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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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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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collected from the Reykjanes Ridge on two separate cruises were therefore examined in an effort to redefine the taxonomy of this and several other problematic ophiuroid families. Additionally, the genus *Ophioplinthus* was re-evaluated in order to elucidate its convoluted taxonomic history. Range extensions and species accounts are also given for the ophiuroid material collected from the Reykjanes Ridge taken by the RV *Akademik Mstislav Keldysh* in 1982 and the *G.O. Sars* cruise as part of the MAR-ECO 2004 project. For example, species of the genus *Ophiocamax* in the North Atlantic were recorded only from the Caribbean region and off the Sahara prior to this study. During the MAR-ECO programme a new species of this genus was discovered from the Charlie-Gibbs Fracture Zone and the Mid-Atlantic Ridge north of the Azores. Up to now, only one species of the genus *Ophiophyllum* was described from the Mid-Atlantic, *O. atlanticum* Stöhr & Segonzac, 2005. The present study discovered a new, second Atlantic species of *Ophiophyllum* from the Reykjanes Ridge.

Material and methods

The present work is based on numerous samples from the Reykjanes Ridge taken by the RV *Akademik Mstislav Keldysh* in 1982 and recent sampling during the *G.O. Sars* cruise under the framework of the MAR-ECO project in 2004 (www.mar-eco.no). Epibenthic fauna on the *G.O. Sars* MAR-ECO cruise was collected using a modified version of a semi-commercial otter trawl (the Campelen 1800 shrimp trawl) lined with a 5 mm mesh at the cod end (Bergstad & Gebruk 2008). The trawl had a mouth opening of 17 m × 12 m × 4.5 m. Ophiuroids in the MAR-ECO material occurred at 18 stations (Table I). Specimens were preserved in 80% ethanol. The collection of the MAR-ECO ophiuroids was examined during a two-week visit to the Museum of Zoology, University of Bergen.

On the fourth cruise of *Akademik Mstislav Keldysh* to the Reykjanes Ridge in 1982 samples were collected using a 2.5 m Sigsbee trawl. Ophiuroids were found at 21 stations (Table II). Specimens were preserved in 80% ethanol.

Additionally, ophiuroids from one trawl station in the north-west Atlantic taken in 2001 on the 46th cruise of *Akademik Mstislav Keldysh* were also examined (Table II).

Abbreviations

IORAS, P.P. Shirshov Institute of Oceanology, Moscow, Russia; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; SMNH, Swedish Museum of Natural History, Stockholm, Sweden; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; YPM, Yale Peabody Museum, Yale University, New Haven, CT, USA; ZMBN, Museum of Zoology at the University of Bergen, Norway; ZMMU, Zoological Museum, Moscow State University, Russia; ZSM, Zoologische Staatssammlung München, Germany.

Table I. MAR-ECO trawl stations on which ophiuroids were sampled.

				Sampling location		Trawling depth (m)		
Areas sampled	Super station	Trawl station	Date	Latitude	Longitude	Mean	Max.	Min.
North of the	40	367	7 July 2004	42°55′N	30°20′W	2961	2968	2954
Azores	42	368	8 July 2004	42°48′N	29°38′W	2078	2107	2063
	44	369	9 July 2004	42°55′N	29°32′W	1742	1767	1702
	46	372	11 July 2004	42°46′N	29°16′W	3031	3050	3005
	50	373	12 July 2004	43°01′N	28°33′W	2600	2607	2593
	52	374	13 July 2004	42°55′N	28°08′W	2977	2979	2973
Faraday seamount	53	375	15 July 2004	49°51′N	29°37′W	990	1003	981
South-east of	54	377	16 July 2004	51°19′N	28°52′W	3512	3527	3505
Charlie-Gibbs	56	378	17 July 2004	51°45′N	29°33′W	1916	1950	1872
Fracture Zone	60	379	19 July 2004	51°33′N	30°18′W	1263	1296	1237
	62	380	20 July 2004	51°55′N	30°25′W	1910	1959	1872
	64	381	21 July 2004	51°32′N	30°58′W	3461	3465	3452
	65	382	23 July 2004	52°16′N	31°00′W	753	979	607
North-west of	66	383	24 July 2004	53°01′N	33°36′W	3030	3071	2995
Charlie-Gibbs	68	384	25 July 2004	53°08′N	34°46′W	2350	2374	2306
Fracture Zone	70	385	26 July 2004	52°58′N	34°52′W	1650	1670	1630
	72	386	27 July 2004	53°16′N	35°31′W	2548	2567	2522
	74	387	28 July 2004	53°17′N	36°46′W	3055	3063	3048

Table II. List of the stations of the fourth and 46th cruise of RV *Akademik Mstislav Keldysh*.

Station[a]	Date	Sampling location		Depth (m)
		Latitude	Longitude	
268	30 July 1982	58°52′03″N	24°09′08″W	2667
268	30 July 1982	58°53′09″N	24°02′07″W	2665
275	2 August 1982	58°30′03″N	31°29′04″W	1684
316	7 August 1982	58°45′00″N	27°13′05″W	2190
316	7 August 1982	58°45′05″N	27°12′01″W	2200
317	8 August 1982	58°40′05″N	28°41′07″W	2132
317	8 August 1982	58°40′08″N	28°39′06″W	2151
319	8 August 1982	58°34′04″N	30°43′01″W	1967
319	8 August 1982	58°34′04″N	30°41′02″W	1984
354	11 August 1982	58°23′09″N	31°43′01″W	1785
364	11 August 1982	58°31′02″N	31°33′07″W	1300
364	11 August 1982	58°31′03″N	31°33′04″W	1330
385	12 August 1982	58°27′01″N	31°33′06″W	1680
385	12 August 1982	58°27′05″N	31°32′08″W	1800
390	21 August 1982	58°34′01″N	34°54′05″W	2930
390	21 August 1982	58°33′09″N	34°52′04″W	2951
413	24 August 1982	58°20′02″N	31°38′07″W	1590
415	25 August 1982	58°20′06″N	31°34′09″W	1535
415	25 August 1982	58°21′02″N	31°27′05″W	1785
418	25 August 1982	58°23′00″N	31°33′08″W	1915
418	25 August 1982	58°23′01″N	31°34′01″W	1815
445	31 August 1982	58°21′01″N	31°35′01″W	1650
445	31 August 1982	58°21′07″N	31°33′00″W	1860
446	31 August 1982	58°23′09″N	31°49′02″W	1650
446	31 August 1982	58°24′01″N	31°47′03″W	1750
464	3 September 1982	58°21′01″N	31°36′09″W	1670
464	3 September 1982	58°21′00″N	31°35′06″W	1750
465	4 September 1982	58°21′03″N	31°38′05″W	1620
465	4 September 1982	58°20′08″N	31°37′00″W	1650
478	6 September 1982	58°27′03″N	31°45′00″W	1800
478	6 September 1982	58°26′09″N	31°44′01″W	1780
489	7 September 1982	58°21′07″N	31°39′08″W	1560
489	7 September 1982	58°22′00″N	31°41′00″W	1550
492	8 September 1982	58°21′08″N	31°44′07″W	1875
492	8 September 1982	58°21′07″N	31°45′02″W	1895
499	9 September 1982	58°03′03″N	30°26′01″W	2440
499	9 September 1982	58°04′00″N	30°17′02″W	2429
500	20 September 1982	46°08′02″N	15°11′05″W	4297
500	20 September 1982	46°07′07″N	16°10′03″W	4287
526	2 October 1982	36°35′07″N	14°11′02″W	1350
526	2 October 1982	36°36′03″N	14°12′03″W	920
4226	20 August 2001	41°43′14″N	49°49′17″W	3600
4226	20 August 2001	41°43′59″N	49°48′01″W	3630

[a]First line: start of trawl; second line: end of trawl.

Species account

Family Asteronychidae

Astrodia tenuispina (Verrill, 1884)
(Figure 1A)
Astronyx tenuispina: Verrill 1884: 219.
Astrodia tenuispina: Verrill 1899: 74; Paterson 1985: 15–6, Figure 9.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 50/373, two specimens.

Distribution

North Atlantic: in the western part – the east coast of the USA, in the east Atlantic – Rockall Trough, Bay of Biscay, off Portugal, at 1560–3659 m (Paterson 1985). Present study: Mid-Atlantic Ridge, north of the Azores, at 2593–2607 m.

Family Asteroschematidae

Asteroschema inornatum Koehler, 1906
(Figure 1B)

Asteroschema inornatum: Koehler 1906: 30–1, Plate 3, Figures 46, 47; Paterson 1985: 16, Figure 10.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 56/378, one specimen; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 364, two specimens.

Distribution

North Atlantic: Rockall Trough, Bay of Biscay, off north-west Spain, off Azores, 1478–2170 m (Paterson 1985). Present study: the Reykjanes Ridge and the Mid-Atlantic Ridge south of the Charlie-Gibbs Fracture Zone, at 1300–1950 m.

Family Ophiuridae

Ophiura irrorata (Lyman, 1878)
(Figure 1C)

Ophioglypha irrorata: Lyman 1878: 73, Plate 4, Figures 106–108.
Ophiura irrorata: H.L. Clark 1911: 62.
Ophiura (*Ophioglypha*) *irrorata irrorata*: Paterson 1985: 123–4, Figures 46, 47.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 46/372, one specimen; St. 50/373, eight specimens; St. 52/374, eight specimens; St. 72/386, 13 specimens.

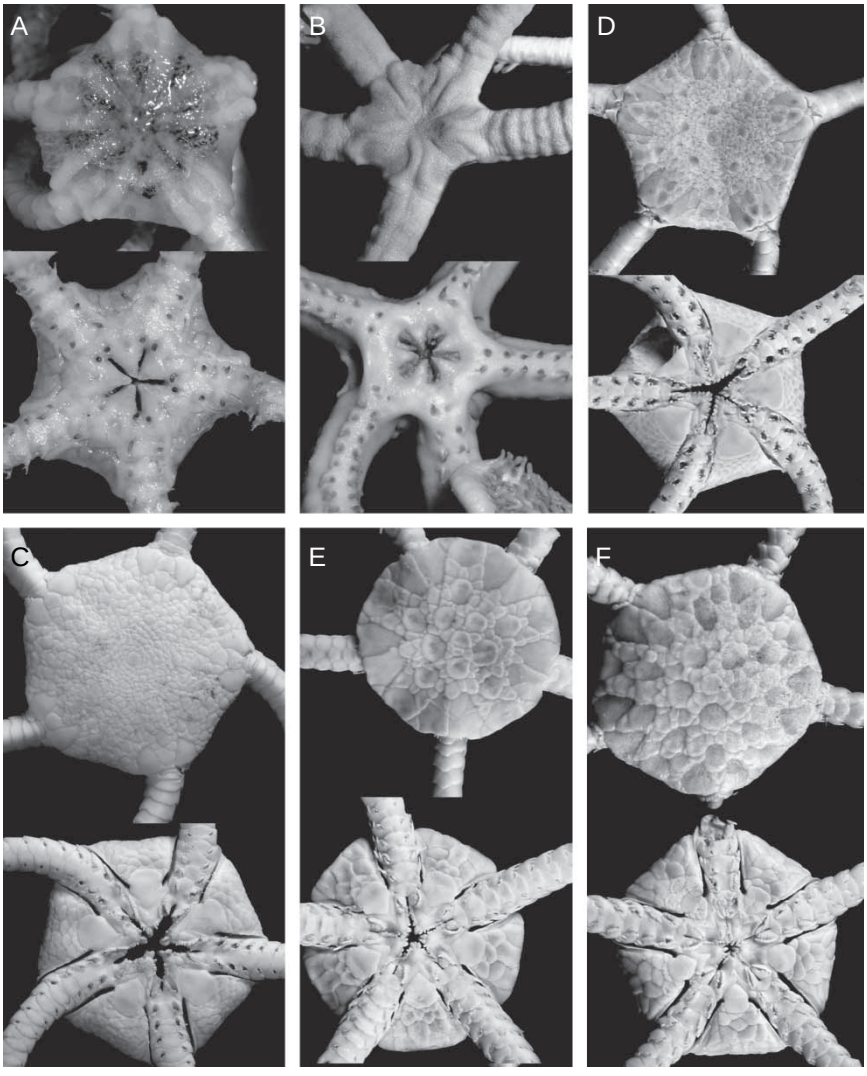

Figure 1. (A) *Astrodia tenuispina* (Verrill, 1884), MAR-ECO, St. 50/373, disk diameter 10 mm; (B) *Asteroschema inornatum* Koehler, 1906, ZMMU D-732, RV *Akademik Mstislav Keldysh*, St. 364, disk diameter 14 mm; (C) *Ophiura irrorata* (Lyman, 1878), MAR-ECO, St. 72/386, disk diameter 23 mm; (D) *Ophiura ljungmani* (Lyman, 1878), MAR-ECO, St. 40/367, disk diameter 10 mm; (E) *Ophiura nitida* Mortensen, 1933, MAR-ECO, St. 72/386, disk diameter 7.8 mm; (F) *Ophiura violainae* (Cherbonnier & Sibuet, 1972), MAR-ECO, St. 70/385, disk diameter 11 mm. Dorsal and ventral views are shown. Photographs: Tanya Korshunova (A, B); Konstantin Tabachnik (C–F).

Distribution

All oceans, except Arctic, at 403–7340 m. North Atlantic records: Cape Cod, south-western Iceland, Bay of Biscay – off North Africa. It is a predominantly abyssal species, inhabiting mostly depths below 2000 m (Paterson 1985). Present study: the Charlie-Gibbs Fracture Zone, the Mid-Atlantic Ridge north of the Azores, at 2522–3050 m.

Remarks

Paterson (1985) considered three subspecies of *O. irrorata* within the same regions of the North Atlantic (e.g. *O. irrorata irrorata* inhabited the Bay of Biscay along with another subspecies *O. irrorata concreta*). Whether these subspecies represent separate species or rather a single polymorphic species is currently unclear. However, several subspecies cannot inhabit the same geographical region (e.g. Bay of Biscay), and we therefore consider *O. irrorata* without the subspecies division.

Ophiura ljungmani (Lyman, 1878)
(Figure 1D)

Ophioglypha ljungmani: Lyman 1878: 71, Plate 3, Figure 77.
Ophiura ljungmani: Farran 1913: 31.
Ophiura (*Ophiura*) *ljungmani*: Paterson 1985: 118–20, Figure 44.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 40/367, two specimens; St. 53/375, one specimen; St. 54/377, five specimens; St. 66/383, two specimens; St. 72/386, two specimens; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 268, 70 specimens; St. 316, seven specimens; St. 319, two specimens; St. 390, three specimens; St. 445, four specimens.

Distribution

Eastern Brazil, off Florida, at 101–2750 m. North Atlantic records: Labrador basin, south-eastern Iceland, North Africa (Paterson 1985). Present study: from the Reykjanes Ridge, including the Charlie-Gibbs Fracture Zone to the Azores, at 981–3527 m.

Ophiura nitida (Mortensen, 1933
(Figure 1E)

Ophiura nitida: Mortensen 1933: 84–6, Text figure 47, Plate 3: 18, 19.
Ophiura (*Ophiura*) *nitida*: Paterson 1985: 121–2, Figure 45.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 68/384, two specimens; St. 72/386, three specimens.

Distribution

Ophiura nitida is a rare ophiurid that has been recorded only from the Reykjanes Ridge, from a depth of 2065 m (Mortensen 1933). The present study revealed this species in the Charlie-Gibbs Fracture Zone at 2306–2567 m.

Remarks

This is the first record of this species since the description by Mortensen (1933).

Ophiura violainae (Cherbonnier & Sibuet, 1972)
(Figure 1F)

Homalophiura violainae: Cherbonnier & Sibuet 1972: 1378.
Ophiura (*Ophiura*) *violainae*: Paterson 1985: 122, Figure 45.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 70/385, one specimen; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 465, two specimens.

Distribution

Bay of Biscay, off Portugal, at 2210–2399 m (Cherbonnier & Sibuet 1972; Paterson 1985). Present study: the Reykjanes Ridge, the Charlie-Gibbs Fracture Zone at 1620–1670 m.

Remarks

This is the first record of the species on the Reykjanes Ridge.

Ophiura saurura (Verrill, 1894) comb. nov.
(Figure 2A–C)

Ophioglypha saurura:Verrill 1894: 288.
Ophioglypha aspera: Koehler 1898: 40, Plate 6, Figures 19–21.
Amphiophiura saurura: H.L. Clark 1915: 315; Paterson 1985: 134–5, Figure 50.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 40/367, 19 specimens; St. 42/368, one specimen; St. 52/374, five specimens; St. 53/375, seven specimens; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 465, four specimens; St. 489, two specimens; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 445, one specimen.

