

Ophiura paucilepis, a new species of brittlestar (Echinodermata, Ophiuroidea) from the Pliocene of the southern North Sea Basin

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Abstract The first articulated ophiuroids to be recorded from Neogene deposits in the southern North Sea Basin are described as a new species, *Ophiura paucilepis*, based on two discs with portions of proximal arms preserved, plus an isolated arm fragment. The specimens were collected from the Oosterhout Formation (Pliocene, lower Zanclean to mid-Piacenzian, ca. 4.9–2.8 Ma) at sandpit ‘De Kuilen’ near Langenboom (province of Noord-Brabant, the Netherlands). A comparison with extant taxa from the North Sea and North Atlantic, such as *O. albida*, *O. ophiura*, *O. sarsii* and *O. carnea*, shows the fossil species to be characterised by a coarse disc scalation, which may be an ancestral state or a pedomorphic condition, similar to immature stages of extant taxa. The new species is compared to and distinguished from other records of mid-Cretaceous to Cenozoic taxa that have been assigned to the genus *Ophiura* either routinely, indiscriminately or with a query.

Keywords Neogene · Pliocene · North Sea Basin · The Netherlands · Ophiuridae · Taxonomy

Abbreviations

dd	Disc diameter
MAB	Oertijdmuseum De Groene Poort, Boxtel, the Netherlands
MGUH	Statens Naturhistorisk Museum, København, Denmark
NHM	The Natural History Museum, Department of Palaeontology, London, United Kingdom
NHMW	Naturhistorisches Museum Wien, Austria
SGWG	Ernst-Moritz-Arndt Universität, Sektion Geologische Wissenschaften, Greifswald, Germany
SMNH	Swedish Museum of Natural History, Stockholm, Sweden
SWBI	Southwest Biostratigraphic Research Institute, Department of Geological Sciences, University of Texas, El Paso, Texas

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Introduction

Neogene (Miocene–Pliocene) strata in the southern North Sea Basin (central and southern Netherlands, northwest Belgium) are locally rich in echinoderm remains, but ophiuroids constitute only a minor component of such assemblages (see e.g., Engel 1941; Sieverts-Doreck 1953). In the majority of cases, only dissociated ossicles, mostly vertebrae and arm plates, are preserved, making generic and specific identification difficult, if not impossible. Until now, records of more or less complete discs with arms,

which attest either to rapid burial and lack of subsequent scavenging and bioturbation or to exceptional circumstances (see e.g., Böhm 1889; Berry 1939; Clark 1959; Wienberg Rasmussen 1972; Kerr and Twitchett 2004; Kroh 2007), were lacking from the study area.

Slightly silty, fine-grained and well-sorted, glauconitic quartz sands assigned to the Oosterhout Formation, which are suction-dredged at sandpit ‘De Kuilen’ near Langenboom (Fig. 1), have now yielded the first articulated ophiuroids to be recorded from the southern North Sea Basin. Two discs with proximal portions of arms preserved, plus an isolated arm fragment, are shown to be conspecific and are described here as a new species of the genus *Ophiura* Lamarck, 1801, *O. paucilepis* sp. nov. At sandpit ‘De Kuilen’, Unit B (sensu Wijnker et al. 2008) has produced most macrofossil remains including molluscs, brachiopods, echinoderms, serpulids, bryozoans, plant and vertebrate remains (Wijnker et al. 2008; Klompmaker 2009). It is from this level that the present brittlestar

material is inferred to have originated, because other units contain little or no carbonate and the holotype disc was covered in shell fragments when it was collected. On molluscan and dinoflagellate evidence (see Wijnker et al. 2008), an early Zanclean to mid-Piacenzian date (Pliocene; ca. 4.9–2.8 Ma) has been established for this part of the sequence (Fig. 2).

The new species is compared with extant taxa from the North Sea and North Atlantic Ocean, as well as with a number of fossil species of mid-Cretaceous (Albian-Cenomanian) to Cenozoic age which have been placed in the genus *Ophiura*, either more or less routinely, indiscriminately or with a query. However, a revision of these extinct taxa is deferred to another occasion.

