

The taxonomy and zoogeography of the genus *Ophiocten* (Echinodermata: Ophiuroidea) in the North Atlantic Ocean

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Introduction

Since the late nineteenth century a large number of samples containing species of the genus *Ophiocten* have been recovered by many expeditions to the North Atlantic Ocean. These were described by various authors under several names. Mortensen (1927), attempting the first revision of the North Atlantic *Ophiocten* species, recognised four species in British waters: *O. sericeum* (Forbes), *O. scutatum* Koehler, *O. latens* Koehler and *O. hastatum* Lyman. Subsequently Mortensen (1933a) tried to clarify the confusion surrounding *Ophiocten sericeum* by referring *Ophioglypha signata* Verrill, 1882, *Ophioglypha gracilis* G. O. Sars, 1871, *Ophiocten le danteci* Koehler, 1897, *Ophiocten amitinum* var. *boreale* Hertz, 1927, and *Ophiocten abyssicolum* (Forbes, 1843), to the synonymy of *O. sericeum*. He recognised two varieties of *O. sericeum*, one in the 'warm water' area and one in the 'cold water' area of the North Atlantic Ocean. Semenova, Mileikovsky and Nesis (1964) treated these varieties as subspecies; *Ophiocten sericeum gracilis* (G. O. Sars) from the warm water region and *O. sericeum sericeum* (Forbes), the cold water subspecies.

The Scottish Marine Biological Association's deep sea sampling programme has collected many specimens of *Ophiocten* from bathyal depths on the Wyville Thomson Ridge, within the Rockall Trough and along the continental slope to the south west of Ireland. Close examination of these samples has thrown light on the controversy surrounding the taxonomy of *Ophiocten sericeum*. The present study also examines the affinities between the abyssal *Ophiocten hastatum* Lyman and the other deep water species outside the Atlantic Ocean, and a new abyssal species from the Bay of Biscay is described.

Systematic description

Genus *OPHIOCTEN* Lütken, 1855

Ophiocten: Lütken, 1855 : 97; 1858 : 51–52; Lyman, 1865 : 53; Ljungman, 1865 : 360; 1867 : 307; Lyman, 1882 : 78; Bell, 1892 : 113; Clark, 1915 : 328; Matsumoto, 1915.
Ophiura (pt): Guille, in press.

TYPE SPECIES. *Ophiocten kröyeri* Lütken, 1855, by monotypy, later considered by Ljungman (1865) to be conspecific with *Ophiura sericea* Forbes, 1852 which he referred to *Ophiocten*.

A genus of the subfamily Ophiurinae, family Ophiuridae, with a flat disk covered with small plates amongst which the primary plates are usually distinct; margin of the disk generally

sharp; the disk not, or only weakly, indented above the arms; arm combs often continuous over the base of the arms; the jaw with a spiniform or angular apical papilla flanked by oral papillae of which the distalmost ones become blocklike; the adoral plates narrow; the oral shield ranges from being distinctly broader than long to longer than broad, depending on the species; the second oral tentacle pore emerging superficially outside the mouth slit; the genital slits distinct and in some species lined with papillae; lateral arm plates often striated, usually bearing three arm spines; the ventral arm plates separated distally, the distal edge usually convex and the proximal edge flat or angular, being either very obtuse or extended to form a more acute angle; the proximal tentacle pores large and open distally with one or two small tentacle scales on the proximal edge of the pore. This genus is cosmopolitan with species in all oceans.

REMARKS. *Ophiocten* is closely related to the genus *Ophiura* with *Ophiura affinis* occupying an isolated intermediate position between the two genera as shown in Table 1. Certain characteristics of *O. affinis*, such as a well developed arm comb, suggest an affinity with *Ophiura* while others, such as the emergence of the second oral tentacle pore outside the mouth slit, the shape of the tentacle pores and ventral arm plates, suggest affinities with *Ophiocten*.

This intermediate position was first noted by Mortensen (1927, 1933*b*, 1936) who questioned the validity of *Ophiocten*. Clark and Courtman-Stock (1976) also commented on the lack of distinction between these two genera and Guille (in press) considers that the evidence provided by *Ophiura affinis* and *Ophiura affinis simulans* is sufficient to warrant merging *Ophiocten* with *Ophiura*.

Certainly *O. affinis* has features common to both genera, but it appears to be the only such species. No gradation is evident from the literature between species of *Ophiura* such as the type species, *Ophiura ophiura* Linnaeus (formerly *O. texturata* Lamarck) and *Ophiura ljungmani* (Lyman) through *Ophiura affinis* to *Ophiocten*. Rather the two genera appear to be easily distinguished, with *Ophiocten* being well defined. *Ophiura* and *Ophiocten* are compared together with *Ophiura affinis* in Table 1.

Despite the apparently intermediate position of *Ophiura affinis* we consider the characters exhibited by *Ophiocten* justify the generic separation. Table 1 shows that the only characters which relate *Ophiura affinis* to *Ophiura* are the form of the arm combs and the indented

Table 1 Comparison of *Ophiocten*, *Ophiura affinis* and *Ophiura* (characters arranged in decreasing order of importance)

Characters	<i>Ophiocten</i>	<i>Ophiura affinis</i>	<i>Ophiura</i>
Emergence of second oral tentacle pore	Away from mouth slit (fig. 1d)	Away from mouth slit (fig. 1d)	Via a furrow into mouth slit (fig. 1e)
Arm combs	Simple (fig. 1a)	Intermediate (fig. 1b)	Well developed (fig. 1c)
Disk margin above arm bases	Without a notch	With well developed notch	With well developed notch
Shape of the ventral arm plates	Proximal side produced distal side rounded (fig. 1h, i)	Proximal side produced distal side rounded (fig. 1h, i)	Scallop-shaped, irregularly hexagonal but not as <i>Ophiocten</i> (fig. 1j, k)
Tentacle pore and scales of the proximal arm segments	Large with only a small tentacle scale (fig. 1f)	Large with only small tentacle scale (fig. 1f)	Large with many, often large, tentacle scales (fig. 1g)

