



Research article

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Morphological diagnoses of higher taxa in Ophiuroidea (Echinodermata) in support of a new classification

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Abstract. A new classification of Ophiuroidea, considering family rank and above, is presented. The new family and superfamily taxa in O'Hara *et al.* (2017) were proposed to ensure a better readability of the new phylogeny but are unavailable under the provisions of the ICZN. Here, the morphological diagnoses to all 33 families and five superfamilies are provided. Ten new families, Ophiosphalmidae fam. nov., Ophiomusaidae fam. nov., Ophiocamacidae fam. nov., Ophiopteridae fam. nov., Clarkcomidae fam. nov., Ophiopezidae fam. nov., Ophiernidae fam. nov., Amphilimnidae fam. nov., Ophiothamnidae fam. nov. and Ophiopholidae fam. nov., are described. The family Ophiobyrsidae Matsumoto, 1915, not yet discovered in the previous publication, is added, based on new molecular data. A new phylogenetic reconstruction is presented. Definitions of difficult-to-apply morphological characters are given.

Keywords. Taxonomy, brittle-stars, morphology, phylogeny, nomenclature.

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Introduction

In their new phylogeny of the Ophiuroidea, O'Hara *et al.* (2017) named the new families suggested by their phylogeny for the sake of readability but deferred the morphological delimitation of the new families, and supplied no diagnoses, leaving the proposed names unavailable in that publication. The new classification was presented in an electronic supplement and as such nomenclaturally unavailable (Krell 2015) with respect to ranks that are governed by the ICZN (family group names and below).

Here, we provide the diagnoses, required by the ICZN, to make the new family names available and valid. In addition to newly formed families, several previously proposed but later synonymized families are resurrected. We reconsidered a few decisions on the composition of some families, compared to the preliminary classification presented in O'Hara *et al.* (2017). A new monophyletic clade corresponding to the Ophiobursidae Matsumoto, 1915 was identified with new molecular data and morphological characters. Of the 256 currently recognized genera (Stöhr *et al.* 2017), many remain to be analysed and possibly revised, which may affect their final placement in the classification. New family-level clades may also be discovered in the future. With respect to previously existing names, it should be noted that the concepts of many of the taxa delimited herein differ considerably from the concepts held by the original authors of these taxon names. Meier (2017) stressed the difference between taxon naming and taxon delimitation, the former being a technical housekeeping exercise and the latter being hypothesis driven. This difference becomes quite obvious in the work presented here. For the sake of nomenclatural stability, naming conventions require that existing names are preserved, even when the concept associated with that name changes beyond recognition. Taxon concepts are clearly scientific hypotheses of evolutionary relationships, and may change over time, being tested against new data. Phrases such as “taxon A is polyphyletic/paraphyletic” refer to the concept of the respective taxon, i.e., the assortment of genera included in a family, or species included in a genus. They do not question the monophyly of a clade but the application of the name to a component of the clade.

Material and methods

Data collection

This study is the result of years of taxonomic work and data collection by the authors and therefore the material used comes from a variety of sources. Specimens were sourced from museum collections all over the world, in particular from the Swedish Museum of Natural History (Stockholm), the Zoological Museum of Moscow State University, the Muséum national d'Histoire naturelle (Paris), as well as from the authors' personal research material. The brittle stars were examined, dissected, photographed, subjected to scanning electron microscopy, and used for molecular work. The data used here were produced and accumulated over the past 20 years, originally for other projects, published in part (Stöhr 2005; Stöhr & Segonzac 2005; O'Hara & Stöhr 2006; Stöhr, Conand & Boissin 2008; Stöhr, Boissin & Chenuil 2009; Martynov 2010a, 2010b; Stöhr & Muths 2010; Stöhr 2011; Thuy & Stöhr 2011; Thuy 2013; Thuy & Stöhr 2016; Stöhr & Martynov 2016; O'Hara *et al.* 2017).

We analysed original images from our respective collections, as well as text and illustrations from original descriptions of genera and families (for a complete list of original works see Appendix A), and from other literature (Paterson 1985; Martynov 2010b; Thuy & Stöhr 2011; Pineda-Enriquez *et al.* 2014), to identify synapomorphies of the various taxa, diagnosed below. Species were identified using identification keys (Mortensen 1927; Clark & Rowe 1971; Paterson 1985), and recent revisions and new descriptions (O'Hara *et al.* 2004; O'Hara & Stöhr 2006; Benavides-Serrato & O'Hara 2008; Martynov & Litvinova 2008; Okanishi & Fujita 2009; Okanishi *et al.* 2011a, 2011b; Stöhr 2011; Okanishi & Fujita 2011; Okanishi *et al.* 2013; Pineda-Enriquez *et al.* 2014; Baker 2016). One family, Ophiobursidae Matsumoto, 1915, not included in O'Hara *et al.* (2017), but presented here, was identified by molecular

methods and phylogenetic analyses as described in that publication, and diagnosed morphologically here. This slightly changed phylogenetic reconstruction is shown in Fig. 1.

Only a limited number of genera and species has been subjected to detailed morphological examination so far. Particularly the characteristics of the internal skeleton are unknown for the majority of the about 2100 described species (Stöhr *et al.* 2017). Although O'Hara *et al.* (2017) collected molecular data for more than a quarter of all known species, within- and between-family relationships may change when more data are available. The diagnoses provided herein are based foremost on some of the characters presented by the type species of each family (Thuy & Stöhr 2016), to comply with nomenclatural rules, although the type species are in some cases rather specialized with many novelties that are absent in other members of the same family (e.g., *Astrophiura* Sladen, 1879). Such novelties or autapomorphies of genera were excluded from the diagnosis of a family to accommodate a wider range of included genera. Other genera than the type genus are included based on molecular data alone (O'Hara *et al.* 2017), when the available morphological data are insufficiently known. Many rarely collected species are still unavailable for study, and strongly paedomorphic species are difficult to place without molecular data due to their aberrant morphology suggesting false homologies that are actually homoplasies, as well as pseudoplesiomorphies (Stöhr & Martynov 2016). The following diagnoses present synapomorphies that support the monophyly of each taxon, and characters that distinguish the families within a higher taxon. We do not provide full descriptions for each family, because at this point it is unclear which characters are common to all members (genera) of a family, in addition to the synapomorphies so far identified. Some families are surprisingly heterogeneous in morphology but clearly monophyletic according to our molecular data (O'Hara *et al.* 2017). Characters may have been reduced during evolution within a family and other characters may have appeared as novelties in one or more genera. The phylogenetic relationships on lower taxonomic level (below family rank) will be the subject of future molecular and morphological studies.

Character definitions

Many significant characters require dissection and examination of micromorphology, sometimes only visible by scanning electron microscopy. For the purpose of routine identifications this is unfortunate but previous attempts at reconstructing the ophiuroid phylogeny were clearly hampered by the almost exclusive use of external and macromorphological characters, as has been shown by the most recent morphological phylogenetic analysis (Thuy & Stöhr 2016). The terminology used for the ophiuroid skeleton has varied widely over the last two centuries. Stöhr *et al.* (2012) proposed a standardized list of terms, but clear definitions are hampered by our limited understanding of ophiuroid morphology. Recent work (Martynov 2010b; Thuy & Stöhr 2011, 2016) has provided insights that allow us to refine existing terms and define new structures. Here we provide our definitions for some of the more difficult or confusing characters used, with example illustrations (Fig. 2A–J).

Disc scales and plates (Fig. 2A) are terms that are often used in a random fashion, perhaps based on size, scales being considered smaller than plates. Instead, the term 'plate' should be used for external disc or arm ossicles with fixed position and exact number, which makes them individually identifiable (e.g., primary disc plates, radial shields, dorsal, ventral and lateral arm plates) and predictable during ontogeny (Sumida *et al.* 1998; Stöhr 2005). Some internal ossicles are also called plates, e.g., oral and genital plates. In contrast, scales are found mainly on the disc, rarely on the arms, and they cannot be identified individually, their number varies between individuals and ontogenetic stages and they do not always appear in the exact same position. In species with reduced numbers of disc scales, these can become individually recognizable, fixed in position and number, and predictable in ontogeny. There is thus a certain flexibility in these terms that cannot be eliminated.