Systematic palaeontology

Order Ophiurida MÜLLER & TROSCHEL, 1840

Family Ophiuridae MÜLLER & TROSCHEL, 1840

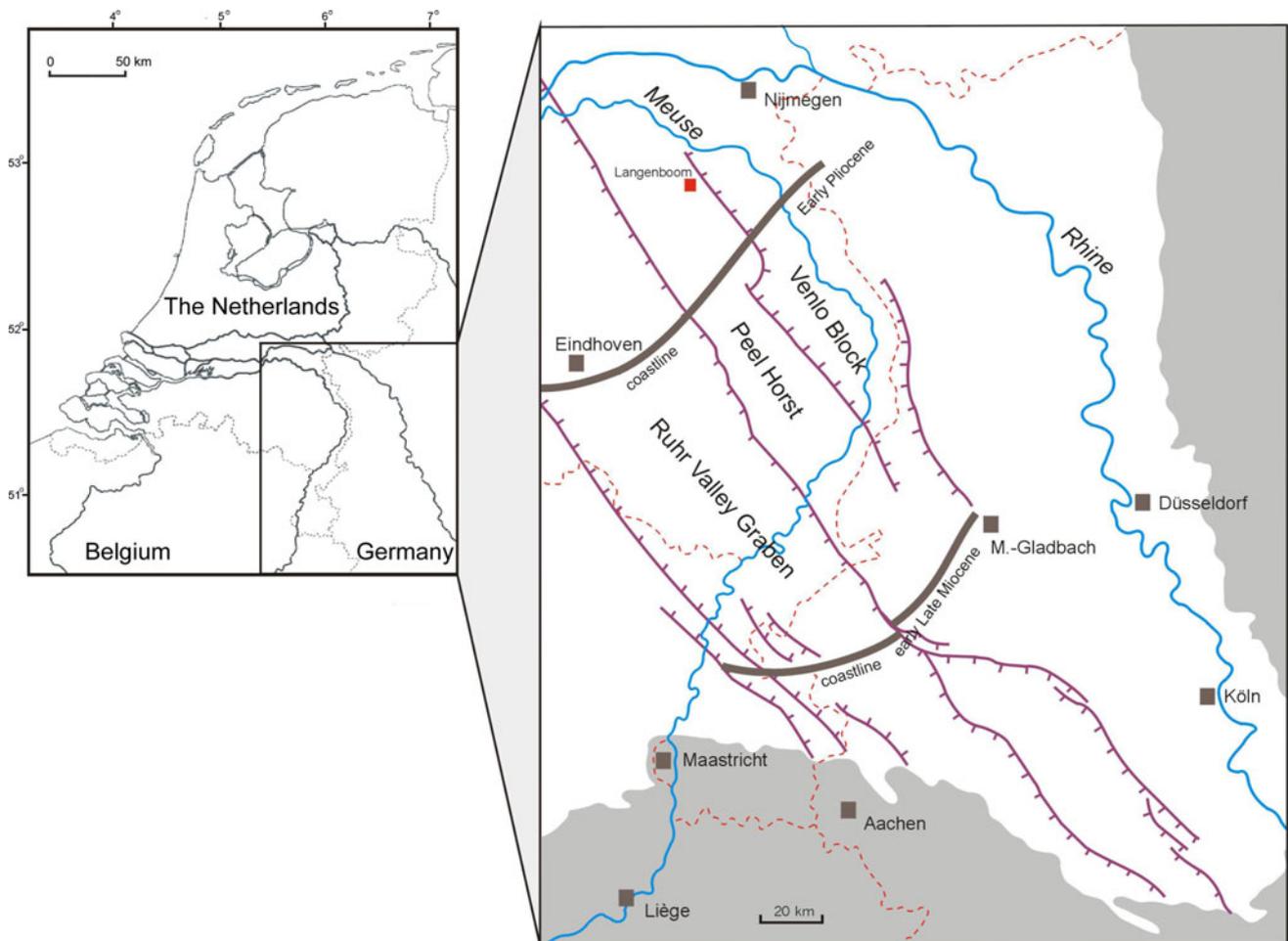


Fig. 1 Map of the Langenboom area (province of Noord-Brabant, the Netherlands), showing the locality of sandpit ‘De Kuilen’ (copy of Wijnker et al. 2008, fig. 1, reproduced with permission)

