



Ophiuroid (Echinodermata) systematics—where do we come from, where do we stand and where should we go?*

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Abstract

Over 2,000 Recent species of brittle star are currently known. The most active period of species discovery was between 1850 and 1950, with an average rate of about 20 new species per year, but even today, an average of 7 species per year are described. The most prolific authors were R. Koehler, H.L. Clark, T. Lyman, T. Mortensen and C. Lütken. Early classifications divided the Ophiuroidea into Euryalida and Ophiurida. Matsumoto suggested in 1917 further subdivision, accepted by some authors, rejected by others. His classification is still the most comprehensive work available. A first modern cladistic analysis was presented in 1995 by Smith *et al.*, but despite its shortcomings, no further attempts at reconstructing the phylogeny of the whole class have been made. It is becoming increasingly clear that Ophiuroidea have undergone rapid evolution after the great extinction event at the Permian/Triassic boundary, complicating phylogenetic analysis both with morphological and molecular data. Palaeozoologists still debate which ophiuroid group(s) survived the extinction. It has been suggested that the modern families Ophiuridae and Ophiolepididae may be traced back to the Palaeozoic, but the traditional view puts Ophiacanthidae and Ophiomyxidae at the root of the tree, with Euryalida as ancient sister group to Ophiurida. Unusual species with aberrant traits abound, but are still poorly understood. New morphological approaches, such as the study of the internal skeleton (jaws, dental plates, lateral arm plates), ontogeny and the role of paedomorphosis, as well as the extensive use of SEM for microstructure examinations, attempt to improve our understanding of the diversity and evolution of brittle stars.

Key words: Echinodermata, Ophiuroidea, diversity, morphology, history of science

Introduction

The latest census counted 2,064 species of ophiuroid (Stöhr *et al.* 2012), a number that has since grown with the description of 13 new species, according to the World Ophiuroidea Database (Stöhr & O'Hara 2012). The number has probably decreased again though, because among known species some have been recognized as conspecific with others. Nevertheless, brittle stars form the largest class among extant echinoderms, rivalled only by the sea stars with about 1,900 species (Mah & Blake 2012). Compared to megataxa such as molluscs, crustaceans or polychaetes, they represent a small part of global animal diversity. It is therefore surprising that we still know relatively little about them. Many species are only known from the type material, *e.g.*, *Ophiolimna opercularis* Koehler, 1907 (Paterson 1985), or a few other specimens and have not been found again for a hundred or more years. In some cases this may be, because the species was described on a juvenile specimen without

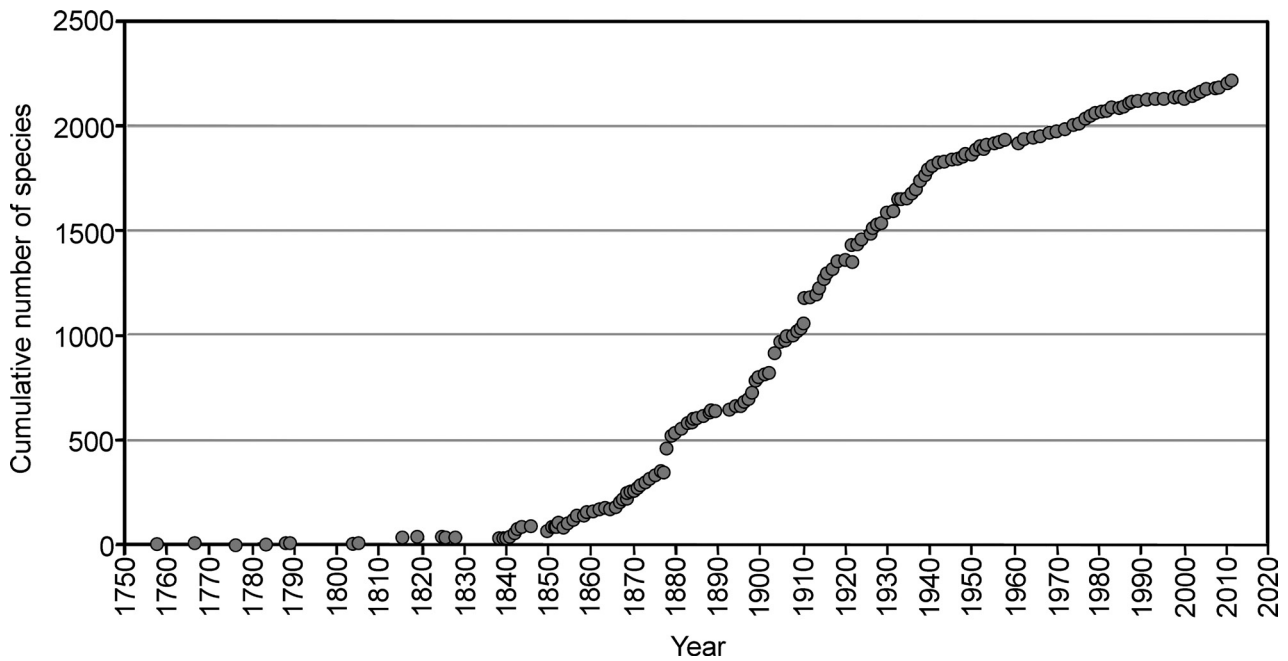


FIGURE 1. Discovery rate of Ophiuroidea species from 1758 till today (created by the World Ophiuroidea Database). Updated from Stöhr *et al.* (2012).

recognizing its true identity, as is probably the case with *Ophiacantha spinosella* Mortensen, 1933 (Paterson 1985).