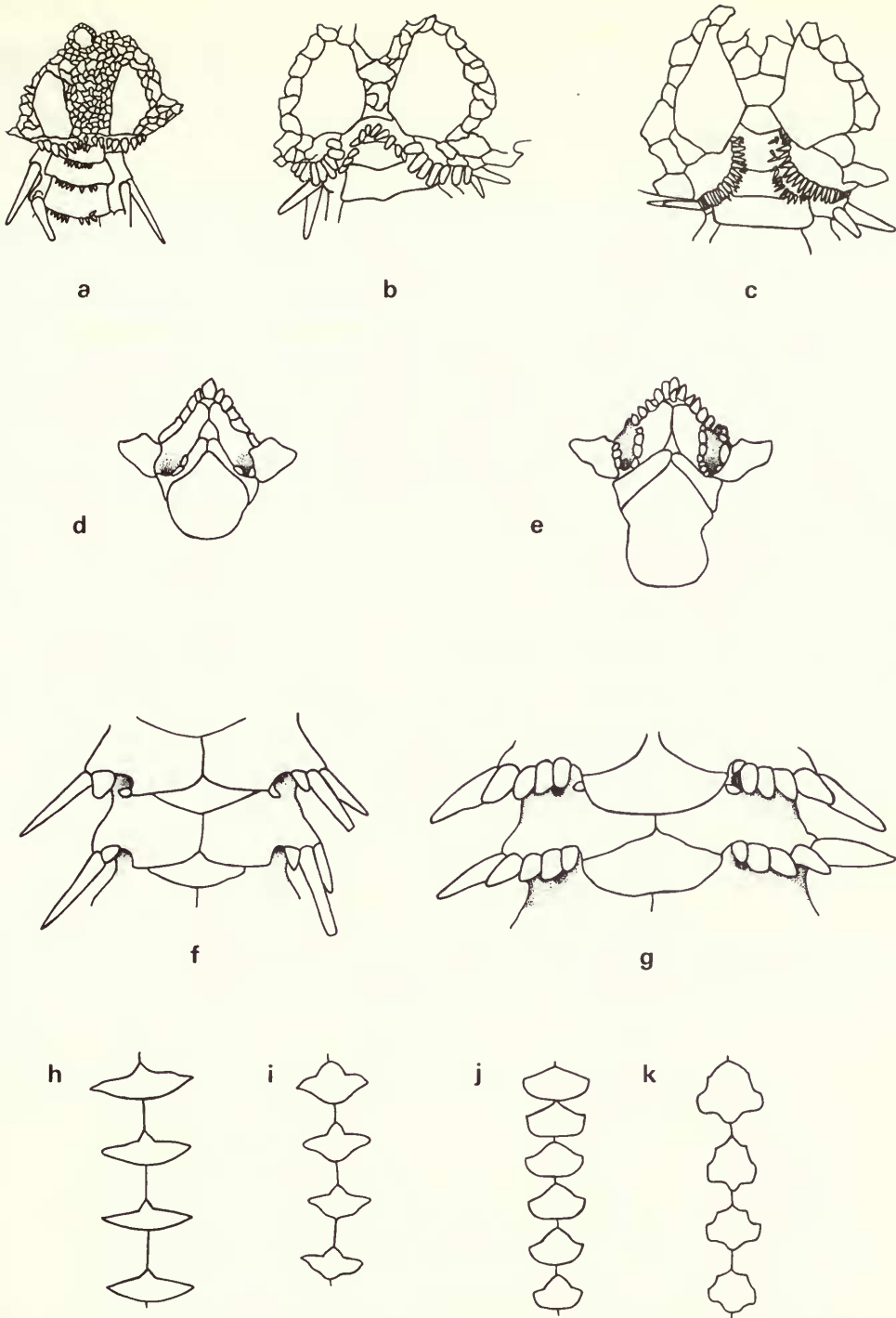


Fig. 1 Diagrams of characters referred to in Table 1. The arm comb of, (a) *Ophiocten sericeum*; (b) *Ophiura affinis*; (c) *Ophiura ophiura*; (d) the jaw shape characteristic of *Ophiocten* and *Ophiura affinis*; (e) the jaw shape characteristic of *Ophiura*; (f) the ventral side of the arm, characteristic of *Ophiocten* and *Ophiura affinis*; (g) the ventral side of the arm characteristic of many *Ophiura* species; (h)–(k) the ventral arm plate arrangement of, (h) *Ophiocten sericeum*; (i) *Ophiocten gracilis*; (j) *Ophiura ophiura*; and (k) *Ophiura ljunghmani*. Figures are not drawn to the same scale.

disk, while the other characters indicate a closer affinity with *Ophiecten*. Indeed, Koehler (1897) described some small *Ophiura affinis* as a new species of *Ophiecten*, *O. scutatum*. Possibly *O. affinis* should be referred to a separate genus but this is inadvisable until *Ophiura* itself is revised.




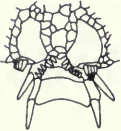




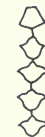






Characters of taxonomic value

a *The oral shield*: the main features of this plate considered are: 1 its overall shape; 2 the length to breadth ratio; 3 the extent of the proximal inner angle. Mortensen (1927) considered the shape of the oral shield to be of great taxonomic value. The identities of *Ophiecten sericeum* and *O. gracilis* (Sars, 1871) were confused by many authors who failed to notice the different shape of this plate in these species.

b *The second and subsequent ventral arm plates*: the important features are: 1 the shape of the plates; 2 whether the proximal angle is obtuse, as in *O. sericeum*, or produced into a point as in *O. gracilis* and *O. abyssicolum* (Forbes, 1843); 3 the distal edge, whether round as in *O. sericeum*, indented as in *O. gracilis* or angular as in *O. abyssicolum*.

c *Occurrence of genital papillae*: the present study indicates that the extent of these spinelets along the genital plates is a useful taxonomic character which was previously unconsidered.

Table 2 Comparison of the five species of *Ophiecten* occurring in the North Atlantic

SPECIES	CHARACTERS				
	Arm comb	Dorsal arm plate	Oral shield	Genital papillae	Ventral arm plate
<i>sericeum</i>		weakly arched slightly convex distal edge		line full length of genital slit	
<i>abyssicolum</i>		strongly arched almost straight distal edge		extend only half way down genital slit	
<i>gracilis</i>		strongly arched slightly convex distal edge		extend only half way down genital slit	
<i>hastatum</i>		may be ridged with convex distal edge		confined to edge of disk or absent	
<i>centoli</i>		weakly arched with convex distal edge		line full length of genital slit	

d Arm combs: several features of the arm comb should be considered: 1 whether its spinelets are confined to the disk edge on either side of the arm base or more usually form a continuous fringe over the arms; 2 whether supplementary spinelets are found on the dorsal arm plates; 3 the arm comb spinelets themselves may be characteristic and either thin and needlelike as in *O. gracilis*, or have slightly blunt tips as in *O. abyssicolum*, or they may be short, rounded triangular and toothlike as in *O. sericeum*. In some cases the spinelets may be rubbed off in preservation but their bases can usually be seen. Mortensen (1933a) did not consider arm-comb characters to be of value, particularly in the case of *O. latens* (now *O. hastatum*) where arm-comb spinelets (and also genital papillae) are often absent. However, we consider that these characters have proved useful for separating the individual species.

e Dorsal arm plates: in some species these plates may be arched giving the arm a carinate appearance. However, in some specimens this feature is less obvious.

Key to the species of *Ophiecten* (see also Table 2)

- | | | |
|---|--|---|
| 1 | Oral shield broader than long or square with obtuse proximal angle | 2 |
| - | Oral shields longer than broad | 4 |
| 2 | Genital papillae absent. Dorsal arm spine very long, up to 2 arm segments long | |
| | <i>Ophiecten hastatum</i> Lyman, 1878 p. 117 | |
| - | Genital papillae present | 3 |
| 3 | Genital papillae extending along the distal half of the genital slit. Radial shields separated and longer than broad | <i>Ophiecten gracilis</i> (G. O. Sars, 1871) p. 115 |
| - | Genital papillae extending the full length of the genital slit. Radial shields contiguous and broader than long | <i>Ophiecten centobi</i> sp. nov. p. 119 |
| 4 | Genital papillae extending along the distal half of the genital slit. Ventral arm plates wider than long with a distinctly convex outer edge | <i>Ophiecten abyssicolum</i> (Forbes, 1843) p. 114 |
| - | Genital papillae extending along the entire length of the genital slit. Ventral arm plates much wider than long and widely separated | <i>Ophiecten sericeum</i> (Forbes, 1852) p. 113 |

Ophiecten sericeum (Forbes, 1852)

(Fig. 2)

Ophiura sericea Forbes, 1852 : 215.

Ophiecten sericeum: Ljungman, 1867 : 307; Duncan & Sladen, 1881 : 65-66; Bell, 1892 : 113-114 (part); Grieg, 1893 : 9-10 (part); 1900 : 246; 1903 : 26 (part); Michailovskij, 1903 : 492, 531; 1904 : 173; Koehler, 1909 : 166; Mortensen, 1927 : 247 (part); 1932 : 34; 1933 : 96-98 (part); Thorson, 1934 : 4; Djakanov, 1954 : 92; Grainger, 1955 : 910; Semenova, Mileikovskiy, Nesis, 1964 (part).

Ophiecten kröyeri Lütken, 1855 : 102; 1858 : 52; 1859 : 28, 52-53; Lyman, 1865 : 53.

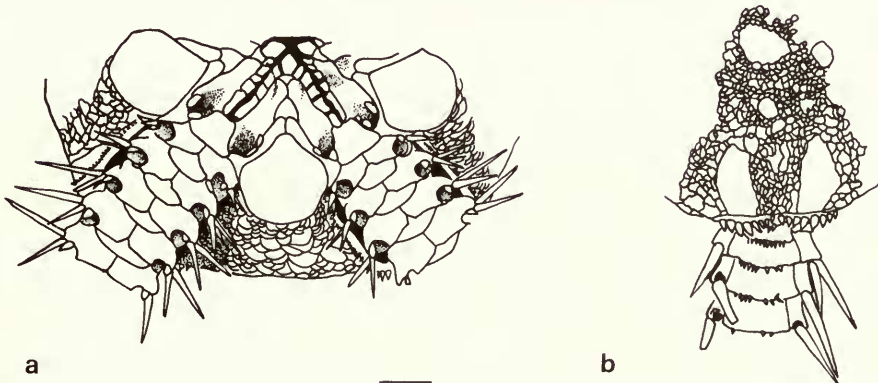


Fig. 2 *Ophiecten sericeum* (Forbes), (a) Ventral; and (b) dorsal views of part of the disk. Bar scale = 1 mm.