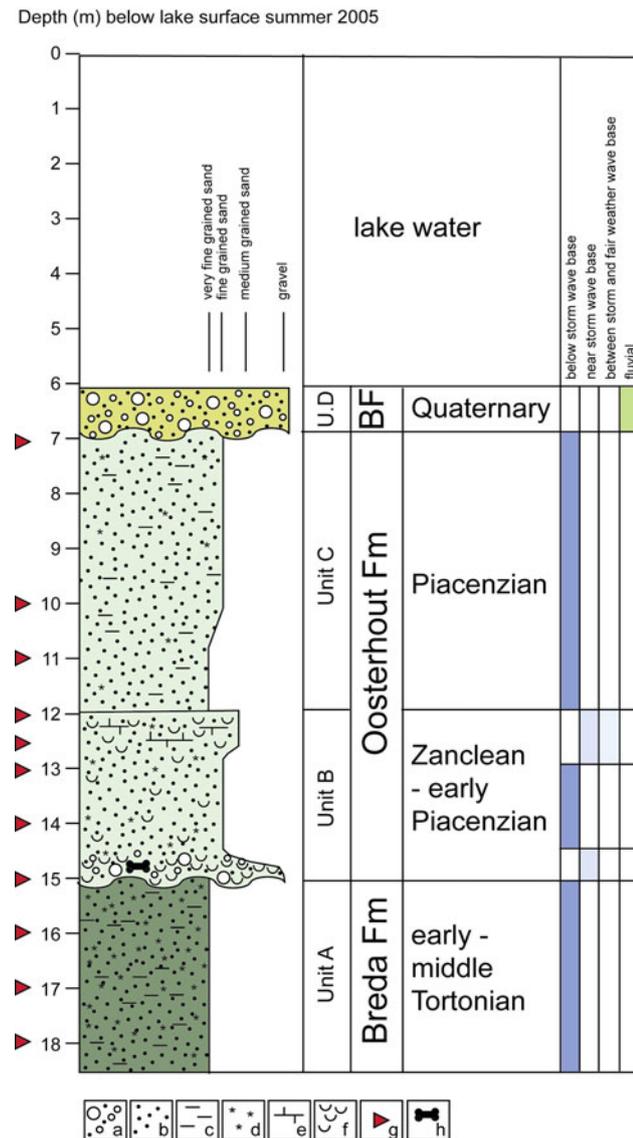


Fig. 2 Facies interpretation and litho- and chronostratigraphy of the Langenboom section at sandpit ‘De Kuilen’ (copy of Wijunker et al. 2008, fig. 6, reproduced with permission). *a* gravel, *b* sand, *c* silt, *d* glauconite, *e* carbonate cement, *f* shells, *g* sample location, *h* bone. Unit B is here inferred to be the source of *Ophiura paucilepis* sp. nov. (see text)

Genus *Ophiura* LAMARCK, 1801

Type species: Asterias ophiura LINNAEUS, 1758, by ICZN ruling (Opinion 1152; see Melville 1980).

Diagnosis: Disc low, flat, covered by small, imbricating plates, primary rosette usually distinct. Radial shields more or less separated. Arms not stout, gradually tapering, usually deep incisions next to arm bases (distal bursal slits). Dorsal arm plates well developed, adjacent plates usually contiguous, several proximal dorsal plates included in the disc, separating radial shields. Genital papillae well developed, arm combs present. Second oral tentacle pore

opens into mouth slit, beset with numerous small papillae, which often form a continuous row with the oral papillae. Ventral arm plates much wider than long, usually separated, at least outside disc.

Ophiura paucilepis sp. nov. (Fig. 3a–k)

Types: MAB 4280 (holotype; leg. A. A. Klompmaker) and MAB 4281 (paratype; leg. N. Taverne).

Additional material: MAB 4282, an arm fragment, which might well have belonged to either of the holotype or paratype discs, but this cannot be ascertained beyond doubt.

Comparative recent material: *Ophiura albida* Forbes, 1839: SMNH-52141 (one specimen on SEM stub, 4 mm dd; Kattegat, Sweden, Halland, Värö, 57°16.5’N, 12°05’E, depth 19 m, sand bottom, leg. S. Smith) and SMNH-87672 (one specimen on SEM stub, 8 mm dd; same locality); SMNH-115527, one specimen, 8 mm dd, on SEM stub, same locality. *Ophiura sarsii* Lütken, 1855: SMNH-42832 (one specimen on SEM stub, 7 mm dd; BIOICE station 2585, Iceland, 67°24.79’N, 22°24.43’W, depth 450 m) and SMNH-45845 (one specimen on SEM stub, 6 mm dd; BIOICE station 2673, Iceland, 66°50.22’N, 16°16.26’W, depth 222 m).

Locality and stratigraphy: Sandpit ‘De Kuilen’ near Langenboom, province of Noord-Brabant (the Netherlands); Oosterhout Formation, Unit B (12–15 m below surface), lower Zanclean to mid-Piacenzian, Pliocene.

Etymology: Latin *pauci*, meaning ‘few’ and *lepis*, meaning ‘scale’.

Diagnosis: Species of *Ophiura* with few large disc scales, among which the primary rosette is distinct. The oral shield is almost twice as long as wide and covers about two-thirds of the ventral interradial disc space. Dorsal arm plates fan shaped, three times wider than long. Two (or three) short conical arm spines. The known maximum size of the species (disc diameter) is 8 mm.

Description of MAB 4280 (holotype): Disc diameter of approximately 8 mm and five arms, which are all broken off close to the disc. The dorsal disc is formed by large scales, among which the primary rosette, consisting of a round central primary plate and a circle of five round radial primary plates, is distinct (Fig. 3a). Distal to the primary rosette, two to three interradial plates extend to the disc margin. The radial shields are round, but at their proximal ends they are partially overlapped by interradial plates and a wedge plate (‘k-plate’), which separates adjacent radial shields proximally (Fig. 3b). Distally, the radial shields are separated by the small, wedge- or possibly cordiform, first dorsal arm plate. The dorsal arm plates beyond the first three are about three times as wide as long, with straight lateral and proximal edges, convex distal edge, and wider