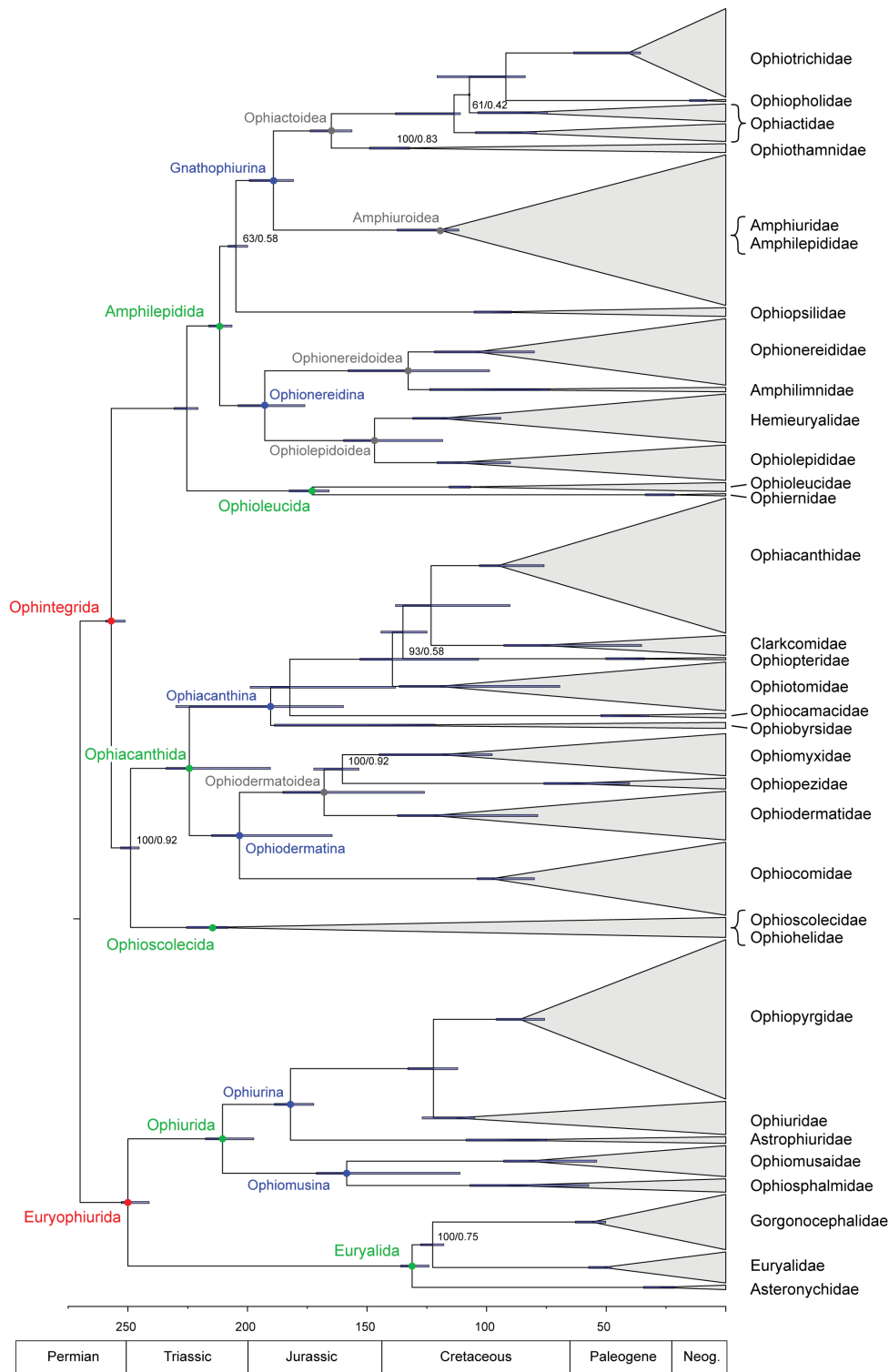


Fig. 1. Summary phylogenetic tree of the ophiuroid higher taxonomy. Modified from O'Hara *et al.* (2017: fig. 1), with Ophiobysidae included based on O'Hara *et al.* (2017: fig. S3) sample *Ophiuroidea*_sp_IE.2009.1713 (= *Ophiophrinx*_confinis) and additional unpublished exon-capture data on samples *Ophiobysa*_rudis_F222711 and *Ophiomilax*_sp_IE.2207.6967. All-sites PLRS/RAXML tree with node support and age confidence intervals (coloured bars). Node support shows all-sites RAXML BS followed by the proportion of the data subset trees in agreement. For all other nodes support was 100/1. The root was fixed according to O'Hara *et al.* (2014) at 270 Ma.

The terms **oral papillae**, **apical papillae**, **infradental papillae**, **tooth papillae** and **teeth** (Fig. 2B–C, G) cause considerable confusion, as they have been applied to non-homologous structures across the diversity of Ophiuroidea. We have studied the dental plates and jaws of numerous species and propose here a clear way to distinguish between these structures (Martynov 2010b; Thuy & Stöhr 2016; Stöhr & Martynov 2016). Oral papillae at the ventral or ventrolateral edge of the dental plate lack corresponding sockets on the dental plate. Ontogenetically, these develop laterally at the dental plate and move below the teeth (= in infradental position) (Hendler 1978; Stöhr 2005) to varying degree, depending on the species. Thus defined, infradental papillae are found in more taxa than previously assumed (see diagnoses below). In contrast, teeth and so called tooth papillae sit on sockets on the dental plate (Fig. 2H). Consequently, the term **apical papilla**, commonly used in the literature, usually refers to a ventral tooth, whereas the **infradental papillae** are oral papillae. **Tooth papillae** should better be viewed as teeth, since they cannot unambiguously be distinguished from apical tooth clusters, and both