MATERIAL EXAMINED. See Appendix

DIAGNOSIS. Disk diameter up to 18 mm; dorsal surface of disk with distinct primary plates showing radiating structure; radial shields longer than broad, approximately equal in length to half disk radius, only part of the distal edge reaching the disk edge; arm combs consisting of well developed spines and some massive papillae, extending across the base of the arm.

Dorsal arm plates not strongly arched with only a slightly convex distal edge; up to eight of the proximal dorsal arm plates with their distal edges fringed with papillae (this can be seen in specimens with disk diameter greater than 4 mm); second ventral arm plate flat or with a very slightly convex distal edge; other ventral arm plates much wider than long, separated, with the distal edge gently curved; three arm spines of approximately similar size, although the dorsalmost spine may be longer than the other two; the longest spine is about one arm segment long.

Oral shields always longer than broad, with an acute proximal angle and an almost semi-circular distal edge; the apical papilla stout and spinelike or sometimes angular; three or four oral papillae; the proximal ones spinelike the distal becoming blocklike; genital papillae fringing the whole length of the genital slit.

RANGE. This species has its centre of distribution in the shallow high Arctic Ocean but may penetrate the deeper waters of the Norwegian Basin to a depth of about 2000 m. It has been recorded from the Kara Sea, Barents Sea, Spitzbergen, northern Greenland, Davis Strait and Baffin Bay.

REMARKS. Development is planktotrophic (Thorson, 1934). *O. sericeum* is a distinctive species easily recognised by the shape of the oral shield, the extent of the genital papillae, the presence of papillae on the proximal dorsal arm plates and the shape of the arm comb spinelets. This is the cold water form of Grieg (1903), Mortensen (1933a) and Semenova, Mileikovsky and Nesis (1964).

Ophiecten abyssicolum (Forbes, 1843)

(Fig. 3a-c)

Ophiura abyssicola Forbes, 1843 : 146.

Ophiecten abyssicolum: Marenzeller, 1895 : 190; Koehler, 1907 : 269; Cherbonnier, 1958 : 37; Cherbonnier & Guille, 1967 : 322.

Ophiura signata: Kemp, 1905 : 193 (part); Farran, 1913 : 30 (part); Mortensen, 1927 : 245 (part).

Ophiecten sericeum: Mortensen, 1927 : 247 (part); Nobre, 1931 : 92-93.

Ophiecten sericeum: Cherbonnier, 1970 : 344; 1267 (*non O. sericeum* Forbes, 1852).

MATERIAL EXAMINED. See Appendix.

DIAGNOSIS. Disk diameter up to 8 mm; dorsal surface matt when dried with large obvious primary plates each encircled by a ring of small contiguous plates; radial shields small, less than one third disk radius, separated radially by a line of overlapping small plates; the distal edge of the radial shields extending to the disk edge; four or five comb papillae arise at the interradiial edge of each radial shield but not forming a continuous comb across the base of the arm, a few small papillae arising on the first or second arm plate giving the impression of an inner arm comb, however, this is not as extensive or well developed as the secondary arm combs found in *Ophiura* species (see Fig. 1).

Dorsal arm plates strongly arched; only the first dorsal arm plate with any spinelets; the ventral arm plates widely separated, the proximal edge with an acute peak in the middle and an angular distal edge (Fig. 3a); the tentacle scale large and triangular; arm spines stubby in appearance and of equal size, just shorter than the corresponding arm segment.

Oral shield longer than broad, equal in length to half disk radius, the proximal angle acute, with parallel sides and a semi-circular distal end; the apical papilla conelike and flanked by three mouth papillae each side, spine-like proximally, broad and block-like distally; genital papillae limited to the distal half of the genital slit.

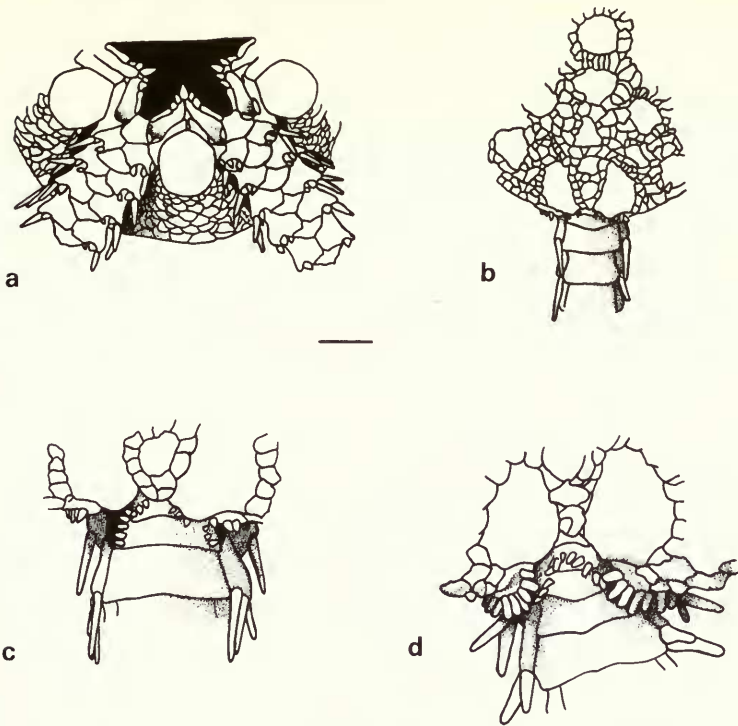


Fig. 3 (a)–(c) *OphiocTEN abyssicolum* (Forbes), (a) ventral and (b) dorsal views of part of the disk; (c) an arm base showing the arrangement of the arm comb. The black areas are covered by skin in the specimen (d) *Ophiura affinis*, the arrangement of the arm comb. Bar scales = 1 mm.

RANGE. This species is found from the Mediterranean as far north as S.W. Ireland. It is found at depths below 100 m in the Mediterranean, 300–500 m in the Bay of Biscay and between 300–1000 m off S.W. Ireland.

REMARKS. The form of the papillae on the dorsal arm plates may suggest an affinity with *Ophiura affinis* but there are a number of differences. Firstly the form of the genital plate is different, being well developed and widest in the dorso-ventral plane on each side of the arm in *Ophiura affinis*, while in *OphiocTEN abyssicolum* (and *OphiocTEN* in general) it is thin and compressed laterally, being widest at the edge of the disk. Secondly, there is a distinct notch in *Ophiura affinis* which is absent in *OphiocTEN abyssicolum*.

Kemp (1905) confused this species and *OphiocTEN gracilis* and considered both as variations of one species which he thought was Verrill's *Ophiura signata*. The specimens from the *Helga* (Kemp, 1905, Plate 35, Fig. 6) are in fact *O. abyssicolum*.

***OphiocTEN gracilis* (G. O. Sars, 1871)**
(Fig. 4)

Ophioglypha gracilis G. O. Sars, 1871 : 18.

Ophioglypha signata Verrill, 1882 : 220; Hoyle, 1884 : 718.

OphiocTEN pattersoni Lyman, 1883 : 244.

OphiocTEN sericeum: Hoyle, 1884 : 718 (part); Bell, 1892 : 113–114 (part); Grieg, 1893 : 9–10; 1903 : 26 (part); Mortensen, 1927 : 247 (part).

OphiocTEN le danteci Koehler, 1896 : 72.

Ophiura signata: Kemp, 1905 : 193 (part); Farran, 1913 : 30 (part).

OphiocTEN hastatum: Koehler, 1914 : 37; Schoener, 1971 : 153–160; (*non O. hastatum* Lyman, 1878).

OphiocTEN amittinum var. *boreale* Hertz, 1927a : 64.

Ophiocten sericeum var. *gracilis* Mortensen, 1933a : 98.

