Marine Biology Research, 2008; 4: 76–111

ORIGINAL ARTICLE

Deep-water Ophiuroidea of the northern Atlantic with descriptions of three new species and taxonomic remarks on certain genera and species

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Abstract

Based on material from the fourth cruise of the RV *Akademik Mstislav Keldysh* and the MAR-ECO cruise of the RV *G.O. Sars*, 31 species of Ophiuroidea were identified from the section of the Mid-Atlantic Ridge between the Reykjanes Ridge and the Azores. The taxonomy of the group of genera with reduced arm comb and tentacle pores restricted only to the proximal arm segments is reviewed. It is suggested that the genera *Homalophiura* H.L. Clark, 1915, *Ophiurolepis* Matsumoto, 1915, *Theodoria* Fell, 1961 and *Homophiura* Paterson, 1985 should be regarded as synonyms of the genus *Ophioplinthus* Lyman, 1878. From examination of the type specimens, it is demonstrated that the six-armed species *Ophiacantha anomala* G.O. Sars, 1871 also includes five-armed specimens previously identified as the separate species *Ophiacantha cuspidata* Lyman, 1878. The latter taxon is considered here as the junior synonym of *O. anomala*. Previously mentioned 'deep-water populations of the common shallow water species *Ophiacantha bidentata* (Retzius, 1805)' represent a separate species, *Ophiacantha fraterna* Verrill, 1885, which is well distinguished by the shape of the spicules of the disk, narrow outer oral papilla and narrower tentacle scale as well as a hermaphroditic nature. Three new species, i.e. *Ophioplinthus pseudotessellata* sp. nov., *Ophiocamax patersoni* sp. nov. and *Ophiophyllum nesisi* sp. nov., are described.

Key words: *Distribution, North Atlantic, Ophiuroidea, Reykjanes Ridge, taxonomy*

Introduction

The North Atlantic deep-water Ophiuroidea have a long history of study. The first deep-water ophiuroid from the North Atlantic was found during sounding of Baffin Bay at a depth of 1460 m in the early 19th century. This species was *Gorgonocephalus eucnemis* (Müller et Troschel, 1842) brought up wound around the plummet (Menzies et al. 1973). Regular collecting of ophiuroids took place during the famous deep-water expeditions, such as *Porcupine* and *Lightning* (Wyville Thomson 1873), Norwegian expeditions (Sars 1871), *Challenger* (Lyman 1878, 1882), *Travailleur* and *Talisman* (Koehler 1906, 1907a), *Albatross* (Verrill 1885a,b, 1894), *Caudan* (Koehler 1895, 1896a), *Princesse Alice* (Koehler 1896b, 1901a, 1909), *L'Hirondelle* (Koehler 1898), *Michael Sars* (Grieg 1921), *Tjalfe*, *Thor*, *Dana*, *Ingolf* (Mortensen 1913, 1933) and others. More recently, ophiuroids of the North Atlantic have been studied by Cherbonnier & Sibuet (1972); cruises of the RV *Jean Charcot*), Gage et al. (1983); mainly RRS *Challenger*), Paterson (1985); campaign BIOGAS), and Bartsch (1987, 1991) (RV *Meteor*). Paterson (1985) summarized scattered data and reviewed all North Atlantic Ophiuroidea. Most recently, a new amphiurid species was described from deep waters around Iceland (Stöhr 2003). Stöhr & Segonzac (2005) described several new species from hydrothermal vents and methane cold seeps of the North Atlantic, including also records from non-vent habitats. Tyler et al. (2005) presented results of a study of Ophiuroidea around the Faeroe Islands, including both shallow- and deep-water species. Preliminary results of the study of the ophiuroid fauna from waters around Iceland were presented by Stöhr (oral communication).

Despite numerous studies, taxonomic problems still remain, even with common species. Species

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Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

(Accepted 3 November 2007; Printed 18 February 2008)

