between spine articulations equal. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc pentagonal or circular; high (above arm level). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; with granules; length more than half of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with spines. Scales on ventral interradii absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of lateral papillae; spiniform. Adoral shield spine present. Lyman's ossicle present. Oral shield covering more than one third of the length of an interradius; about as long as wide. Madreporite no data. Adoral shield separated. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate dorsal half widest; entire. Dental sockets heart-shaped(?); equal to or more than 50% of the width. Teeth flat (with round or slightly pointed tip, but never spine-like).

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Clarkcomidae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Clarkcoma Devaney, 1970. (No other genera)

Description

ARM. Arm shape unbranched; length 3–4× disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section oval. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines flat; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines longer than two segments. Tentacle scales present; pores visible along most of the arm; more than two times as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs with constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; with a fully developed sigmoidal fold; arranged over entire distal LAP edge; dorsalwards increasing in size. Distance between spine articulations equal. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; with granules; length more than half of the disc radius.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with granules. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius no data. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of lateral papillae; paddle-shaped. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; about as long as wide. Madreporite no data. Adoral shield meeting in front of the

oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over; entire (single plate). Dental sockets slit-shaped and circular; equal to or more than 50% of the width. At least one socket on DP as perforation with septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as a single row on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophiacanthidae** Ljungman, 1867

Type genus

Ophiacantha Müller & Troschel, 1842.

Other genera

Ophialcaea Verrill, 1899; *Ophientrema* Verrill, 1899; *Ophiocanops* Koehler, 1922; *Ophiochondrus* Lyman, 1869; *Ophiohamus* O'Hara & Stöhr, 2006; *Ophiolebes* Lyman, 1878; *Ophiolimna* Verrill, 1899; *Ophiomitrella* Verrill, 1899; *Ophiomoeris* Koehler, 1904; '*Ophiophthalmus*' Matsumoto, 1917; *Ophioplinthaca* Verrill, 1899; *Ophioripa* Koehler, 1922; *Ophiosemmotes* Matsumoto, 1917; *Ophiurothamnus* Matsumoto, 1917.

Description

ARM. Arm shape unbranched; length $3\times$ disc diameter, or length $3-4\times$ disc diameter, or length more than $4\times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9, or 0.9–1 (*Ophiochondrus*). Arm spines pointed; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between one and two segments long (*Ophiolimna*), or longer than two segments. Tentacle scales present; pores visible along most of the arm; nearly as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs with constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; with a fully developed sigmoidal fold; arranged over entire distal LAP edge; dorsalwards increasing in size (*Ophiacantha bidentata* (Bruzelius, 1805), *Ophiolimna*), or all similar (*Ophiacantha abyssicola* G.O. Sars, 1872, *Ophioplinthaca*). Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms) or high (above arm level) (*Ophiochondrus*). Integument obscuring plates. Dorsal disc with granules (*Ophioplinthaca*, *Ophiolimna*); with concealed primary plates; with scales; with spines (*Ophiacantha*, *Ophiolimna*) or without spines. Dorsal disc scale/plate without tubercles. Radial shield present; with spines and with granules; length between one third and half of the disc radius (*O. bidentata*, *Ophioplinthaca*), or length more than half of the disc radius (*O. abyssicola*, *Ophiochondrus*); isosceles (mirror-symmetric) triangular to pear-shaped, or bar-like.

VENTRAL DISC. Gonads restricted to the disc or not restricted to the disc (*Ophiocanops*). Ventral interradii with spines (*O. abyssicola*) or with granules (*O. bidentata*, *Ophiochondrus*, with spine and granules in *Ophiolimna*). Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius about 7–14. Ventral teeth single. Infradental papillae on oral plate present.

Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of lateral papillae; spiniform. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; much wider than long. Madreporite one or multiple; with one pore or with numerous pores. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over, or dorsal half widest (*Ophiolimna*); entire (single plate). Dental sockets slit-shaped; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Suborder Ophiodermatina Ljungman, 1867
Superfamily Ophiodermatoidea Ljungman, 1867

Family **Ophiodermatidae** Ljungman, 1867

Type genus

Ophioderma Müller & Troschel, 1840.

Other genera

Bathypectinura H.L. Clark, 1909; *Cryptopelta* H.L. Clark, 1909; *Diopederma* H.L. Clark, 1913; *Ophiarachnella* Ljungman, 1872; *Ophiochasma* Grube, 1868; *Ophiocormus* H.L. Clark, 1915; *Ophiocryptus* H.L. Clark, 1915; *Ophiocypris* Koehler, 1930; *Ophiomidas* Koehler, 1904; *Ophiopsammus* Lütken, 1869.

Description

ARM. Arm shape unbranched; length 3–4× disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section oval. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines flat; mainly lateral; predominantly parallel to arm axis (adpressed). Longest arm spines shorter than half a segment. Tentacle scales present; pores visible along most of the arm; slightly longer than wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; with a weakly developed sigmoidal fold; arranged over entire distal LAP edge; ventralwards increasing in size. Distance between spine articulations equal. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc pentagonal to circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; with granules; length less than one third of the disc radius; isosceles (mirror-symmetric) triangular to pear-shaped.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with granules. Scales on ventral interradii absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of

lateral papillae; spiniform. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; much wider than long. Madreporite multiple; with one pore. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits two per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over; fragmented. Dental sockets slit-shaped and circular; less than 50% of the width or equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth block-like (with square tip). Teeth on DP arranged as a single row on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophiopezidae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Ophiopeza Peters, 1851.

Other genera

Ophiochaeta Lütken, 1869.

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly parallel to arm axis (adpressed). Longest arm spines shorter than half a segment. Tentacle scales present; pores visible along most of the arm; slightly longer than wide; shorter than the spine nearby. Dental plate ventral half widest; entire (single plate). Position of lateral arm plate (LAP) only lateral. Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and thin ventral lobes and a fully developed sigmoidal fold; arranged over entire distal LAP edge; larger in middle of arm. Distance between spine articulations equal. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc pentagonal; flat (about same level as arms). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; without scales; with spines. Dorsal disc scale/plate without tubercles. Radial shield present; covering, length and shape no data.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with granules. Scales on ventral interradii absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of lateral papillae; spiniform. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; about as long as wide. Madreporite no data. Adoral shield separated. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental sockets slit-shaped or circular; less than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth spine-shaped. Teeth on DP arranged as a single row on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophiomyxidae** Ljungman, 1867

Type genus

Ophiomyxa Müller & Troschel, 1842.