Although early workers such as A.H. Clark, H.L. Clark, Mortensen and others thought in terms of evolution and phylogeny, few attempts at reconstructing the tree of Ophiuroidea have been made yet. Matsumoto (1915, 1917) proposed the most comprehensive classification of the whole class, but it was not universally accepted by his peers. It took almost 80 years to propose a new, modern phylogeny (Smith *et al.* 1995), which remains the only cladistic analysis of all Ophiuroidea, including both morphological and molecular data. The fossil record is inconclusive about the origin of Ophiuroidea, but it is assumed that some palaeozoic groups in the order Ophiurida survived the mass extinction at the Permian/Triassic boundary (Chen & McNamara 2006), while most modern groups are of later origin. Fast radiation has been postulated for the Ophiuroidea in the Triassic period (Smith *et al.* 1995; Chen & McNamara 2006), and recently it was claimed that this fast diversification has led to a lack of evolution of morphological and molecular synapomorphies, hampering the reconstruction of the Ophiuroidea phylogeny (Perseke *et al.* 2010). This review will summarize the current knowledge of ophiuroid morphology and point out problems, arguing that this perceived lack of apomorphies may instead be due to our lack of understanding of ophiuroid morphology and evolution.

A brief history of ophiuroid taxonomy

Our knowledge of brittle star diversity has increased from the two species, *Asterias ophiura* Linnaeus, 1758 and *Asterias caputmedusae* Linnaeus, 1758, included in the *Systema Naturae* (Linnaeus 1758) to currently 2,135 valid species and subspecies (Stöhr & O'Hara 2012). According to the World Ophiuroidea Database (Stöhr & O'Hara 2012) these are sorted in 16 families and 272 genera. The largest families are Amphiuridae (34 genera, 471 species), Ophiuridae (44 genera, 341 species) and Ophiacanthidae (35 genera, 325 species), and the largest genera are *Amphiura* Forbes, 1843 (203

TABLE 1. Numbers of species described by some ophiuroid workers, based on the World Ophiuroidea database (Stöhr & O'Hara 2012). Records sorted by species numbers, with Linnaeus at the top as the founder of modern nomenclature. Dates of publication refer to the first and last species name by each author. The total number of species is lower than the sum of these names, since some authors co-published with each other. Authors who have described fewer than 10 valid species have been left out.

Author (publ. dates)	Valid species	Total names
Carl von Linné (1758, 1767)	3	3
René Koehler (1895–1930)	456	600
Hubert Lyman Clark (1901–1946)	313	439
Theodore Lyman (1860–1883)	292	348
Theodor Mortensen (1897–1952)	130	204
Christian Frederik Lütken (1855–1859)	111	140
Axel Vilhelm Ljungman (1865–1872)	62	85
Austin Hobart Clark (1916–1964)	41	50
Addison Emery Verrill (1867–1899)	39	54
Hikoshichiro Matsumoto (1911–1941)	38	47
Mathilde Hertz (1926/27)	37	43
Ludwig Döderlein (1896–1930)	35	47
Alain Guille (1972–2001)	33	37
Johannes Müller (1840–1844)	29	48
Franz Herrmann Troschel (1840–1844)	29	48
Gustave Cherbonnier (1957–1978)	29	34
Sabine Stöhr (2001–)	29	29
Alan N. Baker (1974–2001)	28	35
Shiro Murakami (1937–1963)	27	33
Alexander Mikhailovitch Djakonov (1929–1954)	26	28
Donald G. McKnight (1967–2003)	23	25
Ailsa M. Clark (1952–1974)	22	26
Nina Litvinova (1971–2008)	22	27
Fred C. Ziesenhenné (1935–1951)	21	22
Yulin Liao (1978–2004)	20	21
Theophil Studer (1876–1885)	20	41
P. Martin Duncan (1878–1887)	19	29
Luiz Roberto Tommasi (1965–1976)	19	21
Gordon Hendler (1984–2005)	16	16
Jean Baptiste de Lamarck (1801, 1816)	14	20
Johann Brock (1888)	13	18
Eigil Nielsen (1932)	13	14
Jeffrey Bell (1884–1917)	13	25
Barracough Fell (1946–1961)	12	21
Timothy Damian O'Hara (2006–)	12	12
Perceval de Loriol (1893–1900)	10	30
Edward Forbes (1839–1854)	10	15
Jensenius Madsen (1947–1970)	10	12
Thomas Say (1825)	10	10
Dennis M. Devaney (1974, 1981)	10	10

species) and *Ophiacantha* Müller & Troschel, 1842 (129 species). After an initial slow increase, the most prolific time of species discovery took place in the hundred year period of 1850–1950, when on average about 20 species of brittle star were described per year (Fig. 1). In comparison, in the decade of 2000–2010 about seven species have been described each year. However, these numbers underestimate the scientific effort, because many species have been described more than once over the years and the total number of nominal species is about 3,000. The number of synonyms, including taxonomic revisions, amounts to about 4,000 species names.

The most productive ophiuroid researcher in terms of described species was René Koehler, with 600 nominal species, 456 of which are still valid today (Table 1). Hubert L. Clark and Theodore Lyman described about 300 still valid species each, Christian F. Lütken and Theodor Mortensen are responsible for over 100 valid species each. A large number of echinoderm workers described smaller numbers of ophiuroid species, work that is continued by a handful of specialists today. Interestingly, the number of species described by an individual researcher was less affected by the number of still unknown species than probably by opportunity (times of ocean exploration by famous expeditions known by the name of the research vessels such as the “Challenger” and the “Albatross”) and research interest. Many of these authors worked on a variety of taxa, Mortensen for example is well known for his echinoid work, Austin H. Clark for his crinoid studies, and R. Koehler worked on other echinoderms, isopods and molluscs. More than 50 additional authors have been left out of this compilation, although some of them have contributed greatly to ophiuroid taxonomy in other ways than by describing new species. Others have just begun their career and may in the future add to the known diversity of brittle stars.

