

Article

The Northernmost Occurrence of the Tropical-Subtropical Brittle Star *Ophiocoma* (Echinodermata, Ophiuroidea) from a Late Cretaceous Rocky Shore in Southern Sweden [†]

Ben Thuy *  and Lea D. Numberger-Thuy

Natural History Museum Luxembourg, Department of Palaeontology, 25 Rue Münster, 2160 Luxembourg, Luxembourg

* Correspondence: bthuy@mnhn.lu; Tel.: +352-462233-412

† LSID: urn:lsid:zoobank.org:pub:90109747-8209-47FB-8893-293EE9ADB4CF.

Abstract: In spite of considerable progress during the last few years, the fossil record of the ophiuroids, or brittle stars, is still poorly known, especially with respect to taxa restricted to specific environments. Here, we describe new ophiuroid fossils collected from an Upper Cretaceous rocky shore in Ivö Klack, southern Sweden, consisting of fully disarticulated skeletal remains retrieved from the sediments deposited between boulders and hummocks. The fossils are identified as a new species of the extant ophiocomid genus *Ophiocoma*. In a critical revision of the ophiocomid fossil record, we show that all fossils previously assigned to the Ophiocomidae belong to other families. Thus, the fossil record of the Ophiocomidae is currently restricted to the new species described herein, and *Amphiura? gigantiformis* from the Miocene of Austria which, in fact, is a species of *Ophiocoma*. Since recent species of *Ophiocoma* exclusively occur in tropical to subtropical shallow subtidal environments, our discovery of a fossil *Ophiocoma* species in the rocky shore sediments of Ivö therefore conforms with the previously assumed subtropical palaeotemperatures prevailing in southern Sweden during the Late Cretaceous. Most notably, it represents the northernmost occurrence of an ophiocomid recorded to date.



Citation: Thuy, B.; Numberger-Thuy, L.D. The Northernmost Occurrence of the Tropical-Subtropical Brittle Star *Ophiocoma* (Echinodermata, Ophiuroidea) from a Late Cretaceous Rocky Shore in Southern Sweden [†]. *Taxonomy* **2023**, *3*, 346–355. <https://doi.org/10.3390/taxonomy3030020>

Academic Editor: Ingi Agnarsson

Received: 14 February 2023

Revised: 24 May 2023

Accepted: 19 June 2023

Published: 25 June 2023



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Keywords: Ophiuroidea; Ophiocomidae; microfossils; fossil record; new species; Cretaceous

1. Introduction

During the Late Cretaceous, some 70 million years before present, southern Sweden was located on the shores of a shallow, subtropical sea [1]. The sedimentary rocks formed in this particular environment document a variety of depositional settings and yield a rich marine fauna with occasional terrestrial elements. The most notable site is the ancient rocky shore exposed in the disused kaolin quarries of Ivö Klack near Kristianstad (Figure 1). Here, a steep palaeo-coast consisting of Precambrian gneiss formed a rocky shoreline with a wave-cut platform and large hummocks and gneiss boulders encrusted by oysters and other epizoic invertebrates [1–3]. The carbonate sediments deposited between these boulders and hummocks yield an exceptionally rich and well-preserved fauna, including more than 200 species of invertebrates, some 50 species of sharks, rays, marine reptiles and other aquatic vertebrates and occasional terrestrial elements such as bird and non-avian dinosaur bones [1]. Rocky shores often harbour biotic elements that are not found in other marine environments (e.g., [4]). At the same time, however, rocky shores are only rarely preserved in the fossil record. The site at Ivö Klack therefore offers a unique insight into an otherwise inaccessible part of the Upper Cretaceous marine biodiversity.

Among the most abundant echinoderm groups occurring in the detrital deposits of the ancient rocky shore at Ivö Klack are the ophiuroids, or brittle stars. They are the slender-armed cousins of the starfish and live in almost every corner of the present-day oceans, including the shallow subtidal and intertidal environments [5]. The ophiuroid skeleton

is composed of a multitude of microscopic plates, called ossicles. Although the skeleton tends to fall apart very quickly after death, the individual ossicles are taphonomically stable and readily fossilize even in high-energy depositional settings such as rocky shores. Specific types of ophiuroid ossicles, in particular the spine-bearing lateral arm plates, are character-rich and identifiable to species level [6].