Distribution

North Atlantic: off Nantucket and Newfoundland, south of Iceland to Bay of Biscay, at 844–2245 m (Paterson 1985). Present study: the Reykjanes Ridge, the Mid-Atlantic Ridge north of the Azores, at 981–2979 m.

Remarks

Specimens from St. 445 (Figure 2B) are similar to the type specimen (YPM 9419) (Figure 2A) in having numerous elevated disk plates, connected radial shields, straight distal edge of the dorsal arm plates, rounded proximal outline of the jaws and whitish colour. At the same time, most of the other specimens from various stations (e.g. Figure 2C) somewhat differ from the type specimen and the specimen from St. 445 in the presence of a superficially smooth disk with non-elevated plates, radial shields conspicuously separated, triangular distal edge of the dorsal arm plates, triangular proximal outline of the jaws and maculated colour. Despite these differences, evidently intermediate specimens between these forms were discovered, therefore we consider both forms within a single species. Traditionally, *O. saurura* is considered within the genus *Amphiophiura* (Clark 1915; Mortensen 1933; Paterson 1985), but this placement was never discussed. Almost all species of the genus *Amphiophiura* (including the type species *A. bullata* (Wyville Thomson, 1877) have a peculiarly stocky general appearance with strong disk and arm plates and differ considerably from *O. saurura*. The latter is similar to the species of the genus *Ophiura* in general shape of the disk and arms, especially to *O. irrorata*. Differences between *O. saurura* and *O. irrorata* are smaller than with species from the genus *Amphiophiura* and clearly are non-generic. Therefore, we consider *O. saurura* as species of the genus *Ophiura*.

Amphiophiura convexa (Lyman, 1878)
(Figure 2D)

Ophioglypha convexa: Lyman 1878: 84, Plate 3, Figures 83, 84.
Amphiophiura convexa: Matsumoto 1915: 77.
Amphiophiura bullata convexa: Paterson 1985: 132–3, Figure 51.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 64/381, two specimens; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 500, two specimens; 46th cruise, St. 4226, three specimens.

Distribution

Atlantic, Pacific and Indian Oceans. North Atlantic records: Labrador Basin, Rockall Trough, Bay of Biscay, off the Azores, at 1997–6480 m (Litvinova 1971; Paterson 1985). Present study: Mid-Atlantic Ridge, south of Charlie-Gibbs Fracture Zone and the Biscay Bay region, at 3452–4297 m.

Ophiotjalfa vivipara Mortensen, 1913
(Figure 2E)

Ophiotjalfa vivipara: Mortensen 1913: 40, Figures 4–6; Paterson 1985: 139, Figure 53.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 446, one specimen; St. 464, one specimen; St. 478, three specimens.

Distribution

Previously known only from two records – in the Davis Strait and off south-west Iceland, at 1438 m (Mortensen 1913, 1933). In the present study this species was recorded on the Reykjanes Ridge at 1650–1800 m.

Ophiotypa simplex Koehler, 1897
(Figure 2F)

Ophiotypa simplex Koehler 1897: 281–3, Plate 5, Figures 1–3; Paterson 1985: 144–5, Figure 55.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 464, two specimens; St. 500, two specimens.

Distribution

Atlantic, Pacific and Indian Oceans. North Atlantic records: off the Azores and Cape Verde at 3595–4366 m (Paterson 1985). Present study: the Reykjanes Ridge and the Bay of Biscay at 1670–4297 m.

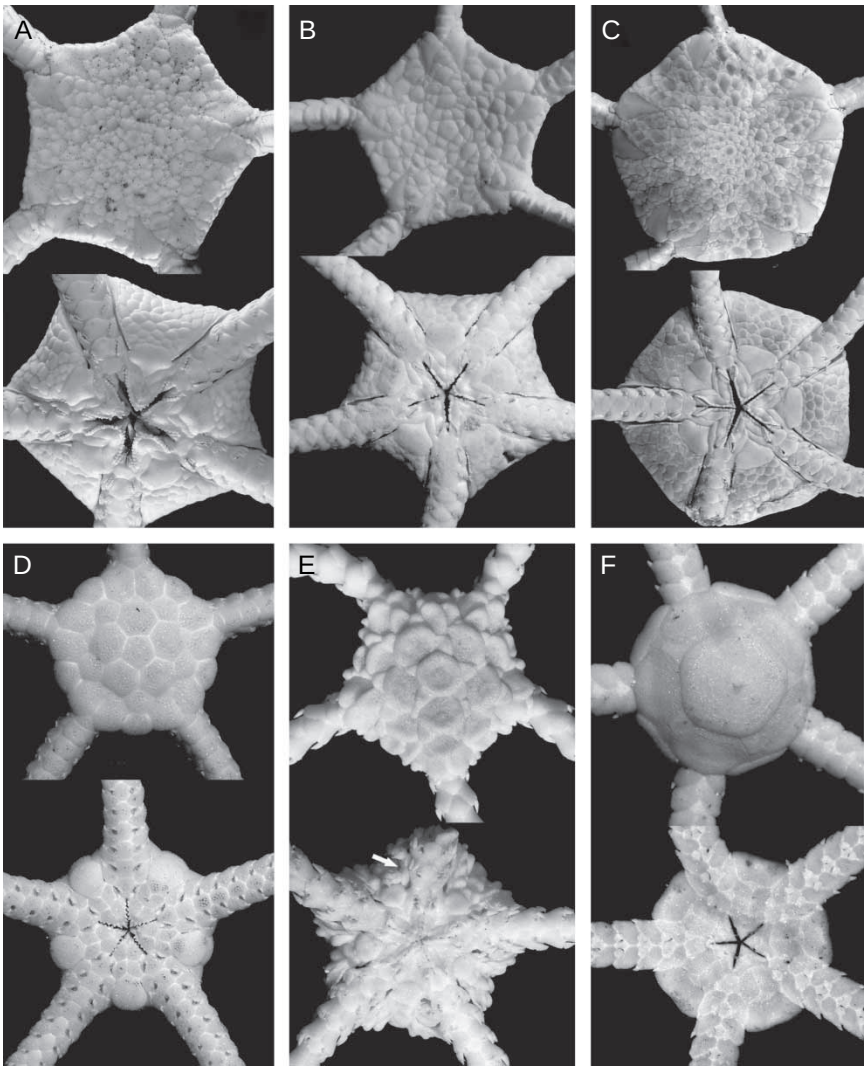

Figure 2. (A–D) *Ophirua saurura* (Verrill, 1894): (A) syntype, YPM 9419, RV *Albatross*, cruise of 1885, St. 2528, 41°47′N, 65°37′30″W, depth 1232 m, disk diameter 14 mm; (B) IORAS 14.818, RV *Akademik Mstislav Keldysh*, St. 445, disk diameter 8.2 mm; (C) MAR-ECO, 40/367, disk diameter 17 mm; (D) *Amphiophiura convexa* (Lyman, 1878), IORAS 14.468, RV *Akademik Mstislav Keldysh*, St. 500, disk diameter 6.5 mm. (E) *Ophiotjalfa vivipara* Mortensen, 1913, ZMMU D-646, RV *Akademik Mstislav Keldysh*, St. 464, disk diameter 4 mm. Juvenile within genital slit indicated by arrow. (F) *Ophiotypa simplex* Koehler, 1897, IORAS 14.193, RV *Akademik Mstislav Keldysh*, St. 500, disk diameter 4 mm. Dorsal and ventral views are shown. Photographs: Alexander Martynov (A); Tanya Korshunova (B, D–F); Konstantin Tabachnik (C).

Remarks

The present findings are the most northern record for the species.

Ophiophycis mirabilis Koehler, 1901
(Figure 3A)

Ophiophycis mirabilis Koehler 1901a: 222, Figures 1, 2; Paterson 1985: 141, Figure 54.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 445, one specimen; St. 478, one specimen; St. 489, five specimens; St. 526, one specimen.

Distribution

Prior to this study the species was recorded only from the Bay of Biscay at 1175–1662 m (Paterson 1985). Present study: the Reykjanes Ridge and off Portugal, 920–1860 m.

Ophiopleura inermis (Lyman, 1878)
(Figure 3B)

Ophioglypha inermis: Lyman 1878: 95, Plate 5, Figures 123–125.
Ophiopleura inermis: Gage et al. 1983: 295; Paterson 1985: 128, Figure 48.

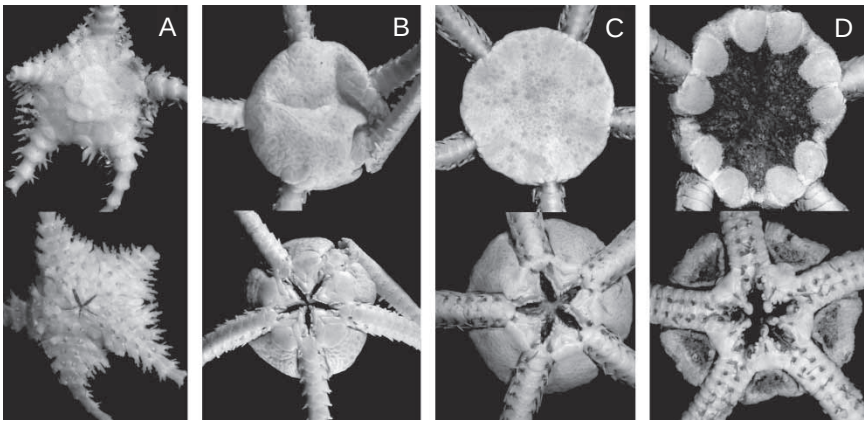

Figure 3. (A) *Ophiophycis mirabilis* Koehler, 1901, IORAS 14.718, RV *Akademik Mstislav Keldysh*, St. 526, disk diameter 2.8 mm; (B) *Ophiopleura inermis* (Lyman, 1878), MAR-ECO, St. 53/375, disk diameter 8 mm; (C) *Ophiocten hastatum* Lyman, 1878, ZMMU D-730, RV *Akademik Mstislav Keldysh*, St. 390, disk diameter 14 mm; (D) *Ophiernus vallincola* Lyman, 1878, ZMMU D-731, RV *Akademik Mstislav Keldysh*, St. 415, disk diameter 13 mm. Dorsal and ventral views are shown. Photographs: Alexander Martynov (A); Konstantin Tabachnik (B); Tanya Korshunova (C, D).

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 53/375, one specimen.

Distribution

North Atlantic: off Martha's Vineyard, New England north to western Greenland, east of Faeroe Islands, south of the Azores, at 150–1740 m (Paterson 1985). Present study: the Mid-Atlantic Ridge south of the Charlie-Gibbs Fracture Zone, at 981–1003 m.

Ophiocten hastatum Lyman, 1878
(Figure 3C)

Ophiocten hastatum: Lyman 1878: 103, Plate 5, Figures 133, 134; Paterson et al. 1982: 117–9, Figure 5; Paterson 1985: 129, Figure 49.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 42/368, one specimen; St. 44/369, one specimen; St. 72/368, two specimens; St. 268, eight specimens; RV *Akademik Mstislav Keldysh*, fourth cruise; St. 316, 11 specimens; St. 317, one specimen; St. 390, 68 specimens; St. 445, one specimen; St. 465, five specimens.

Distribution

Atlantic, Pacific and Southern Oceans, at depths of 1600–4700 m. North Atlantic records: off Rockall Trough, south of the Azores, at 1970–4700 m (Paterson et al. 1982). Present study: the Reykjanes Ridge and the Mid-Atlantic Ridge south of the Charlie-Gibbs Fracture Zone, the Mid-Atlantic Ridge, north of the Azores, at 1620–2951 m.

Ophiernus vallincola Lyman, 1878
(Figure 3D)

Ophiernus vallincola Lyman 1878: 122, Plate 6, Figures 170–172.
Ophiernus abyssalis Koehler 1896b: 242.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 415, one specimen; St. 445, 12 specimens; St. 464, one specimen; St. 465, two specimens.

Distribution

East Atlantic, from south of Ireland to off South Africa, Indian Ocean, western Pacific, at 840–4065 m (Madsen 1977). Present study: the Reykjanes Ridge, at 1535–1860 m.

Ophioplinthus tessellata (Verrill, 1894) comb. nov.
(Figures 4A, C, 5A–C)

Ophioglypha tessellata: Verrill 1894: 290.
Homalophiura tessellata H.L. Clark 1915: 327.
Homophiura tessellata: Paterson 1985: 137–8, Figure 52.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 50/373, 11 specimens; St. 53/375, 47 specimens; St. 54/377, three specimens; St. 72/386, one specimen.

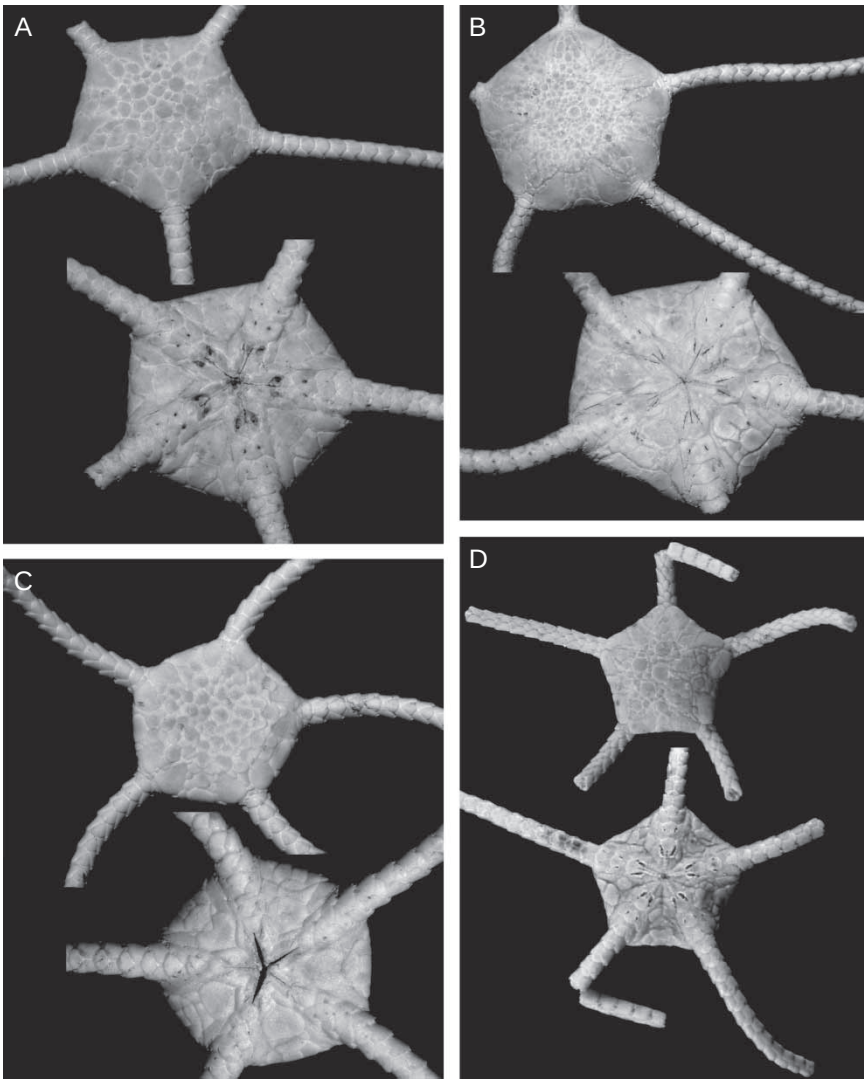

Figure 4. (A) *Ophioplinthus tessellata* (Verrill, 1894), MAR-ECO, St. 53/375, disk diameter 17 mm; (B) *Ophioplinthus pseudotessellata* sp. nov., holotype ZMBN 77852, MAR-ECO, St. 40/367, disk diameter 17.5 mm; (C) *Ophioplinthus tessellata* (Verrill, 1894), MAR-ECO, St. 53/375, disk diameter 10 mm; (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