ISSN 1745-1000 print/ISSN 1745-1019 online
DOI: 10.1080/17451000701840066

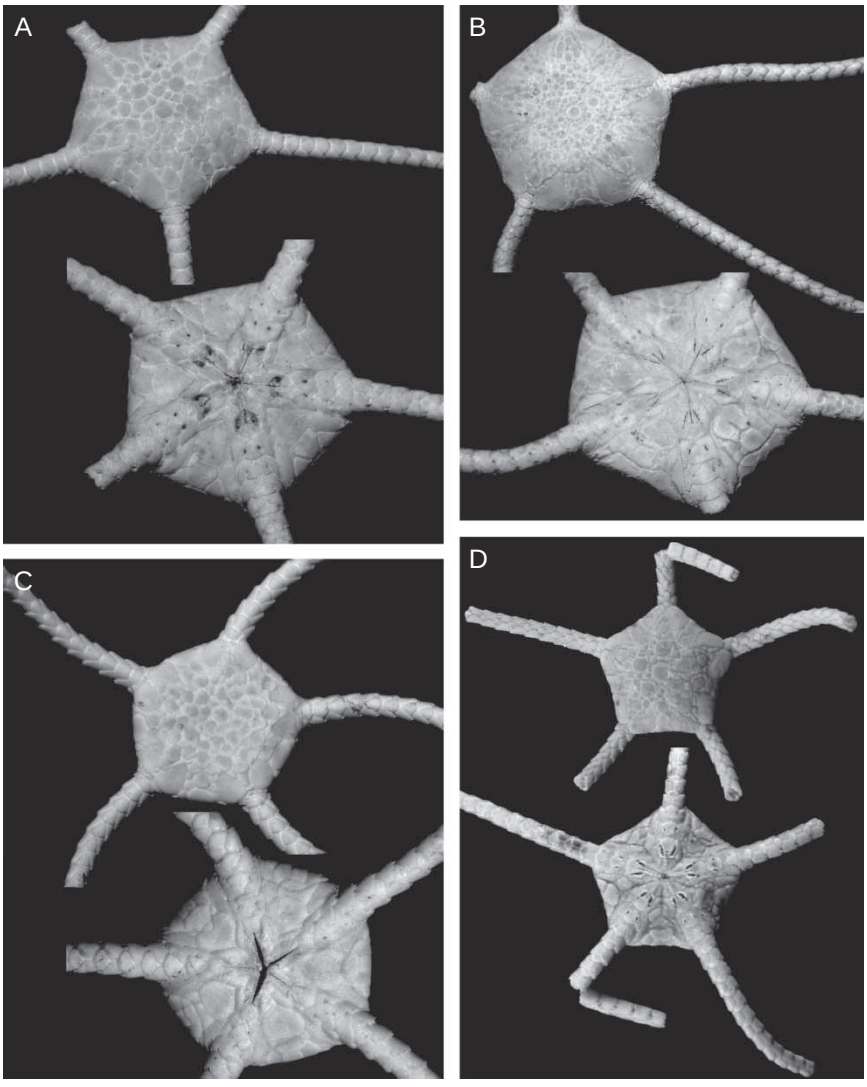

Figure 4. (A) *Ophioplinthus tessellata* (Verrill, 1894), MAR-ECO, St. 53/375, disk diameter 17 mm; (B) *Ophioplinthus pseudotessellata* sp. nov., holotype ZMBN 77852, MAR-ECO, St. 40/367, disk diameter 17.5 mm; (C) *Ophioplinthus tessellata* (Verrill, 1894), MAR-ECO, St. 53/375, disk diameter 10 mm; (D) *Ophioplinthus pseudotessellata* sp. nov., paratype ZMBN 77853, MAR-ECO, St. 40/367, disk diameter 7 mm. Dorsal and ventral views are shown. Photographs: Alexander Martynov (A–C); Konstantin Tabachnik (D).

Distribution

North Atlantic: off New England to Labrador Basin, southern Iceland to Azores, at 433–4706 m (Paterson 1985). Present study: the Charlie-Gibbs Fracture Zone, the Mid-Atlantic Ridge south of the Charlie-Gibbs Fracture Zone and north of the Azores at 981–3527 m. It is interesting to note that despite numerous samples on the Reykjanes Ridge during the fourth cruise of *Akademik Mstislav Keldysh* this species was not found.

Remarks

Ophiurids with strongly reduced arm comb and tentacle pores restricted only to the few proximal segments have a long and tangled taxonomic history. Lyman (1878, 1882) erected the genus *Ophioplinthus* for two species with the above-mentioned characters. However, Lyman considered other species with similar characters (e.g. *Ophioglypha inornata* Lyman, 1878, *O. abyssorum* Lyman, 1883) to be within his large genus *Ophioglypha* (now a synonym of the genus *Ophiura*). Several *Ophioplinthus*-like species were described by Studer (1876) and Koehler (1901b, 1908, 1911) also within the genus *Ophioglypha*. In 1915, Matsumoto and H.L. Clark created two genera, *Ophiurolepis* and *Homalophiura*, almost simultaneously. The type species of these genera are different, but both have reduced arm combs and tentacle pores restricted to proximal arm segments. Clark (1915) listed a number of species previously assigned to the genus *Ophiura* (or *Ophioglypha*) under the generic name *Homalophiura*. Hertz (1927a,b) for the first time suggested that all three