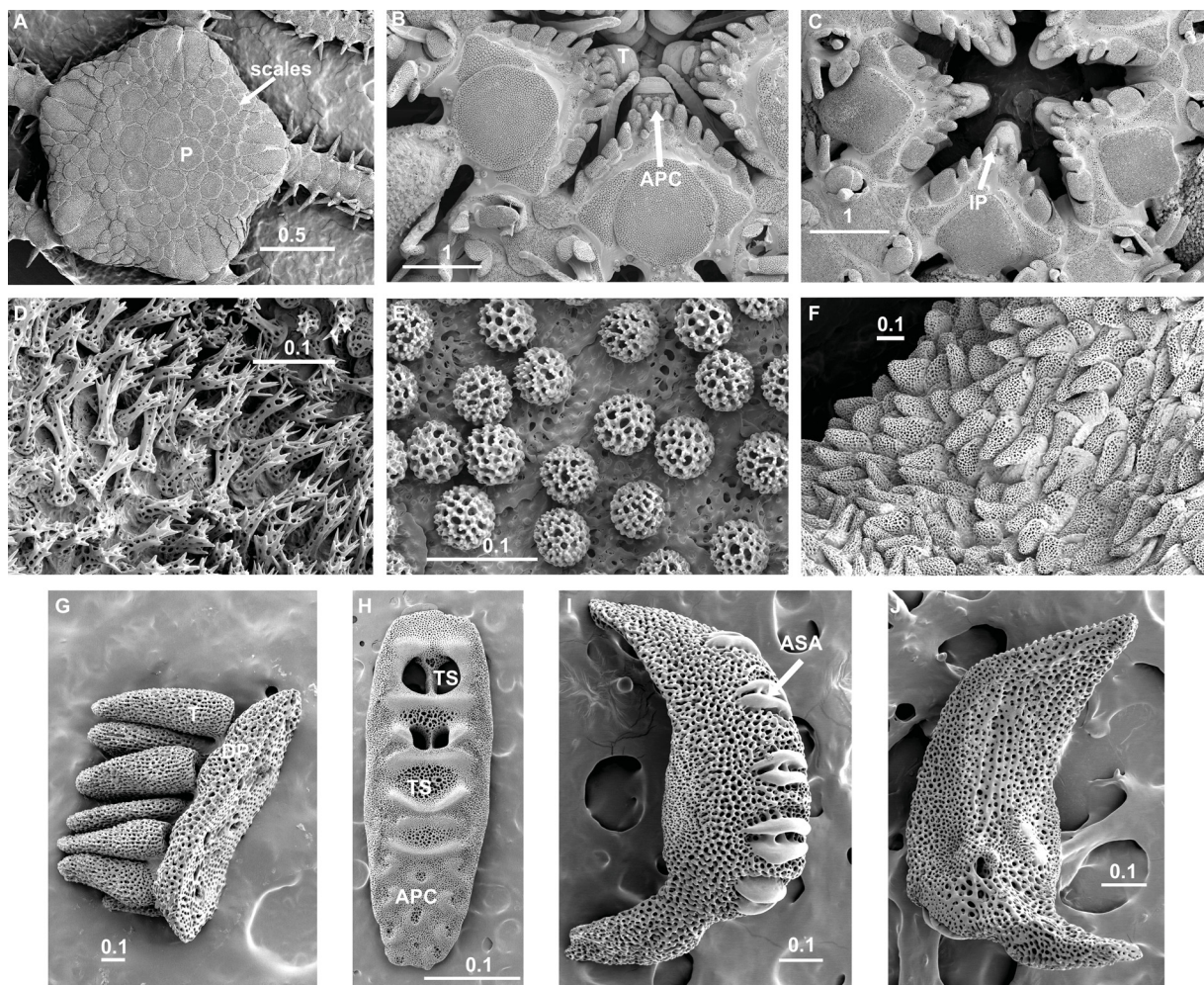


Fig. 2. Examples of skeletal structures of brittlestars. **A.** Dorsal disc with scales and plates in *Amphiura* Forbes, 1843 (P). **B.** Oral frame with teeth (T) and apical tooth cluster (APC) in *Ophiocoma* L. Agassiz, 1836. **C.** Oral frame with infradental oral papillae (IP) in *Ophioplax* Lyman, 1875. **D.** Disc spines in *Ophiacantha* Müller & Troschel, 1842. **E.** Disc granules in *Ophiocoma* L. Agassiz, 1836. **F.** Disc tubercles in *Acrocnida* Gislén, 1926. **G.** Dental plate (DP) in *Ophiura* Lamarck, 1801, with teeth attached. **H.** Dental plate with sockets for regular teeth (TS) and for apical tooth cluster (APC) in *Ophiocoma* L. Agassiz, 1836. **I–J.** Lateral arm plate in *Amphiura* Forbes, 1843. **I.** External view with arm spine articulations (ASA). **J.** Internal view. Scale bars in millimetres.

tooth papillae and tooth clusters have evolved multiple times. In addition, both teeth and tooth papillae articulate to the dental plate on sockets, whereas infradental oral papillae have no sockets. Instead, dental plates with infradentals are usually laterally tapered at their ventral end.

Disc granules and **disc spines** (Fig. 2D–F) refer to different shapes of the same structure, and there are numerous variations of intermediate forms between granule and spine, all are articulated to disc scales and/or plates, sometimes extending onto the arms. **Tubercles** are outgrowths of ossicles, not articulated. **External, epidermal or dermal ossicles** are terms that have been used for granule- or scale-like ossicles in the epidermis covering the disc and arms of Euryalida (Okanishi *et al.* 2011a, 2013), giving the impression that these are novel structures, found only in this order. There is however no evidence against a homology of granules and scales across all Ophiuroidea and the same terminology should be used until found otherwise.

The **arm spine articulations** (Fig. 2I) have been treated in detail by Martynov (2010a, 2010b), who demonstrated their strong phylogenetic signal. They consist of a large variety of lobes, ridges and knobs, bordering usually two, sometimes one, opening(s) for muscle and nerve, passing through to the spine. Thuy & Stöhr (2011) studied the lateral arm plates (Fig. 2I–J) and later identified a total of 42 characters on these alone (Thuy & Stöhr 2016), phylogenetically important on various taxonomic levels.

Arm vertebrae are subject to ecological adaptation and show convergent evolution. Thus, hourglass-shaped vertebral articulations are found in several taxa with epizoic life style, whereas their relatives have zygospondylous articulations. This character cannot therefore be used on its own but it is helpful in combination with other characters or to differentiate closely related groups. In some Euryalidae, the ventral vertebral furrow, in which the radial water vascular canal and radial nerve are placed, is closed by a structure known as “oral bridge” (Mortensen 1933; Okanishi *et al.* 2011b).

Results

New classification scheme of Recent Ophiuroidea (family and higher ranks)

Phylum Echinodermata Bruguière, 1791
 Subphylum Asterozoa von Zittel, 1895
 Class Ophiuroidea Gray, 1840
 Subclass Myophiuroidea Matsumoto, 1915
 Infraclass Metophiurida Matsumoto, 1913 (crown-group of Ophiuroidea)
 Superorder Euryophiurida O’Hara *et al.*, 2017
 Order **Euryalida** Lamarck, 1816

Diagnosis

Arm spine articulations with muscle and nerve openings well separated. Arm spines ventral only. Lateral arm plates devoid of ornamentation. Vertebrae with hourglass-shaped articulations.

Family **Asteronychidae** Ljungman, 1867

Type genus

Asteronyx Müller & Troschel, 1842 (type species: *A. loveni* Müller & Troschel, 1842).

Other genera

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

Diagnosis

Dorsal disc with thickened skin, few or no scales, radial shields bar-like, almost meeting in disc centre. Long, tapering arms, covered by thickened skin, lacking dorsal plates. Multiple columns of spiniform teeth, dental plate entire. Arms not branching. All vertebrae without oral bridge. Gonads restricted to disc. Arm spine articulation as slightly tumid regular stereom with large oval or round opening.

Family **Euryalidae** Gray, 1840

Type genus

Euryale Lamarck, 1816 (type species: *E. aspera* Lamarck, 1816).

Other genera

Asteromorpha Lütken, 1869, *Asteroschema* Örstedt & Lütken, 1856, *Asterostegus* Mortensen, 1933a, *Astrobrachion* Döderlein, 1927, *Astroceras* Lyman, 1879, *Astrocharis* Koehler, 1904, *Ophiocreas* Lyman, 1869, *Squamophis* Okanishi *et al.* 2011, *Sthenocephalus* Koehler, 1898, *Trichaster* Agassiz, 1836.

Diagnosis

Dorsal disc with thickened skin and embedded external ossicles. Single column of teeth, dental plate fragmented. Arms branching in *Euryale*, *Trichaster* and *Sthenocephalus*. Distal vertebrae with oral bridge in *Asteromorpha*, *Asterostegus*, *Astrobrachion*, *Astroceras*, *Euryale*, *Sthenocephalus* and *Trichaster* (Okanishi *et al.* 2011b). Gonads may extend into the arms. Arm spine articulation with large muscle opening separated from the nerve opening by a large, swollen ridge.

Family **Gorgonocephalidae** Ljungman, 1867

Astrochelidae Verrill, 1899a: 79.

Type genus

Gorgonocephalus Leach, 1815 (type species: *G. caputmedusae* (Linnaeus, 1758)).

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, 1899b, *Astroclon* Lyman, 1879, *Astrocnida* Lyman, 1872, *Astrocarius* 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, 1909a, *Astrotoma* Lyman, 1875, *Astrozona* Döderlein, 1930, *Conocladus* H.L. Clark, 1909b, *Ophiocrene* Bell, 1894, *Ophiozeta* Koehler, 1930, *Schizostella* A.H. Clark, 1952.