Here, we describe new finds of ophiuroid microfossils retrieved from detrital deposits within the Cretaceous rocky shore of Ivö Klack. The material belongs to the Ophiocomidae, an ophiuroid clade that is very common and widespread in present-day tropical to subtropical shallow marine environments [7] but very poorly represented in the fossil record [8]. We assess the taxonomy of the new fossils and discuss previously published reports of fossil ophiocomids.

2. Materials and Methods

For the purpose of the present study, we analysed several hundred ophiuroid microfossils handpicked from the dried sieving residues of bulk sediment samples taken from the fossil-rich carbonate deposits between the boulders and hummocks of the Ivö Klack rocky shore located on the northern slope of Ivö Island (56°08'21.6'' N, 14°24'05.8'' E) in Skåne, southern Sweden. The deposits in question are dated to the *Belemnellocamax mammilatus* belemnite biozone of the latest early Campanian, Late Cretaceous [1] (Figure 2). A total of 103 lateral arm plates were identified as remains of the new species described in the present paper. Nine arm spines and ventral and dorsal arm plates were found to belong to that same species based on similarities in size of the spine base and spine articulation and in outer surface ornamentation, respectively. Selected microfossils were cleaned in an ultrasonic bath, mounted on aluminum stubs and gold-coated for scanning electron microscopy using a Hitachi FE-SEM 4300. Type and figured specimens were deposited in the collection of the Natural History Museum Luxembourg (acronym MNHNL). We used the terminology by Stöhr et al. [5] and Thuy and Stöhr [6,9], and the classification of O'Hara et al. [10,11].

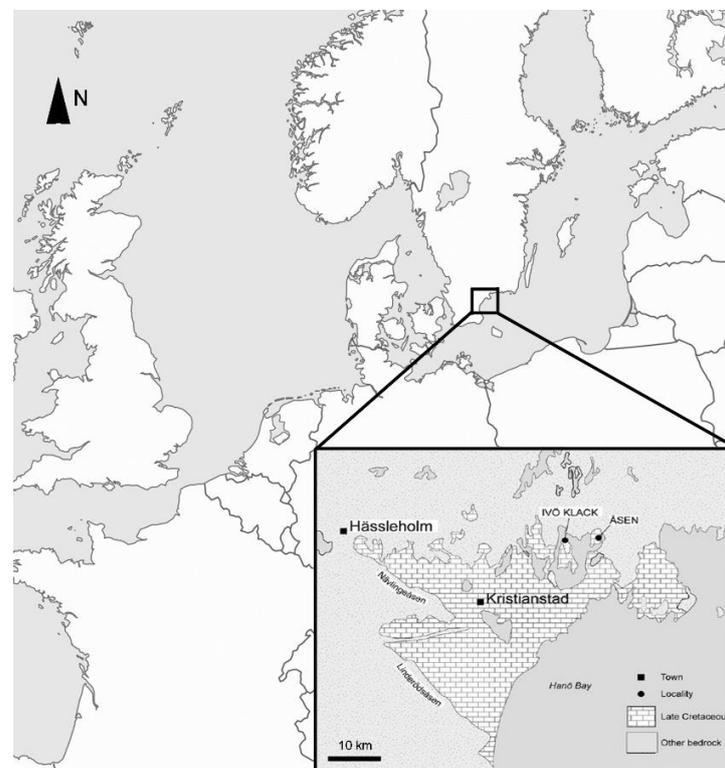


Figure 1. Map showing the location of the Ivö Klack rocky shore section in southern Sweden, modified after Einarsson et al. [12].