Ophiocten sericeum gracilis Semenova, Mileikovsky & Nesis, 1964.

MATERIAL EXAMINED. See Appendix

DIAGNOSIS. Disk diameter up to 12 mm; dorsal surface matt when dried with obvious primary plates; radial shields less than half disk radius, extending to the edge of the disk; arm comb moderately well developed but spinelets more slender than in *O. sericeum* (Fig. 4b, d); first dorsal arm plate with spinelets, other proximal plates rarely if ever with spinelets on the distal edge.

Dorsal arm plates usually strongly ridged; second ventral arm plate longer than broad with an acute proximal angle and a very convex distal edge; distal arm plates with a convex distal edge and lateral indentations; arm spines of similar length, nearly one arm segment long proximally, in some cases the dorsal spine is longer than the other two.

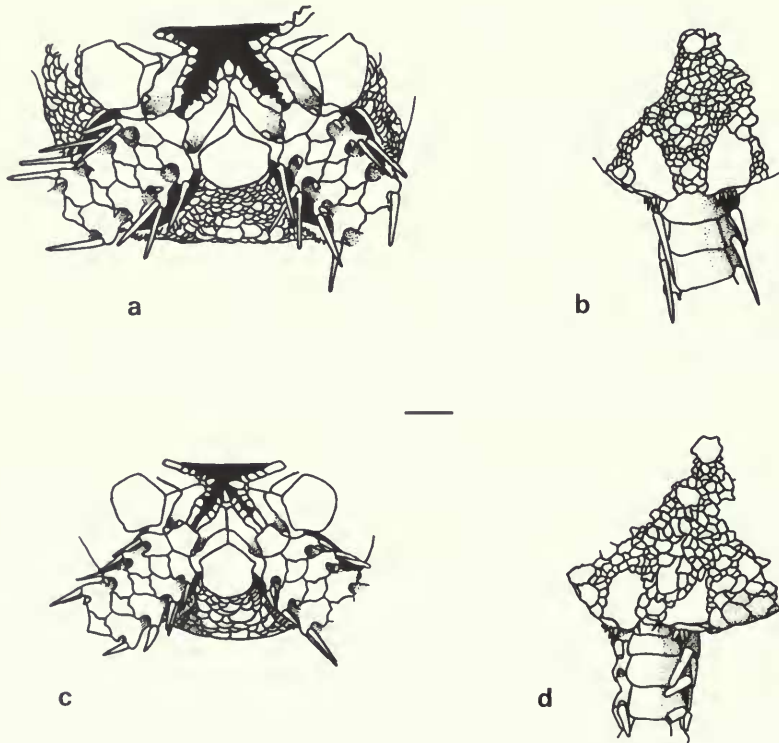


Fig. 4 *Ophiocten gracilis* (G. O. Sars), (a) ventral and (b) dorsal views of part of the disk of a specimen from the Rockall Trough; (c) ventral and (d) dorsal views of part of the disk of a specimen from Albatross Stn. 2582, off Rhode I. Bar scale = 1 mm.

Oral shields broader than long or almost square, the proximal angle being very obtuse, often with lateral projections giving the shield a squat, arrow-shape, the distal edge gently convex; the apical papilla stout with three to four oral papillae each side, which become blocklike distally; often the distal papillae with secondary points; genital papillae only extend along the distal half (i.e. from the arm combs towards the oral shield) of the genital slit.

RANGE. This is an upper bathyal species with a vertical distribution of 600–1200 m, found within the Rockall Trough from the southern slope of the Wyville Thomson Ridge and as far south as western Ireland, and off the eastern seaboard of North America. *O. gracilis* has also

been recorded by the *Ingolf* (see Appendix) from the Norwegian Sea north of Iceland from depths of 106–1909 m. Whether its occurrence in these waters represents part of its range, or is a result of settlement of larvae accidentally brought into the Norwegian Sea by surface currents from neighbouring populations, has yet to be determined. It is highly probable that *Ophiopluteus ramosus* Mortensen, 1898 is the larva of this species (Semenova, Mileikovsky & Nesis, 1964). Postlarvae of this species have been identified in samples taken in the summer months at depths to 2925 m in the Rockall Trough. They do not appear to survive into the following winter at these depths (Gage & Tyler, 1981).

REMARKS. The true identity of this species has been subject to considerable confusion. G. O. Sars (1871) described it as an *Ophioglypha*, a synonym of *Ophiura*, but subsequently Lyman (1878) and then Grieg (1893), assigned it to *Ophiecten*. However Grieg synonymized *O. gracilis* with *Ophiecten sericeum*, since he doubted the importance of the arm combs as specific characters. In taking this action, he overlooked the different shape of the oral shield. Later Grieg (1903) recognised two forms of *Ophiecten sericeum*, a warm water form, the *Ophiecten gracilis* of this study, and a more robust cold water form, *O. sericeum*, but he did not name them. Mortensen (1933a) also recognised these two varieties and Semenova, Mileikovsky & Nesis (1964) proposed that they should be considered as subspecies.

On the Atlantic seaboard of North America the situation was equally confused. Verrill (1882) described *Ophioglypha signata* and Lyman (1883) *Ophiecten pattersoni* both from specimens now considered to be conspecific with *Ophiecten gracilis* (Sars). Koehler (1914) perhaps not realising the existence of these previous names, erroneously identified his specimens as *Ophiecten hastatum*. In fact, there are no published records of *Ophiecten hastatum* Lyman (sensu stricto) occurring in the western basin of the Atlantic.

Several authors, including Hoyle (1884), Kemp (1905) and Farran (1913), studying specimens from S.W. Ireland, overlooked the existence and priority of *O. gracilis* and named their specimens *Ophiura signata* using Verrill's name.

Mortensen (1927, 1933a) synonymized all of these names with *Ophiecten sericeum* although as stated previously he recognised two varieties of *O. sericeum*.

Ophiecten gracilis differs from *O. sericeum* in the shape and dimensions of the oral shield, the extent of the genital papillae lining the genital slit and the form of the arm comb spinelets.

Ophiecten hastatum Lyman, 1878

(Fig. 5)

Ophiecten hastatum Lyman, 1878 : 103; 1882 : 82; Koehler, 1898 : 42–44; 1909 : 165.

Ophiecten longispinum Koehler, 1896a : 204–205; 1896b : 243.

Ophiecten sericeum: Hoyle, 1884 : 718 (part); Bell, 1892 : 113–114 (part) (*non O. sericeum* (Forbes, 1852)).

Ophiecten pacificum Lütken & Mortensen, 1899 : 131; H. L. Clark, 1911 : 96–97; H. L. Clark, 1923 : 364; Hertz, 1927b : 11–12; Jumars, 1976 : 244.

Ophiecten latens Koehler, 1906 : 13; 1907 : 267; 1921 : 5; Grieg, 1921 : 33; 1932 : 33; Mortensen, 1927 : 246; 1932 : 35; 1933a : 98–99; 1933b : 392–393; Cherbonnier & Sibuet, 1972 : 1384; A. M. Clark & Courtman-Stock, 1976 : 189.

Ophiura hastata Guille, in press.

MATERIAL EXAMINED. See Appendix

DIAGNOSIS. Disk diameter up to 12 mm; dorsal surface matt when dried with indistinct primary plates showing a 'mottled' centre and radiating striations; secondary plates small and overlapping; radial shields approximately half disk radius with their distal edges reaching the disk edge, the two shields of each pair separated radially by at least three secondary plates; arm combs reduced, sometimes absent altogether.