Other genera

Neoplax Bell, 1884; *Ophiarachna* Müller & Troschel, 1842; *Ophioconis* Lütken, 1869; *Ophiostiba* Matsumoto, 1915; *Ophiurochaeta* Matsumoto, 1915.

Description

ARM. Arm shape unbranched; length 3–4 × disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines shorter than half a segment, or longer than two segments (*Ophiarachna*). Tentacle scales present; pores visible along most of the arm; slightly longer than wide, or more than two times as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without or with a weakly developed sigmoidal fold; arranged over entire distal LAP edge; ventralwards increasing in size. Distance between spine articulations equal. Nerve and muscle openings separated by small ridge if at all. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc pentagonal; flat (about same level as arms). Integument not obscuring plates. Dorsal disc with granules (*Ophiarachna*) or without granules; with concealed primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length less than one third of the disc radius; isosceles (mirror-symmetric) triangular to pear-shaped.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines, or with granules (*Ophiarachna*). Scales on ventral interradii absent. Ventral teeth single or with several tooth papillae (*Ophiarachna*). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of lateral papillae; paddle-shaped. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; about as long as wide. Madreporite one; with one pore. Adoral shield separated. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate ventral half widest; fragmented. Dental sockets slit-shaped and circular; less than 50% of the width or equal to or more than 50% of the width. At least one socket on DP as perforation with septum. Teeth block-like (with square tip). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Superfamily **Ophiocomoidea** Ljungman, 1867

Family **Ophiocomidae** Ljungman, 1867

Type genus

Ophiocoma L. Agassiz, 1836.

Other genera

Breviturma Stöhr Stöhr, Boissin & Hoareau, 2013; *Ophiarthrum* Peters, 1851; *Ophiocomella* A.H. Clark, 1939; *Ophiomastix* Müller & Troschel, 1842.

Description

ARM. Arm shape unbranched; length 3–4× disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section oval. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9, or 0.9–1. Arm spines flat, or cylindrical, or pointed; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines longer than two segments. Tentacle scales present; pores visible along most of the arm; nearly as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; with a fully developed sigmoidal fold; arranged over entire distal LAP edge; dorsalwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc pentagonal to circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; with scales; with smooth spines (O'Hara *et al.* 2018) or without spines. Dorsal disc scale/plate without tubercles. Radial shield present; with granules; length less than one third of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with granules. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius more than 21. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present or absent; multiple rows of lateral papillae; rounded. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; about as long as wide. Madreporite one; with one pore. Adoral shield separated. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over; entire (single plate). Dental sockets circular to heart-shaped; equal to or more than 50% of the width. At least one socket on DP as perforation with septum. Teeth block-like (with square tip). Teeth on DP arranged as a single row on half of dental plate and other half with a cluster of tooth papillae (ventral cluster), or a single row on 2/3 and a cluster of tooth papillae on 1/3 of dental plate.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Order Ophioleucida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Family **Ophiernidae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Ophiernus Lyman, 1878. (No other genera)

Description

ARM. Arm shape unbranched; length 3–4× disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present.

Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines not all similar in shape. The atypical spines are bristles (Fig. 2H). Arm spine cross section oval. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly parallel to arm axis (adpressed). Longest arm spines between half and one segment long. Tentacle scales present; pores visible along most of the arm; slightly longer than wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) only lateral. Dorsal and/or ventral edge(s) of LAPs with constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation without dorsal and ventral lobes or with weak lobes (O’Hara *et al.* 2018); arranged over entire distal LAP edge; dorsalwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by large, prominent ridge or regular stereom. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc pentagonal to circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length less than one third of the disc radius; isosceles (mirror-symmetric) triangular to pear-shaped.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradial with granules. Scales on ventral interradial covering the whole area of an interradius. The number of scales on H line of an interradius fewer than 7. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of lateral papillae; spiniform. Adoral shield spine present. Lyman’s ossicle present. Oral shield covering less than one third of interradius; about as long as wide. Madreporite one; with one pore. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over; entire (single plate). Dental sockets circular; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophioleucidae** Matsumoto, 1915

Type genus

Ophioleuce Koehler, 1904.

Other genera

Ophiopallas Koehler, 1904; *Ophiopyren* Lyman, 1878; *Ophiostratus* Madsen, 1983.

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar or not all similar in shape (*Ophiopallas*). The atypical spines are hook-shaped. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly parallel to arm axis (adpressed). Longest arm spines between half and one segment long. Tentacle scales present; pores visible along most of the arm; nearly as long as wide; shorter than the spine nearby; cross section round. Position of lateral arm plate (LAP)

arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; larger in middle of arm. Distance between spine articulations dorsalwards increasing, or not applicable (two spine articulations) (*Ophioleuce seminudum* Koehler, 1904). Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc with granules; with concealed primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; with granules; length less than one third of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with granules. Scales on ventral interradii absent. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine absent. Lyman's ossicle present. Oral shield covering less than one third of interradius; much longer than wide. Madreporite multiple; with numerous pores. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae present (*Ophiopallas*) or absent. Dental plate ventral half widest; entire (single plate). Dental sockets slit-shaped; less than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth spine-shaped. Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae hourglass-shaped (streptospondylous); beyond segment 5 with short keel; without oral bridge.

Order Amphilepidida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Suborder Ophionereidina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Superfamily Ophiolepidoidae Ljungman, 1867

Family **Ophiolepididae** Ljungman, 1867

Type genus

Ophiolepis Müller & Troschel, 1840.

Other genera

Ophioleichus H.L. Clark, 1938; *Ophiotypa* Koehler, 1897.

Description

ARM. Arm shape unbranched; length $3 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate present. Ventral arm plate present. Accessory ventral arm plate absent or present in other genera or species of *Ophiolepis* (Koehler 1922 and Pineda-Enriquez 2014). Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly parallel to arm axis (addressed). Longest arm spines shorter than half a segment. Tentacle scales present; pores visible along most of the arm; slightly longer than wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal

fold; arranged over entire distal LAP edge; larger in middle of arm. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc pentagonal to circular; flat (about same level as arms). Integument not obscuring plates. Dorsal disc without granules; with obvious primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length between one third and half of the disc radius; isosceles (mirror-symmetric) triangular to pear-shaped.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii absent. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; much longer than wide. Madreporite one. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over, or dorsal half widest; entire (single plate). Dental sockets circular to heart-shaped; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth block-like (with square tip). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Hemieuryalidae** Verrill, 1899

Type genus

Hemieuryale von Martens, 1867.