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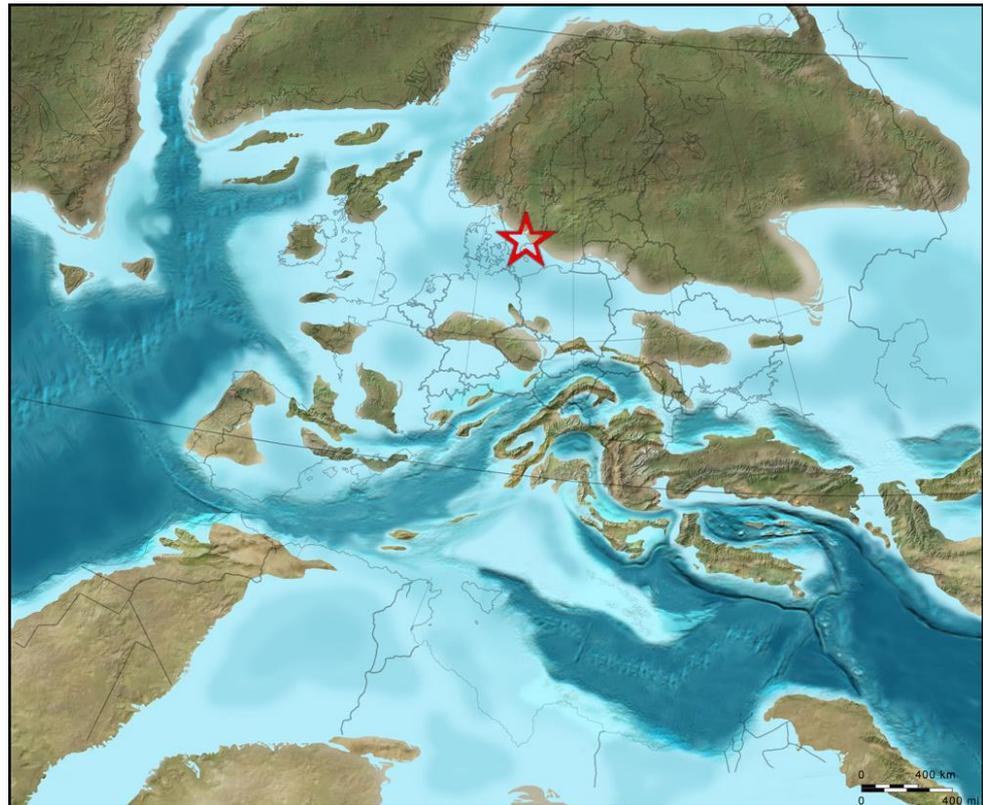


Figure 2. Palaeogeographical map showing a reconstruction of oceans, epicontinental seas and landmasses during the Late Cretaceous (c. 75 Ma, map provided by Colorado Plateau Geosystems Inc., Scottsdale, Arizona). Red star indicates position of Ivö Klack.

3. Systematic Palaeontology

Class Ophiuroidea Gray, 1840;

Subclass Myophiuroida Matsumoto, 1915;

Infraclass Metophiurida Matsumoto, 1913;

Superorder Ophintegrida O'Hara, Hugall, Thuy, Stöhr and Martynov, 2017;

Order Ophiacanthida O'Hara, Hugall, Thuy, Stöhr and Martynov, 2017;

Suborder Ophiodermatina Ljungman, 1867;

Superfamily Ophiocomoidea Ljungman, 1867;

Family Ophiocomidae Ljungman, 1867;

Genus *Ophiocoma* L. Agassiz, 1836.

Diagnosis (emended specifically for lateral arm plate morphology): Ophiocomid genus with stout, strongly arched and high lateral arm plates, with a very large, strongly ventro-proximalwards protruding ventral portion showing a thickened, widened ventral tip; outer proximal edge devoid of spurs, lined by a narrow band of more finely meshed stereom; outer surface with coarse tuberculation, often restricted to areas surrounding spine articulations and to ventral and dorsal areas; very large, conspicuous spine articulations

in shallow, round depressions on a strongly raised distal portion of the lateral arm plate, with spine articulation composed of thick, smooth dorsal and ventral lobes merged into an ear-shaped volute with a well-developed sigmoidal fold; strong dorsalward increase in size of spine articulations; inner side with a slender, well defined vertebral articular ridge with two kinks and a ventro-proximalwards pointing projection associated with the dorsal kink, with the dorsal part of the ridge vertical, closely lining the distal edge of the lateral arm plate and beset with several knobs; single, large perforation close to ventral kink in ridge; knob on the internal side of the ventral tip of the lateral arm plate.

Ophiocoma avatar sp. nov. (Figures 3 and 4)

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Holotype: MNHNL OPH191.

Paratypes: MNHNL OPH192—MNHNL OPH197.

Type horizon and locality: Coarse-grained skeletal carbonates from between the hummocks and boulders of the rocky shore at Ivö Klack (56°08'21.6'' N, 14°24'05.8'' E), southern Sweden, dated to the latest early Campanian *Belemnellocomax mammilatus* belemnite biozone, Late Cretaceous.

Etymology: Species named in honour of Swedish metal band Avatar, to honour their outstanding musical creativity that has been inspiring our research activities during the last years.

Diagnosis: Relatively small species of *Ophiocoma* with up to four large spine articulations, and outer surface largely covered by coarse tubercles, freestanding in dorsal and ventral parts of outer surface and between the spine articulations, and merged into an irregular vertical striation in a narrow band proximally bordering the spine articulations.