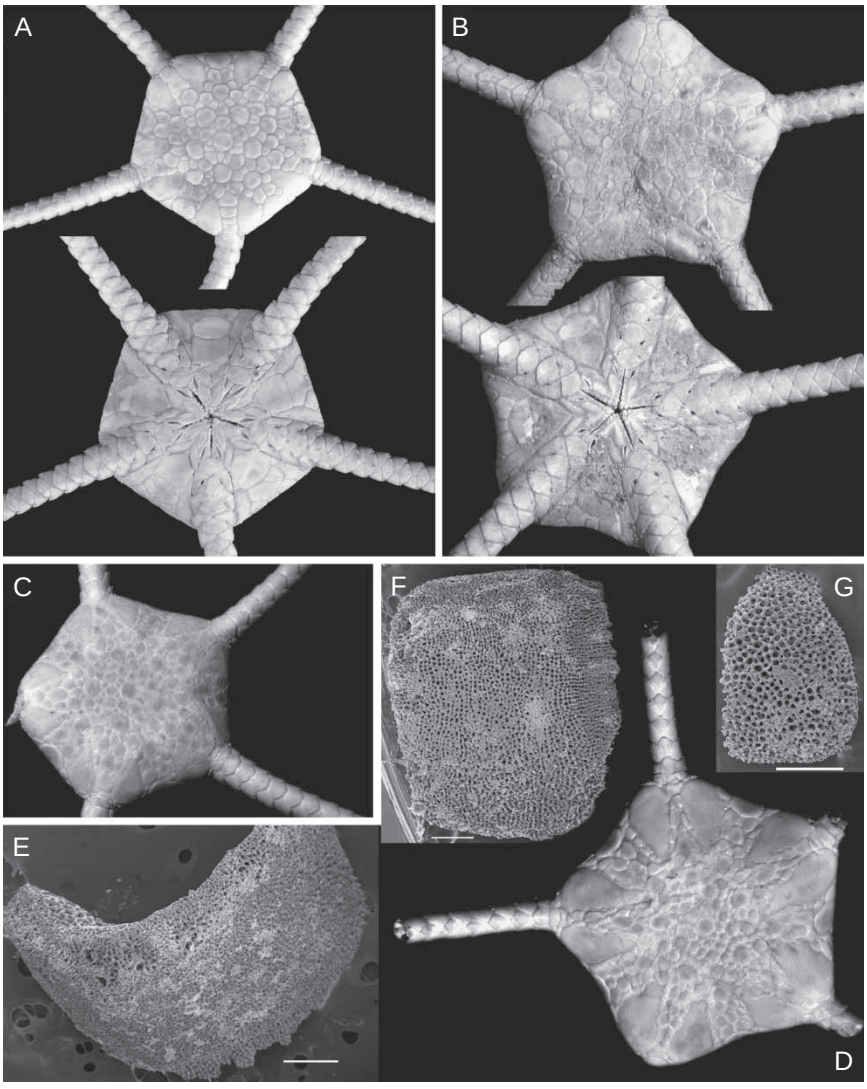

Figure 5. (A–C) *Ophioplinthus tessellata* (Verrill, 1894): (A) lectotype YPM 39095, RV *Albatross*, cruise of 1886, St. 2710, off Nantucket I., 40°06′00″N, 68°01′30″W, depth 1800 m, disk diameter 19 mm, dorsal and ventral views; (B) paralectotype USNM 9070, RV *Albatross*, St. 2083, Massachusetts, Georges Bank, 40°26′40″N, 67°05′15″W, depth 1754, disk diameter 20 mm, dorsal and ventral views; (C) MAR-ECO, St. 50/373, disk diameter 19 mm, dorsal view. (D–G) *Ophioplinthus pseudotessellata* sp. nov.: (D) paratype ZMMU D-749, MAR-ECO, St. 40/367, disk diameter 17.5 mm, dorsal view; (E) scanning electron micrograph of lateral arm plate, basal segments, showing arm spine articulation ridges; (F) scanning electron micrograph of lateral arm plate, basal segments; (G) scanning electron micrograph of dorsal arm plate, basal segments. Scale bars: 300 μm (E–G). Photographs: Eric Lazo-Wasem (A); Cynthia Ahearn (B); Alexander Martynov (C–G).

genera, *Ophioplinthus*, *Ophiurolepis* and *Homalophiura*, be united under the same name, using the oldest name *Ophioplinthus*. Despite this Hertz (1927a,b), as well as Koehler (1922, 1923), for most Antarctic species of this group, used the generic name *Ophiurolepis*. Later this decision was widely accepted (Mortensen 1936; Fell 1961; Madsen 1967; McKnight 1967; Bernasconi & D'Agostino 1975; Smirnov 2006). Bartsch (1982) gave a short historical overview of the taxonomy of the *Homalophiura–Ophiurolepis* group and placed *H. inornata* (type species of the genus *Homalophiura*) within the genus *Ophiurolepis*. In addition, Madsen (1967) listed without discussion *Homalophiura inornata* (Lyman, 1878) under the generic name *Ophiurolepis* and thus acted as the first reviser. Fell (1961) described one more genus with tentacle pores restricted only to proximal segments of the arms, *Theodoria*. This genus is distinguished from *Ophiurolepis* mainly by the degree of development of the tentacle scales and excavated jaws.

Paterson (1985) briefly reviewed the genus *Homalophiura* and divided it into four informal groups. Paterson argued that species with reduced arm comb and tentacle pores restricted only to the proximal segments belonged to several different

genera. According to Paterson, the genus *Ophiurolepis* included species with short genital slits (including the type species of the genus *Homalophiura*, *H. inornata*), whereas for species with long genital slits (*Homalophiura tessellata*, *H. abyssorum*) Paterson created a new genus *Homophiura*. Other species from the former genus *Homalophiura* were referred to the genus *Ophiura* s.l. The relation between *Homalophiura*, *Ophiurolepis*, *Homophiura* and *Ophioplinthus* was not investigated. According to the present study, the length of the genital slits is not a very reliable character. First of all, the type species of the genus *Ophiurolepis*, *O. carinata* (Studer, 1876) (Figure 6E), and most of the other species of the genus *Ophiurolepis* have long genital slits. Secondly, the type species of the genus *Homalophiura*, *H. inornata* (Lyman, 1878) (Figure 6G) (according to illustration given by Lyman 1882: Plate 3, Figure 10), and the type species of the genus *Homophiura*, *H. tessellata* (Figures 4A, C, 5A–C) both have long genital slits. In general, it is hard to evaluate an exact length of the genital slits due to closing of the distal part, and this may cause misinterpretation. For instance, Lyman (1882) figured the type species of the genus *Ophioplinthus*, *O. medusa*, as having short genital slits. However, re-examination of the type material of *O. medusa* (Figure 6A) revealed the presence of long genital slits at least in one interradius, whereas in other interradii the genital slits are closed distally. Thus, there are no real differences in length of the genital slits (according to Paterson 1985 one of the main diagnostic characters) between type species of the genera *Ophioplinthus*, *Homalophiura*, *Ophiurolepis* and *Homophiura*. *Homophiura* Paterson, 1985, therefore, is a clear synonym of the genus *Homalophiura* H.L. Clark, 1915. The latter, in turn does not have reliable differences from *Ophioplinthus* Lyman, 1878. Bartsch (1991) did not support the genus *Homophiura* and maintained *H. abyssorum* (Lyman, 1883) within the genus *Homalophiura*.