Taxonomic practice and quality of work have developed and improved over the centuries, but varied greatly between researchers. Some early descriptions were limited to a few sentences that barely allow identification of the species in question. For example, the description of the common and well-studied *Ophiactis savignyi* (Müller & Troschel, 1842) omits the fact that the species is hexamerous, but refers to a drawing in Savigny’s accounts of his collections in Egypt, where the species was figured, but not described (Müller & Troschel 1842). Some species, such as *Amphipholis kinbergi* Ljungman, 1872 were first described solely by inclusion in a key or list (Ljungman 1872), and many lack illustrations. These short treatments have without doubt lead to misunderstandings and multiple descriptions of species, but the majority of the species descriptions from the late 19th century on are detailed and informative.

Typically, a description of a new species of ophiuroid has been (and still is) based on a more or less limited set of external, mostly skeletal, structures (Fig. 2), such as disc and arm plates and scales, disc and arm spines, oral frame plates and papillae; but attempts have been made to increase the number of taxonomically valuable characters. Here should be mentioned Lyman’s (1882) anatomical work on the internal skeleton, *e.g.*, vertebrae, oral, dental and genital plates, which was continued by Matsu-moto (1917) and formed the basis of his classification, by Murakami (1963) with a special treatment of the mouth skeleton, lately by Martynov (2010a; 2010b) who added a novel approach of studying the arm spine articulations, followed by in depth studies of lateral arm plates by Thuy & Stöhr (2011). Internal characters are still not standard components of all new species descriptions though, partially because type series are often small and do not allow the complete dissection of a specimen. Most species descriptions are based on adult specimens or rather what was believed to be adult, but studies of juvenile development began in the late 19th century with Ludwig’s work (1881, 1899), followed in recent years by some larger studies (Schoener 1967; Sumida *et al.* 1998; Stöhr 2005). Still, juvenile

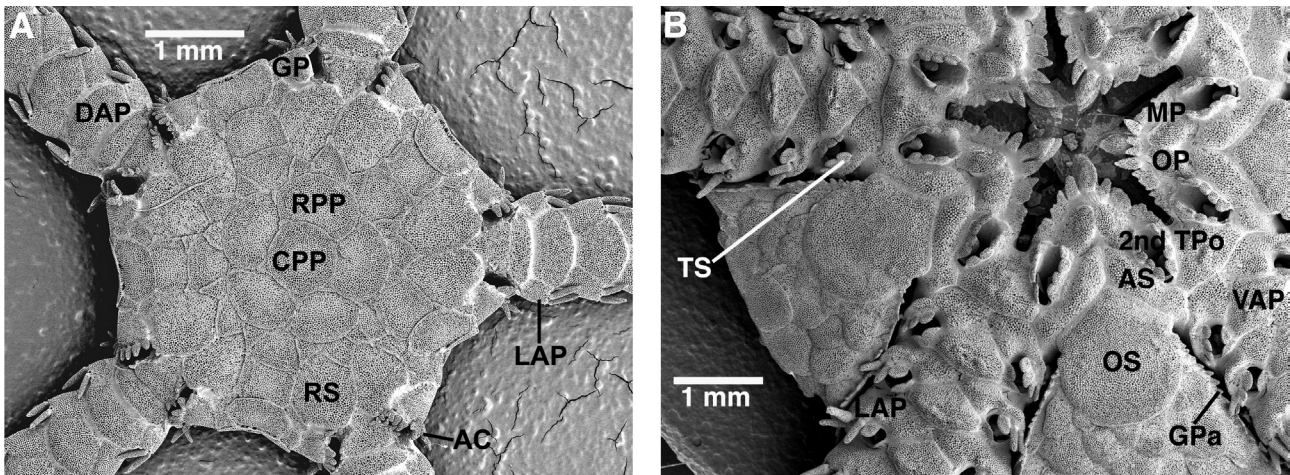


FIGURE 2. Brittle star external morphology and key characters demonstrated on *Ophiura albida*. A, dorsal/aboral aspect at 4 mm disc diameter, B, ventral/oral aspect at 9 mm disc diameter. AC—arm comb (present only in Ophiuridae), AS—adoral shield, CPP—central primary plate, DAP—dorsal arm plate, GP—genital plate, GPa—genital papillae, LAP—lateral arm plate, MP—mouth papillae, OP—oral plate (half-jaw), OS—oral shield, RPP—radial primary plate, RS—radial shield, TPo—tentacle pore, TS—tentacle scale, VAP—ventral arm plate.

forms are known for less than 50 species, although juvenile characters often differ considerably from adult ones and may potentially be valuable for phylogenetic considerations (Figure 3). This lack of understanding of ontogenetic changes has led to a number of erroneous species descriptions that were based on juveniles of already known species. A striking example of this is the description of the postlarva of *Asteronyx loveni* Müller & Troschel, 1842, as new species *Ophiuraster patersoni* Litvinova, 1998. The juvenile appearance of the animals was interpreted as paedomorphic (Litvinova 1998). This example also illustrates the necessity of keeping the old literature alive by active taxonomists, because Mortensen (1912) had described the postlarva of *A. loveni* in detail, but none of the researchers who examined and ultimately described these specimens some 80 years later knew about it (Stöhr 2005). Clearly, despite 250 years of effort, our understanding of ophiuroid morphology is still limited.