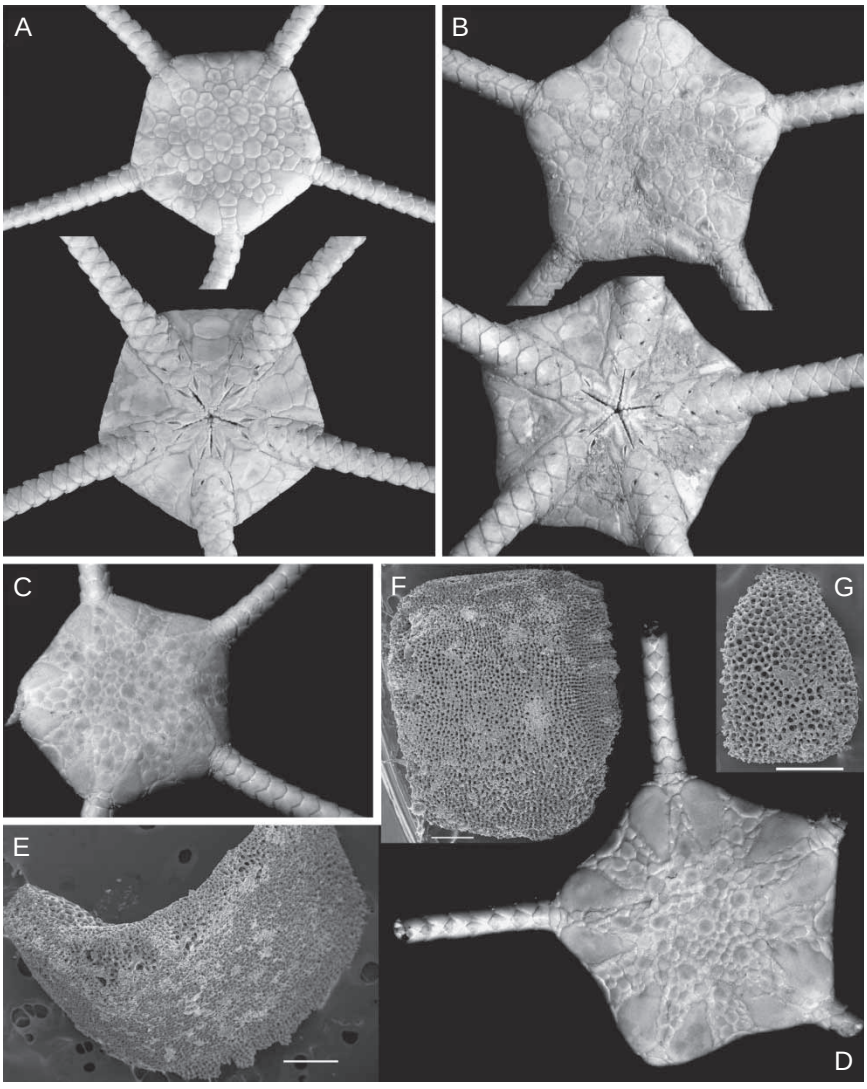

Figure 5. (A–C) *Ophioplinthus tessellata* (Verrill, 1894): (A) lectotype YPM 39095, RV *Albatross*, cruise of 1886, St. 2710, off Nantucket I., 40°06′00″N, 68°01′30″W, depth 1800 m, disk diameter 19 mm, dorsal and ventral views; (B) paralectotype USNM 9070, RV *Albatross*, St. 2083, Massachusetts, Georges 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

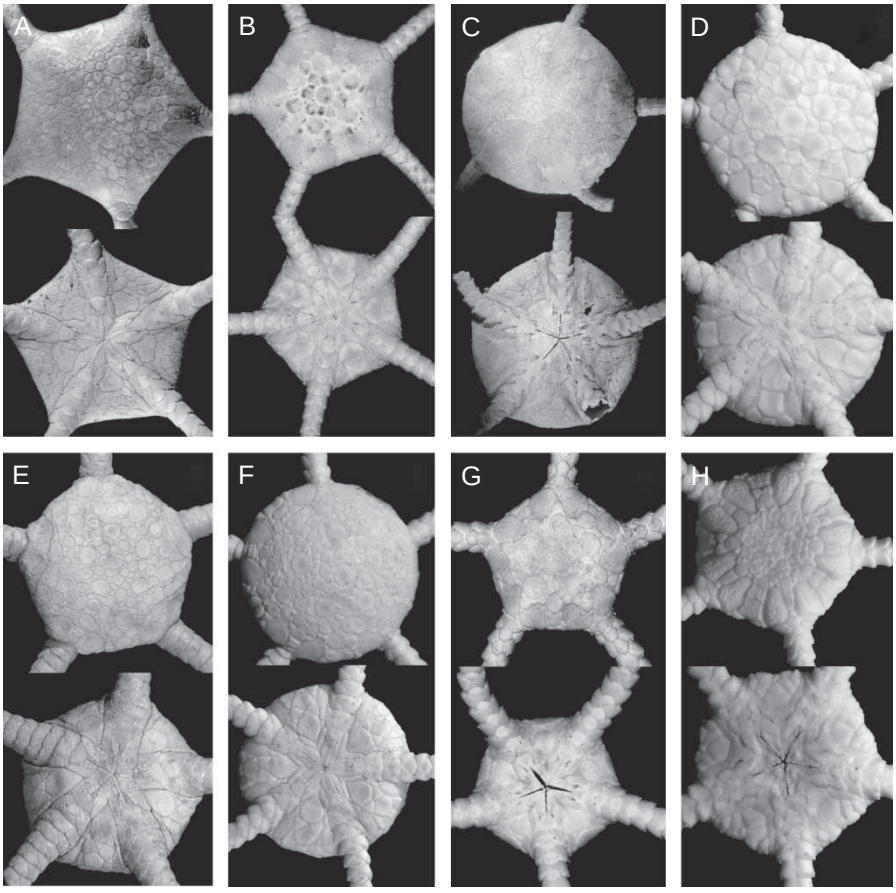

Figure 6. (A) *Ophioplinthus medusa* Lyman, 1878, syntype, MCZ 378, HMS *Challenger*, St. 156, Antarctic, off Kaiser Wilhelm II Land, depth 3594 m, disk diameter 12.5 mm; (B) *Ophioplinthus abyssorum* (Lyman, 1883), holotype, MCZ 532, *Blake*, St. 140, off Virgin Gorda, depth 1997 m, disk diameter 11 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.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 40/367, two specimens; St. 50/373, one specimen; St. 52/374, one specimen; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 316-5, 108 specimens; St. 317, three specimens; St. 445, two specimens; St. 499, 172 specimens.

Type and historically important material studied. USNM 6610, 11 specimens identified by M. Rathbun, Steamer *Albatross*, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00′′N, 73°03′50′′W, depth 2551 m.

USNM 12669, lectotype, here designated, specimen identified by R. Koehler, Steamer *Albatross*, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00′′N, 73°03′50′′W, depth 2551 m.

USNM 27900, one specimen identified by A.E. Verrill, Steamer *Albatross*, cruise of 1886, St. 2725, Virginia Beach, 36°34′00′′N, 73°48′00′′W, depth 2513 m.

USNM 1100627, three paralectotypes, specimens identified by R. Koehler, Steamer *Albatross*, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00′′N, 73°03′50′′W, depth 2551 m.

Distribution

North Atlantic: from off Virginia to New England, east of Rockall Trough, Bay of Biscay, Iberian Basin, at 2500–3584 m (Verrill 1885a,b; Paterson 1985). Present study: the Reykjanes Ridge, Mid-Atlantic Ridge north of the Azores, at 1650–2979 m.

Remarks

See discussion on *Ophiacantha fraterna* below.

Ophiacantha anomala G.O. Sars, 1871
(Figure 7B–J)

Ophiacantha anomala: G.O. Sars 1871: 12; Paterson 1985: 24–5, 34, Figure 14.
Ophiacantha cuspidata: Lyman 1878: 143, Plate 10, Figures 248–250, syn. nov.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 65/382, two specimens; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 385, 17 specimens; St. 418, one specimen; St. 446, four specimens; St. 464, 15 specimens; St. 478, 55 specimens.

Distribution

Ascension I., 785 m (Lyman 1878, type locality of *O. cuspidata*), North Atlantic: from Florida to south-west Iceland and from east Iceland to Norway and Rockall Trough, at 141–1500 m (Paterson 1985) and off Morocco, 1750 m (Bartsch 1987, as *O. cuspidata*). Present study: the Reykjanes Ridge, the Charlie-Gibbs Fracture Zone at 607–1915 m.

Remarks

Mortensen (1933) mentioned two findings of five-armed *O. anomala* collected off southern Iceland and from Trondheimsfjord. Moreover, Mortensen also mentioned six-armed juveniles in the bursae of the five-armed specimens. Despite this, Paterson (1985) strictly distinguished five- and six-armed species of the genus *Ophiacantha* in the North Atlantic. New material from the Reykjanes Ridge (geographically close to one of Mortensen's specimens) includes apparently one species, though with a different number of arms – five or six. The general appearance, shape of the spicules of the disk, oral shield and oral papillae, and tentacle scale are the same in five- and six-armed specimens (compare Figure 7C, F, I and 7B, G, H). Both five- and six-armed specimens fit the diagnosis of *O. anomala* well. At the same time, five-armed *O. cuspidata* are very similar to *O. anomala* and five-armed specimens of *O. anomala* have never been mentioned as a synonym of *O. anomala*. We examined two paratypes of *O. cuspidata* from the Museum of Comparative Zoology (Harvard University) (Figure 7D). They do not differ from the five-armed *O. anomala*, therefore *O. cuspidata* is considered here as a synonym of *O. anomala*. We also discovered one seven-armed juvenile of *O. anomala* (Figure 7E). The six-armed specimens differ from the five-armed specimens in slightly narrower jaws and oral shields because development of the additional arm results in tighter packing of the oral structures.

Ophiacantha fraterna Verrill, 1885
(Figures 8A, B, F, H, 9, 11A)

Ophiacantha fraterna: Verrill 1885b: 545; Koehler 1914: 83–6, Plate 11, Figures 5, 6.
Ophiacantha bidentata var. *fraterna* Mortensen 1933: 21–2, Figures 6, 7.
? *Ophiacantha hibernica*: Farran 1913: 39, Figures 10, 11.
= *Ophiacantha bidentata* auct. non Retzius, 1805.

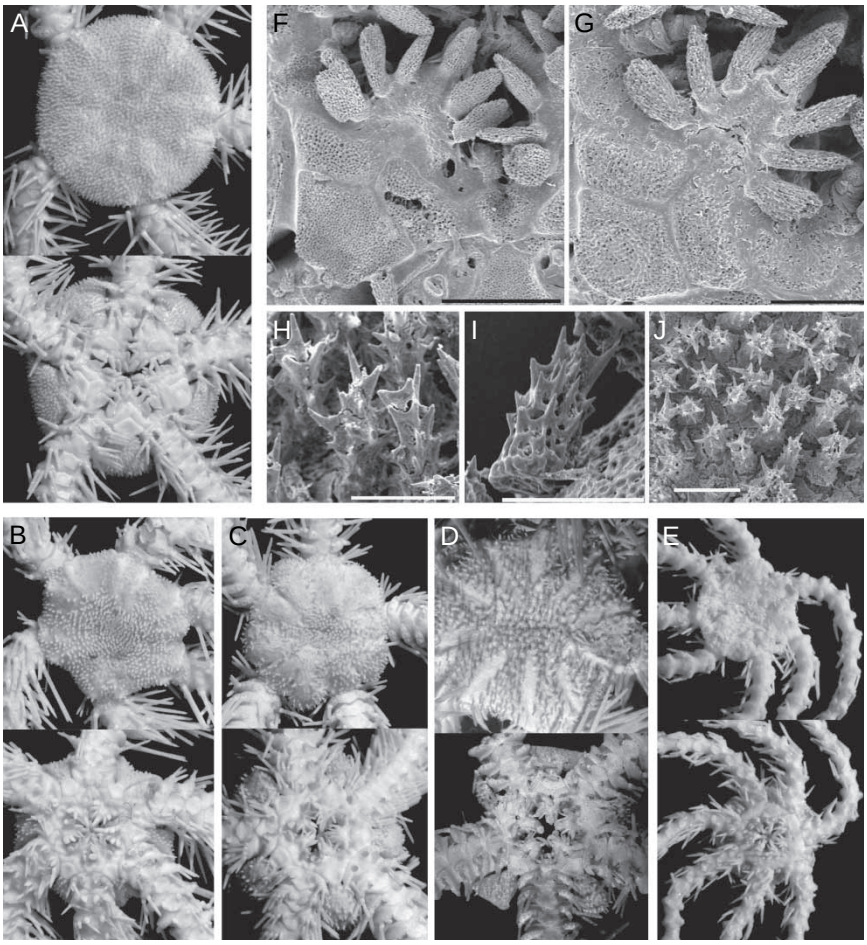

Figure 7. (A) *Ophiacantha aculeata* Verrill, 1885, ZMMU D-641, RV *Akademik Mstislav Keldysh*, St. 499, disk diameter 9 mm. (B, C, E–J) *Ophiacantha anomala* G.O. Sars, 1871: (B) ZMMU D-661, six-armed specimen, RV *Akademik Mstislav Keldysh*, St. 464, disk diameter 9 mm; (C) ZMMU D-658, five-armed specimen, RV *Akademik Mstislav Keldysh*, St. 464, disk diameter 9 mm; (E) ZMMU D-659, seven-armed specimen, RV *Akademik Mstislav Keldysh*, St. 478, disk diameter 3.1 mm; (F) ZMMU D-658, five-armed specimen, RV *Akademik Mstislav Keldysh*, St. 464, scanning electron micrographs of oral structures; (G) ZMMU D-659, six-armed specimen, RV *Akademik Mstislav Keldysh*, St. 478, scanning electron micrographs of oral structures; (H, J) ZMMU D-659, six-armed specimen, RV *Akademik Mstislav Keldysh*, St. 478, scanning electron micrographs of spicules from dorsal side of the disk; (I) ZMMU D-658, five-armed specimen, RV *Akademik Mstislav Keldysh*, St. 464, scanning electron micrographs of spicules from dorsal side of the disk. (D) Syntype MCZ 1942 of *Ophiacantha cuspidata* Lyman, 1878, HMS *Challenger*, St. 344, Ascension I., depth 764 m, disk diameter 10 mm. Dorsal and ventral views are shown in (A–E). Scale bars: 1 mm (F); 600 μm (G); 150 μm (H, J); 200 μm (I). Photographs: Tanya Korshunova (A–C, E); Alexander Martynov (D, F–J).

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 60/379, one specimen; St. 68/384, one specimen; St. 70/385, one specimen; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 316, 72 specimens; St. 317, three specimens; St. 415, 18 specimens; St. 418, two specimens; St. 445, 19 specimens; St. 464, three specimens; St. 478, one specimens; St. 499, 10 specimens.

Type and historically important material studied. *Ophiacantha spinulosa* Müller & Troschel, 1842: SMNH-Type-3289, syntype, Svalbard, West Spitsbergen.

'*Ophiocoma*' *arctica* Müller & Troschel, 1842: SMNH-Type-5144, syntype, Svalbard, West Spitsbergen.

Ophiacantha fraterna Verrill, 1885: USNM 7905, specimen identified by A.E. Verrill, Steamer *Albatross*, cruise of 1884, St. 2206, New Jersey, Hudson Canyon, 39°35′00″N, 71°24′30″W, depth 1907 m.

USNM 11451, three specimens identified by A.E. Verrill, Steamer *Albatross*, cruise of 1885, St. 2532, Massachusetts, SE of Georges Bank, 40°34′30″N, 66°48′00″W, depth 1289 m.