Many authors mention *Ophiurolepis* as closely related to *Homalophiura* and *Ophioplinthus* (Hertz 1927a,b; Mortensen 1933, 1936; Paterson 1985). Apart from the tentacle pores being restricted to the proximal segments, *Ophiurolepis* can be distinguished by a round swollen disk, relatively few (compared to *Ophioplinthus*) distinct large disk plates including quite distinct primary plates in a rosette pattern, relatively large radial shields, slender arms, carinate dorsal arm plates and a fragmented oral shield. At first glance, all these characters taken together distinguish *Ophiurolepis* from *Ophioplinthus*. However, if all species referred to *Ophiurolepis* are considered, the above-mentioned characters turn into a tendency rather than a clear separation. For instance, some species do not have carinate dorsal arm plates and fragmented oral shield (e.g. *O. martensi* (Studer, 1885)). We examined a number of specimens of *Homalophiura confragosa* (Lyman, 1878), the species with unclear generic placement, collected off the Falkland Islands. Some specimens of this species had round and conspicuously swollen disks (Figure 6F) and were similar to species of the genus *Ophiurolepis*, whereas other specimens, with round or pentagonal and flattened disks (Figure 6D) did not differ from species of the genera *Ophioplinthus* and *Homophiura*. On the other hand, some small specimens of the type species of the genus *Homophiura*, *H. tessellata*, have quite well-developed distinct disk plates and weakly carinated dorsal arm plates. The type species of the genus *Homalophiura*, *H. inornata* (Figure 6G), has quite distinct disk plates and thick dorsal arm plates with a weak ridge, similar to the species of the genus *Ophiurolepis* with well-developed dorsal ridges, as well as relatively small oral papillae characteristic for the type species of the genera *Ophioplinthus* and *Homophiura*. An additional character mentioned by Paterson as separating *Homophiura* from *Ophiurolepis* is the fragmented oral and adoral shields in the latter genus. Despite this, in the present material a new species *Ophioplinthus pseudotessellata* sp. nov. (Figures 4B, D, 5D–G), closely related to the type species of the genus *Homophiura*, *H. tessellata*, has partially fragmented oral and adoral shields. Thus *Homalophiura inornata* can be equally referred to the genera *Homophiura* or *Ophiurolepis*.

Moreover, the genus *Theodoria* Fell, 1961 is closely related to the genus *Ophiurolepis* in most characters including distinct dorsal plates of the disk. A difference of the type species of the genus *Theodoria*, *T. relegata* (Koehler, 1922), from the type species of the genus *Ophiurolepis*, *O. carinata* (and from the genus *Ophioplinthus*), is well-defined proximal tentacle pores and tentacle scales. However, this character is not stable. Even among species referred to the genus *Theodoria*, for instance *T. wallini* (Mortensen, 1925), tentacle scales are much less developed than in the type species, and are more similar to those in some species of the genus *Ophiurolepis*. At the same time, in one species, initially included by Lyman in his genus *Ophioplinthus*, *O. grisea* Lyman, 1878 (Figure 6C), tentacle scales are well developed. The general shape of the disk and absence of distinct plates in *O. grisea* separates it from *Theodoria* and *Ophiurolepis*. Thus, *O. grisea* by morphology of the tentacle scales is similar to *Theodoria*, whereas the shape of the disk corresponds to the type species of the genus *Ophioplinthus*. Similarly, *Ophiurolepis scissa* (Koehler, 1908) has an intermediate position between *Theodoria* and *Ophiurolepis* based on the degree of