Description: The holotype specimen (MNHNL OPH191, Figure 3A–C) is a dissociated proximal lateral arm plate, strongly arched, approximately two times higher than long, with a pointed dorsal tip, an evenly convex distal edge and an evenly concave proximal edge devoid of spurs but lines by a narrow, slightly raised band of more finely meshed stereom; ventral portion of lateral arm plate strongly protruding ventro-proximalwards, with an enlarged ventral tip; outer surface covered by coarse tubercles freestanding in dorsal and ventral parts of the outer surface and between the spine articulations, and merged into an irregular vertical striation in a narrow band proximally bordering the spine articulations (Figure 3A); four very large spine articulations (Figure 3B) in shallow, large depressions on a strongly raised distal portion of the lateral arm plate; size of spine articulations and distance separating them increasing in size dorsalwards; spine articulations composed of large, smooth dorsal and ventral lobes merged into an ear-shaped volute with a well-developed sigmoidal fold separating a large muscle opening and a smaller nerve opening (Figure 3B); inner side of lateral arm plate with a slender, sharply defined vertebral articular ridge (Figure 3C), composed of three parts connected by two sharp kinks, the dorsal one with a ventro-proximalwards pointing angular projection, damaged; dorsal part of ridge closely lining the proximal edge of the lateral arm plate, beset with at least four small, prominent, poorly preserved knobs; single, conspicuous perforation on ventro-distal border of ventral kink of ridge (Figure 3C); large, poorly defined knob on inner side of ventral tip of lateral arm plate; tentacle notch large and deep.

Paratype supplements and variation: MNHNL OPH192 (Figure 3D–F) is a dissociated median lateral arm plate, slightly longer than holotype; plate outline, outer surface ornamentation (Figure 3D) and spine articulations (Figure 3E) as in holotype; inner side slightly better preserved, showing at least three small knobs on dorsal part of vertebral articular ridge (Figure 3F) paralleling the proximal edge of the lateral arm plate, with knobs becoming smaller and less prominent dorsalwards.