Other genera

Actinozonella Stöhr, 2011; *Astrogymnotes* H.L. Clark, 1914; *Ophioholcus* H.L. Clark, 1915; *Ophioplocus* Lyman, 1861; *Ophioplus* Verrill, 1899; *Ophiozonella* Matsumoto, 1915; *Ophiozonoida* H.L. Clark, 1915; *Quironia* A.H. Clark, 1934; *Sigsbeia* Lyman, 1878.

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate present or absent (*Actinozonella*). Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round or oval (*Sigsbeia*). The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.9–1. Arm spines cylindrical; at proximal segments only on ventral side of arms; predominantly parallel to arm axis (adpressed). Longest arm spines shorter than half a segment (*Sigsbeia*, *Ophiozonella falklandica* Mortensen, 1936), or between half and one segment long (*Hemieuryale*, *Ophiozonella longispina* (H.L. Clark, 1908), *Ophioplus*). Tentacle scales present; pores visible along most of the arm; nearly as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) only lateral or arched (wrapped around the arm) (*Sigsbeia*). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; restricted to (the ventral or central) portion of the distal edge; ventralwards increasing in size. Distance between spine articulations not applicable (two spine articulations). Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening, or approximately as large as muscle opening (*Ophiozonella*).

DORSAL DISC. Disc pentagonal to circular; high (above arm level). Integument not obscuring plates. Dorsal disc without granules; with obvious primary plates; with scales; without spines. Dorsal disc scale/plate with tubercles. Radial shield present; without granules/spines; length between one third and half of the disc radius, or length more than half of the disc radius (*Ophioplus*); isosceles (mirror-symmetric) triangular to pear-shaped.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius fewer than 7. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP absent. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; one lateral papilla along each side of the jaw; block-shaped. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; much wider than long. Madreporite no data. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit shorter than half interradius. Genital papillae absent. Dental plate dorsal half widest; entire (single plate). Dental sockets slit-shaped and circular; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae hourglass-shaped (streptospondylous) or zygospondylous (*Ophiozonella longispina*); beyond segment 5 with short keel; without oral bridge.

Superfamily Ophionereidoidea Ljungman, 1867

Family **Amphilimnidae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Amphilimna Verrill, 1899. (No other genera)

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section oval. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines flat; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between one and two segments long. Tentacle scales present; pores visible along most of the arm; more than two times as long as wide; shorter than the spine nearby; cross section round. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; ventralwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc pentagonal or circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc without granules; with concealed primary plates; with scales; with spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length between one third and half of the disc radius; scalene (oblique) triangular or bar-like.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius about 14–21.

Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP present; single row of lateral papillae; rounded and spiniform. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; about as long as wide. Madreporite no data. Adoral shield meeting in front of the oral shield. Abradial genital plate twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate dorsal half widest; entire (single plate). Dental sockets slit-shaped and circular; equal to or more than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophionereididae** Ljungman, 1867

Type genus

Ophionereis Lütken, 1859.

Other genera

Ophiochiton Lyman, 1878; *Ophiodoris* Koehler, 1904; *Ophioneroides* Cherbonnier & Guille, 1978; *Ophioplax* Lyman, 1875.

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate present or sometimes absent (*Ophiodoris* sp.). Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9, or 0.9–1 (*Ophioplax*, *Ophiodoris*). Arm spines pointed or cylindrical (*Ophioplax*, *Ophiodoris*); mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between half and one segment long, or between one and two segments long (*Ophioplax*). Tentacle scales present; pores visible along most of the arm; slightly longer than wide; shorter than the spine nearby; cross section oval or round. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; larger in middle of arm. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc pentagonal to circular; flat (about same level as arms) to high (above arm level). Integument obscuring plates. Dorsal disc without granules or with granules along the genital slit, extending onto disc edge; with concealed primary plates; with scales; with spines (*Ophiodoris*) or without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length less than one third of the disc radius; isosceles (mirror-symmetric) triangular to pear-shaped.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines or with granules (*Ophioplax*). Scales on ventral interradii covering the whole area of an interradius or absent (*Ophioplax*, *Ophiodoris*). The number of scales on H line of an interradius about 14–21. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle present. Oral shield covering

less than one third of interradius; about as long as wide. Madreporite one; with one pore. Adoral shield separated. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae present. Dental plate of equal width all over, or ventral half widest (*Ophioplax*); entire (single plate). Dental sockets circular to heart-shaped; equal to or more than 50% of the width. At least one socket on DP as perforation with septum. Teeth block-like (with square tip). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with extended keel, or with short keel; without oral bridge.

Suborder Ophiopsilina Matsumoto, 1915
Superfamily Ophiopsiloidea Matsumoto, 1915

Family **Ophiopsilidae** Matsumoto, 1915

Type genus

Ophiopsila Forbes, 1843. (No other genera)

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section oval. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.9–1. Arm spines flat; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between one and two segments long. Tentacle scales present; pores visible along most of the arm; more than two times as long as wide; longer than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; ventralwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms). Integument obscuring plates. Dorsal disc without granules; with concealed primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length between one third and half of the disc radius; bar-like.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius more than 21. Ventral teeth several (tooth papillae). Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle present. Oral shield covering more than one third of the length of an interradius; about as long as wide. Madreporite multiple; with numerous pores. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate dorsal half widest; entire (single plate). Dental sockets slit-shaped; equal to or more than 50% of the width. At least one socket on DP as perforation with septum. Teeth block-like (with square tip). Teeth on DP arranged as a single row on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Suborder Gnathophiurina Matsumoto, 1915
Superfamily Amphiuroidea Ljungman, 1867

Family **Amphiuridae** Ljungman, 1867

Type genus

Amphiura Forbes, 1843.

Other genera

Acrocnida Gislén, 1926; *Amphichondrius* Nielsen, 1932; *Amphicontus* Hill, 1940; *Amphigyptis* Nielsen, 1932; *Amphiodia* Verrill, 1899; *Amphiomya* H.L. Clark, 1939; *Amphioncus* H.L. Clark, 1939; *Amphioplus* Verrill, 1899; *Amphipholis* Ljungman, 1866; *Amphipholizona* H.L. Clark, 1915; *Amphistigma* H.L. Clark, 1938; *Dougaloplus* A.M. Clark, 1970; *Microphiopholis* Turner, 1985; *Nannophiura* Mortensen, 1933; *Nudamphiura* Tommasi, 1965; *Ophiocentrus* Ljungman, 1867; *Ophiocnida* Lyman, 1865; *Ophiodaphne* Koehler, 1930; *Ophionephthys* Lütken, 1869; *Ophiophragmus* Lyman, 1865; *Ophiosphaera* Brock, 1888; *Ophiostigma* Lütken, 1856; *Paracrocnida* Mortensen, 1940; *Paramphichondrius* Guille & Wolff, 1984; *Paramphiura* Koehler, 1895; *Triplodia* Turner & Hallan, 2011.