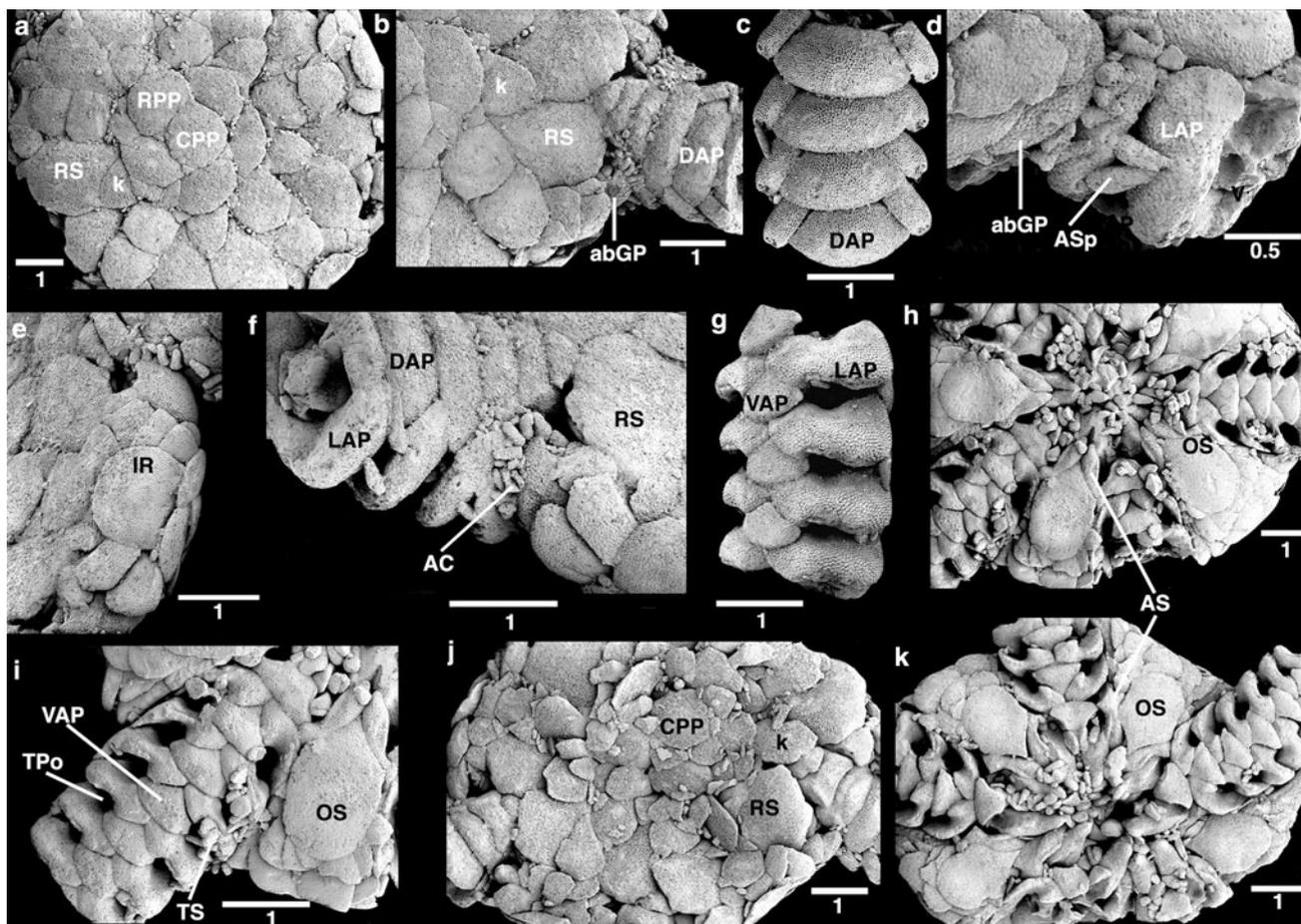


Fig. 3 SEM images of *Ophiura paucilepis* sp. nov., Pliocene, Langenboom; holotype (MAB 4280), dorsal view (a), detail of radial shields and dorsal arm plates (b), lateral view of arm with spines (d), interradial lateral view of disc (e), detail of arm comb and lateral arm plates (f), disc in ventral view (h) and detail of ventral arm plates (i); j, k paratype (MAB 4281) in dorsal and ventral views, respectively; c, g arm fragment (MAB 4282) in dorsal and ventrolateral views,

respectively. *abGP* abradial genital plate, *AC* arm comb, *adGP* adradial genital plate, *AS* adoral shield, *ASp* arm spine, *CPP* central primary plate, *DAP* dorsal arm plate, *GS* genital scales; *k* k-plate, *LAP* lateral arm plate, *IR* interradial plate, *OS* oral shield, *RPP* radial primary plate, *RS* radial shield, *TPo* tentacle pore, *TS* tentacle scale, *V* vertebra, *VAP* ventral arm plate. Scale bars in millimetres

at their distal end than at their proximal end (Fig. 3c). The first dorsal arm plate is the smallest and has an acute proximal angle, the following two plates increase in size and are similar in shape to the remaining plates (Fig. 3b, c). Lateral arm plates from the fourth segment bear two, probably three, conical spines, which are appressed and shorter than an arm segment (Fig. 3d). At the vertical disc edge, a large round plate is visible, bordered by smaller, round to oval plates to either side, creating the appearance of a rosette (Fig. 3e).

Below the radial shields, a well-developed arm comb is present, consisting of at least eight, probably slightly more, elongated papillae on the edge of the abradial genital plate (Fig. 3c, f). The abradial genital plate extends onto the ventral side, where it is continued by a row of small genital scales along the bursal slit, as is typical for the genus

Ophiura (Fig. 4a). The genital scales appear to bear genital papillae, which are, however, difficult to distinguish from the scattered tentacle scales (Fig. 3h).