Diagnosis

Dorsal disc and arms with scales and plates, which bear thorny granules or spines. Girdles of small hyaline hooks on the arms. Arms branching or simple. All vertebrae without oral bridge. Gonads restricted to disc. Multiple teeth in irregular columns, dental plate entire. Arm spine articulation with slit-shaped muscle opening proximally bordered by vertical ridge, small nerve opening at a distance.

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

Diagnosis

Arms never branching. Spine articulation with muscle opening generally surrounded by ridges and/or knobs and separated from nerve opening by vertical ridge, lateral arm plates generally with external ornamentation (tubercles, striation, spurs). Strong influence of paedomorphosis (Stöhr & Martynov 2016).

Suborder **Ophiomusina** O'Hara *et al.*, 2017

Diagnosis

Dental plate entire, sockets shallow, single row of teeth. Tentacle openings minute within-plate perforations of the lateral arm plate, except on proximal arm joints. Lateral arm plates conspicuously thick and meeting dorsally and ventrally. Genital papillae restricted to ventral side. Second tentacle pore concealed inside mouth slit.

Family **Ophiosphalmidae** fam. nov.

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Type genus

Ophiosphalma H.L. Clark, 1941 (type species: *O. planum* (Lyman, 1878b) = *O. armigerum* (Lyman, 1878a)).

Other genera

Ophiolipus Lyman, 1878b, *Ophiomusium* Lyman, 1869 (only species *O. eburneum* Lyman, 1869).

Diagnosis

Numerous disc scales, small primary plates. Dorsal and ventral arm plates present along most of the arm. Lateral arm plate with a finely meshed proximal band that lacks spurs. Longer genital slits than *Ophiomusa*. Three (rarely 2–5) visible proximal pairs of tentacle pores. Frequently with small disc spines distal to the genital slit around the disc margin. In our molecular analysis, the genus *Ophiolipus* (lacking disc plates) is polyphyletic.

Family **Ophiomusaidae** fam. nov.

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Type genus

Ophiomusa Hertz, 1927 (type species: *O. lymani* (Wyville-Thomson, 1873)).

Diagnosis

Disc scales few, primary plates obvious, radial shields enlarged. Ventral arm plates, and in some species also dorsal arm plates, present on few proximal arm joints only. Lateral arm plates with numerous spurs along proximal edge. Extremely short genital slits, rarely as long as first arm joint. Two visible proximal pairs of tentacle pores.

Remarks

Hertz (1927) included 11 species in the genus *Ophiomusa* – *canaliculata* (H.L. Clark, 1917), *facunda* (Koehler, 1922a), *fallax* (Koehler, 1904), *luetkeni* (Lyman, 1878), *lunaris* (Lyman, 1878), *lymani*, *muta* Hertz, 1927 (as subspecies of *facunda*), *relicta* (Koehler, 1904), *scalare* (Lyman, 1878), *trychna* (H.L. Clark, 1911) and *ultima* Hertz, 1927 – many of them with a more simplified skeleton than the type species *O. lymani* (Baker 2016). The type species of *Ophiomusium*, *O. eburneum*, is genetically and morphologically related to *Ophiosphalma* and not to the other described species of *Ophiomusium*. It has 2–3 pairs of visible tentacle pores and persistent ventral and dorsal arm plates, and rounded, almost bulging lateral arm plates. The remaining species of *Ophiomusium* form a distinct family-level clade with typically 2 (rarely 0 or 1) pairs of visible tentacle pores. Consequently, we transfer these remaining species to the only available genus name, *Ophiomusa* Hertz, 1927, which until now has been treated as a synonym of *Ophiomusium*. A future molecular and morphological revision of the Ophiomusaidae fam. nov. may reveal several monophyletic clades at genus level.

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

Diagnosis

Genital papillae on adradial genital plate form an arm comb (secondarily lost in Astrophuriidae) at the distal end of the plate. Cluster of teeth on ventral part of dental plate. Lateral arm plates generally much more fragile than in Ophiomusina. Many strongly paedomorphic taxa in which arm combs and oral tooth clusters may be reduced or absent. Second tentacle pore outside of mouth slit or opening into it but never concealed.

Family **Astrophuriidae** Sladen, 1879a

Type genus

Astrophuri Sladen, 1879a (Type species: *A. permira* Sladen, 1879b).

Other genera

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

Diagnosis

Dorsal disc composed of very obvious primary plates, interradial plates and radial shields, few or no disc scales. Single apical ventralmost tooth. No genital papillae, no arm combs. Strongly paedomorphic genera with reduced skeleton; *Astrophuri* with highly modified lateral arm plates on proximal joints. Arm spine articulation as simple muscle opening, bordered by thickened stereom, nerve opening reduced.

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

Type genus

Ophiura Lamarck, 1801 (type species: *O. ophiura* (Linnaeus, 1758)).

Other genera

Ophiocrossota H.L. Clark, 1928, *Ophiocten* Lütken, 1855, *Ophioctenella* Tyler *et al.*, 1995, *Ophionotus* Bell, 1902.

Diagnosis

Flat disc, usually fully scaled but naked in some species. Genital papillae and arm combs present, although combs in *Ophionotus* reduced. Dental plate entire, sockets small round holes, not perforating,

with low borders; single, offset column, ventral cluster. Lateral arm plates commonly divided in two halves by central, distalwards-pointing tentacle notch. Arm spine articulation with large, irregularly round muscle opening on an elevation, nerve opening at base of elevation.

Remarks

Ophiura may be polyphyletic and needs to be revised (e.g., *O. robusta* (Ayres, 1852) has hooked spines on the distal arm, a character of Ophiopyrgidae Perrier, 1893). The subgenus *Ophiuroglypha* Hertz, 1927 is herein raised to genus-rank and referred to the Ophiopyrgidae. The available genus name *Glaciacantha* Fell, 1961b is used herein to contain two Southern Ocean species of *Ophiecten* (*dubium* Koehler, 1901 and *doederleini* Hertz, 1927) with raised disc plates and hooked distal arm spines, and also transferred to the Ophiopyrgidae.

Family **Ophiopyrgidae** Perrier, 1893

Type genus

Ophiopyrgus Lyman, 1878a (type species: *O. wyvillethomsoni* Lyman, 1878a).

Other genera

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

Diagnosis

High disc with few to many scales, primary plates obvious (but *Ophiosparte* with thickened skin covering the disc scales and plates; *Ophiopleura* with scales embedded in thickened skin). Arm combs present but often not as well expressed as in Ophiuridae. Lateral arm plates generally with ventro-distalwards-pointing tentacle notch, often with within-plate tentacle perforation in median to distal arm portions. Distal arm spines often hooked. Arm spine articulation oval to slit-shaped with lower lip, nerve opening at a distance, in paedomorphic taxa such as *Ophiopyrgus* weakly expressed as slightly larger pore in the stereom of the lateral arm plate.

Remarks

Ophiopyrgus is a paedomorphic species with reduced morphology. It is therefore not ideal as typical genus for the characterization of a family but the name Ophiopyrgidae has priority. The expression of typical characters varies greatly among the included genera, many specializations occur.

Ophiurida incertae sedis

Abyssura Belyaev & Litvinova, 1976, *Anophiura* H.L. Clark, 1939, *Anthophiura* H.L. Clark, 1911, *Bathylepta* Belyaev & Litvinova, 1972, *Haplophiura* Matsumoto, 1915, *Ophiochalcis* Koehler, 1930, *Ophiochrysis* Koehler, 1904, *Ophiochytra* Lyman, 1880, *Ophiobella* Mortensen, 1936, *Ophiomaria* A.H. Clark, 1916, *Ophiomastus* Lyman, 1878a, *Ophiopenia* H.L. Clark, 1911, *Ophiophyllum* Lyman, 1878a, *Ophiotjalfa* Mortensen, 1913, *Ophiotrochus* Lyman, 1878a, *Ophiuraster* H.L. Clark, 1939, *Perlophiura* Belyaev & Litvinova, 1972, *Uriopha* Paterson, 1980. (Most of these fit morphologically with Ophiopyrgidae, but in the light of their paedomorphic morphology and lack of genetic data, we refrain from placing them at this time).