Making sense of ophiuroid morphology

Studies of postlarval development in ophiuroids have shown that growth changes to the shape, position and number of particular skeletal elements require great care in the differentiation of species, and related species should always be compared at similar size. Characters shown to be of limited or no taxonomic value if the growth stage of a particular animal is not known include, but are not limited to, the number of arm spines, oral papillae and tentacle scales, size and shape of disc spines, absence of structures such as tentacle scales, oral papillae, disc spines and granules, extent of disc scalation, as well as width:length proportions of a variety of skeletal elements (Sumida *et al.* 1998). For practical reasons, these characters are usually described in relation to disc diameter, as a good approximation of ontogenetic stage, but they are still subject to interpretation. These insights are important for character evaluations in phylogenetic reconstructions, but have so far had little impact. True juvenile characters may be confused with paedomorphic structures and ancient character states may be mistaken as paedomorphic. A paedomorphic nature and origin has been proposed for whole families, such as the Ophiuridae (Vadon 1988) as well as for certain species (Vadon 1991). A comprehensive study on the importance of heterochrony for ophi-

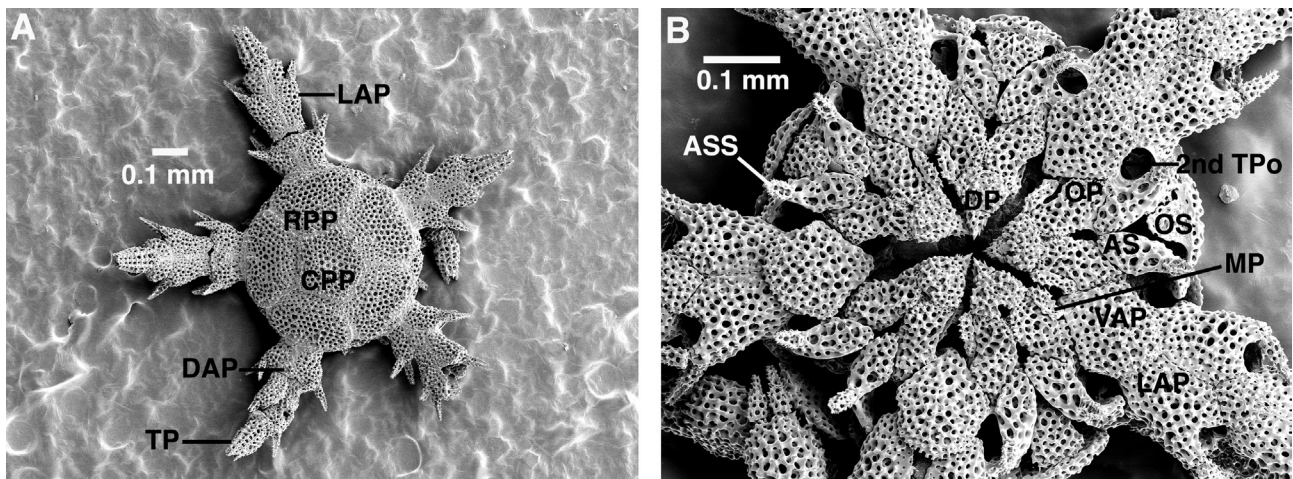


FIGURE 3. Postlarval morphology of brittle stars demonstrated on *Ophiura albida*. A, dorsal/aboral aspect, B, ventral/oral aspect. Abbreviations as in Figure 2, and ASS—adoral shield spine, DP—dental plate, TP—terminal plate.

uroid evolution is in preparation (Stöhr & Martynov, unpubl. results).

The external skeleton has been used to differentiate taxa on all taxonomic levels, but usually in a limited descriptive way and comparative studies of specific structures are rare. The diagnostic value of disc spines has been stressed for Ophiacanthidae (O'Hara & Stöhr 2006), but in most other groups the importance of the disc covering is unexplored, although many species have granules, spines or tubercles.

Among the structures that have been studied in greater detail are the ophiuroid arm ossicles or vertebrae (Fig. 4A–D), the genital plates and the dental and oral plates or jaws (Fig. 4E–J). Historically, the vertebrae have been classified into two main types, streptospondylous (Fig. 4D) and zygospondylous (Fig. 4A–C), which were used to divide the Ophiuroidea into two major groups, the Euryalida and the Ophiurida. Litvinova (1989, 1994) proposed five types of vertebral ossicles, based on the articulation surface, with ecological and functional considerations and a proposed evolutionary trajectory between the types. LeClair (1996) studied the vertebrae in 35 species from seven families and found two main types, keeled, with a proximal dorsal depression and a distally directed dorsal process (Fig. 4B, C), and non-keeled. The keeled form is universal in Ophiotrichidae and Ophionereididae, but occurs also in the family Ophiactidae in the genus *Ophiopholis* Müller & Troschel, 1842, although not in *Ophiactis* Lütken, 1856. This similarity may suggest a sister taxon relationship between Ophionereididae and Ophiotrichidae, and a closer relationship between Ophiotrichidae and *Ophiopholis* than between *Ophiopholis* and *Ophiactis*. Serially along the arm, the first few vertebrae are always of the non-keeled form; in Ophiotrichidae and Ophionereididae, the third vertebra distal from the jaw turns into the keeled form, in *Ophiopholis* it is the fifth (LeClair 1996). This difference is not understood yet, but may suggest an independent origin of the keeled type of vertebra in the different taxa. Martynov (2010a) interpreted the vertebrae of some ophiomyxids and ophiacanthids as keeled, although they lack the deep proximal depression and distally extending process found in the other taxa. All other studied taxa possess non-keeled vertebrae. Vertebral articulations (proximal and distal faces) vary within families and are most likely subject to ecological selection and functional adaptation. Epizoid taxa in various groups tend to have a vertebral articulation more similar to the euryalid streptospondylous type than to the zygospondylous type, e.g., *Ophiurothamnus clausa* (Lyman, 1878), in the family Ophiacanthidae (O'Hara & Stöhr 2006), likely because they promote vertical flexibility and curling of the arms. Thus, similar types of vertebrae may have evolved by convergence, but we do not understand yet how to identify these from true homologies.