The numerous oral papillae are scattered across all jaws and their original number and position is unclear. The second tentacle pore is superficial. The adoral shields are narrow and curved, bordering the proximal edges of the oral shield, which is almost twice as long as wide, with acute proximal angle and convex distal edge. The madreporite is not distinguishable among the oral shields. Few scales of different sizes and shape form the ventral disc distal of the oral shield (Fig. 3g, h).

The ventral arm plates have an acute proximal angle and a convex distal edge, which is twice as wide as the plate is long (Fig. 3h, i). Adjacent plates are separated by the lateral plates, which meet on the mid-line of the arm. The

large tentacle pores bear numerous small tentacle scales, which are scattered and their exact number and position cannot be determined.

Paratype MAB 4281 differences: The paratype is of approximately the same size as the holotype, with about 8 mm dd, and largely agrees with the holotype. However, part of the disc is missing. The dorsal disc plates are in disarray, but the primary rosette is distinguishable, as are the radial shields, k-plate and interradiial plates (Fig. 3j). In contrast to the holotype, some smaller plates are present between the radial shields and the primaries. The rosette at the disc margin is not visible and the plates look broken and compressed. No arm spines are preserved in this specimen, but articulation ridges are visible, suggesting that three arm spines were present. Fewer oral papillae and tentacle scales are preserved in the paratype (Fig. 3k).

Discussion

The genus *Ophiura* is differentiated from *Amphiophiura* Matsumoto, 1915 by its low, flat disc, the small ventral arm plates and the position of the second tentacle pore closer to the mouth slit (see also Matsumoto 1917). However, the latter, which is closely related, currently includes species that probably would fit better in *Ophiura* (see Martynov and Litvinova 2008), which obscures the generic boundaries. *Amphiophiura* is in need of revision, as are the related genera *Stegophiura* Matsumoto, 1915 and *Ophiomastus* Lyman, 1878. The matter is complicated by the fact that the whole family of the Ophiuridae appears to have been affected by heterochronic development, leading to various states of reduced skeleton (Stöhr and Martynov, in preparation).

Without doubt, the new species described here belongs to the genus *Ophiura*, on account of the position of the second tentacle pore close to the mouth slit, the well-developed arm comb and deep incisions at the arm bases, the presence of tentacle pores along the entire arm, the wide dorsal arm plates, three of which are part of the dorsal disc, and the wide, separated ventral arm plates (compare Fell 1960; Paterson 1985). Judging from the appearance of its type species, *A. bullata* (Wyville Thomson 1878), the genus *Amphiophiura* has a stocky appearance with stout arms which are not that far inserted into the disc as in *Ophiura*. Its arm bases lack the deep incisions, while dorsal, ventral and lateral arm plates are tumid, the ventral ones being quadrangular to axe shaped and contiguous and the second tentacle pore is positioned further from the mouth slit than in *Ophiura*. The genus *Amphiophiura* includes species with large oral shields and a small ventral disc, but these characters likely are the effect of heterochronic development, rather than homologies. Therefore, we dismiss a close relationship of the new species with *Amphiophiura*.

Recent studies have shown that the number of skeletal elements, such as disc scales, increases during ontogeny, but the final number of scales varies between species and higher taxa (see e.g., Sumida et al. 1998; Stöhr 2005 and references therein). The dorsal scalation pattern in *O. paucilepis* sp. nov. resembles conditions seen in many extant species during ontogeny, e.g., in *Ophiura albida* Forbes, 1839 at 4 mm dd (Fig. 4b). The low number of disc scales and their size might thus suggest that the type specimens of *O. paucilepis* sp. nov. represent juvenile individuals. However, the oral elements are similar in shape and number to those of larger specimens, e.g., *O. albida* at 8 mm dd (Fig. 4c). Thus, the coarse disc scalation sets *O. paucilepis* sp. nov. apart from most extant species. Coarser scalation is found in *O. imprudens* (Koehler 1906) and *O. carnea* Lütken 1858, but both differ in the shape of the dorsal and ventral arm plates and barely reach 8 mm dd (see Paterson 1985).

Ophiura paucilepis sp. nov. shows greatest affinities with *O. sarsii* Lütken 1855, *O. albida* and *O. ophiura* (Linnaeus 1758), all of which have more or less similar shapes of dorsal and ventral arm plates, arm spines and oral shields (Fig. 4) (compare Ishida 2004; Stöhr 2005). However, they all have smaller and more numerous disc scales at a similar size, longer and more slender arm spines, and reach a larger maximum size than is currently known for *O. paucilepis* sp. nov. However, they may be descendants from the same lineage.

Absence of certain skeletal elements in adult Ophiuroidea has been interpreted as a paedomorphic state (Vadon 1991). Assuming that coarse scalation is a juvenile character state, *O. paucilepis* sp. nov. may have retained an early ontogenetic stage into adulthood. It is, however, also plausible that a limited number of scales or other elements represent an ancestral state of shorter development, since externally only the disc shows any signs of possible paedomorphosis. In that case, modern forms would have a prolonged development known as peramorphosis. Almost nothing is known about the adaptational significance of the presence or absence of ophiuroid skeletal elements, their shape and number. In addition, the phylogenetic interrelationships of the species assigned to the genus *Ophiura*, as well as among genera within the family Ophiuridae, are still poorly understood (compare also Smith et al. 1995). It is therefore difficult to draw any conclusions from the appearance of *O. paucilepis* sp. nov., which may be a predecessor of Recent species, or an extinct sister taxon to modern forms.