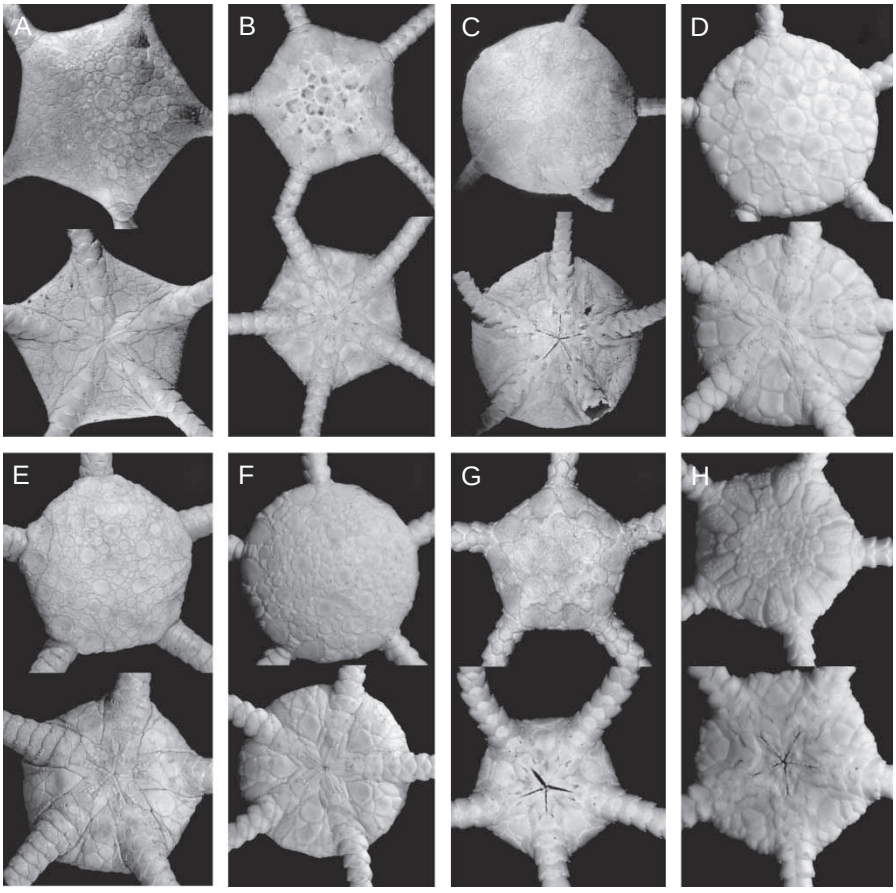

Figure 6. (A) *Ophioplinthus medusa* Lyman, 1878, syntype, MCZ 378, HMS *Challenger*, St. 156, Antarctic, off Kaiser Wilhelm II Land, depth 3594 m, disk diameter 12.5 mm; (B) *Ophioplinthus abyssorum* (Lyman, 1883), holotype, MCZ 532, *Blake*, St. 140, off Virgin Gorda, depth 1997 m, disk diameter 11 mm; (C) *Ophioplinthus grisea* Lyman, 1878, syntype, MCZ 377, HMS *Challenger*, St. 156, Antarctic, off Kaiser Wilhelm II Land, depth 3594 m, disk diameter 18 mm; (D) *Ophioplinthus confragosa* (Lyman, 1878), flattened specimen, ZMMU D-733, RV *Akademik Kurchatov*, cruise 11, St. 928, 52°15′S, 56°51′W, off Falkland Is., depth 1105 m, disk diameter 13 mm; (E) *Ophioplinthus carinata* (Studer, 1876), IORAS 14.672, RV *Ob'*, St. 122, Kerguelen I., disk diameter 18 mm; (F) *Ophioplinthus confragosa* (Lyman, 1878), swollen specimen, ZMMU D-733, RV *Akademik Kurchatov*, cruise 11, 52°15′S, 56°51′W, off Falkland Is., depth 1105 m, disk diameter 15 mm. (G) *Ophioplinthus inornata* (Lyman, 1878), syntype, MCZ 611, HMS *Challenger*, St. 106, tropical Atlantic, depth 3367 m, disk diameter 8 mm; (H) *Ophiomusium lymani* Wyville Thompson, 1873, ZMMU D-744, RV *Akademik Mstislav Keldysh*, St. 385, disk diameter 19 mm. Dorsal and ventral views are shown. Photographs: Alexander Martynov (A, C); Jessica Cundiff (B, G); Tanya Korshunova (D–F, H).

development of tentacle scales. *Homalophiura nana* (Lütken & Mortensen, 1899) and *H. madseni* Belyaev & Litvinova, 1972 have quite well-developed tentacle scales. *Homalophiura abyssorum* (Lyman, 1883) (Figure 6B) in the structure and shape of disk is similar to *H. madseni*, but has strongly reduced tentacle scales. Another character, mentioned as a distinguishing feature of *Theodoria*, is the excavated jaws. Despite the fact that many species of the *Ophioplinthus–Ophiurolepis* group have rather flattened jaws, we found distinctly excavated jaws in small specimens of *Ophioplinthus pseudotessellata* sp. nov. (Figure 4D), whereas one species of *Theodoria*, *T. wallini*, has somewhat flattened jaws. One of the species originally included by Lyman in the genus *Ophioplinthus*, *O. grisea*, also has slightly excavated jaws. Finally, *Homalophiura madseni* has clearly excavated jaws.

Summarizing, it should be noted that the degree of development of the tentacle scales varies considerably among different species from the genera *Ophioplinthus*, *Homalophiura* and *Ophiurolepis*. This means that *Theodoria* cannot remain as a separate genus. Even if we try to retain the genus *Theodoria* as independent, including only species with more or less well-defined tentacle scales, there is no evidence of monophyly.