Dorsal arm plates sometimes strongly arched with convex distal edge, distal edge not lined by papillae; second ventral arm plate broader than long, in some specimens contiguous with

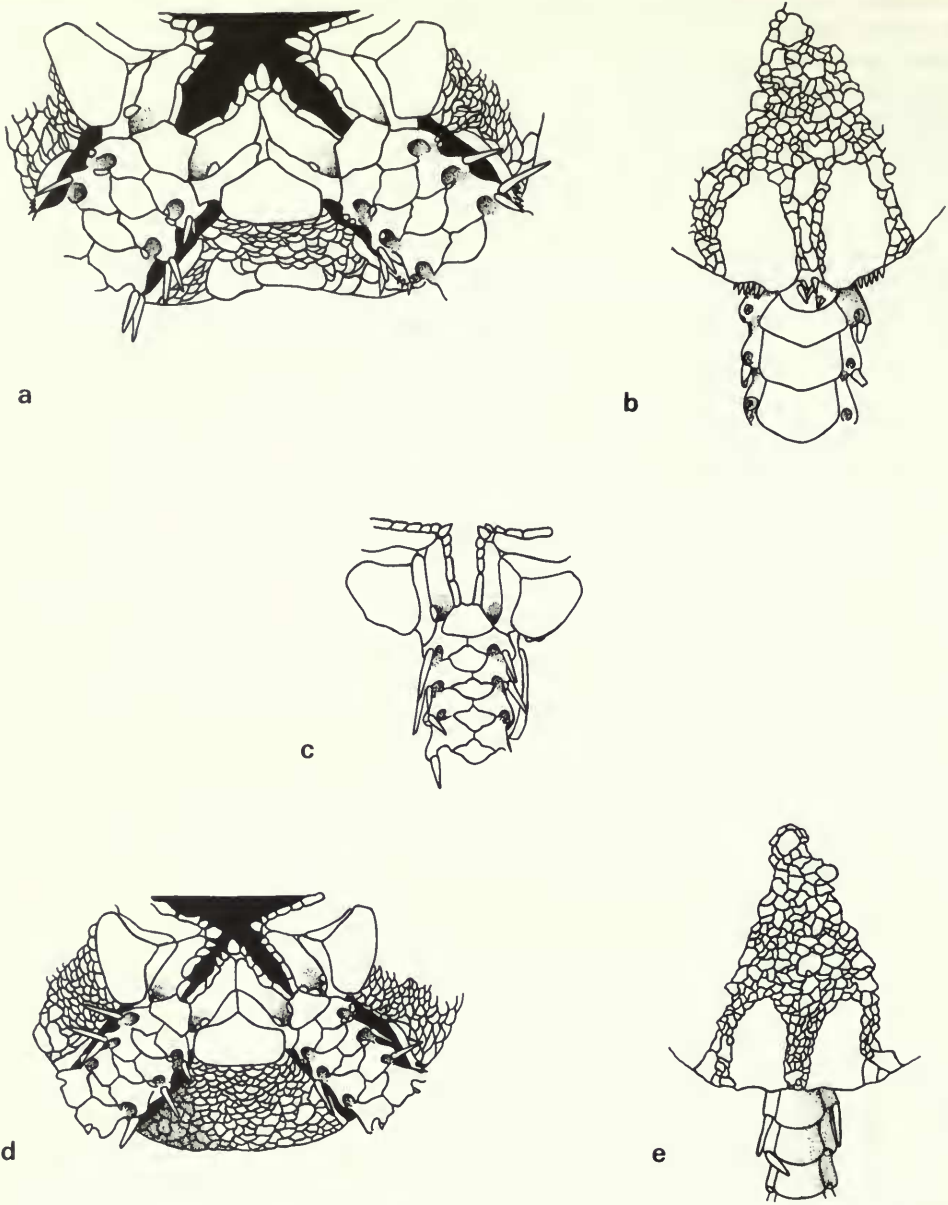


Fig. 5 *Ophiocten hastatum* Lyman, (a) ventral and (b) dorsal views of part of the disk of one of the paratypes; (c) ventral view of part of the disk of the syntype of *Ophiocten pacificum* Lütken & Mtsn.; (d) ventral and (e) dorsal view of part of the disk of a specimen from the Bay of Biscay. Bar scale = 1 mm.

the third ventral armplate; subsequent ventral armplates separated, with an obtuse proximal angle and a rounded distal edge; three arm spines, the dorsal spine twice the length of the lower spine and up to 1–1.5 arm segments long.

Oral shields considerably broader than long with a flat or slightly convex distal edge, sometimes with small lateral projections as in *O. gracilis* giving a squat arrow-shaped appearance; apical papilla stout with two pointed and distally two blocklike oral papillae on each side;

genital papillae absent (except in a few cases when they are confined to the distal edge of the genital plate).

RANGE. This species is found between 1130–4700 m. It appears to be cosmopolitan, being recorded from the Eastern Atlantic, off southern Africa, Kerguelen and Prince Edward Island in the Southern Ocean, in the east Pacific off southern California and Panama and in the west Pacific off Japan.

REMARKS. A comparison of the type specimens of *Ophiecten hastatum* and *O. latens* using the characters mentioned above has not revealed any significant specific differences between them and we conclude that they are conspecific. The differences that do exist, such as the extent of the arm comb and the length of the arm spines, once thought to separate them, are now considered to be intraspecific variations.

Although Mortensen (1933*b*) refuted H. L. Clark's (1923) suggestion that *O. pacificum* was present off southern Africa, an examination of one of the syntypes (Albatross Stn. 3393, 1836 m E. Pacific) together with the description given by Lütken and Mortensen (1899) confirms that *O. pacificum* is conspecific with *O. hastatum*. The disk of the syntype of *O. pacificum* in the BM(NH) is badly damaged but the other features are consistent with those of *O. hastatum*.

Ophiecten australis Baker, 1979, from off southern Tasmania, 800–1772 m, may also be conspecific with *O. hastatum*. Certainly the figures and description resemble Atlantic specimens of *O. hastatum*.

Ophiecten centobi sp. nov.

(Figs. 6, 7)

The holotype has a disk diameter of 4.5 mm, the two paratypes 4 mm and 3.5 mm respectively. The disk is round with very large, conspicuous centrodorsal and primary plates which are nearly contiguous but are separated from one another by a ring of much smaller plates. The radial shields are small, nearly twice as broad as long and contiguous for most of their length. The arm comb forms a continuous fringe over the arm base and is comprised of stout, pointed papillae. The ventral interradial areas are covered with large plates.

The dorsal arm plates are not strongly arched. They are contiguous, fan shaped with a convex distal edge. None of the dorsal arm plates carry spinelets on their distal edge. The ventral arm plates are widely separated. The distal edge of the plate is rounded while the proximal angle is acute. The tentacle pores are of the typical *Ophiecten* kind (see Fig. 1*f*). The proximal pores have two, sometimes three tentacle scales, the distal ones, two then one tentacle scale. There are 3 long pointed arm spines of which the dorsalmost is usually the longest.

There is one pointed apical papilla at the apex of the jaw flanked on either side by 3 to 4 oral papillae. The proximal oral papillae are pointed but the distalmost one is blocklike. The adoral shields are long and thin. The oral shield is as broad as or broader than long with an acute proximal angle and a convex distal edge. In some cases the oral shield may be quite rounded while in others there is a suggestion of small lateral projections. The genital slits are conspicuous and are lined along their entire length by stout, pointed papillae.

DERIVATION OF NAME. The specific name is derived from the initials of the Centre National de Tri d'Océanographie Biologique (CENTOB).

TYPE LOCALITY. *Cymor* drague 15 : 47°44' N : 8°21' W. Bay of Biscay. 2420 m.

The holotype is deposited in the Museum National d'Histoire Naturelle, Paris, one paratype is deposited in the British Museum (Natural History), London, the other in the Centre Océanologique de Bretagne at Brest.