Comparisons to other fossil taxa

Added below are some preliminary notes on mid-Cretaceous to Cenozoic ophiuroids that have been assigned to

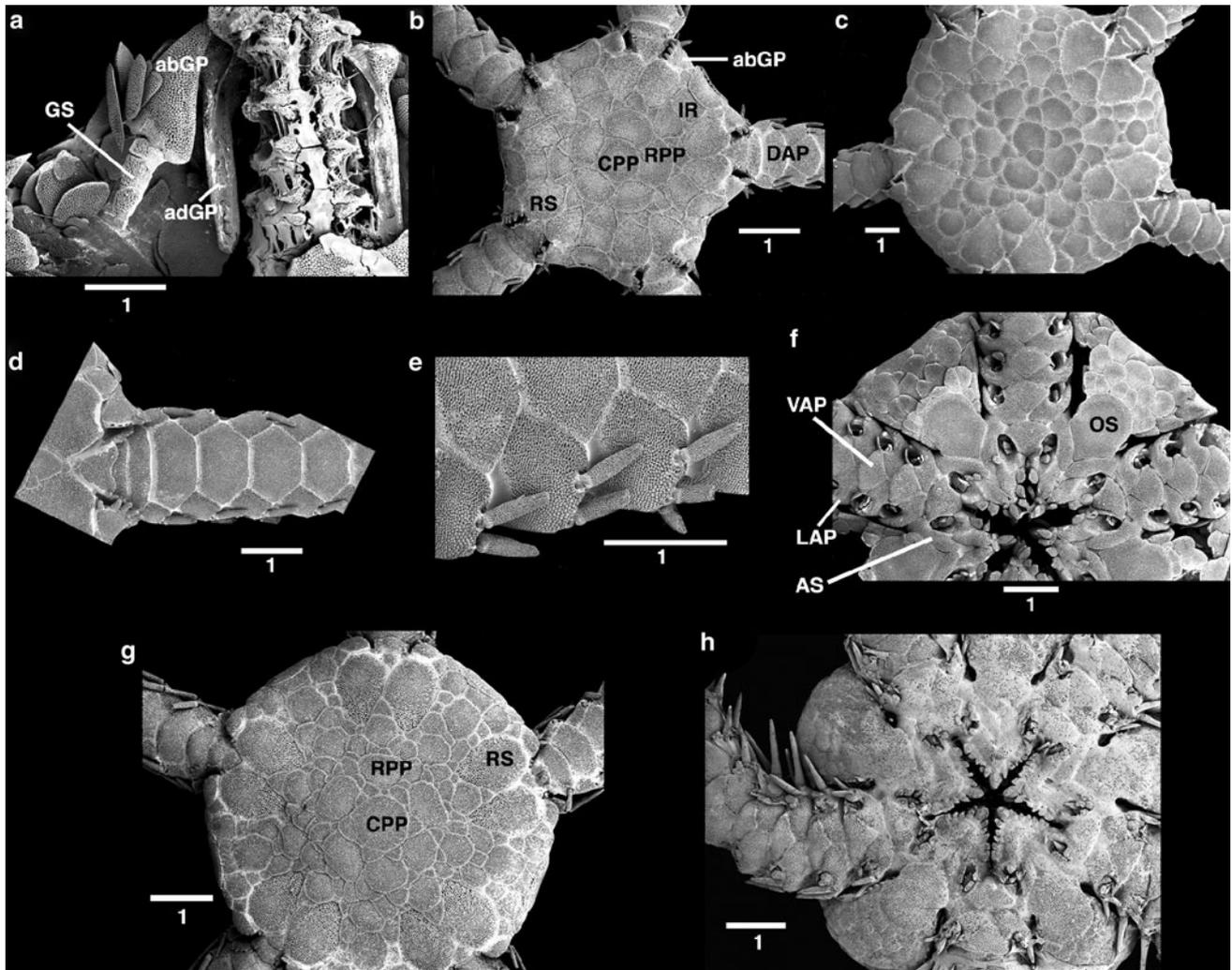


Fig. 4 SEM images of extant species of *Ophiura* from the North Sea and North Atlantic; *O. sarsii* Lütken, 1855, off Iceland, genital plates and scales as typical of the genus *Ophiura* (a); *O. albida* Forbes, 1839, Kattegat, 4 mm dd, with coarse disc scalation (b), at 8 mm dd, dorsal view (c), dorsal arm plates (d), lateral arm plates

with spines (e), ventral view, slightly overbleached (f); *O. sarsii*, dorsal disc, 6 mm dd (g), ventral disc, 7 mm dd (h). Specimens have all been bleached with household NaOCl to remove the integument, dd disc diameter, other abbreviations as in Fig. 3. Scale bars in millimetres