USNM 33816, lectotype, here designated, one specimen identified by R. Koehler, Steamer

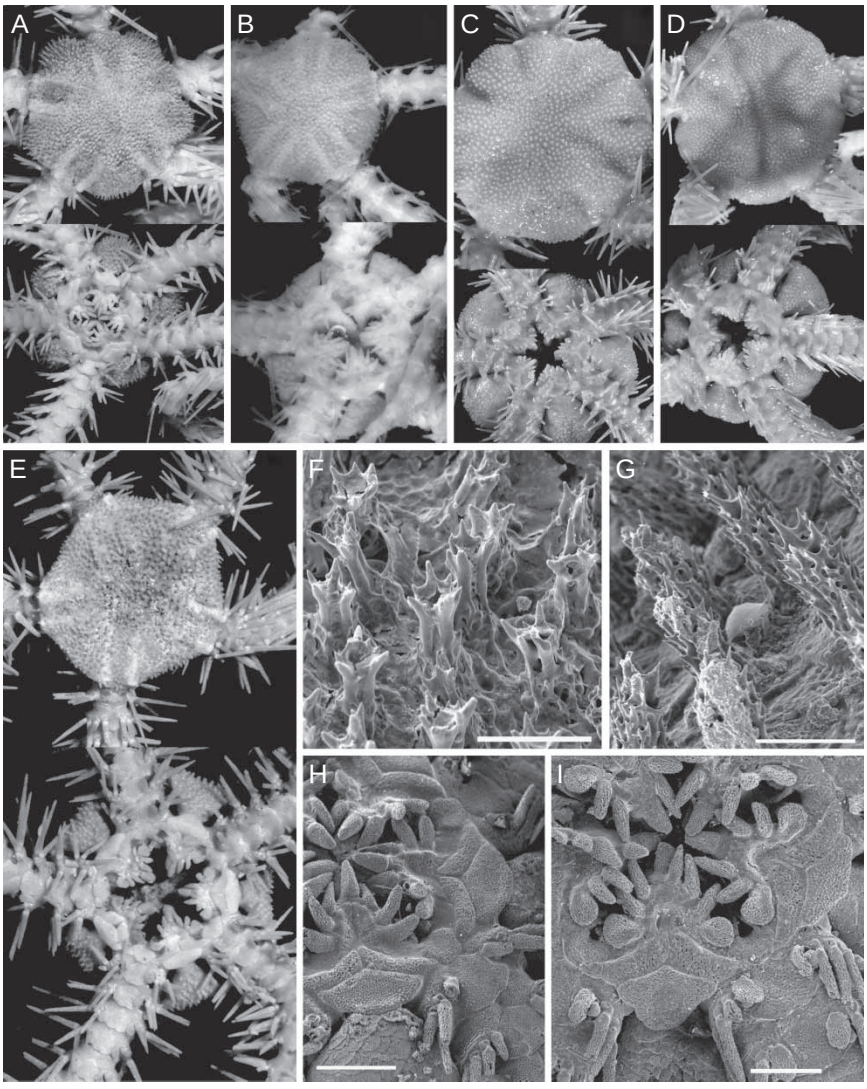

Figure 8. (A) *Ophiacantha fraterna* Verrill, 1885, ZMMU D-635, RV *Akademik Mstislav Keldysh*, St. 415, disk diameter 5.7 mm; (B) *Ophiacantha fraterna* Verrill, 1885, YPM 7241, specimen identified by A.E. Verrill, Steamer *Albatross*, St. 2562, off New Jersey, depth 2609 m, disk diameter 5.5 mm; (C) *Ophiacantha bidentata* (Retzius, 1805), syntype of *Ophiacantha spinulosa* Müller & Troschel, 1842, SMNH-Type-3289, Svalbard, West Spitsbergen, probably collected by Sven Lovén, no date, no depth, disk diameter about 15 mm; (D) *Ophiacantha bidentata* (Retzius, 1805), syntype of '*Ophiocoma*' *arctica* Müller & Troschel, 1842, SMNH-Type-5144, Svalbard, West Spitsbergen, probably collected by Sven Lovén, no date, no depth, disk diameter 10 mm; (E) *Ophiacantha bidentata* (Retzius, 1805), ZMMU D-727, RV *Sergei Vavilov*, Cruise 13, St. 1132, Barents Sea, 70°22.6′N, 55°37.1′E, depth 80–109 m, disk diameter 6.5 mm; (F) *Ophiacantha fraterna* Verrill, 1885, ZMMU D-635, RV *Akademik Mstislav Keldysh*, St. 415, disk diameter 7.2 mm, scanning electron micrograph of the spicules from dorsal side of the disk; (G) *Ophiacantha bidentata* (Retzius, 1805), ZMMU D-728, RV *Sergei Vavilov*, Cruise 11, St. 1035, Barents Sea, 70°22′N, 57°39.1′E, depth 70–90 m, disk diameter 7.5 mm, scanning electron micrograph of the spicules from dorsal side of the disk; (H) *Ophiacantha fraterna* Verrill, 1885, ZMMU D-635, RV *Akademik Mstislav Keldysh*, St. 415, scanning electron micrograph of the oral structures and proximal arm segments; (I) *Ophiacantha bidentata* (Retzius, 1805), ZMMU D-750, RV *Sevastopol*, cruise 5, St. 1238, 71°00′N, 12°56′W, depth 380 m, scanning electron micrograph of the oral structures and proximal arm segments. Dorsal and ventral views are shown in (A–E) . Scale bars: 150 μm (F, G); 1 mm (H, I). Photographs: Tanya Korshunova (A, E); Alexander Martynov (B, F–I); Sabine Stöhr (C, D).

Albatross, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00′′N, 73°03′50′′W, depth 2551 m.

USNM 1100626, paralectotypes, seven specimens identified by R. Koehler, Steamer *Albatross*, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00′′N, 73°03′50′′W, depth 2551 m.

Re-identified specimens of *O. fraterna* removed from *O. aculeata* USNM lots: USNM 24783, one specimen, re-identified by A.V. Martynov, Steamer *Albatross*, cruise of 1883, St. 2042, Massachusetts, SE of Nantucket Shoals, 39°33′00′′N, 68°26′45 W, depth 2844 m.

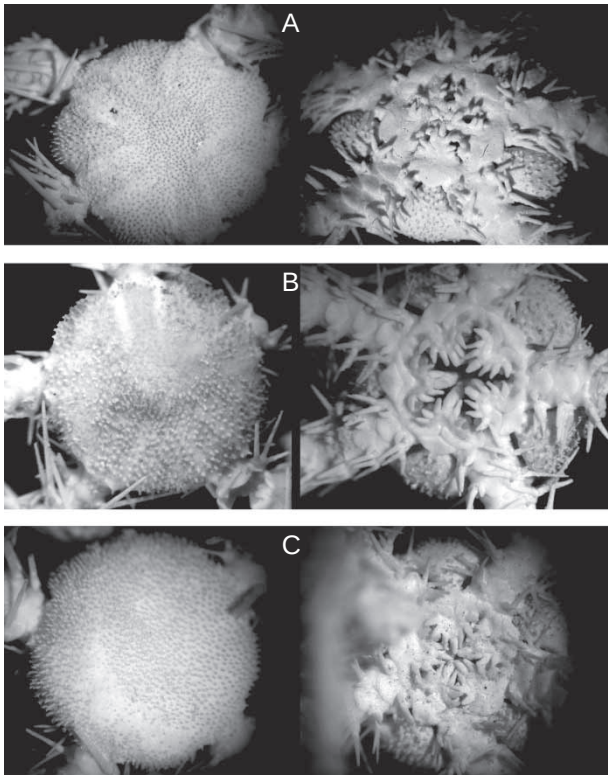

Figure 9. *Ophiacantha fraterna* Verrill, 1885. (A) USNM 7905, specimen identified by A.E. Verrill, Steamer *Albatross*, cruise of 1884, St. 2206, New Jersey, Hudson Canyon, 39°35′00″N, 71°24′30″W, depth 1907 m, disk diameter 6.5 mm; (B) lectotype USNM 33816, specimen identified by R. Koehler, Steamer *Albatross*, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00″N, 73°03′50″W, depth 2551 m, disk diameter 6.5 mm; (C) USNM 24783, specimen identified by A.E.Verrill as *Ophiacantha aculeata*, Steamer *Albatross*, cruise of 1883, St. 2042, Massachusetts, SE of Nantucket Shoals, 39°33′00″N, 68°26′45″W, depth 2844, disk diameter 7.5 mm. Dorsal and ventral views are shown. Photographs: Cynthia Ahearn.

USNM 1100630, one specimen removed from USNM 6610 *O. aculeata* lot, re-identified by A.V. Martynov, Steamer *Albatross*, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00″N, 73°03′50″W, depth 2551 m.

YPM 7679, two specimens labelled as '*Ophiacantha aculeata*, Type', actually belong to *Ophiacantha fraterna*, Steamer *Albatross*, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00″N, 73°03′50″W, depth 2551 m.

Distribution

Reliable records from south-east of New England (Verrill 1885b), from the Reykjanes Ridge, the Charlie-Gibbs Fracture Zone and the Mid-Atlantic Ridge south of the Charlie-Gibbs Fracture Zone (present study) at 1237–2440 m, from northern Rockall Trough (Tyler & Gage 1982). Specimens from BIOGAS, at least those occurring below 1500 m, identified as *O. bidentata* by Paterson (1985), also correspond to *O. fraterna*.

Remarks

Since 1885 it has been known that there is a deep-water Atlantic species similar to the shallow-water *Ophiacantha bidentata.* Verrill (1885b, 1899) was the first to separate it as *Ophiacantha fraterna*. This decision was supported only by Koehler (1914). Most authors maintained *O. fraterna* just as a variety of *O. bidentata* (Farran 1913; Grieg 1921; Mortensen 1933). Dyakonov (1954) considered deep-water specimens of *O. bidentata* under the same name as shallow-water specimens, but did not mention in the synonymy the name *fraterna* even as a variety. Baranova & Kunzevich (1969) indicated *O. fraterna* as a synonym of *O. bidentata*. In the study of reproductive biology of deep-water *Ophiacantha bidentata*, Tyler & Gage (1982) demonstrated the hermaphroditic nature of deep-water specimens, whereas the shallow-water *O. bidentata* was known as gonochoristic (Kaufman 1974; Tyler & Gage 1982). Tyler & Gage (1982) and Gage et al. (1983) concluded that the deep-water populations might represent a distinct species. However, Paterson (1985) did not find any reasons to maintain a separate deep-water species and also included *O. fraterna* into the synonymy of *O. bidentata*.

The present study confirms the view of Verrill (1885b) and Koehler (1914) that the deep-water Atlantic species *O. fraterna* differs from *O. bidentata*. *Ophiacantha fraterna* is well distinguished from *O. bidentata* by the following characters: (1) spicules of the disk of *O. fraterna* have a rosette of denticles at the top whereas in *O. bidentata* they are more club-shaped and acute at the top with denticles mainly along the sides of the spicules (compare Figure 8F and 8G); (2) the outer oral papilla in *O. fraterna* is always narrow, whereas *O. bidentata* typically has a widened outer oral papilla (compare Figure 8H and 8I); (3) the tentacle scale of *O. fraterna* is more or less narrow, acute, not widened, whereas *O. bidentata* has a widened tentacle scale (compare Figure 8A, H and 8E, I); (4) *Ophiacantha fraterna* is hermaphroditic, whereas *O. bidentata* is gonochoristic. In addition, *O. fraterna* is smaller than *O. bidentata*.

All these characters are enough to keep the species separate. Since Retzius' types of *O. bidentata* in Lund University are not traceable (Lars R. Lundqvist, personal communication), for comparative purposes in the present study we examined syntypes of the two species that had been regarded as junior synonyms of *O. bidentata*. These are *Ophiacantha spinulosa* Müller & Troschel, 1842 (SMNH-Type-3289) (Figure 8C)

and '*Ophiocoma*' *arctica* Müller & Troschel, 1842 (Figure 8D) (SMNH-Type-5144) as well as *O. bidentata* from distant regions, i.e. from Norway, the Barents Sea, the Sea of Okhotsk and the Sea of Japan. All these specimens demonstrated clear differences from deep-water Atlantic *O. fraterna*.

Ophiacantha fraterna and *O. aculeata* – two common North Atlantic species – have often been found together in considerable quantity at the same stations. Both species were described by Addison Emery Verrill in two successive works (Verrill 1885a,b). While for *Ophiacantha fraterna* already in the first description (Verrill 1885b), a diagnosis sufficient for the separation from other species even without illustrations was provided, the first description of *O. aculeata* (Verrill, 1885a) is very short and ambiguous. However, already in the same year as the first description, Verrill (1885b) published an extended description of *O. aculeata*, where diagnostic features of this species were expressed clearly. According to Verrill (1885b), *O. fraterna* is characterized by very small, rough disk spinelets terminated by several minute sharp thorns, and about three rather long, acute and spiniform oral papillae, the distalmost of which does not differ from the others. These features agree well with the specimens used in the present study. Verrill did not give the exact station where *O. fraterna* was discovered, but it is known that for both of Verrill's works of 1885 material collected during the cruise of the RV *Albatross* in 1883 was used (Verrill 1885a,b). In addition, records of the depth accompany the first description of *O. fraterna* – from 908 to 1608 fathoms. Thus we can estimate the approximate number of stations that can be included into the type series. Specimens of *O. fraterna* from the Yale Peabody Museum (e.g. YPM 7241) originated from the cruise of the *Albatross* of 1885 and therefore cannot be syntypes. At the same time, USNM keeps some specimens of *O. fraterna* which, although not labelled as syntypes, were collected during the cruise of the *Albatross* of 1883, at St. 2105, depth 2551 m (Figure 9B). These specimens were identified by Rene Koehler and used by him for the re-description of *O. fraterna* (Koehler, 1914). In the latter work Koehler mentioned that these specimens were compared with specimens identified by Verrill from *Albatross* St. 2573 in 1885. Data of the label of the eight ethanol specimens from the lot USNM 33816 (1883, St. 2105) agree well with those mentioned in Verrill's first description. All eight specimens display essentially the same structure of the disk spinelets and oral papillae and agree well with the first description of *O. fraterna*. It is necessary to highlight that the type series of both *O. fraterna* and *O. aculeata* were never located. From all the available materials from Yale Peabody Museum and the Smithsonian Institution, only the above-mentioned specimens from *Albatross* cruise 1883 lot USNM 33816 may represent syntypes of *O. fraterna*. All other specimens, even those identified personally by Verrill, originated from cruises of the *Albatross* in other years. In summary, despite some potential problems with the decision, we prefer to consider lot USNM 33816 as syntypes of *O. fraterna*.

Contrary to *O. fraterna*, the situation with *O. aculeata* is more complex. In the first description Verrill (1885a) mentioned very slender rough disk spinelets and four to five rather slender acute oral papillae. As far as very slender disk spinelets clearly point to *O. aculeata*, the 'rather slender, acute' oral papillae may apply equally to both *O. aculeata* and *O. fraterna*. However, in the extended description (Verrill 1885b) of *O. aculeata*, Verrill unambiguously mentioned the long slender disk spinelets (including specially highlighting that the spinelets are longer and more slender than in *Ophiacantha bidentata*) together with broad and flat distalmost oral papillae. Since these very broad distalmost oral papillae have an acute tip, it probably explains why he mentions the 'all acute oral papillae' in the first description. Thus, both the first and following descriptions of *O. aculeata* agree in the presence of 'long slender disk spinelets', the features characteristic exactly for *O. aculeata* and not for *O. fraterna* (Figure 10). Koehler (1914) performed a detailed study of both *Ophiacantha aculeata* and *O. fraterna* including descriptions of specimens either identified by Verrill or brought to Koehler from the same stations as those of the first description. Koehler's re-description of *O. aculeata* was based on non-identified specimens from St. 2105, *Albatross* cruise of 1883, and on specimens identified by Verrill from St. 2725, *Albatross* cruise of 1886. Current usage of the name *O. aculeata* (e.g. Paterson 1985) is thus based on Verrill's (1885b) extended description without illustrations and the re-description by Koehler (1914) including illustrations of the above-mentioned specimens. We have studied all available specimens of *O. aculeata* from various *Albatross* cruises. However, after examination of two specimens (YPM 7679) labelled as '*Ophiacantha aculeata*, Type' (Figure 11A) it was discovered that they do not belong to the species *O. aculeata*. Short disk spinelets and clearly slender oral papillae, all similar in width, including the distalmost papilla, of both YPM 7679 specimens unambiguously point to *O. fraterna*. Further study of old specimens of *O. aculeata* from USNM also discovered a similar contradiction of the current usage of the name '*O. aculeata*' including usage of this name in Verrill's descriptions and own identifications of Verrill. For

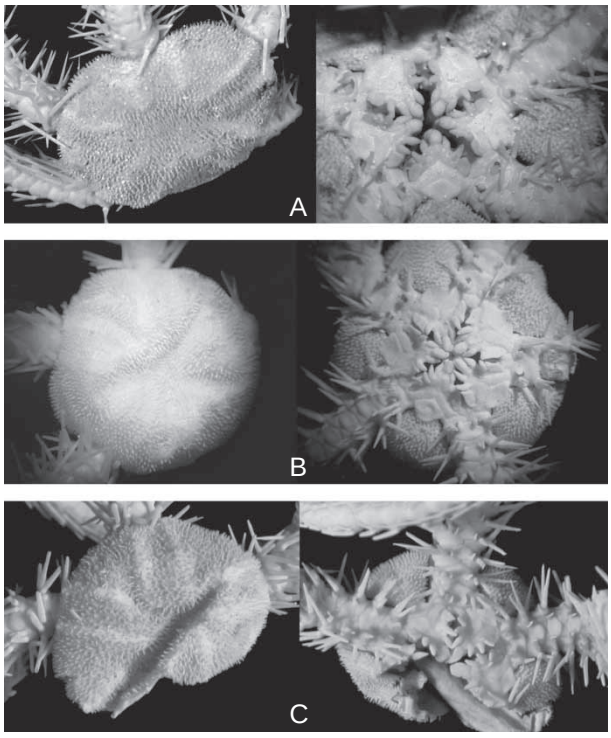

Figure 10. *Ophiacantha aculeata* Verrill, 1885. (A) USNM 27900, specimen identified by A.E. Verrill, Steamer *Albatross*, cruise of 1886, St. 2725, Virginia Beach, 36°34′00″N, 73°48′00″W, depth 2513 m, disk diameter 13 mm; (B) lectotype USNM 12669, specimen identified by R. Koehler, Steamer *Albatross*, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00″N, 73°03′50″W, depth 2551 m, disk diameter 12 mm; (C) paralectotype USNM 1100627, same data as in the lectotype, disk diameter ca. 14 mm. Dorsal and ventral views are shown. Photographs: Cynthia Ahearn.

instance, a specimen from St. 2042, *Albatross* cruise 1883 (USNM 24783) undoubtedly belongs to *O. fraterna*, but was identified by Verrill as *O. aculeata* (Figure 9C). At the same time, a specimen from St. 2725, *Albatross* cruise 1886, identified by Verrill as *O. aculeata* (Figure 10A), actually belongs to this species. Since the two specimens labelled as '*O. aculeata*, Type' (YPM 7679) and actually belonging to the species *O. fraterna* originated from the same station (*Albatross*, St. 2105, 1883) as recorded for *O. aculeata* in the first description (Verrill 1885a), further usage of these exemplars as types will lead to confusion between two common North Atlantic deep-water species of *Ophiacantha*. As was already mentioned above, Verrill (1885a,b) in two works published in the same year unambiguously differentiated the species, *O. aculeata* and *O. fraterna*. Thus we consider the discovered confusion with identifications of *O. aculeata* by Verrill as secondary. It may be explained by further incorrect determination of various specimens, some of which then were designated as a 'type'. To preserve the current usage of the species names *O. aculeata* and *O. fraterna*, which are based on correct interpretations of Verrill's first descriptions (1885a,b), Verrill's extended description of *O. aculeata* (1885b) and re-descriptions of both species by Koehler (1914), and to avoid further confusion, we here designate lectotypes for both species. For *O. fraterna* the designated lectotype is selected from syntypes of the lot USNM 33816 (Figure 9B), for *O. aculeata* the designated lectotype is selected from syntypes of the lot USNM 12669 (Figure 10B). Paralectotypes of *O. fraterna* are seven specimens, USNM 1100626, paralectotypes of *O. aculeata* are three specimens, USNM 1100627 correspondingly.