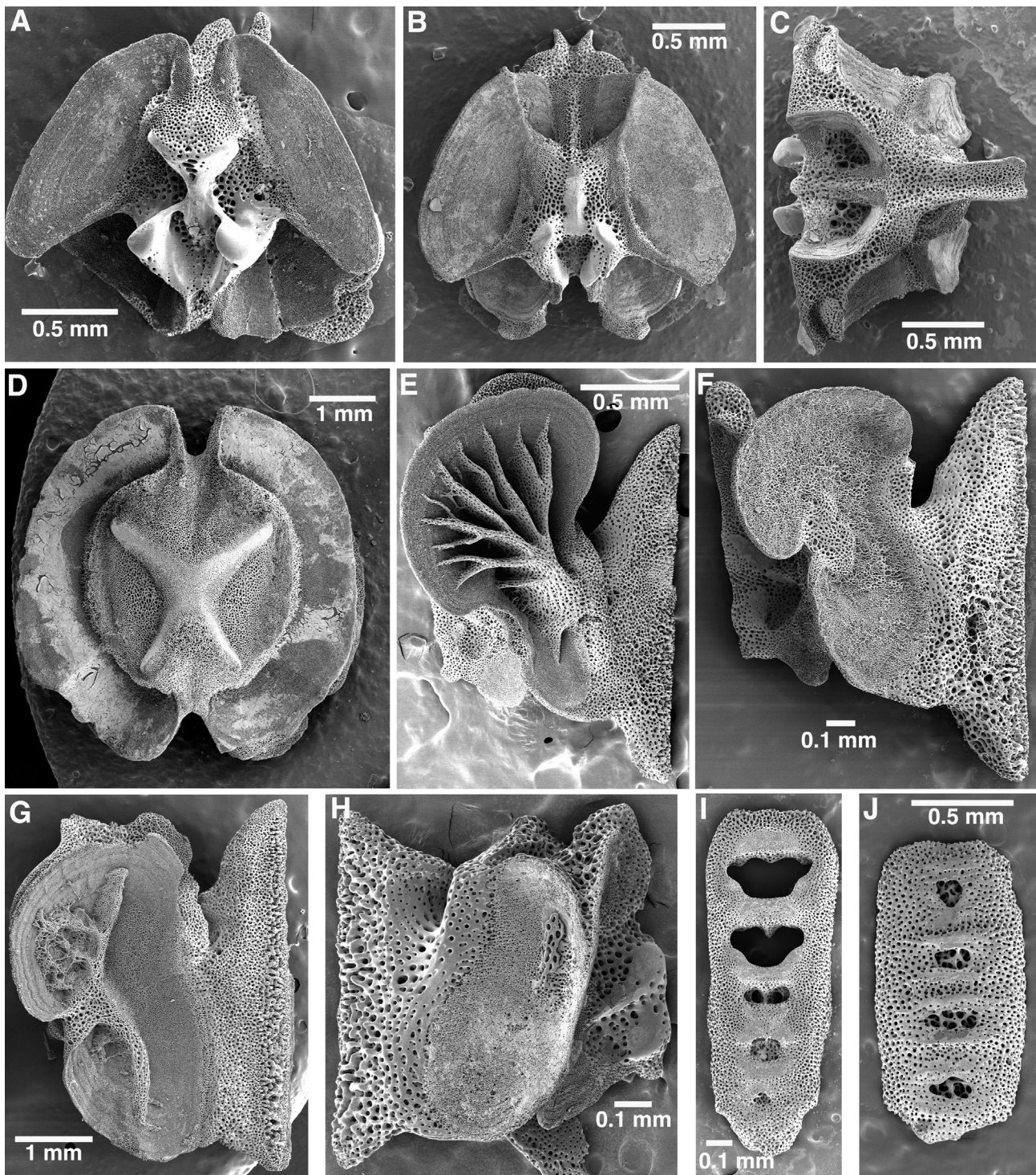


FIGURE 4. Comparison of some internal skeletal parts of brittle stars. A–D, arm vertebrae, E–H, oral plates (half-jaws), adradial aspect, I, J, dental plates, external view. All except C orientated with the dorsal end upwards. A, zygospondylous articulation, non-keeled type, proximal face (*Ophiacantha bidentata*); B, C, zygospondylous, keeled type (*Ophiothrix fragilis*), B, proximal face, C, dorsal aspect, D, streptospondylous articulation, proximal face (*Gorgonocephalus eucnemis*). E, *Acrocnida spatulispina*; F, *Amphiura filiformis*, Kattegat form; G, *Ophiothrix fragilis*; H, *Ophiactis abyssicola*. I, *Amphiura chiajei*, J, *Ophiacantha bidentata*.

Possibly the first detailed treatment of the ophiuroid mouth skeleton was presented by J. Müller (1854). Later, Lyman (1874) commented on the homologies of the ‘chewing apparatus’ in Ophiuroidea and also Ludwig (1879) described the mouth skeleton, but these pioneering works were limited to a few species. Murakami’s (1963) extensive study of the dental and oral plates (jaws) across the whole class