Superorder Ophintegrida O'Hara *et al.*, 2017

Order **Ophioscolecida** O'Hara *et al.*, 2017

Remarks

The radial shields are small and concealed by disc scales or absent in most of the included genera, which may suggest reduction of radial shields as synapomorphy of Ophioscolecida.

Family **Ophiophilidae** Perrier, 1893

Ophiomycetidae Verrill, 1899b: 359 (see Thuy & Meyer 2013; Parameswaran *et al.* 2016).

Type genus

Ophiophilus Lyman, 1880 (type species: *O. umbella* Lyman, 1880).

Other genera

Ophiomyces Lyman, 1869, *Ophiotauma* H.L. Clark, 1938, *Ophiophilia* Lyman, 1880.

Diagnosis

Disc fully scaled but radial shields absent, giving the disc a sac-like shape. Jaws (oral plates) covered by numerous flat papillae, except in *Ophiotauma*. Large flat teeth. Arm spine articulations separated from distal edge by a fragile ledge with a distalwards pointing ventral extension. Articulation with nearly vertical dorsal and ventral lobes, connected at their proximal ends, opening into a wide y- or horseshoe-shape, bordering a single muscle/nerve opening, dorsal lobe larger and bent. Lateral arm plates generally with irregular, smooth vertical striation. Conspicuous parasol-shaped arm spines in *Ophiophilus* and *Ophiophilia*. Ventral arm plates often with sockets for tentacle scales.

Family **Ophioscolecidae** Lütken, 1869 (emended, paraphyletic assemblage, see Fig. 2)

Type genus

Ophioscolex Müller & Troschel, 1842 (type species: *O. glacialis* Müller & Troschel, 1842).

Other genera

Ophiocymbium Lyman, 1880, *Ophiogeron* Lyman, 1878a, *Ophiophyalus* Matsumoto, 1915, *Ophiophymen* H.L. Clark, 1911, *Ophiopletoplax* H.L. Clark, 1911, *Ophiologimus* H.L. Clark, 1911, *Ophiolycus* Mortensen, 1933a, *Ophiophrura* H.L. Clark, 1911, *Ophioplexa* Martynov, 2010, *Ophioprium* H.L. Clark, 1915a, *Ophiorupta* Martynov, 2010, *Ophiosyzygus* H.L. Clark, 1911, *Ophiuroconis* Matsumoto, 1915.

Diagnosis

Dorsal disc and arms with thickened skin, thin glassy disc scales, reduced in number or absent in some genera (*Ophioscolex*), mostly naked but scattered smooth disc spines or dense granules occur in some species. Spiniform teeth, forming apical clusters in some genera, spiniform oral papillae. Paired ventralmost teeth, dental plate entire, round sockets, not penetrating. Arm spine articulations adjacent to distal edge of lateral plate, as single opening for both muscle and nerve, with a horseshoe-shaped border in some genera (*Ophioscolex*, *Ophiogeron*), as separate nerve and muscle openings bordered by a larger dorsal and smaller ventral lobe in others (*Ophiolycus*).

Order **Ophiacanthida** O'Hara *et al.*, 2017

Diagnosis

Radial shields often with distal portion exposed (or only proximal tip concealed). Arm spine articulations with bent dorsal and ventral lobes merged at their proximal tips, and generally with sigmoidal fold.

Suborder **Ophiacanthina** O'Hara *et al.*, 2017

Diagnosis

Abradial genital plate without conspicuous ridges or perforations. Arm spines smooth or with lateral thorns. Dorsalward increase in size of spine articulations. Lateral arm plates commonly with constriction leading to raised distal portion. Generally row of small perforations (putatively associated with arm spine innervation) in shallow vertical furrow on inner side of lateral arm plates.

Family **Ophiobyrsideae** Matsumoto, 1915 stat. nov. (raised to family-rank)

Type genus

Ophiobyrsa Lyman, 1878a (type species: *O. rudis* Lyman, 1878a).

Other genera

Ophiobyrsellia Verrill, 1899b, *Ophiosmilax* Matsumoto, 1915, *Ophiophrixus* H.L. Clark, 1911.

Diagnosis

Disc and arms covered by thickened skin bearing pointed spines, large radial shields. Vertebrae with hourglass-shaped articulation. Multiple columns of spiniform teeth on round, knob-like sockets, not perforating the dental plate. Ventral tooth cluster. Spine articulation asymmetrical with large, swollen dorsal lobe and small, indistinct ventral lobe. No sigmoidal fold. Lateral arm plates without ornamentation.

Remarks

New molecular data indicates that the genera *Ophiobyrsa*, *Ophiophrixus* and *Ophiosmilax* form a clade that is sister to all remaining ophiacanthid families. Consequently, the former subfamily Ophiobyrsinae Matsumoto, 1915 is raised to family-level rank.

Family **Ophiocamacidae** fam. nov.

urn:lsid:zoobank.org:act:30C91042-C4FE-4373-9C62-B0D906F16541

Type genus

Ophiocamax Lyman, 1878a (type species: *O. vitrea* Lyman, 1878a).

Diagnosis

Dorsal disc with spines with multipointed crowns. Ventral cluster of spiniform teeth, dental plate entire, sockets small, not penetrating. Numerous spiniform oral papillae clustered at lateral jaw edges. Vertebral articulation hourglass-shaped. Arm spines thin, round in cross section, with lateral thorns. Pointed thorn-like tubercles on dorsal, ventral and lateral arm plates. Proximal tentacle pores with multiple elongated erect scales, forming a sheath through which the foot emerges, distally a single thorny scale, penetrated by foot (*O. vitrea*). Arm spine articulations conspicuously large muscle opening encompassed by rather thin dorsal and ventral lobes forming an irregular circle. Row of spine articulations on midline of raised distal portion of lateral arm plate. Second or third dorsalmost spine articulation often much larger than others.

Family **Ophiotomidae** Paterson, 1985 stat. nov.

Ophiotretidae O'Hara *et al.*, 2017: 421, figs 1–2 (nomen nudum).

Type genus

Ophiotoma Lyman, 1883 (type species: *O. coriacea* Lyman, 1883).

Other genera

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

Diagnosis

Dorsal disc with granules or long, thorny spines. Abradial genital plate with concave adradio-distal tip. Arm spines flattened, laterally serrated. Dental plate fragmented (*Ophiotreta*, *Ophiocopa*) or entire (*Ophiocomina*, *Ophiotoma*), sockets shallow. Ventral clusters of short, papilliform teeth in *Ophiotreta* and *Ophiocomina*. Arm spine articulation lobes with small perforations or imperforate. Ridge on the inner side of the lateral arm plates with two kinks and a ventro-proximalwards pointing projection associated with the dorsal kink. This family was mistakenly named Ophiotretidae in O'Hara *et al.* (2017).

Remarks

The species *Ophiocomina australis* H.L. Clark, 1928 is a *Clarkcoma* species (Naughton *et al.* 2014; O'Hara *et al.* 2017), which leaves *Ophiocomina* monotypic. *Ophiotoma* is polyphyletic (O'Hara *et al.* 2017).

Family **Ophiopteridae** fam. nov.

urn:lsid:zoobank.org:act:28D7ECF8-2D03-4F4B-874B-8D998E39561D

Type genus

Ophiopteris E.A. Smith, 1877 (type species: *O. antipodum* E.A. Smith, 1877).

Diagnosis

Dorsal disc with dense cover of low granules, obscuring scales and plates. Ventral disc with short spines. Several small, conical lateral oral papillae. Long, smooth, cylindrical, erect arm spines, the two dorsalmost small, scale-like. Several columns of small papilliform teeth all over dental plate, no regular teeth. Dental plate entire. Tooth sockets on dental plate without foramina and teeth without glassy tips (Devaney 1970). Arm spine articulation lobes merged, with proximal and dorsal swellings, nerve and muscle openings widely separated.