the genus *Ophiura*, either routinely, indiscriminately or with a query, listed according to stratigraphic age. Full revisions of these taxa are deferred to another occasion. Currently, no comparative basis exists that would allow the identification of dissociated ophiuroid remains to the species level. Possible exceptions may be certain types of vertebrae (i.e., the 'keeled' type) found exclusively in the families Ophiothrichidae Ljungman, 1867 and Ophionerididae Ljungman, 1867, as well as the genus *Ophiopholis* Müller & Troschel, 1842 (but not in the confamilial *Ophiactis* Lütken, 1856), as demonstrated by LeClair (1996) or the peculiar branching vertebrae that are found only in members of the families Gorgonocephalidae Ljungman, 1867 and Euryalidae Gray, 1840, or the ventrally closed vertebrae of the latter family. Those ossicles are, however,

only useful at the family level. Martynov (2010) has recently suggested that ophiuroid families might be identifiable by arm spine articulation type, but more data are needed to validate this hypothesis. The majority of extant ophiuroid species cannot be identified solely on either the ventral or dorsal side, so that in the majority of cases, also in fossils, both sides need to be present. Often the ventral side is more informative, though, because the oral skeleton is critical for the classification of modern brittle stars.

At a disc diameter of 5–6 mm, *Ophiura straini* Cornell, LeMone & Norland, 1991 (p. 1010, figs. 2.1–2.4; holotype is SWBI 90-01), from the Smelertown Formation (Albian) of New Mexico (USA) and referred by the authors to *Ophiura* with a query (aff.), has more numerous disc scales than *O. paucilepis* sp. nov. and the arm structure is

different as well, with triangular dorsal arm plates. The overall habit of this species certainly is ophiurid, but details of the ventral disc surface and arm structure are needed to substantiate such an assignment. This same holds true for other mid-Cretaceous taxa from North America, such as *Ophioglypha texana* W.B. Clark, 1893 (p. 30, pl. 4, fig. 1a–c) from the Weno Member (upper Albian) of Texas (see also Berry 1941, p. 61, pl. 9, fig. 11; pl. 10, figs. 9, 11) and *Ophioglypha graysonensis* Alexander, 1931 (p. 152, pl. 20, figs. 19, 20) from the Grayson Member (lower Cenomanian) of Texas (see also Berry, 1941, p. 62, pl. 9, figs. 1, 10; pl. 10, figs. 1, 6–7, 10; pl. 11, figs. 8, 10, as *Ophiura*).

Later, Clark (1959) referred specimens from the Austin Chalk (Campanian) of Texas to *O. graysonensis*, but this assignment appears doubtful and a revision of this material is called for.

Arm fragments and dissociated arm ossicles from the Santonian to Maastrichtian of northwest Europe from the basis for the record of *Ophiura serrata* Roemer, 1840 by Wienberg Rasmussen (1950, p. 111, pl. 16, figs. 1–8), which is now assigned to the ophiidermatid genus *Ophiotitanos* Spencer, 1907 (see Jagt 2000). A new species from the lower Maastrichtian of southeast England, assigned with a query to *Ophiura* is Wienberg Rasmussen's (1950, p. 114, pl. 17, figs. 1–5) *O?. hagenowi*, which Kutscher & Jagt (in Jagt, 2000, p. 69, pl. 24, figs. 1–6; pl. 33, fig. 1) provisionally transferred to the ophiurid genus *Stegophiura* Matsumoto 1915. A third species, *Ophiura? substriata* Wienberg Rasmussen, 1950 (p. 116, pl. 18, figs. 1–9), from the Santonian to Maastrichtian of northwest Europe appears to be an ophiidermatid, which Jagt (2000, p. 28) listed as *Ophioderma? substriatum*.

On the basis of dissociated ossicles from the Kemp Clay (Upper Cretaceous, Maastrichtian) of Texas, Berry (1941, p. 64, text-fig. 1; pl. 9, figs. 2–9, 12–14; pl. 10, figs. 2–5, 8; pl. 11, figs. 1, 3–4, 7, 11–15) erected *Ophiura travisana*. His reconstruction suggests this form to differ clearly from *O. paucilepis* sp. nov. on the basis of adoral and oral shields.

Again with only dissociated ossicles at hand, Berry (1938, p. 66, pl. 14, figs. 1–10, 13–25) introduced *Ophiura kunradeca*. However, as noted by Jagt (1991, 2000) this 'taxon' comprises ossicle types of more than one species. In particular, the lateral arm plates and radial shields have been shown to belong to *Felderophiura vanderhami* Jagt, 1991, of which numerous discs with arms preserved are available for study. *Felderophiura*, originally considered to be an ophiurid, is an ophiolepidid.

Ophiura achatae Wienberg Rasmussen 1972 (p. 61, pl. 6, fig. 3; holotype is MGUH 12799), from the Sonja Sandstone Member (Agatdal Formation, upper Danian) of Nûgssuaq, West Greenland, is based on a single arm

fragment. Compared to *O. paucilepis* sp. nov. this has longer arm spines (three in number), which are also in a different position, and contiguous ventral arm plates.

Ophiura bognoensis Wienberg Rasmussen, 1972 (p. 66, pl. 8, figs. 1–10; pl. 14, fig. 1; holotype is NHM E 13761), from the lower Eocene London Clay of Bognor Regis, Sussex (UK), has more numerous disc scales (at 12 mm dd), larger-sized radial shields and the arm combs have more papillae. Moreover, ventral arm plates appear to have been smaller than in *O. paucilepis* sp. nov., even in proximal arm portions.