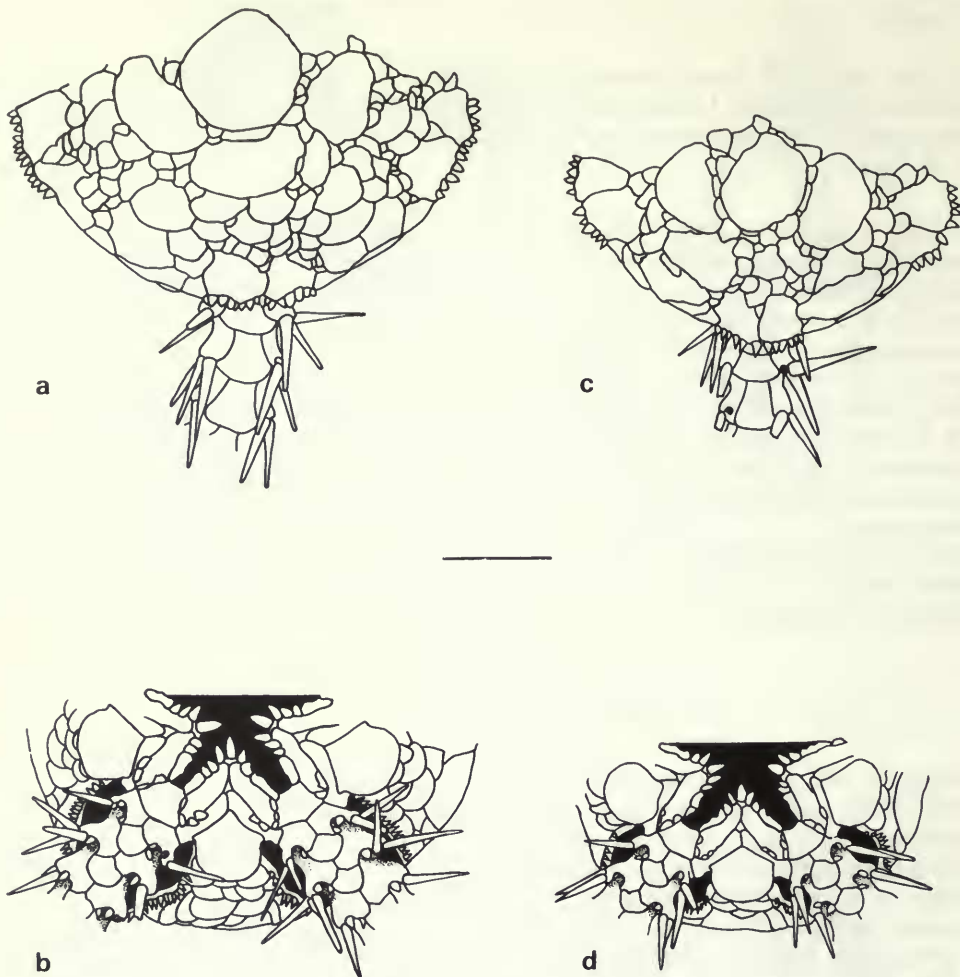


Fig. 6 *Ophiocten centobi* sp. nov., (a) dorsal and (b) ventral view of part of the disk of the holotype; (c) dorsal and (d) ventral view of part of the disk of a paratype. Bar scale = 1 mm.

REMARKS. As shown in Table 2, the scaling of the disk, the form of the arm combs, the contiguous radial shields and the extent and composition of the genital papillae differentiate *Ophiocten centobi* from the other N. Atlantic species. A large conspicuous primary rosette is also found in the Antarctic species *Ophiocten ultimum* Hertz, 1927, *O. carinatum* Hertz, 1927, *Ophiocten megaloplax* Koehler, 1901 and *Ophiocten banzareii* Madsen, 1967. *O. centobi* differs from the first two in the form of the radial shields which are broader than long while in *O. ultimum* and *O. carinatum* they are larger and longer than broad. *O. megaloplax*, and also *O. carinatum*, differ mainly because they lack genital papillae on the genital slit. The lack of an arm comb and the presence of four arm spines differentiates *O. banzareii* from *O. centobi*.

None of the characters, particularly the large primary rosette, are merely due to the small size of the specimens. Similar sized specimens of *O. gracilis*, *O. abyssicolum* and *O. hastatum* all show recognisable adult features and the primary rosette is very much smaller.

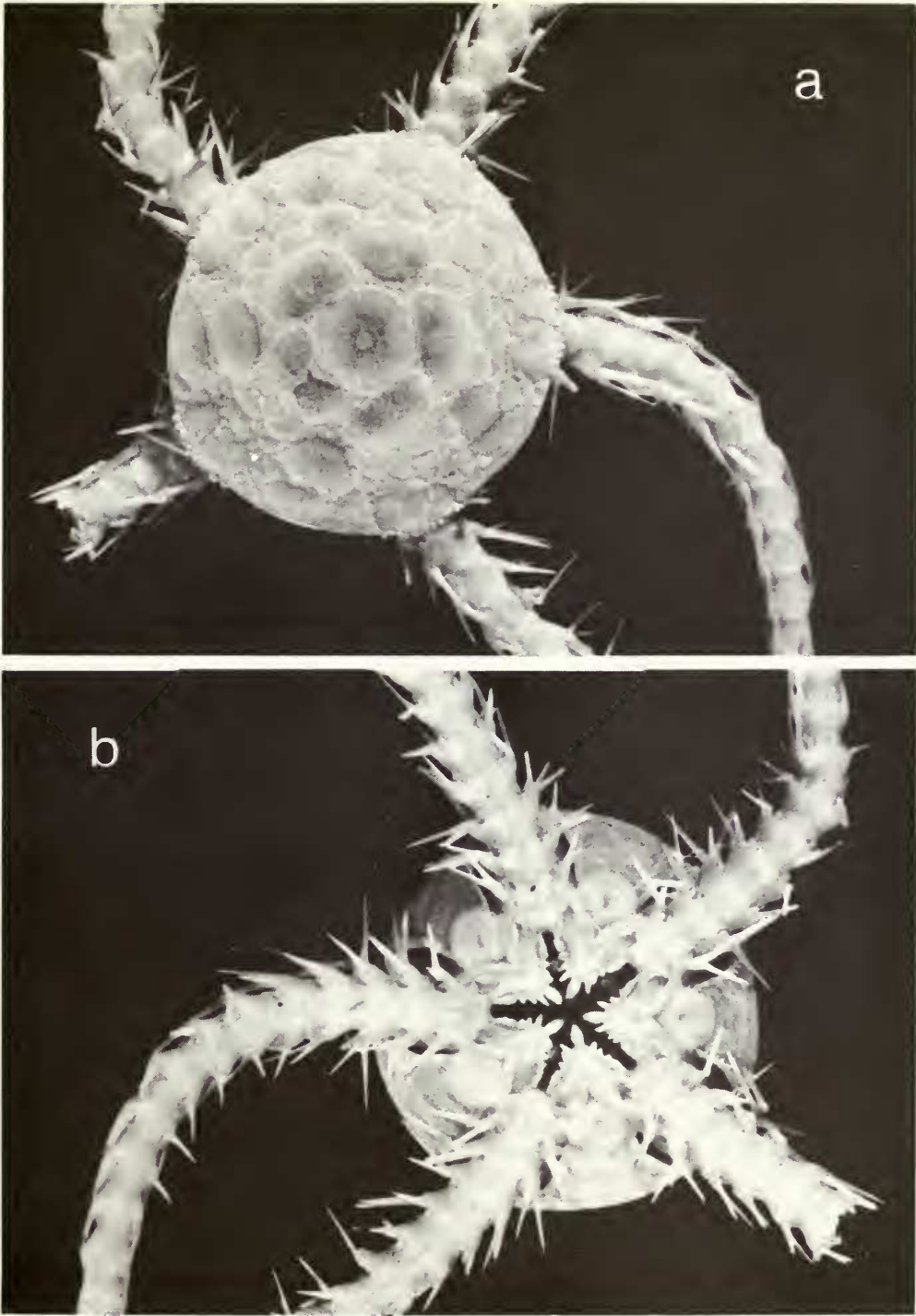


Fig. 7 *Ophiocten centobi* sp. nov., (a) dorsal and (b) ventral view of the holotype.

Discussion

To summarise our taxonomic conclusions, five species are recognised: *Ophiecten sericeum* (Forbes), which is restricted to Arctic Seas; *O. gracilis* (Sars), a boreal species found off Ireland, the Rockall Trough, S. Iceland, south Greenland and off eastern N. America (previously described under a variety of names and often confused with *O. sericeum*, see page 117); *O. abyssicolum* (Forbes), recorded from the Mediterranean as far north as south west Ireland; *O. hastatum* Lyman, an abyssal species (which we consider to be conspecific with *O. latens* Koehler and *O. pacificum* Lütken and Mortensen); and *O. centobi*, a new abyssal species from the Bay of Biscay. *O. scutatum* Koehler, 1896, is considered conspecific with *Ophiura affinis*.