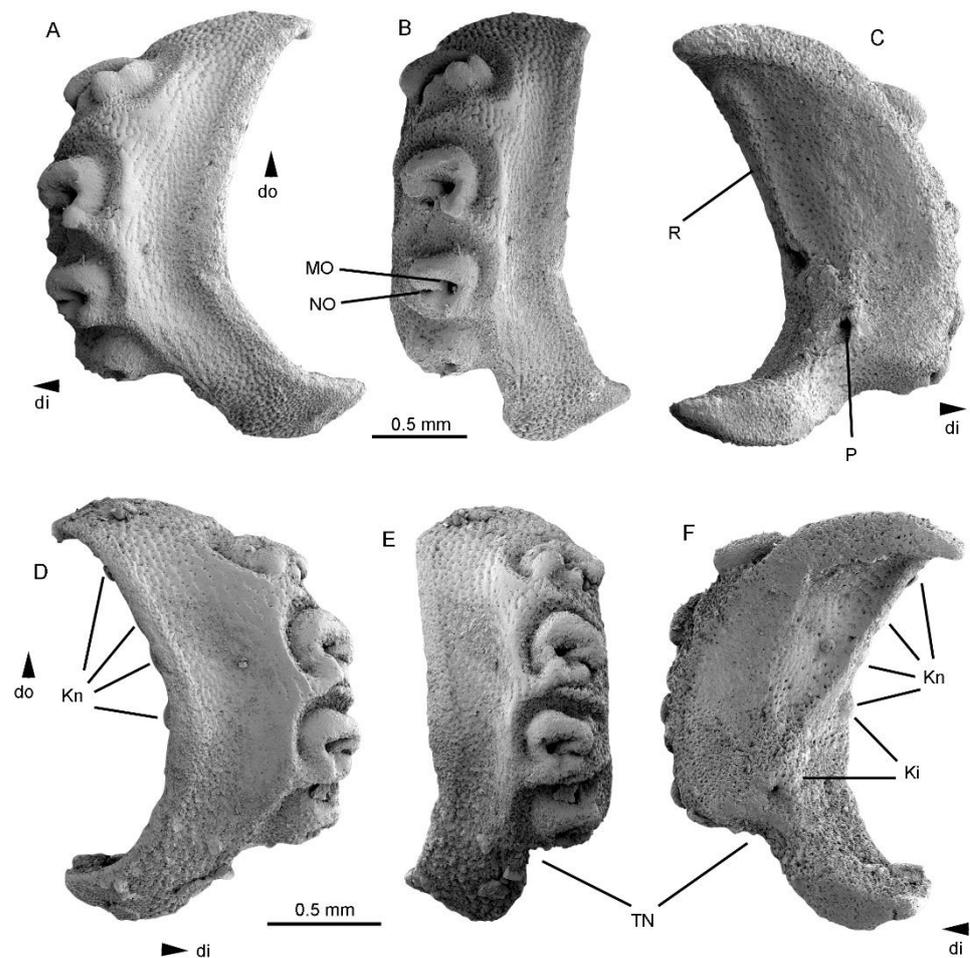


Figure 3. *Ophiocoma avatar* sp. nov. from the latest early Campanian *Belemnellocomax mammilatus* belemnite biozone, Late Cretaceous, of Ivö Klack, Sweden. Holotype (MNHNLK OPH191), dissociated proximal lateral arm plate in external oblique (A), external frontal (B) and internal (C) views; paratype (MNHNL OPH192), dissociated median lateral arm plate in external oblique (D), external frontal (E) and internal (F) views. Arrows indicating orientation. Abbreviations: di: distal; do: dorsal; Ki: kinks in vertebral articular ridge; MO: muscle opening; NO: nerve opening; P: perforation; R: vertebral articular ridge; Sp: knobs on vertebral articular ridge; and TN: tentacle notch.

MNHNL OPH193 (Figure 4A,B) is a dissociated distal lateral arm plate, slightly higher than long, with a rounded dorsal edge, an evenly convex distal edge and a strongly ventro-proximalwards protruding ventral portion; proximal edge concave, with a poorly defined, weakly prominent central elevation; outer surface (Figure 4A) with coarse tubercles merged into an irregular vertical striation close to spine articulations, in the dorsal and, to a lesser extent, the ventral part of the lateral arm plate; three large spine articulations (Figure 4A) similar to those of holotype; inner side with a large but poorly preserved vertebral articular ridge (Figure 4B) composed of three parts connected via two sharp kinks, the dorsal one of which with a ventro-proximalwards pointing extension; single large, conspicuous perforation adjacent to ventral kink of vertebral articular ridge; no knobs preserved on ridge; tentacle notch wide, deep.

MNHNL OPH194 (Figure 4C) is a dissociated proximal dorsal arm plate, fan-shaped, approximately two times wider than long with an evenly convex distal edge and an obtuse, rounded proximal angle, damaged but showing the remains of an articular surface devoid of tubercles but with a poorly defined spur; outer surface evenly covered by large tubercles.

MNHNL OPH195 (Figure 4D) is a dissociated median to distal dorsal arm plate, fan-shaped, as long as wide, with an unevenly convex distal edge and an acute, rounded

proximal angle with a small articular surface devoid of tubercles and showing a small, poorly defined spur; outer surface evenly covered by large tubercles.

MNHNL OPH196 (Figure 4E) is a dissociated proximal ventral arm plate, approximately 1.5 times wider than long; outline reminiscent of a dog head, with pointed latero-distal tips; distal edge with two incisions; lateral edges with a pointed extension; proximal edge convex, much narrower than distal edge; outer surface covered by large tubercles.

MNHNL OPH197 (Figure 4F) is a dissociated arm spine, four times longer than wide, conical, with a blunt tip, covered in small scale-like tubercles pointing towards the spine tip.