Description

ARM. Arm shape unbranched; length 3–4× or more than 4× disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9, or 0.9–1. Arm spines tapering (conical), cylindrical, or pointed; mainly lateral; predominantly parallel to arm axis (adpressed). Longest arm spines between half and one, or between one and two segments long. Tentacle scales present or absent (*Ophiophragmus*); pores only proximally visible along the arm; nearly as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) only lateral. Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP not projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation without dorsal and ventral lobes, or with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; ventralwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc pentagonal to circular; flat (about same level as arms) to high (above arm level). Integument not obscuring plates. Dorsal disc without granules; with obvious primary plates or with concealed primary plates; without scales; without spines or with spines, granules and tubercles in some genera (O'Hara *et al.* 2018). Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length between one third and half of the disc radius; scalene (oblique) triangular, or isosceles (mirror-symmetric) triangular to pear-shaped, or bar-like.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines or with spines. Scales on ventral interradii covering the whole area of interradius or absent. The number of scales on H line of an interradius about 14–21. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius;

much wider than long or about as long as wide (*Amphipholis*). Madreporite one; with one pore or with numerous pores. Adoral shield separated or meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate dorsal half widest, entire (single plate). Dental sockets slit-shaped to heart-shaped, equal to or more than 50% of the width of dental plate. At least one socket on DP as perforation with septum. Teeth block-like (with square tip). Teeth on DP arranged as single column.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Amphilepididae** Matsumoto, 1915

Type genus

Amphilepis Ljungman, 1867.

Other genera

Ophiomonas Djakonov, 1952.

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between one and two segments long. Tentacle scales absent. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; ventralwards increasing in size. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening smaller than muscle opening.

DORSAL DISC. Disc pentagonal to circular; flat (about same level as arms). Integument not obscuring plates. Dorsal disc without granules; with obvious primary plates; with scales; without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length more than half of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius about 14–21. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; much wider than long. Madreporite one; with one pore. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over; entire (single plate). Dental sockets slit-shaped and heart-shaped; less than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Superfamily Ophiactoidea Ljungman, 1867

Family **Ophiothamnidae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Ophiothamnus Lyman, 1869.

Other genera

Histampica A.M. Clark, 1970; *Ophioleila* A.H. Clark, 1949.

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between one and two segments long. Tentacle scales present; pores visible along most of the arm; nearly as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; larger in middle of arm. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc pentagonal to circular; flat (about same level as arms). Integument not obscuring plates. Dorsal disc without granules; with concealed primary plates; with scales; with spines or without spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length between one third and half of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius about 7–14. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; about as long as wide. Madreporite one; with one pore. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate ventral half widest; entire (single plate). Dental sockets circular; less than 50% of the width. At least one socket on DP as depression or perforation without septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophiactidae** Matsumoto, 1915

Type genus

Ophiactis Lütken, 1856.

Other genera

Hemipholis Lyman, 1865.

Description

ARM. Arm shape unbranched; length 3–4× disc diameter, or length more than 4× disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9, or 0.9–1. Arm spines pointed; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between half and one segment long, or between one and two segments long. Tentacle scales present; pores visible along most of the arm; slightly longer than wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; larger in middle of arm. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc pentagonal or circular; high (above arm level). Integument not obscuring plates. Dorsal disc without granules; with obvious primary plates; with scales; with spines. Dorsal disc scale/plate without tubercles. Radial shield present; without granules/spines; length more than half of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii without granules/spines. Scales on ventral interradii covering the whole area of an interradius. The number of scales on H line of an interradius about 14–21. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; much longer than wide or about as long as wide. Madreporite one; with one pore. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate of equal width all over, or dorsal half widest; entire (single plate). Dental sockets slit-shaped; equal to or more than 50% of the width. At least one socket on DP as perforation with septum. Teeth block-like (with square tip). Teeth on DP arranged as single row.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with short keel; without oral bridge.

Family **Ophiophilidae** O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018

Type genus

Ophiophilis Müller & Troschel, 1842. (No other genera)

Description

ARM. Arm shape unbranched; length 3–4× disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate present. Ventral arm plate present. Accessory ventral arm plate present. Girdle of tiny hooks on the arms absent. Spines not all similar in shape. The atypical spines are hook-shaped. Arm spine cross section round. The ratio of thickness of distal 1/3 of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines

pointed; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines between one and two segments long. Tentacle scales present; pores visible along most of the arm; nearly as long as wide; shorter than the spine nearby; cross section oval. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs with constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes; without sigmoidal fold; arranged over entire distal LAP edge; larger in middle of arm. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms). Integument not obscuring plates. Dorsal disc with granules; with obvious primary plates; with scales; with spines. Dorsal disc scale/plate with tubercles. Radial shield present; with granules and with tubercles grown out of plate; length between one third and half of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with spines. Scales on ventral interradii absent. Ventral teeth single. Infradental papillae on oral plate present. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine present. Lyman's ossicle present. Oral shield covering less than one third of interradius; much wider than long. Madreporite one; with one pore. Adoral shield meeting in front of the oral shield. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate ventral half widest; entire (single plate). Dental sockets circular; equal to or more than 50% of the width. At least one socket on DP as perforation with septum. Teeth block-like (with square tip). Teeth on DP arranged as a single row on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate.

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with extended keel; without oral bridge.

Family **Ophiotrichidae** Ljungman, 1867

Type genus

Ophiotrix Müller & Troschel, 1840.

Other genera

Gymnolophus Brock, 1888; *Lissophiotrix* H.L. Clark, 1938; *Macrophiotrix* H.L. Clark, 1938; *Ophiocnemis* Müller & Troschel, 1842; *Ophiogymna* Ljungman, 1866; *Ophiolophus* Marktanner-Turneretscher, 1887; *Ophiomaza* Lyman, 1871; *Ophiophthirius* Döderlein, 1898; *Ophiopsammium* Lyman, 1874; *Ophiopteron* Ludwig, 1888; *Ophiothela* Verrill, 1867; *Ophiotrichoides* Ludwig, 1882.