Ophiacantha simulans Koehler, 1896
(Figure 11B)

Ophiacantha simulans: Koehler 1896a: 82, Plate 4, Figures 37, 38; Paterson 1985: 39–40, Figure 17.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 415, one specimen; St. 464, two specimens.

Distribution

The North Atlantic, in the west – off Carolinas, in the east – from Iceland to the Azores, at 1575–3018 m (Paterson 1985) and of Morocco, at the depth 1750 m (Bartsch 1987). Present study: the Reykjanes Ridge, at 1535–1785 m.

Ophiacantha spectabilis G.O. Sars, 1871
(Figure 11C)

Ophiacantha spectabilis: G.O. Sars 1871: 10; Paterson 1985: 41, Figure 18.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 464, one specimen.

Distribution

The North Atlantic: off Nova Scotia, south of Iceland, Norway, south-west Ireland, Bay of Biscay, at depths 145–1700 m (Paterson 1985). Present study: Reykjanes Ridge, at 1670–1750 m.

Ophiacantha veterna Koehler, 1907
(Figure 11D)

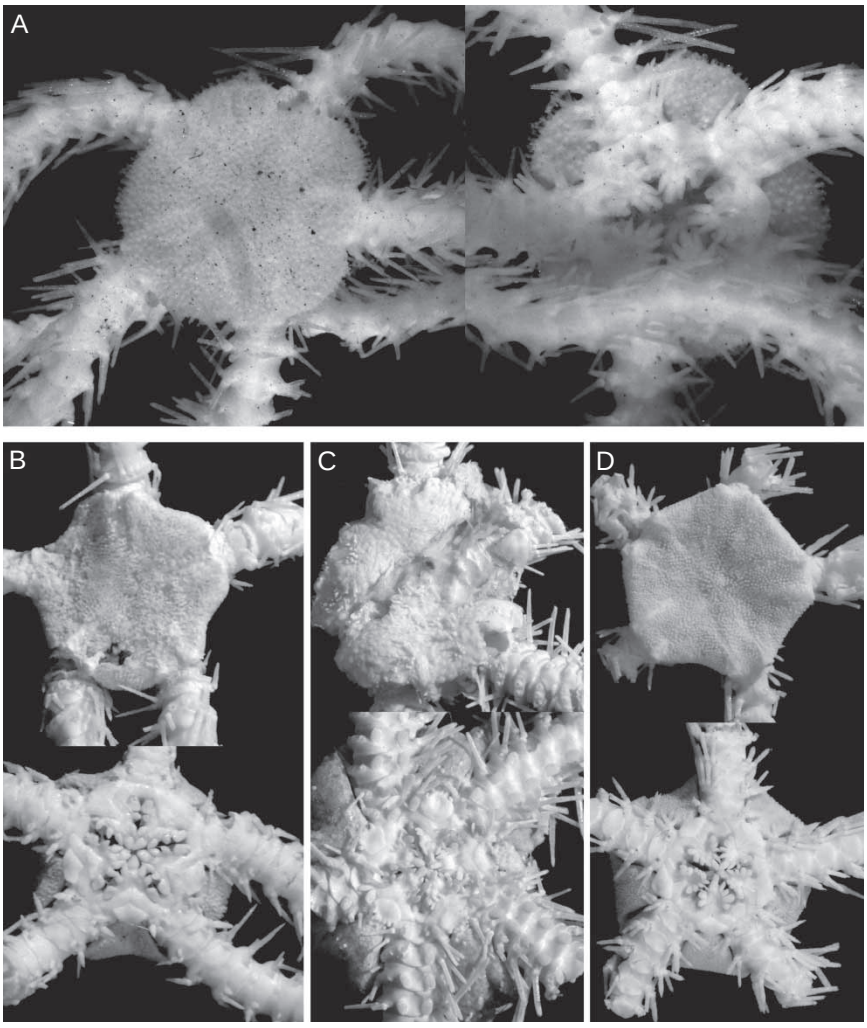

Figure 11. (A) *Ophiacantha fraterna* Verrill, 1885, specimen labelled as '*Ophiacantha aculeata*, Type', YPM 7679, Steamer *Albatross*, cruise of 1883, St. 2105, off Delaware Bay, 37°50′00″N, 73°03′50″W, depth 2551 m, disk diameter 6 mm; (B) *Ophiacantha simulans* Koehler, 1896, ZMMU D-640, RV *Akademik Mstislav Keldysh*, St. 464, disk diameter 6 mm; (C) *Ophiacantha spectabilis* G.O. Sars, 1871, ZMMU D-660, RV *Akademik Mstislav Keldysh*, St. 464, disk diameter ca. 11 mm; (D) *Ophiacantha veterna* Koehler, 1907, ZMMU D-657, RV *Akademik Mstislav Keldysh*, St. 464, disk diameter 7.5 mm. Dorsal and ventral views are shown. Photographs: Tanya Korshunova.

Ophiacantha veterna: Koehler 1907b: 41.
Ophiacantha enopla veterna: Paterson 1985: 37, Figure 16.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 464, three specimens.

Distribution

Prior to this study *O. veterna* was recorded only from the Bay of Biscay and south of the Azores and Madeira at 101–2300 m (Koehler 1907b; Paterson 1985; Stöhr & Segonzac 2005). Now the range is extended to the north to the Reykjanes Ridge, at 1670–1750 m.

Remarks

Paterson (1985) considered *O. veterna* as a subspecies of *O. enopla* Verrill, 1985. We believe that characters distinguishing *O. enopla enopla* from *O. enopla veterna* listed by Paterson are enough to maintain them as separate species. Especially characteristic is the shape of tentacle scales in *O. veterna*: these are very small compared to those of *O. enopla* and are missing on distal arm segments.

Ophiocamax patersoni sp. nov.
(Figures 13D, 14, 15C, F, 16H, I)

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 52/374, holotype (ZMBN 77854, dried), one paratype

(ZMBN 77855, dried), St. 50/373, 10 paratypes (ZMBN 77856, in ethanol), two paratypes (ZMMU D-748, dried), St. 72/386, one paratype (ZMBN 77857, in ethanol).

Etymology

This species is named in honour of Gordon L.J. Paterson (The Natural History Museum, London) for his important contribution in studying North Atlantic Ophiuroidea.

Description of the holotype

The disk has diameter 17.5 mm, is domed and circular, but indented interradially to various degrees – from minor to considerable. The disk plates are numerous, different in size and shape, from small to moderate, irregular-rhomboidal and -polygonal, bearing one or few long spines. Some spines bearing at about mid-length a few irregularly placed short thorns, whereas others lack distinct thorns. Proximal to the radial shields the disk plates are larger and fewer, whereas in the centre of the disk and in the interradii the plates are smaller. Radial shields (2–3 mm in length) are relatively small, about one-sixth of the disk diameter, irregularly triangular in outline, proximally narrowed and obtuse pointed, distally widened, joined at almost their length, but in two interradii have irregular row of spinelets in-between. At the distal border of the radial shields and between the first dorsal arm plate there is a dense irregular row of spines. The interradii are swollen, ventrally covered by spines; close to the oral shields the interradial scales bear short tubercle-like spines or are naked. Each jaw bears two or three irregularly placed narrow spiniform apical papillae. The latter are hardly distinguished from teeth and from adjacent lateral oral papillae. Nevertheless, the first pair of the lateral papillae is quite distinct. Other papillae are placed along jaws in two irregular rows – one internal and one external. At least two pairs placed dorsally in the middle of the jaws. The distal papillae are similar to the proximal ones in shape, differing only in length, but forming a semicircular comb around the second tentacle pore. The first papillae are pointed, narrow. Sometimes additional papillae are placed between apical and first papillae. The shape of the oral shield can be described as wide-arrowhead with straight rather long distal part attached to the interradius and triangular proximal part, completely separated from the first lateral arm plate by the wide adoral shields. The madreporic oral shield is swollen and has lost its usual shape. One to five rough spindle-shaped papillae (in one interradius these papillae probably are lost) are placed on the proximal edge of the madreporite. Two oral shields also have two tubercles at their distal edge. Arm length is about four times the disk diameter. The dorsal arm plates are broad, fan-shaped, rather large, entirely separated by the lateral arm plates, even on most basal segments. The proximal edge of the dorsal arm plate is almost straight throughout the length of the arm, whereas on the basal segments this edge is slightly triangular. The distal edge of the dorsal arm plate is semicircular and distinctly covered with sparse quite long thorns. These thorns are present already on most basal segments and placed in few irregular rows – one more close to the distal edge, whereas others are placed farther from the edge of the dorsal arm plate. The proximal area of the dorsal arm plate is also covered sparsely with short thorns or spiny small tubercles. On the basal segments these proximal thorns are more developed, whereas towards the distal end of the arm they tend to be reduced. The middle area of the dorsal arm plates has few and weakly developed thorns or is fully devoid of them. Most distal dorsal arm plates have ca. five blunt tubercle-shaped distal thorns and few prominent needle-shaped thorns on the middle line of the lateral plates. Arms have distinct nodes and form a strong lateral ridge on which the spine arm articulation ridges are placed. On most proximal segments there are eight or nine spines, in the middle of the arm – six or seven, distally – five or six. The dorsalmost spine is shortest, the second slightly longer and the third is longest and strongest (about four segments in length). The next spine is considerably shorter and following spines are gradually reduced in size. Sparse quite long thorns cover the dorsal spines including the longest, whereas the more ventrally placed spines have a rough surface with some short denticles. The first ventral arm plate is rather small, trapezoid. The second ventral arm plate is very remarkable – distally rhomboid, proximally with two semicircular lateral wings corresponding to the large basal tentacle pore. The third and fourth ventral arm plates are also distally rhomboid (about two times wider than long) and proximally show traces of the above described structure, which disappears towards the middle of the arm and again becomes more developed on more distal segments. Further ventral arm plates towards the middle of the arm have a triangular proximal lobe, while they are polygonal with rounded angles distally. Some segments have nearly ovoid ventral arm plates. The distalmost segments have a rather trapezoid distal part of the ventral arm plate. Ventral plates throughout the length of the arm are separated. The tentacle pores are larger and more conspicuous proximally than towards the distal end

of the arm, where they become small and inconspicuous. Basally around the tentacle pores at least four tentacle scales are placed. The basal tentacle scales are large, narrowly conical, with widened base and gradually sloped towards top. Towards the distal end of the arm the number of tentacle scales reduced to two and then to one. About at mid-length of the arm the tentacle scales became spindle-shaped, and at the distalmost segments they turn into a rather short tubercle.

Paratype variations

The smallest paratype with disk diameter 8.5 mm (radial shields approximately 0.8–0.9 mm) is different compared to the large specimen disk spine structure. These spines, both in the centre and periphery have a well-developed basal rosette of four or five long thorns and several also have long denticles towards the top of the spine. At the distal border of the radial shields similar spines are placed, with a basal rosette of denticles. The radial shields are very short and irregularly square in outline, entirely joined in some radii, whereas in others slightly divergent proximally. The dorsal arm plates, especially on the seven or eight proximal segments at their distal edge heavily covered by long spines (15–20 spines on the mentioned segments), which are arranged in two irregular rows. Towards the middle of the arm the spines become more tubercle-shaped and reduced in number. The oral papillae are more irregular than in the holotype, the single large, and small additional rows of papillae encircling the second tentacle pores are especially well developed. The additional papillae are placed on the adoral shields instead of on the oral shield, and the shape of the papillae are approaching the shape of the disk spines but more massive and with lesser developed rosette of denticles. The oral shields are more or less hourglass-shaped. The tentacle scales on all segments, including the proximalmost, are spiniform and not massive conical. At least one tentacle scale has a wide base contrasting with its narrow remaining part. The tentacle scales are rough, some have distinct thorns. Proximally there are seven to nine spines, five or six towards the distal end of the arm. The largest paratype of 19.5 mm disk diameter (radial shields 3–4 mm in length) has disk spines that are roughly spiniform but without thorns. Only a few spines in the interradii have two or three blunt thorns. The radial shields are triangular, some with obtuse proximal angle, whereas others have an acute angle. The radial shields are in contact for most of their length, but in two radii there is a distinct narrow insertion plate in-between. Proximally the radial shields are divergent. All dorsal arm plates bear on their distal edge a set of, to a various degree developed, blunt short spines (on proximal segments) or tubercles, 15–20 in number on proximal segments. Few short sharp spines or tubercles are placed also proximally on the dorsal arm plate. The dorsal arm plates are rhomboidal, wider than long. Towards the middle of the arm the dorsal plates became wider and shorter. All dorsal arm plates are not contiguous but the basalmost plates lie very close to each other due to somewhat dorsally shifted arms.

The oral papillae have a more irregular appearance than in the holotype, but they also have two distinct irregular rows around the tentacle pore (laterally they are adjoining true tentacle scales). The tentacle scales at the second and third segments are very long, narrow, up to five in number, with a smooth surface. The oral shield is shaped with a proximal wide triangular part with slightly convex sides, and a triangular lobe of considerable size. At the lateral sides of the distal edge of the triangular lobe there are usually one or two pairs of long narrow papillae. The distal part of the oral shield is short and wide.

Distribution

The Charlie-Gibbs Fracture Zone, the Mid-Atlantic Ridge north of the Azores, 2522–2979 m.