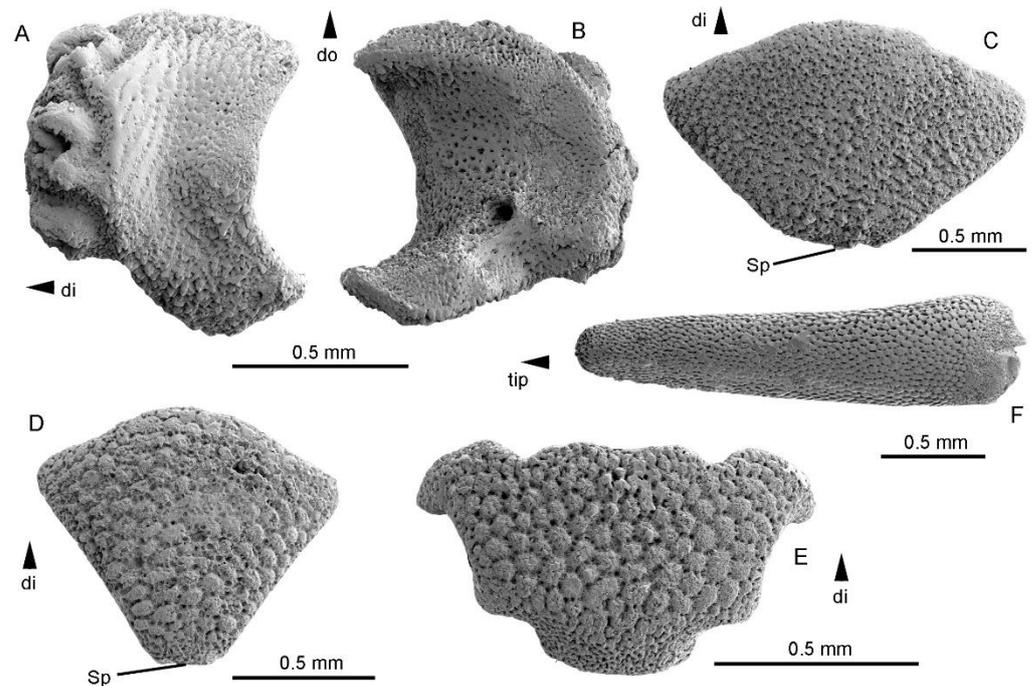


Figure 4. *Ophiocoma avatar* sp. nov. from the latest early Campanian *Belemnellocomax mammilatus* belemnite biozone, Late Cretaceous, of Ivö Klack, Sweden. Paratype (MNHNL OPH193), dissociated distal lateral arm plate in external (A) and internal (B) views; paratype (MNHNL OPH194), dissociated proximal dorsal arm plate in external view (C); paratype (MNHNL OPH195), dissociated median to distal dorsal arm plate in external view (D); paratype (MNHNL OPH196), dissociated proximal ventral arm plate in external view (E); and paratype (MNHNL OPH197), dissociated arm spine (F). Arrows indicating abbreviations. Abbreviations: di: distal; do: dorsal; and Sp: spur.

4. Discussion

4.1. Taxonomic Affinities

The lateral arm plates described in the present paper show a remarkable similarity with those of recent *Ophiocoma* species, including the type species *O. echinata* [5]. The fossil specimens show all the diagnostic features that characterize the lateral arm plate morphology of the Ophiocomidae, in particular the very large ear-shaped spine articulations, the large proximalwards-protruding ventral portion, the coarse tubercles on the outer surface ornamentation, the vertebral articular ridge with two sharp kinks and the single large perforation. The combination of coarse tubercles on the outer surface, a series of knobs on the dorsal part of the vertebral articular ridge and a continuous series of spine articulations that increase in size dorsalwards is exclusively found in *Ophiocoma* and tells this genus apart from the other ophiocomids, e.g., [13]. We therefore assign the fossil lateral arm plates described in the present paper to *Ophiocoma*.

The ventral and dorsal arm plates shown in Figure 4 can be associated with the fossil *Ophiocoma* lateral arm plates because of similarities in outer surface ornamentation and

plate size, and because they match the respective morphology of recent *Ophiocoma* species. The arm spine associated with the fossil *Ophiocoma* lateral arm plates shows an articulation that matches the spine articulations of the lateral arm plates, and it shows the scale-like tubercles on the outer surface that are typically found in ophiocomids [6].

There are currently five fossil species tentatively assigned to the genus *Ophiocoma*. In ascending stratigraphic order, these are: *Ophiocoma? nereida* (Wright, 1880) [14] from the Oxfordian (Upper Jurassic) of Dorset, Great Britain, *Ophiocoma? rasmussenii* Hess, 1960 [15] originally from the Cenomanian (Lower Cretaceous) of Kent, Great Britain (Hess 1960), *Ophiocoma senonensis* (Valette, 1915) [16] originally from the Campanian (Upper Cretaceous) of Yonne, France, *Ophiocoma? ishidaei* Kutscher and Jagt, 2000 [17] from the Maastrichtian (Upper Cretaceous) of Rügen, Germany and *Ophiocoma hessi* Rasmussen, 1972 [18] from the Upper Eocene of Hampshire, Great Britain. None of them are similar to the lateral arm plates described in the present paper, which is why we introduce the new species *Ophiocoma avatar* sp. nov. to accommodate them. The new species differs from the recent relatives in having a more pronounced merging of outer surface tubercles into a vertical striation.