A characteristic feature of the genus *Ophiura* is a rapid decrease in size of the tentacle pores and number of tentacle scales in the distal direction. Paterson (1985): 135), discussing the taxonomy of the genus *Homalophiura*, noted that 'this character

is more widespread…'. In fact, the most characteristic feature of the *Ophioplinthus–Ophiurolepis* group is a reduction of distal tentacle pores. This tendency is most pronounced in the genus *Ophioplinthus* and it is present in the genus *Ophiura*. There is a possibility that species similar in morphology to the group *Ophioplinthus–Ophiurolepis* may have evolved several times from different species of the genus *Ophiura* by means of further reduction of the arm comb and tentacle pores on distal segments. Thus, it is necessary to have additional characters for confirmation or for disproof of the monophyly of the *Ophioplinthus–Ophiurolepis* group. One such character could be the position of the second tentacle pore. Species of the genus *Ophiura* with reduced arm comb and reduced tentacle scales, like *O. maculata*, have the second tentacle pore rather opened inside the mouth between the jaws. At the same time, in species of the genera *Ophioplinthus*, *Ophiurolepis*, *Theodoria* and *Homophiura*, as well as in the type species of the genus *Homalophiura*, the second tentacle pore does not open inside the mouth and is nearly completely enclosed by the jaw. This character corresponds to the shape of the jaws: in the genus *Ophiura* the jaws have nearly parallel edges distally and rounded edges proximally, whereas in *Ophioplinthus*, *Ophiurolepis*, *Theodoria* and *Homophiura* the jaws are triangular.

Thus, *Ophioplinthus*, *Homalophiura*, *Ophiurolepis*, *Theodoria* and *Homophiura* represent a single morphological unit supported by several characters. The type species of the genera *Ophioplinthus* and *Homophiura* differ only slightly from each other and these genera are considered here as clear synonyms. From most characters *Ophiurolepis* is also similar to *Ophioplinthus*. There are differences, mainly the more distinct and more regular shape of the plates in *Ophiurolepis*. However, this character is quite hard to use as diagnostic since it is difficult to determine the degree of the distinctness of disk plates. As already mentioned, *Homalophiura inornata* can equally belong to the genus *Homophiura* or the genus *Ophiurolepis.*

In addition, some species, for instance *Ophiurolepis martensi* (Studer, 1885), *Homalophiura abyssorum* (Lyman, 1883), *Homalophiura confragosa* (Lyman, 1878) and *Homalophiura madseni* Belyaev & Litvinova, 1972, are hardly unambiguously referred to *Ophioplinthus* or *Ophiurolepis*. An interesting ecological characteristic of *Ophioplinthus sensu lato* are commensal hydroids recorded on e.g. *O. medusa*, *O. tessellata* and *O. relegata* (Lyman 1882; Svoboda et al. 1995). These species earlier were included in the genera *Ophioplinthus*, *Homophiura* and *Theodoria*. Most recently, Hunter (2007) has presented a phylogenetic analysis based on morphological characteristics of the genus *Ophiurolepis*. According to this study genus *Ophiurolepis* is not a monophyletic group comprising from three clades including species from other closely related genera. For instance, *Ophiurolepis scissa* is more closely related to *Homalophiura confragosa* and *H. inornata* than to other species of the genus *Ophiurolepis.* These data also support the taxonomic division suggested here.

In summary, we consider *Homalophiura* H.L. Clark, 1915, *Ophiurolepis* Matsumoto, 1915, *Theodoria* Fell, 1961 and *Homophiura* Paterson, 1985 as synonyms of the genus *Ophioplinthus* Lyman, 1878. Lyman (1878) used the name *Ophioplinthus* as a noun of the feminine gender. The following species we consider within the genus *Ophioplinthus* Lyman, 1878:

Ophioplinthus abyssorum (Lyman, 1883) comb. nov.
Ophioplinthus accomodata (Koehler, 1922) comb. nov.
Ophioplinthus anceps (Koehler, 1908) comb. nov.
Ophioplinthus banzarei (Madsen, 1967) comb. nov.
Ophioplinthus brevirima (Mortensen, 1936) comb. nov.
Ophioplinthus brucei (Koehler, 1908)
Ophioplinthus carinata (Studer, 1876) comb. nov.
Ophioplinthus clasta (H.L. Clark, 1911) comb. nov.
Ophioplinthus confragosa (Lyman, 1878) comb. nov.
Ophioplinthus divisa (Lütken & Mortensen, 1899) comb. nov.
? *Ophioplinthus euryplax* (H.L. Clark, 1939) comb. nov.
Ophioplinthus frigida (Koehler, 1901) comb. nov.
Ophioplinthus gelida (Koehler, 1901) comb. nov.
? *Ophioplinthus glypta* (H.L. Clark, 1939) comb. nov.
Ophioplinthus granulifera (Bernasconi & D'Agostino, 1973) comb. nov.
Ophioplinthus grisea Lyman, 1878
Ophioplinthus inflata (Koehler, 1897) comb. nov.
Ophioplinthus inornata (Lyman, 1878) comb. nov.
Ophioplinthus intorta (Lyman, 1878) comb. nov.
Ophioplinthus madseni (Belyaev & Litvinova, 1972) comb. nov.
Ophioplinthus medusa Lyman, 1878
Ophioplinthus martensi (Studer, 1885) comb. nov.
Ophioplinthus mordax (Koehler, 1922) comb. nov.
Ophioplinthus nexila (Kyte, 1987) comb. nov.
Ophioplinthus olstadi (Madsen, 1955) comb. nov.
Ophioplinthus partita (Koehler, 1908) comb. nov.
Ophioplinthus relegata (Koehler, 1922) comb. nov.
Ophioplinthus scissa (Koehler, 1908) comb. nov.
? *Ophioplinthus scutata* (Lyman, 1883) comb. nov.
Ophioplinthus tessellata (Verrill, 1994) comb. nov.
Ophioplinthus tuberosa (Mortensen, 1936) comb. nov.
Ophioplinthus tumescens (Koehler, 1922) comb. nov.
Ophioplinthus turgida (Mortensen, 1936) comb. nov.
Ophioplinthus wallini (Mortensen, 1925) comb. nov.