Remarks

For comparative purposes we studied type material of various species of the genus *Ophiocamax* as well as non-type specimens of *O. dominans* Koehler, 1906 identified by Ilse Bartsch. Since species of the genus *Ophiocamax* are difficult to distinguish, we illustrate here the above-mentioned material. From the geographically closest species *O. dominans* Koehler, 1906 (known presently only off Sahara, and never reported from the Reykjanes Ridge), *Ophiocamax patersoni* sp. nov. clearly differs in the following characters. Disk plates are more numerous, radial shields are relatively small (from one-fifth to one-tenth of the disk diameter in *Ophiocamax patersoni* sp. nov. and from one-half to three-quarters in *O. dominans*; the latter according to Paterson (1985) (compare Figures 12A, 15A and 13D, 14A, B, 15C, F). In the specimens identified by Bartsch we found the length of the radial shield to the disk diameter to be one-third to one-fifth, thus not considerably different from *Ophiocamax patersoni* sp. nov. Disk spines of *Ophiocamax patersoni* sp. nov are narrow elongated cones, almost devoid of the long thorns in large specimens (few can be found in the interradial area), whereas in large specimens of *O. dominans* most disk spines presented massive spines with

conspicuous thorns. The distal edges of the radial shields of *Ophiocamax patersoni* sp. nov. are heavily covered with long spines (Figure 15C), whereas *O. dominans* has radial shields almost devoid of spines at their distal edge (Figure 15A). The dorsal arm plates of *Ophiocamax patersoni* sp. nov. are rhomboidal, slightly convex at their proximal edge, and form an obtuse angle at the distal edge, wider than long, not contiguous even on most basal segments (Figures 13D, 14A–C, 15C, F) (*O. dominans* has dorsal arm plates clearly triangular, distal edge convex, proximal edge represented by an acute angle, clearly contiguous at the basal segments and still nearly in contact (Figures 12A, 15A).) In *Ophiocamax patersoni* sp. nov. most dorsal arm plates have distal edges heavily covered with relatively long spines or obtuse tubercles (Figures 14C–E, 15C, F), whereas in *O. dominans* they are entirely devoid of spines (Figure 15A), except for the distal part of the arms where two tiny spines appear (according to Bartsch 1987). The shape of the oral shield of *Ophiocamax patersoni* sp. nov. is an arrow-head (proximal part is large, acutely triangular with slightly concave lateral sides) (Figure 16H, I), whereas *O. dominans* has the oral shield irregularly hour-glass-shaped (Figure 16A). Another Atlantic species, *O. fasciculata* Lyman, 1883 from the Caribbean region, also differs considerably from *Ophiocamax patersoni* sp. nov. by a number of features: dorsal arm plates clearly triangular, distal edge convex, proximal edge represented by an acute angle, clearly contiguous on the basal segments and still nearly in contact, most dorsal arm plates entirely devoid of spines (Figures 12B, 15B), oral shields with large ovoid proximal part with small triangular lobe and short wide distal edge (Figure 16B), apical and oral papillae are very irregular, tentacle scales with considerably widened base (Figures 12B, 16B). The only other Caribbean species, *O. hystrix* Lyman, 1878 (and very similar to this species *Ophiocamax austera* Verrill, 1899), has slightly rugose dorsal and lateral arm plates (Figure 15D), but in other characters it differs greatly from *Ophiocamax patersoni* sp. nov.: distinctly lobed disk, deeply notched interradially thus forming a very small central area (Figure 12C), disk covered with short massive conical stumps or blunt tubercles, trapezoid dorsal arm plates contiguous basally (Figure 15D), oral papillae placed proximally in two distinct clusters (Figure 16C), ovoid proximal part of the oral shield with small triangular proximal lobe and distinct swollen tubercle on distal edge (Figure 16C). The North Atlantic *Ophiocamax patersoni* sp. nov. is by general appearance and shape and structure of the dorsal arm plates even more similar to Antarctic species of the genus – *O. gigas* Koehler, 1901 and especially to *O. drygalskii* Hertz, 1927. *Ophiocamax gigas* differs from *Ophiocamax patersoni* sp. nov. in the numerous short spinelets of the disk having few thorns at the top (Figure 13A), dorsal arm plates with convex proximal edge and distal edge forming an obtuse angle covered by a single regular row of rounded tubercles (Figure 15E), the oral shield heavily covered with thorny spines (Figure 16E) and tentacle scales with few denticles at the top. *Ophiocamax drygalskii* Hertz, 1927 differs from *Ophiocamax patersoni* sp. nov. in the numerous short spinelets of the disk having few denticles at the top or along their sides (even in large specimens) (Figure 13B, C), proximal edge of the dorsal arm plate distinctly triangular – from acute to obtuse angle, nearly contiguous on basal segments (Figures 13B, C, 15G, H), oral shield hour-glass-shaped or with very elongated proximal part (Figure 16F, G). It is necessary to note that in the studied type specimens of *O. drygalskii* the shape of the oral shield is quite variable. Different shapes of the oral shields were observed even within single specimen (madreporic oral shield is not considered). At the same time, *Ophiocamax patersoni* sp. nov. does not display such polymorphism and all studied large specimens have essentially the same shape of the oral shield, well distinguished from *O. drygalskii* by this character. *Ophiocamax applicatus* Koehler, 1922 described off Tasmania, Australia is considerably larger than *Ophiocamax patersoni* sp. nov. and has proximally contiguous triangular dorsal arm plates. *Ophiocamax brevicetra* Baker, 1974, off Otago, New Zealand, differs from *Ophiocamax patersoni* sp. nov. in shape of disk spinelets, structure of spines, shape of thorns at distal edge of the dorsal arm plates and in shape of the oral shield.

Finally, the common Indo-West Pacific deep-water species *O. vitrea*, which was recently shown as being very polymorphic (O'Hara & Stöhr 2006), is well distinguished from *Ophiocamax patersoni* sp. nov. by the shape and structure of the disk spines and spines of the arm (Figures 12D, 15I), numerous irregular oral papillae and the shape of the oral shield (Figure 16D).

Thus, in the North and Middle Atlantic there are several locally distributed, but well-distinguished species – in the Caribbean region *O. fasciculata* and *O. hystrix*; off Northern Africa *O. dominans*; and on the Charlie-Gibbs Fracture Zone and the Mid-Atlantic Ridge north of the Azores *Ophiocamax patersoni* sp. nov.

Ophiolimna bairdi (Lyman, 1883)
(Figure 17A)

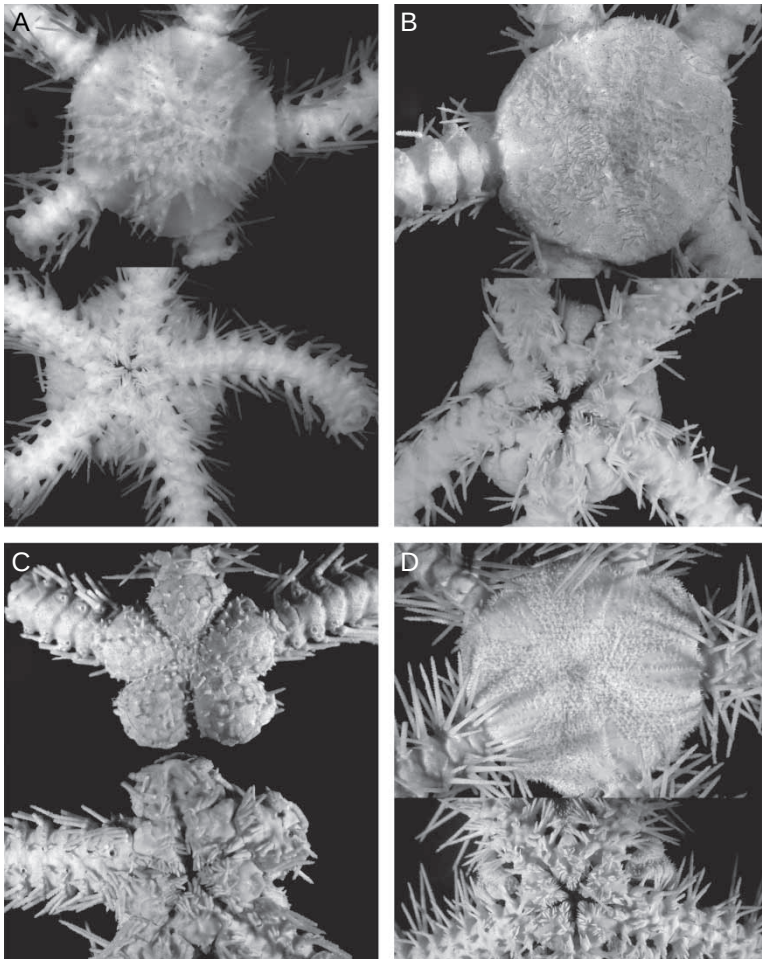

Figure 12. (A) *Ophiocamax dominans* Koehler, 1906, ZSM 20043260, RV *Meteor*, Cruise 36, St. 98/ES 148, off Spanish Sahara, 25°40.8′N, 16°02.0′W, depth 883–992 m, disk diameter 11.1 mm; (B) *Ophiocamax fasciculata* Lyman, 1883, holotype MCZ 2082, *Blake*, St. 209, off Martinique, depth ca. 344 m, disk diameter 14 mm; (C) *Ophiocamax hystrix* Lyman, 1878, holotype MCZ 2084, *Blake*, off Havana, Cuba, depth ca. 318 m, disk diameter 13 mm; (D) *Ophiocamax vitrea* Lyman, 1878, syntype MCZ 2096, *Challenger*, St. 219, off Admiralty Is., depth ca. 273 m, disk diameter 17 mm. Dorsal and ventral views are shown. Photographs: Tanya Korshunova (A); Alexander Martynov (B–D).

Ophiacantha bairdi: Lyman 1883: 256, Plate 5, Figures 70–72.
Ophiolimna bairdi: Verrill 1899: 40, 44; Paterson 1985: 60, Figure 24.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 316-5, 56 specimens; St. 415, one specimen; St. 445, three specimens; St. 478, one specimen; St. 499, 10 specimens.

Distribution

Arctic Ocean; North Atlantic: in the west – south of Martha's Vineyard, east – from the Rockall Trough to south of Portugal, at 620–2600 (Dyakonov 1954; Paterson 1985). Present study: the Reykjanes Ridge, at 1535–2440 m.

Family Ophiactidae

Histampica duplicata (Lyman, 1875)
(Figure 17B)

Amphiura duplicata: Lyman 1875: 19–20, Text figure 87, Plate 5, Figure 78.
Ophiactis duplicata: Lütken & Mortensen 1899: 142–3, Plate 6, Figures 1–3.
Amphiactis duplicata: Matsumoto 1915: 66–7.
Histampica duplicata: A.M. Clark 1970: 73–4.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 418, two specimens.

Distribution

The Caribbean, the Pacific Ocean. North Atlantic records: Bay of Biscay to north Africa, at 125–2870 m

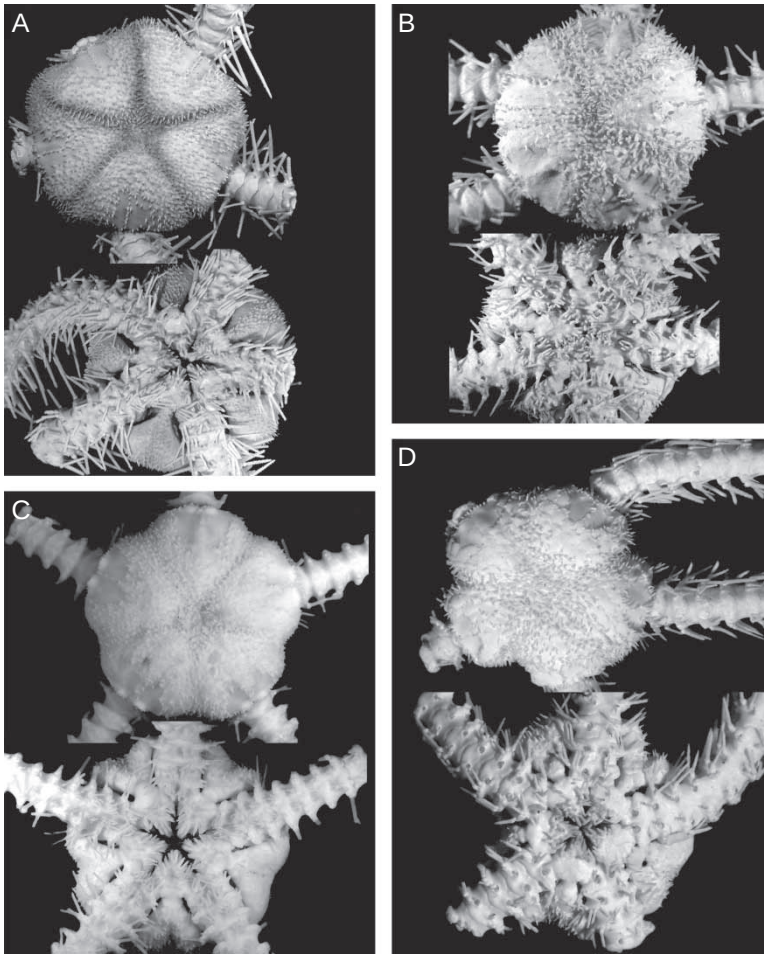

Figure 13. (A) *Ophiocamax gigas* Koehler, 1901, IORAS 5.1, RV *Akademik Kurchatov*, Cruise 11, St. 881, 57°8′S, 26°42′W, depth 932 m, disk diameter 34 mm; (B) *Ophiocamax drygalskii* Hertz, 1927, syntype ZSM 20001015/2, Deutsche Südpolar-Expedition, 65°31′S, 85°14′W, depth 2450 m, disk diameter 19.8 mm; (C) *Ophiocamax drygalskii* Hertz, 1927, syntype ZSM 20001015/1, 65°31′S, 85°14′W, depth 2450 m, disk diameter 20.1 mm; (D) *Ophiocamax patersoni* sp. nov., holotype ZMBN 77854, MAR-ECO St. 52/374, disk diameter 17.5 mm. Dorsal and ventral views are shown. Photographs: Alexander Martynov (A, D); Tanya Korshunova (B, C).

(Paterson 1985). Present study: the Reykjanes Ridge, at 1815–1915 m.

Ophiactis abyssicola (M. Sars, 1861)
(Figure 17C–E)

Amphiura abyssicola: M. Sars 1861: 18.
Ophiactis abyssicola: Ljungman 1867: 324; Paterson 1985: 76–8, Figure 32.
Ophiactis poa: Lyman 1882: 119.
Ophiactis echinata: Koehler 1898: 48.
Ophiactis corallicola: Koehler 1896a: 75.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 42/368, one specimen; St. 53/375, one specimen; St. 60/379, 25 specimens; St. 62/380, 13 specimens; St. 65/382, five specimens; St. 70/385, seven specimens; RV *Akademik Mstislav Keldysh*, fourth cruise, St. 319, 13 specimens; St. 364, five specimens; St. 385, 56 specimens; St. 415, three specimens; St. 418, one specimen; St. 445, 40 specimens; St. 446, three specimens; St. 464, one specimen; St. 465, 65 specimens; St. 478, one specimen; St. 489, 15 specimens.

Distribution

North Atlantic: Davis Strait, off Iceland, Faeroe Islands, from Norway to southern Africa, at 121–4721 m (Paterson 1985). Present study: the Reykjanes Ridge, at 607–2107 m.