4.2. The Ophiocomid Fossil Record

Re-examination of the specimen originally described as *Ophiurella nereida* and tentatively transferred to the genus *Ophiocoma* [19], housed at the Natural History Museum in London, suggests that the preservation is too poor to allow for an unambiguous assessment of diagnostic characters. We therefore consider it as a *nomen dubium*. The arm fragment described as *Ophiocoma? rasmussenii*, also housed at the Natural History Museum in London, turned out to show characters typically found in members of the Ophiotomidae. Given the similarities with *Ophiotreta striata* (Kutscher and Jagt, 2000) from the Maastrichtian of Rügen, we transfer the species to the ophiotomid genus *Ophiotreta*. The arm fragments and arm ossicles assigned to *Ophiocoma? senonensis* are incompatible with the diagnosis of the genus *Ophiocoma* and the family Ophiocomidae altogether, especially with respect to the shape of the spine articulations. Instead, the material in question shows strong affinities with recent ophiionereids. Given the absence of accessory dorsal arm plates in the type specimens illustrated by Valette [16], and given the shape of the lateral arm plates, we suggest transfer to the ophiionereid genus *Ophiodoris* Koehler, 1904. The lateral arm plates described as *Ophiocoma? ishidaei* show a spine articulation morphology that is not found in ophiocomids. Instead, the spine articulations suggest ophiionereid affinities, although the outer general outline of the lateral arm plates combined with their surface ornamentation is typically found in the Ophiotomidae. A correct genus-level assignment of *O. ishidaei* should be based on a detailed reassessment of the type material, with high-resolution views of the spine articulations and the vertebral articular ridge and perforations on the inner side of the lateral arm plates. Until then, we tentatively transfer the species to the ophiionereid genus *Ophiodoris*. *Ophiocoma hessi* is clearly not an ophiocomid but instead shows characters typically found in the Amphiuroidae [5,6]. We therefore transfer the species to *Amphiura*, stressing, however, that the genus-level assignment is tentative and should be further substantiated by a detailed reassessment of the type specimens.

As a conclusion, none of the fossil species previously assigned to *Ophiocoma* are compatible with the diagnosis of the genus or, more general, the family Ophiocomidae. We therefore suggest removing them from the fossil record of the family. Interestingly, however, the dissociated lateral arm plates from the Miocene of Mannersdorf, Austria, described by Küpper [20] as *Amphiura? gigantiformis*, in fact, show strong a combination of characters typically found in Ophiocomidae. Examination of material from the same locality confirms the ophiocomid affinities, prompting us to transfer the species to *Ophiocoma*.

Following our revision, the fossil record of the genus *Ophiocoma* currently comprises two formally named species, *Ophiocoma gigantiformis* comb. nov. from the Miocene and *Ophiocoma avatar* sp. nov. from the Upper Cretaceous. The species described in the present paper thus significantly adds the very sparse fossil record of the family. Most significantly,

it represents by far the oldest record of the family and shows that the genus *Ophiocoma* has been a part of shallow subtidal communities since at least the Late Cretaceous. Thanks to their size, abundance and semi-cryptic lifestyle (e.g., emerging at low tide to suspension feed), *Ophiocoma* species are among the most conspicuous elements of the shallow tropical intertidal areas [7]. Yet, their fossil record is extremely sparse. We speculate that the scarcity of ophiocomid fossils and the excessively long ghost range between the Cretaceous and the Miocene records are due to a lack of sampling in the appropriate palaeoenvironments, i.e., tropical to subtropical shallow subtidal settings (see below). Given the taphonomic conditions prevailing in these environments [21], generally involving high wave energy and normal oxygen levels, leading to complete disarticulation of multi-element skeletons, sampling efforts ignoring dissociated ossicles likely overlook ophiocomid remains.

4.3. Palaeoecological Implications

Present-day representatives of the genus *Ophiocoma* are restricted to the tropical to subtropical shallow seas of the world oceans [22] (Figure 5). The discovery of *Ophiocoma* in the Campanian rocky shore sediments of Ivö therefore corroborates the previously assumed subtropical palaeotemperatures prevailing in southern Sweden during the Late Cretaceous [2].