Ophioplinthus pseudotessellata sp. nov.
(Figures 4B, D, 5D–G)

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 40/367, holotype (ZMBN 77852, dried), 27 paratypes (ZMBN 77853, in ethanol), one paratype (ZMMU D-749, dried).

Etymology

Species epithet *pseudotessellata* (from the Greek *pseudos* – false – and species epithet *tessellata*) refers to close similarity of this species to *Ophioplinthus tessellata*.

Description of holotype

The disk diameter of the holotype is 17.5 mm. It is pentagonal, moderately swollen and slightly concave in the interradii. The central area of the disk is distinctly depressed. The disk scales are numerous (about 150–160 in number), small, but various in size, irregular-rounded in shape. There is a conspicuous primary rosette of six plates, clearly separated from most disk plates by their larger sizes. Radial shields are irregularly pear-shaped in outline, proximally narrowed, distally considerably widened and lie close to each other, but do not touch. Maximum width of radial shields is 3 mm. Along both internal and external edges of the radial shields there are irregular rows of small plates. In some radii these plates are smaller, in others larger. Distally in-between the radial shields few irregularly rectangular plates are placed which together with plates along the internal edges form a more or less evident Y-shaped structure between a pair of radial shields. The surface of the radial shields is smooth. Each jaw bears two or three quite irregularly placed conical or blunt apical oral papillae and seven or eight pairs of rectangular lateral papillae. Distal papillae are more elongated, block-shaped, whereas more proximally placed papillae are rounded. The oral shield is large, irregularly oval or irregularly pear-shaped and fragmented different edges in different interradii: ventrally, dorsally or laterally. The distal edge of the oral shield is bordered by an irregular line of quite small scales. Adoral shields are triangular narrow bands, about three times as long as broad. Between adoral shields and oral shields sometimes an insertion plate appears as an additional adoral shield, whereas in some interradii between adoral shields there are several irregular small plates. Genital slits are long, extending from first to fourth ventral arm plates, but for most of their length tightly closed, therefore appearing as quite short or inconspicuous. The papillae of the arm comb are greatly reduced and very short, but distinguishable. There are several short papillae placed on the distal part of the genital slit, arranged in two more or less distinct rows, up to 10 papillae per row. In some interradii these papillae are almost indistinct. Dorsally few tubercle-shaped papillae are placed at the distal edge of the radial shields. Arms slender, broken, about 1.5 times disk diameter. The dorsal arm plates are small, a few basal segments bear spear-shaped plates, while starting from the third or fifth segments the plates become almost rhomboid and very narrow. The first ventral arm plate is trapezoid. Most ventral arm plates are irregularly rhomboidal, lengthened triangular and widely separated from each other. The two first plates are nearly contiguous. Distal ventral arm plates are irregularly rhombic or wide spear-shaped, and widely separated by lateral plates. Lateral arm plates are massive. Arm spines on most segments are absent and eroded, more or less retained only on few basal segments. Spines generally are four (in a single segment five), extremely short and conical. The ventral spine on more distal segments (starting approximately from 15th segment) is considerably longer than the others and also longer than the corresponding ventral spine on the proximal segments. Arm spine articulation ridges are separated from each other by conspicuous elevations and more dorsally placed ridges are separated from each other by a distinct gap, while ventral ridges are closer together. The second tentacle pore is slit-shaped and surrounded by two rows of four to seven tentacle scales. The lateral plate has smaller and more numerous square scales, whereas the rows on the ventral plate include few larger almost oval swollen scales. The same pattern of two different rows of tentacle scales is found on three following basal segments but to a considerably lesser degree. The third segment has three scales on the lateral plate and three to four on the ventral plate. Fourth and fifth segments usually have one or two on the lateral plate and two or three on the ventral plate. Starting from the sixth segment there are no tentacle pores and tentacle scales.

Paratype variations

Generally, all paratypes, including small specimens, are essentially similar to the holotype. Small paratypes of *Ophioplinthus pseudotessellata* sp. nov. have about 100 dorsal plates on the disk and even more narrow, almost ovoid dorsal arm plates. The tentacle scales of the small specimens are more distinct than in the holotype. Large paratypes have a more flattened disk and more distinct disk plates. Tentacle scales are

more numerous – up to eight scales at the second pore, up to five, usually four scales at the third pore.

Distribution

Mid-Atlantic Ridge north of the Azores, at 2954–2968 m.