Remarks

Mortensen (1933) recorded six- and seven-armed specimens of this species as a rare abnormality. This feature was confirmed in the present study (Figure 17C–E). Other characters are essentially the same as in common five-armed specimens. In our material

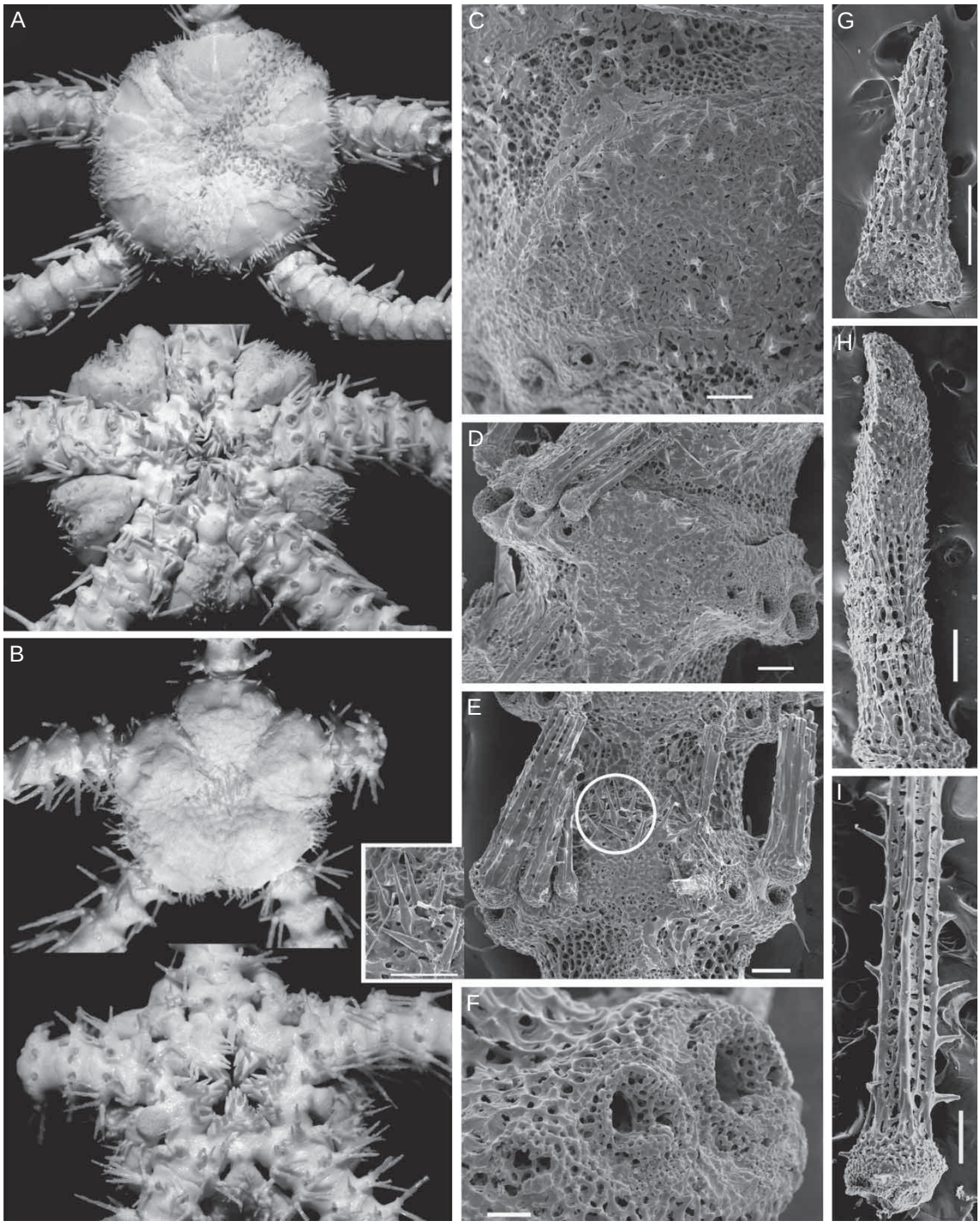

Figure 14. *Ophiocamax patersoni* sp. nov. (A) Paratype ZMMU D-748, MAR-ECO St. 50/373, disk diameter 19.5 mm, dorsal and ventral views; (B) paratype ZMMU D-748, MAR-ECO St. 50/373, disk diameter 8.5 mm, dorsal and ventral views; (C) holotype ZMBN 77854, scanning electron micrograph of dorsal arm plate, basal segments; (D) holotype ZMBN 77854, scanning electron micrograph of dorsal arm plate, distal segments; (E) paratype ZMMU D-748, disk diameter 8.5 mm, scanning electron micrograph of dorsal arm plate, basal segments (enlarged view of spines also shown); (F) paratype ZMMU D-748, disk diameter 8.5 mm, scanning electron micrograph of arm spine articulation ridges, middle segments; (G) paratype ZMMU D-748, disk diameter 19.5 mm, scanning electron micrograph of tentacle scale, basal segments; (H) paratype ZMMU D-748, disk diameter 19.5 mm, scanning electron micrograph of ventral arm spine, middle segments; (I) paratype ZMMU D-748, disk diameter 19.5 mm, scanning electron micrograph of basal part of third arm spine, middle segments. Scale bars: 300 μm (C–E, G–I); 100 μm (F). Photographs: Alexander Martynov.

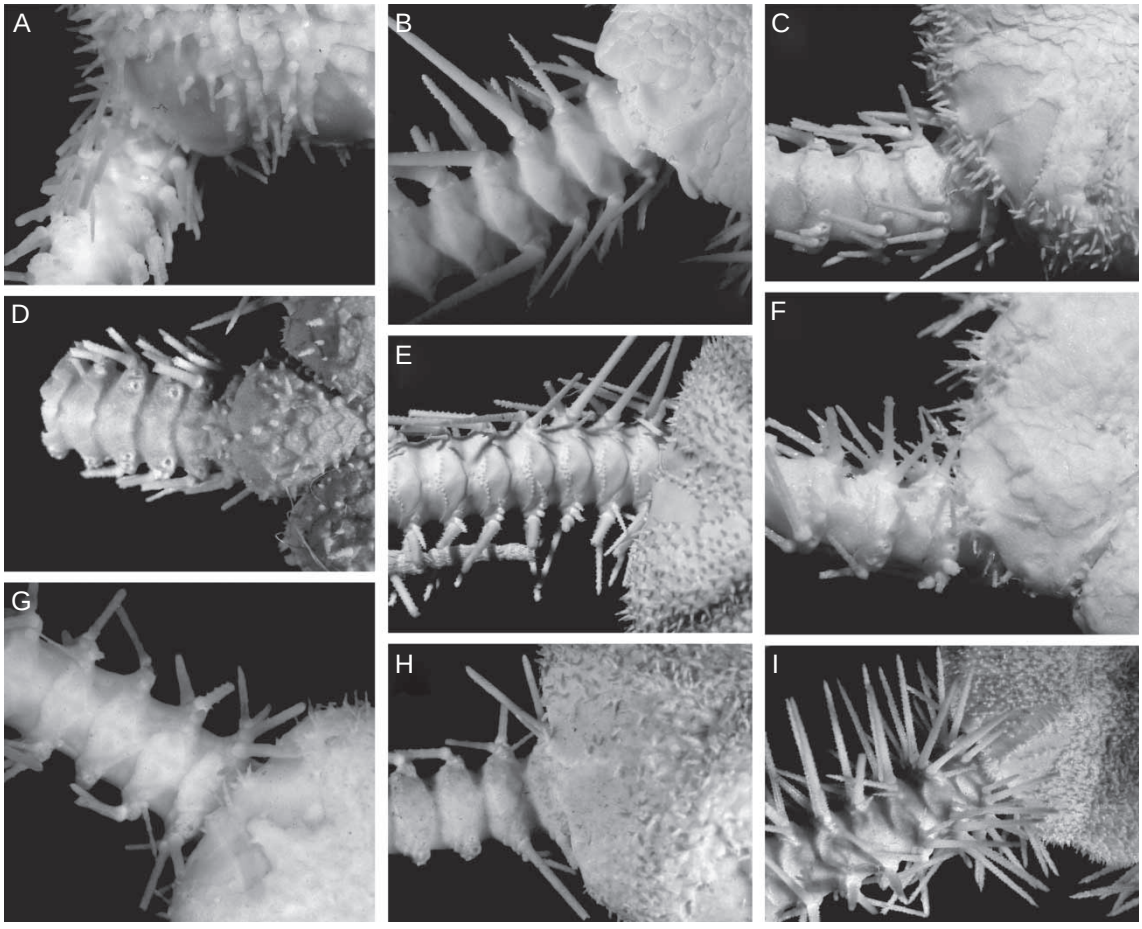

Figure 15. Segment of the disk and basal part of the arm of various *Ophiocamax* species. (A) *Ophiocamax dominans* Koehler, 1906, ZSM 20043261, RV *Meteor*, Cruise 36, St. 98/AT 149, off Spanish Sahara, 25°31′05″N, 16°02′00″W, depth 658–888 m, disk diameter 16.5 mm; (B) *Ophiocamax fasciculata* Lyman, 1883, paratype MCZ 4613, *Blake*, St. 145, 147, 148, off St Kitts, 378–491 m, disk diameter 18 mm; (C) *Ophiocamax patersoni* sp. nov., paratype ZMMU D-748, MAR-ECO St. 50/373, disk diameter 19.5 mm; (D) *Ophiocamax hystrix* Lyman, 1878, holotype MCZ 2084, *Blake*, off Havana, Cuba, depth ca. 318 m, disk diameter 13 mm; (E) *Ophiocamax gigas* Koehler, 1901, RV *Akademik Kurchatov*, Cruise 11, St. 881, 57°8′S, 26°42′W, depth 932 m, disk diameter 34 mm; (F) *Ophiocamax patersoni* sp. nov., paratype ZMMU D-748, MAR-ECO St. 50/373, disk diameter 8.5 mm; (G) *Ophiocamax drygalskii* Hertz, 1927, syntype ZSM 20001015/1, 65°31′S, 85°14′W, depth 2450 m, disk diameter 18.1 mm; (H) *Ophiocamax drygalskii* Hertz, 1927, syntype ZSM 20001015/2, Deutsche Südpolar-Expedition, 65°31′S, 85°14′W, depth 2450 m, disk diameter 20.9 mm; (I) *Ophiocamax vitrea* Lyman, 1878, syntype MCZ 2096, *Challenger*, St. 219, off Admiralty Is., depth ca. 273 m, disk diameter 17 mm. Photographs: Tanya Korshunova (A, G, H); Alexander Martynov (B–F, I).

this species was found associated with the sponge *Hertwigia falcifera* Schmidt, 1880.

Ophiothamnus chariis H.L. Clark, 1915
(Figure 17F, G)

Ophiacantha gracilis Verrill 1885b: 548.
Ophiothamnus gracilis: Verrill 1899: 41.
Ophiothamnus chariis H.L. Clark 1915: 208; Mortensen 1933: 44–5, Figure 27.

Material

RV *G.O. Sars*, MAR-ECO cruise, St. 60/379, one specimen.

Distribution

Off Nova Scotia, 400–1561 m (Verrill 1885b) and Davis Strait, at 700–1055 m (Mortensen 1933). Present study: the Reykjanes Ridge, at 1237–1296 m. This species was omitted by Paterson (1985) and recorded here for the first time after 70 years.

Family Ophiochitonidae

Ophiochiton ternispinus Lyman, 1883
(Figure 17H)
Ophiochiton ternispinus Lyman 1883: 255–6, Plate 5, Figures 67–69; Paterson 1985: 96–7, Figure 39.

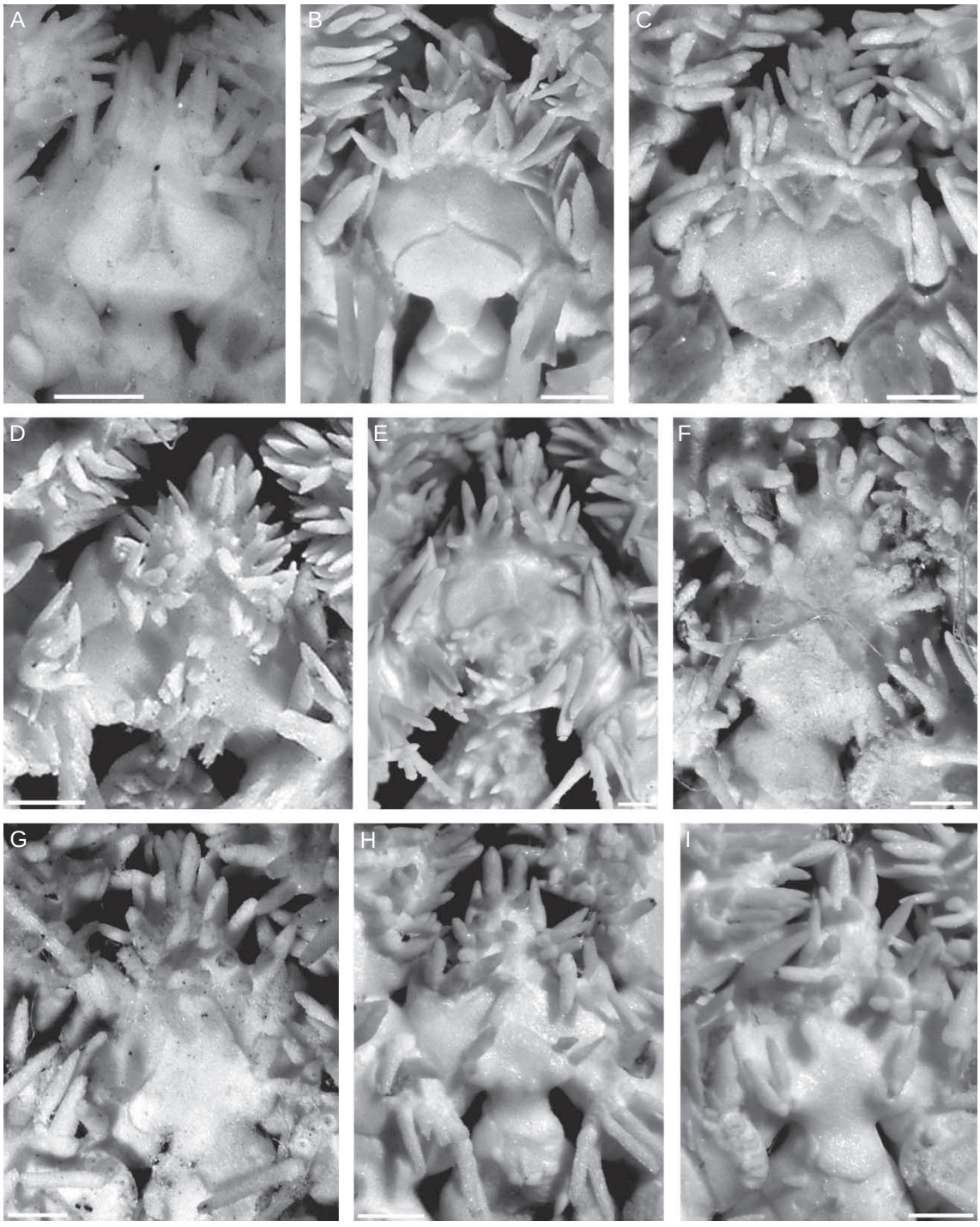

Figure 16. Oral frame showing shape of the oral shield of various *Ophiocamax* species. (A) *Ophiocamax dominans* Koehler, 1906, ZSM 20043261, RV *Meteor*, Cruise 36, St. 98/AT 149, off Spanish Sahara, 25°31.5′N, 16°02.0′W, depth 658–888 m. (B) *Ophiocamax fasciculata* Lyman, 1883, paratype MCZ 2083, *Blake*, St. 295, off Barbados, ca. 328 m. (C) *Ophiocamax hystrix* Lyman, 1878, holotype MCZ 2084, *Blake*, off Havana, Cuba, depth ca. 318 m. (D) *Ophiocamax vitrea* Lyman, 1878, syntype MCZ 2096, *Challenger*, St. 219, off Admiralty Is., depth ca. 273 m. (E) *Ophiocamax gigas* Koehler, 1901, RV *Akademik Kurchatov*, Cruise 11, St. 881, 57°08′S, 26°42′W, depth 932 m. (F, G) *Ophiocamax drygalskii* Hertz, 1927, syntype ZSM 20001015/2, Deutsche Südpolar-Expedition, 65°31′S, 85°14′W, depth 2450 m. (H, I) *Ophiocamax patersoni* sp. nov.: (H) holotype ZMBN 77854, MAR-ECO St. 52/374; (I) paratype ZMMU D-748, MAR-ECO St. 50/373, disk diameter 19.5 mm. Scale bars: 1 mm. Photographs: Tanya Korshunova (A, F, G); Alexander Martynov (B–E, H, I).