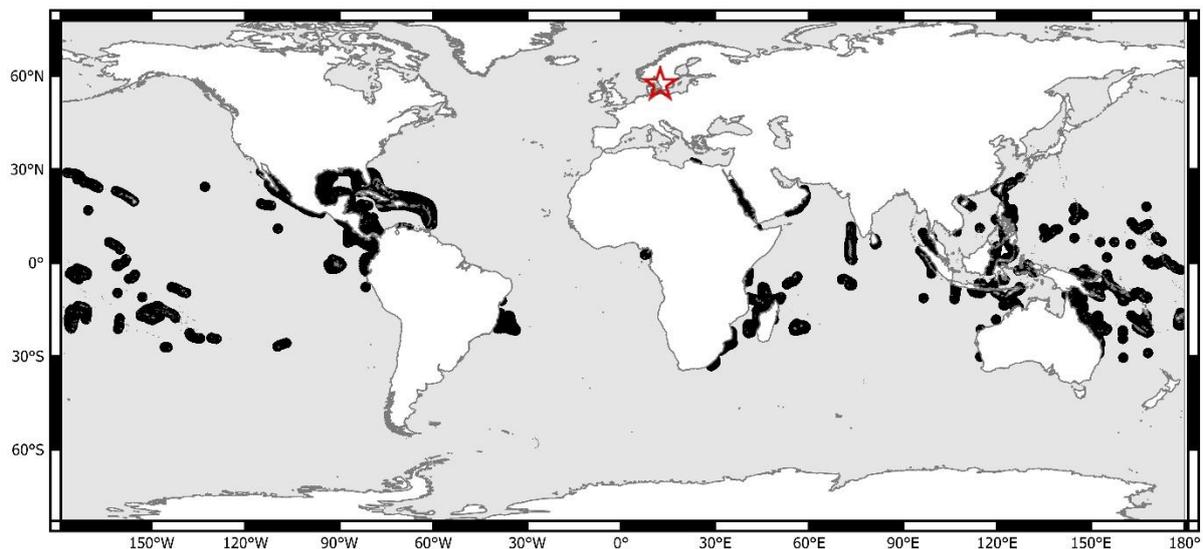


Figure 5. Map showing the distribution of recent *Ophiocoma* species (in black) [22] and the location of *Ophiocoma avatar* sp. nov. (red star) from the Upper Cretaceous.

Recent *Ophiocoma* species have been the subject of extensive investigations regarding photoreception and colour-change in response to light intensity, e.g., [23,24]. Initially, it was thought that the conspicuous tubercles on the arm ossicles of some recent *Ophiocoma* species, also called enlarged peripheral trabeculae, were calcitic lenses focalizing incumbent light as part of the photoreceptor system of the animals [24]. Later, however, it was shown that photoreceptor systems are present in *Ophiocoma* species with and without lens-like tubercles, and that the structural optics of the latter represent an exaptation [25,26]. While Sumner-Rooney et al. [26] did not fully reject the hypothesis that enlarged peripheral trabeculae are somehow involved in the visual system of ophiuroids, they clearly showed that these structures are not involved directly in vision, in particular in focusing the light onto putative photoreceptors, but rather play role indirectly in this process. More specifically, they demonstrated that photoreceptors in the recent *Ophiocoma wendtii* are distributed in pores surrounding the enlarged peripheral trabeculae, and the convex morphology of the “microlenses” increases the acceleration of the dispersion of chromatophores (acting as filters covering the photoreceptors) producing a more dramatic colour change in animals, thus leading to more effective phototaxis.

The lens-like tubercles are therefore not directly related to photoreception in ophiuroids, and their presence in fossil ossicles cannot be interpreted as an indication of a visual system, unlike previously made claims [27]. As long as the chromatophore and photoreceptive properties of ophiuroids cannot be unambiguously linked with special skeletal features, it remains impossible to deduce whether extinct species such as *Ophiocoma avatar* sp. nov. were capable of colour-change and/or light detection. Interestingly, aside from the putative role in photoreception, the “microlenses”, or enlarged peripheral trabeculae, display a unique nanostructural design, resembling the so-called Guinier–Preston zones, enhancing skeleton strength [28]. In this respect, the new species aligns with previous evidence for an increased occurrence of lens-shaped tubercles on the surface of echinoderm ossicles by the Late Cretaceous [27].

Author Contributions: Conceptualization, B.T. and L.D.N.-T.; methodology, B.T. and L.D.N.-T.; validation, B.T. and L.D.N.-T.; formal analysis, B.T.; investigation, B.T. and L.D.N.-T.; writing—original draft preparation, B.T.; writing—review and editing, B.T. and L.D.N.-T.; visualization L.D.N.-T. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: Not applicable.

Acknowledgments: We thank Manfred Kutscher (Rügen, Germany) who collected the material described in the present paper and generously made it available for research. We furthermore thank the reviewers whose comments greatly improved an earlier version of this manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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