revealed a variety of types and his phylogenetic analysis confirmed the classification of Matsumoto (1917). His findings have not been tested yet and only occasionally have oral and dental plates been used to differentiate between closely related species (Devaney 1970; Benavides-Serrato & O'Hara 2008; Stöhr & Muths 2010) or to confirm the familial placement of a new species (Stöhr & Segonzac 2006). Martynov (2010a) explored the taxonomic value of dental plates, but barely discussed the oral plates. A recent study (Stöhr & Muths 2010) found two different types of oral plates in the genus *Amphiura*, which raised the question of the evolution and phylogenetic importance of these structures anew. The ear-shaped abradial muscle flanges found in some *Amphiura filiformis* (O.F. Müller, 1776) (Fig. 4F) seem to be similar to some *Ophiothrix* species (Murakami 1963), although not *O. fragilis* (Abildgaard, in O. F. Müller, 1789) (Fig. 4G), but Murakami's description of a branched indentation is similar to that in *Amphiura* spp. and it turns out that some of his text may be ambiguous. His study did not document the stereom structure, whereas the scanning electron microscopic (SEM) study by Stöhr & Muths (2010) showed a rough mesh-like stereom on the muscle flanges in *A. filiformis* (Fig. 4F) and a smooth, imperforate structure in *Amphiura chiajei* Forbes, 1843 and *Acrocnida* spp. (Fig. 4E). The branching structure found in *Amphiura chiajei* (the generic type) and *Acrocnida* spp. appears to be typical for Amphiuroidae, as it has been observed also in *Ophiophragmus acutispina* (Koehler, 1914), *Amphipholis nudipora* Koehler, 1914 and possibly in *Amphioplus aurensis* A.M. Clark, 1955, where it is reduced to a central patch (Stöhr & Alme, unpublished results), but as well in *Ophiothrix fragilis* and possibly much reduced in *Ophiactis abyssicola* (M. Sars, 1861) (Fig. 4H). There are also indications that the stereom structure and shape of the oral plate may vary with habitat or else *A. filiformis* may be a cryptic species complex (Stöhr, unpublished results). It is still largely unknown, which functional and ecological selection pressures act on the evolution of the oral plates and their appendages. Again, homologous structures have not yet been differentiated from homoplasious ones and we do not understand which of the contradicting characters are most important for phylogeny reconstruction.

Medeiros-Bergen (1996) showed that ophiuroid teeth are homoplasious structures, evolved by functional convergence. Since teeth are attached to dental plates, these should be analyzed in combination. A first attempt at understanding the functional aspects of the mouth parts was made by Boos (2012), but empirical evidence is still scarce.

Additional structures examined by early workers (Lyman 1874, 1882) and used by Matsumoto (1917) for his classification are the genital plates, two of which line each bursal slit, abradially and adradially. Both genital plates articulate with each other distally and with the underside of the radial shield. Variations in their shape and in the articulation have been described, most recently by Martynov (2010a), but again, the knowledge is limited and few morphological studies or species descriptions have included these details.

Recently, an extensive study of ophiuroid arm spine articulations proposed some taxonomic changes (Martynov 2010a), but other characters, such as jaws, vertebrae and dental plates may contradict the evidence provided by the spine articulations, requiring explanations. This is the case in *Amphilimna olivacea* (Lyman, 1869), which shows a jaw similar to Ophiacanthidae and spine articulations similar to *Ophiopsila* Forbes, 1843. These in turn are more similar to Amphiuroidae than Ophiocomidae, which has prompted Martynov (2010a) to place *Amphilimna* Verrill, 1899 in Amphiuroidae instead of Ophiacanthidae. The taxonomic placement of *Amphilimna* is however still open for debate and more data, as well as a phylogenetic analysis are necessary.

Another character potentially valuable for phylogenetic inferences is found in the calcareous spicules that have first been described from the ovarian and bursal wall (Mortensen 1924) and from

the stomach wall of *Ophiomyxa* Müller & Troschel, 1842 spp. (Mortensen 1933a). Irimura (1988) examined 70 species of ophiuroid and proposed five basic types of stomach ossicles with numerous sub-types, from rod, comma and double-anchor shapes to triradiate hooks, hook-less multi-rayed star shapes and various types of perforated scales. He showed that oral and aboral parts of the stomach wall may contain ossicles of different shape, and he suggested possible systematic implications. Stomach ossicles are absent in Ophiotrichidae, most Amphiuridae, and in *Ophiopholis* (except orally in *O. aculeata* Linnaeus, 1767), but present in *Ophiactis*. This finding further differentiates *Ophiopholis* from *Ophiactis* and may be evidence of closer affinities with Amphiuridae or Ophiotrichidae than with Ophiactidae.

Skeletal structures that have received little attention until recently include the lateral arm plates and the mouth papillae. The lateral arm plates present several potentially useful characters (Martynov 2010a; Thuy & Stöhr 2011) and their examination is important for the interpretation of fossil remains, many of which have been described as distinct species, based mainly on lateral arm plates, but originally without a comparative analysis of their specificity. Thuy & Stöhr (2011) showed that lateral arm plates indeed often show high specificity on species level, but they also pointed out some problematic taxa. Another ophiuroid specialization, the mouth papillae show a remarkable variation between species, but also stability that has led to them being used in many identification keys, on species, genus and family level (Mortensen 1927; Fell 1960; Paterson 1985). Apart from ontogenetic studies regarding their development and homologies (Hendler 1978; Sumida *et al.* 1998; Stöhr 2005), the mouth papillae have not been subjected to a comparative analysis. Their function and evolution are unknown (but see Boos 2012).

Soft parts such as tube feet, gonads and other tissues are largely unexplored with regard to their systematic potential. A general overview of ophiuroid anatomy, including soft tissues was presented by Byrne (1994).

So-called cryptic species are increasingly being proposed by molecular workers (Boissin *et al.* 2008). Strictly speaking, the term implies that no morphological differences exist between genetically isolated populations. However, at least in some cases, morphological differences are found when these putative species are examined in detail (Stöhr & Muths 2010). It is likely that a lack of understanding of intraspecific character variations causes species to go unrecognized for a long time. When indeed no phenotypic differences can be found, the genetic differences are difficult to understand, since selection acts on the phenotype. Species should thus not be described exclusively on molecular characters.