Description

ARM. Arm shape unbranched; length more than $4 \times$ disc diameter; covering without granules/spines/tubercles. Arm combs absent. Dorsal arm plate present. Accessory dorsal arm plate absent. Ventral arm plate present. Accessory ventral arm plate absent. Girdle of tiny hooks on the arms absent. Spines all similar in shape. Arm spine cross section round. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) 0.6–0.9. Arm spines pointed; mainly lateral; predominantly erect, standing perpendicular to arm axis. Longest arm spines longer than two segments long. Tentacle scales present; pores visible along most of the arm; more than two times as long as wide; as long as the spine nearby; cross section round. Position of lateral arm plate (LAP) arched (wrapped around the arm). Dorsal and/or ventral edge(s) of LAPs without constriction. Ventral position of LAP projecting ventro-proximalwards. Ventro-distal tip of LAP not projecting ventralwards. Arm spine articulation with dorsal and ventral lobes;

without sigmoidal fold; arranged over entire distal LAP edge; larger in middle of arm. Distance between spine articulations dorsalwards increasing. Nerve and muscle openings separated by small ridge if at all. Nerve opening approximately as large as muscle opening.

DORSAL DISC. Disc circular; flat (about same level as arms). Integument not obscuring plates. Dorsal disc without granules; with concealed primary plates; with scales; with spines. Dorsal disc scale/plate without tubercles. Radial shield present; with spines; length more than half of the disc radius; scalene (oblique) triangular.

VENTRAL DISC. Gonads restricted to the disc. Ventral interradii with spines. Scales on ventral interradii absent. Ventral teeth single or with several tooth papillae (O'Hara *et al.* 2018). Infradental papillae on oral plate absent. Buccal scales on OP present. Accessory oral papillae on OP absent. Lateral oral papillae on OP absent. Adoral shield spine absent. Lyman's ossicle absent. Oral shield covering less than one third of interradius; much wider than long. Madreporite one; with one pore. Adoral shield separated. Abradial genital plate not twisted. Number of genital slits one per bursa. Genital slit longer than half the length of an interradius. Genital papillae absent. Dental plate ventral half widest; entire (single plate). Dental sockets slit-shaped and circular; less than 50% of the width of to equal to or more than 50% of the width. At least one socket on DP as perforation with septum. Teeth flat (with round or slightly pointed tip, but never spine-like). Teeth on DP arranged as a single row on half of dental plate and other half with a cluster of tooth papillae (ventral cluster).

VERTEBRAE. Vertebrae zygospondylous; beyond segment 5 with extended keel; without oral bridge.

Discussion

One of the main results of this study is the analysis of previously introduced characters (Smith *et al.* 1995; Pomory 2007; Thuy & Stöhr 2016; O'Hara *et al.* 2018) and selection of those most useful for family identification. To illustrate, the dental plate was described in greater detail in Thuy & Stöhr (2016) than in Smith *et al.* (1995), i.e., the geometry of the dental plates, as well as the shape, depth, and size of its sockets. Moreover, the arrangement of teeth and the cluster of tooth papillae is here categorized into four groups to cover all available variations, regarding single/multiple columns and the ratio of teeth to tooth papillae for each family. In addition, dorsal and ventral covering of arm and disc are modified, following the terminology described above, to better define what 'scale', 'plate', 'tubercle' and 'granule' mean and how they are assessed in an organized classification. Although Pomory (2007) illustrated the arm spine shapes, it was not applicable at the family level, and still some details were overlooked. We revise the classification of the arm spine shapes by integrating the tip and cross-sectional shapes, to define all types of arm spine, including flat, tapering, pointed, and circular. Hendler's study (2018) was instrumental in clarifying the confusion about the development and homologies of the oral papillae, and for the first time his new terminology has been applied in the current identification key. Tentacle scales were termed 'podial scales' in some earlier publications (Pomory 2007) and ambiguously described with subjective terminology (Pomory 2007; O'Hara *et al.* 2018). Here, apart from the visibility of the tentacle pores along the arm, the tentacle scale length is described relative to the nearest spine to overcome subjective terms such as long or short. Moreover, different descriptions of shape suggested earlier (Thuy & Stöhr 2016) are substituted by a comparison of the length of each tentacle scale with its width combined with the shape (oval/round) of its cross-section. The definition of 'keel' based on LeClair (1996) occurs only in *Ophiopholis*, *Ophiotrichidae* and *Ophionereis*. We use "extended keel" as an equivalent to LeClair's definition and "short keel" in the broader sense of an arrow-shaped projection. According to this definition, the families *Ophiopholidae*, *Ophiotrichidae* and *Ophionereididae* have an extended keel and all others with the exception of *Euryalida* (non-keeled) have a short keel. To conclude, our result of creating a functional key suggests that the chosen states for each family are in good agreement with those mentioned

in previous studies (Mortensen 1927; Fell 1960; Clark & Rowe 1971; Paterson 1985; Pomory 2007; Martynov 2010a; Gondim *et al.* 2013).

The possibilities offered by computer-based multi-access keys (interactive keys) have rarely been explored for brittle stars. Possibly the first of its kind was presented by Smirnov *et al.* (2006), for species of the Arctic and Antarctica, but he used a specially developed software that is unfortunately not available anymore. A key to Antarctic species created with DELTA was available on the website of the Melbourne museum but can no longer be accessed. The only interactive key to brittle stars still freely available online comprises 16 species from south-eastern Brazil (Alitto *et al.* 2016) and was created using the software Xper (Ung *et al.* 2010), which is similar in functionality to DELTA. Walter & Winterson (2007) mentioned DELTA as a standard format for taxonomic descriptions and also as a database for interactive keys, despite the fact that the format is rather inflexible compared with the Structure of Descriptive Data (SDD) format, which was proposed as a standard for taxonomic descriptions by the association for biodiversity information standards, TDWG (www.tdwg.org). Coleman *et al.* (2010) also described the advantage of the software package DELTA for taxonomists and prepared an introduction to the software for beginners. The interactive identification key (Intkey) shows an advantage over conventional keys, due to its flexibility of applying characters in any order, interactive techniques such as automatically showing relevant images and allowing choice of states by clicking on an image, the possibility of updating the key (character deletion and change), when more data are available, and setting error tolerance and expressing uncertainty while using the intkey.