Remarks

Ophioplinthus pseudotessellata sp. nov. is clearly different from the sympatric congener *Ophioplinthus tessellata* in having more numerous and smaller plates on the disk (comparing specimens of similar size), small narrow rhomboid dorsal arm plates and partially fragmented oral and adoral shields. For comparative purposes type series from different stations of *O. tessellata* from USNM and YPM were studied. All six studied specimens ranging 10–21 mm in disk diameter invariably have wide dorsal arm plates, whereas both small and large specimens of *Ophioplinthus pseudotessellata* sp. nov. have very narrow dorsal arm plates. The shape of the dorsal arm plate is thus the most reliable character for distinguishing *Ophioplinthus pseudotessellata* sp. nov. from *O. tessellata*. Small specimens of *Ophioplinthus pseudotessellata* sp. nov. differ even more in this character from *O. tessellata* of comparable size in having very narrow, almost ovoid dorsal arm plates (compare Figure 4C and Figure 4D). Large specimens of *Ophioplinthus pseudotessellata* sp. nov. (17.5 and 18.5 mm disk diameter) have 150–160 dorsal disk plates, whereas large specimens of *O. tessellata* 19 mm disk diameter as well as a paralectotype of *O. tessellata* (USNM 9070) 21 mm disk diameter have only about 110–120 dorsal plates on the disk (compare Figures 4B, 5D and 4A, 5A–C). The small paratypes of *Ophioplinthus pseudotessellata* sp. nov. (disk diameter 7 mm) have 100 dorsal disk plates, whereas small *Ophioplinthus tessellata* (disk diameter 10 mm) have 70–75 dorsal disk plates. To avoid further confusion between these two closely related species we designate here a lectotype of *O. tessellata* – specimen YPM 39095. Paralectotypes are correspondingly YPM 9246 (nine specimens), YPM 39096 (one specimen) and USNM 8094 (three specimens), USNM 8124 (three specimens), USNM 9070 (one specimen), USNM 9172 (one specimen), USNM 11522 (one specimen), USNM 11523 (three specimens), USNM 14993 (one specimen), USNM 21231 (two specimens), USNM 24735 (one specimen), USNM 27888 (one specimen). The only other species of *Ophioplinthus* known from the North Atlantic is *O. abyssorum* (Lyman, 1883) (Figure 6B). This species (including variety *O. abyssorum* var. *africana* Madsen, 1947) differs clearly from *Ophioplinthus pseudotessellata* sp. nov. in a significantly smaller number of dorsal plates (50–60 in syntype 11.5 mm disk diameter), the shape of the radial shields, the widely rhombic shape of the dorsal arm plates, not fragmented oral and radial shields, and much less developed tentacle scales at the second tentacle pore. Some species of the genus *Ophioplinthus*, e.g. the type species *O. medusa* as well as *O. clasta*, and *O. madseni* are similar to *O. pseudotessellata* sp. nov. in having very narrow dorsal arm plates but differ considerably in a number of other characters (e.g. by general appearance of the disk and shape of the dorsal arm plates in *O. medusa*, thick skin of the disk of *O. clasta* and well-developed tentacle pores in *O. madseni*).

Ophiomusium lymani Wyville Thompson, 1873
(Figure 6H)

Ophiomusium lymani Wyville Thomson 1873: 174; Paterson 1985: 147–8, Figure 58. *Ophiomusa lymani*: Hertz 1927a: 103–5.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 44/369, five specimens; St. 68/384, one specimen; St. 70/385, 14 specimens; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 316, 11 specimens; St. 317, nine specimens; St. 319, 20 specimens; St. 354, three specimens; St. 385, one specimen; St. 415, 89 specimens; St. 418, 26 specimens; St. 445, 36 specimens; St. 446, 11 specimens; St. 464, seven specimens; St. 465, five specimens; St. 478, one specimen; St. 489, one specimen; St. 492, two specimens; St. 499, two specimens.

Distribution

Atlantic, Pacific and Indian Oceans. North Atlantic records: from West Indies to Davis Strait and from south-west Iceland to south of Cape Blanc, at 651–4829 m (Paterson 1985). Present study: the Reykjanes Ridge, the Charlie-Gibbs Fracture Zone, the Mid-Atlantic Ridge north of the Azores, at 1535–2440 m.

Family Ophiacanthidae

Ophiacantha aculeata Verrill, 1885
(Figures 7A, 10)

Ophiacantha aculeata: Verrill 1885a: 153; Verrill 1885b: 547; Koehler 1914: 74–7, Plate 11, Figures 1, 2; Paterson 1985: 38–9, Figure 17.

loan of Verrill's ophiacanthid type specimens and making photographs of some types. We deeply appreciate Jon Kongsrud (Zoological Museum, University of Bergen), who kindly made photographs of the type series of *Ophioplinthus pseudotessellata* sp. nov. Konstantin R. Tabachnik (P.P. Shirshov Institute of Oceanology) kindly photographed ophiuroid specimens from the MAR-ECO expedition. We are thankful to Jessica D. Cundiff (Museum of Comparative Zoology, Harvard University) for photographs of some ophiuroid types. Many thanks to Jens M. Bohn and Eva Lodde (Zoologische Staatssammlung, München) for help during the visit of one of the authors to ZSM. Some ophiacanthid types were photographed during the visit of one of the authors (A.V. Martynov) to the Museum of Comparative Zoology, Harvard University, supported by The Ernst Mayr Travel Grant in Animal Systematics. Andrey V. Gebruk and Alan J. Southward (Marine Biological Association, Plymouth) kindly improved the English. Three anonymous referees kindly helped to improve the manuscript. This work was an element of MAR-ECO, a field project under the Census of Marine Life programme.

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