Phylogeny of Ophiuroidea

To date, the only attempt at reconstructing the phylogeny of Ophiuroidea with cladistic methods was carried out by Smith *et al.* (1995). Their analysis placed the Ophiocanopidae as sister taxon to all other extant taxa. This idea had been controversial for decades and was supported mainly by the incomplete (probably reduced) skeleton of the then only known extant species *Ophiocanops fugiens* Koehler, 1922. Recently, two additional species of *Ophiocanops* Koehler, 1922 with more complete skeleton and additional characters have been found and *Ophiocanops* has been transferred to the Ophiomyxidae, eliminating the family Ophiocanopidae completely (Stöhr *et al.* 2008).

The analysis of Smith *et al.* (1995) left the Ophiacanthidae unresolved as a paraphyletic taxon and the Hemieuryalidae as a taxon with changeable position. The old division in Euryalida and Ophiu-

rida was confirmed by Smith *et al.* (1995), although the bootstrap value supporting the Ophiurida as a monophyletic taxon is rather low, and reliable fossil evidence of Euryalida older than Miocene is lacking (Kroh 2003). Several of the branches within Ophiurida are based on bootstrap support lower than 50%, some are less than 10%. Smith *et al.* (1995) attributed the difficulties with obtaining a good resolution on their tree to long terminal branches and short internal branches, caused by rapid evolution in the early history (Triassic–Jurassic) of the extant Ophiuroidea, a hypothesis suggested also by the fossil record (Chen & McNamara 2006), but our limited understanding of ophiuroid characters may also be to blame.

The phylogeny proposed by Smith *et al.* (1995) was built on 43 morphological family and subfamily characters, which were collected mainly from published morphological descriptions. When a character is represented by several different states in different species of the same family they decided, which state should be typical for the family and be used in the data matrix, apparently favouring the most common state among documented species, sometimes the ‘most developed’ state, which is subjective if the direction of evolution is unknown. Only in ambiguous cases they explicitly scored the type genus (not necessarily the type species though). The notes in the appendix of Smith *et al.* (1995) do not allow an evaluation of all decisions made, since only family names or at best genus names are given. This highly subjective approach poses some problems: 1. published data may be incorrect, incomplete or misunderstood, 2. a family (or a genus) may not be monophyletic to begin with.

For instance, in the ophiacanthid subfamily Ophioplinthacinae, some genera have zygospondylous vertebrae, others streptospondylous ones. Smith *et al.* (1995) decided to score them as zygospondylous, but did not explain why. Species and genera of Ophiuroidea are still quite unstable as recent taxonomic works show, with every larger study turning up new species and revising the taxonomic status of known species (Stöhr & Segonzac 2005; O’Hara & Stöhr 2006; Martynov & Litvinova 2008; Martynov 2010a). To avoid this problem when analyzing higher taxa, the type taxon should be scored, in this case the genus *Ophioplinthaca* Verrill, 1899, which indeed has zygospondylous vertebrae (personal observation on *O. plicata* [Muséum National d’Histoire Naturelle, Paris specimen no. Ech Os 22634]), or better the type species [here *O. dipsacos* (Lyman, 1878)], to avoid the possibility of non-monophyletic genera. In this particular example, the subfamilies of Ophiacanthidae were proposed by Paterson (1985), but only recently (Martynov 2010a) critically revised and ultimately rejected. Their putative monophyly had thus not been proven in 1995 and it is generally advisable to choose the type taxa for any analysis. The type taxon is by definition the basis against which all other taxa have to be evaluated. According to this definition, the type taxon cannot be aberrant and if it differs in a character state from most other species included in the same higher taxon, this character is probably not a synapomorphy for the taxon in question or the taxon is not monophyletic.

Smith *et al.* (1995) assumed that *Ophiacantha bidentata* (Bruzellius, 1805) has streptospondylous vertebrae, referring to Matsumoto (1917), but there must have occurred some mistake in his work. In reality, *O. bidentata* has zygospondylous vertebrae (Figure 4A), which also illustrates the importance of primary data collection instead of re-using dated publications. Since *O. bidentata* is the generic, subfamilial (Ophiacanthinae) and familiar (Ophiacanthidae) type species, zygospondylous vertebrae are to be regarded as typical for all these higher taxa. However, since also some taxa with streptospondylous vertebrae are included in these higher taxa, a phylogenetic reconstruction of the family may be necessary before it can be included in an analysis of the class. On the other hand, as pointed out above, these types of vertebral articulation may be too plastic and poorly understood to be informative in a phylogeny reconstruction.

Gorgonocephalidae were scored by Smith *et al.* (1995) as not having arm spines, which is an error, since the lateral arm plates evidently have spine articulations (Martynov 2010b). Neither do all gorgonocephalids have non-retractable tube feet.

It appears that many of the extant ophiuroid families are poorly delimited, due to a rather large number of intermediate species that seem to possess a combination of characters from several families. Such overlaps exist between Ophiomyxidae (*e.g.*, *Ophiolycus* Mortensen, 1933) and Ophiacanthidae (some ‘Ophiotominae’); Ophiocomidae and Ophiacanthidae with the species *Ophiocomina nigra* (Abildgaard, in O.F. Müller, 1789), currently best supported as an ophiacanthid (Wilkie 1980; Medeiros-Bergen 1996); Amphiuroidae and Ophiacanthidae through the genus *Amphilimna* (Thomas 1967, 1975), which also bears similarities to *Ophiopsila* (Ophiocomidae, but possibly needs to be transferred); Ophiuridae (*Ophiomastus* Lyman, 1878) and Ophiolepididae (some species of *Ophiolonella* Matsumoto, 1915; Martynov & Stöhr, unpublished observations); and between Ophiuridae and Ophiacanthidae with *Ophiosparte* Koehler, 1922 (Martynov 2010a). Reconstructing a phylogeny based on assumed family characters is therefore problematic and as Smith *et al.* (1995) conclude, the higher ophiuroid taxonomy is in need of revision. Martynov (2010a; 2010 b) has proposed some taxonomic changes that may resolve some of these problems, but further critical evaluation with the addition of more characters is necessary.