The keys presented in this study are the first conventional and interactive keys for the 33 currently accepted families, albeit still based on a limited selection of examined species, and the first release version still has limitations. Identification to the family level is more difficult than species identification, because many families are composed of a large number of species, usually grouped in several genera. The morphological diversity is thus considerably higher than within a species, and the delimitation of a family must be based on the selection of characteristics shared by as many species as possible. Pending the full taxonomic revision of each family, we attempted to delimit the families from one another by examination of selected species, but the (non-)availability of material (particularly of rare species) and a reasonable effort with highly time-consuming methods, limited the number of included species. Possibly, not all family-specific characters needed to correctly assign all species to a family have been recognized yet. While nomenclatural rules require that the type species of a family must be the basis of that family, the type species does not always share many characters with the majority of other included species. For example, the Ophiomyxidae as currently understood, include genera (e.g., *Ophioconis*) that are superficially more similar to Ophiidermatidae than to *Ophiomyxa* and were previously placed in that family. On the other hand, Ophiomusaidae and Ophiosphalmidae are separated by few characters. These limitations highlight the difficulty of collecting data from morphological characters and interpreting the available states. Direct observation (albeit on images) is a painstaking and highly time-consuming task. However, it has been shown that keys created from published data alone, without direct observation, are less accurate (Drinkwater 2009). Nevertheless, there might be some obstacles during the observation, since some characters might not be discriminate enough with different preservation methods, either wet or dried, e.g., thick/thin skin. We categorized the surface of the arm spine into five different states, but excluded them from our study in the end since the wet/dry preservation had an effect on arm spine surface shape. Technically, missing data are handled in DELTA Intkey and in conventional keys, but inadequate data can prevent the separation of some taxa. We tested the separability of taxa in Intkey (using diagnosis level 1) and the result showed that the tested taxa were separated using the current characters and chosen states. Given the above considered limitations, the result from such an analysis should of course be treated with considerable caution.

The polychotomous conventional key created by DELTA from the full dataset is limited to a single entry point and a single pathway that must be followed to identify a specimen to family level. If any of the choices are impossible, because the specimen is incomplete or lacks the character in question (which can be the case with species not included in this study), an identification may not be possible. To facilitate its use in the field, where computers may not be available and preparations and microscopy may be difficult, the conventional key was built with priority on external characters, which may make it less accurate, though, because recent studies have emphasized the taxonomic importance of internal and microscopic features (Martynov 2010a; Thuy & Stöhr 2016; O'Hara *et al.* 2018). In contrast, a tabular key has multiple entry points and may be a better alternative. The full data matrix can serve as a tabular key, but with 77 characters and 33 taxa, it is unwieldy. A condensed tabular key was created with DELTA as a more manageable compromise (Appendix 2).

Our approach should lend itself well for use by both general users of the key and specialist researchers. We conclude that an interactive software-based key is a practical and effective alternative to the conventional printed key. Further work should look into finding new characters and further observation of more genera from each family to construct a reliable and up to date identification key. We compared two different types of freely available software for the creation of identification keys and conclude that both are sufficient for this purpose, although users may favor one of them for particular features.

The family descriptions derived from this study are more detailed than the diagnoses provided by O'Hara *et al.* (2018), but they are still based on a small number of species and genera, and will need to be updated in the future. Some families were newly created by O'Hara *et al.* (2018) and consequently, they have never been described in detail before.

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Supplementary material

Supp. file 1. Condensed tabular key to the ophiuroid families. Only diagnostic characters for each family are included. Usage: find the family whose characters concur with your specimen. <https://doi.org/10.5852/ejt.2021.766.1483.4955>

Supp. file 2. The full matrix of characters and items in ophiuroid family identification (tabular key). <https://doi.org/10.5852/ejt.2021.766.1483.4957>

Supp. file 3. Conventional key for ophiuroid family identification (OFID) exported from Xper3 (online application). <https://doi.org/10.5852/ejt.2021.766.1483.4959>

Supp. file 4. Comparison of Xper2 and Xper3 with DELTA (CSIRO and ALA) platforms in providing conventional and interactive keys in taxonomy. <https://doi.org/10.5852/ejt.2021.766.1483.4961>

Appendix I. Character list

Arm

- #1. Arm <simple/branched>/
 - 1. shape unbranched/
 - 2. shape branched/

 - #2. Arm <relative length>/
 - 1. length less than 2x disc diameter/
 - 2. length 3x disc diameter/
 - 3. length 3– 4x disc diameter/
 - 4. length more than 4x disc diameter/

 - #3. Arm <covering/structure>/
 - 1. covering without granules/spines/tubercles/
 - 2. covering with granules/
 - 3. covering with tubercles grown out of scales/plates/

 - #4. Arm combs <presence/absence>/
 - 1. present/
 - 2. absent/

 - #5. Dorsal arm plate <absence/presence>/
 - 1. present/
 - 2. absent/

 - #6. Accessory dorsal arm plate <absence/presence>/
 - 1. present/
 - 2. absent/

 - #7. Ventral arm plate <absence/presence>/
 - 1. present/
 - 2. absent/

 - #8. Accessory ventral arm plate <absence/presence>/
 - 1. present/
 - 2. absent/

 - #9. Girdle of tiny hooks on the arms <hook girdle>/
 - 1. present/
 - 2. absent/
- Note: The hooks are not arm spines and they do not occur anywhere else, these are tiny hooks in bands across the dorsal arm.
- #10. Spines <shape>/
 - 1. all similar in shape/
 - 2. not all similar in shape/

 - #11. The atypical spines <hooks/bristles>/
 - 1. are hook-shaped/
 - 2. are bristles/
 - 3. are umbrella-shaped/

#12. Arm spine cross section <shape>/

1. round/
2. oval/

#13. The ratio of thickness of distal $\frac{1}{3}$ of arm spine to maximum thickness (in a given cross-sectional plane) <arm spine>/

1. 0.2–0.6/
2. 0.6–0.9/
3. 0.9–1/

#14. Arm spines <shape>/

1. tapering (conical) <distally $\frac{1}{3}$ as thick as proximal diameter with round cross section>/
2. flat <distally half as thick as proximal diameter or same with oval cross section>/
3. cylindrical <same thickness at both ends with flat/round tip>/
4. pointed <distally half as thick as proximal diameter with round cross section>/

#15. Arm spines <position>/

1. mainly lateral/
2. at proximal segments only on ventral side of arms/

#16. Arm spines <direction>/

1. predominantly parallel to arm axis (adpressed)/
2. predominantly erect, standing perpendicular to arm axis/

#17. Longest arm spines <relative length>/

1. shorter than half a segment/
2. between half and one segment long/
3. between one and two segments long/
4. longer than two segments/

#18. Tentacle scales <absence/presence>/

1. present/
2. absent/

#19. Tentacle pores <visibility>

1. visible only on proximal arm /
2. visible along most of the arm /

#20. Tentacle scales <length>/

1. nearly as long as wide/
2. slightly longer than wide/
3. more than two times as long as wide/

#21. Tentacle scales <length compared with the spine nearby>/

1. shorter than the spine nearby/
2. as long as the spine nearby/
3. longer than the spine nearby/