The type species of *Ophiecten*, *O. sericeum* is a shallow or bathyal Arctic species found to a depth of 2000 m. This species was originally thought to occur commonly to the south of the Wyville Thomson Ridge in progressively deeper water and also in the Mediterranean (Mortensen, 1933a). Though the pelagic larvae of *O. sericeum* could be carried south, Mileikovsky (1971) has shown that this is unlikely because the larvae of Arctic ophiuroids are not dispersed far from their breeding grounds. The supposed Mediterranean population has been shown by Cherbonnier (1958) to be *Ophiecten abyssicolum* (Forbes, 1843).

We believe that those specimens found at intermediate depths along the slope to the west of the British Isles, and originally described as *Ophiecten sericeum* or *Ophiura signata*, are *Ophiecten gracilis* and *Ophiecten abyssicolum*. These two species are distinguished by the shapes of the mouth shield, the ventral arm plates and the arm comb arrangement. *Ophiecten gracilis* has a wide distribution on the upper slope of the N. Atlantic from western Scotland round the Faroes, Iceland-Greenland Ridge down to the eastern United States. On the slope southwards from western Scotland *O. gracilis* is replaced by *Ophiecten abyssicolum* which extends along the western European slope to the Straits of Gibraltar and the Mediterranean. The distribution of these two species clarifies the confusion over the identity of the *Ophiecten* species found on the slope to the west of the British Isles described by Kemp (1905). In water greater than 2000 m deep, the species found are: *Ophiecten hastatum* (recorded as *O. latens*), which is easily distinguishable from the other species by the very broad mouth shield, and the long upper arm spine, the reduced arm comb and extent of the genital papillae, and *Ophiecten centobi*.

The distribution of the five species within the North Atlantic is closely related to the hydrography of the main water masses.

The water masses of the N.E. Atlantic have been described by Cooper (1952) and Ellett and Martin (1973), and the northward modification of the intermediate water originating from the Mediterranean outflow has been discussed in detail by Pingree & Morrison (1973) and Reid (1979). We believe that *O. sericeum* is indicative of cold Norwegian Sea Deep Water and, as this species has a pelagic larva, it may occasionally cross the Scotland-Greenland ridges in the Norwegian Sea overflow to live as a 'guest' population (*sensu* Madsen, 1961) around the northern fringes of the North Atlantic where the incoming water is least modified. *O. abyssicolum* is found as far north as S.W. Ireland on the eastern Atlantic slopes in association with the salinity maximum due to Gibraltar water (Cooper, 1952; Cooper, Jones & Lee, 1962). Further north, off western Scotland, where the intermediate salinity maximum is not evident and Gibraltar influence can only be traced by lower oxygen content (Ellett & Martin, 1973), *O. gracilis* is found. Finally, *O. hastatum* and *O. centobi* are found in the colder deep waters (Labrador Sea water and Northeast Atlantic Deep water in the European Basin; Ellett & Martin, 1973) beneath the Gibraltar water layers.

These conclusions on the taxonomy and zoogeography of the different North Atlantic species of *Ophiecten*, especially in relation to the water mass distribution, help to clarify the confusion found in previous accounts.

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Appendix

Samples examined:

- (i) *Ingolf* specimens from the Zoologisk Museum, Copenhagen identified by Mortensen (1933a) as *Ophiocten sericeum*.

	Locality		Depth	Our identification
Stn 100	66° 23' N	14° 12' W	111 m	<i>Ophiocten gracilis</i>
Stn 124	67° 40' N	15° 40' W	932 m	<i>Ophiocten gracilis</i>
Stn 104	66° 23' N	7° 25' W	1802 m	<i>Ophiocten gracilis</i>
Stn 118	68° 27' N	8° 20' W	1996 m	<i>Ophiocten gracilis</i>
Stn 138	63° 26' N	7° 56' W	887 m	<i>Ophiocten gracilis</i>
Stn 103	66° 23' N	8° 52' W	1090 m	<i>Ophiocten gracilis</i>
Stn 27	64° 51' N	55° 10' W	740 m	<i>Ophiocten gracilis</i>
Stn 120	67° 29' N	11° 32' W	1666 m	<i>Ophiocten gracilis</i>
Stn 5	64° 40' N	12° 09' W	279 m	<i>Ophiocten gracilis</i>
Stn 4	64° 07' N	11° 12' W	446 m	<i>Ophiocten gracilis</i>

- (ii) *Albatross* specimens from the United States National Museum, Washington, cited by Koehler (1914) as *O. hastatum*.

Stn 2415	30° 44' N	79° 26' W	900 m	<i>O. gracilis</i>
Stn 2429	45° 55' 30" N	50° 51' W	857 m	<i>O. gracilis</i>
Stn 2542	40° 00' 15" N	20° 42' 20" W	235 m	<i>O. gracilis</i>
Stn 2582-3	39° 50' N	71° 43' W	249 m	<i>O. gracilis</i>

- (iii) *Blake* specimen from the Museum of Comparative Zoology, Harvard, identified by Lyman 1883 as *Ophiocten pattersoni*.

Stn 344	40° 1' N	70° 58' W	HOLOTYPE	<i>O. gracilis</i>
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- (iv) Specimens from the Museum National d'Histoire Naturelle, Paris

- (a) identified as *Ophiocten latens*

Travailleur et *Talisman* 1883

Stn 134	42° 19' N	23° 26' W	4060 m	SYNTYPES	<i>O. hastatum</i>
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- (b) identified as *Ophiocten hastatum*

Marion Island (Antarctique)		Southern Ocean			<i>O. hastatum</i>
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- (v) Specimens from the 'Biogas' and 'Polygas' Investigations (Centre Oceanologique de Bretagne, Brest) in the Bay of Biscay.

ES = epibenthic sledge samples, T = Trawl samples

Stn 1	ES 47° 30' - 47° 39' N : 8° 30' - 8° 46' W				
	2100 m (average)	ES 340 specimens			<i>O. hastatum</i>

Stn 2	ES 47° 25'–47° 36' N : 9° 00'–9° 15' W 3000 m (average)	ES 124 specimens	<i>O. hastatum</i>
	ES 47° 25'–47° 36' N : 9° 00'–9° 15' W 3000 m (average)	T 57 specimens	<i>O. hastatum</i>
Stn 3	47° 30'–47° 40' N : 9° 28'–9° 44' N 4200 (average)	ES 37 specimens	<i>O. hastatum</i>
Stn 5	44° 20'–44° 32' N : 4° 45'–4° 56' W 4500 m (average)	ES 578 specimens T 295 specimens	<i>O. hastatum</i>
Stn 6	44° 03'–44° 12' N : 4° 10'–4° 23' N 2000 m (average)	ES 16 specimens T 53 specimens	<i>O. hastatum</i>
(vi) Specimens from <i>Discovery</i> Investigations, Institute of Oceanographic Sciences.			
Stn 8511	1 41° 55' N : 11° 15' W	2399–2384 m	<i>O. hastatum</i>
8512	4 42° 15' N : 11° 36' W	2281–2465 m	<i>O. hastatum</i>
(vii) Specimens from the British Museum (Natural History).			
(a) <i>Challenger</i> specimens identified as <i>Ophiocten hastatum</i> by Lyman (1878–1882).			
Stn 146	40° 46' S : 45° 31' E	2515 m	
		Holotype and Paratypes	1882.12.23.352
Stn 146	40° 46' S : 45° 31' E	2515 m	
		7 specimens	1956.10.2.21.24
Stn 78	37° 34' N : 25° 13' W	1829 m	
		1 specimen	1882.12.23.351
Stn 168	40° 28' S : 177° 43' E	2012 m	
		3 specimens	1882.12.23.220
Stn 168	40° 28' S : 177° 43' E	2012 m	
		3 specimens	1956.10.2.16–17
(b) Specimens originally identified as <i>Ophiura signata</i> .			
Oxford University Expedition. Spitzbergen.			
		4 specimens	1923.7.6.12–14
J. M. Wordie.	Baffin Island, Eglington Fjord.		
		2 specimens	1935.10.19.1
Oxford University Ellesmere I. Expedition. Faylfe Fjord, Greenland			
		5–21 specimens	1936.5.26.4
<i>Rosaura</i> .	Stn 1 65° 35' N : 37° 20' W	25–50 m	
		6 specimens	1949.1.19.80
<i>William E. Ripley</i> .	71° 34' N : 150° 22' W		
			1955.6.23.14
<i>Ernest Holt</i> .	70° 20' N : 33° 32' E	165 m	
		20 specimens	1969.6.12.246–255
Spitzbergen. 60–64 m			
		1 specimen	1969.8.25.33
<i>Porcupine</i> .	Stn. 47 59° 34' N ; 7° 18' W	975–6 m	
			1908.2.19.28–34
<i>Procupine</i> .	Stn 88. 59° 26' N : 8° 23' W	1057 m	
			1890.2.19.147.160
<i>Porcupine</i> .	Stn 77. 60° 34' N : 4° 40' W	1124 m	
		12 specimens	1890.2.19.191–195
Thomson Collection. Lofoten Island 18–30 m			
		2 specimens	1890.2.20.202
<i>Triton</i> .	Wyville Thomson Ridge	829 m	
		15 specimens	1925.10.30.21.31
<i>Triton</i> .	West of Wyville Thomson Ridge	513–779 m	
		16 specimens	1925.10.30.52–59
<i>Porcupine</i> .	Stn 23a 56° 13' N : 14° 18' W	768 m	
		2 specimens	1890.2.19.25