Molecular evidence

Smith *et al.* (1995) included sequence data from the 28S ribosomal RNA of ten ophiuroid species from nine families in their phylogenetic analysis, based on Matsumoto’s (1917) four suborders. The result was a limited dataset with support for certain branches of the tree in congruence with the morphological data, but also weak support for other branches. Molecular techniques were still in their infancy in 1995, but surprisingly little progress has been made with regard to ophiuroid molecular phylogeny. A search in GenBank (on 5th Oct. 2012) turns up 2,873 nucleotide sequence records for Ophiuroidea, over 1,700 of these from the seven most frequently sequenced species. The barcode of life project currently lists 7,322 records of Ophiuroidea. Most of these are identified to species, which is an improvement compared to just two years ago. Compared to over 300,000 echinoid sequences, a taxon of less than 1,000 species, Ophiuroidea is still a neglected group. Apparently, ophiuroids present some difficulties for sequencing (Hoareau & Boissin 2010), but promising results for identifying possible cryptic species complexes have been obtained from COI sequence data (Muths *et al.* 2006; Ward *et al.* 2008). DNA analyses and particularly barcoding data are also useful for matching and identifying different life stages. The basis for any successful sequencing is of course a correctly identified specimen, for which skilled taxonomists with a good understanding of morphology are indispensable.

Recently, Perseke *et al.* (2010) presented a study of the complete mitochondrial genome of six species of ophiuroid from five families, four brittle stars and a basket star. They found five different gene orders and suggested that four of them can be derived from the mitochondrial gene order of *Ophiocomina nigra*. They further suggest that the gene order of *O. nigra* may be basal to all Ophiuroidea, which would require this species or rather its ancestors to be of pre-Triassic origin. There is however no fossil evidence yet in support of this hypothesis. Notably, no support was found for the historical division in Euryalida and Ophiurida, on the contrary, the former may be rooted in the latter. This hypothesis is supported by Hotchkiss & Glass (2012), who reinterpret vertebrae of Palaeozoic

Onychaster Meek & Worthen, 1868 as not of euryalid type, thus rejecting the idea that Euryalida trace back to Palaeozoic groups. Instead they may have developed from Ophiacanthidae, a family in which various types of vertebrae are present. The idea that streptospondylous vertebrae may have developed from zygospondylous ones was proposed already by Litvinova (1989), although she also erroneously placed *Ophiacantha bidentata* at the streptospondylous end of the trajectory. It cannot be excluded yet, that streptospondylous vertebrae have evolved more than once. Like Smith *et al.* (1995), Perseke *et al.* (2010) encountered difficulties with phylogeny reconstruction and attributed them to the fast speciation of the group after the Permian/Triassic mass extinction, which may cause long branch artefacts. However, their dataset was rather limited and may not allow such conclusions.

Suggestions for the future

Humans have tried to name and classify organisms probably for as long as they have existed, but documenting all the earth's biodiversity is a huge task. Morphology still plays an important role in achieving that goal, because many other biological disciplines need means of identifying their study subjects in the field, and understanding fossil remains requires a solid understanding of the morphology of extant forms. Initiatives such as DNA barcoding can only be successful if the organisms that are barcoded have been reliably identified by morphological means.

It is obvious from the published attempts at reconstructing ophiuroid phylogeny that the taxon must have undergone rapid evolution in its early history, apparently more rapidly than the other echinoderm classes. Understanding the relationships among the extant (and fossil) taxa is made more difficult by the great diversity of character states and seemingly contradicting combinations of states, but there is no lack of apomorphies, although we need to better understand which ones provide phylogenetic information. Progress has also been hampered by a lack of taxonomic specialists. Further research should concentrate on documenting ophiuroid morphology using modern methods such as SEM, perhaps also TEM (transmission electron microscopy) for tissue microstructures, because the available documentation in the literature needs to be verified and partially corrected. X-ray-microtomography has shown promising results in the examination of internal structures in fossils, but it does not reach the level of detail that can be achieved with SEM. Data from all available disciplines (morphology, molecular biology, paleontology, ecology, ethology *etc.*) should be combined to increase our understanding of the diversity of brittle stars and their interrelationships.

The understanding of ophiuroid morphology, as of morphology in general, is somewhat hampered by the historical lack of standardization of the used terminology. Through the centuries, different terms have been used for the same structures and even today, different authors may use different terms or the same author may use different terms in different publications. This causes confusion and creates discouraging difficulties for beginners. It may also limit our way of thinking, when terminology implies assumed function, as with terms such as jaw, which leads the thought to specialized structures for feeding and thereby somewhat obscures their homology with ambulacrals. In addition, specialists of echinoderms use a different terminology for each class, further creating obstacles for the understanding of related structures. Creating a defined and controlled formal vocabulary or ontology based solely on morphological observation without functional or developmental definitions would facilitate communication and the use of databases for handling morphological data in a more objective way, which is not a trivial task. A good theoretical overview of the subject has been given by Vogt

(2008). Stöhr *et al.* (2012) offered an illustrated list of preferred terms that may be used as a starting point for the development of a standardized terminology.

Last, but not least, we should also embrace the tools provided by the growing field of cyber taxonomy. Taxonomic databases, such as the World Register of Marine Species, image repositories, such as Morphbank, online libraries, such as the Biodiversity Heritage Library, and DNA databases, such as GenBank and Barcode of Life, for the first time offer easy access to a wealth of data and the possibility of creating a detailed picture of each organism so that we may better understand them.

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