#22. Tentacle scales <oval/round>/

1. cross section round/
2. cross section oval/

- #23. Position of lateral arm plate (LAP) <lateral/arched>/
1. only lateral/
2. arched (wrapped around the arm)/
- #24. Dorsal and/or ventral edge(s) of LAPs <with/without constriction=concave>/
1. with constriction/
2. without constriction/
- #25. Ventral position of LAP <projecting ventro-proximalwards>/
1. projecting ventro-proximalwards/
2. not projecting ventro-proximalwards/
- #26. Ventro-distal tip of LAP <projecting ventralwards, e.g., *Ophiopallas*>/
1. projecting ventralwards/
2. not projecting ventralwards/
- #27. Arm spine articulation <with/without dorsal and ventral lobes>/
1. without dorsal and ventral lobes/
2. with dorsal and ventral lobes/
- #28. Arm spine articulation <with/without sigmoidal fold>/
1. without sigmoidal fold/
2. with a weakly developed sigmoidal fold/
3. with a fully developed sigmoidal fold/
- #29. Arm spine articulation <central/entire>/
1. restricted to (the ventral or central) portion of the distal edge/
2. arranged over entire distal LAP edge/
- #30. Arm spine articulation <size>/
1. dorsalwards increasing in size/
2. ventralwards increasing in size/
3. larger in middle/
4. all similar/
- #31. Distance between spine articulations/
1. dorsalwards increasing/
2. ventralwards increasing/
3. equal/
4. not applicable (two spine articulations)/
- #32. Nerve and muscle openings separated <related to arm spine articulation>/
1. by small ridge if at all/
2. by large, prominent ridge or regular stereom/
- #33. Nerve opening <size - related to arm spine articulation>/
1. smaller than muscle opening/
2. approximately as large as muscle opening/

Dorsal disc

- #34. Disc <circular/pentagonal>/
1. pentagonal/
2. circular/

- #35. Disc <flat/high>/
1. flat (about same level as arms)/
2. high (above arm level)/
3. a sac-like shape (much higher than wide)/
- #36. integument <skin obscuring plates>/
1. not obscuring plates/
2. obscuring plates/
- #37. Dorsal disc <cover - granules>/
1. with granules/
2. without granules/
- #38. Dorsal disc <cover - primary plates>/
1. with obvious primary plates/
2. with concealed primary plates/
- #39. Dorsal disc <cover - scale>/
1. with scales/
2. without scales/
- #40. Dorsal disc <cover - spines>/
1. with spines/
2. without spines/
- #41. Dorsal disc scale/plate <tubercles growing out of scales/plates>/
1. with tubercles/
2. without tubercles/
- #42. Radial shield <absence/presence>/
1. present/
2. absent/
- #43. Radial shield <covering>/
1. without granules/spines/
2. with spines/
3. with granules/
4. with tubercles grown out of plate/
- #44. Radial shield <length>/
1. length less than one third of the disc radius/
2. length between one third and half of the disc radius/
3. length more than half of the disc radius/
- #45. Radial shield <shape>/
1. scalene (oblique) triangular/
2. isosceles (mirror-symmetric) triangular to pear-shaped/
3. bar-like/
- Ventral disc**
- #46. Gonads <position>/
1. restricted to the disc/
2. not restricted to the disc (extending into the basal portion of the arms)/

#47. Ventral interradii <cover>/

1. without granules/spines/
2. with spines/
3. with granules/

#48. Scales on ventral interradii <covering - from disc edge>/

1. covering the whole area of an interradius/
2. covering half/less than half of an interradius/
3. absent/

#49. The number of scales on H line of an interradius <the interradius is assumed as a triangle and H gives its height>/

1. fewer than 7/
2. 7–14/
3. 14–21/
4. more than 21/

#50. Ventral teeth <the number of oral papillae *sensu lato* on DP>/

1. single/
2. several (tooth papillae)/

A cluster is not the same as the tooth papillae but in some species, the cluster is large and very similar to tooth papillae.

#51. Infradental papillae on oral plate <absence/presence>/

1. present/
2. absent/

#52. Buccal scales on OP <absence/presence>/

1. present/
2. absent/

#53. Accessory oral papillae on OP <absence/presence>/

1. present/
2. absent/

#54. Lateral oral papillae on OP <absence/presence>/

1. present/
2. absent/

#55. Lateral oral papillae <number>/

1. one lateral papilla along each side of the jaw/
2. single row of lateral papillae/
3. multiple rows of lateral papillae/

#56. Lateral oral papillae <shape>/

1. block-shaped/
2. rounded/
3. paddle-shaped/
4. spiniform/

#57. Adoral shield spine <absence/presence>/

1. present/
2. absent/

#58. Lyman's ossicle <absence/presence>/

1. present/
2. absent/

#59. Oral shield <length - distance between proximal tip of OS and disc margin>/

1. covering less than one third of interradius/
2. covering more than one third of the length of an interradius/

#60. Oral shield <shape>/

1. much longer than wide/
2. about as long as wide/
3. much wider than long/

#61. Madreporite <number>/

1. one/
2. multiple/
3. absent/

#62. Madreporite <number of pores on each madreporite>/

1. with one pore/
2. with numerous pores/

#63. Adoral shield <separated or meeting in front of oral shield>/

1. separated/
2. meeting in front of the oral shield/

#64. Abradial genital plate <shape>/

1. twisted/
2. not twisted/

#65. Number of genital slits <1/2 slits per bursa>/

1. one per bursa/
2. two per bursa/

#66. Genital slit <length>/

1. shorter than half interradius/
2. longer than half the length of an interradius/

#67. Genital papillae <absence/presence>/

1. present/
2. absent/

#68. Dental plate <geometry>/

1. of equal width all over/
2. ventral half widest/
3. dorsal half widest/

#69. Dental plate <entire/fragmented>/

1. entire (single plate)/
2. fragmented/

#70. Dental sockets <shape>/

1. slit-shaped/
2. circular/
3. heart-shaped/

#71. Dental sockets <size>/

1. less than 50% of the width/
2. equal to or more than 50% of the width/

#72. At least one socket on DP as <depression/perforation - with/without septum>/

1. depression or perforation without septum/
2. perforation with septum/

#73. Teeth <shape>/

1. spine-shaped/
2. flat (with round or slightly pointed tip, but never spine-like)/
3. block-like (with square tip)/

#74. Teeth on DP arranged as <the ratio of teeth and tooth papillae on dental plate>/