Family **Clarkcomidae** fam. nov.

urn:lsid:zoobank.org:act:3A1F5F7F-3A02-406F-8D81-D6CF66472181

Type genus

Clarkcoma Devaney, 1970 (type species: *C. canaliculata* (Lütken, 1869)).

Diagnosis (Devaney 1970)

Dorsal disc with low rounded granules, obscuring scales and plates. Blunt, thin, compressed, minutely serrated arm spines. Dental plate entire. Cluster of papilliform teeth on ventral half, regular teeth on

dorsal half. Teeth with glassy tips. Tooth sockets on dental plate with thickened lobes, dorsal ones as penetrating, large foramina.

Family **Ophiacanthidae** Ljungman, 1867

Synonyms

Ophiochondrinae Verrill, 1885: 355.

Ophioplinthacinae Paterson, 1985: 61.

Ophiocanopidae Mortensen, 1932: 8.

Type genus

Ophiacantha Müller & Troschel, 1842 (type species: *O. bidentata* (Bruzelius, 1805)).

Other genera

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

Diagnosis

Dorsal disc fully scaled, with thorny spines or granules, or with thickened skin. No tooth clusters. Dental plate entire with single column of wide sockets with low dorsal and ventral border, not penetrating. Arm spine articulations bordered by raised, dorsoventrally striated ridge. Ventral portion of lateral arm plates (the portion below the row of spine articulations) small and not protruding ventro-proximalwards. Ridge on inner side of lateral arm plates with two kinks and a dorsal tip with a ventro-proximalwards pointing projection.

Remarks

The genera *Ophiacantha*, *Ophiomitrella* and *Ophiolebes* are polyphyletic and require revision.

Suborder **Ophiodermatina** Ljungman, 1867

Diagnosis

Abradial edge of radial shield excavated. Abradial genital plate with a longitudinal groove and a large perforation. Arm spines commonly with minute scale-like tubercles. Dorsal arm plates with spur on the proximal edge.

Superfamily **Ophiodermatoidea** Ljungman, 1867

Diagnosis

Arm spine articulations inserted in distal edge of lateral plate. Ventral arm plates commonly with spur on proximal edge.

Family **Ophiodermatidae** Ljungman, 1867

Type genus

Ophioderma Müller & Troschel, 1840 (type species: *O. longicauda* (Bruzelius, 1805)).

Other genera

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

Diagnosis

Dorsal disc covered with granules. Dental plate fragmented, with finely meshed stereom, tooth sockets as broadly oval, not penetrating depressions with swollen borders, small tooth cluster on ventral end. Lateral arm plate with two proximal spurs, visible on external and internal surface. Arm spine articulation with weak sigmoidal fold, sunken in notches of distal plate edge.

Remarks

Ophiarachnella is polyphyletic and requires revision. The type species *O. gorgonia* Müller & Troschel, 1842, however, is a confirmed ophiidermatid (O'Hara *et al.* 2017).

Family **Ophiopezidae** fam. nov.

urn:lsid:zoobank.org:act:5CB2AA19-60FA-4483-A659-998AF13B3E55

Type genus

Ophiopeza Peters, 1851 (type species: *O. fallax* Peters, 1851).

Other genera

Ophiochaeta Lütken, 1869.

Diagnosis

Dorsal disc covered with granules (*Ophiopeza*) or needle-like spines (*Ophiochaeta*). Dental plate entire, with coarsely porous stereom, tooth sockets as small, not penetrating holes with indistinct borders, on the ventral end a pair of sockets. Arm spine articulation with swollen dorsal lobe and thin ventral lobe, well defined sigmoidal fold. Lateral arm plates with conspicuous ornamentation (tubercles of variable size in *Ophiopeza*).

Family **Ophiomyxidae** Ljungman, 1867

Synonym

Ophiarachninae Matsumoto, 1915: 83.

Type genus

Ophiomyxa Müller & Troschel, 1842 (type species: *O. pentagona* (Lamarck, 1816)).

Other genera

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

Diagnosis

Dorsal disc covered with granules or naked thickened skin, scales reduced in *Ophiomyxa*. Dental plate fragmented, sockets with flat borders, not penetrating. *Ophiarachna* with small ventral tooth cluster.

Hyaline, large, flat, serrated teeth in *Ophiomyxa* and *Ophioconis*. Lateral arm plates reminiscent of an upside-down Y-shape. Arm spine articulation without sigmoidal fold. Arm spine articulations generally larger than in Ophiidermatidae and Ophiopezidae fam. nov. and in shallower notches or on same level as plate stereom (*Ophiomyxa*), of rounded shape with smooth stereom.

Remarks

Ophiomyxa has a specialized morphology with many reductions of the skeleton and is thus not typical for this family but the name has priority. Ophiocanopidae Mortensen, 1932 was synonymized with Ophiomyxidae by Stöhr *et al.* (2008) but *Ophiocanops* is now a member of Ophiacanthidae.

Superfamily **Ophiocomoidea** Ljungman, 1867

Diagnosis

As for Ophiocomidae Ljungman, 1867 (see below).

Family **Ophiocomidae** Ljungman, 1867

Type genus

Ophiocoma L. Agassiz, 1836 (type species: *O. echinata* (Lamarck, 1816)).

Other genera

Breviturma Stöhr *et al.* 2013 stat. nov., *Ophiarthrum* Peters, 1851, *Ophiocomella* A.H. Clark, 1939, *Ophiomastix* Müller & Troschel, 1842.

Diagnosis

Dorsal disc with granules, smooth spines or naked thickened skin. Oral plate with large abradial flange with horizontal grooves. Dental plate entire, dorsalmost sockets as large penetrating holes, with vertical septum, large cluster of teeth ventrally. Teeth with hyaline tip. Spine articulations very large, with dorsalward increase in size, freestanding on raised distal portion of lateral arm plates. Lateral arm plates with very small proximal spurs if any. Inner side of lateral arm plates with single, large perforation (putatively for bundled arm spine nerves).

Remarks

We raise *Breviturma* from subgeneric to generic level. *Ophiocoma* is polyphyletic and requires revision.

Ophiacanthida incertae sedis

Microphiura Mortensen, 1910, *Ophioblenna* Lütken, 1859, *Ophiobranchion* Lyman, 1883, *Ophiacanthella* Verrill, 1899a, *Ophiochondrella* Verrill, 1899b, *Ophioclastus* Murakami, 1943, *Ophiodaces* Koehler, 1922b, *Ophiodelos* Koehler, 1930, *Ophiodictys* Koehler, 1922a, *Ophiodyscrita* H.L. Clark, 1938, *Ophiogema* Koehler, 1922a, *Ophiolamina* Stöhr & Segonzac, 2006, *Ophiomedeia* Koehler, 1906, *Ophiomora* Koehler, 1907, *Ophioncus* Ives, 1889, *Ophiopaepale* Ljungman, 1872, *Ophioparva* Guille, 1982, *Ophiosciasma* Lyman, 1878a, *Ophiostyracium* H.L. Clark, 1911, *Pectinura* Forbes, 1843, *Ophiambix* Lyman, 1880. (Some of the above genera were previously placed in Ophiomyxidae. They may belong in Ophioscolecidae instead but more data are needed.)

O'HARA T. *et al.*, New classification of Ophiuroidea

Order **Ophiroleucida** O'Hara *et al.*, 2017

Diagnosis

Dorsal disc with granules. Radial shields with distal adradial portion exposed. Abradial genital plate with concave adradio-distal tip. Dorsal arm plates rectangular to trapezoid with straight edges. Arm spine articulations irregularly rhombic, framing large, dorsoventrally elongated muscle opening, small nerve opening ventral to articulation. Lateral arm plates fragile. Arm spine articulations commonly separated from distal plate edge by a ledge. Vento-distal edge of lateral arm plates protruding ventralwards.

Family **Ophiernidae** fam. nov.

urn:lsid:zoobank.org:act:4FF0D5F3-DF26-4CA0-A6FD-F4C6B6696C1A

Type genus

Ophiernus Lyman, 1878a (type species: *O. vallincola* Lyman, 1878a).