<i>Knight Errant.</i>	N. of N. Rona	972 m			
	6 specimens		1925.10.30.177-179		<i>O. gracilis</i>
<i>Manahine.</i>	Stn 5 S.W. Ireland	720-819 m			
	20 specimens		1950.8.14.20.26		<i>O. gracilis</i>
Irish Fisheries.	Stn SR	1173 m			
	5 specimens		1914.1.30.62-63		<i>O. gracilis</i>
Norman Collection.	Off Martha's Vineyard	N.E. America	140 m		
	2 specimens		1910.2.1.197-198		<i>O. gracilis</i>
Norman Collection.	Faeroe Channel	838 m			
	8 specimens		1910.2.1.214-217		<i>O. gracilis</i>
Norman Collection.	Off Cleggin Head, Ireland				
	5 specimens		1910.2.1.2.18		<i>O. abyssicolum</i>
Irish Dept. Agriculture.	Off Kerry	606 m			
	10 specimens		1904.1.2.4.2-6		<i>O. abyssicolum</i>
E. W. L. Holb.	52° 2' N : 12° 8' W	817 m			
	7 specimens		1914.6.12.11.14		<i>O. abyssicolum</i>
(c) Other material examined					
Greenland.	1 specimen		1858.9.10.18		<i>O. sericeum</i>
Spitzbergen.	90 m				
	2 specimens		1868.6.19.25		<i>O. sericeum</i>
Arctic Expedition 1875.	Winter Quarters	20 m			
	1 specimen		1880.10.1.27		<i>O. sericeum</i>
Franz Joseph Land.					
	1 specimen		1880.11.2.17		<i>O. sericeum</i>
Kara Sera (Kara Haven).					
	1 specimen		1890.1.9.6-9		<i>O. sericeum</i>
Norman Collection.	Greenland.				
	2 specimens		1914.6.12.19-22		<i>O. sericeum</i>
<i>Porcupine.</i>	Stn 37	48° 38' N : 12° 8' W	4563 m		
	4 specimens		1890.2.19.92		<i>O. hastatum</i>
<i>Albatross.</i>	Stn 3393	1836 m			
	Syntype of <i>O. pacificum</i>		1901.4.9.48		<i>O. hastatum</i>
<i>Discovery.</i>	Investigations	Stn 7711/57	54° 48' N : 20° 03' W		
	2658-2656 m.		1976.7.30.122-130		<i>O. hastatum</i>

(viii) Specimens from sampling undertaken by the Scottish Marine Biological Association, mainly from R.R.S. *Challenger*.

ES = Epibenthic sledge; SBC = spade box corer; AT = Agassiz Trawl.

ES 10	56° 37' N : 11° 04' W	2540 m	43 486 specimens	<i>O. gracilis</i>
ES 18	56° 44' N : 09° 20' W	1392 m	4441 specimens	<i>O. gracilis</i>
ES 20	56° 46' N : 09° 17' W	1271 m	7465 specimens	<i>O. gracilis</i>
ES 22	56° 41' N : 09° 22' W	1028 m	6761 specimens	<i>O. gracilis</i>
ES 23	56° 37' N : 09° 10' W	704 m	5665 specimens	<i>O. gracilis</i>
ES 27	54° 40' N : 12° 16' W	2880 m	3 specimens	<i>O. gracilis</i>
ES 54	54° 40' N : 12° 16' W	2878 m	1 specimen	<i>O. gracilis</i>
ES 59	54° 40' N : 12° 20' W	2900 m	2281 specimens	<i>O. gracilis</i>
ES 69	53° 39' N : 07° 12' W	1050 m	48 specimens	<i>O. gracilis</i>
ES 90	60° 05' N : 05° 55' W	1040 m	10 specimens	<i>O. gracilis</i>
ES 99	60° 00' N : 10° 35' W	1160 m	2 specimens	<i>O. gracilis</i>
ES 115	56° 29' N : 10° 22' W	1000 m	113 specimens	<i>O. gracilis</i>
ES 129	54° 39' N : 12° 17' W	2900 m	5 specimens	<i>O. gracilis</i>
ES 135	54° 39' N : 12° 16' W	2900 m	15 561 specimens	<i>O. gracilis</i>
ES 137	54° 34' N : 12° 19' W	2900 m	35 specimens	<i>O. gracilis</i>
ES 147	54° 36' N : 12° 19' W	2921 m	10 263 specimens	<i>O. gracilis</i>
ES 164	54° 37' N : 12° 24' W	2925 m	417 specimens	<i>O. gracilis</i>
ES 172	54° 39' N : 12° 17' W	2910 m	1650 specimens	<i>O. gracilis</i>
ES 176	57° 15' N : 10° 26' W	2200 m	10 380 specimens	<i>O. gracilis</i>
ES 178	56° 33' N : 09° 17' W	997 m	147 specimens	<i>O. gracilis</i>
ES 180	54° 42' N : 12° 11.5' W	2886 m	8 specimens	<i>O. gracilis</i>

ES 184	57° 14' N : 10° 24' W	2260 m	650 specimens	<i>O. gracilis</i>
SBC 65	56° 39' N : 09° 40' W	1600 m	21 specimens	<i>O. gracilis</i>
SBC 66	56° 39' N : 09° 23' W	1200 m	57 specimens	<i>O. gracilis</i>
SBC 67	56° 39' N : 09° 13' W	1000 m	26 specimens	<i>O. gracilis</i>
AT 90a	60° 05' N : 05° 57' W	1040 m	1 specimen	<i>O. gracilis</i>
AT 1		750 m	77 specimens	<i>O. gracilis</i>
AT 141	54° 44' N : 12° 14' W	2909 m	2 specimens	<i>O. gracilis</i>
ES 6	55° 03' N : 12° 29' W	2900 m	9 specimens	<i>O. hastatum</i>
ES 27	54° 40' N : 12° 16' W	2880 m	1 specimen	<i>O. hastatum</i>
ES 52	54° 40' N : 12° 16' W	2886 m	2 specimens	<i>O. hastatum</i>
ES 55	54° 40' N : 12° 16' W	2886 m	1 specimen	<i>O. hastatum</i>
ES 111	54° 40' N : 12° 16' W	2886 m	1 specimen	<i>O. hastatum</i>
ES 129	54° 39' N : 12° 17' W	2960 m	1 specimen	<i>O. hastatum</i>
ES 137	54° 34' N : 12° 19' W	2900 m	2 specimens	<i>O. hastatum</i>
ES 140	54° 40' N : 12° 16' W	2912 m	7 specimens	<i>O. hastatum</i>
ES 147	54° 36' N : 12° 19' W	2921 m	7 specimens	<i>O. hastatum</i>
AT 107a	57° 07' N : 12° 06' W	2000 m	10 specimens	<i>O. hastatum</i>
AT 119	54° 40' N : 12° 14' W	2908 m	1 specimen	<i>O. hastatum</i>
AT 121	54° 37' N : 12° 09' W	2910 m	187 specimens	<i>O. hastatum</i>

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