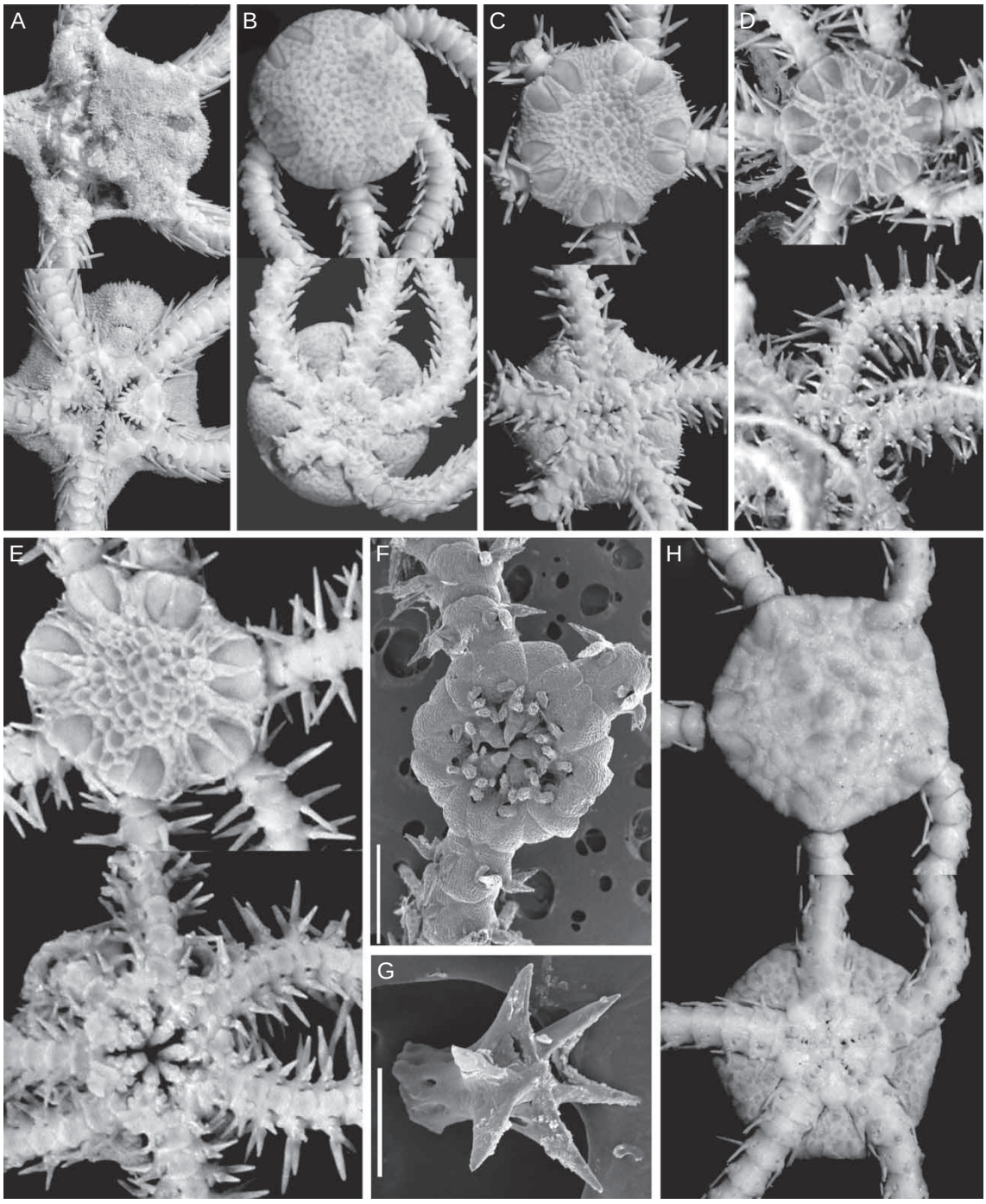

Figure 17. (A) *Ophiolimna bairdi* (Lyman, 1883), ZMMU D-648, RV *Akademik Mstislav Keldysh*, St. 499, disk diameter 11 mm. (B) *Histampica duplicata* (Lyman, 1875), ZMMU D-729, RV *Akademik Mstislav Keldysh*, St. 445, disk diameter 5.5 mm. (C) *Ophiactis abyssicola* (M. Sars, 1861), ZMMU D-634, RV *Akademik Mstislav Keldysh*, St. 478, five-armed specimen, disk diameter 6.5 mm. (D) *Ophiactis abyssicola* (M. Sars, 1861), MAR-ECO, St. 60/379, six-armed specimen, disk diameter 5 mm. (E) *Ophiactis abyssicola* (M. Sars, 1861), MAR-ECO, St. 60/379, seven-armed specimen, disk diameter 4.8 mm. (F, G) *Ophiothamnus chariis* H.L. Clark, 1915, MAR-ECO, St. 60/379: (F) scanning electron micrograph of the ventral side; (G) scanning electron micrograph of the spicule of the disk. (H) *Ophiochiton ternispinus* Lyman, 1883, ZMMU D-743, RV *Akademik Mstislav Keldysh*, St. 445, disk diameter 5.5 mm. Dorsal and ventral views are shown in (A–E, H) . Scale bars: 600 μm (F); 60 μm (G). Photographs: Tanya Korshunova (A, B, H); Konstantin Tabachnik (C–E); Alexander Martynov (F, G).

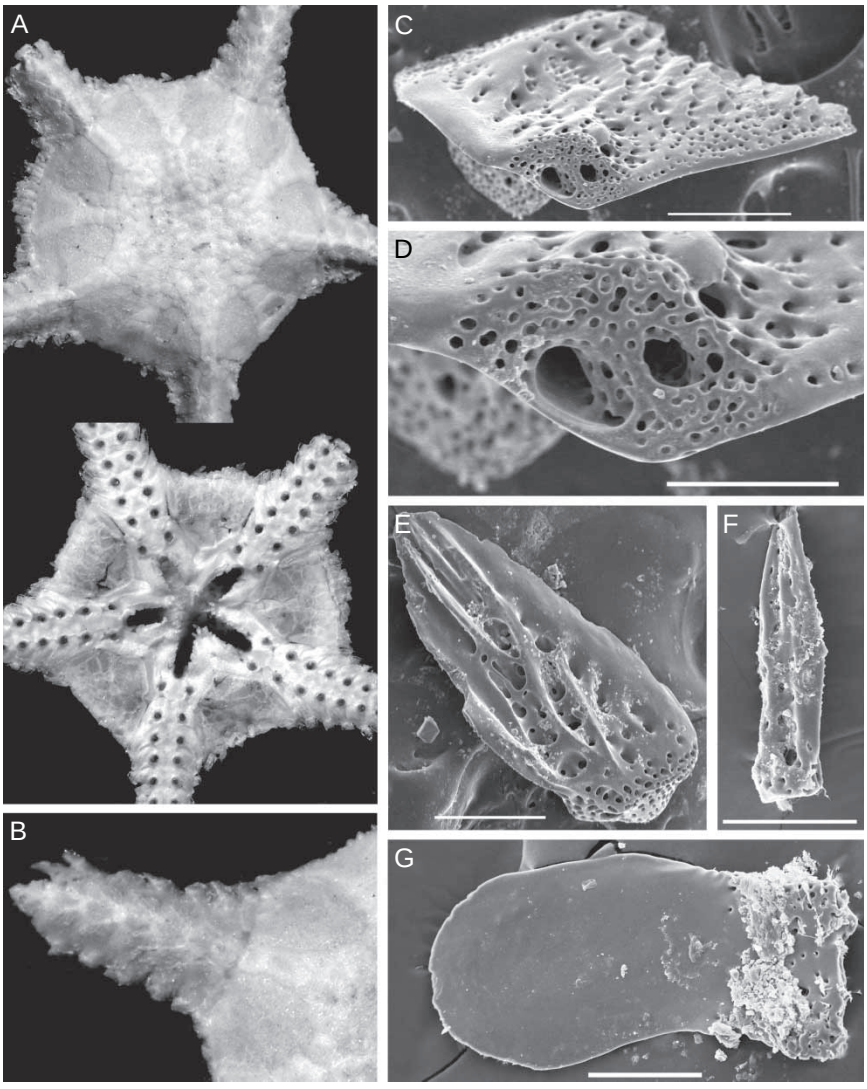

Figure 18. *Ophiophyllum nesisi* sp. nov. (A) Holotype ZMMU D-746, RV *Akademik Mstislav Keldysh*, St. 464, disk diameter 7 mm, dorsal and ventral views; (B) segment of the disk and the arm of the holotype; (C) scanning electron micrograph of the lateral arm plate of the holotype; (D) scanning electron micrograph of the arm spine articulation ridges of the holotype; (E) scanning electron micrograph of the ventral spine from distal arm segments of the holotype; (F) scanning electron micrograph of the dorsal spine of the paratype, RV *Akademik Mstislav Keldysh*, St. 492; (G) scanning electron micrograph of the spine from the disk fringe of the paratype. Scale bars: 200 μm (C); 100 μm (D, F, G); 120 μm (E). Photographs: Alexander Martynov.

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 316, one specimen; St. 413, one specimen; St. 445, five specimens; St. 446, one specimen; St. 489, one specimen.

Distribution

North Atlantic: in the west – from the Gulf of Mexico to Davis Strait, in the east – from south-eastern Iceland to south of the Azores, at 425–2220 m. Present study: the Reykjanes Ridge, at 1550–2200 m.

Family Ophiolepididae

Ophiophyllum nesisi sp. nov.
(Figure 18)

Material

RV *Akademik Mstislav Keldysh*, fourth cruise, St. 464 holotype (ZMMU D-746, dried), St. 492, one paratype (ZMMU D-747, dried).

Etymology

This species is named in honour of the prominent cephalopod taxonomist Kir Nesis, whose early works were devoted to the North Atlantic benthic fauna.

Description of the holotype

The disc diameter of the holotype is 7 mm. It is subcircular, moderately swollen and distinctly concave in the interradii. The dorsal disk surface is clearly divided into two areas – a concave, oblique peripheral area including large radial shields and few (including at least one large) inserted plates between it and a slightly depressed central area covered with numerous (about 110 in number) small, almost uniform in size overlapping irregular-rounded plates. The plates are elevated towards forming tubercle-shaped structures. There are no conspicuous primary plates. A single subcentral plate is slightly larger and more elevated than the neighbouring ones. The surface of the disk plates is smooth. The radial shields are large, elongated narrowly and cup-shaped in outline, proximally obtuse, distally slightly widened. The radial shields are entirely separated from each other by one to two narrow slightly carinated plates. In the interradii the radial shields are separated by one large trapezoid plate distally and few irregularly square plates proximally. The surface of the radial shields is smooth. In the interradii at the border of the disk there is a fringe comprised of a single row of flattened spines. In two interradii the spine fringe is almost completely lost. The jaws are dorsally concave, each bearing three short spiniform irregular-appearing apical papillae of different length and six to eight pairs of rectangular lateral oral papillae. The lateral papillae are formed along the entire jaw edges without gap. The outermost papillae are wide, often with a sharpened edge directed towards the mouth slit. The middle papillae are irregularly rectangular, whereas the most proximal papillae are more spiniform or tubercle-shaped. Both outermost and middle papillae at some jaws have a general appearance as a single block-like scalloped structure. There is a single long spiniform tooth on each short dental plate. The oral shield is large, irregularly rhomboidal in shape, wider than long. In one interradius the oral shield is fragmented by two middle insertion plates. Ventrally there are few irregularly polygonal plates proximally in contact with the oral shield and distally with the spine fringe. The adoral shields are long narrow bands thickened where they are in contact, about five times as long as wide. Genital slits are short, extending from second to third ventral arm plates, in some interradii quite distinct, whereas in others tightly closed and inconspicuous. All arms are broken, maximal number of the saved segments is nine. The saved segments have a quite massive general appearance. Together with the adjacent parts of the disk spine fringe the arms appear conical. The dorsal arm plates are small, narrowly hexagonal in shape and distinctly carinated, contiguous throughout the saved segments of the arms. Distal edges of the dorsal plates are concave. The lateral plates are abruptly sloping giving the arms a high and carinated general appearance. Spines are placed only at the ventral border of the lateral plates. There are two spines: a spiniform one is placed more dorsally, while another is wide and flat, and placed almost ventrally at nearly the same level as the ventral plates. On basal segments the ventral spines are wider than on more distal segments. The ventral spine has a concave surface and few ridges. Ventrally the dorsal plates are placed distinctly obliquely in relation to the ventral plates. The first ventral arm plate is rather square with slightly concave lateral sides. Other ventral arm plates have quite straight proximal and distal edges and deeply concave lateral sides. All ventral arm plates are contiguous. The tentacle pores are large, bordered by deep incisions in the ventral arm plates and oblique lateral arm plates. Tentacle scales are entirely reduced, but at a few basal segments there are two to five thickened, rarely even formed very small, short tubercle-like tentacle scales.

Paratype variation

The single paratype is generally similar to the holotype in size and structure, but differs by more separated, not block-shaped middle oral papillae and the presence of several (the holotype has a single) spiniform teeth.

Distribution

Reykjanes Ridge, at 1670–1895 m.

Remarks

A species named after the Atlantic, *Ophiophyllum atlanticum* Stöhr & Segonzac, 2005, was recently described from a depth of 4078 m from the Mid-Atlantic Ridge in the Central Atlantic (Stöhr & Segonzac 2005). Before the discovery of that species, only a single record of the genus was known from the Atlantic, the Caribbean *O. petilum* Lyman, 1878, but that record was dubious, because the species had originally been described from the Pacific Ocean (Clark 1915). Despite that *Ophiophyllum nesisi* sp. nov. like *O. atlanticum* was also discovered from the Mid-Atlantic Ridge (but considerably more northerly at almost half the depth), it differs clearly from the latter in a number of characters. In *Ophiophyllum nesisi* sp. nov., basal segments of arms together with adjacent parts of the disk clearly form a cone in outline whereas the corresponding parts of the arms in *O. atlanticum* have a cylindrical appearance. The dorsal arm plates of *O. atlanticum* are triangular,

with straight distal edge, whereas in *Ophiophyllum nesisi* sp. nov. they are polygonal, with distinctly concave distal edge. The ventral spine articulation ridges of the lateral arm plates have a distinctly subparallel appearance with two openings in *Ophiophyllum nesisi* sp. nov., whereas *O. atlanticum* has a semicircular ridge with hardly conspicuous openings. The dorsal small spine of *Ophiophyllum nesisi* sp. nov. is almost straight and narrow, whereas *O. atlanticum* has a distinctly conical dorsal spine with wide base. The oral shield, despite its variability, is large rhomboidal in *Ophiophyllum nesisi* sp. nov. and rather small and rounded pentagonal in *O. atlanticum*, and, finally, the appearance of the oral frame is very different in *Ophiophyllum nesisi* sp. nov. and *O. atlanticum* – in the latter the middle oral papillae are rounded and there is a distinct gap devoid of papillae between middle and apical papillae, whereas *Ophiophyllum nesisi* sp. nov. has square or block-shaped middle oral papillae and no gap. Holotype and paratype of *Ophiophyllum nesisi* sp. nov. are originated from two different stations but show essentially the same features. *Ophiophyllum nesisi* sp. nov. is more similar to the New Zealand species *O. teplium* McKnight, 2003 than to its Atlantic congeners. From *O. teplium*, *Ophiophyllum nesisi* sp. nov. differs clearly in its elongated cup-shaped and not triangular radial shields, the rhomboidal and not ovoid oral shield, fewer (six to eight in *Ophiophyllum nesisi* sp. nov. and seven to ten in *O. teplium*) and often block-shaped oral papillae. Type species of the genus, *O. petilum* Lyman, 1878 differs from *Ophiophyllum nesisi* sp. nov. by absence of the small dorsal arm spine, and even if the dorsal spine is considered easily lost, it differs clearly in its flat, thin not domed disk (Lyman 1882: 102 in his description of *O. petilum* specially highlighted this as 'disk flat and very thin', given thus the genus name *Ophiophyllum*). Genital slits of *O. petilum* are relatively long and extending from the oral shield to the fringe of disk spines, whereas in *Ophiophyllum nesisi* sp. nov. they are short and extending from adoral shield to lateral plate of the third segment. Arms of *O. petilum* have cylindrical appearance (conical in *Ophiophyllum nesisi* sp. nov.) and considerably fewer segments within the disk (two in *O. petilum* and four in *Ophiophyllum nesisi* sp. nov.). *Ophiophyllum petilum* has short and wide ventral side of the lateral arm plate, whereas in *Ophiophyllum nesisi* sp. nov. it is narrow, relatively long and oblique. In *Ophiophyllum petilum* there is a clear gap between spines of the adjacent segments, whereas in *Ophiophyllum nesisi* sp. nov spines are overlapping. First ventral arm plate is triangular in *Ophiophyllum petilum* and square with concave lateral sides in *Ophiophyllum nesisi* sp. nov., same length as width (or wider) of the other ventral arm plates in *Ophiophyllum petilum* and distinctly longer than broad in *Ophiophyllum nesisi* sp. nov. Shape of distalmost and other oral papillae is similar in *Ophiophyllum petilum*, whereas *Ophiophyllum nesisi* sp. nov. has a markedly different distalmost oral papilla in shape and size. *Ophiophyllum concinnus* Litvinova, 1981 is considerably different from *Ophiophyllum nesisi* sp. nov. in having a flattened disk, not clearly divided into central and peripheral areas, a cylindrical appearance of the arms, triangular dorsal arm plates, a distinct gap between spines of the adjacent segments, less differentiated oral papillae and a small rounded oral shield. *Ophiophyllum borbonica* Vadon & Guille, 1984 is clearly different from *Ophiophyllum nesisi* sp. nov. in having larger disk plates, a rounded shape of the radial shields, considerably fewer block-shaped oral papillae, and two distinct tentacle scales. *Ophiophyllum novacaledoniae* Vadon, 1991 has fewer dorsal disk plates compared to the distinct primary plates, large triangular radial shields, triangular dorsal arm plates, and two distinct tentacle scales. All these characters are enough to separate the latter species from *Ophiophyllum nesisi* sp. nov. Finally *O. marginatum* A.H. Clark, 1918 is clearly separated from *Ophiophyllum nesisi* sp. nov. by the presence of only ventral arm spines and two distinct tentacle scales.

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