Diagnosis

Lateral arm plates without vertical striations, but with horizontally striated proximal band (under adjacent plate). Bristle-shaped accessory arm spines. Narrow, broad, imperforate tooth sockets with flat borders. Vertebrae with radiating rib-like structures on distal muscle flanges. Lateral arm plates with several rib-like spurs on external proximal/internal distal band (where adjacent plates overlap). Arm spine articulations with weak lobes.

Family **Ophiroleucidae** Matsumoto, 1915 (restricted)

Type genus

Ophiroleuce Koehler, 1904 (type species: *O. seminudum* Koehler, 1904).

Other genera

Ophiopallas Koehler, 1904, *Ophiopyren* Lyman, 1878a, *Ophiostriatus* Madsen, 1983.

Diagnosis

Tooth sockets as round holes with indistinct borders. Vertebrae with smooth distal muscle flanges. No accessory arm spines. Lateral arm plates with vertical striations, single spur on dorsal part of external proximal/internal distal edge (where adjacent plates overlap). Arm spine articulations with swollen lobes.

Order **Amphilepidida** O'Hara *et al.*, 2017

Diagnosis

Ventral end of dental plate laterally tapered. Infradental papillae. Abradial genital plate with concave adradio-distal tip. Dorsal and ventral lobes of arm spine articulations parallel (except in Ophiotrichidae).

Suborder Ophionereidina O'Hara *et al.*, 2017

Superfamily **Ophiolepidioidea** Ljungman, 1867

Diagnosis

Disc with stout plates, few or no stout scales, neither granules nor spines. Primary plates usually distinct. Spine articulations small and generally sunken in notches of distal plate edge.

Family **Ophiolepididae** Ljungman, 1867 (restricted)

Type genus

Ophiolepis Müller & Troschel, 1840 (type species: *O. superba* H.L. Clark, 1915).

Other genera

Ophioteichus H.L. Clark, 1938, *Ophiotypa* Koehler, 1897.

Diagnosis

Accessory dorsal and ventral arm plates. Tooth sockets large, round to oval, with low, indistinct borders, deep but not penetrating. Lateral arm plates with single spur on ventral third of proximal half. Arm spine articulation with muscle and nerve openings of similar size. Finely porous stereom in all arm plates.

Family **Hemieuryalidae** Verrill, 1899

Type genus

Hemieuryale von Martens, 1867 (type species: *H. pustulata* von Martens, 1867).

Other genera

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

Diagnosis

Dorsal disc with scales and plates or thickened skin, neither granules nor spines, but in some genera with tubercles. Strongly tuberculous stereom in all arm plates. No accessory arm plates. Arm spine articulation with single small opening (e.g., *Hemieuryale*) or separate muscle and nerve openings (e.g., *Ophiozonella*, *Ophioplocus*); articulations placed at an angle to each other. Tooth sockets shallow with indistinct borders in *Hemieuryale* but in *Ophiozonella* only ventral sockets like this, dorsal ones as large fenestrations with septum.

Remarks

Heteromorphic assemblage of genera with numerous reductions and specializations. The arm spine articulation with only two parallel ridges may be such a reduction, as the type species of *Ophiozonella* (*O. longispina* (H.L. Clark, 1908)) has the dorsal and ventral lobes proximally separated by a strong, irregularly denticulate ridge (or vertical series of merged knobs).

Superfamily **Ophionereidoidea** Ljungman, 1867

Diagnosis

Disc with numerous thin scales and few plates, partially covered by scales, indistinct primary plates, no granules or spines. Large spine articulations not sunken in depressions of distal plate edge. Lateral arm plates with a band of more finely meshed stereom only in the central part of the outer proximal edge.

Family **Amphilimnidae** fam. nov.

urn:lsid:zoobank.org:act:304D30DE-9638-47B8-9AD4-CD1DB5AEDFD4

Type genus

Amphilimna Verrill, 1899a (type species: *A. olivacea* (Lyman, 1869)).

Diagnosis

Dorsal disc fully scaled, with rod-like smooth spines. Arm spines inside disc modified, large, flat scale-like. Long, spiniform tentacle scales. Abradial genital plate twisted. Tooth sockets round with indistinct borders, not perforating. Arm spine articulations with two smooth, parallel ridges, in the proximal space between them a short ridge (absent in some species). Inner side of lateral arm plates with two merged knobs instead of a ridge. Ventral arm plate with spur on the proximal edge.

Family **Ophionereididae** Ljungman, 1867

Synonym

Ophiochitonidae Matsumoto, 1915: 88 (see Smith, Paterson & Lafay 1995).

Type genus

Ophionereis Lütken, 1859 (type species: *O. reticulata* (Say, 1825)).

Other genera

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

Diagnosis

Granules along the genital slit, extending onto disc edge. Accessory dorsal arm plates (*Ophionereis*). Scale-like, flat, oval to round tentacle scales. Tooth sockets dorsally as large fenestrations with septum. Arm spine articulation horse-shoe shaped, with parallel dorsal and ventral lobes proximally separated by vertical row of knobs or merged by ribbed border, framing nerve and muscle openings of almost equal size. Internal of lateral arm plate with large pore close to the dorsal edge of the tentacle pore excavation, at the ventral tip of a large ridge along the inner proximal edge that bends ventro-distalwards. Vertebrae with distally protruding dorsal keel and proximal dorsal groove.

Remarks

Most characters apply only to *Ophionereis* and are modified or reduced in the other genera. The unifying characters are the lateral arm plate characteristics and the arm spine articulation.

Suborder Ophiopsilina Matsumoto, 1915
Superfamily **Ophiopsiloidea** Matsumoto, 1915

Diagnosis

As for Ophiopsilidae stat. nov.

Family **Ophiopsilidae** Matsumoto, 1915 stat. nov. (raised to family rank)

Type genus

Ophiopsila Forbes, 1843 (type species: *O. aranea* Forbes, 1843).

Diagnosis

Dorsal disc fully scaled, neither spines nor granules. Extremely long, flat tentacle scales that cross on the mid-line of the ventral arm. Ventral tooth sockets shallow and indistinct, dorsally increasing in size and penetrating with septum. Oral plate (half-jaw) higher than long, with large dorsodistal muscle flange (similar to *Amphiuridae*). Arm spine articulations with two smooth, parallel, straight lobes, in the proximal space between them a short ridge (similar to *Amphilimna*). Inner side of lateral arm plates with two merged knobs instead of a ridge.

Remarks

The position of this family is variable in our molecular analyses with some trees supporting a sister relationship to the Ophionereidina and others to the Gnathophiurina (O'Hara *et al.* 2017). The morphological analysis supports a relationship within Gnathophiurina, close to *Amphiuridea* (Thuy & Stöhr 2016).

Suborder Gnathophiurina Matsumoto, 1915
Superfamily **Amphiuroidea** Ljungman, 1867

Diagnosis

Disc usually without spines, any occurring spines are not thorny. Arm spine articulations with parallel ridges.

Family **Amphiuridae** Ljungman, 1867

Type genus

Amphiura Forbes, 1843 (type species: *A. chiajei* Forbes, 1843).

Other genera

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

Diagnosis

Dorsal disc cover variable, often naked scales, but simple spines, granules or tubercles occur in some genera. Large infradental papillae. Buccal scale higher on the oral plate than other oral papillae. Dorsalmost tooth socket a large, heart-shaped fenestration with incomplete septum, other dorsal sockets as fenestrations with septum, ventral sockets shallow, not penetrating. Oral plates with large wing-shaped abradial muscle flange, often with branching ribs. Arm spine articulations with two smooth separated, parallel, straight dorsal and ventral lobes. Lateral arm plates commonly sickle-shaped with pointed dorsal tip. Lateral arm plates devoid of ornamentation except for band of more finely meshed stereom in the central part of the proximal edge. Inner side of lateral arm plates with two to three knobs instead of a ridge.