Ophiura furiae Wienberg Rasmussen, 1972 (p. 62, pl. 6, figs. 4–5; pl. 13, fig. 1; holotype is MGUH 12800), from the lower Eocene Mo Clay Formation of Fur, Denmark, is easily distinguished from *O. paucilepis* sp. nov. on details of ventral and dorsal arm plating, adoral and oral shields and dorsal disc scalation.

In *Ophiura wetherelli* Forbes, 1852 (p. 32, pl. 4, fig. 7; see also Wienberg Rasmussen, 1972, p. 64, pl. 7, figs. 1–5; pl. 13, figs. 2–3, with additional synonymy; lectotype is no. 99786, Institute of Geological Sciences, London), from the lower Eocene London Clay of London, disc scales (between 3.5 and 9 mm dd) are much more numerous, ventral arm plates do not abut, dorsal arm plates are narrower and triangular in distal direction, thus precluding confusion with *O. paucilepis* sp. nov.

Ophiura bartonensis Wienberg Rasmussen, 1972 (p. 68, pl. 9, figs. 1–9; pl. 14, figs. 2–4; holotype is NHM E 52158), from the upper Eocene at Barton, Hampshire (UK), has triangular dorsal arm plates, non-contiguous ventral arm plates, an arm comb with more papillae, a large marginal disc plate and more numerous and smaller disc scales arranged in clear radial and interradial series, unlike *O. paucilepis* sp. nov.

Ophiura carpelloides Wienberg Rasmussen, 1972 (p. 71, pl. 10, figs. 1–9; holotype is NHM E 53658), from the upper Eocene of Barton, Hampshire, is based on dissociated ossicles only, and the structure of the oral shield and lateral arm plate suffice to distinguish that taxon easily from *O. paucilepis* sp. nov.

Ophiura costata Wienberg Rasmussen, 1972 (p. 70, pl. 6, figs. 8–9; holotype is NHM E 53637), from the upper Eocene of Barton, Hampshire, is based on dissociated lateral arm plates only. However, their structure suggests them to be asteroid oral ossicles rather than ophiuroid. In addition, the species name is preoccupied by *Ophioglypha* (= *Ophiura*) *costata* Lyman 1878.

Ophiura davisii Wienberg Rasmussen, 1972 (p. 75, pl. 10, figs. 10–15; holotype is NHM E 53668), from the upper Eocene at Barton, Hampshire, is based on dissociated lateral arm plates, which are easily differentiated from those of *O. paucilepis* sp. nov. by their denticulate external and internal articular surfaces.

Arm spine number (4) and length, shape of dorsal and ventral arm plates and the peculiar voids between the radial shields and arm combs serve to distinguish *O. hendleri* Blake & Aronson, 1998 (p. 348, figs. 5.1–5.8, 6.1–6.4, 7.1–7.4, 7.6), from the upper Eocene of Seymour Island, Antarctica.

Ophiura? sp. of Kutscher (1985, p. 8, pl. 3, fig. 1), from the middle Oligocene at Magdeburg, Germany, is based on a single lateral arm plate which appears to be much thinner than those of *O. paucilepis* sp. nov. and finely striate.

Ophiura? sternbergica Kutscher, 1980 (p. 226, pl. 2, figs. 4–7; pl. 3, figs. 4–5; pl. 4, figs. 1–7; holotype is SGWG 64), from the upper Oligocene ‘Sternberger Gestein’ of northeast Germany, is based mainly on dissociated ossicles, although an arm fragment is also known. Arm spines are three in number, but their position differs from that of spines in *O. paucilepis* sp. nov., and proximal lateral arm plates appear narrower while oral shields are medially constricted.

Ophiura? parviformis Küpper, 1954 (p. 161, pl. 15, figs. 4–14), from the ?lower ‘Badenian’ (=Langhian, mid-Miocene) of Austria, is an indeterminate species, based on isolated lateral arm plates only (see also Kroh, 2007, Table 4). It is certainly not an ophiurid, but compares much more favourably with some Late Cretaceous species assigned either to amphiuroids or ophiothrichids (see e.g., Kutscher and Jagt, in Jagt 2000, pl. 29).

Ophiura? vindobonensis Küpper, 1954 (p. 162, pl. 14, figs. 9–17), from the ‘Badenian’ (=Langhian; see also Kroh, 2007, Fig. 4, Table 4) is either an ophiolepidid, close to some Late Cretaceous forms such as *Ophiolepis? linea* Kutscher & Jagt, in Jagt, 2000 (p. 86, pl. 26, figs. 3–6) or an ophiidermatid comparable to *Ophiotitanos serrata*, as based on spine base structure and peg-like articulation bosses.

Ophiura marylandica Berry, 1934 (see Berry, 1939, p. 87, text-fig. 1; pl. 1, figs. 1–3), from the upper Miocene of Maryland, has differently shaped oral and adoral shields and ventral arm plates and arm combs have more numerous papillae than in *O. paucilepis* sp. nov., at comparable diameters.

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