1. single column/
2. a single column on half of dental plate and other half with a cluster of tooth papillae (ventral cluster) <e.g., Ophiotrichidae, Ophiophilidae>/
3. a single column on $\frac{2}{3}$ and a cluster of tooth papillae on $\frac{1}{3}$ of dental plate <e.g., Ophiuridae>/
4. covering the entire dental plate evenly <e.g., Gorgonocephalidae>/

Vertebrae

#75. Vertebrae <streptospondylous/zygospondylous>/

1. hourglass-shaped (streptospondylous)/
2. zygospondylous/

#76. Vertebrae beyond segment 5 <keeled/non-keeled>/

1. with extended keel/
2. with short keel/
3. non-keeled/

#77. Vertebrae <with/without oral bridge>/

1. with oral bridge/
2. without oral bridge/

Appendix 2 (continued on next page). Condensed tabular key to the ophiuroid families (modified from the prt file exported from DELTA). Heteromorphic families appear more than once in the table below (e.g., Ophiopyrgidae = 4) and the number of occurrences in the table is indicated in the second column (No. occ.). Each occurrence represents a different set of diagnostic characters and heteromorphic families can be identified from species with different morphology. This offers multiple entry points to the key. Next to a taxon name and its occurrence, there is a list of the characters that separate it from the other taxa in the key. The characters are presented by numbers combined with a letter for the state. State 1, 2, 3 and 4 become state A, B, C and D; for example, 17A corresponds to state 1 in character 17 (see Appendix 1). The table can also be used to compare families by morphological similarity.

Family	No. occ.	Diagnostic characters
Ophiopyrgidae	4	17A, 14A, 4A, 5A, 10A, 15A
Asteronychidae	1	17A, 14A, 4B, 5B, 10B, 15B
Ophiodermatidae	1	17A, 14B
Astrophiuridae	2	17A, 14C, 45A
Ophiopyrgidae	4	17A, 14C, 45B, 4A, 15A, 20C, 41B
Hemieuryalidae	2	17A, 14C, 45B, 4B, 15B, 20A, 41A
Euryalidae	1	17A, 14C, 45C
Ophiosphalmidae	1	17A, 14D, 20A, 21A, 22A, 34A, 40A
Astrophiuridae	2	17A, 14D, 20A, 21B, 22B, 34B, 40B
Ophiolepididae	1	17A, 14D, 20B, 6A, 38A, 63B, 31A
Ophiopezidae	1	17A, 14D, 20B, 6B, 38B, 63A, 31C, 16A, 36B, 39B, 40A
Ophiomyxidae	3	17A, 14D, 20B, 6B, 38B, 63A, 31C, 16B, 36A, 39A, 40B
Ophiopyrgidae	4	17A, 14D, 20C, 4A, 34B, 67A, 31A
Ophiomusaidae	1	17A, 14D, 20C, 4B, 34A, 67B, 31C, 16A, 21C, 19A, 38A
Ophiomyxidae	3	17A, 14D, 20C, 4B, 34A, 67B, 31C, 16B, 21A, 19B, 38B
Hemieuryalidae	2	17B, 16A, 20A, 14C, 45B, 13C, 15B
Ophioleucidae	1	17B, 16A, 20A, 14D, 45A, 13B, 15A
Ophiuridae	2	17B, 16A, 20B, 4A, 10A, 12A, 36A
Ophiernidae	1	17B, 16A, 20B, 4B, 10B, 12B, 36B
Ophiopyrgidae	4	17B, 16A, 20C
Amphiuridae	2	17B, 16B, 36A, 33B, 20A, 44B, 30B
Ophiactidae	2	17B, 16B, 36A, 33B, 20B, 44C, 30C
Ophionereididae	2	17B, 16B, 36B, 33A, 3A, 12A, 15A, 66B, 18A, 39A, 43A, 50A
Ophiobyrsideae	1	17B, 16B, 36B, 33A, 3A, 12A, 15A, 66B, 18B, 39B, 43C, 50B
Gorgonocephalidae	1	17B, 16B, 36B, 33A, 3B, 12B, 15B, 66A
Ophiuridae	2	17C, 36A, 44B, 4A, 16A, 20B, 50B
Ophiopholidae	1	17C, 36A, 44B, 4B, 16B, 20A, 50A, 6A, 8A, 10B, 24A
Ophiothamnidae	1	17C, 36A, 44B, 4B, 16B, 20A, 50A, 6B, 8B, 10B, 24B, 49B
Amphiuridae	2	17C, 36A, 44B, 4B, 16B, 20A, 50A, 6B, 8B, 10A, 24B, 49C
Ophiactidae	2	17C, 36A, 44C, 18A, 40A, 30C, 33B
Amphilepididae	1	17C, 36A, 44C, 18B, 40B, 30B, 33A
Ophiotomidae	3	17C, 36B, 20A, 14B, 49D, 12B, 50B
Ophiacanthidae	3	17C, 36B, 20A, 14D, 49B, 12A, 50A
Ophiohelidae	1	17C, 36B, 20B, 16A, 42B, 47B, 26A
Ophiotomidae	3	17C, 36B, 20B, 16B, 42A, 47C, 26B, 45A, 49D, 12B, 43C
Ophionereididae	2	17C, 36B, 20B, 16B, 42A, 47C, 26B, 45B, 49C, 12A, 43A
Ophioscolecidae	1	17C, 36B, 20C, 21A, 49C, 59A, 72A, 12A, 22B, 42B, 47A
Amphilimnidae	1	17C, 36B, 20C, 21A, 49C, 59A, 72A, 12B, 22A, 42A, 47B

Appendix 2 (continued).

Family	No. occ.	Diagnostic characters
Ophiopsilidae	1	17C, 36B, 20C, 21C, 49D, 59B, 72B
Ophiocomidae	1	17D, 44A, 45A, 12B, 36B, 43C, 63A, 25A, 35A, 55C
Ophiotomidae	3	17D, 44A, 45A, 12B, 36B, 43C, 63B, 25B, 35B, 55B
Ophiomyxidae	3	17D, 44A, 45B, 12A, 36A, 43A
Ophiacanthidae	3	17D, 44B, 3A, 14D, 20A, 36B
Ophiocamacidae	1	17D, 44B, 3C, 14C, 20B, 36A
Ophiopteridae	1	17D, 44C, 20A, 8A, 22A, 48C, 50B
Ophiacanthidae	3	17D, 44C, 20A, 8B, 22B, 48A, 50A
Clarkcomidae	1	17D, 44C, 20C, 14B, 21A, 12B, 22B
Ophiotrichidae	1	17D, 44C, 20C, 14D, 21B, 12A, 22A