Remarks

This large family requires revision. Preliminary findings (O'Hara *et al.* 2017) indicate that there are at least three major clades within the group that fit our criteria for family status. Important genera, including *Amphiura*, *Amphioplus* and *Amphipholis*, are polyphyletic in their current composition.

Family **Amphilepididae** Matsumoto, 1915

Type genus

Amphilepis Ljungman, 1867 (type species: *A. norvegica* (Ljungman, 1865)).

Other genera

Ophiomonas Djakonov, 1952.

Diagnosis

Tooth sockets with small, slit-shaped, perforating holes with indistinct borders. Infradental papillae minute, single wide lateral oral papilla. Arm spine articulation with two smooth ridges, connected proximally by a depressed bridge.

Remarks

This is a paedomorphic family with reduced characters.

Superfamily **Ophiactoidea** Ljungman, 1867

Diagnosis

Disc usually with thorny spines. Spine articulations with parallel, bent dorsal and ventral lobes.

Family **Ophiothamnidae** fam. nov.

urn:lsid:zoobank.org:act:CD418837-0D1F-47AF-BF52-C7BC76C67EFC

Type genus

Ophiothamnus Lyman, 1869 (type species: *O. vicarius* Lyman, 1869).

Other genera

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

Diagnosis

Dorsal disc with pointed spines (*Ophiothamnus*), naked scales (*Histampica*), or thorny spines (*Ophioleila*). Radial shields large. Infradental papillae small, distal lateral papilla at adoral shield edge widened in *Ophiothamnus*. Arm spine articulations with two smooth, slightly diverging ridges, not connected. Muscle and nerve openings separated by smooth bridge.

Family **Ophiactidae** Matsumoto, 1915

Type genus

Ophiactis Lütken, 1856 (type species: *O. krebsii* Lütken, 1856 = *O. savignyi* (Müller & Troschel, 1842)).

Other genera

Hemipholis Lyman, 1865.

Diagnosis

Dorsal disc with scales and plates, often with conical spines. Large tricuspid teeth. Dorsalmost tooth socket large fenestration with incomplete septum, other dorsal sockets with complete septum, ventral sockets not penetrating depressions. Infradental papillae in lateral position at dental plate. Arm spine articulation with two separated lobes, dorsal one bent and much larger than ventral one, framing two holes for muscle and nerve, separated by thin bridge. Lateral arm plates commonly with outer surface tubercles. Inner side of lateral arm plates with separate knobs sometimes associated with ridge.

Remarks

Ophiactis forms two clades based on number of lateral oral papillae (two or one), which are paraphyletic with respect to each other on some molecular topologies (O'Hara *et al.* 2017).

Family **Ophiopholidae** fam. nov.

urn:lsid:zoobank.org:act:24F78A13-2640-4ACB-8D5F-EDCFFC7E3767

Type genus

Ophiopholis Müller & Troschel, 1842 (type species: *O. aculeata* (Linnaeus, 1767)).

Diagnosis

Dorsal disc with large plates, encircled by small scales that are extended into multi-thorned spines in young individuals. Arm spines smooth, distally hooks and spines. Small cluster of papilliform teeth ventrally, followed by large block-like teeth dorsalwards. Tooth sockets ventrally indistinct round depressions, on middle area of dental plate horizontal ribs and depressions, dorsally fenestrations with septum. Vertebrae with narrow dorsal keel protruding beyond length of vertebra, corresponding deep dorsal groove proximally. Arm spine articulation horizontal, with two strong lobes, dorsal one larger and bent, large muscle and nerve openings. Lateral arm plates with coarse tubercles. Inner side of lateral arm plates with two separate lobes and a dorsal ridge.

Family **Ophiotrichidae** Ljungman, 1867

Type genus

Ophiothrix Müller & Troschel, 1840 (type species: *O. rosula* (Forbes, 1839) = *O. fragilis* (Abildgaard in O.F. Müller, 1789)). Original type designation *O. rosula* by Lyman (1865). H.L. Clark (1915) synonymized *O. rosula* with *O. pentaphyllum* (Pennant, 1777) which may have caused later authors to accept the latter (older) name for the type species for some time but it was then replaced by *O. fragilis* for unknown reasons. Indeed, the name *O. pentaphyllum* has priority over the name *O. fragilis* and the proposal by A.M. Clark (1967) to suppress it appears never to have been decided. Prevailing usage cannot be applied because the name *O. pentaphyllum* was used as a valid species name after 1899 (ICZN article 23.9.1.1). However, to change the name of the well-known *O. fragilis* after a century of usage would not serve the purpose of nomenclatural stability. A ruling by the commission is needed.

Other genera

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

Diagnosis

Dorsal disc with thorny spines or granules, arm spines thorny. Ventral half of dental plate with numerous papilliform teeth, at the outer edge as column of larger papillae, in the centre as lower granules. Dorsal teeth block-shaped. On dental plate ventral half an outer column of small holes at each edge, indistinct small depressions in the centre, dorsal half with fenestrations with septum. Infradental papillae and lateral oral papillae absent. Arm spine articulation diagonal to almost vertical, with two thick lobes, connected by thin proximal bridge, diagonal. Outer surface of lateral arm plates generally without tubercles. Inner side of lateral arm plates with three knobs. Vertebrae with narrow dorsal keel protruding distalwards far beyond vertebra edge, matching large dorsal groove proximally.

Remarks

The Ophiotrichidae forms a large, but genetically and morphologically coherent, family-level taxon. Genetic data (O'Hara *et al.* 2017) indicates that *Ophiothrix* is polyphyletic and suggests that Hoggett (1991) was correct in transferring *Ophiothrix* species with wide dorsal arm plates into an expanded *Macrophiothrix*.

Amphilepidida incertae sedis

Amphicutis Pomory, Carpenter & Winter, 2011, *Ophienigma* Stöhr & Segonzac, 2005, *Ophiopus* Ljungman, 1867, *Ophiothyreus* Ljungman, 1872.

Discussion

The purpose of the proposed new classification is above all to facilitate human communication. It is based as much as possible on inferred phylogenetic relationships but hierarchic ranks will always remain artificial. The latest morphological phylogeny (Thuy & Stöhr 2016) identified the superorders Euryophiurida and Ophintegrida along with several of the orders and lower ranks but, due to the considerably smaller dataset and the high degree of paedomorphosis in some groups (e.g., Ophiurida), the resolution of the tree was lower. Therefore, molecular data (O'Hara *et al.* 2017) were instrumental in the recognition of the phylogenetic clades that are here proposed as taxonomic ranks. Once the clades were identified, it was possible to make sense of morphological characters. Structures that were previously regarded as variation within a group are now recognized as key characters for separate taxa. The large number of genera still without placement is caused by lack of data, both morphological and molecular. Many of these are rare and difficult to obtain. The few known specimens may not be available for the destructive techniques that were used to collect the data for this study. Advancements in non-destructive techniques such as 3D imaging by x-ray microcomputed tomography (Landschoff & Griffith 2015; Okanishi *et al.* 2017), x-ray microscopy and synchrotron imaging open up possibilities for future examinations that may close the present information gaps. The current knowledge on ophiuroid morphology is still quite limited but recent studies (Martynov 2010b; Thuy & Stöhr 2011, 2016) have shown that a wealth of new information can be collected with new approaches.

The new classification recognizes 33 families, a major increase from the hitherto accepted 19 families (Stöhr *et al.* 2017) (Fig. 1). It differs greatly from the latest, until now widely accepted, classification proposed by Smith *et al.* (1995), which had some drawbacks and limitations (Stöhr 2012). The new classification's greatest advantage is the strong support of a large molecular analysis (O'Hara *et al.* 2017) that suggests monophyly for the proposed taxa. On lower taxonomic level, more work is needed. The most heterogeneous families may turn out to contain monophyletic groups that may be placed on subfamily level. Several genera are suspected to be non-monophyletic in their current species composition and further analysis is needed. Identification tools, such as interactive keys, will be produced in the future.

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Appendix A

References to original descriptions of Ophiuroidea taxa, mentioned in the new classification

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